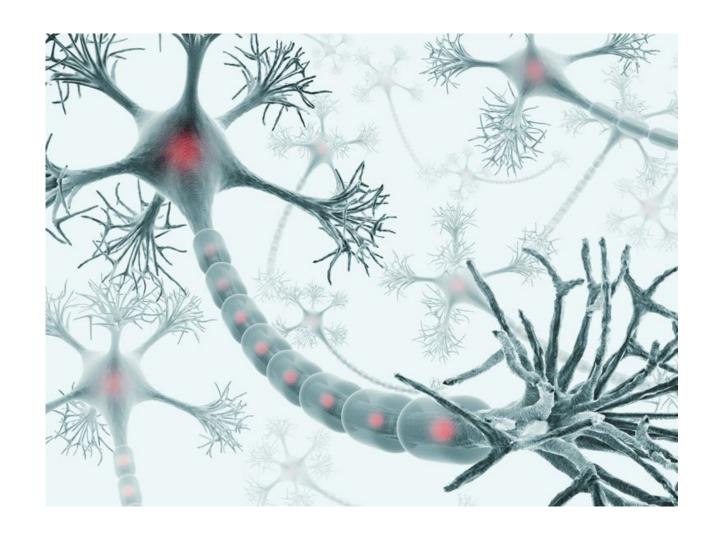


## Neurocomputing

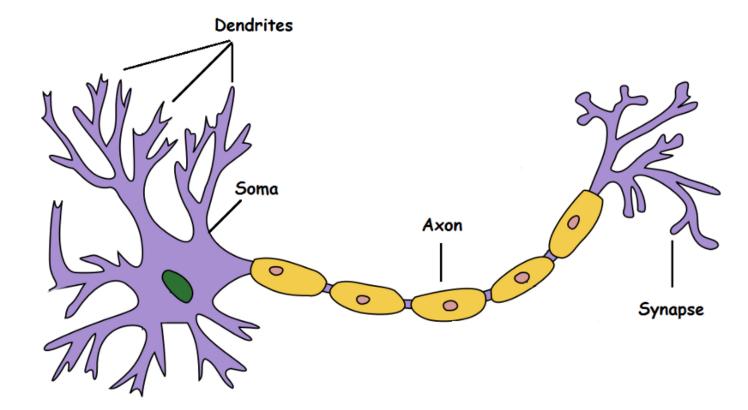
Neurons

Julien Vitay

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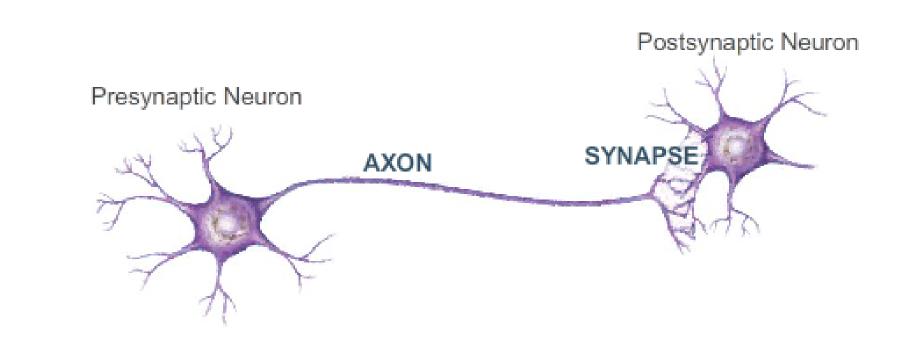


https://www.verywellmind.com/what-is-a-neuron-2794890

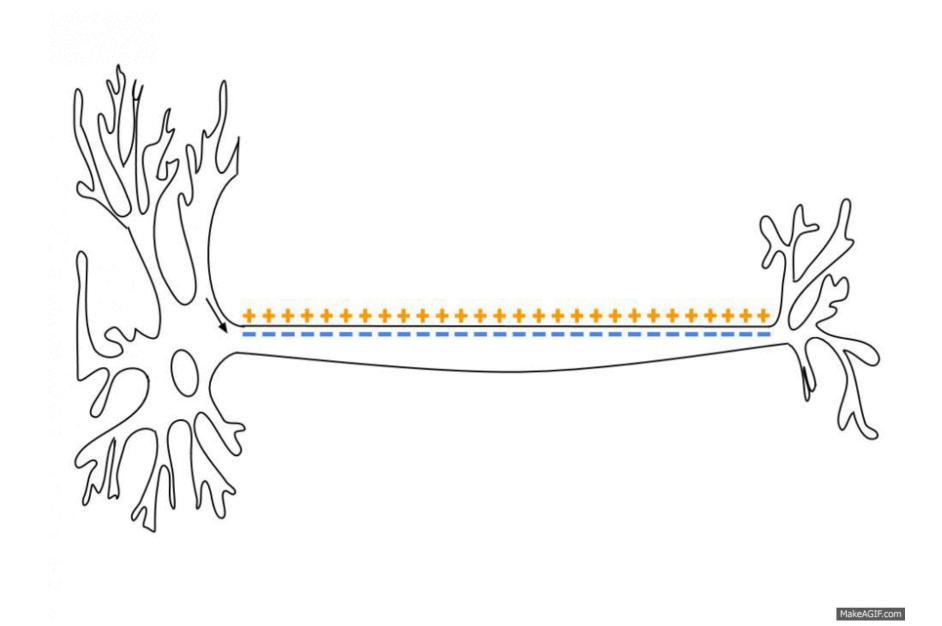


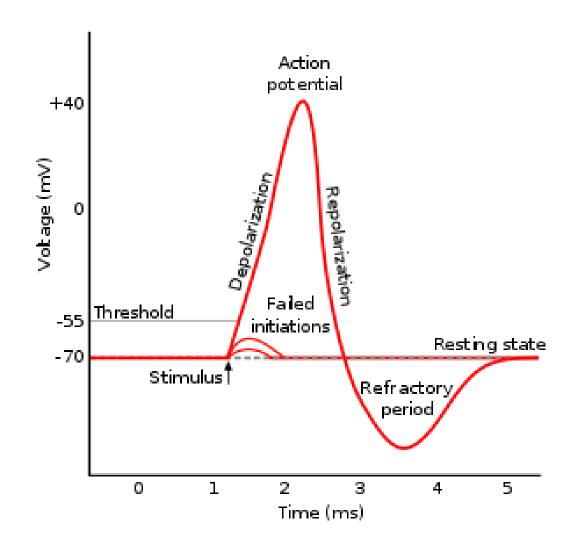
https://en.wikipedia.org/wiki/Neuron

- 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.



