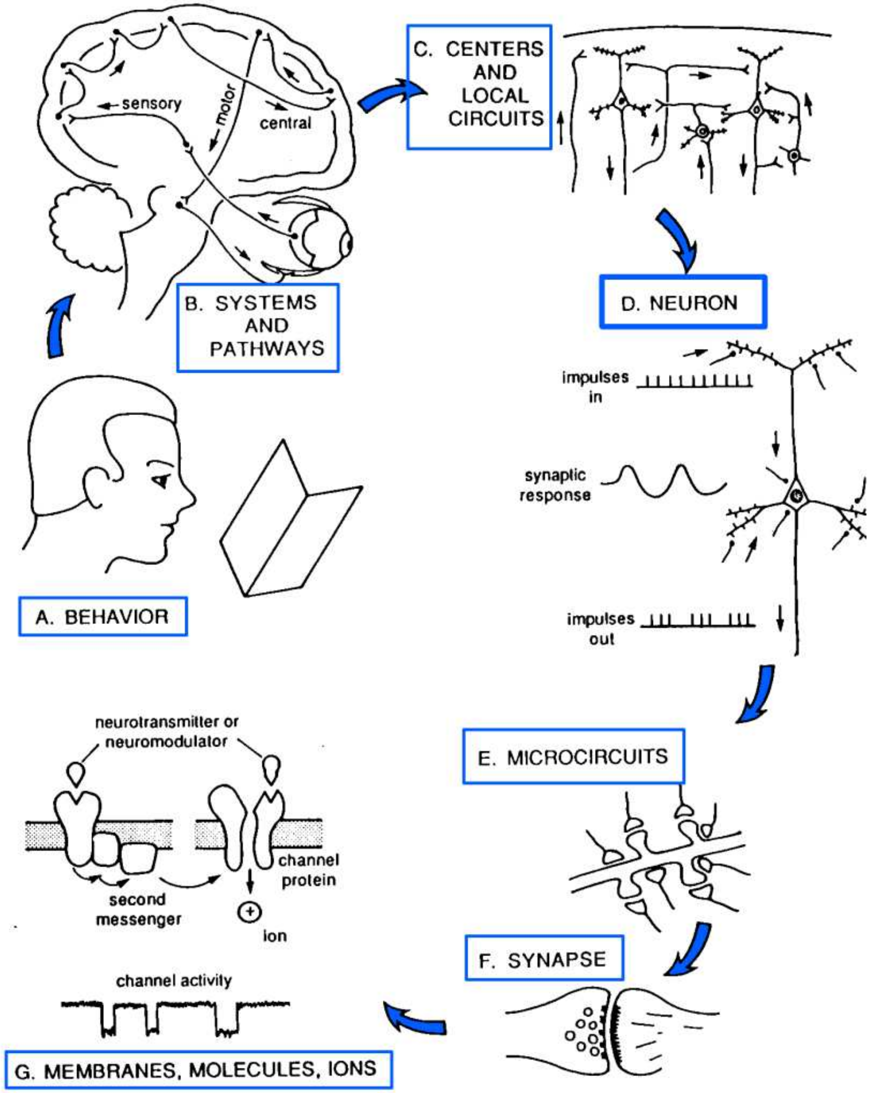
Spatial Scales of the Brain



CNS	1m	10^{0}m
Systeme	10cm	10^{-1} m
Areale	1cm	10^{-2} m
Lokale Netzwerke (Columns)	1mm	10^{-3} m
Neuronen	0.1mm	10^{-4} m
Synapsen	1µm	10^{-6} m
Molekuele	0.1nm	10^{-10} m

Neuron Models Overview

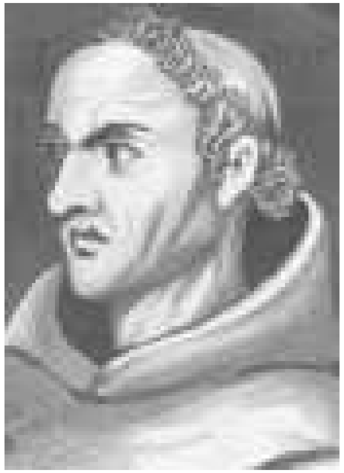
- Nonspiking models
  - Threshold neuron (McCulloch-Pitts neuron, Schwellengatter)
  - Sigmoidal neuron
  - Linear neuron
- Formal spiking neuron models
  - Integrate-and-Fire model
  - Spike response model
- Detailed models
  - Conductance based neuron model
  - Multi-compartment models

From Simple to Complex Models

We start with simple models and switch to more and more complex models.

