

Week 5 – part 1 :Variability



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
- Detour: Poisson model, a modern approach

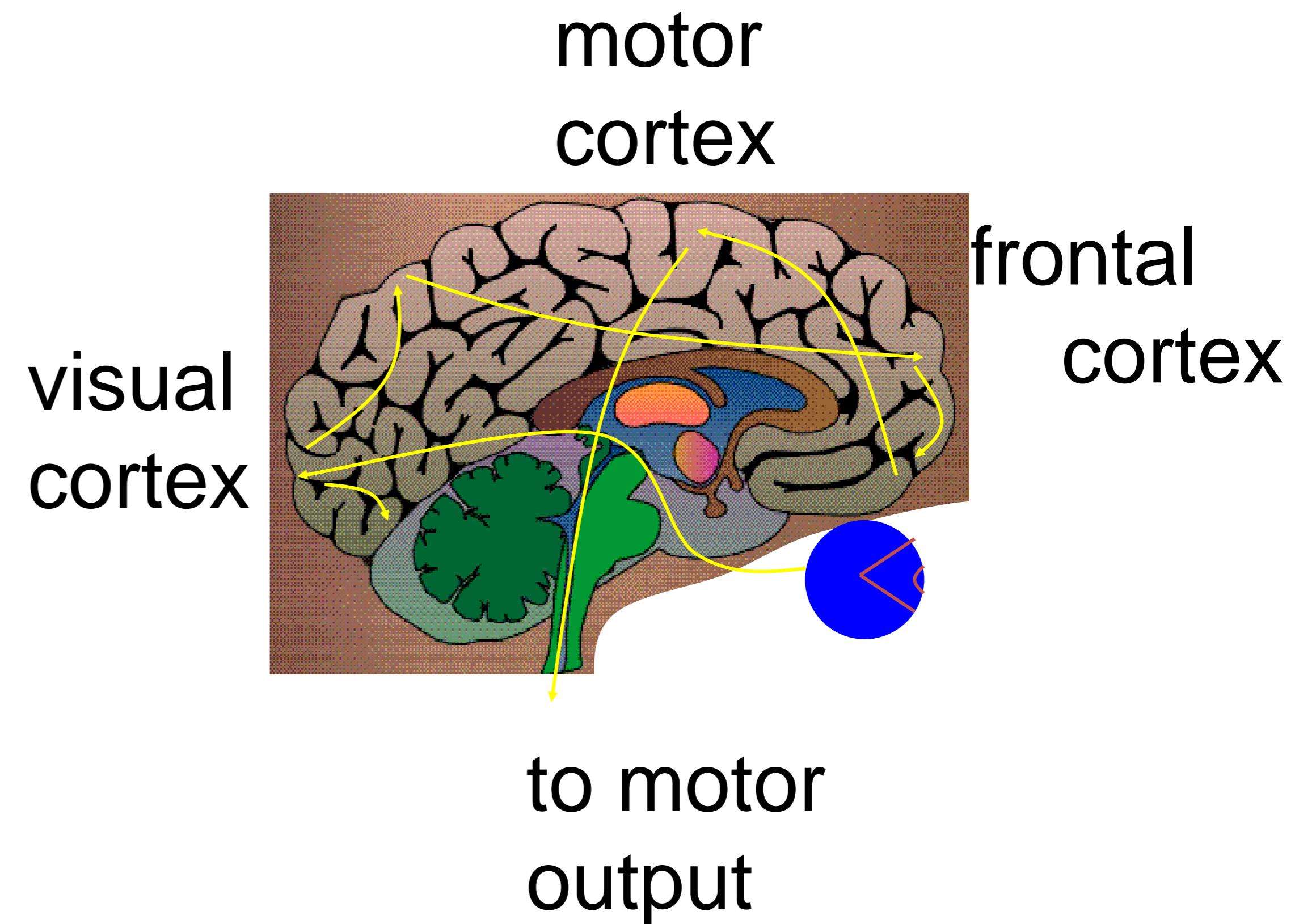
5.4 Stochastic spike arrival

- Membrane potential fluctuations

5.5. Stochastic spike firing