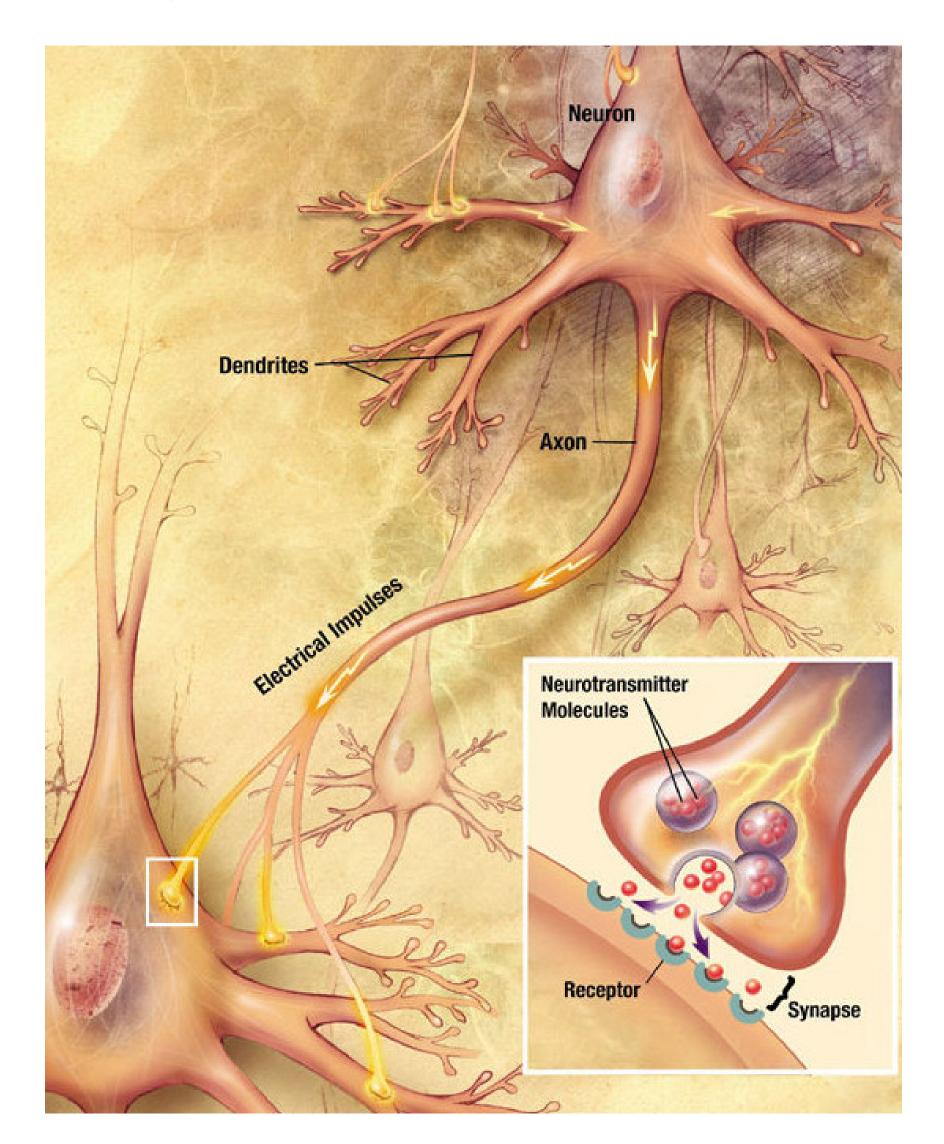
http://bcs.whfreeman.com/webpub/Ektron/Hillis%20Principles%20of%20Life2e/Ani





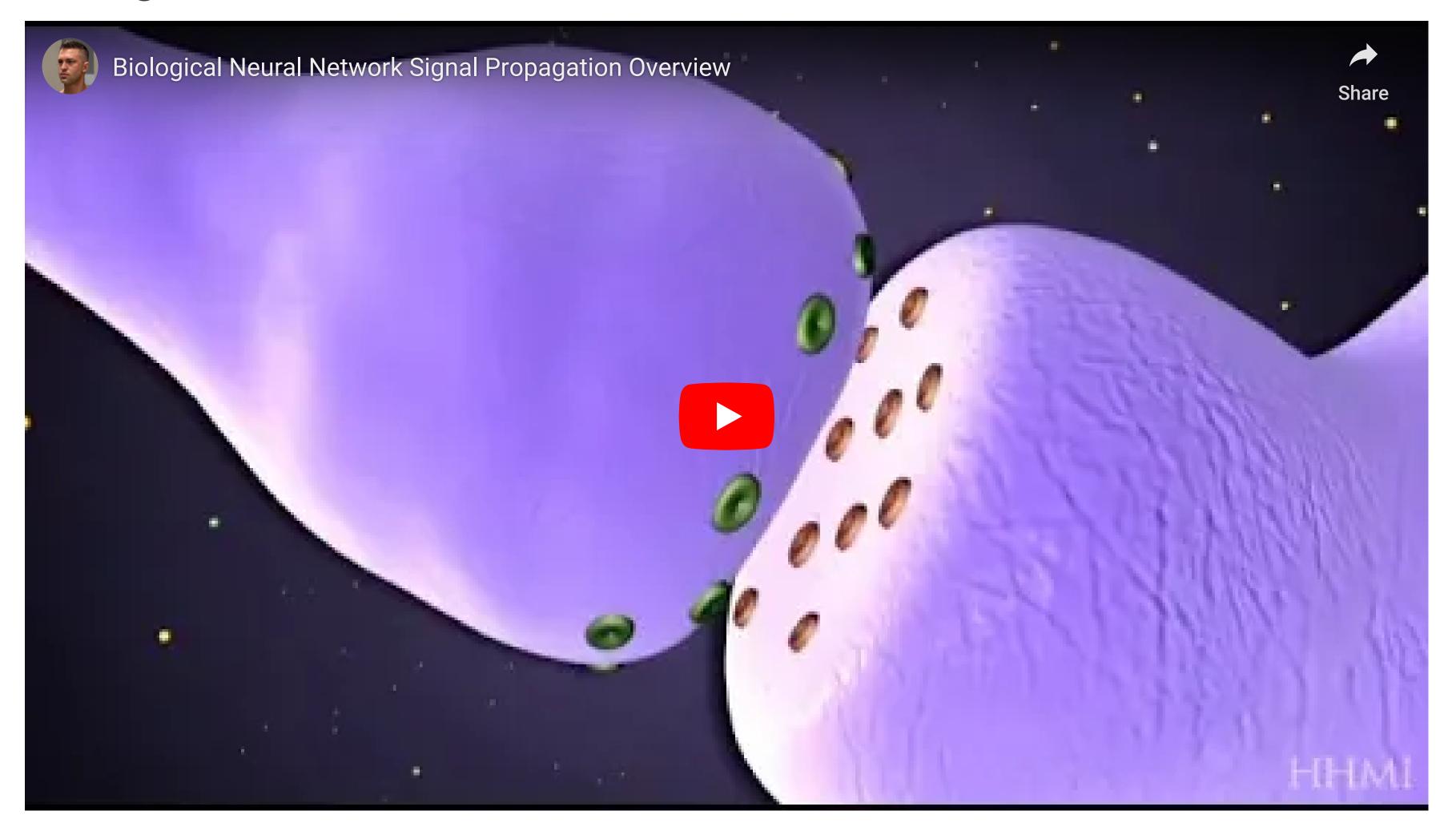
https://en.wikipedia.org/wiki/Action\_potential

- 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.

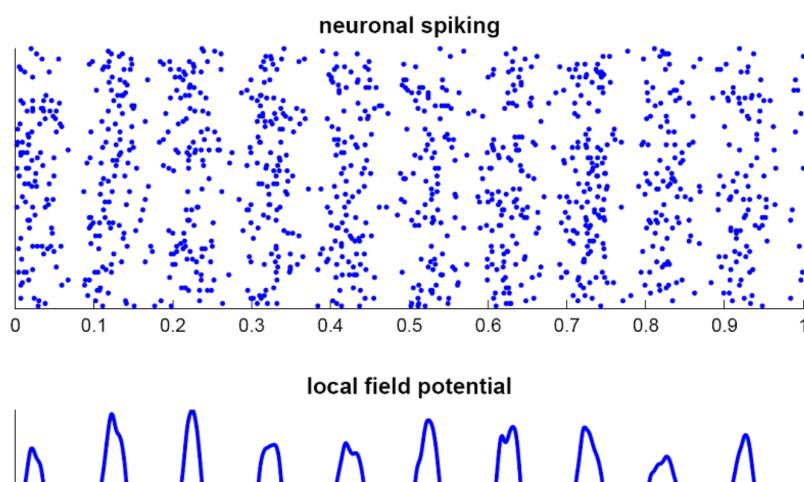


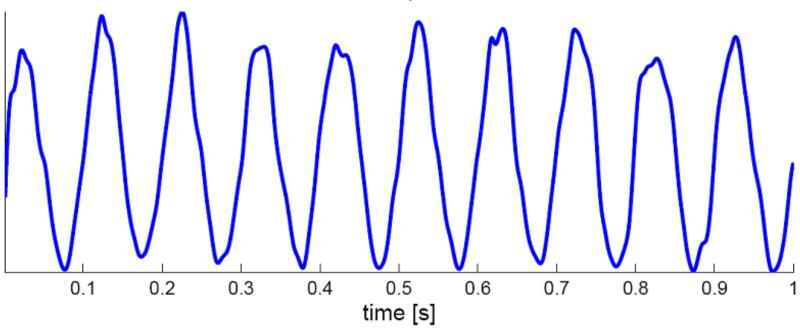
https://en.wikipedia.org/wiki/Neuron

- 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.



