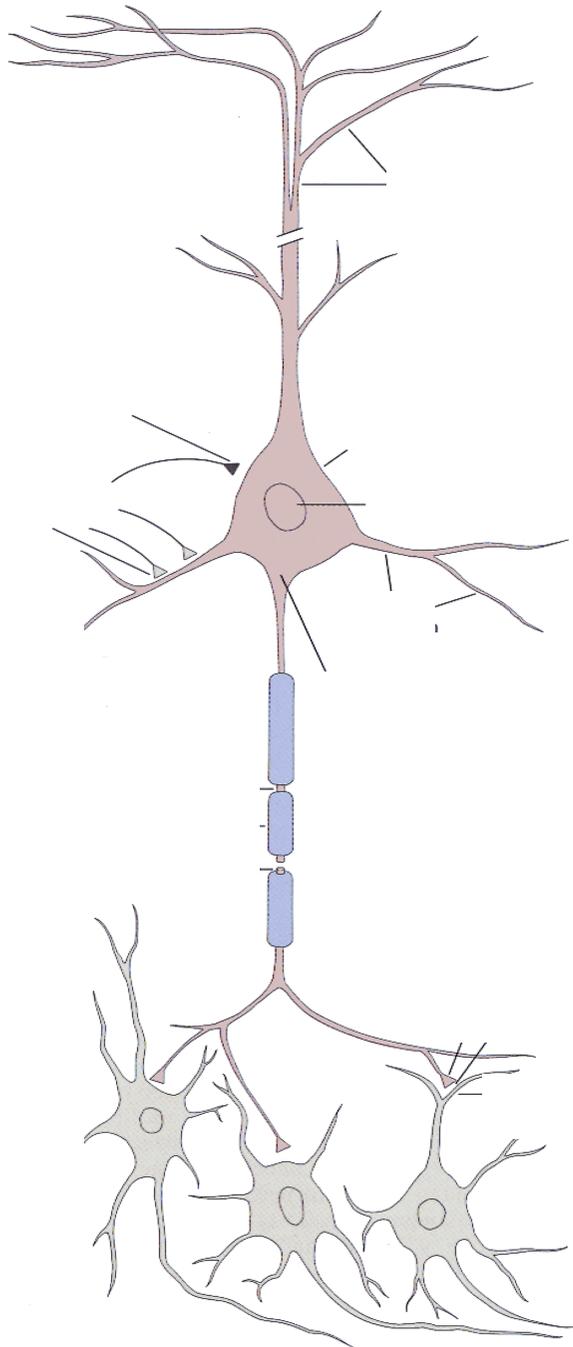


Neuroinformatics

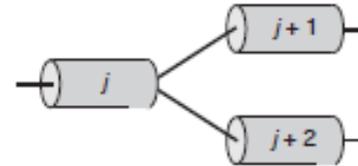
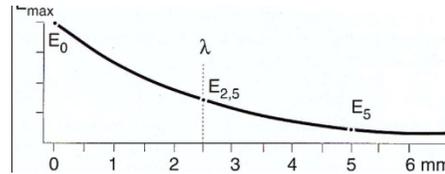
Marcus Kaiser

Week 3: Simplified neuron and population models
(textbook chapter 3)

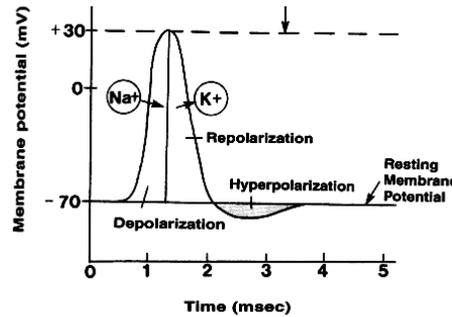


Single-Neuron simulation

Passive propagation (dendrite and soma)



Active propagation (axon hillock and axon) Hodgkin-Huxley



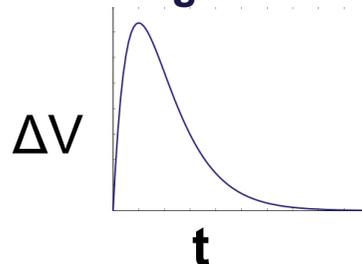
$$C \frac{dV}{dt} = -g_K n^4 (V - E_K) - g_{Na} m^3 h (V - E_{Na}) - g_L (V - E_L) + I(t)$$

$$\tau_n(V) \frac{dn}{dt} = -[n - n_0(V)]$$

$$\tau_m(V) \frac{dm}{dt} = -[m - m_0(V)]$$

$$\tau_h(V) \frac{dh}{dt} = -[h - h_0(V)]$$

Neurotransmitter release -> Ion flow -> change in Postsynaptic potential (PSP)



$$\Delta V_m^{\text{non-NMDA}} \propto t e^{-t/t^{\text{peak}}}$$

Single-Neuron simulation

Benefits

- Can reproduce activity of single neurons
- Can be used to model detailed changes (external currents or the effect of drugs)

Disadvantages

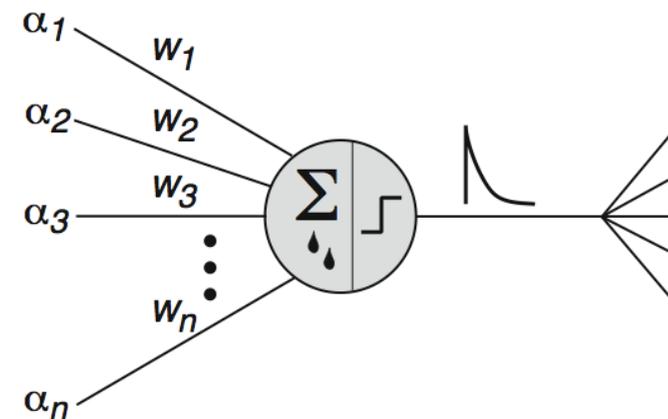
- Needs neuron morphology (dendritic layout)
- Needs information about ion channels, synapse position, neurotransmitter type
- Is slow to calculate for large numbers of neurons

=> Need for simplified neuron models

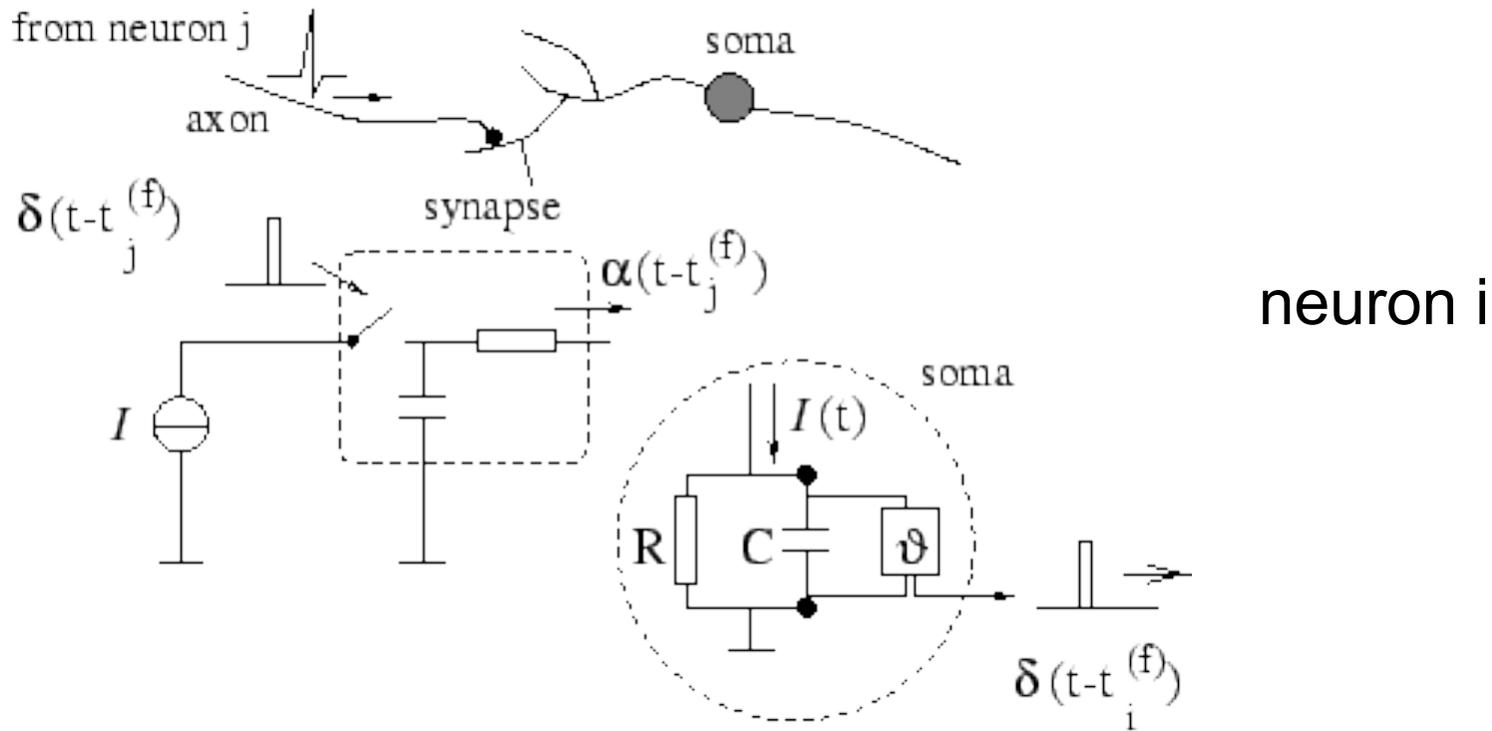
Integrate and Fire Neurons

Simplifications

- The alpha function directly relates to the voltage at the axon hillock (no modelling of passive propagation)
- Spike time rather than the shape of the action potential is important (shapes are similar)
- Synaptic properties are modelled through the synaptic strength value w (also called efficacy)



Integrate and Fire Neurons

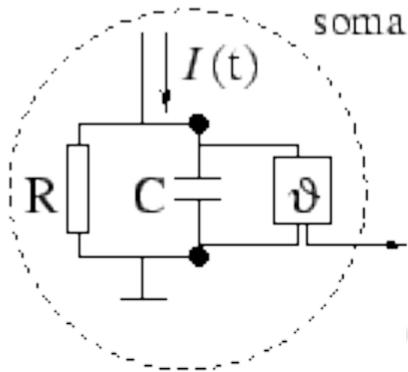


A pre-synaptic spike $\delta(t - t_j^{(f)})$ is low-pass filtered at the synapse and generates an input current pulse $\alpha(t - t_j^{(f)})$

$$I_i(t) = \sum_j w_{ij} \sum_f \alpha(t - t_j^{(f)}) .$$

A current $I(t)$ charges the RC circuit. The voltage $u(t)$ across the capacitance (points) is compared to a threshold ϑ . If $u(t) = \vartheta$ at time $t_i^{(f)}$ an output pulse $\delta(t - t_i^{(f)})$ is generated.

