

# Introduction to Neural Computation

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MIT BCS 9.40 — 2018

Spike trains

# Electrical recordings of brain activity

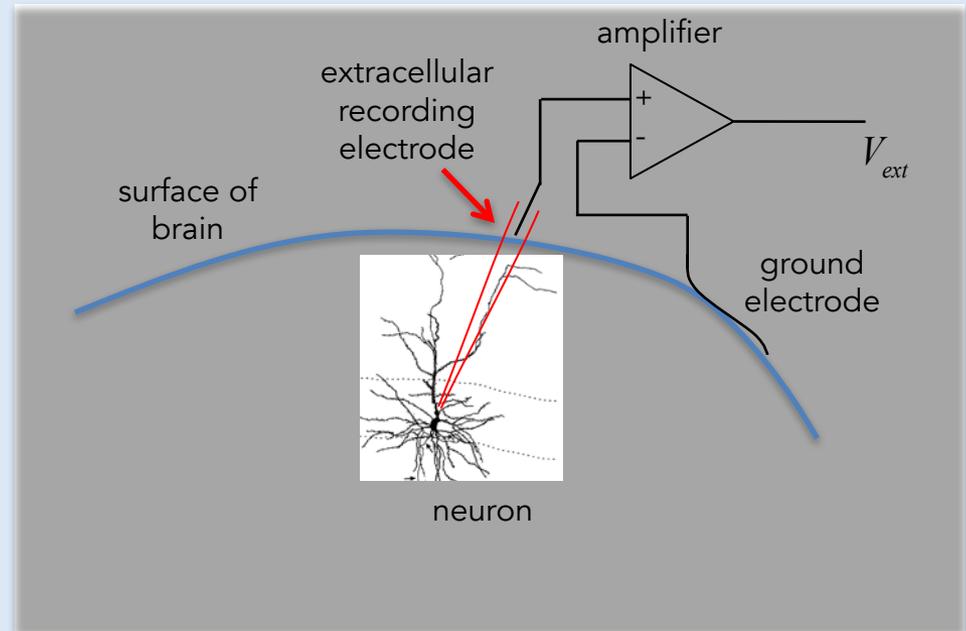
- Electrical recordings in the brain are made with electrodes.
- Recordings can be made inside of single cells
- Most often, in behaving animals, recordings are made of signals outside of neurons.

# Electrical recordings of brain activity

What is the origin of 'extracellular' electrical signals?

- Voltage measurements are always voltage differences
- Extracellular voltages are always measured between the signal electrode and a local ground or reference electrode.
- Voltage differences between the signal and ground electrode are always associated with current flow through the extracellular space.
- Back to Ohm's Law!

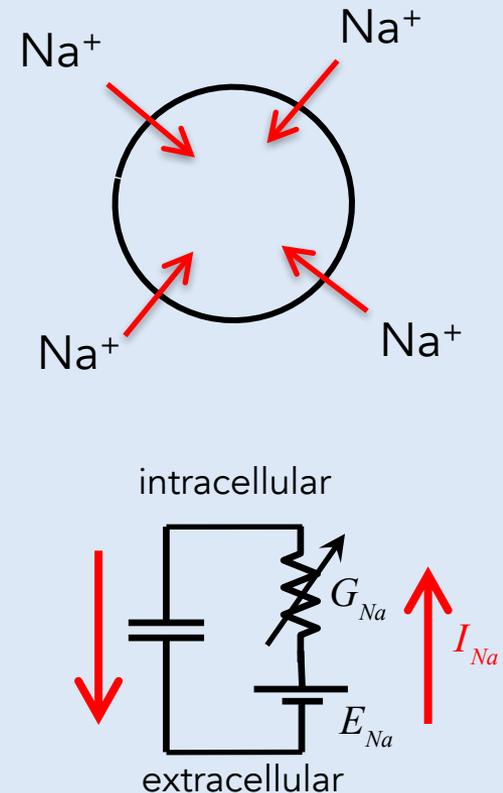
$$\Delta V = IR_{ext} \quad R_{ext} = \frac{\rho l}{A}$$



# Origin of extracellular signals

What happens to the voltage outside our model neuron during an action potential?

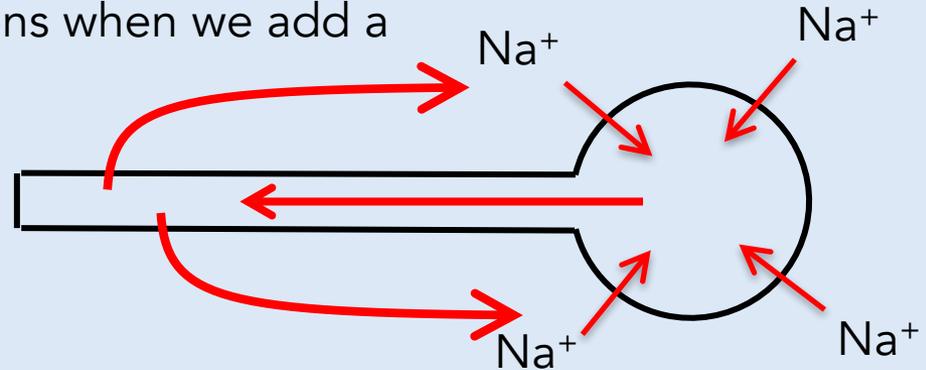
- Let's start with our spherical neuron
- There is no spatial separation between current flows into the neuron and current flow out of the neuron. Thus, no current flow outside the neuron.
- And thus no extracellular voltage changes!



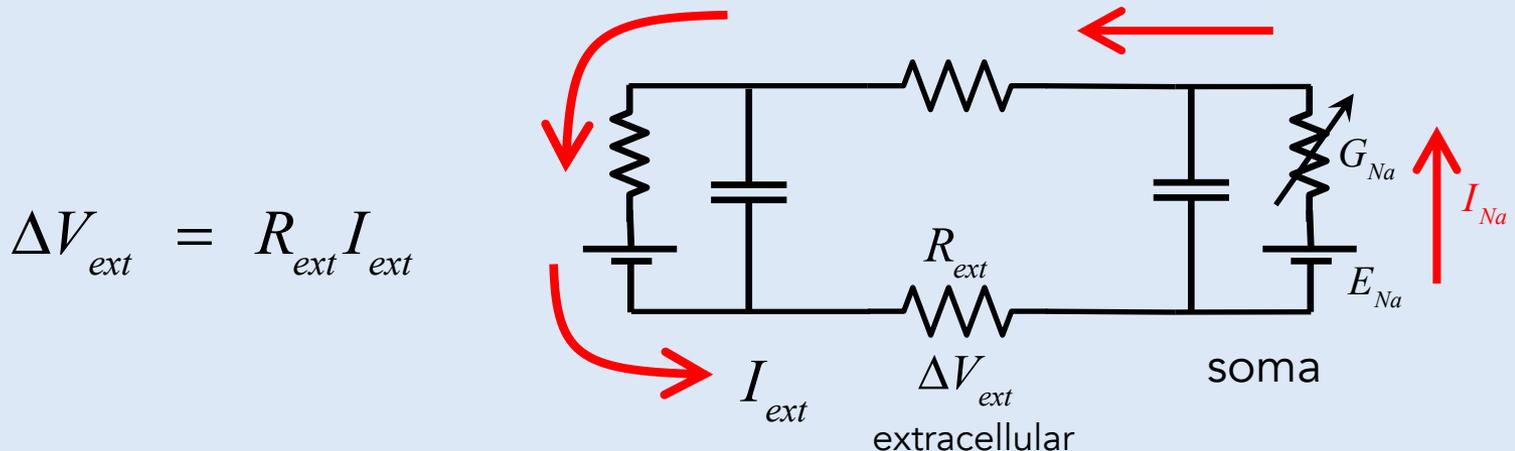
# Origin of extracellular signals

What happens to the voltage outside our model neuron during an action potential?

- Now let's see what happens when we add a dendrite.



- Now there is extracellular current flow

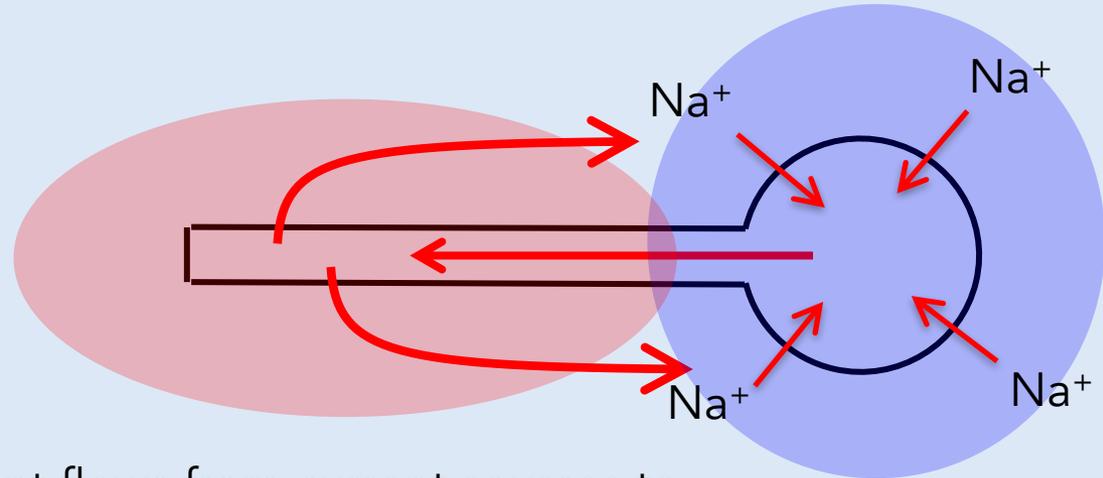


$$\Delta V_{ext} = R_{ext} I_{ext}$$

- And extracellular voltage changes!

# Current sources and sinks

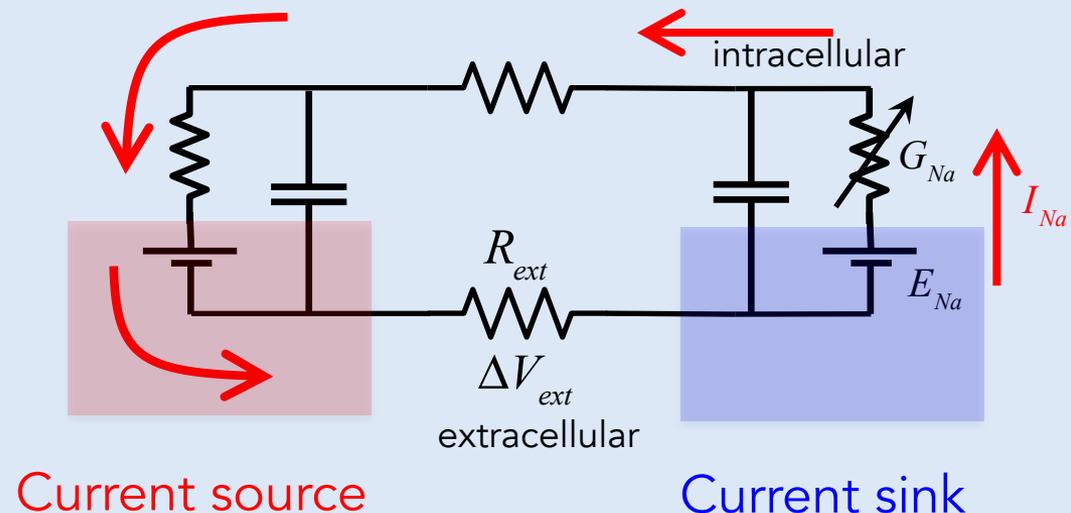
What happens to the voltage outside our model neuron during an action potential?