- subthreshold and superthreshold

Neuronal Dynamics – 5.1. Variability



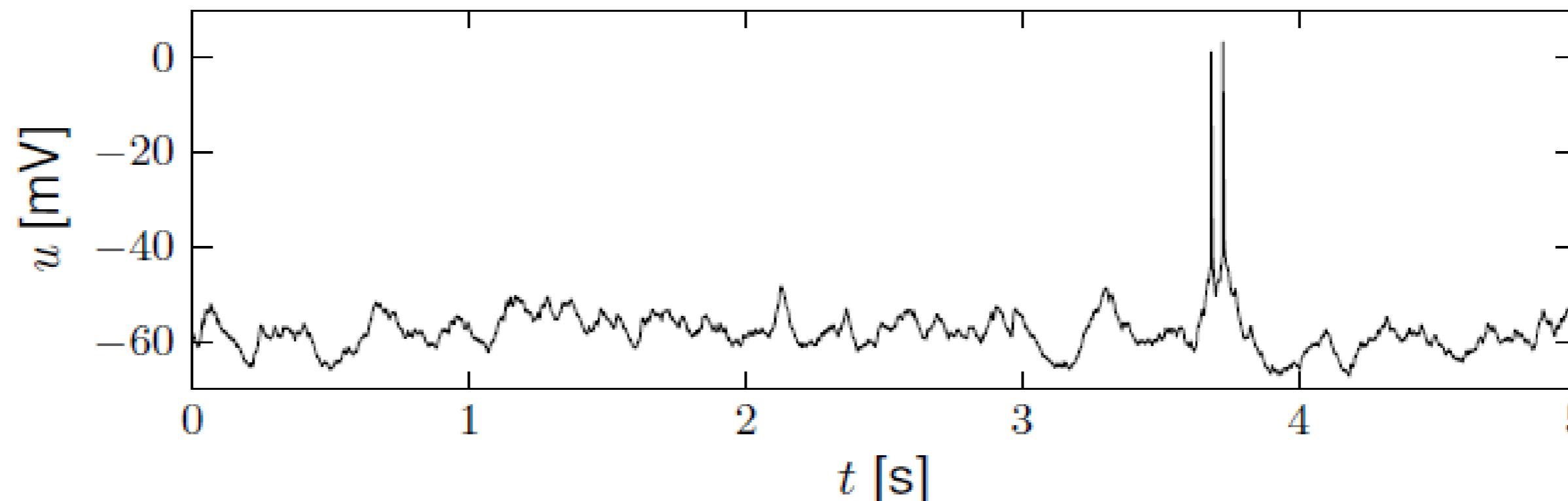
Neuronal Dynamics – 5.1 Variability *in vivo*

Spontaneous activity *in vivo*

Variability

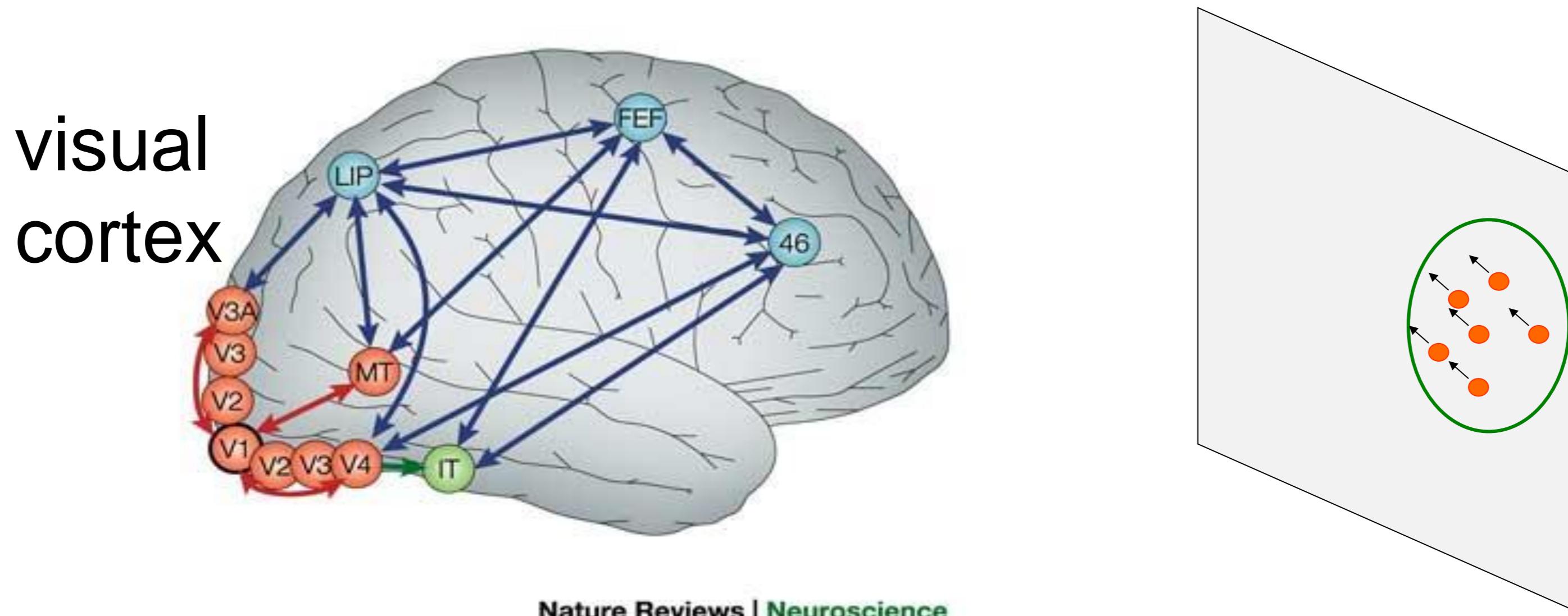
- of membrane potential?
- of spike timing?

