

## Week 5 – part 3a :Three definitions of rate code



# Neuronal Dynamics: Computational Neuroscience of Single Neurons

## Week 5 – Variability and Noise: The question of the neural code

Wulfram Gerstner

EPFL, Lausanne, Switzerland

√ 5.1 Variability of spike trains  
- experiments

√ 5.2 Sources of Variability?  
- Is variability equal to noise?

5.3 Three definitions of Rate code  
- Poisson Model

5.4 Stochastic spike arrival  
- Membrane potential fluctuations

5.5. Stochastic spike firing  
- subthreshold and superthreshold

## Week 5 – part 3a :Three definitions of rate code



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- subthreshold and superthreshold

# Neuronal Dynamics – 5.3. Three definitions of Rate Codes

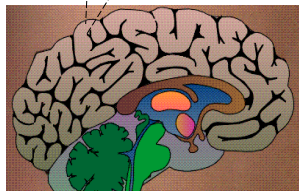
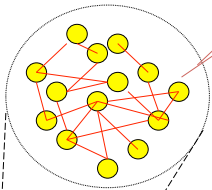
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## 3 definitions

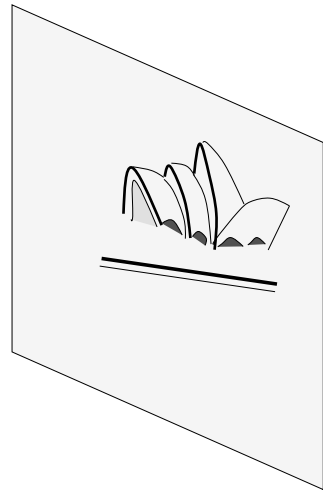
- Temporal averaging
- Averaging across repetitions
- Population averaging ('spatial' averaging)

# Neuronal Dynamics – 5.3. Rate codes: spike count

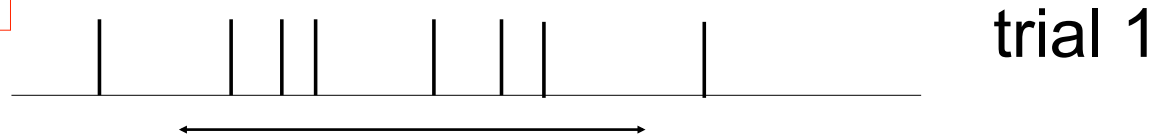
Variability of spike timing



Brain



stim



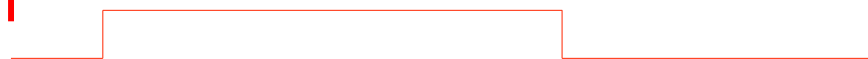
rate as a (normalized) spike count:

$$v(t) = \frac{n^{sp}}{T}$$

single neuron/single trial:  
temporal average



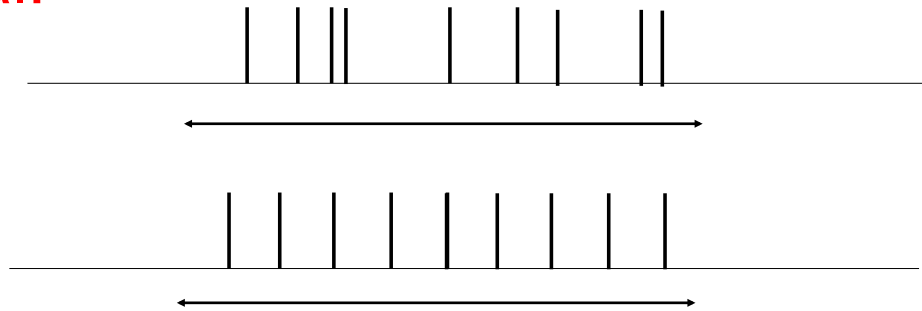
T=1s



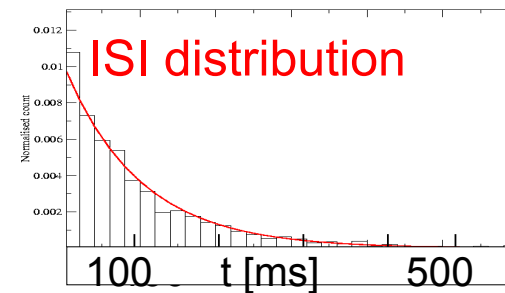
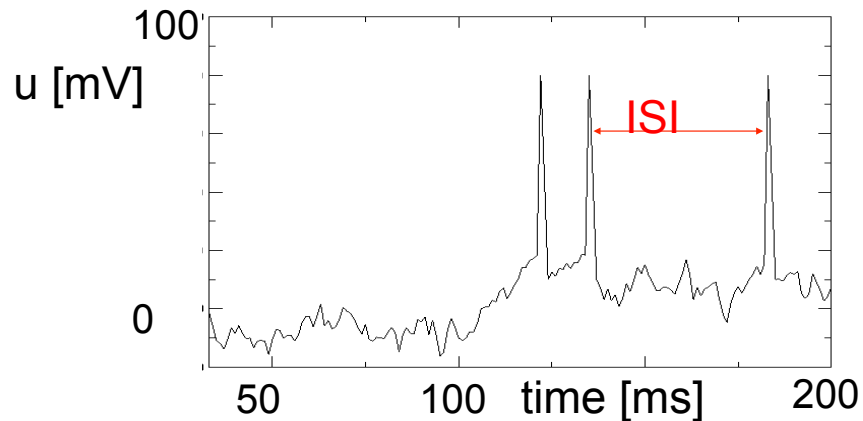
# Neuronal Dynamics – 5.3. Rate codes: spike count

single neuron/single trial:  
temporal average

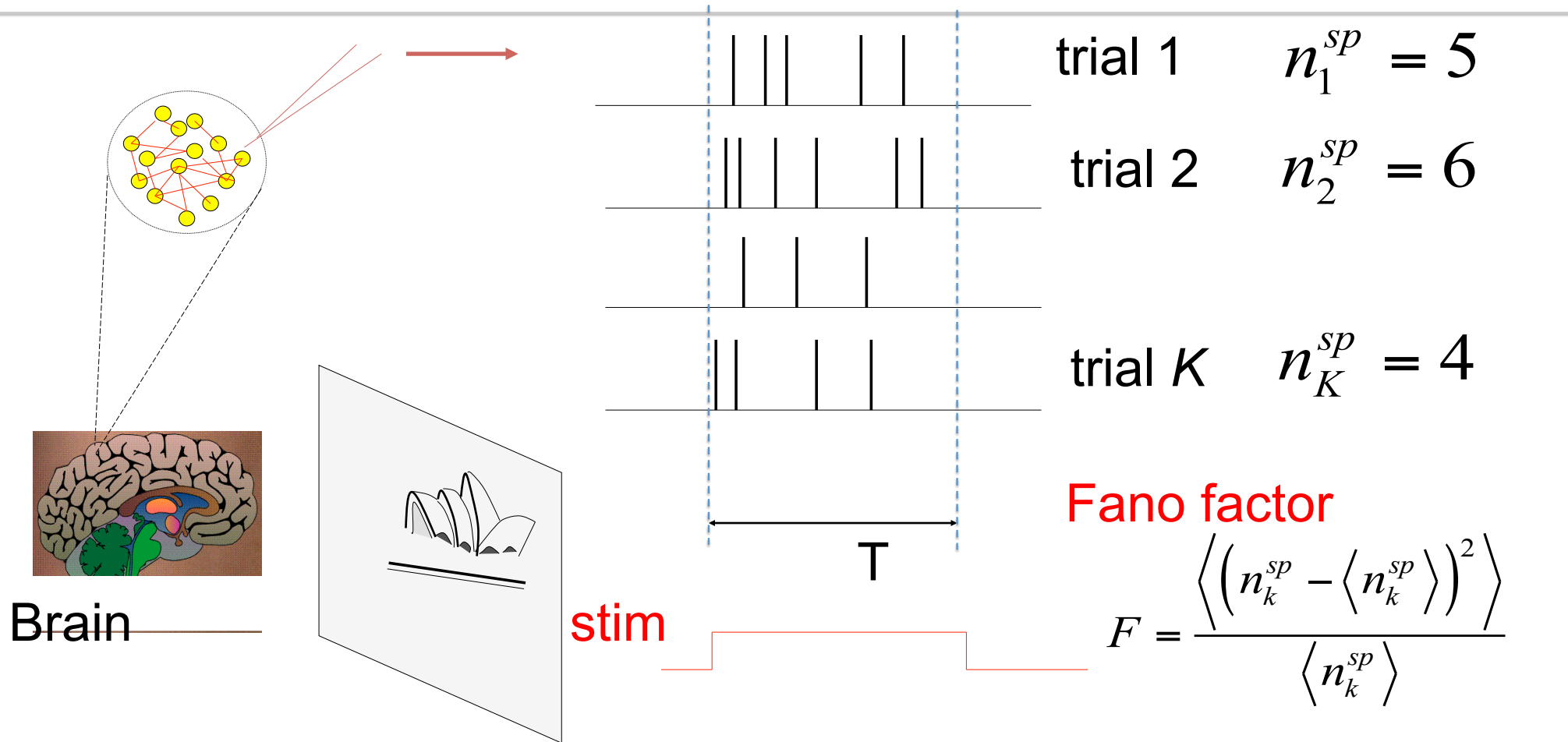
$$v(t) = \frac{n^{sp}}{T}$$



Variability of interspike intervals (ISI) **measure regularity**



# Neuronal Dynamics – 5.3. Spike count: FANO factor



# Neuronal Dynamics – 5.3. Three definitions of Rate Codes

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## 3 definitions

- √ -Temporal averaging (spike count) **Problem: slow!!!**

*ISI distribution (regularity of spike train)*

*Fano factor (repeatability across repetitions)*

- Averaging across repetitions
- Population averaging ('spatial' averaging)