- Extracellular current flows from current sources to current sinks

Current sources are regions of higher extracellular potential

Current sinks are regions of lower extracellular potential



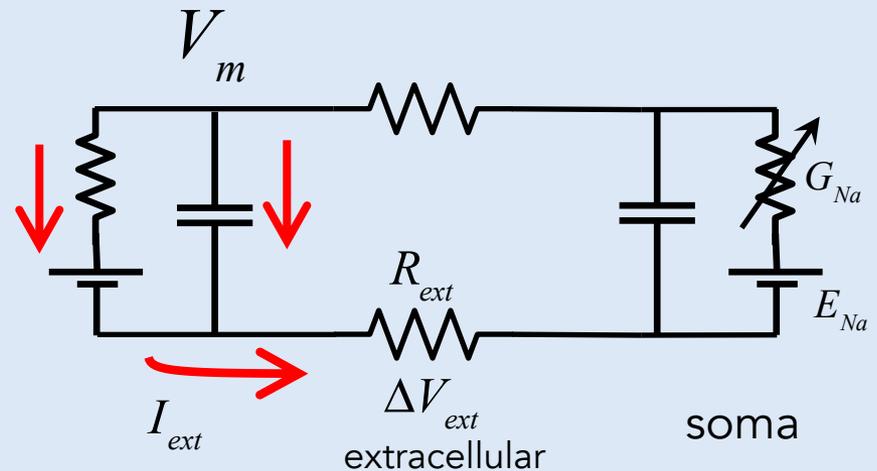
# Relation between membrane potential and extracellular potential

$$\Delta V_{ext} = R_{ext} I_{ext} = R_{ext} (I_c + I_R)$$

$$= R_{ext} \left[ C \frac{dV_m}{dt} + G(V_m - E_L) \right]$$

$$\Delta V_{ext} \approx R_{ext} C \frac{dV_m}{dt}$$

Figure removed due to copyright restrictions. See Henze, D.A., et al. "[Dopamine Increases Excitability of Pyramidal Neurons in Primate Prefrontal Cortex.](#)" *J. Neurophys.* 84 no. 6 (2000): 2799-2809.



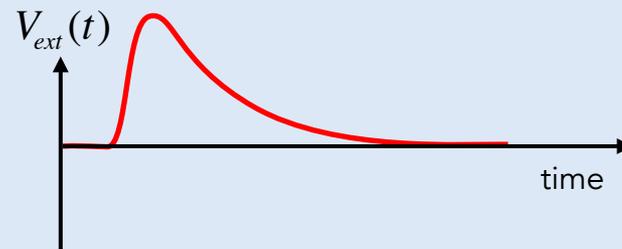
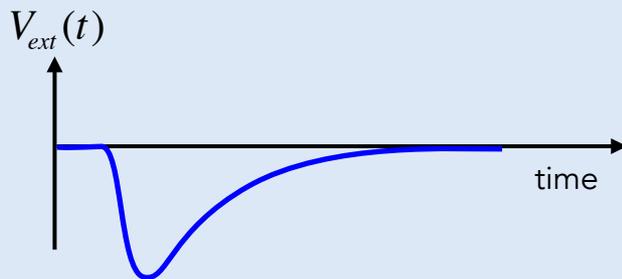
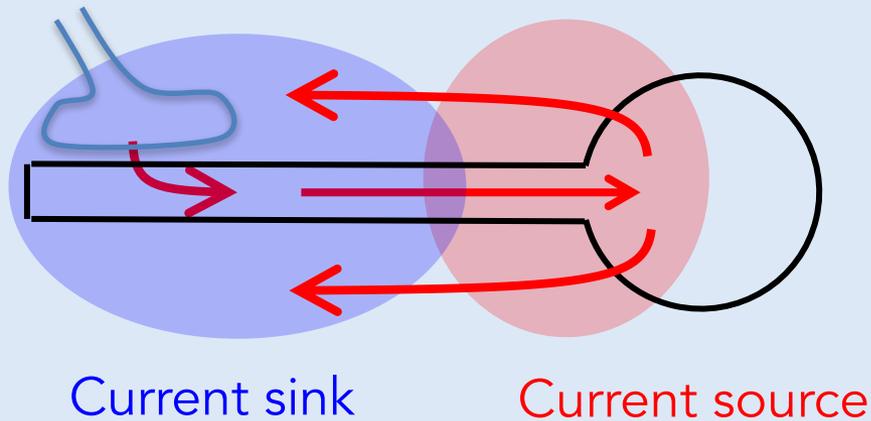
Henze et al, 2000

Extracellular voltages look a lot like the derivative on membrane potential!

# Origin of extracellular signals

What happens to the voltage outside our model neuron during a synaptic input?

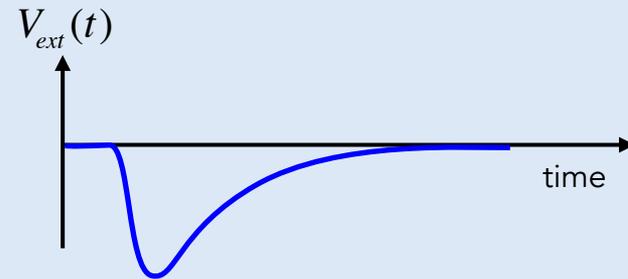
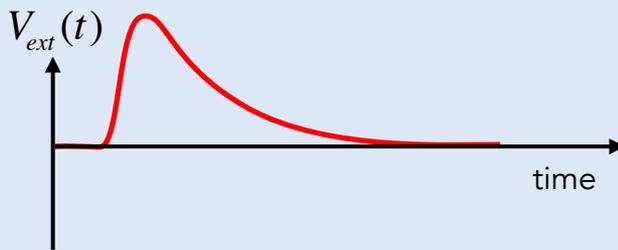
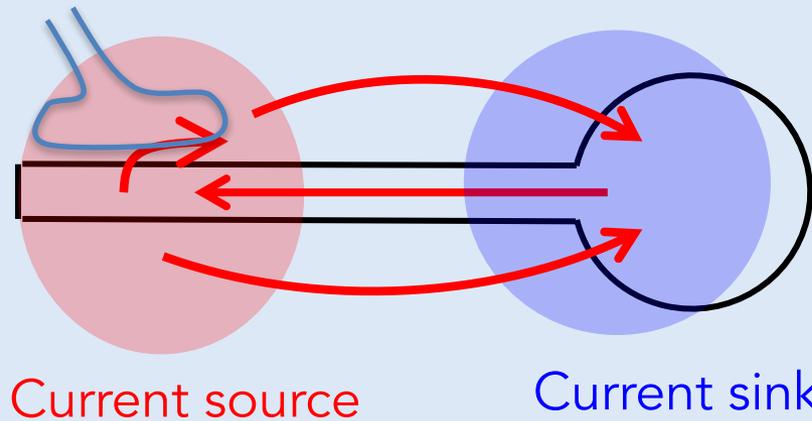
Excitatory synapse



# Origin of extracellular signals

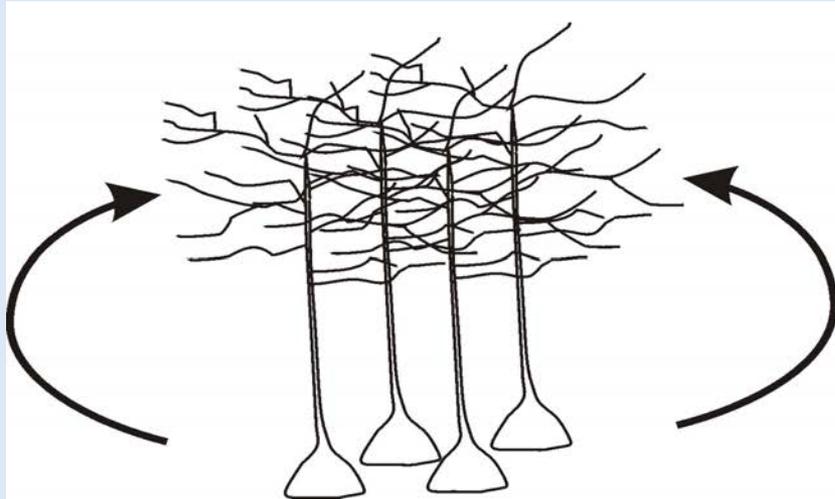
What happens to the voltage outside our model neuron during a synaptic input?

Inhibitory synapse

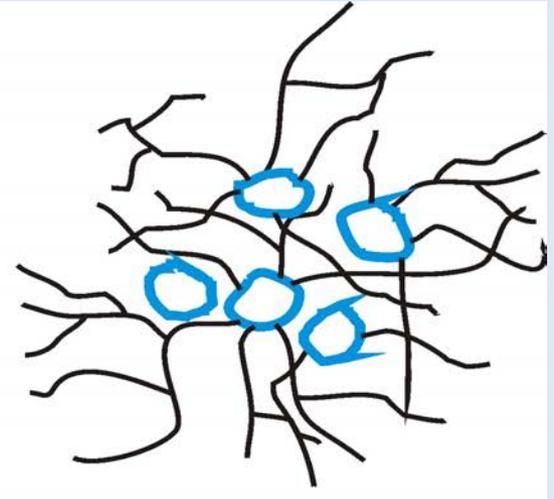


# Local Field Potentials

- Synchronous synaptic input to large populations of neurons
- Depends on linear summation
  - morphology is important