awake mouse, cortex, freely whisking,



Crochet et al., 2011

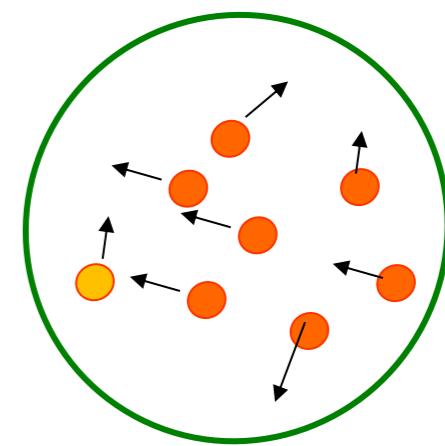
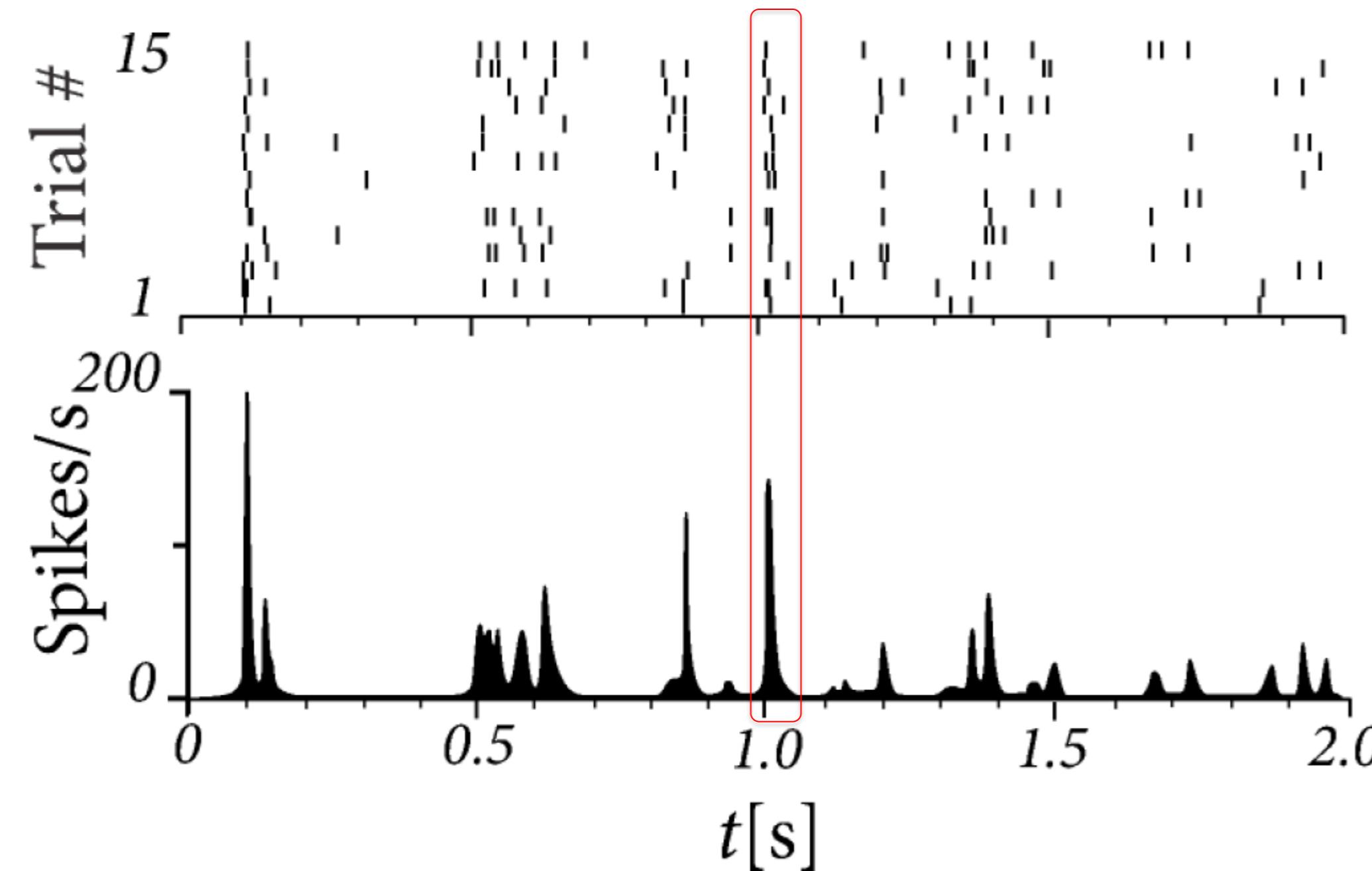
Detour: Receptive fields in V5/MT



cells in visual cortex MT/V5
respond to motion stimuli

Neuronal Dynamics – 5.1 Variability in vivo

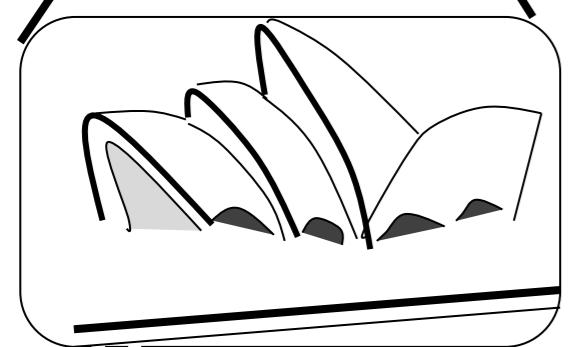
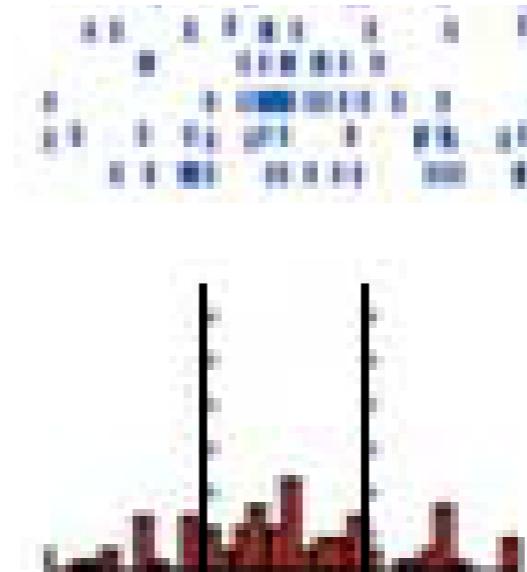
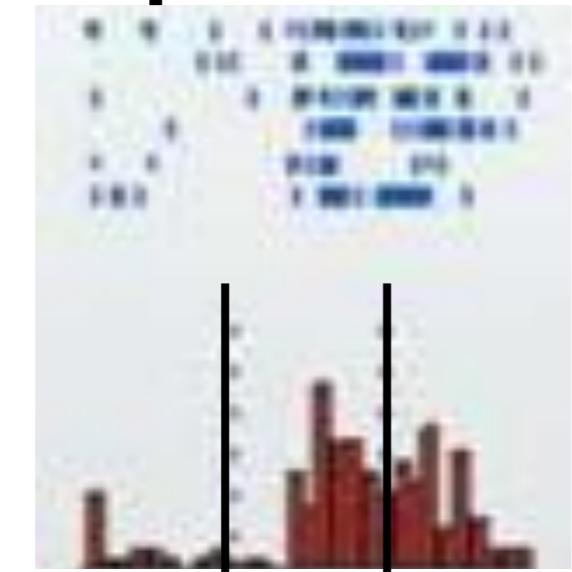
15 repetitions of the **same** random dot motion pattern