### Information is transmitted through spike trains

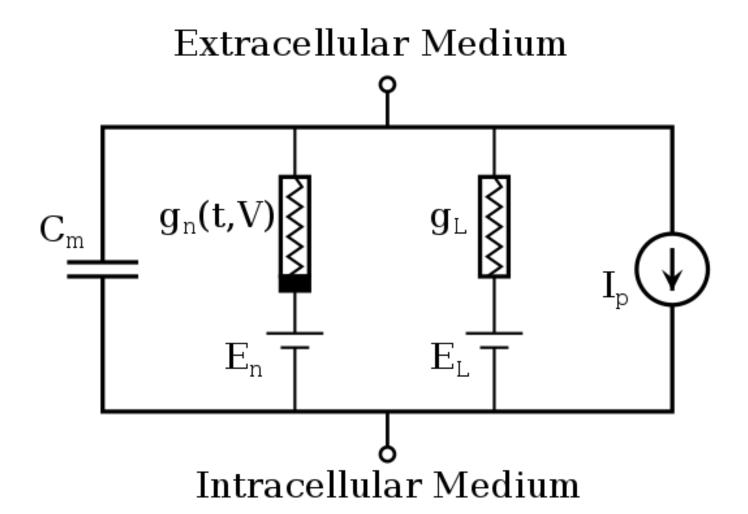




Source: https://en.wikipedia.org/wiki/Neural\_oscillation

- 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.
- ullet 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.

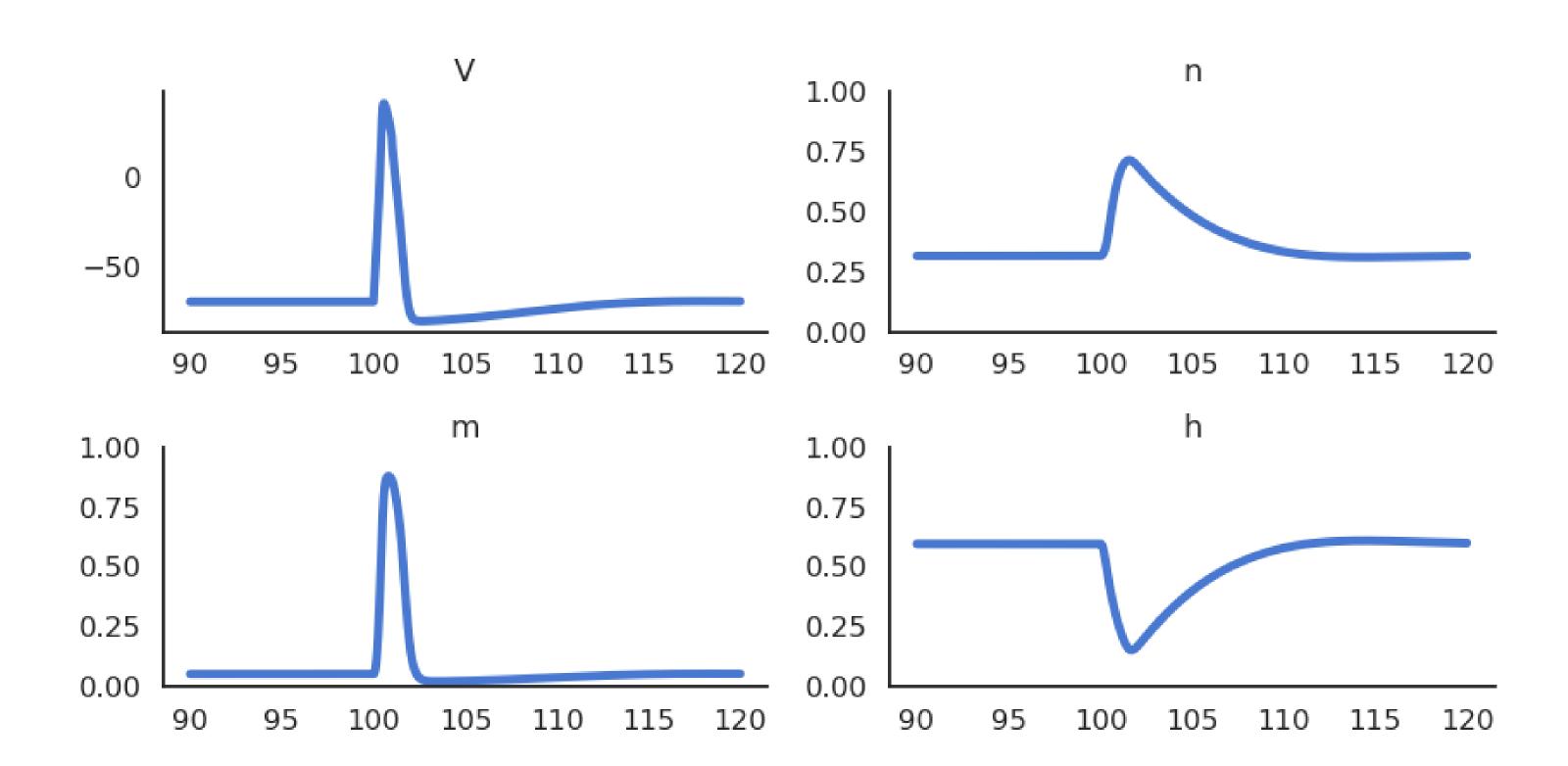
$$egin{aligned} egin{aligned} a_n &= 0.01 \, (v + 60) / (1.0 - \exp(-0.1 \, (v + 60))) \ a_m &= 0.1 \, (v + 45) / (1.0 - \exp(-0.1 \, (v + 45))) \ a_h &= 0.07 \, \exp(-0.05 \, (v + 70)) \ b_n &= 0.125 \, \exp(-0.0125 \, (v + 70)) \ b_m &= 4 \, \exp(-(v + 70) / 80) \ b_h &= 1 / (1 + \exp(-0.1 \, (v + 40))) \ \end{aligned} \ egin{aligned} rac{dn}{dt} &= a_n \, (1 - n) - b_n \, n \ rac{dm}{dt} &= a_m \, (1 - m) - b_m \, m \ rac{dh}{dt} &= a_h \, (1 - h) - b_h \, h \end{aligned}$$