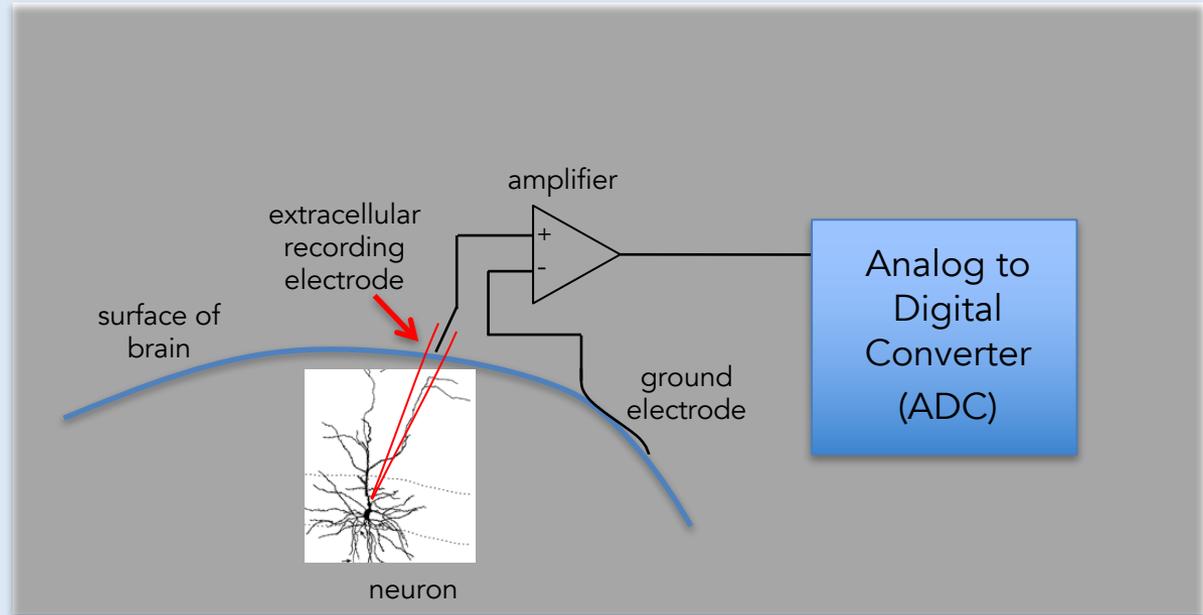


Laminar morphology  
– large LFP



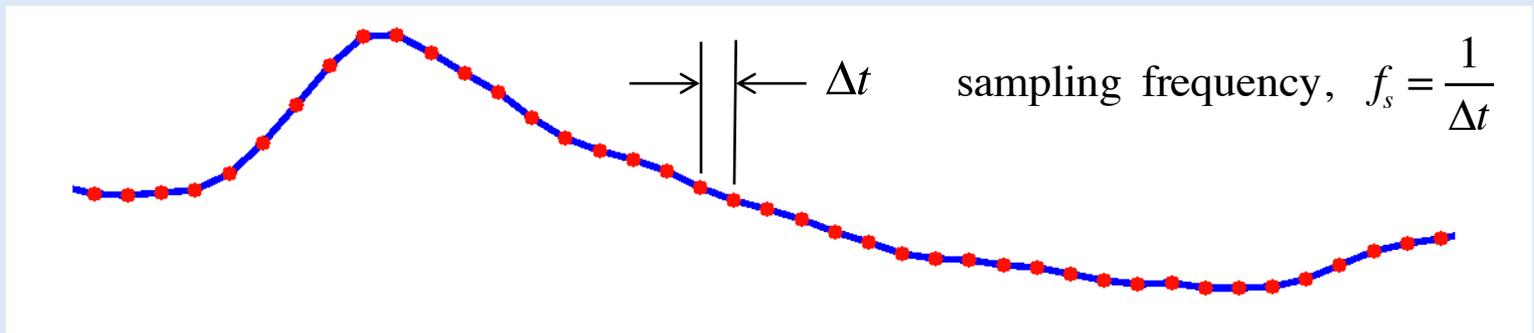
Nuclear morphology  
– small LFP

# Electrical recordings of brain activity



## SAMPLING

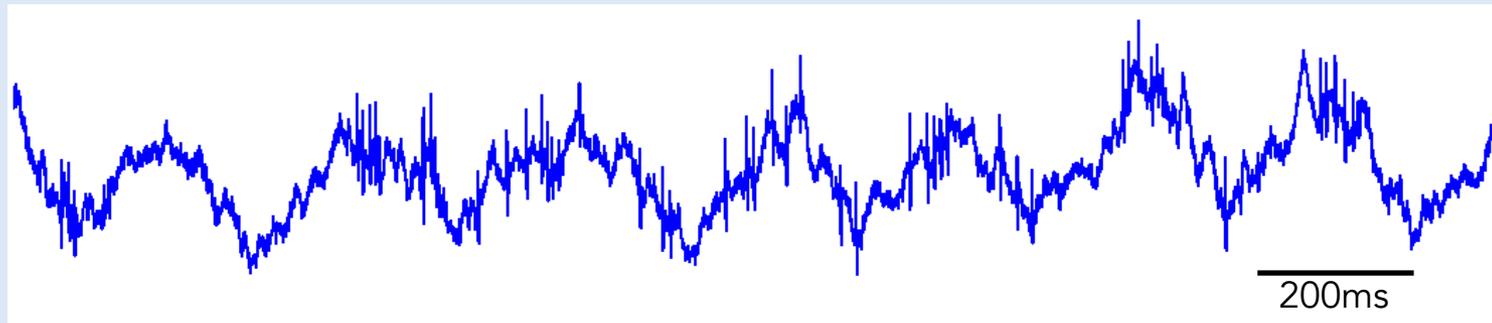
The analog to digital converter samples the voltage from the amplifier at regular intervals in time and stores the result in the computer memory.



The rate at which the samples are acquired is called the sampling rate or sampling frequency.

# Two kinds of signals

- Recording of neural activity in hippocampus of a running rat.

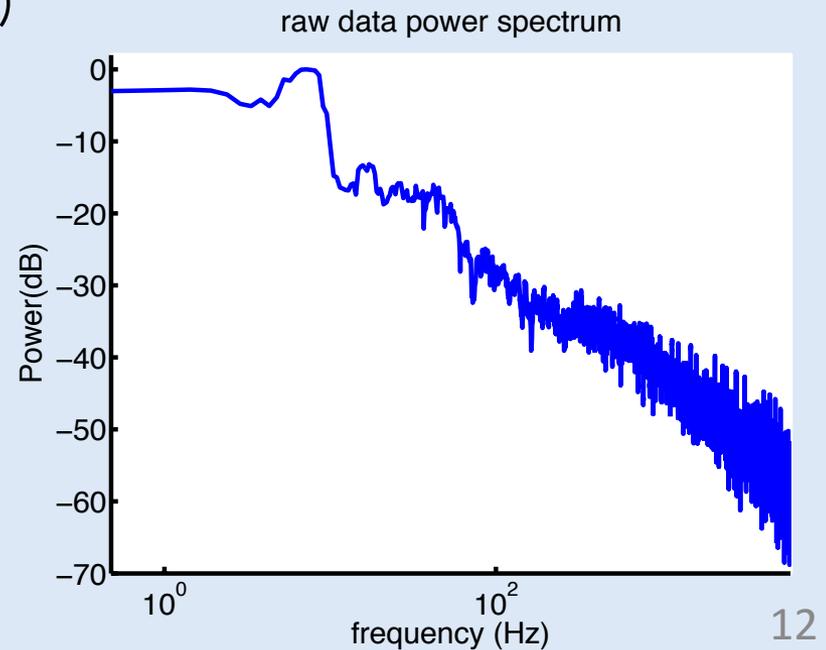
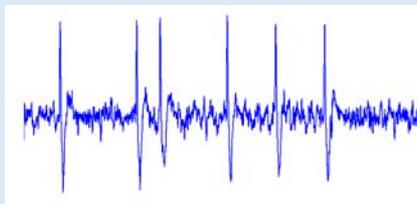


- Slow - Local Field Potentials (LFP)

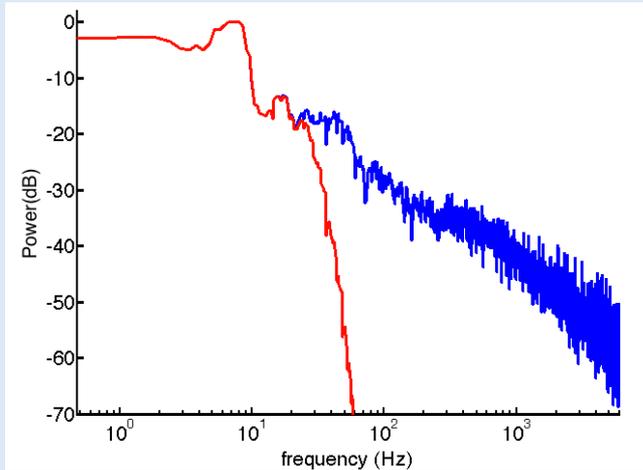
- Synaptic currents

- Fast - Spikes

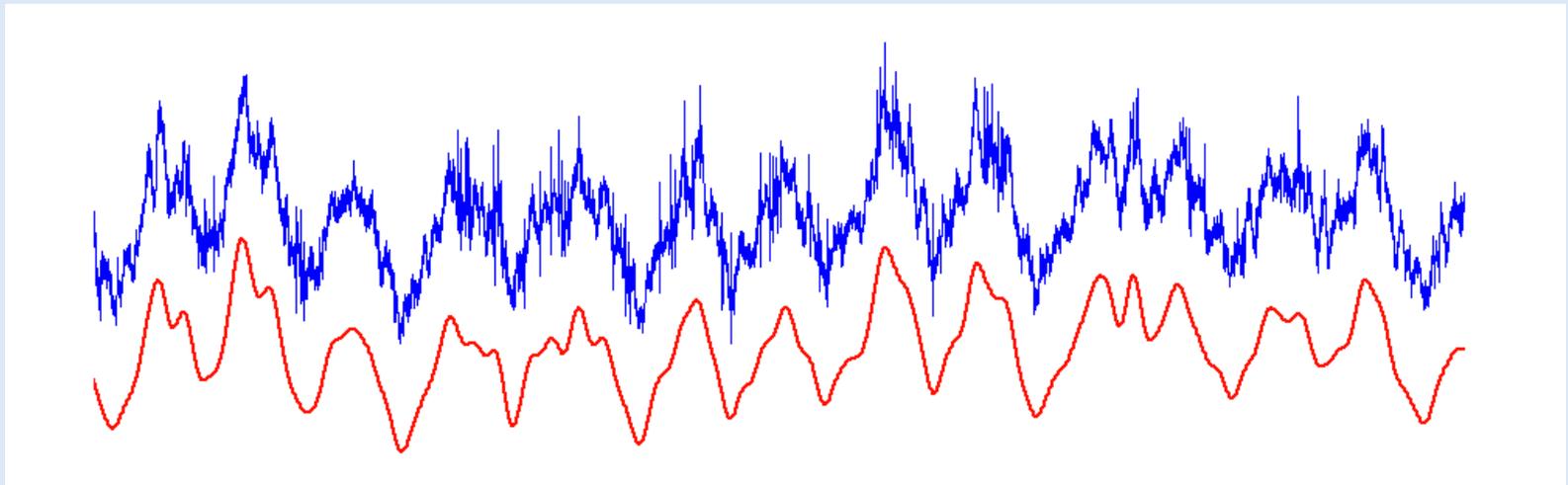
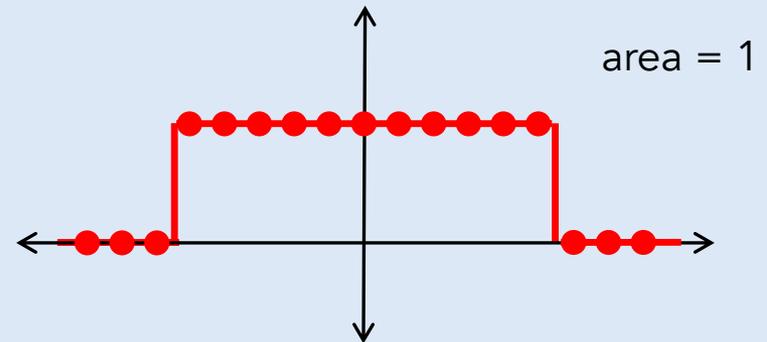
- Action potentials



# Low-pass filtering



Low-pass filtering can be done by convolving the signal with a kernel like this.