# Neuronal Dynamics – 5.3. Three definitions of Rate Codes

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## 3 definitions

- √ -Temporal averaging

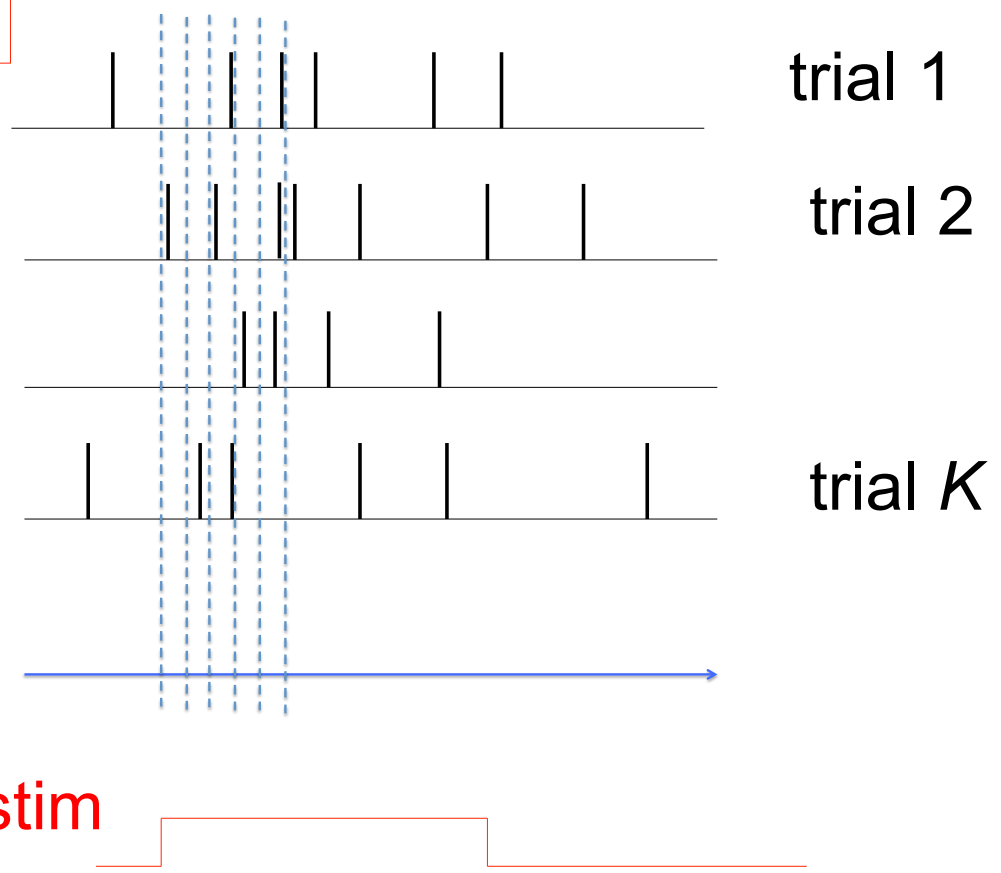
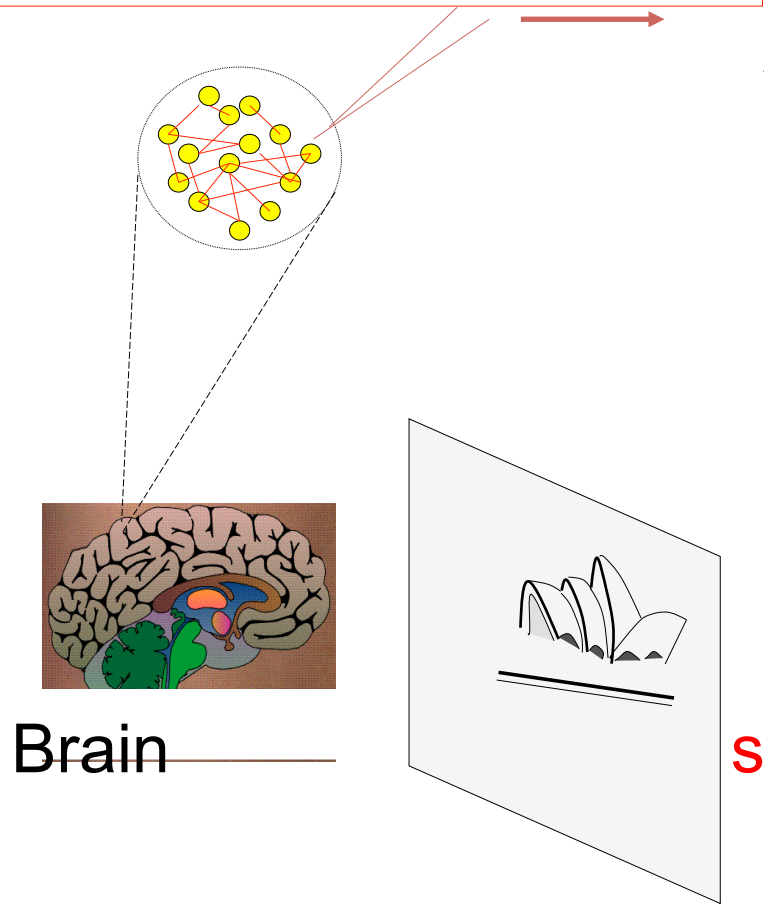
Problem: slow!!!