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

**—** 

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

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

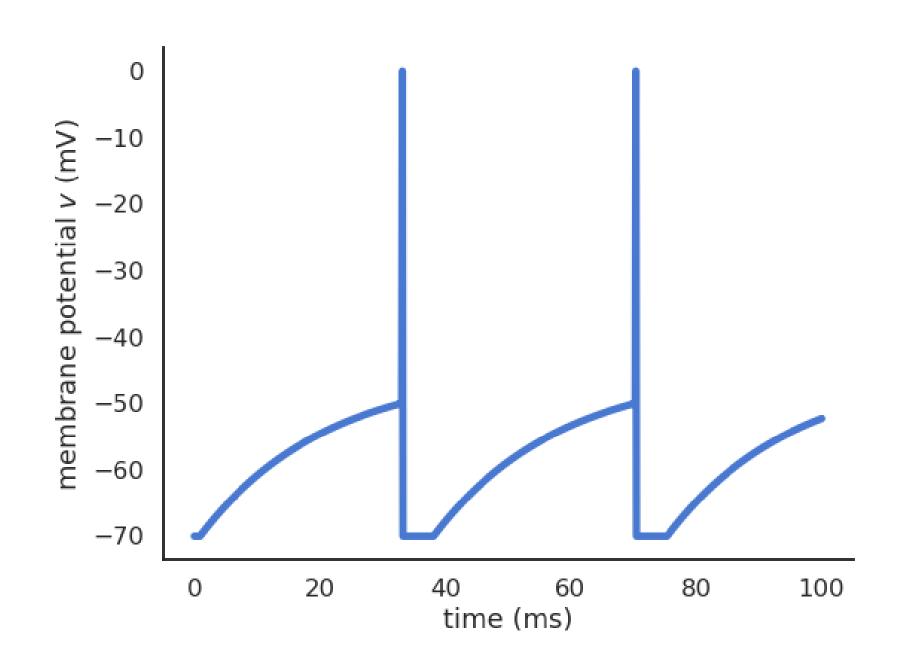


## The leaky integrate-and-fire neuron (Lapicque, 1907)

- 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.

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

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



### Different spiking neuron models are possible

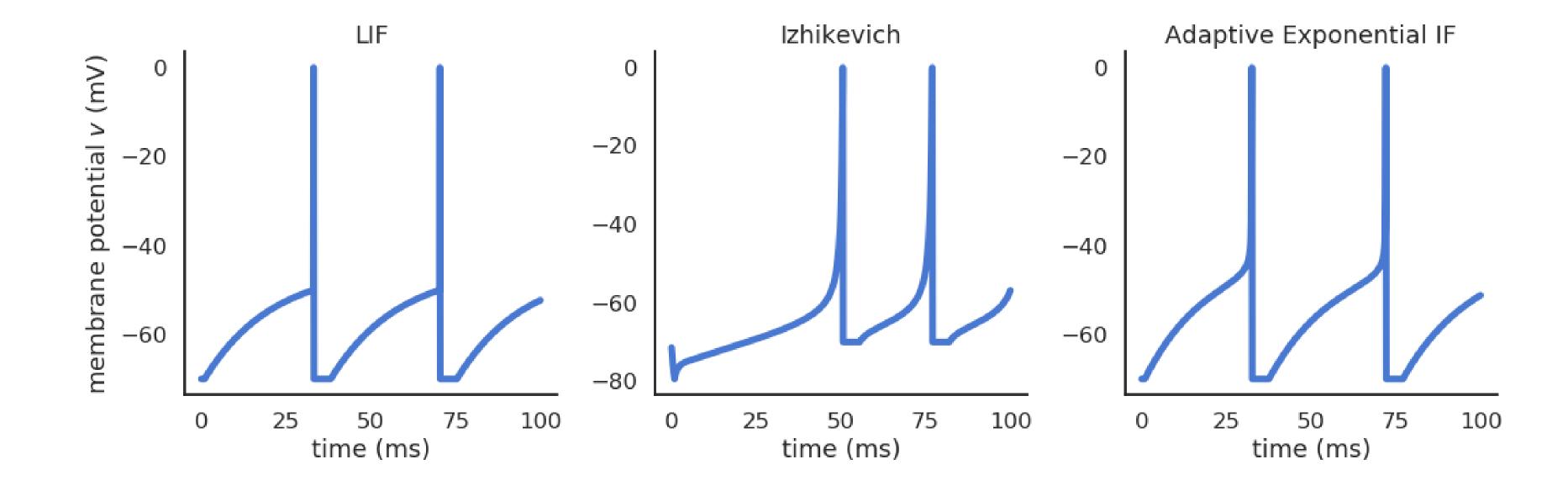
 Izhikevich quadratic IF (Izhikevich, 2001).

$$egin{aligned} rac{dv}{dt} &= 0.04\,v^2 + 5\,v + 140 - u + 100 \ rac{du}{dt} &= a\,(b\,v - u) \end{aligned}$$

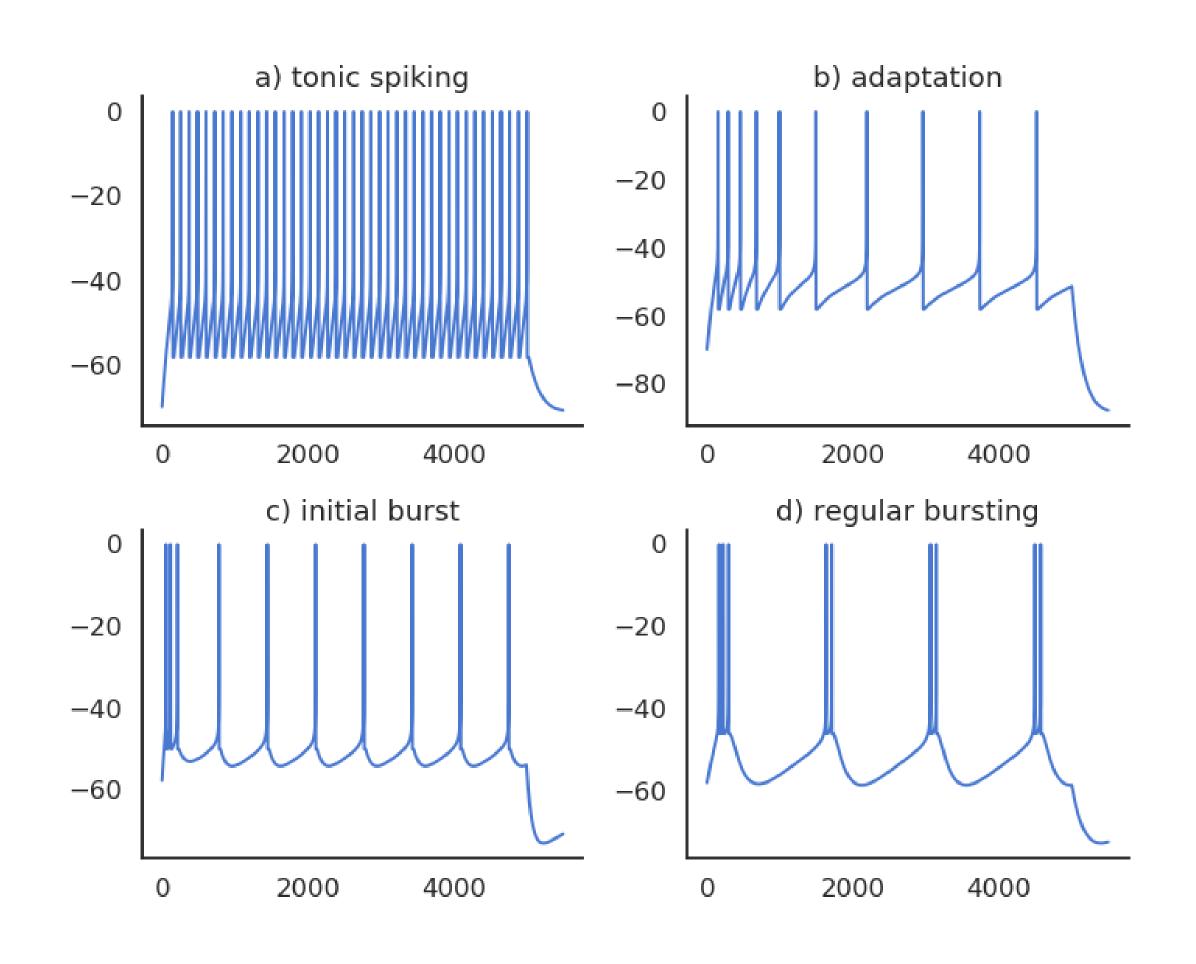
 Adaptive exponential IF (AdEx, Brette and Gerstner, 2005).