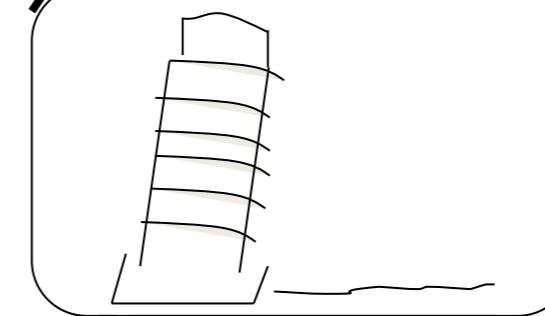
*adapted from Bair and Koch 1996;
data from Newsome 1989*

Neuronal Dynamics – 5.1 Variability in vivo

Human Hippocampus



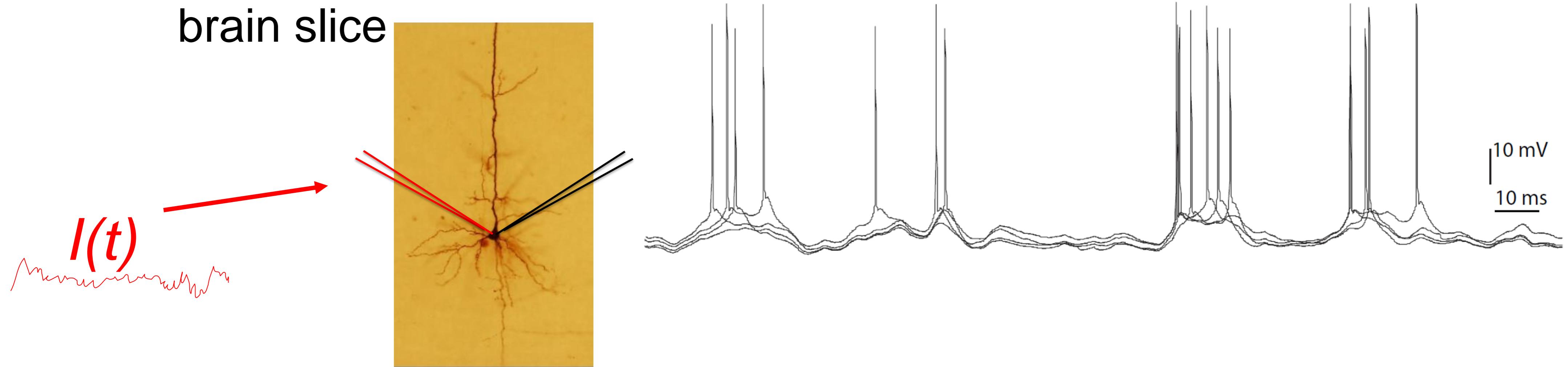
Sidney
opera



*Quiroga, Reddy,
Kreiman, Koch,
and Fried (2005).
Nature, 435:1102-1107.*

Neuronal Dynamics – 5.1 Variability in vitro

4 repetitions of the same time-dependent stimulus,



Neuronal Dynamics – 5.1 Variability

Fluctuations

- of membrane potential
- of spike times

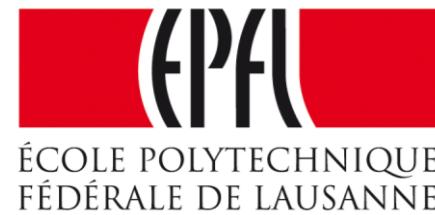
fluctuations=noise?

relevance for coding?

source of fluctuations?

model of fluctuations?