The leaky integrate-and-fire neuron



The driving current can be split into two components, $I(t) = I_R + I_C$. The first component is the resistive current I_R which passes through the linear resistor R . It can be calculated from Ohm's law as $I_R = u/R$ where u is the voltage across the resistor. The second component I_C charges the capacitor C . From the definition of the capacity as $C = q/u$ (where q is the charge and u the voltage), we find a capacitive current $I_C = C du/dt$. Thus

$$I(t) = \frac{u(t)}{R} + C \frac{du}{dt} . \quad \text{Multiply by } R$$

Time constant $\tau_m = RC$ of the 'leaky integrator'. This yields the standard form

Leakage rate 'Leak' Signal

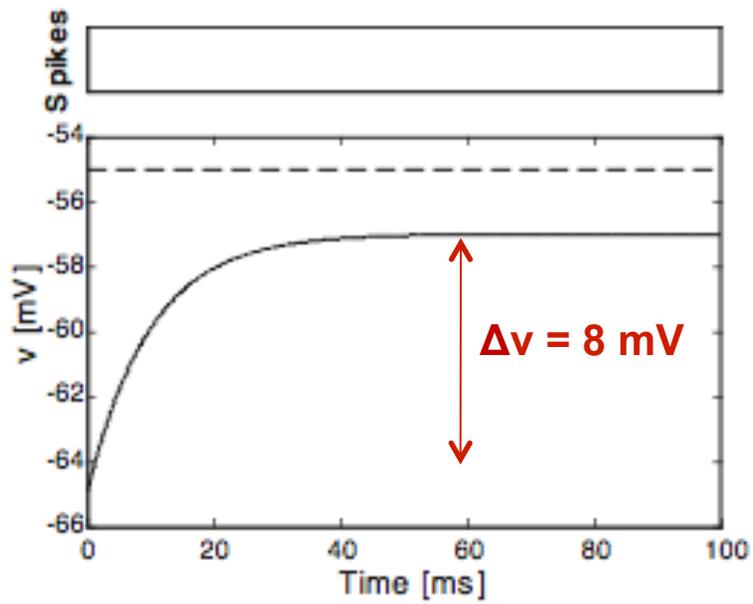
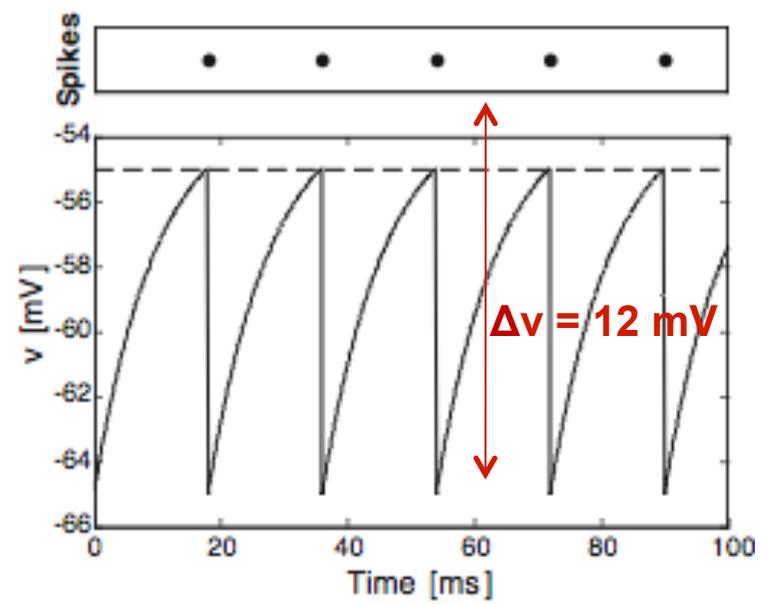
$$\tau_m \frac{du}{dt} = -u(t) + RI(t) .$$

Spikes are events characterized by the 'firing time' $t^{(f)}$ when $t^{(f)} : u(t^{(f)}) = \vartheta$.

Immediately after $t^{(f)}$, the potential is reset to a new value $u_r < \vartheta$,

$$\lim_{t \rightarrow t^{(f)}; t > t^{(f)}} u(t) = u_r .$$

IF simulation

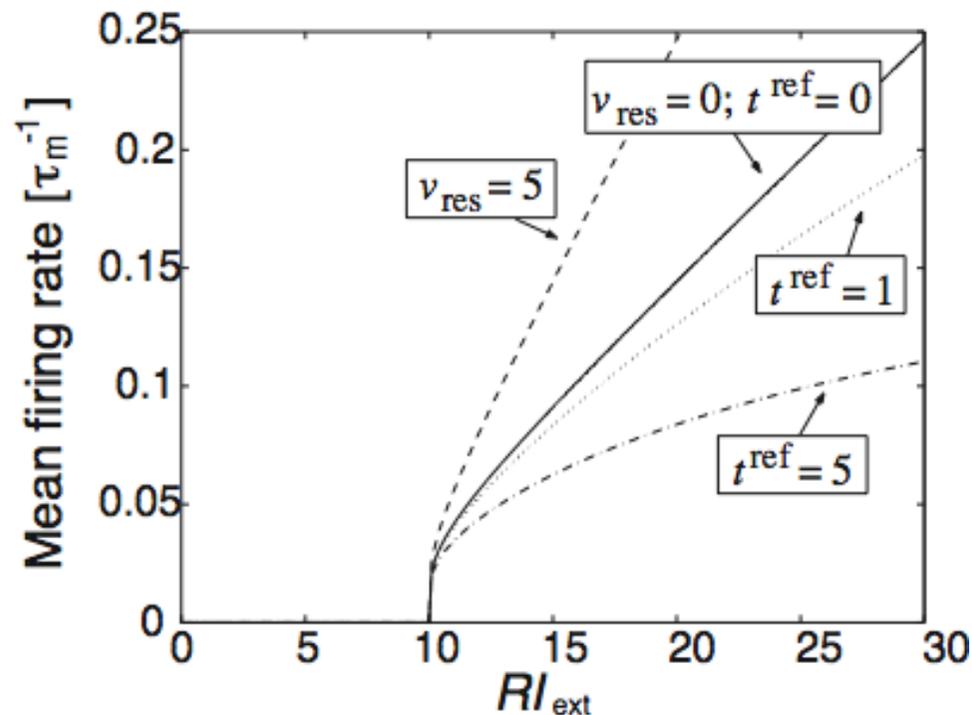
A. External input $RI_{ext} = 8 \text{ mV} < \text{threshold}$ ϑ B. External input $RI_{ext} = 12 \text{ mV} > \text{threshold}$ ϑ 

IF activation function

First passage time: Time a neuron need *for constant input* to reach the threshold and fire

The inverse of the first passage time defines the **firing rate**:

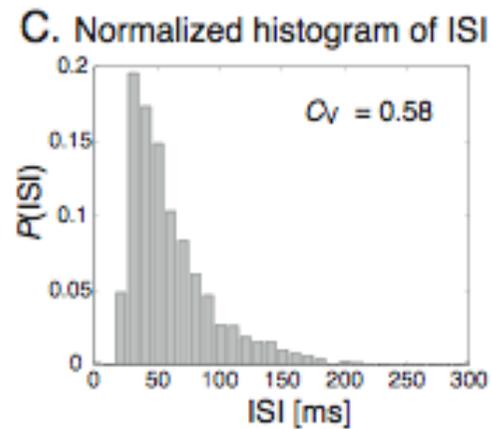
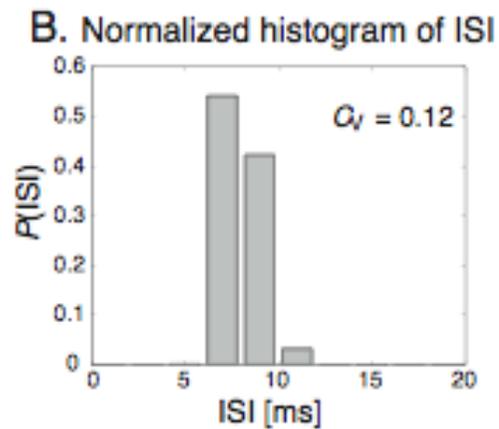
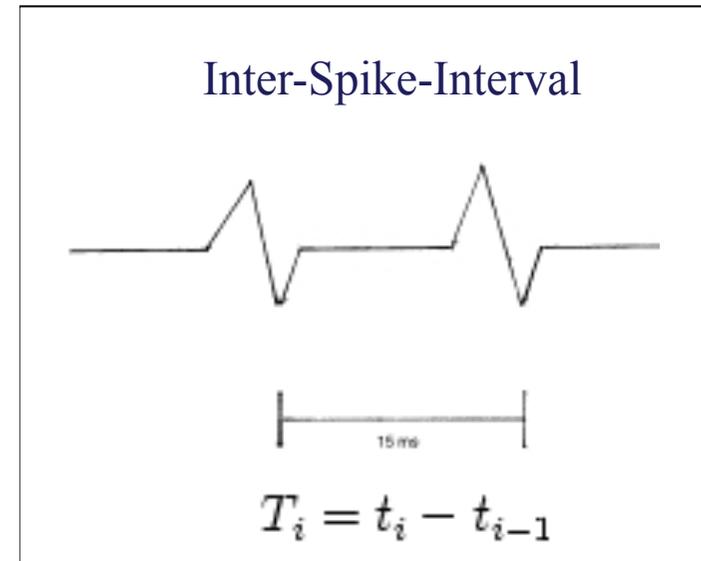
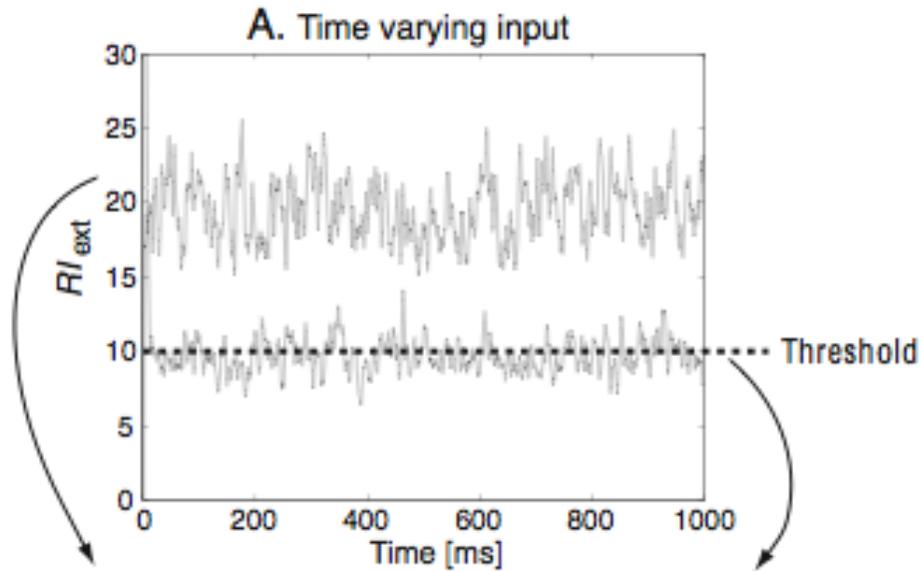
$$\bar{r} = (t^{\text{ref}} - \tau_m \ln \frac{\vartheta - RI}{v_{\text{res}} - RI})^{-1}$$



t^{ref} : refractory time

v_{res} : reset potential

Inter-Spike-Interval (ISI)



The Izhikevich neuron (2003)

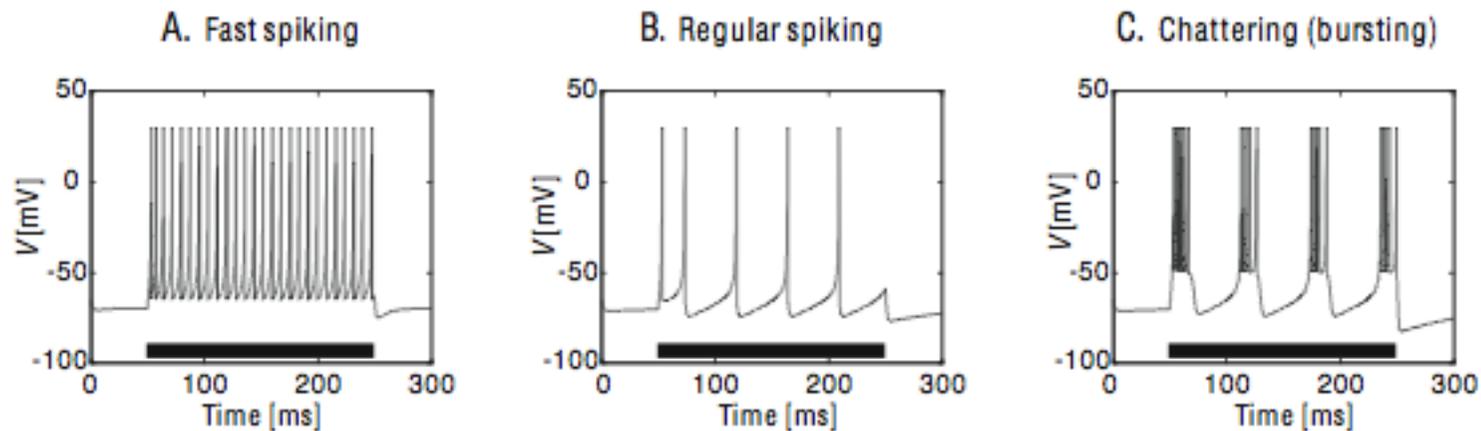
Problems with LIF neurons: does not reproduce the full range of experimentally observed response patterns.

-> Eugene Izhikevich developed a model that can reproduce experiments AND is much simpler than single-neuron models!

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

$$\frac{du(t)}{dt} = a(bv - u)$$

$$v(v > 30) = c \text{ and } u(v > 30) = u + d$$

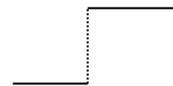


The McCulloch-Pitts neuron (1943)

$$h = \sum_i x_i^{\text{in}}$$

Summation of input (no synaptic weights!)

$$x^{\text{out}} = \begin{cases} 1 & \text{if } h > \Theta \\ 0 & \text{otherwise} \end{cases}$$



Step-wise activation function

-> Birth of artificial neural network (ANN) research

BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 5, 1943

A LOGICAL CALCULUS OF THE IDEAS IMMANENT IN NERVOUS ACTIVITY

WARREN S. MCCULLOCH AND WALTER PITTS

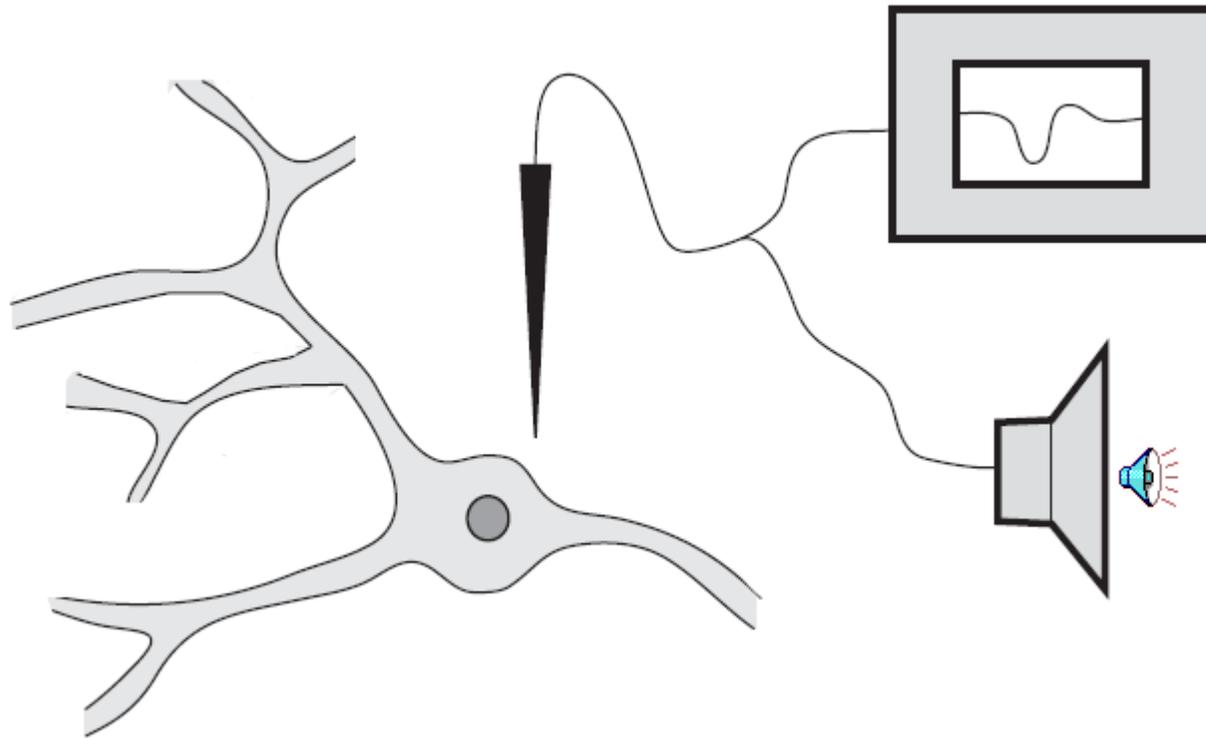
FROM THE UNIVERSITY OF ILLINOIS, COLLEGE OF MEDICINE,
DEPARTMENT OF PSYCHIATRY AT THE ILLINOIS NEUROPSYCHIATRIC INS
AND THE UNIVERSITY OF CHICAGO