- Averaging across repetitions
- Population averaging



# Neuronal Dynamics – 5.3. Rate codes: PSTH

Variability of spike timing



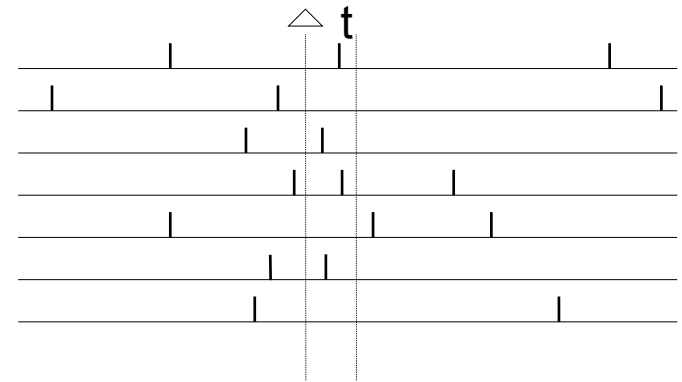
# Neuronal Dynamics – 5.3. Rate codes: PSTH

Averaging across repetitions

single neuron/many trials:  
average across trials

$$PSTH(t) = \frac{n(t; t + \Delta t)}{K \Delta t}$$

$K$  repetitions



Stim(t)



$K=50$  trials

PSTH(t)



# Neuronal Dynamics – 5.3. Three definitions of Rate Codes

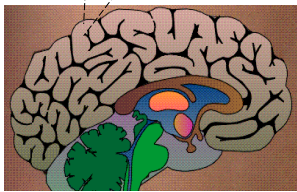
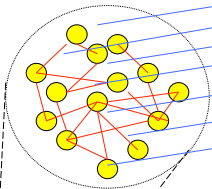
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## 3 definitions

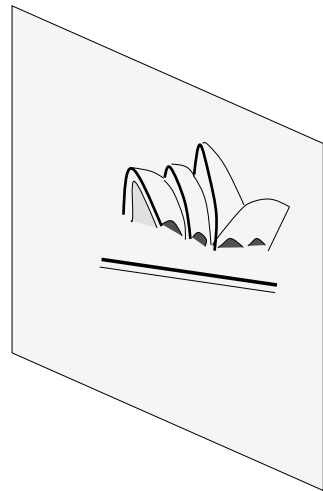
- √ - Temporal averaging
- √ - Averaging across repetitions
  - Problem: not useful for animal!!!
- Population averaging

# Neuronal Dynamics – 5.3. Rate codes: population activity

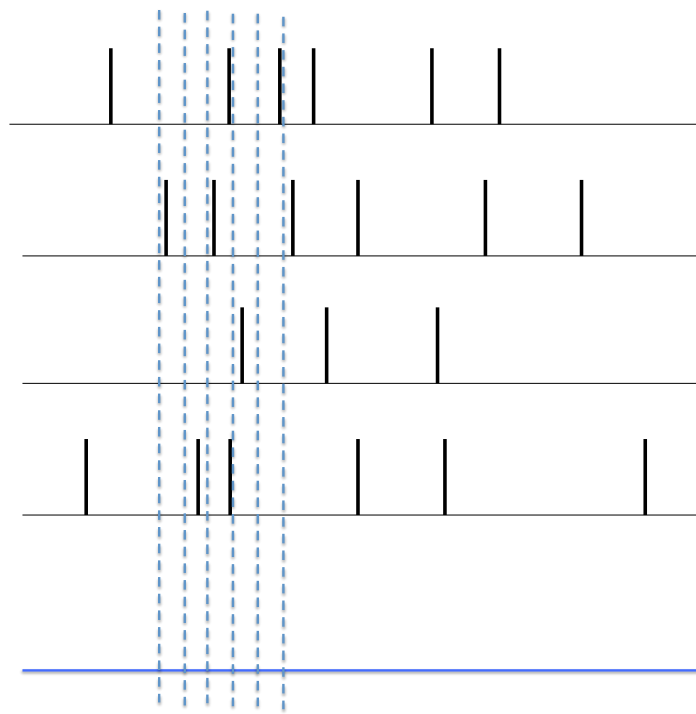
population of neurons  
with similar properties