Week 5 – part 2 : Sources of Variability



Neuronal Dynamics: Computational Neuroscience of Single Neurons

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

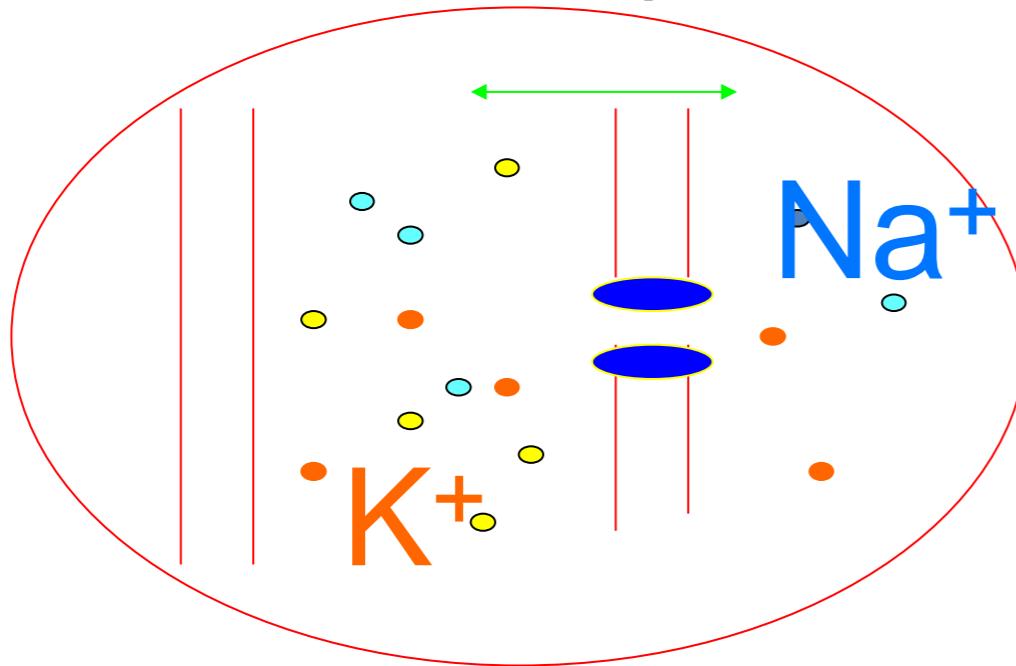
Wulfram Gerstner