Because of the "all-or-none" character of nervous activity, r events and the relations among them can be treated by means of p sitional logic. It is found that the behavior of every net can be desc in these terms, with the addition of more complicated logical mean nets containing circles; and that for any logical expression satis



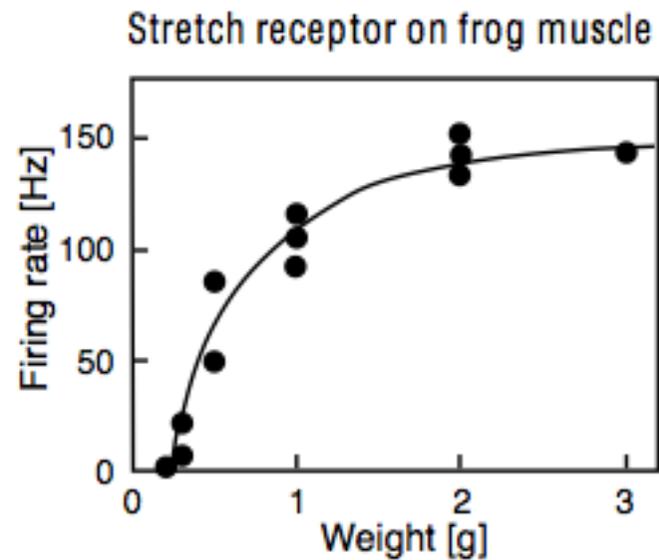
Neural coding

What the brain 'sees'



The firing rate hypothesis

Stimulus features are encoded through the neural firing rate (response curves).

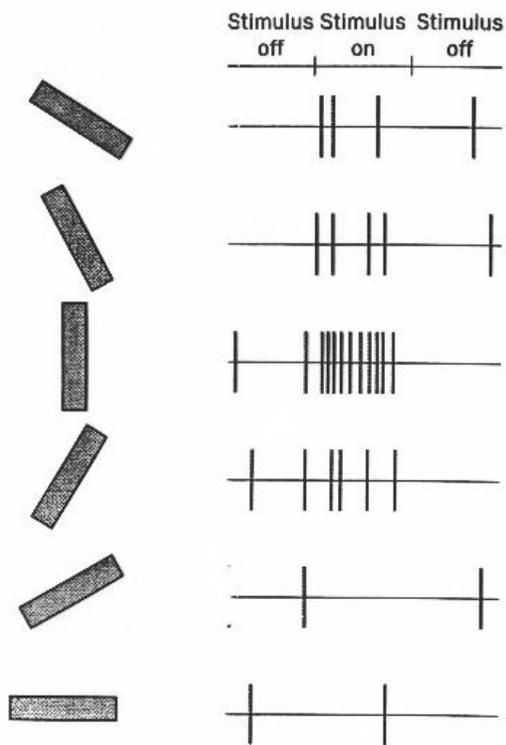


Edgar Adrian
The Nobel Prize in Physiology or Medicine 1932

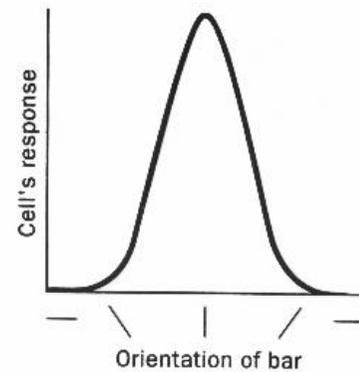
The firing rate hypothesis

Receptive field: area in the outside/physical world for which a neuron is responsive.

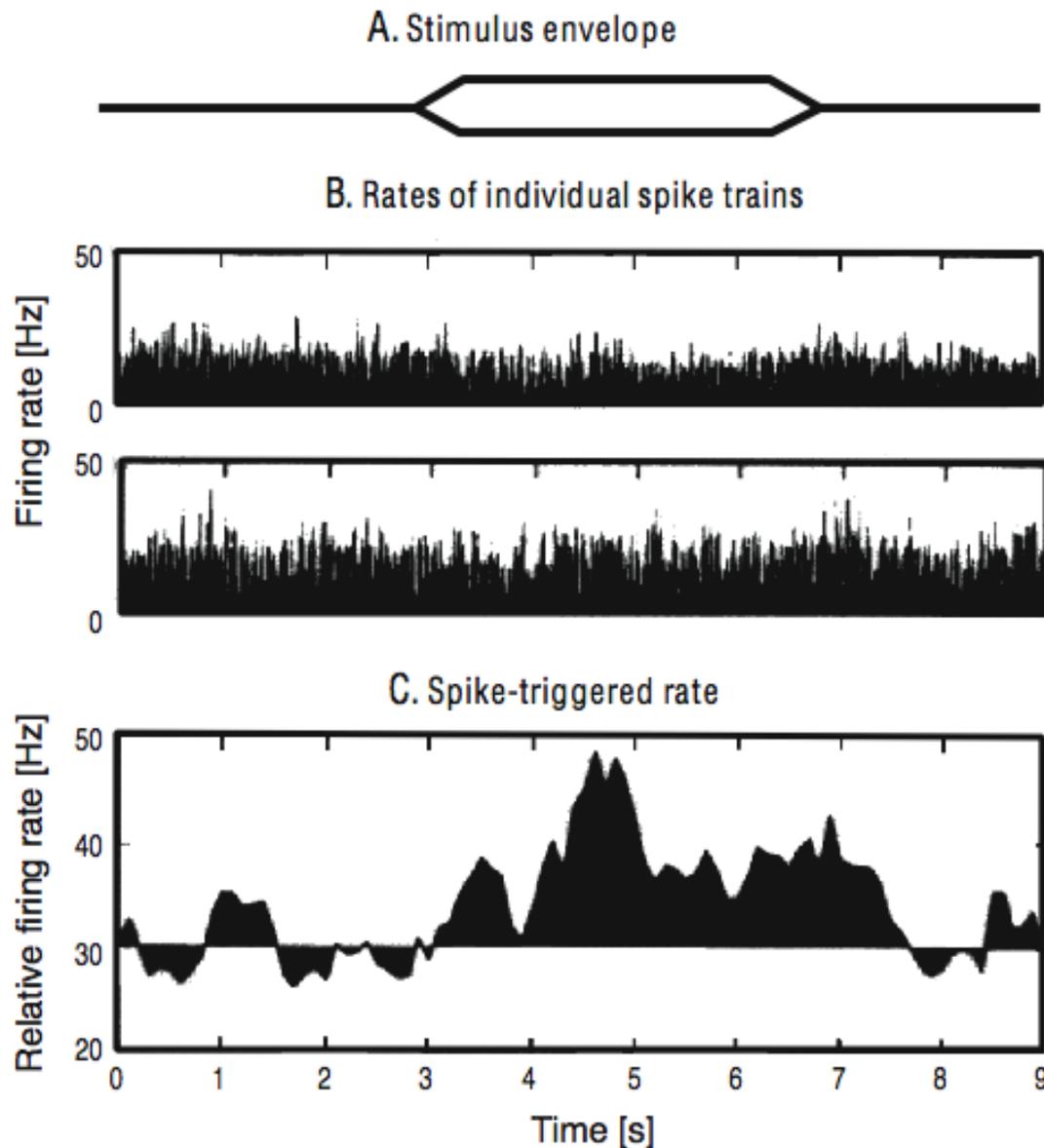
Feature preference



Tuning curve of V1 neuron in cat



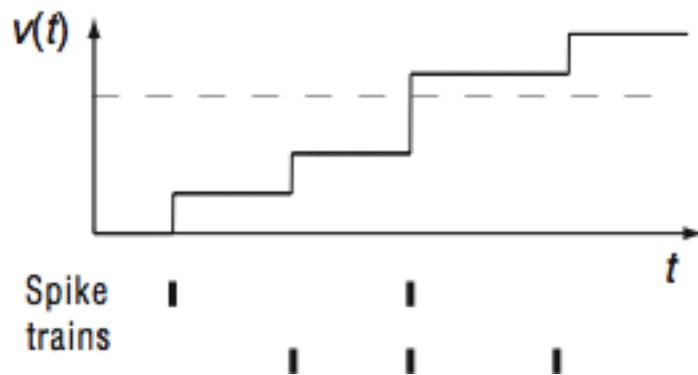
The correlation code hypothesis



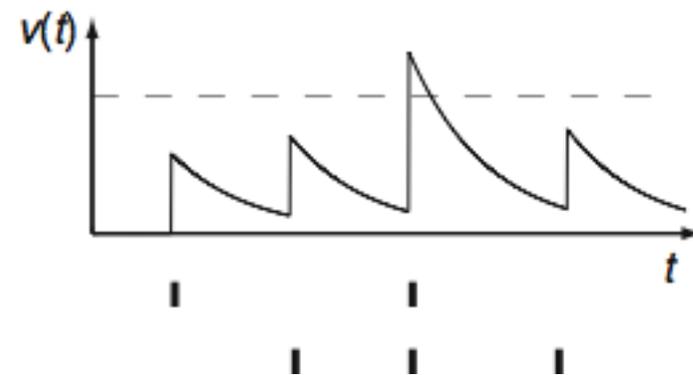
Stimulus features are encoded by neurons firing around the same time

Integrator or coincidence detector?