Brain



stim



neuron 1

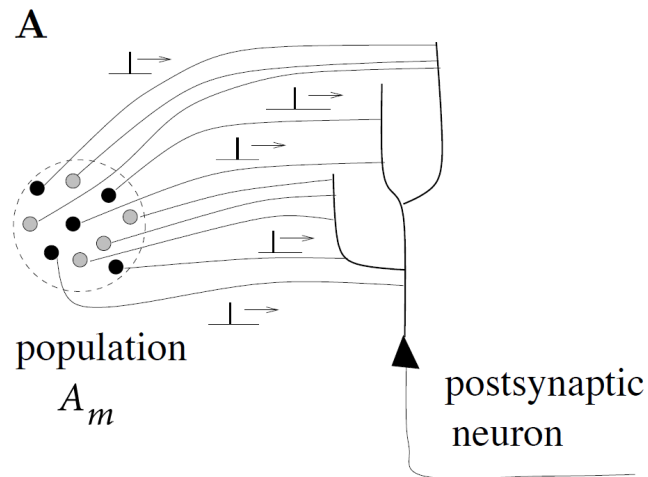
neuron 2

Neuron  $K$



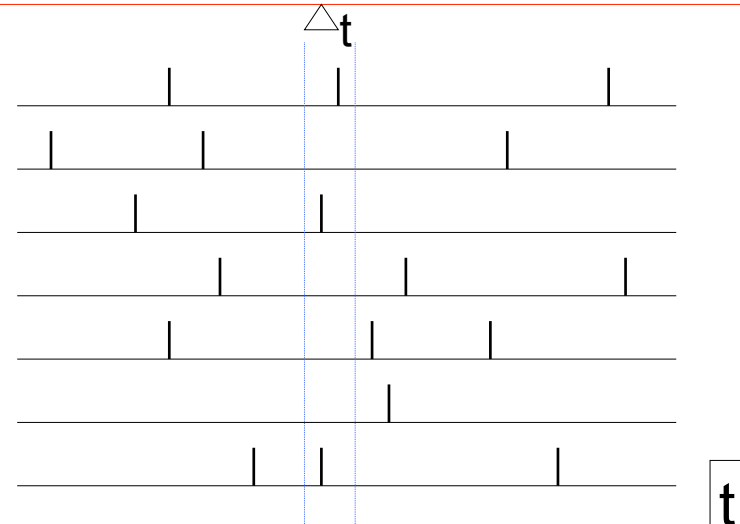
# Neuronal Dynamics – 5.3. Rate codes: population activity

population activity - rate defined by population average



'natural'

population activity



$$A(t) = \frac{n(t; t + \Delta t)}{N\Delta t}$$

# Neuronal Dynamics – 5.3. Three definitions of Rate codes

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## Three averaging methods

-over time

Too slow  
for animal!!!

- over repetitions

Not possible  
for animal!!!

- over population (space)

'natural'

## Neuronal Dynamics – Quiz 5.2.

**Rate codes.** Suppose that in some brain area we have a group of 500 neurons. All neurons have identical parameters and they all receive the same input. Input is given by sensory stimulation and passes through 2 preliminary neuronal processing steps before it arrives at our group of 500 neurons. Within the group, neurons are not connected to each other. Imagine the brain as a model network containing 100 000 nonlinear integrate-and-fire neurons, so that we know exactly how each neuron functions.

Experimentalist A makes a measurement in a single trial on all 500 neurons using a multi-electrode array, during a period of sensory stimulation.

Experimentalist B picks an arbitrary single neuron and repeats the same sensory stimulation 500 times (with long pauses in between, say one per day).

Experimentalist C repeats the same sensory stimulation 500 times (1 per day), but every day he picks a random neuron (amongst the 500 neurons).