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

Neuronal Dynamics – 5.2. Sources of Variability

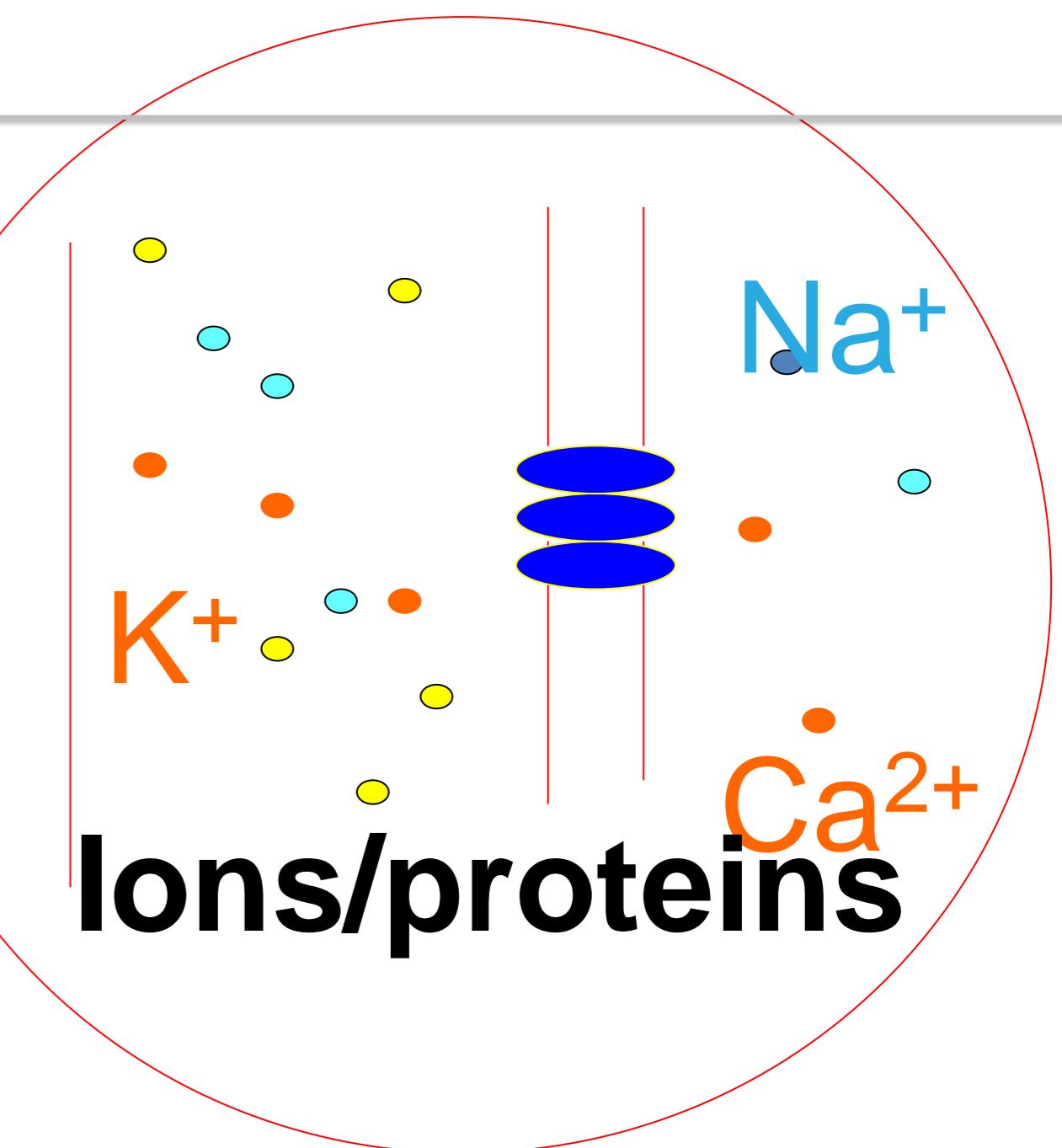
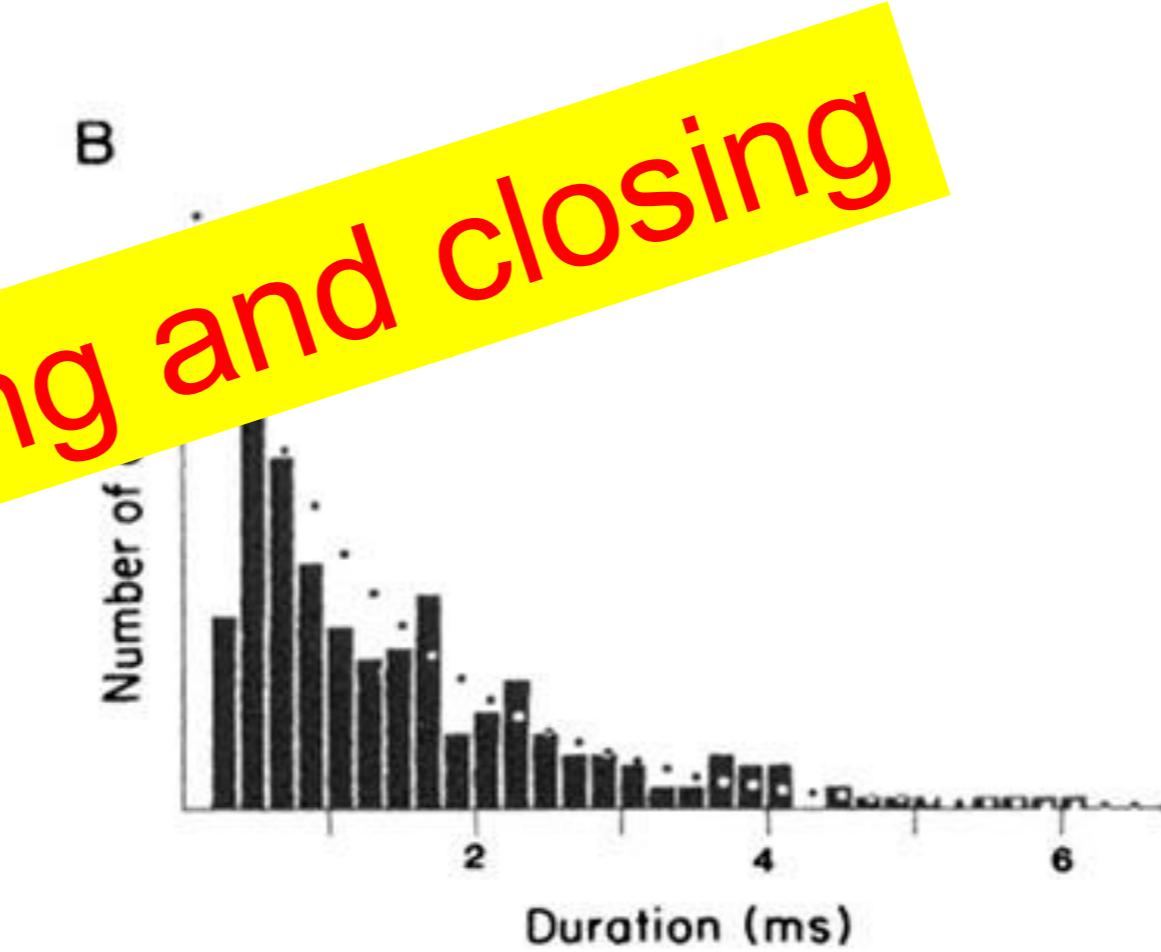
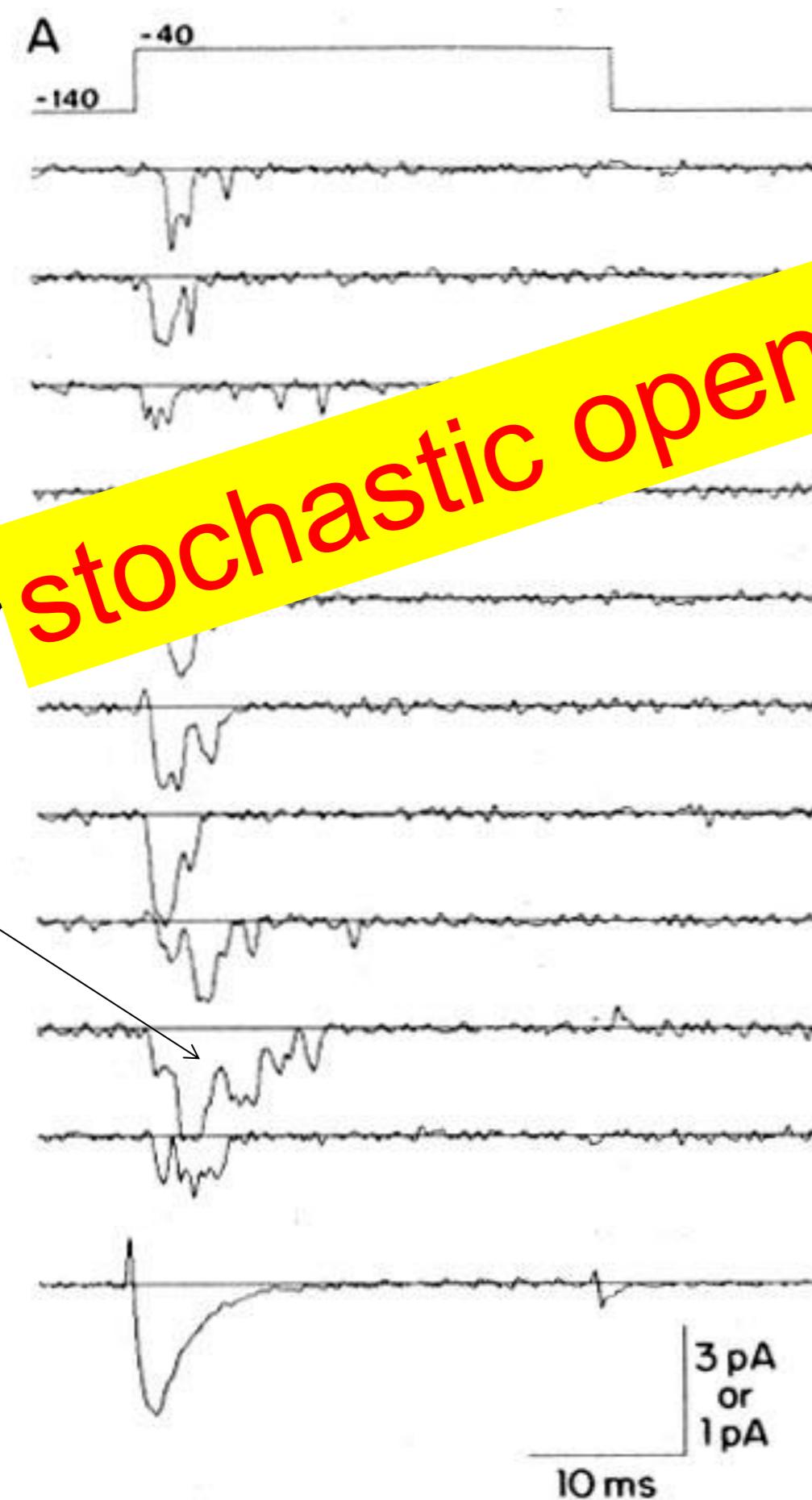
- Intrinsic noise (ion channels)