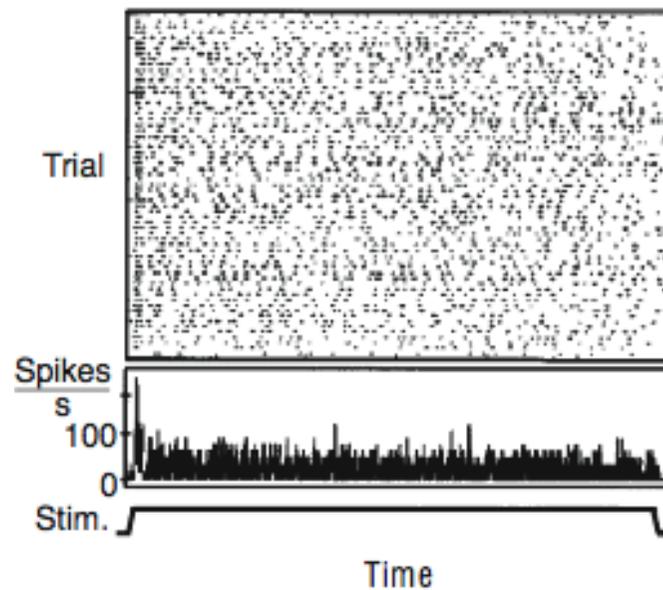
A. Perfect integrator



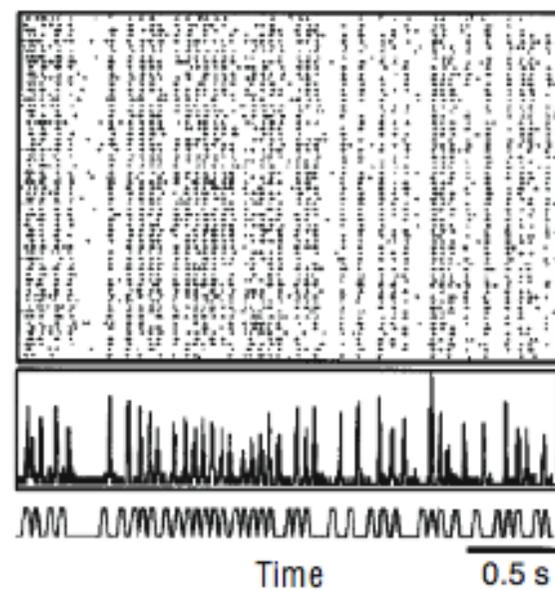
B. Coincidence detector



A. Constant stimulus



B. Rapidly changing stimulus



Seminar papers online at

<http://www.biological-networks.org/t/cneurosci/seminar.zip>

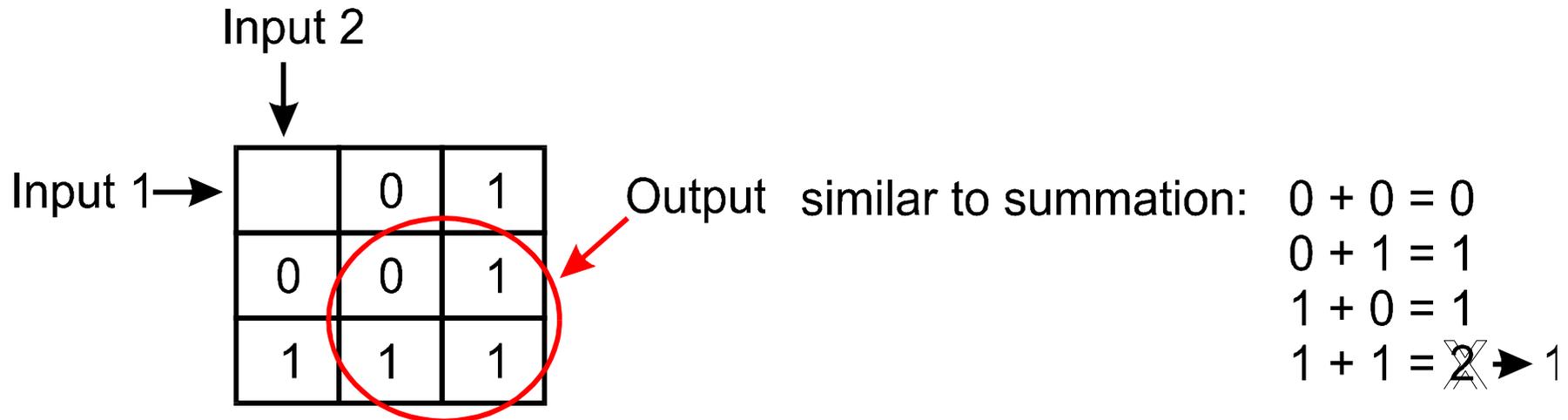
News

Qualcomm Zeroth

Neural computation

LOGICAL OPERATIONS

For example OR:



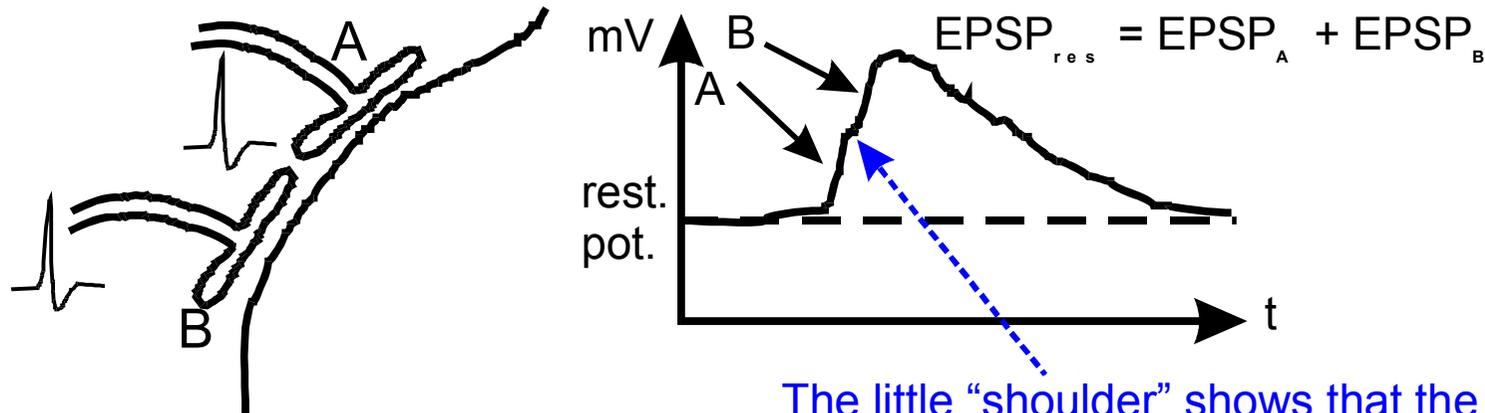
Digital computations with neurons

1 = a spike has occurred

0 = no spike has occurred

Necessary conditions for optimal summation:

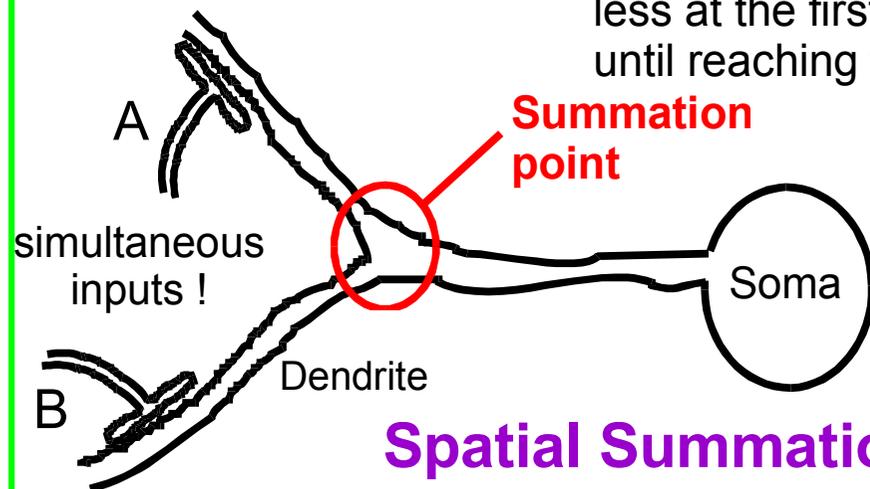
- 1) synapses have to be closely adjacent
- 2) pre-synaptic signals have to arrive simultaneously
- 3) resting potential and reversal potential(s) have to be very different.



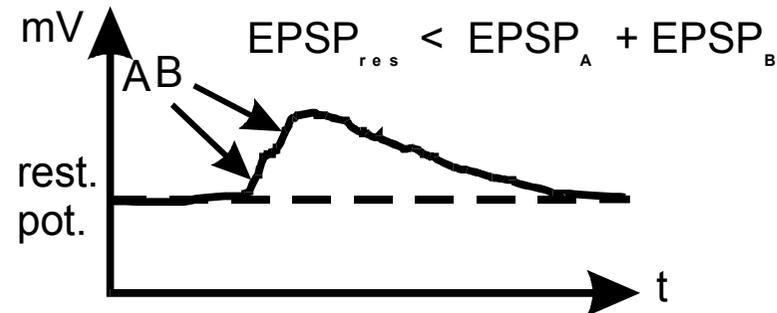
The little "shoulder" shows that the EPSPs were not truly simultaneous.