$$egin{align} rac{dv}{dt} &= 0.04\,v^2 + 5\,v + 140 - u + I & C\,rac{dv}{dt} &= -g_L\;(v-E_L) + g_L\,\Delta_T\,\exp(rac{v-v_T}{\Delta_T}) \ & + I - w \ rac{du}{dt} &= a\,(b\,v-u) & . \end{cases}$$

$$au_w\,rac{dw}{dt}=a\left(v-E_L
ight)-w$$



### Realistic neuron models can reproduce a variety of dynamics

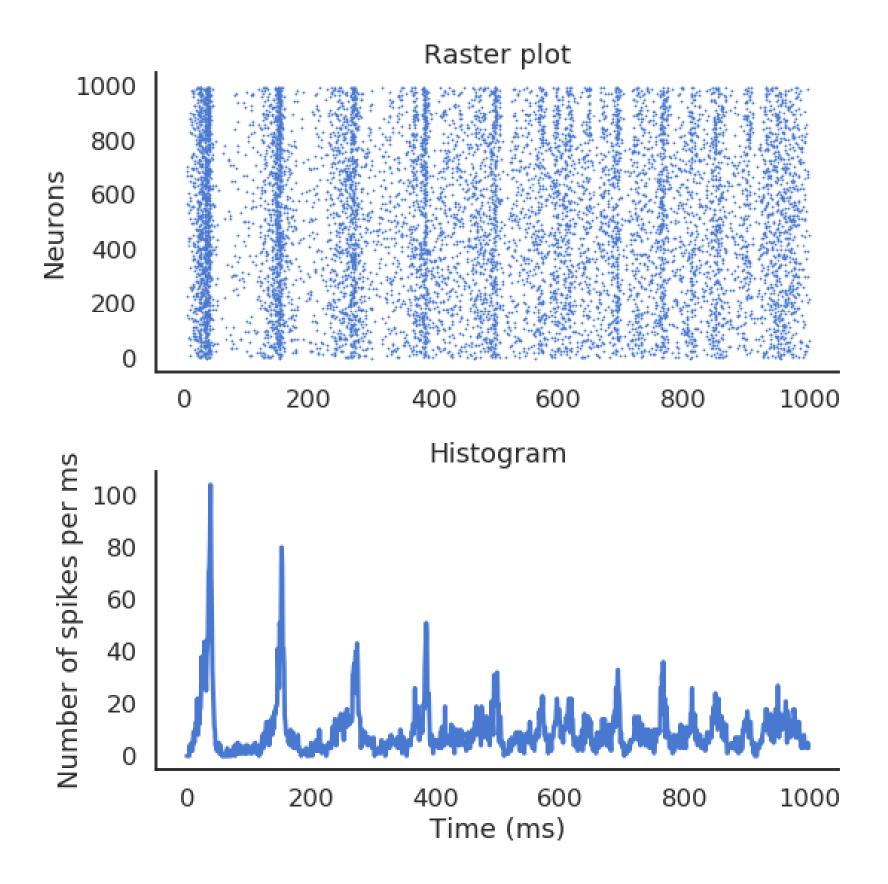


Biological neurons do not all respond the same to an input current.

- 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.

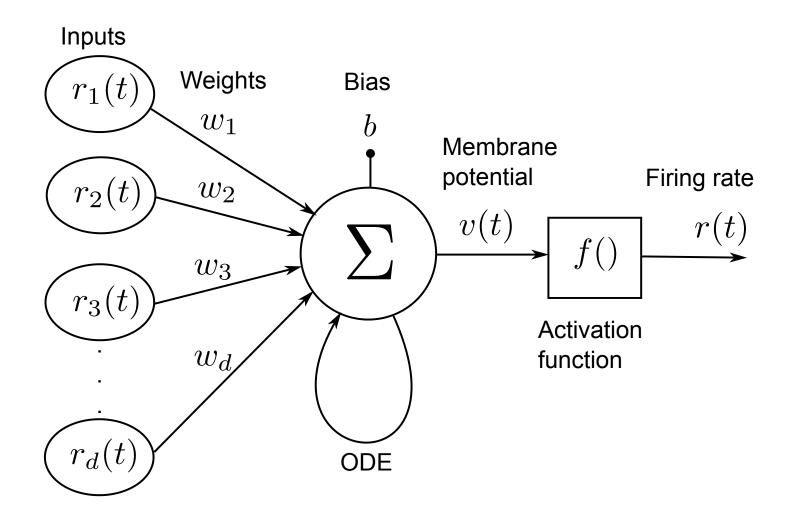
### Populations of spiking neurons



- 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:
  - ullet 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.

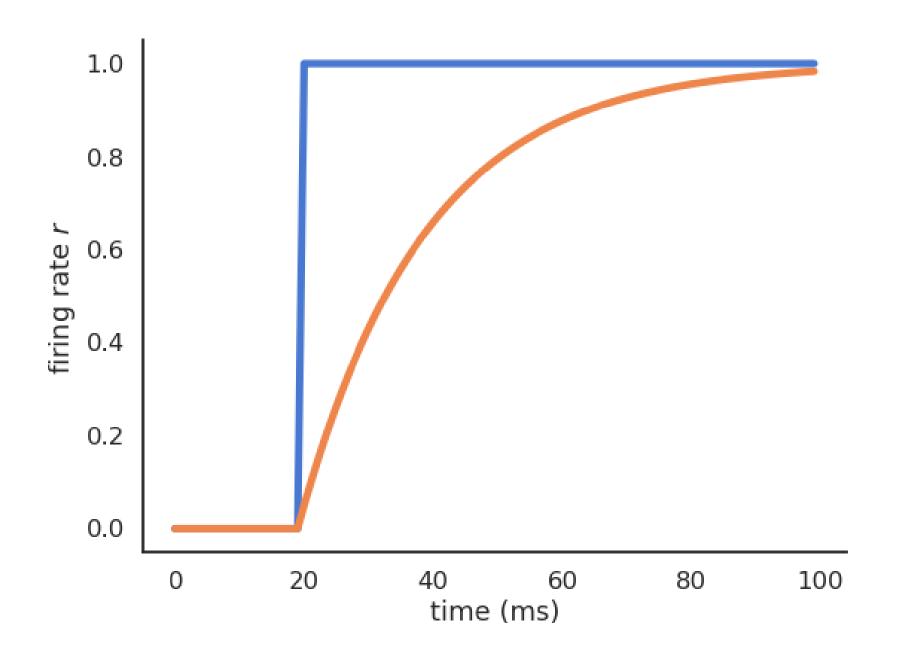


#### Rate-coded neuron

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

• 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:

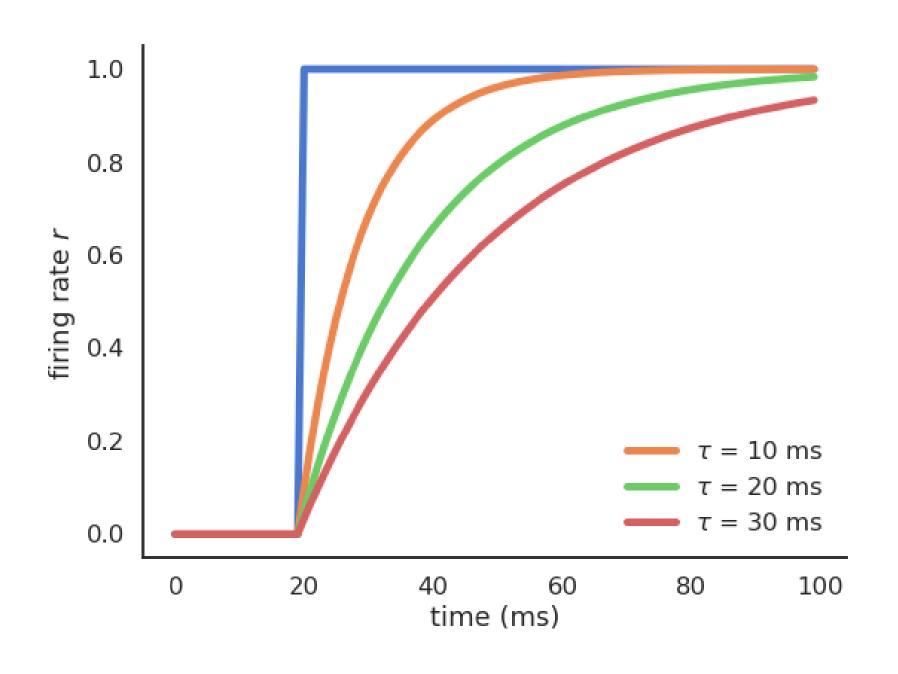
$$au rac{dv(t)}{dt} + v(t) = I(t)$$
  $r(t) = (v(t))^+$ 

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

$$rac{dv(t)}{dt} = rac{I(t) - v(t)}{ au}$$

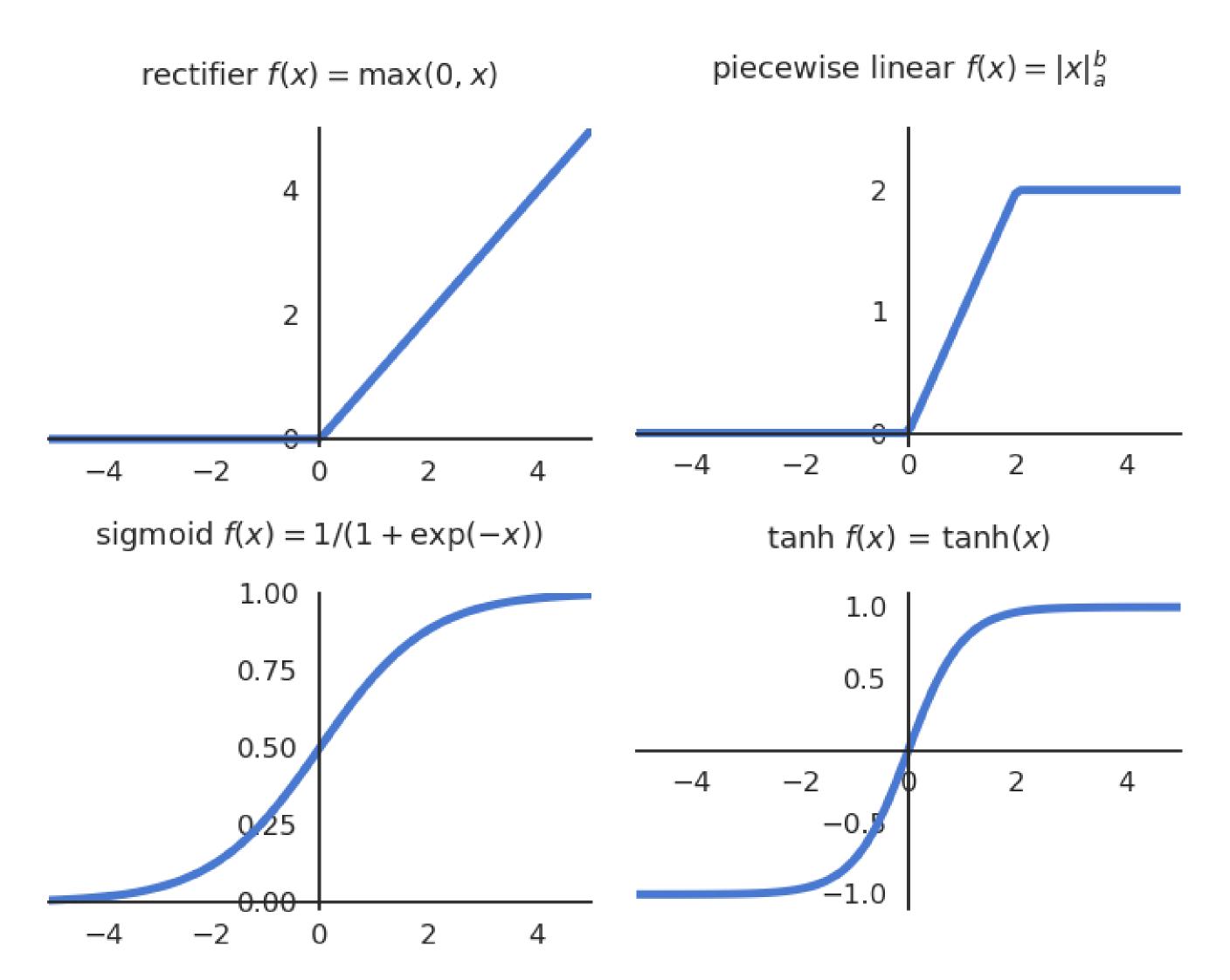
- ullet When v(t) is quite different from I(t), the membrane potential "accelerates" to reduce the difference.
- ullet When v(t) is similar to I(t), the membrane potential stays constant.

#### 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**  $\tau$ .
- The time constant  $\tau$  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**

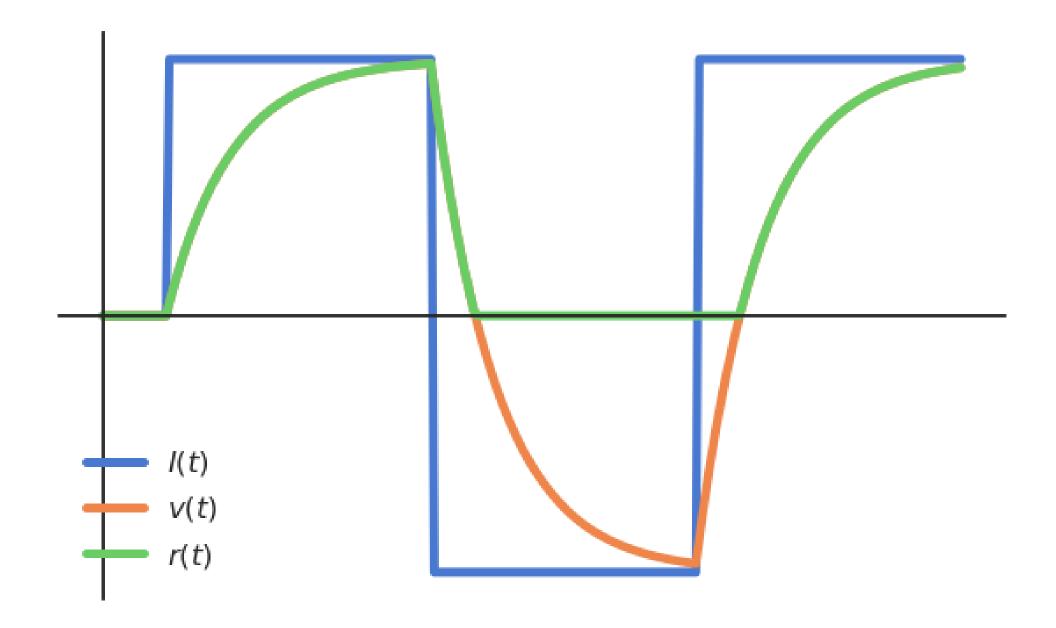


### Rectifier activation function

• 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.