- Finite number of channels
- Finite temperature

Review from 2.5 Ion channels

Steps:
Different numbers
of channels

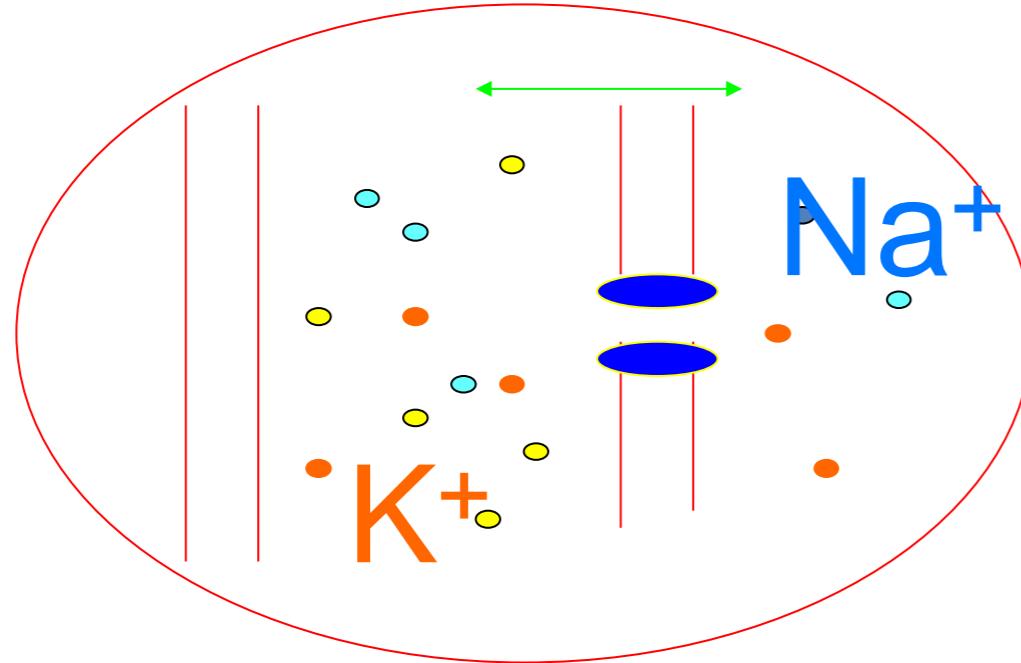


Ions/proteins

Na^+ channel from rat heart (*Patlak and Ortiz 1985*)
A traces from a patch containing several channels.
Bottom: average gives current time course.
B. Opening times of single channel events