We will have to be aware of

- Which aspects of real neurons are ***captured*** by the model?
- Which aspects are ***not captured*** by the model?
- How to understand simpler models as ***special cases*** of more complex models.
- Which new ***mechanisms relevant for information processing*** are captured by more complex models?



Occam's Razor: "Entities should not be multiplied more than necessary"

When you have two competing hypothesis/models which make exactly the same predictions, the one that is simpler is the better.

The most complex model is not necessarily the best one, because

- one often does not understand the true role of additional mechanisms.
- one often does not know the values for additional parameters.
- more complex models are more time intensive to simulate $\longrightarrow$ smaller networks

Threshold Gate

In 1943, the neurophysiologist McCulloch and the logician Pitts proposed a model for the calculations of a neuron i which was quite similar to the following one:

Input: A vector $\boldsymbol{x} = (x_1, \ldots, x_n)^T \in \{0,1\}^n$

Output: A bit $x_i \in \{0,1\}$ defined as follows

$$x_i := \begin{cases} 1, & \text{if } \sum_{i=1}^{n} w_{ij} \cdot x_j \geq \vartheta_i \\ 0, & \text{otherwise} \end{cases}$$

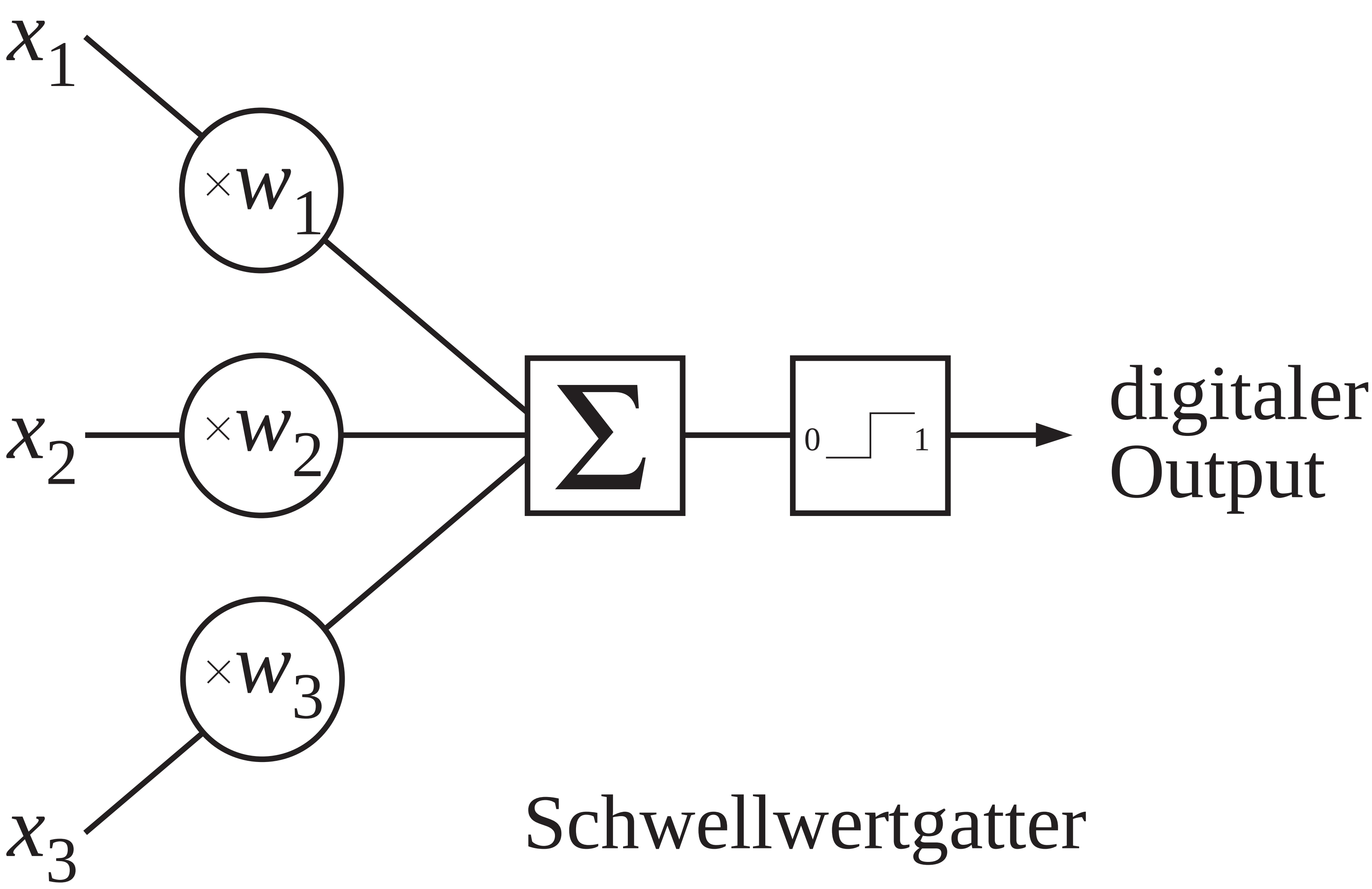
Parameters:

- $\boldsymbol{w} = (w_{i1}, \ldots, w_{in})^T \in \mathbb{R}^n$ ... Weights
- ϑ_i ... Threshold

Vector notation with Θ being the Heaviside step function:

$$x_i = \Theta\left(\mathbf{w}^T \mathbf{x} - \vartheta_i\right)$$

Schema of the Threshold Model



Binary inputs $x_j = 1$ models an active = ”presynaptic neuron j fires” synapse.

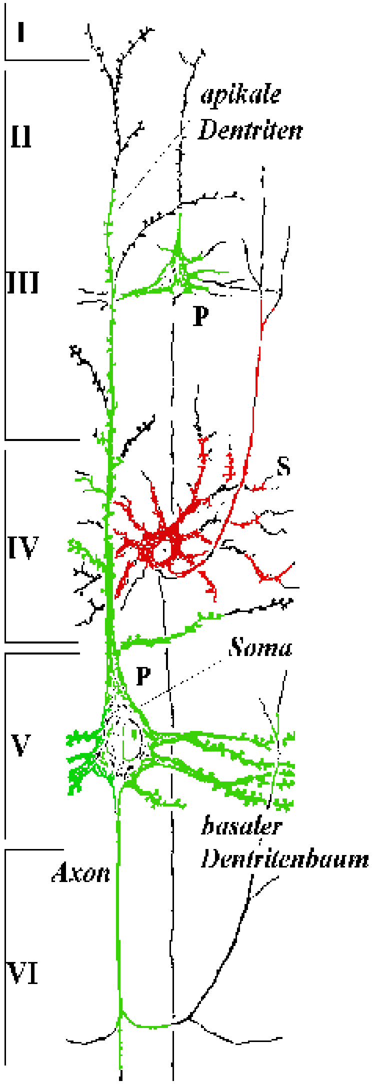
Postsynaptic response The terms $x_j w_{ij}$ model the amplitude of the postsynaptic voltage change due to the active synapse ij.

Nettoinput $u_i := \sum_j w_{ij}\, x_j$ models the membrane potential at the axon hillock of the neuron.

Threshold When the membrane potential u_i exceeds the threshold ϑ_i, the neuron fires an action potential, i.e., $x_i = 1$.

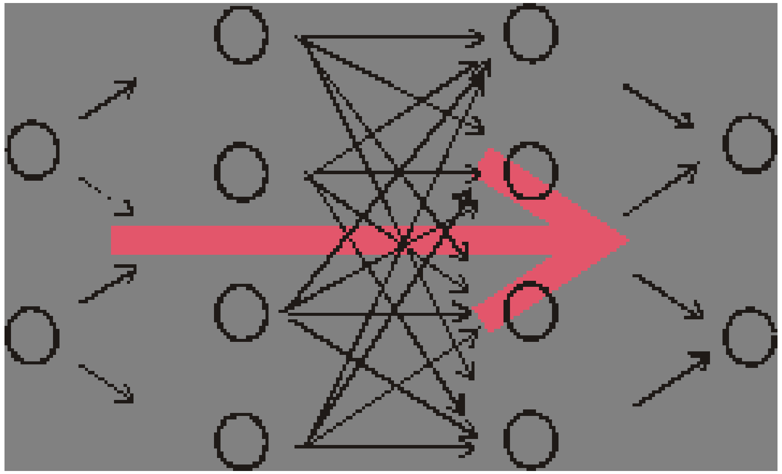
Binary output is like an action potential an all ($x_i = 1$) or nothing ($x_i = 0$) signal.