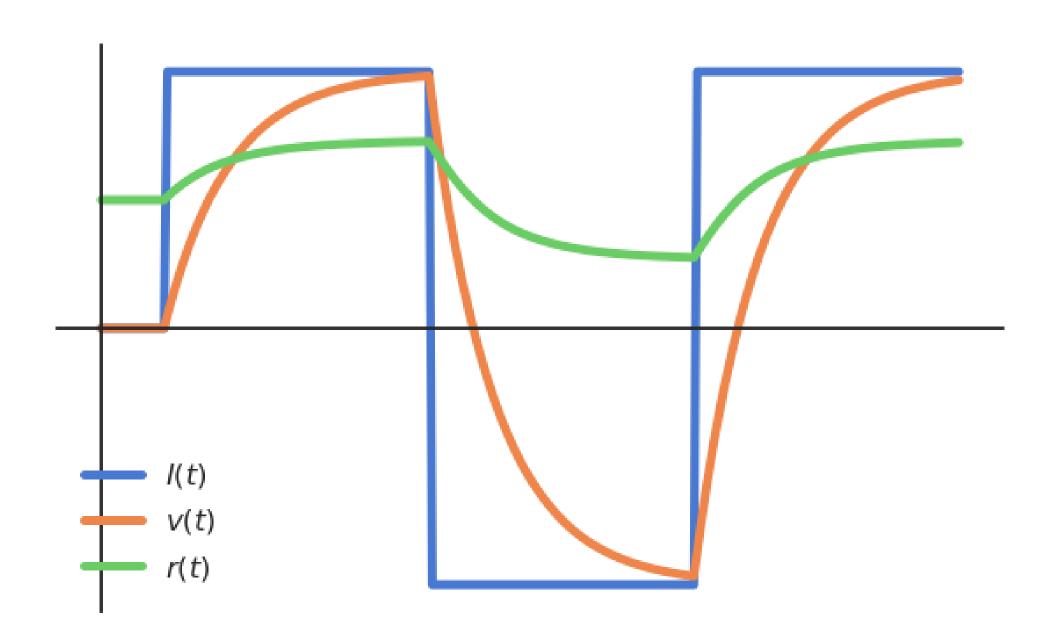


### Logistic activation function

• When using the logistic (or sigmoid) activation function

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

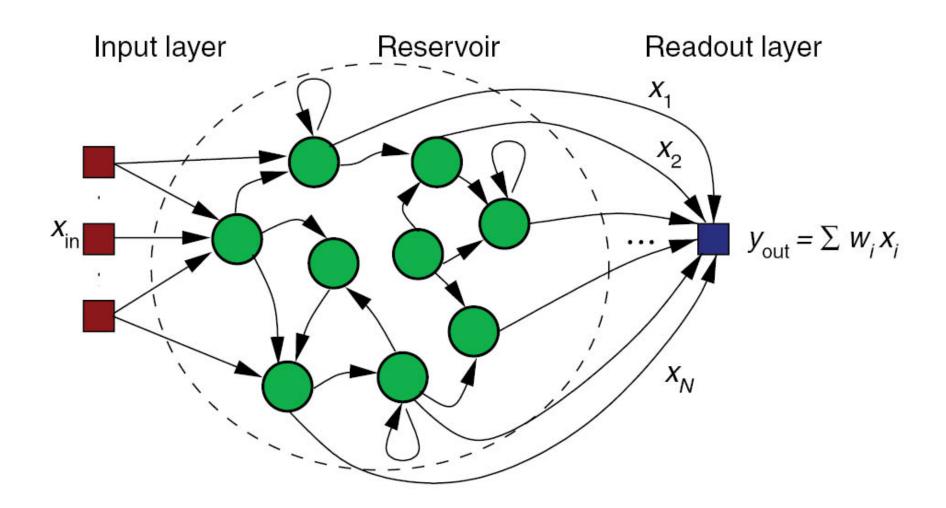
the firing rate r(t) is bounded between 0 and 1, but responds for negative membrane potentials.

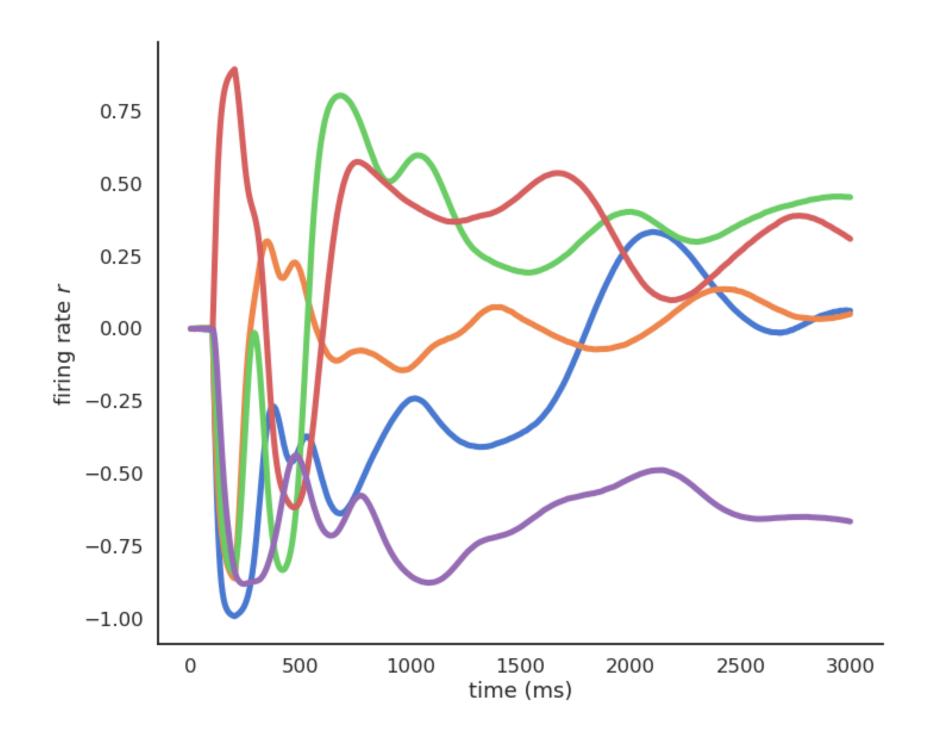


#### **Networks of rate-coded neurons**

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

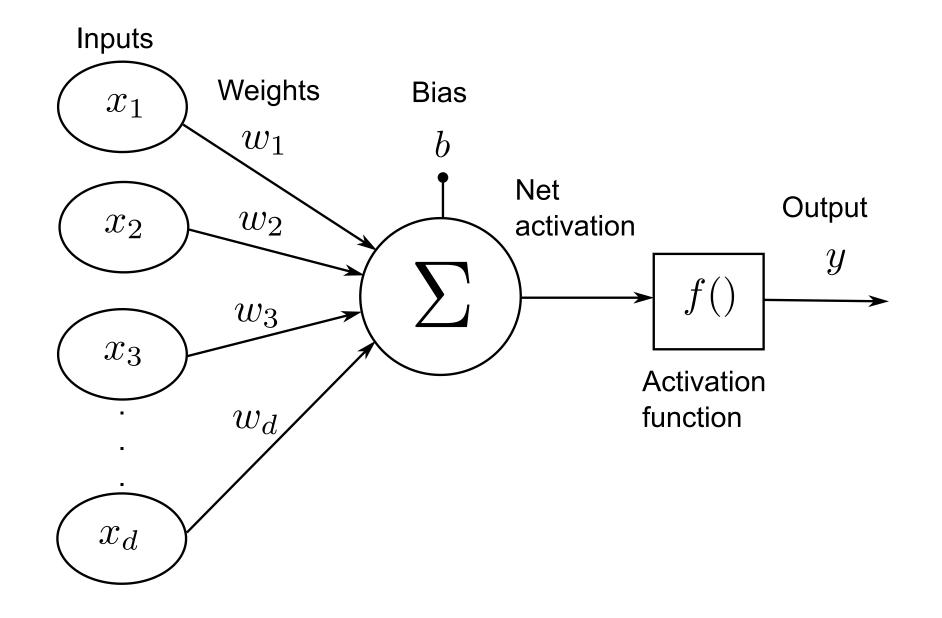
$$au rac{dv(t)}{dt} + v(t) = \sum_{ ext{input}} w^{ ext{I}} \, I(t) + g \, \sum_{ ext{rec}} w^{ ext{R}} \, r(t) + \xi(t)$$
  $r(t) = anh(v(t))$ 