Consider 1:

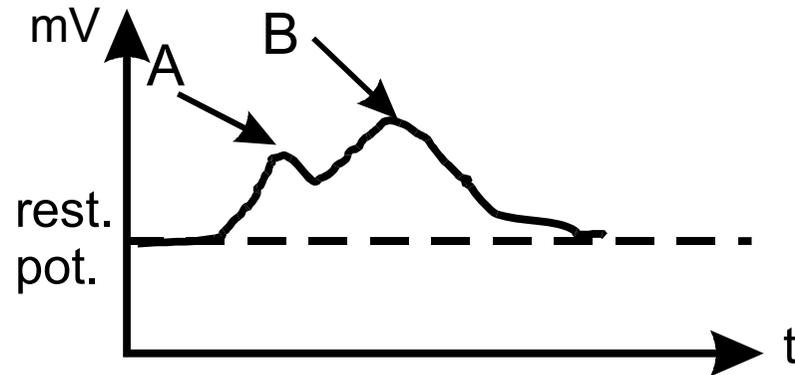
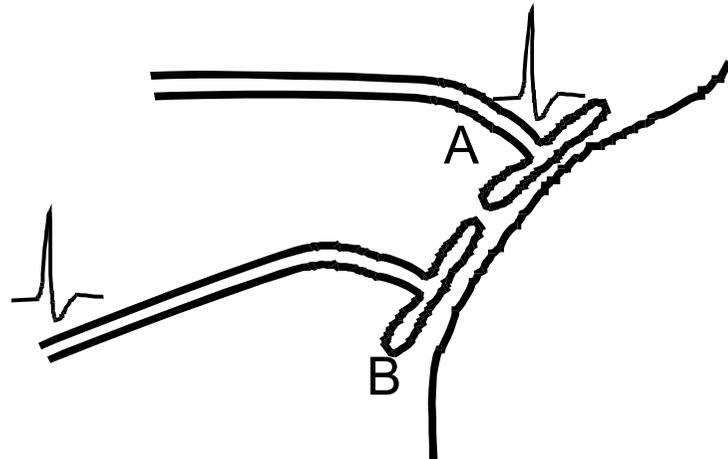
If the synapses are far from each other the amplitude will be less at the first summing point. It will then further decay until reaching the soma.



Spatial Summation



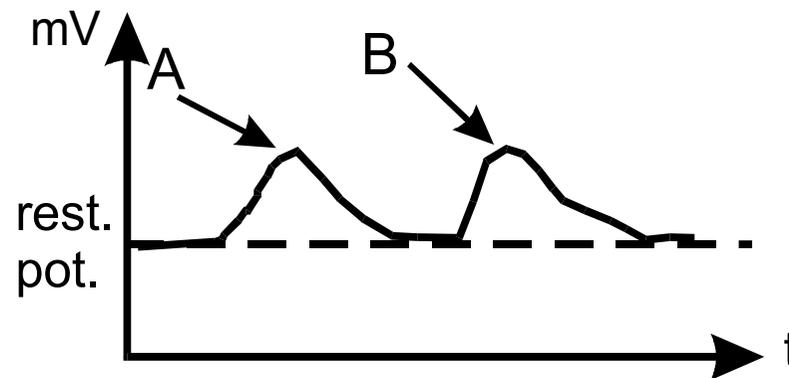
Consider 2: If the signals are not simultaneous then the sum will be smaller



The early signal (A) facilitates the later signal (B). Together the firing threshold might be reached but not alone.

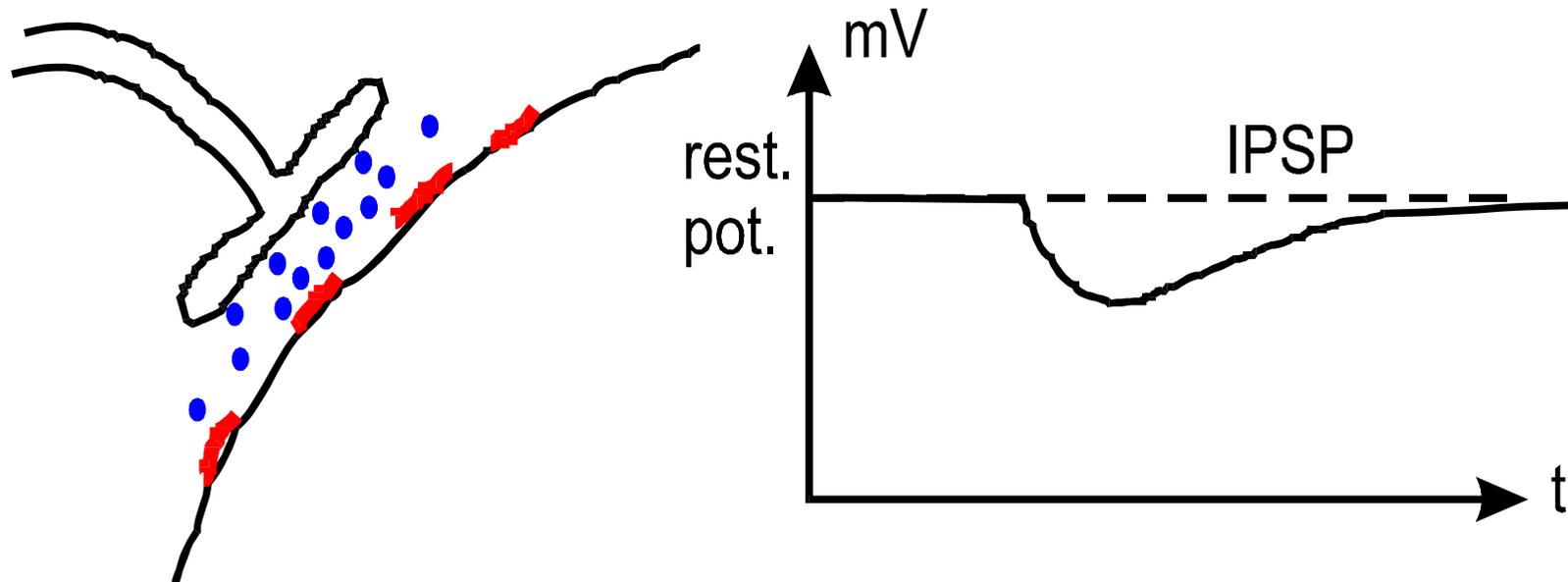
Temporal Summation

If the difference in arrival times is too large, temporal summation does not occur anymore !



Subtraction

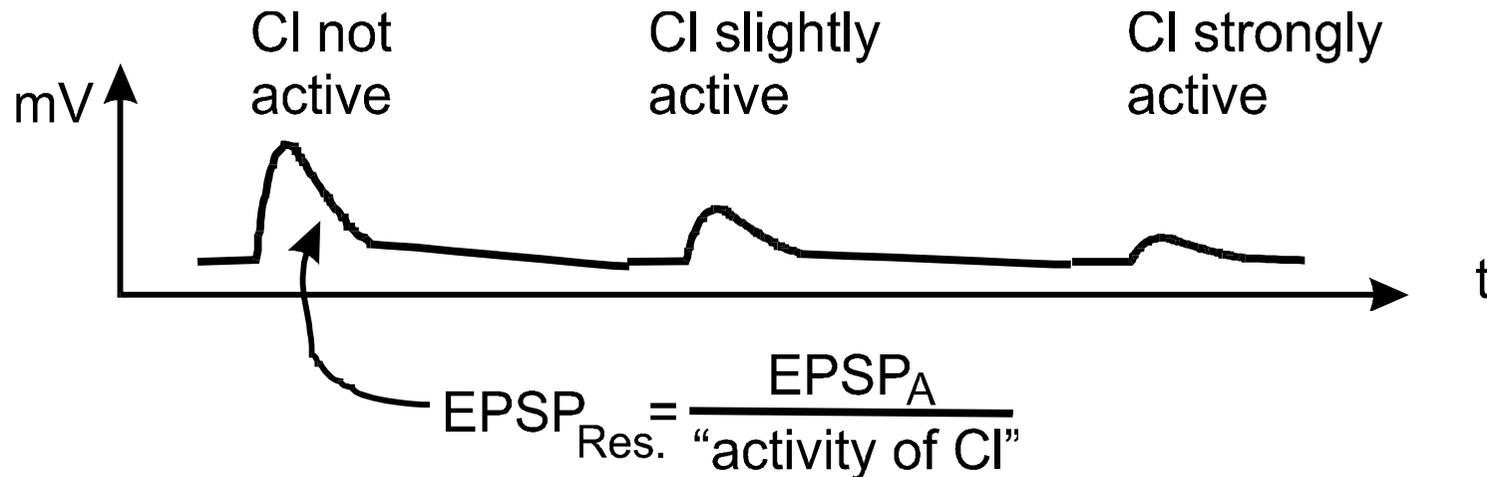
Transmitter release at a synapse leads to an inhibitory postsynaptic potential (IPSP) because ion channels are opening.



The same conditions apply as for summation. Then one can regard an IPSP as a sign-inverted EPSP. “Summation” becomes “Subtraction”.