Weights A weight $\boldsymbol{w_{ij}}$ models the strength of a synapse from the presynaptic neuron j to the postsynaptic neuron i. The weights of synapses are modulated by learning mechanisms.

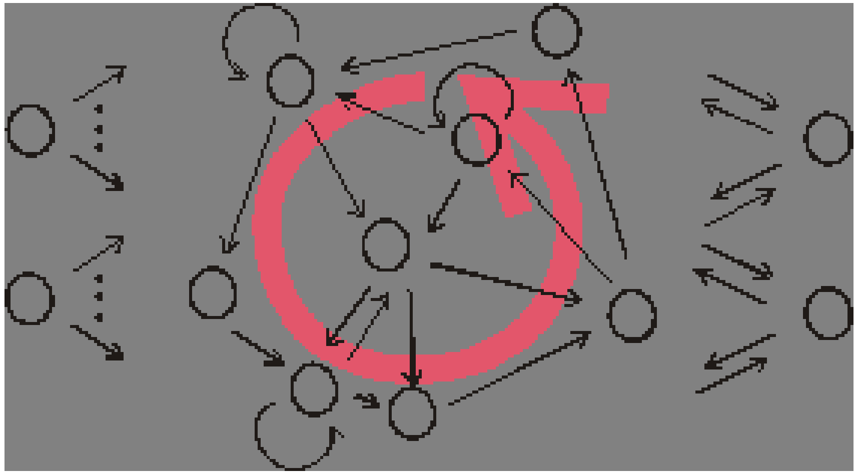


- Excitatory synapses are exciting their targets (i.e., their activity increases the membrane potential of the target). Excitatory synapses are modeled by positive weights $w_{ij} > 0$.
- Inhibitory synapses are inhibiting their targets (i.e., their activity tends to decrease the membrane potential of the target). Inhibitory synapses are modeled by negative weights $w_{ij} < 0$.
- Neurons have either exclusively excitatory or exclusively inhibitory outgoing synapses, i.e., a neuron is either an ***excitatory neuron*** or an ***inhibitory neuron***.
- Therefore, we have $sign(w_{ij}) = sign(w_{kj})$ for all i, j, k.

feed forward networks



recurrent networks



Biological networks are in general highly recurrent.

For recurrent networks, there are two frequently used update schemes

Synchronous

For every (discrete) time step t, the output $x_i(t)$ of neuron i is calculated from the outputs $x_j(t-1)$ of its presynaptic neurons at time $t-1$:

$$x_i(t) = \Theta\left(\sum_j w_{ij}\, x_j(t-1) - \vartheta_i\right)$$

For a network with n neurons, a weight matrix $W = [w_{ij}]_{i,j=1,\ldots,n}$, and a vector of thresholds $\vartheta = (\vartheta_1, \ldots \vartheta_n)^T$, we can write this as

$$\mathbf{x}(t) = \Theta\left(W\mathbf{x}(t-1) - \vartheta\right)$$

Asynchronous/stochastic

Choose a neuron i randomly from the set of neurons in the network and calculate its output $x_i(t)$ from the outputs of its presynaptic neurons at time $t-1$.

Threshold Neuron: Pros and Cons

Simple model: Theoretical analysis is possible, also for learning algorithms (e.g., the perceptron rule).

Abstract model: It captures the most fundamental aspects of neuronal function.

Plausible model: Some cells in the cerebellum seem to work similar to threshold neurons.

Timing: Time has to be discretized.