## 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**

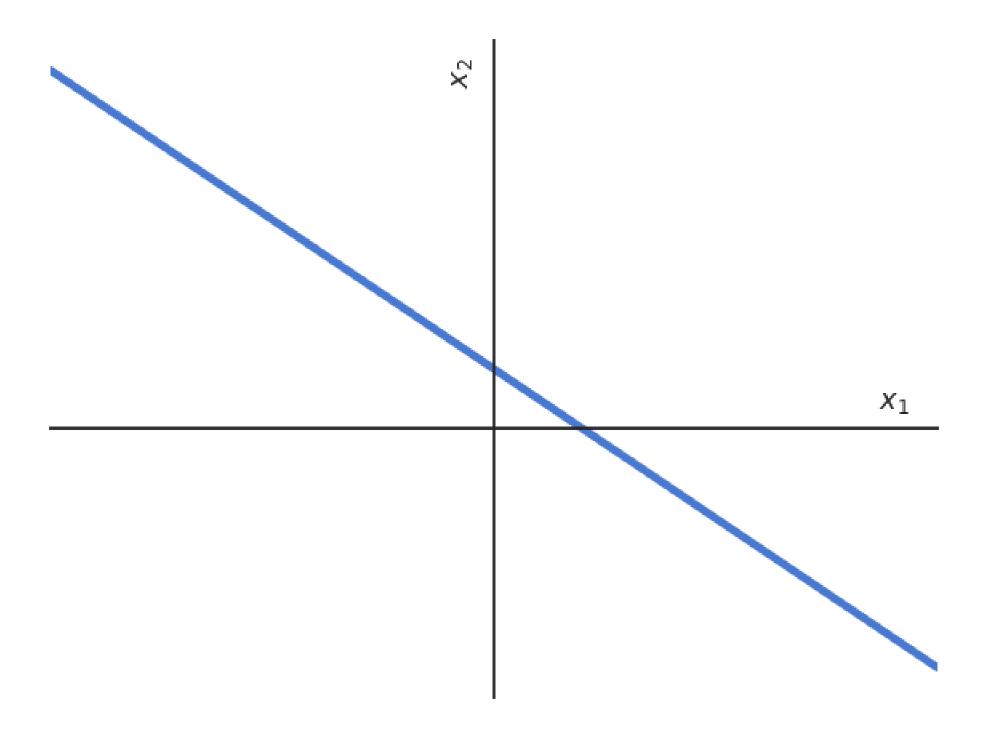
$$y=f(\sum_{i=1}^d w_i\,x_i+b)$$

- 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.

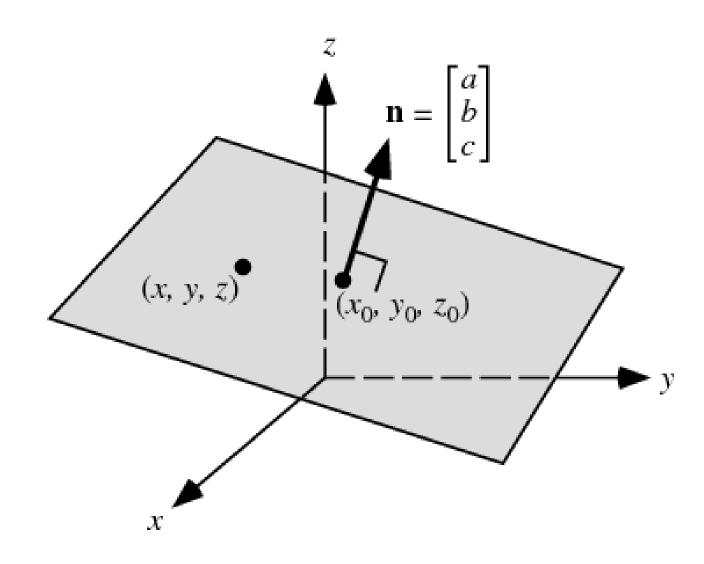
### **Artificial neurons and hyperplanes**

- 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  $(x_1,x_2)$ .

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



### **Artificial neurons and hyperplanes**



https://newvitruvian.com/explore/vector-planes/#gal\_post\_7186\_nonzero-vector.gif

- The net activation defines 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 w and a bias b:

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

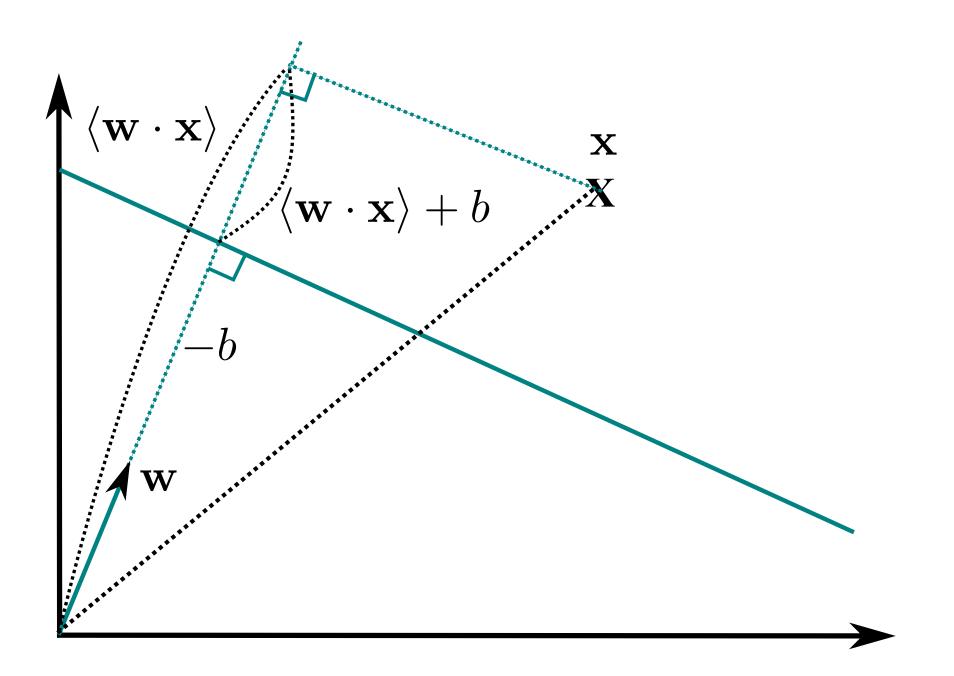
with:

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

- $\langle \cdot \rangle$  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.
  - ullet  $\langle {f w}\cdot{f x}
    angle +b<0$  for all points  ${f x}$  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 Rate-coded Spiking Artificial neuron Hodgkin-Huxley Biological neuron neuron neuron Extracellular Medium Output $g_n(t,V)$ function o Intracellular Medium Machine learning Computational neuroscience

Neurocomputing