# Explanation of low pass filter

Kernel



Signal



Product

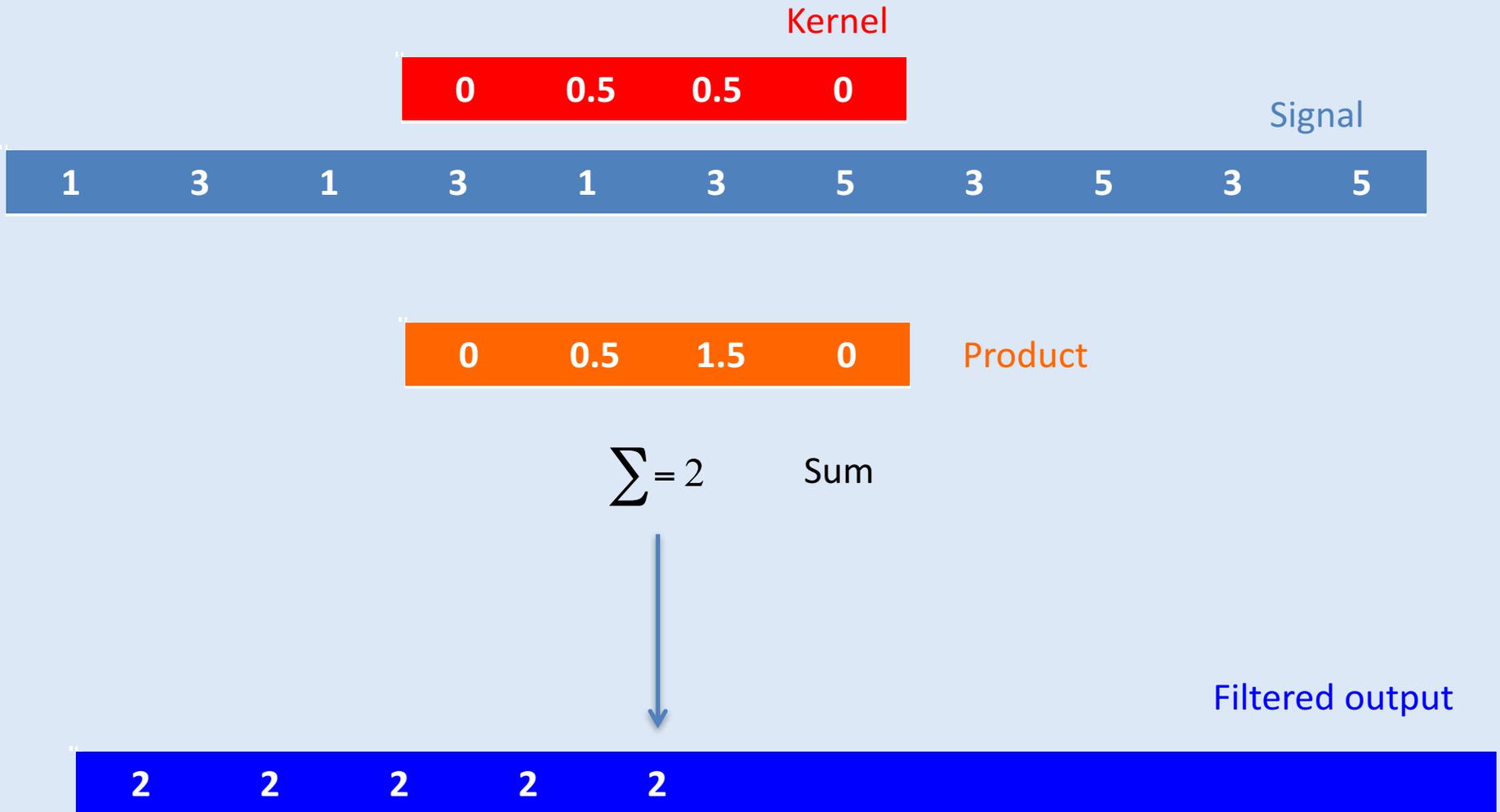
$\sum = 2$  Sum



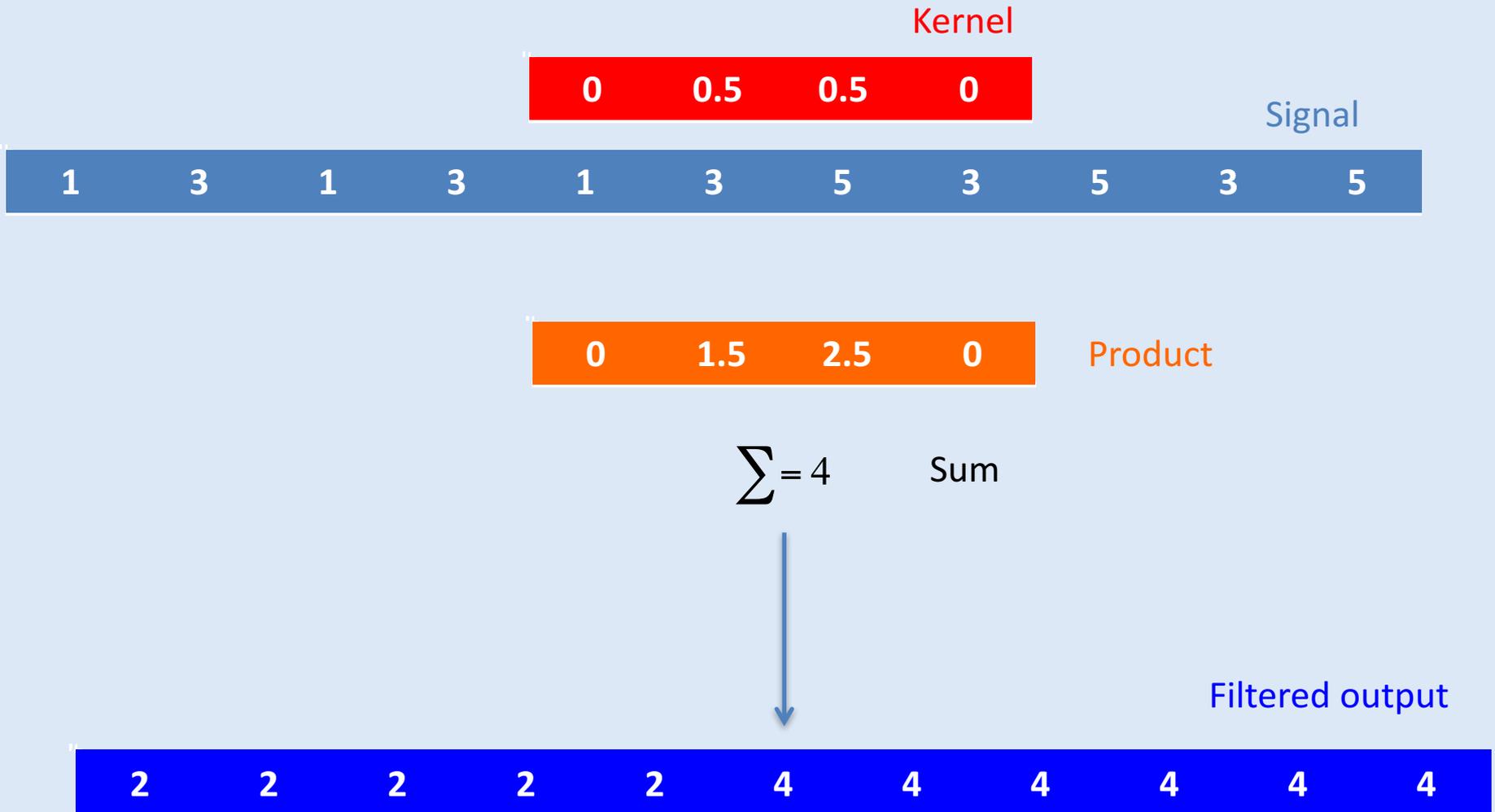
Filtered output



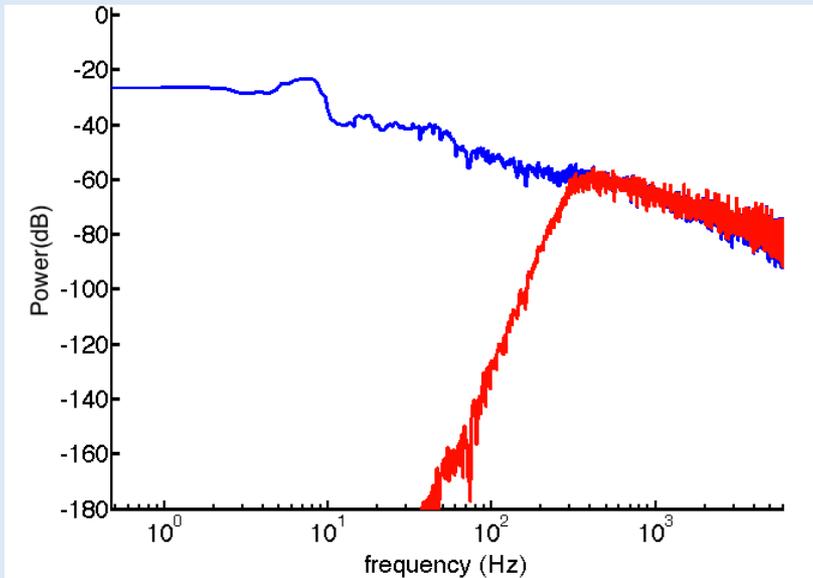
# Explanation of low pass filter



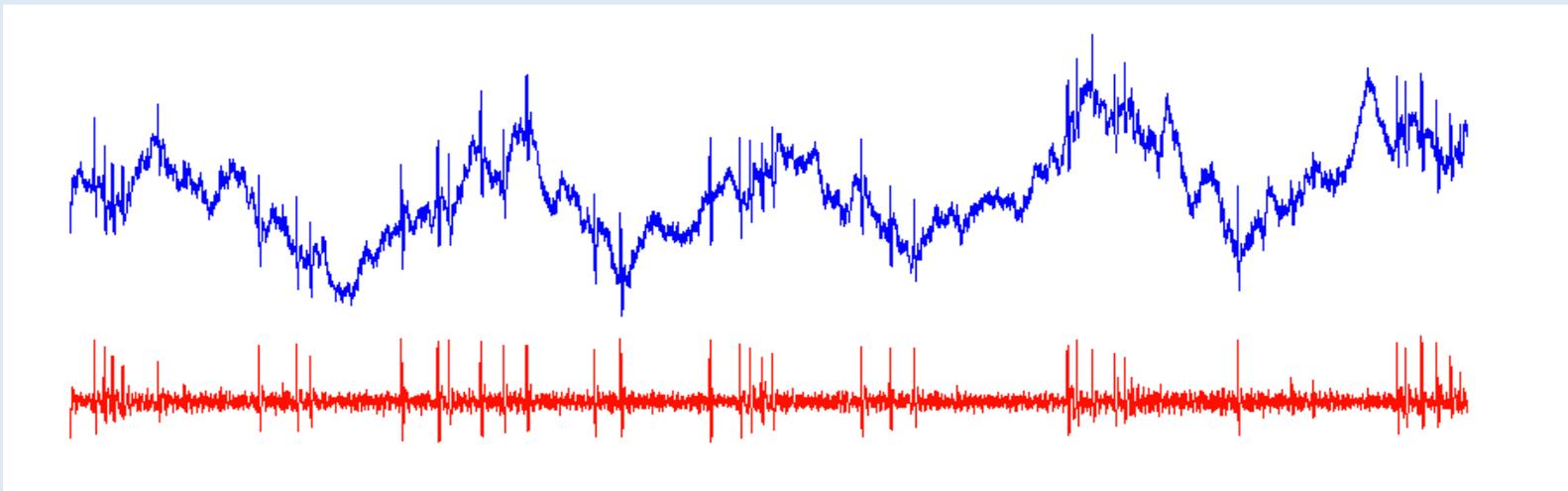
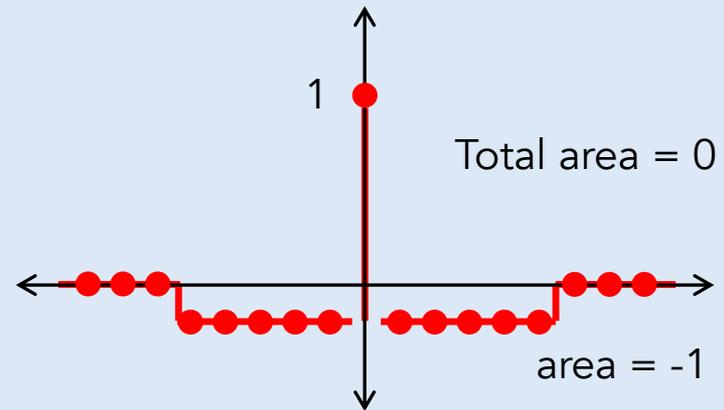
# Explanation of low pass filter