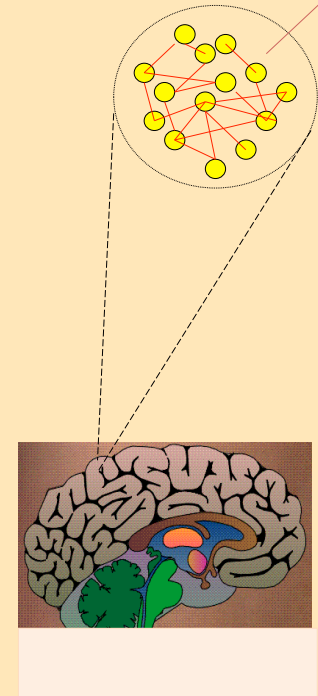
All three determine the time-dependent firing rate.

A and B and C are expected to find the same result.

A and B are expected to find the same result, but that of C is expected to be different.

B and C are expected to find the same result, but that of A is expected to be different.

None of the above three options is correct.



## Week 5 – part 3b :Poisson Model



# Neuronal Dynamics: Computational Neuroscience of Single Neurons

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## Week 5 – part 3b :Poisson Model



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✓ **5.2 Sources of Variability?**  
- Is variability equal to noise?

**5.3 Three definitions of Rate code**

- Poisson Model

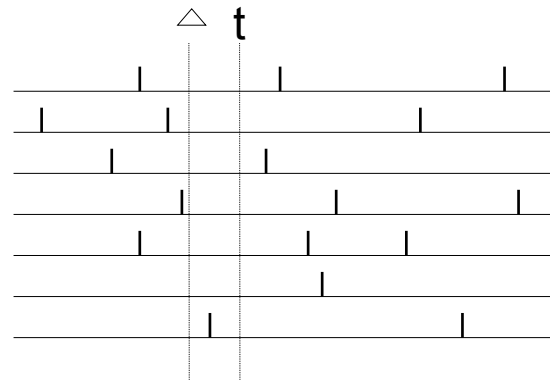
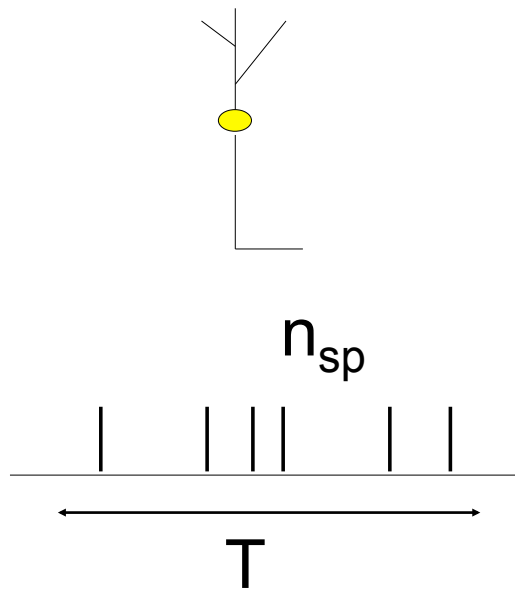
**5.4 Stochastic spike arrival**