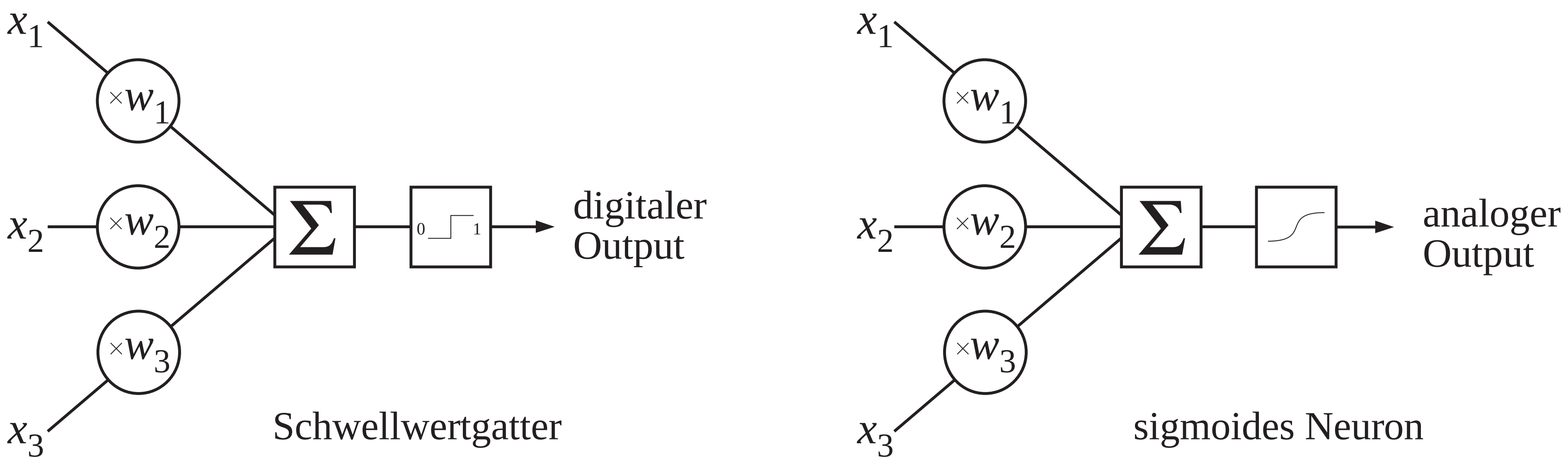
Ignores temporal dynamics: e.g., an output spike is only relevant for the membrane potential of the postsynaptic neurons in the next time step.

Point model: The spatial structure of the dendritic tree and the resulting nonlinear interactions of voltages are not modeled.

Implausible model: Because of its temporal deficits, probably not plausible for most neurons in cortex.

Sigmoidal neuron

Sigmoidal neurons have a “soft” threshold.



The essential difference to a threshold neuron is its sigmoidal ***activation function*** which ensures analog output.

Sigmoidal neuron

Computation of the *analog output* x_i based on *analog inputs* x_j:

$$x_i = \boldsymbol{\sigma}\left(\underbrace{\sum w_{ij}x_j - \vartheta}_{u_i}\right)$$

with the activation function $\boldsymbol{\sigma}$. Often used for $\sigma(u)$:

- logsig: $\sigma(u) = \frac{1}{1+e^{-u}}$
- tansig: $\sigma(u) = \frac{2}{1+e^{-u}} - 1 = \tanh(u)$

Other neuron models are obtained for other activation functions:

- ***Threshold neuron***: $\sigma(u) = \begin{cases} 1, & \text{if } u \geq 0 \\ 0, & \text{otherwise.} \end{cases}$
- ***Linear neuron***: $\sigma(u) = u$.

Interpretation of analog Inputs and Outputs

One can interpret the analog output of a sigmoidal neuron as its *firing rate* $\boldsymbol{\nu}$.