# High-pass filtering

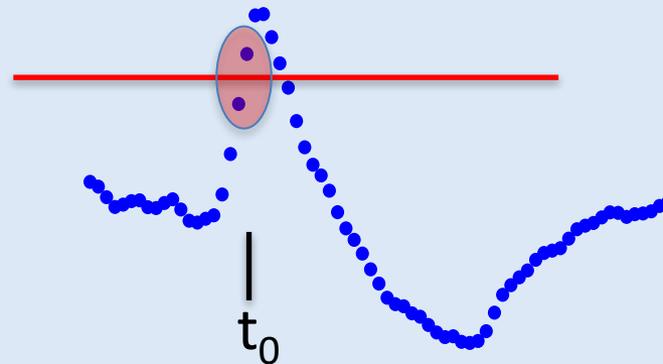
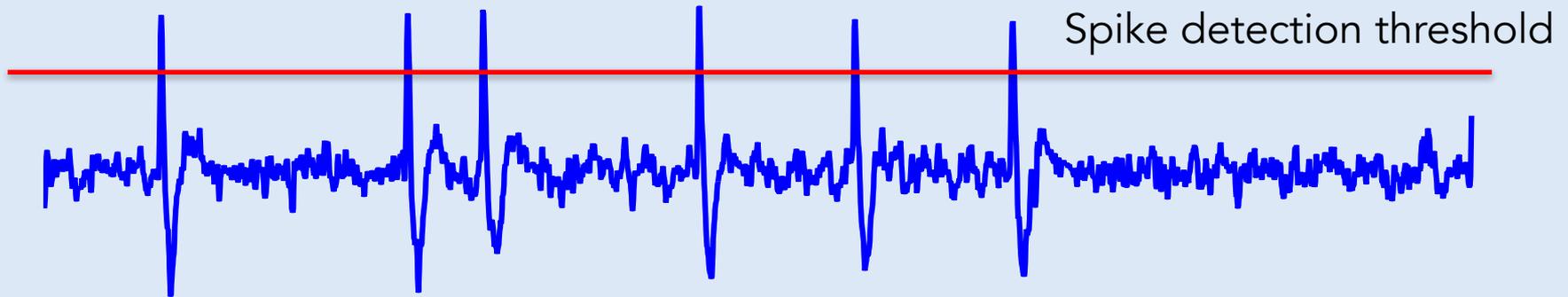


High-pass filtering can be done by convolving the signal with a kernel like this.



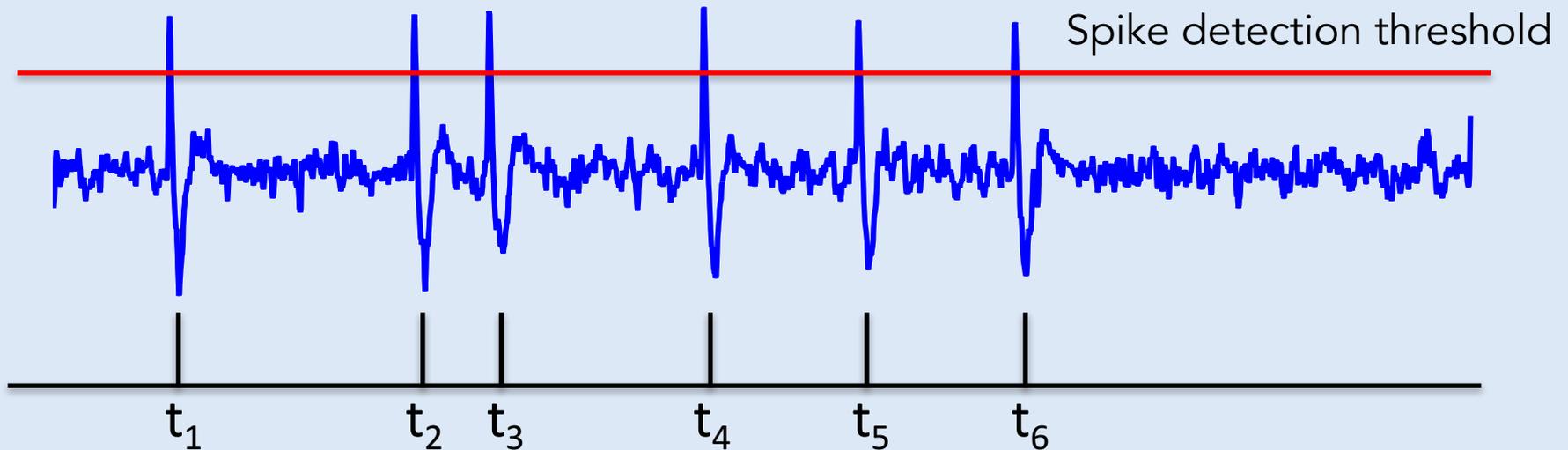
# Spike detecton

- If you are recording from only a single neuron, it is easy to extract spike times...



# Spike trains

- Representation of all the spikes that a neuron generates in a period of time of interest

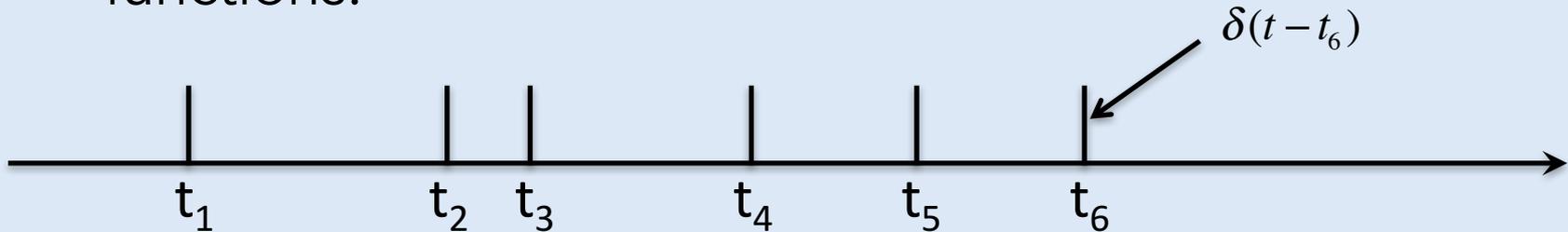


- We can represent a spike train as a list of spike times

$t_i$  for  $i=1$  to  $N$  spikes

# Spike trains

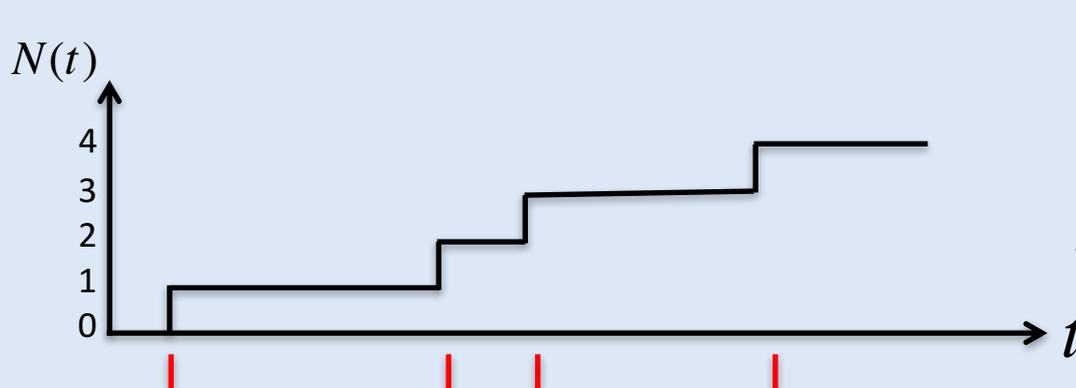
- Spike trains can also be represented a sum of delta functions.



$$\rho(t) = \delta(t-t_1) + \delta(t-t_2) + \delta(t-t_3) + \delta(t-t_4) + \delta(t-t_5) + \delta(t-t_6)$$

$$\rho(t) = \sum_i \delta(t-t_i)$$

- $\rho(t)$  can be thought of as the derivative of a spike count function

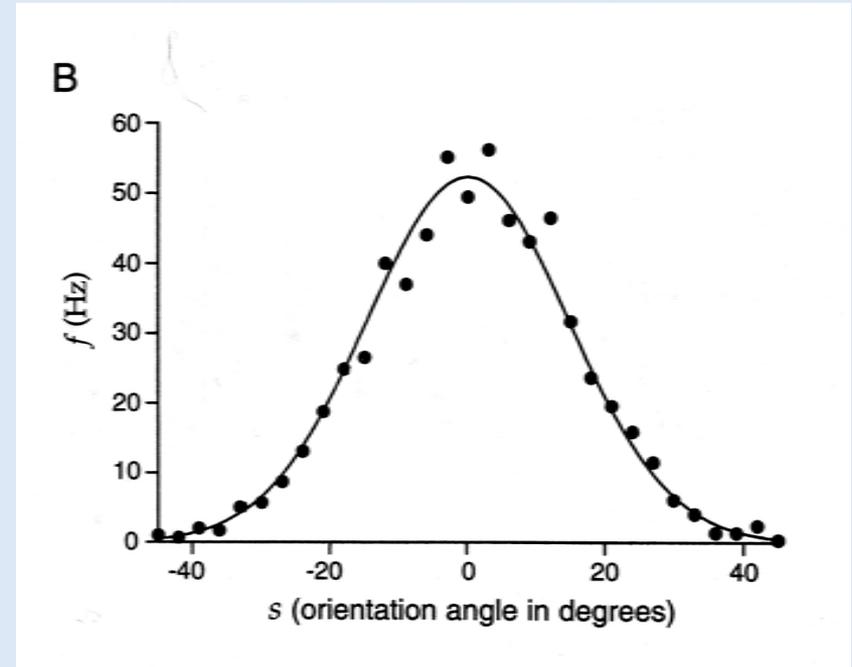
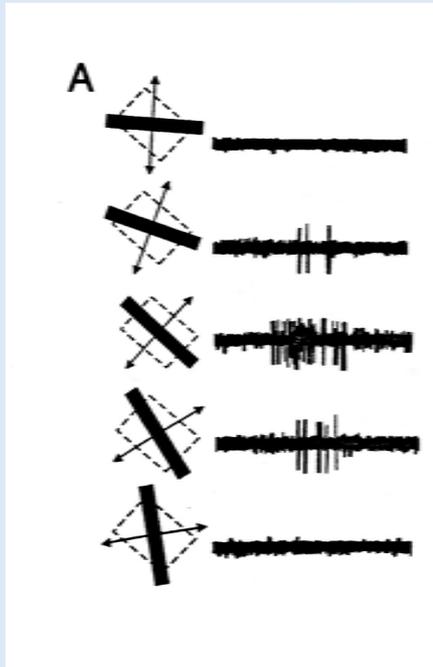


$$\int_0^T \rho(t) dt = N \quad (\# \text{ spikes})$$

$\rho(t)$  has units of spikes per second

# Tuning curves

- Simple cells in primary visual cortex of the cat are responsive to some orientations, but not others.