- Membrane potential fluctuations

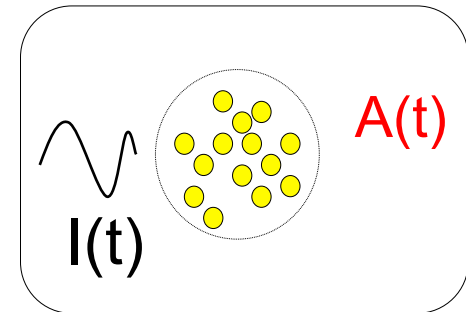
**5.5. Stochastic spike firing**

- subthreshold and superthreshold

# Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process



$$PSTH(t) = \frac{n(t; t + \Delta t)}{K \Delta t}$$



$$A(t) = \frac{n(t; t + \Delta t)}{N \Delta t}$$

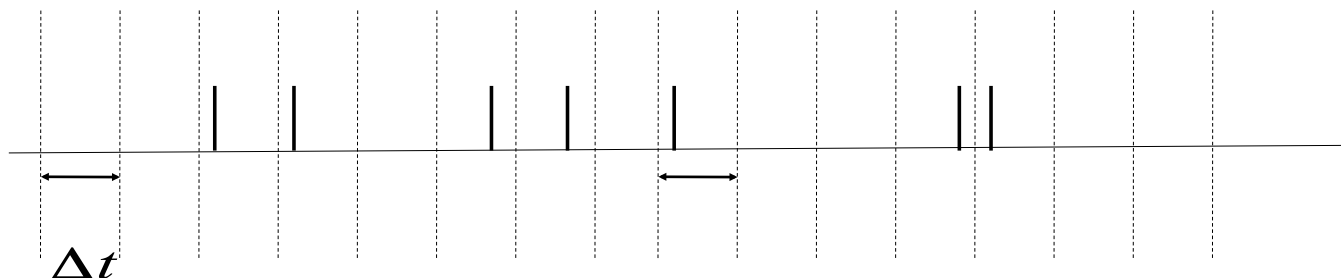
population  
activity

Pure rate code = stochastic spiking  $\rightarrow$  Poisson model

## Neuronal Dynamics – 5.3b. Poisson Model

Homogeneous Poisson model: constant rate

*Math detour:  
Poisson model*



Probability of finding a spike  $P_F = \rho_0 \Delta t$

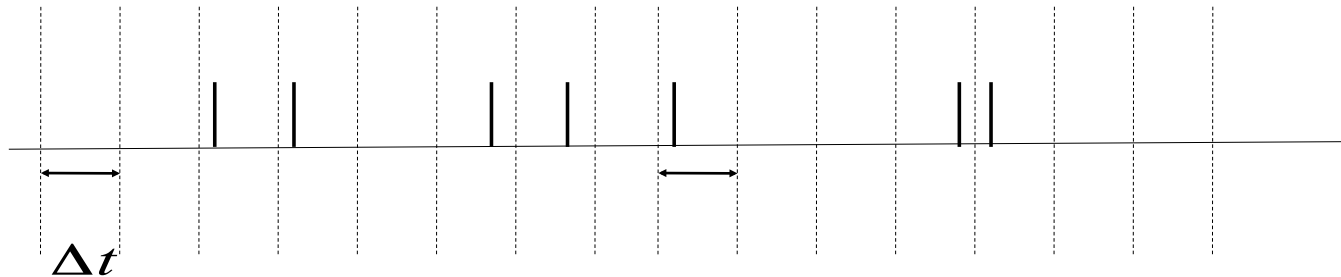
Pure rate code = stochastic spiking  $\rightarrow$  Poisson model

## Neuronal Dynamics – 5.3b. Poisson Model

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Probability of firing:

$$P_F = \rho_0 \Delta t$$



Take  $\Delta t \rightarrow 0$

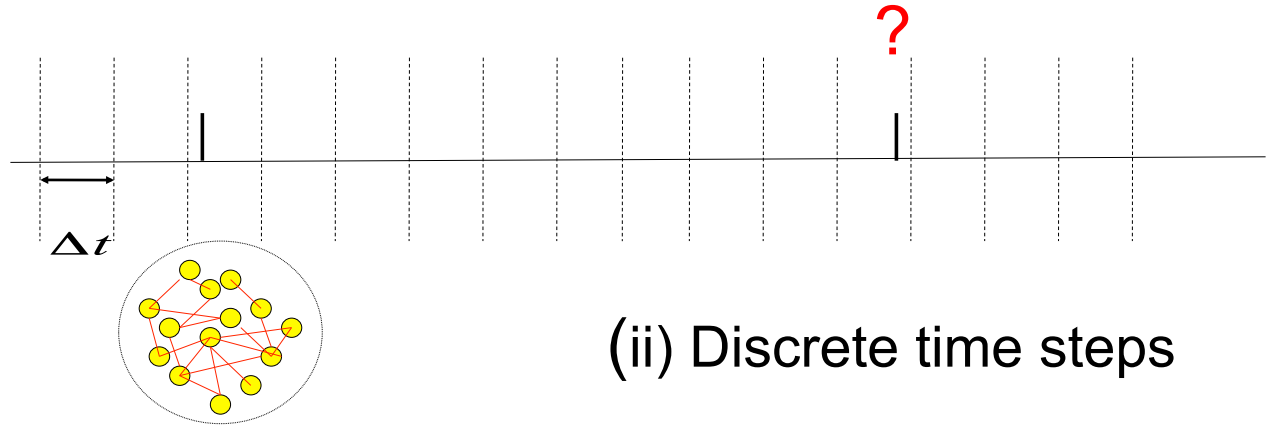
# Neuronal Dynamics – 5.3b. Interval distribution