Shunting inhibition

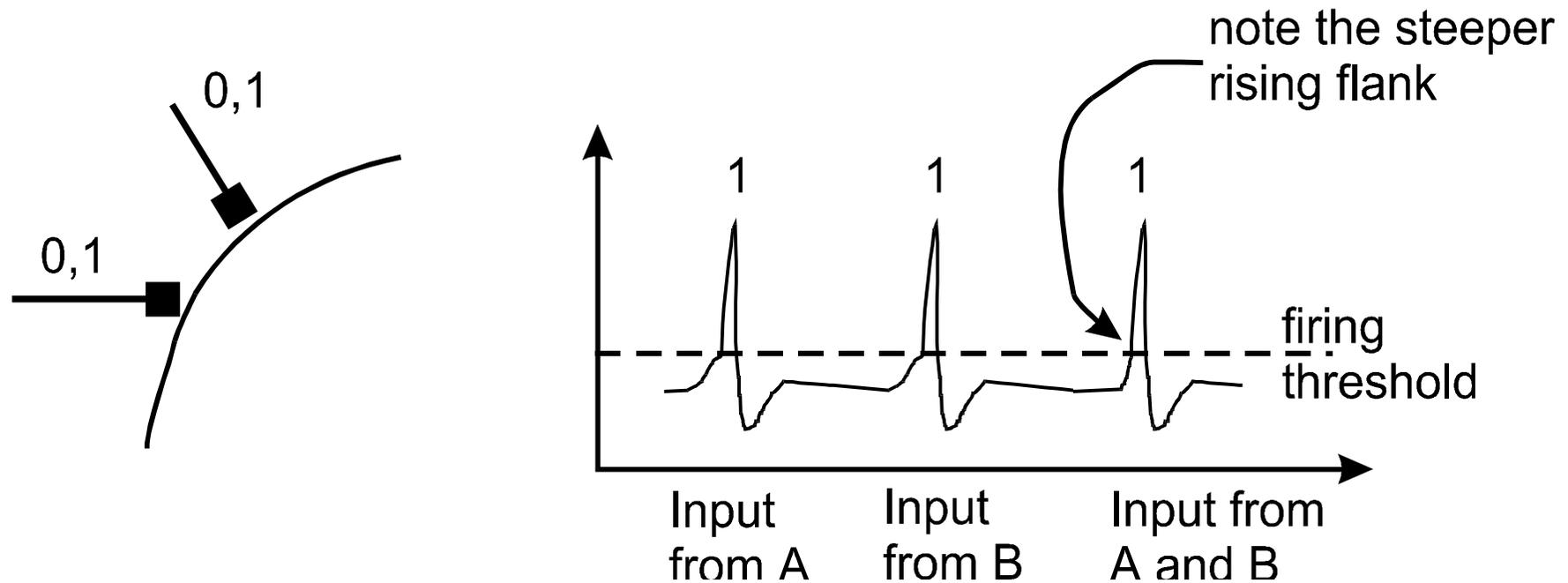
Is often also called “silent inhibition” because by itself no change of the membrane pot. is observed.



Acts like a **“Division”**

shunting inhibition = silent inhibition = divisive inhibition (synonymous terms)

How to realize an OR-gate neuronally:



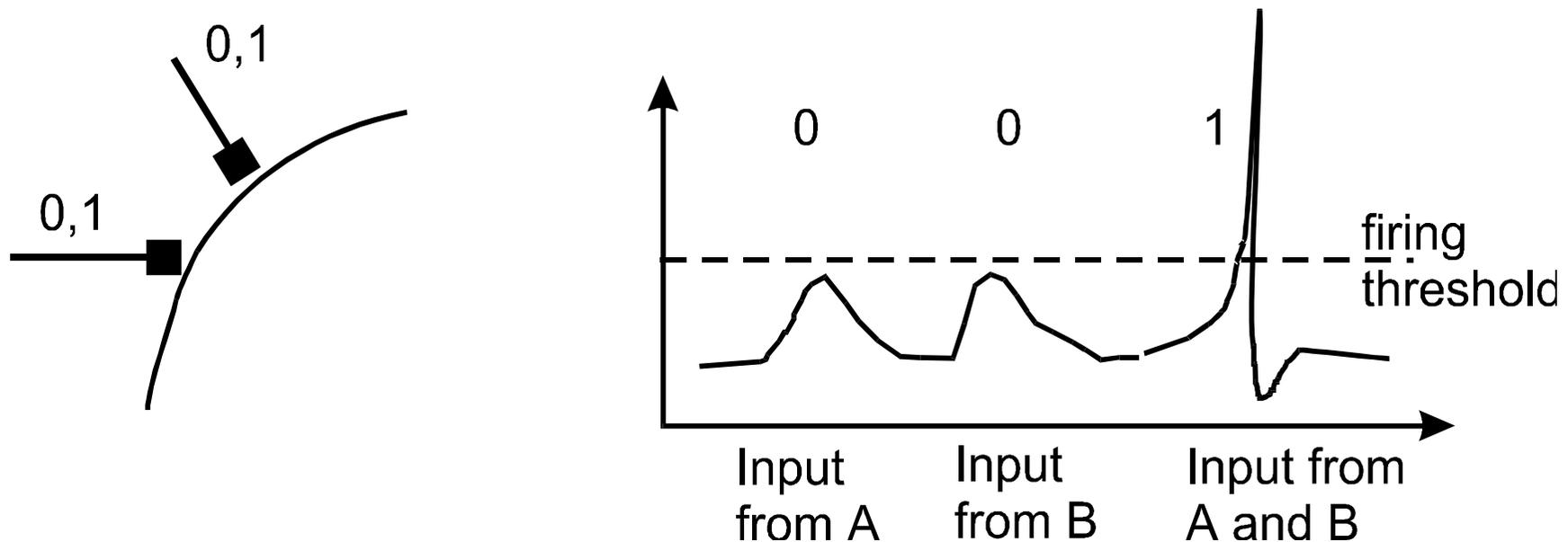
If the **firing threshold is low enough** then every EPSP will elicit a spike.

This emulates the function of an OR-gate.

How to realize an AND-gate neuronally:

| | | |
|-----|---|---|
| | 0 | 1 |
| AND | 0 | 0 |
| | 1 | 1 |

similar to multiplication: $0 \cdot 0 = 0$
 $0 \cdot 1 = 0$
 $1 \cdot 0 = 0$
 $1 \cdot 1 = 1$

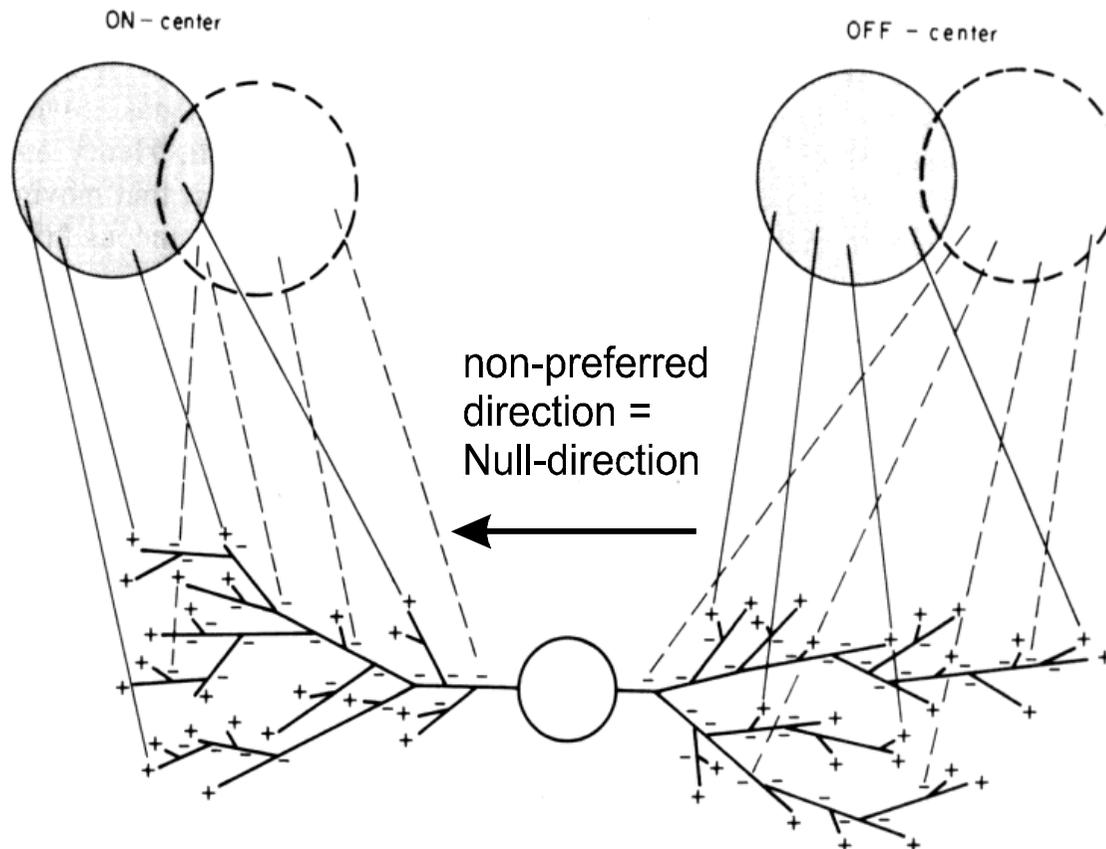
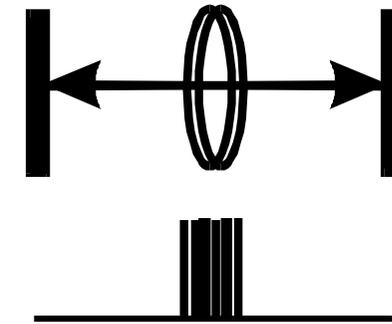


If the **firing threshold is high enough** then a spike will only be elicited when two (or more) EPSPs occur at about the same time. This emulates the function of an AND-gate

Example: Direction selectivity in the visual cortex:

Visual cortical cells usually respond strongly when a moving stimulus is presented. Almost all respond stronger for motion in the one direction as opposed to motion in the opposite direction:

Direction selectivity.



One idea how this might be generated at the single cell level:

(Note other explanations have also been discussed!)

Shunting inhibition

Synaptic signals (EPSPs) travelling along the Null-direction are shunted by inhibition.