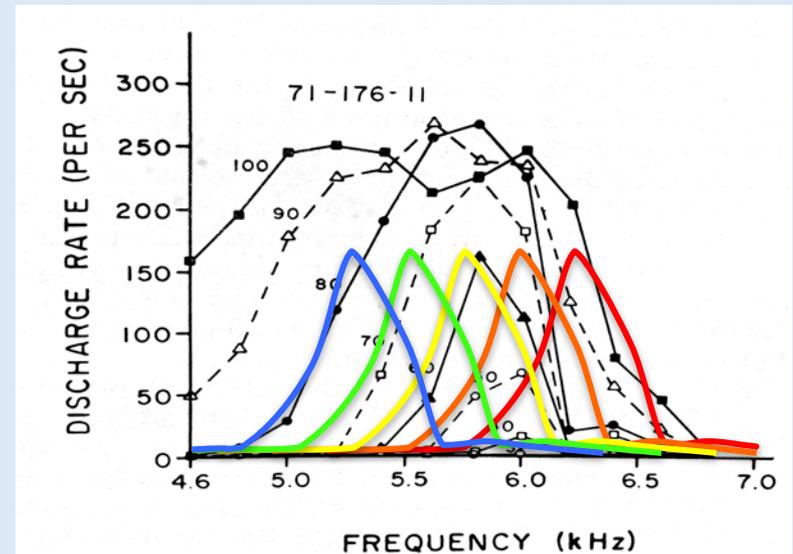
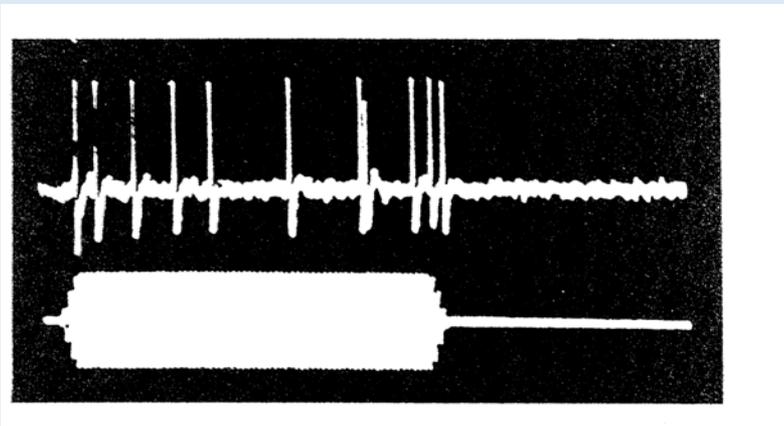


These neurons show 'orientation tuning.'

# Tuning curves

Hearing / ear diagram removed due to copyright restrictions.  
Source unknown.

Unfolded cochlea figure removed due to copyright restrictions.  
Source unknown.



Auditory neurons show frequency tuning

# Tuning curves

- Relation between spiking activity of a neuron in primary motor cortex and the onset of the arm movement.

Figures removed due to copyright restrictions. See Figs. 1 & 3 in Georgopoulos, A.P., et al. "[On the Relations Between the Direction of Two-Dimensional Arm Movements and Cell Discharge in Primate Motor Cortex.](#)" *J. Neurosci.* 2 no. 11(1982): 1527-37.

# Tuning curves

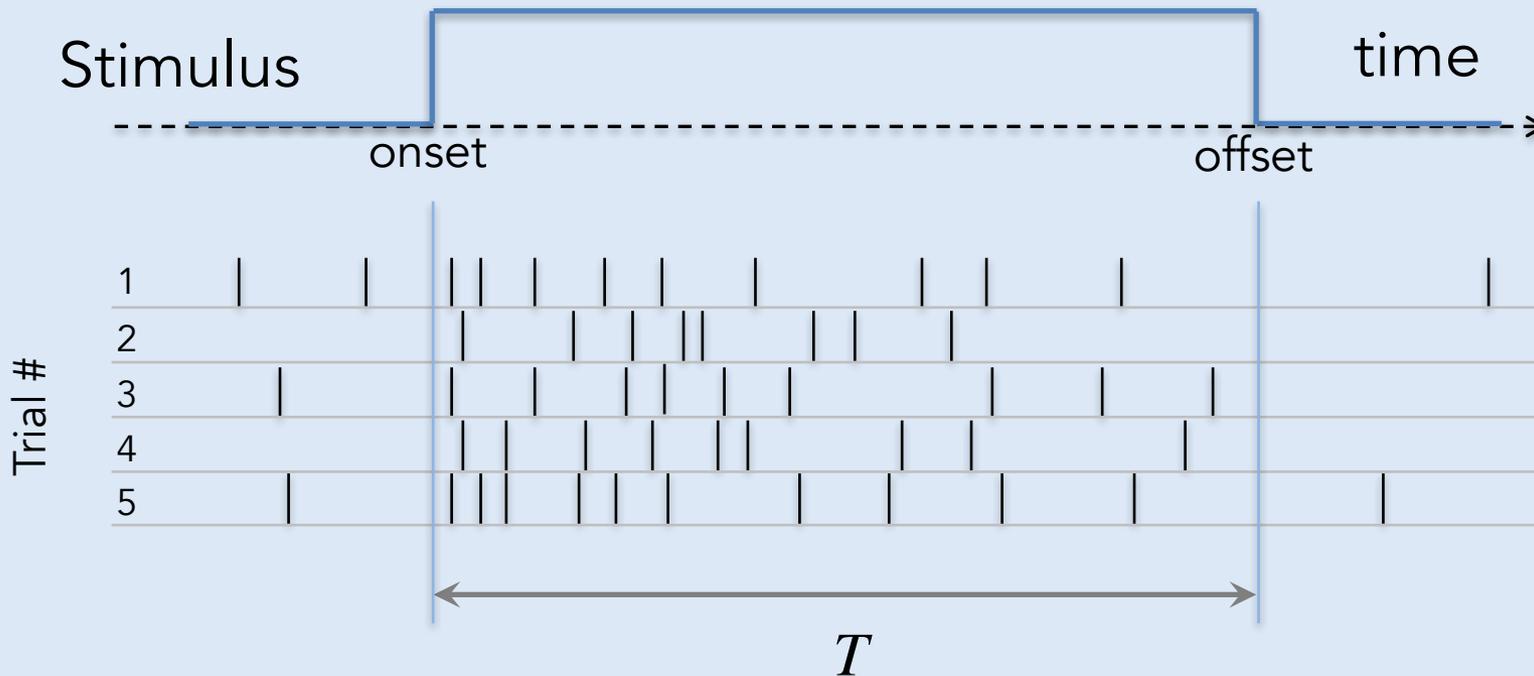
- Relation between spiking activity of a neuron in primate primary motor cortex and the onset of the arm movement.

Figures removed due to copyright restrictions. See Figure 4 in Georgopoulos, A.P., et al. "[On the Relations Between the Direction of Two-Dimensional Arm Movements and Cell Discharge in Primate Motor Cortex.](#)" *J. Neurosci.* 2 no. 11(1982): 1527-37.

M1 neurons show tuning for movement direction.

# Quantifying firing rates

- Method 1: Trial average firing rate.
  - Count the number of spikes in each trial. Average over trials.



$$R = \frac{\langle N_i \rangle_i}{T}$$

$N_i$  = number of spikes on trial  $i$

$\langle \rangle_i$  denotes the average over all trials  $i$

# Quantifying firing rates

- We can get higher temporal resolution by breaking the rate calculation into smaller units in time.



Trial-average rate in time bin  $j$

$$R_j = \frac{1}{\Delta T} \langle N_{i,j} \rangle_i$$

$N_i$  = number of spikes on trial  $i$  in bin  $j$

$\langle \rangle_i$  denotes the average over all trials  $i$

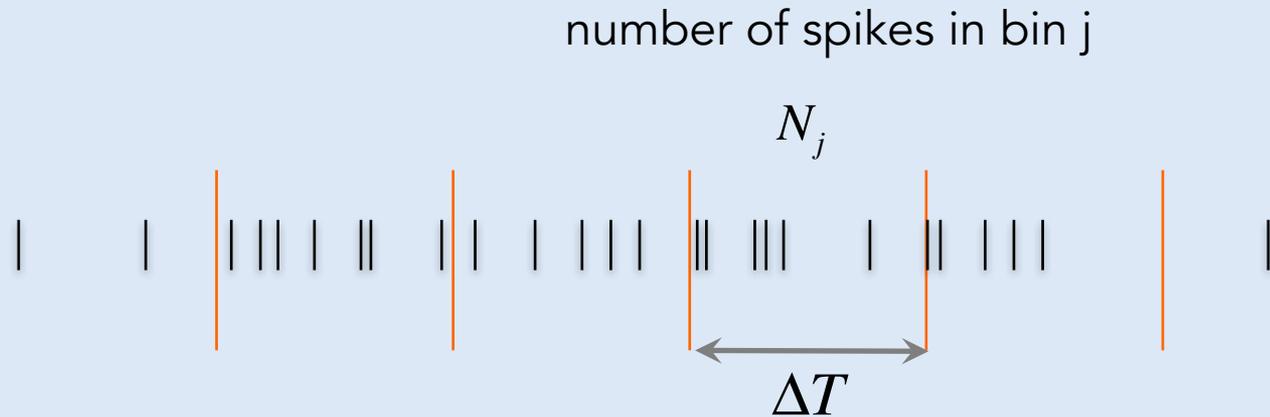
# Quantifying firing rates

- Peri-Stimulus Time Histogram (PSTH)  
or Peri-Event Time Histogram (PETH)

Figures removed due to copyright restrictions. See Figure 2 in Georgopoulos, A.P., et al. "[On the Relations Between the Direction of Two-Dimensional Arm Movements and Cell Discharge in Primate Motor Cortex.](#)" *J. Neurosci.* 2 no. 11(1982): 1527-37.

# Quantifying firing rates

- The same trick can be used to estimate firing rates in continuous spike trains (not associated with trials).