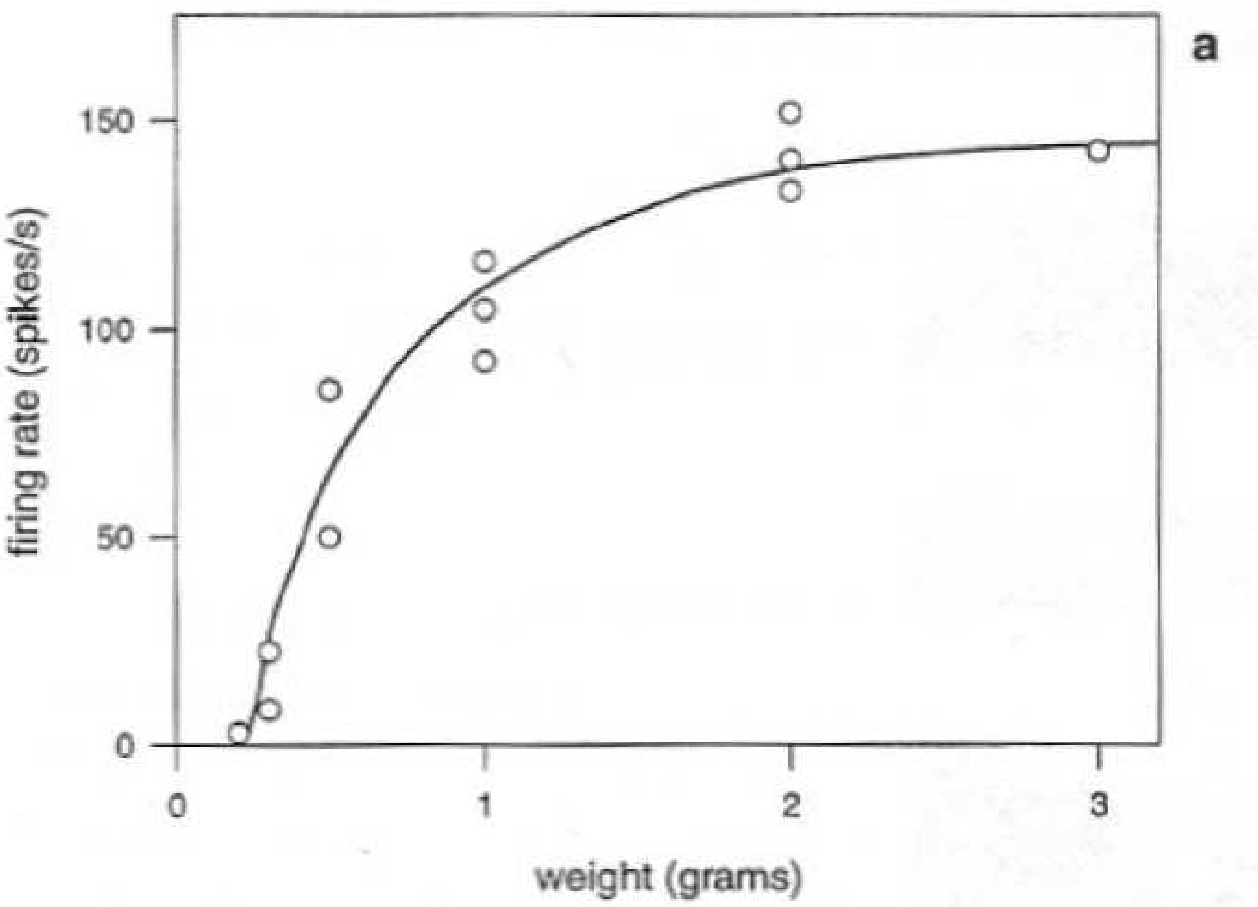
$$\text{firing rate } \nu(t) = \frac{\text{Number of spike in time interval } [t - \Delta T, t]}{\Delta T}$$

Models which are based on the assumption that the firing rate of a neuron codes the information transmitted are called ***rate models***.

Does this model make sense?

Is information transmitted by the firing rate of neurons in biological systems?

Answer by Lord Adrian, 1926



Firing rate of a stretch sensor in a muscle, Adrian 1926.

Discrete time updates

Just like in networks of threshold gates.

Continuous time updates

All neurons in the network update their output x_i continuously such that it changes in the direction of $\sigma(u_i)$.

$$\tau_i \frac{dx_i(t)}{dt} = -x_i(t) + \sigma(u_i(t))$$

with a time constant $\tau_i > 0$ and

$$u_i(t) = \sum_j w_{ij}\, x_j(t) - \vartheta_i$$

Approximation of the continuous update

$$x_i(t) = \alpha_i\, x_i(t - \Delta t) + (1 - \alpha_i)\, \sigma \left(\sum w_{ij}\, x_j(t - \Delta t) - \vartheta \right)$$

with $0 \leq \alpha_i \leq 1$.

Comment:

- $\alpha_i = 1 - \frac{\Delta t}{\tau_i}$
- $\alpha_i \rightarrow 1$ corresponds to $\tau_i \rightarrow \infty$
- $\alpha_i = 0$ corresponds to $\tau_i = \Delta t$ (equivalent to the time-discrete update).
- If Δt is chosen too large (relative to τ_i), the result is not correct.

Sigmoidal Neuron: Pros and Cons

Simple model: Theoretical analysis is possible. Compared to the threshold neuron, the continuous activation function is often advantageous.

Abstract model: It captures the most fundamental aspects of neuronal function.

Plausible model: The firing rate of many neurons as a function of an injected current is sigmoidal-like.

Ignores temporal dynamics: Again, important temporal dynamics of real neurons are ignored.

Point model: The spatial structure of the dendritic tree and the resulting nonlinear interactions of voltages are not modeled.

Implausible model: Many results suggest that the exact spike timing is important for information processing in biological systems, at least in some parts of the brain.