Population models

Population model

Motivation

A set of neurons can sometimes be modeled as a population

-> dealing with populations reduces processing time and complexity

-> useful for cognitive models (high-level functions)

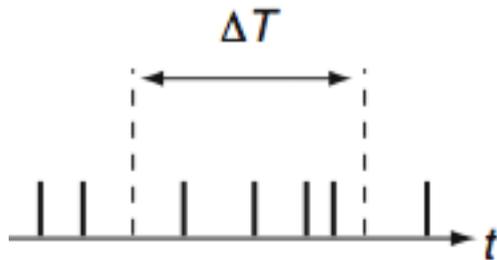
-> abstract away from individual spikes

Assumptions/Limits

Pool of neurons with similar response functions acting in a statistically similar way.

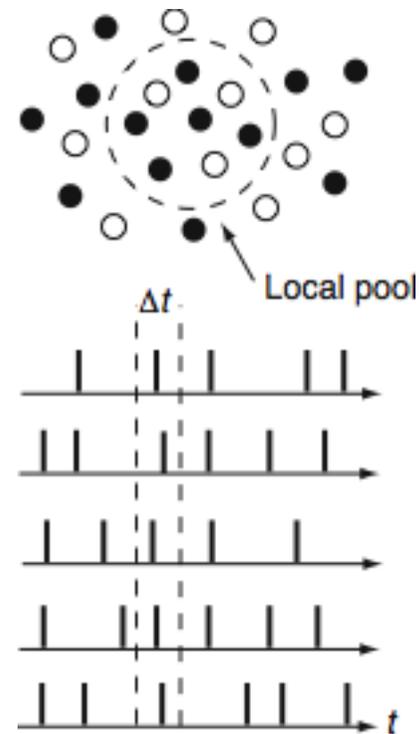
Population model

Temporal averaging
(one neuron)



Averaging over a rectangular time window (Often, a Gaussian time window is used instead).

Population averaging
(many neurons)



Population dynamics

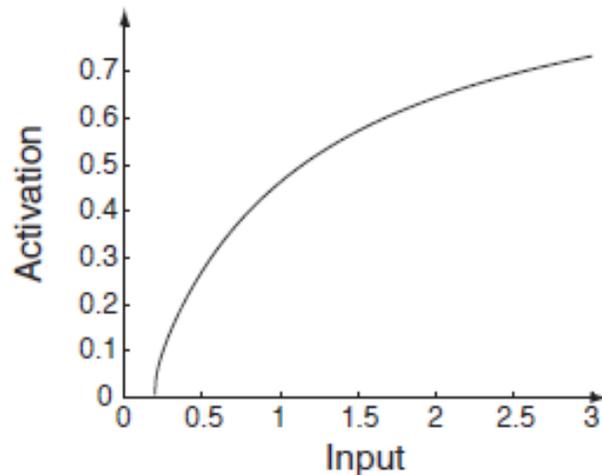
For slow varying input (adiabatic limit), when all nodes do practically the same, and the same input (Wilson and Cowan, 1972):

$$\tau \frac{dA(t)}{dt} = -A(t) + g(RI^{\text{ext}}(t)).$$

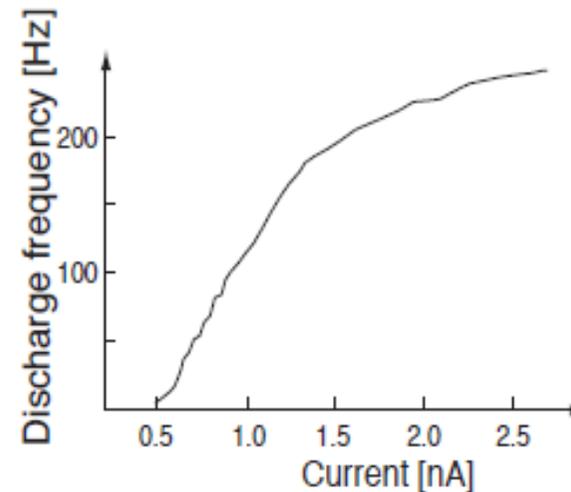
Gain function:

$$g(x) = \frac{1}{t^{\text{ref}} - \tau \log(1 - \frac{1}{\tau x})},$$

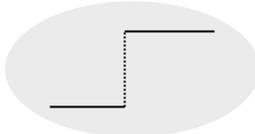
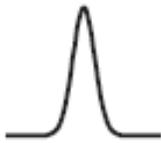
A. Activation function for population average in adiabatic limit



B. Activation function of hippocampal pyramidal neuron



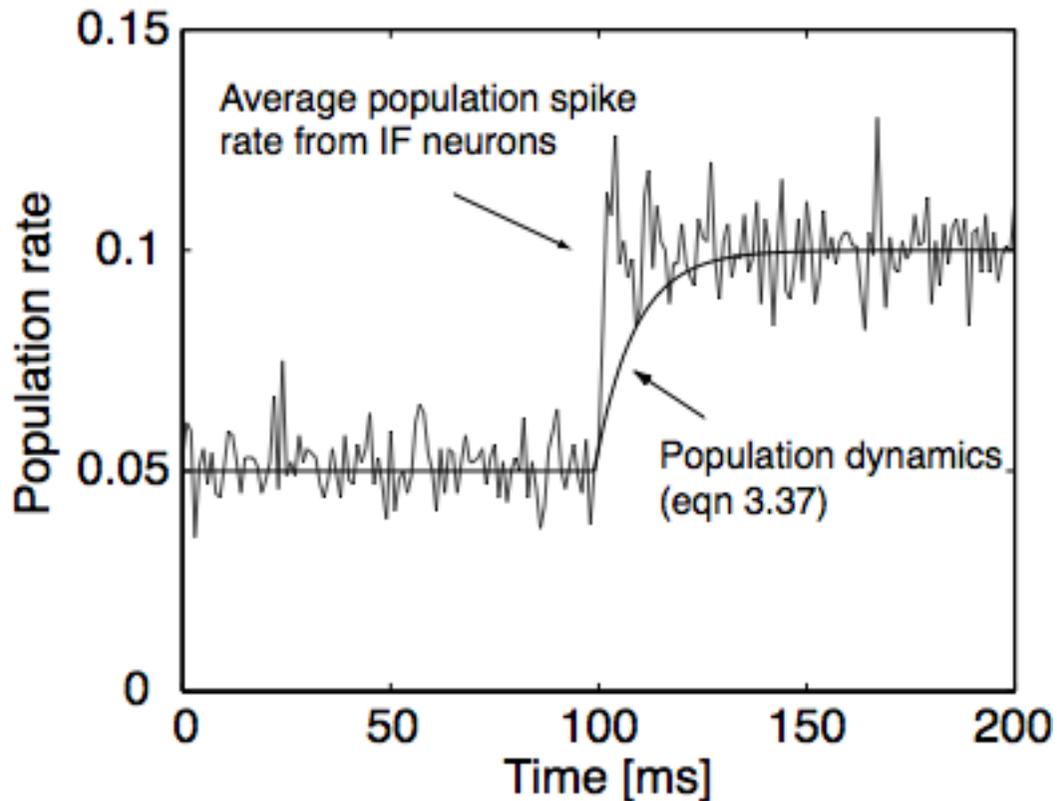
Other gain functions

| Type of function | Graphical represent. | Mathematical formula | MATLAB implementation |
|------------------|-------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|----------------------------------------|
| Linear |  | $g^{\text{lin}}(x) = x$ | <code>x</code> |
| Step |  | $g^{\text{step}}(x) = \begin{cases} 1 & \text{if } x > 0 \\ 0 & \text{elsewhere} \end{cases}$ | <code>floor(0.5*(1+sign(x)))</code> |
| Threshold-linear |  | $g^{\text{theta}}(x) = x \Theta(x)$ | <code>x.*floor(0.5*(1+sign(x)))</code> |
| Sigmoid |  | $g^{\text{sig}}(x) = \frac{1}{1+\exp(-x)}$ | <code>1./(1+exp(-x))</code> |
| Radial-basis |  | $g^{\text{gauss}}(x) = \exp(-x^2)$ | <code>exp(-x.^2)</code> |

Fast population response (rapidly varying input)

A stimulus increase leads to rapid firing rate changes as many neurons in a population are close to the threshold!

Non-adiabatic regime



-> use shorter population time constants when the input varies rapidly

Summary

Simplified models of single neuron activity

- Leaky integrate and fire (LIF) neurons
- Izhikevich neurons
- McCulloch-Pitts neurons

Multiple neurons can be further aggregated

- population models

Further readings

- Wolfgang Maass and Christopher M. Bishop (eds.) (1999), **Pulsed neural networks**, MIT Press.
- Wulfram Gerstner (2000), **Population dynamics of spiking neurons: fast transients, asynchronous states, and locking**, in **Neural Computation** 12: 43–89.
- Eugene M. Izhikevich (2003), **Simple Model of Spiking Neurons**, in **IEEE Transactions on Neural Networks**, 14: 1569–1072.
- Eugene M. Izhikevich (2004), **Which model to use for cortical spiking neurons?**, in **IEEE Transactions on Neural Networks**, 15: 1063–1070.
- Warren McCulloch and Walter Pitts (1943) **A logical calculus of the ideas immanent in nervous activity**, in **Bulletin of Mathematical Biophysics** 7:115–133.
- Huge R. Wilson and Jack D. Cowan (1972), **Excitatory and inhibitory interactions in localized populations of model neurons**, in **Biophys. J.** 12:1–24.
- Nicolas Brunel and Xiao-Jing Wang, (2001), **Effects of neuromodulation in a cortical network model of working memory dominated by recurrent inhibition**, in **Journal of Computational Neuroscience** 11: 63–85.