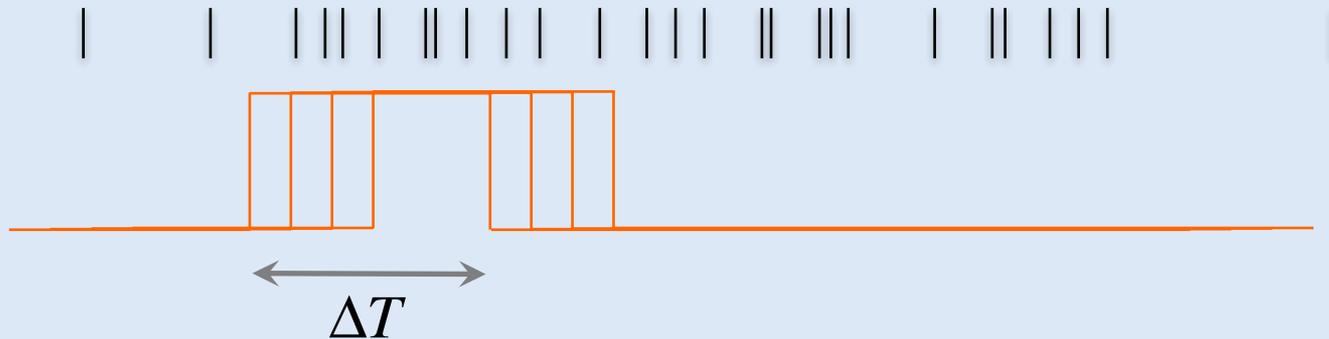


$$R_j = \frac{N_j}{\Delta T}$$

The problem with using fixed bins here is that the answer depends on where the boundaries are

# Quantifying firing rates

- A continuous measure of firing rate.

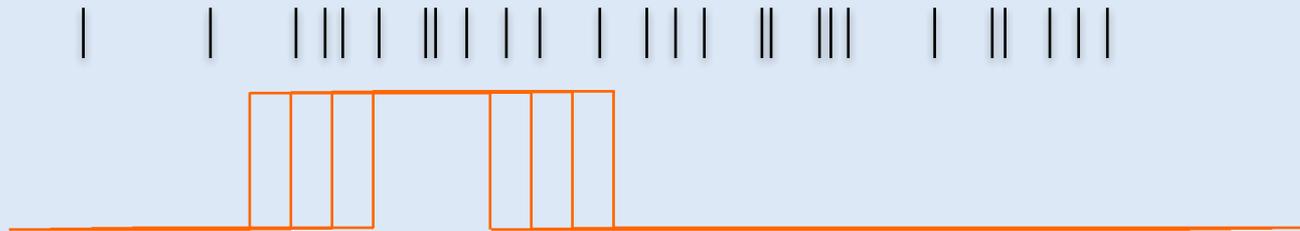


We count the number of spikes in a small window of width  $\Delta T$  and shift the window in smaller steps

How can we describe this mathematically (you ask)?

# Quantifying firing rates

- A continuous measure of firing rate.

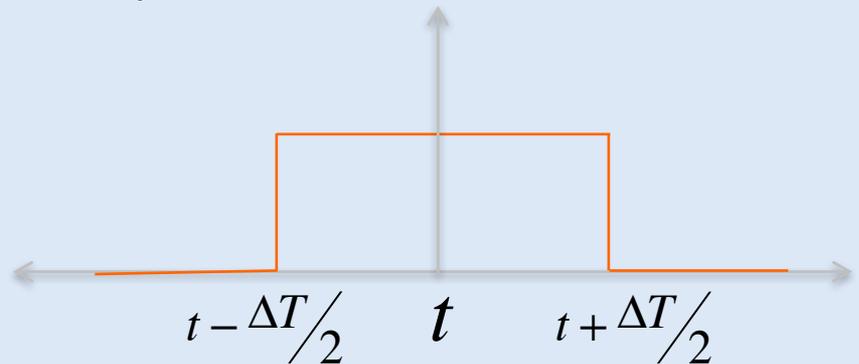


We can write this process down mathematically as follows.

First, we use the fact that the number of spikes in an interval  $t_1$  to  $t_2$  is given by

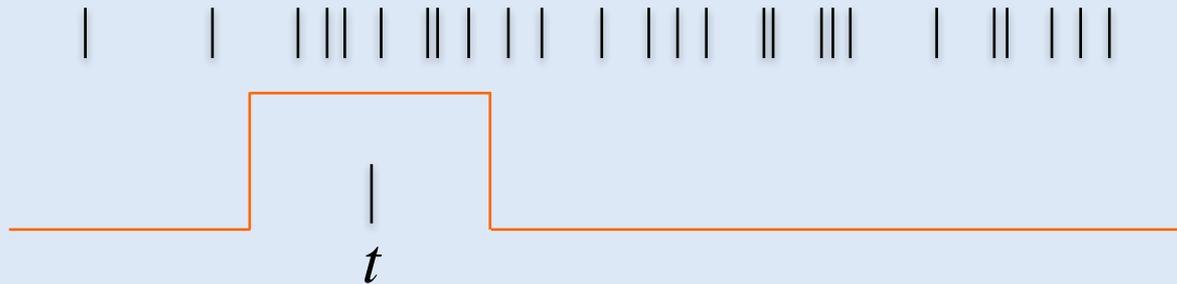
$$N = \int_{t_1}^{t_2} \rho(t) dt$$

$$R(t) = \frac{N}{\Delta T} = \frac{1}{\Delta T} \int_{t-\Delta T/2}^{t+\Delta T/2} \rho(\tau) d\tau$$



# Quantifying firing rates

- A continuous measure of firing rate.

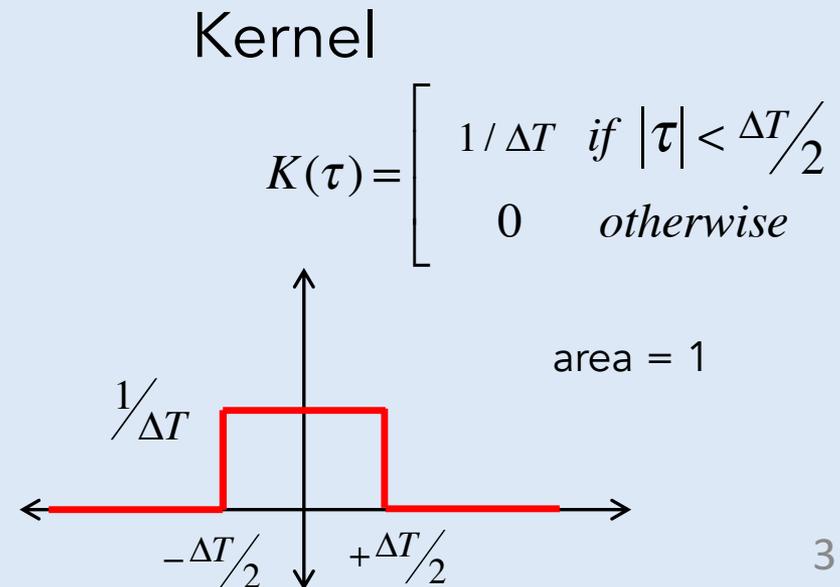


But this is just a convolution! We are convolving our spike train with a square kernel of width  $\Delta T$ .

$$R(t) = \int_{-\infty}^{\infty} \rho(t - \tau) K(\tau) d\tau$$

Notation

$$R(t) = \rho(t) * K$$



# Quantifying firing rates

- A continuous measure of firing rate.

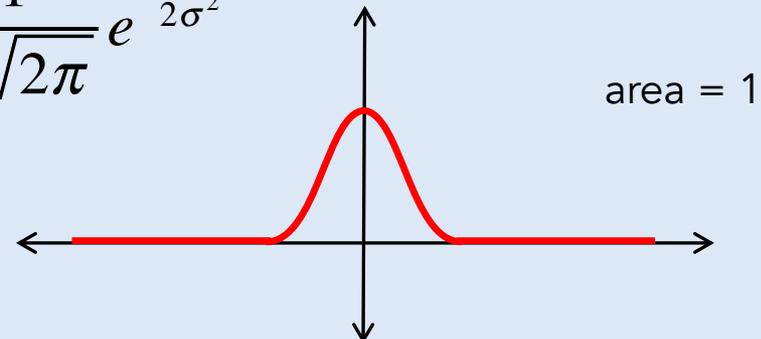


Even better is to convolve with a Gaussian kernel

$$R(t) = \rho(t) * K$$

$$K(\tau) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{\tau^2}{2\sigma^2}}$$

Kernel



Gaussian kernel is still averaging - it is just a weighted average, with less weight at the edges.