Probability of firing:

$$P_F = \rho_0 \Delta t$$

(i) Continuous time

*prob to 'survive'*

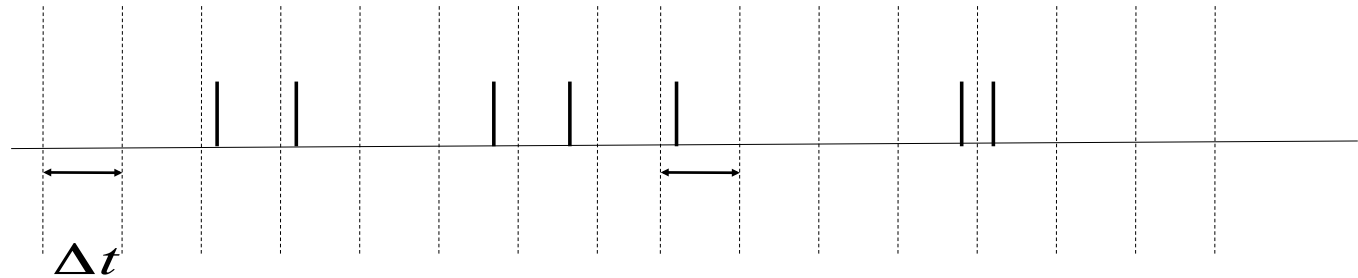


(ii) Discrete time steps

$$\Delta t \rightarrow 0$$

# Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process

rate changes

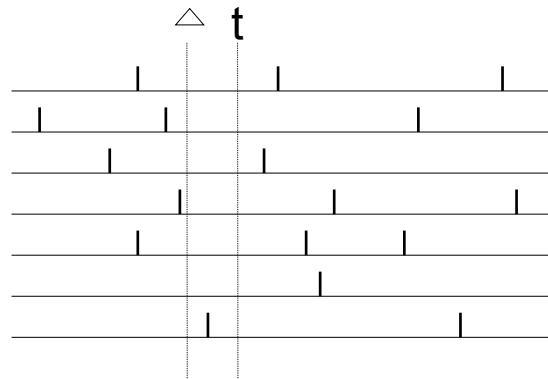
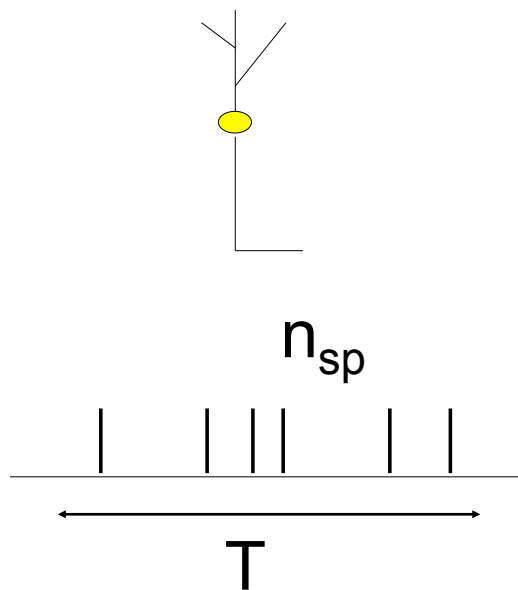


Probability of firing  $P_F = \rho(t) \Delta t$

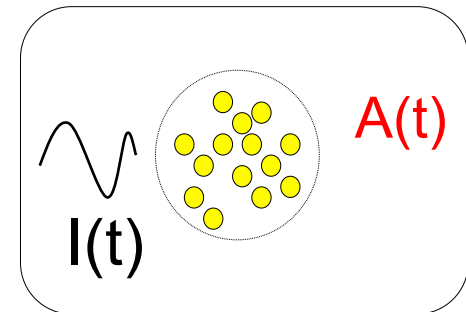
Survivor function  $S(t | \hat{t}) = \exp\left(-\int_{\hat{t}}^t \rho(t') dt'\right)$

Interval distribution

# Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process



$$PSTH(t) = \frac{n(t; t + \Delta t)}{K \Delta t}$$



$$A(t) = \frac{n(t; t + \Delta t)}{N \Delta t}$$

population  
activity

inhomogeneous Poisson model consistent with rate coding

## Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process

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Probability of firing

$$P_F = \rho(t) \Delta t$$

Survivor function

$$S(t | \hat{t}) = \exp\left(-\int_{\hat{t}}^t \rho(t') dt'\right)$$

Interval distribution

$$P(t | \hat{t}) = \rho(t) \exp\left(-\int_{\hat{t}}^t \rho(t') dt'\right)$$



## Neuronal Dynamics – Quiz 5.3.

### A Homogeneous Poisson Process:

A spike train is generated by a homogeneous Poisson process with rate 25Hz with time steps of 0.1ms.

- The most likely interspike interval is 25ms.
- The most likely interspike interval is 40 ms.
- The most likely interspike interval is 0.1ms
- We can't say.

### B Inhomogeneous Poisson Process:

A spike train is generated by an inhomogeneous Poisson process with a rate that oscillates periodically (sine wave) between 0 and 50Hz (mean 25Hz). A first spike has been fired at a time when the rate was at its maximum. Time steps are 0.1ms.

- The most likely interspike interval is 25ms.
- The most likely interspike interval is 40 ms.
- The most likely interspike interval is 0.1ms.
- We can't say.