# Quantifying firing rates

- Summary

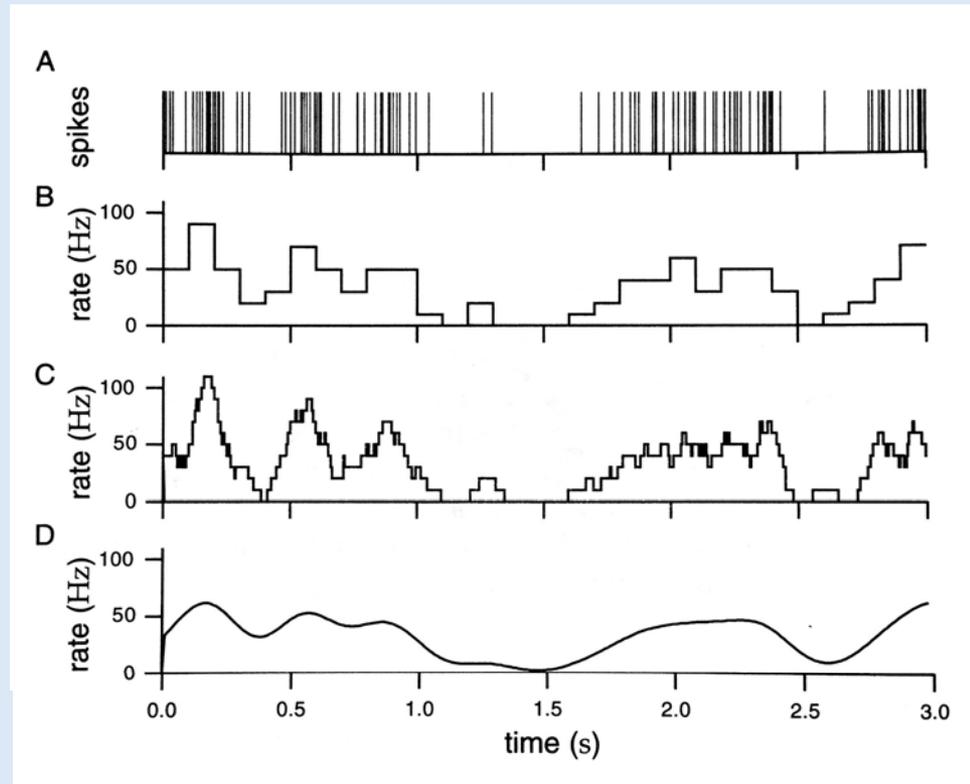
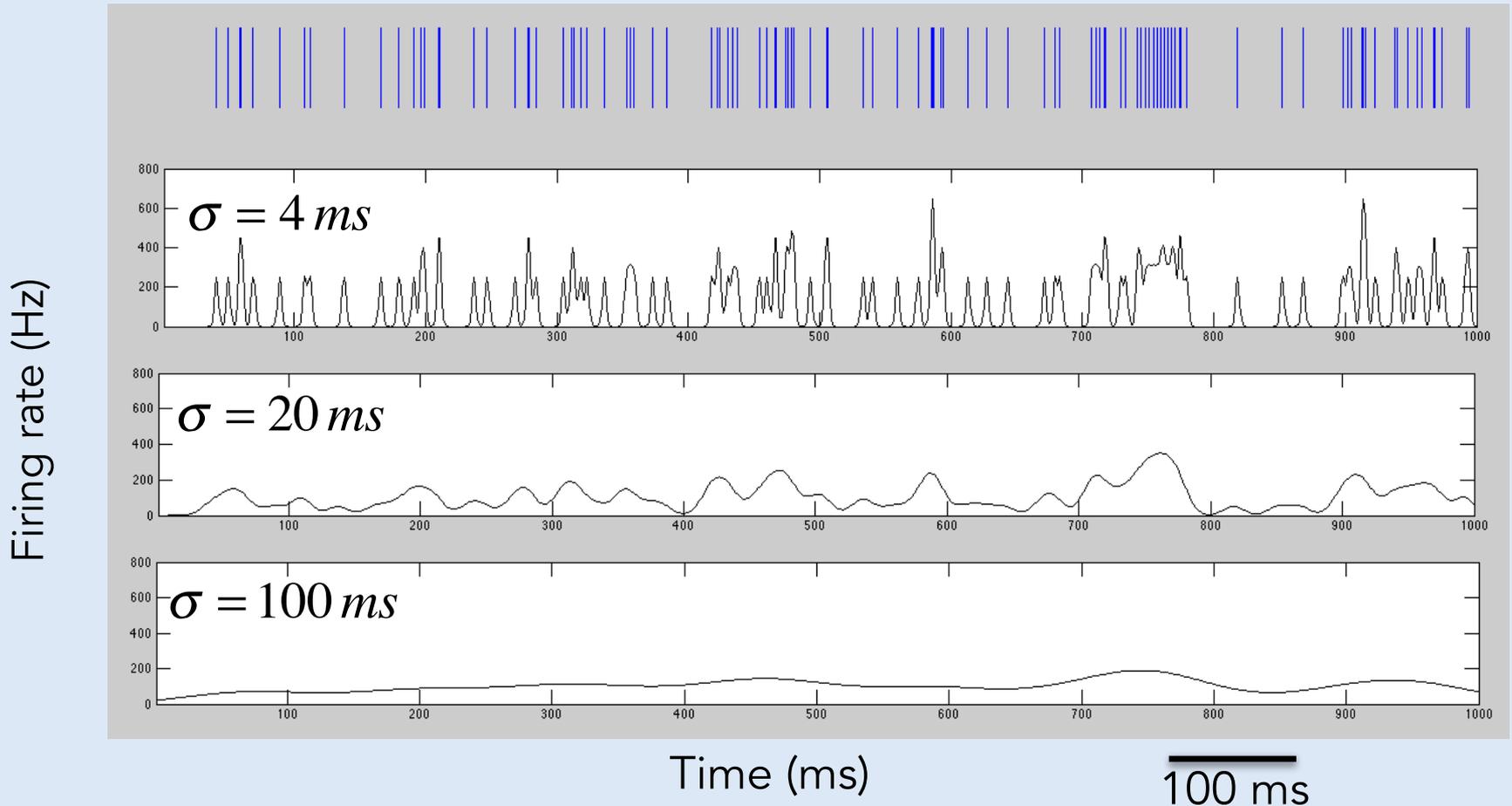


Figure courtesy MIT Press. From Dayan, P. and L. Abbott. [Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems](#). 2001.

# Key problem

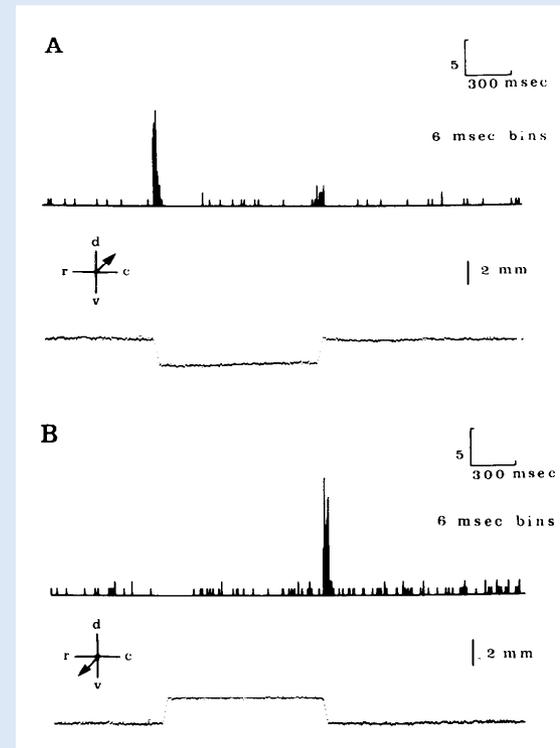
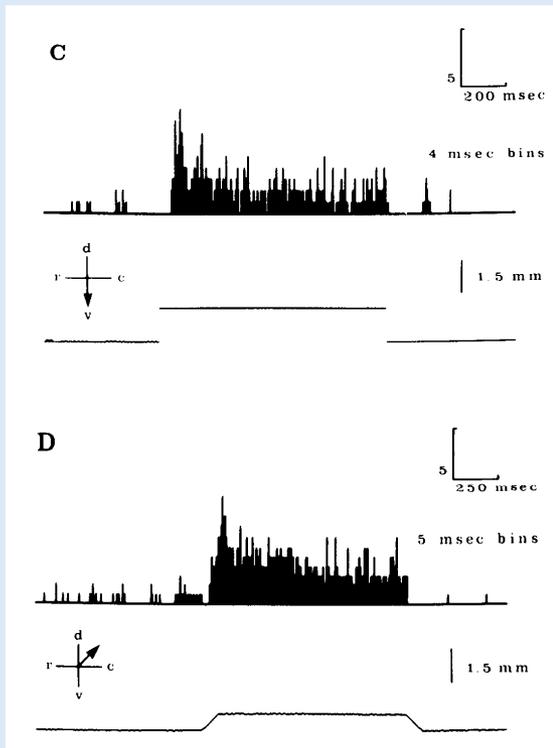
- You have to choose a timescale to measure the firing rate.

But you get a different answer for every different timescale!



# Temporal structure of responses

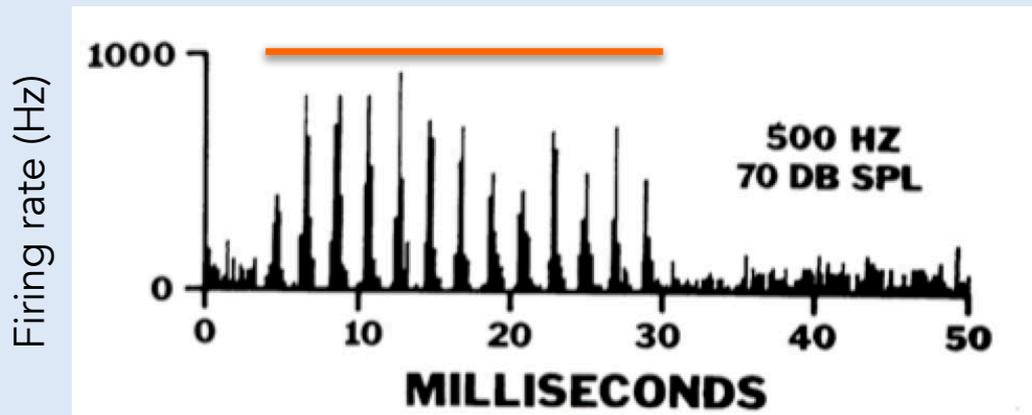
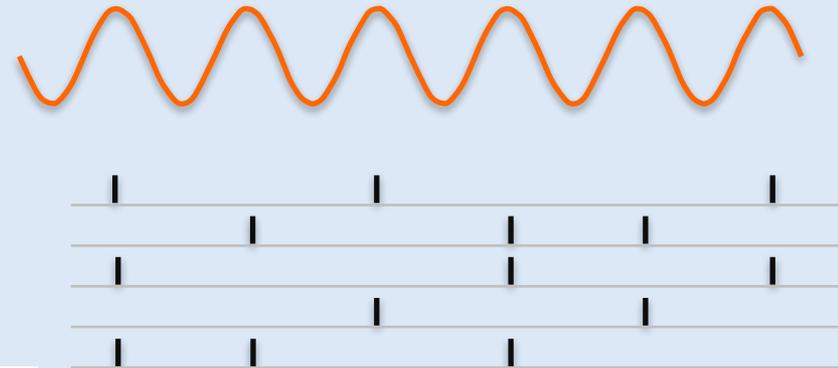
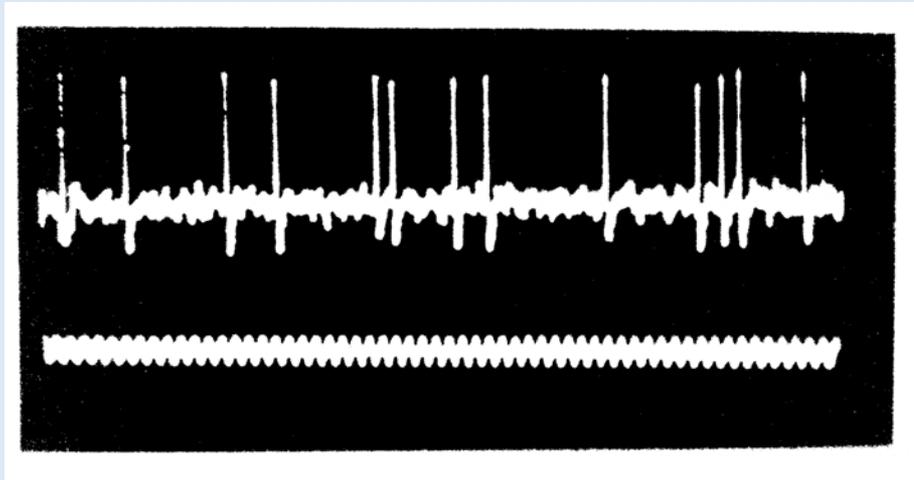
- Neuronal responses are not static. They have a strong temporal structure.



Recordings from vibrissa cortex in the rat. Response to whisker deflections.

# Temporal structure of responses

- Auditory neurons can be strongly locked to the phase of the sound waveform.



The spike timing is precisely controlled.

The firing rate is rapidly modulated in time.

# Rate vs timing?

- Sensory neurons spike more in response to some stimuli than others  
Motor neurons spike more before or during some actions than others

Therefore, information about a stimulus (or motor action) is carried in the numbers of spikes generated.

- All neurons exhibit temporal modulation of their firing rate (or spiking probability per unit time).

If information is carried in the slow modulations spike probability, we say that the information is coded by firing rate.

'Rate coding'

If information is carried in the fast modulations in spike probability, we say the the information is coded by spike timing.

'Temporal coding'

# Rate vs timing?

- You may occasionally hear a debate about 'rate coding' vs. 'temporal coding'.
- This is a false dichotomy. These are two extremes along a spectrum.
- The brain uses information in spike trains at a fast timescale and at a slow timescale.
- How do we determine what timescales are important?

We look at what the downstream neurons do with these spikes!

- What timescale is relevant for the computation being done?
- What are the biophysical processes in the downstream neurons.

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Spring 2018

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