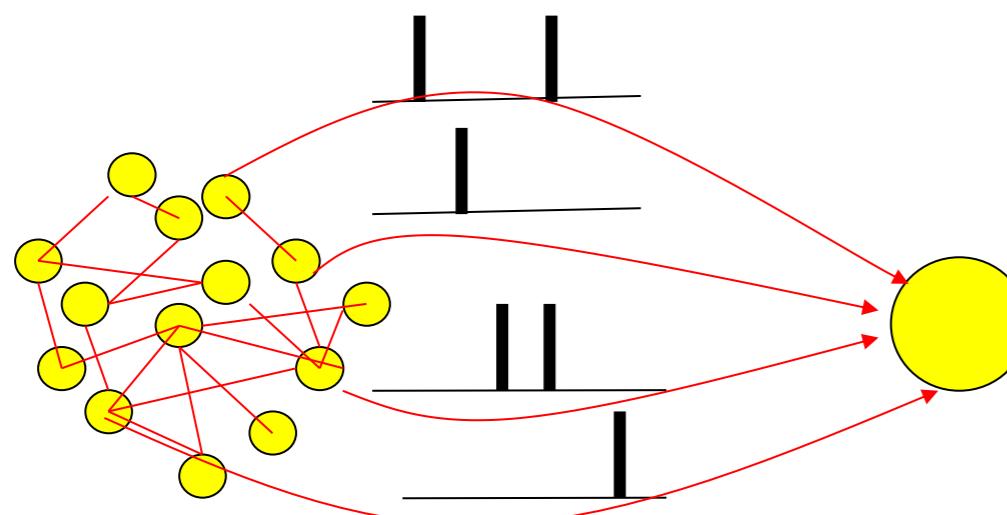
Neuronal Dynamics – 5.2. Sources of Variability

- Intrinsic noise (ion channels)

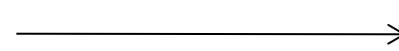


- Finite number of channels
- Finite temperature

- Network noise (background activity)

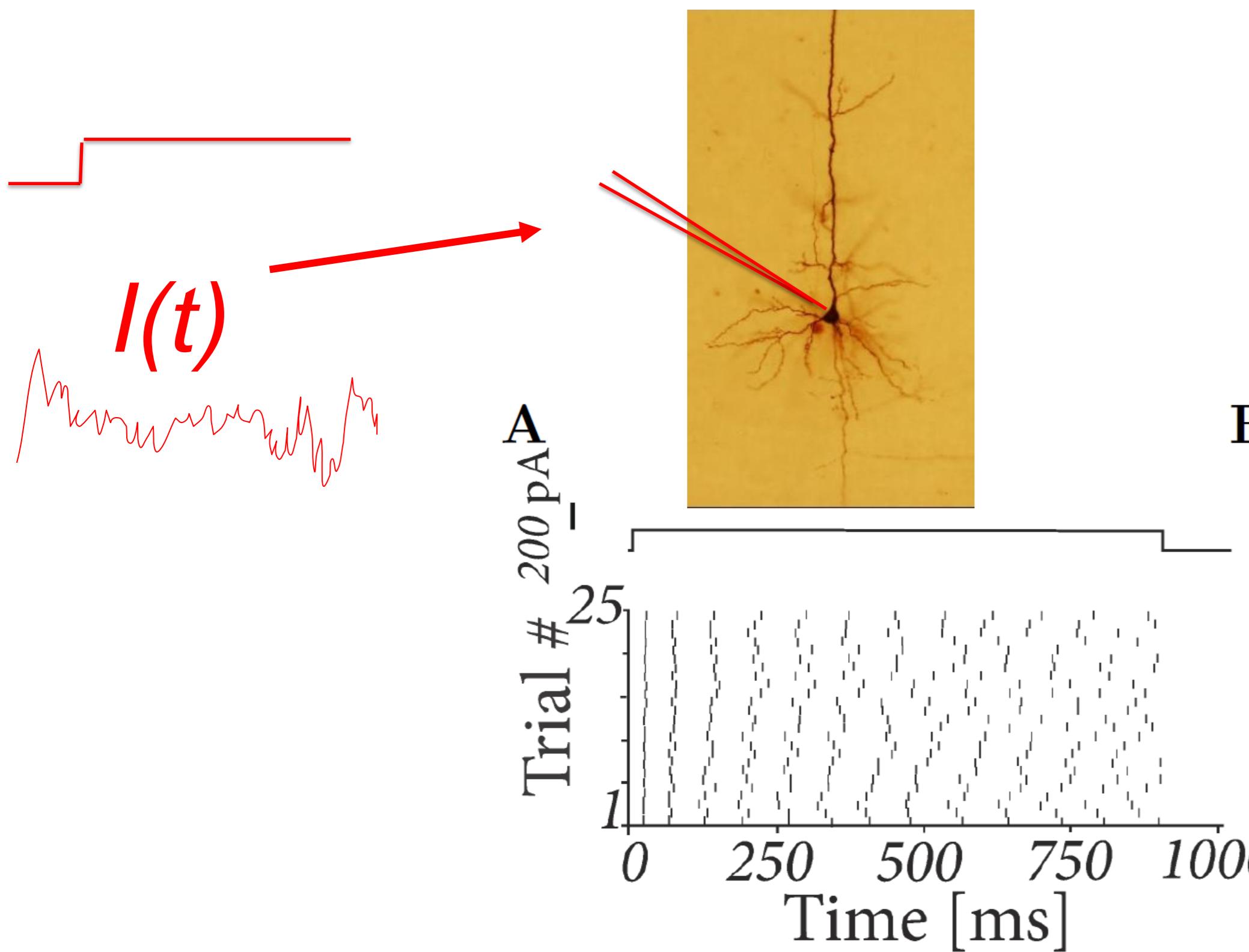


- Spike arrival from other neurons
- Beyond control of experimentalist



Check intrinsic noise by removing the network

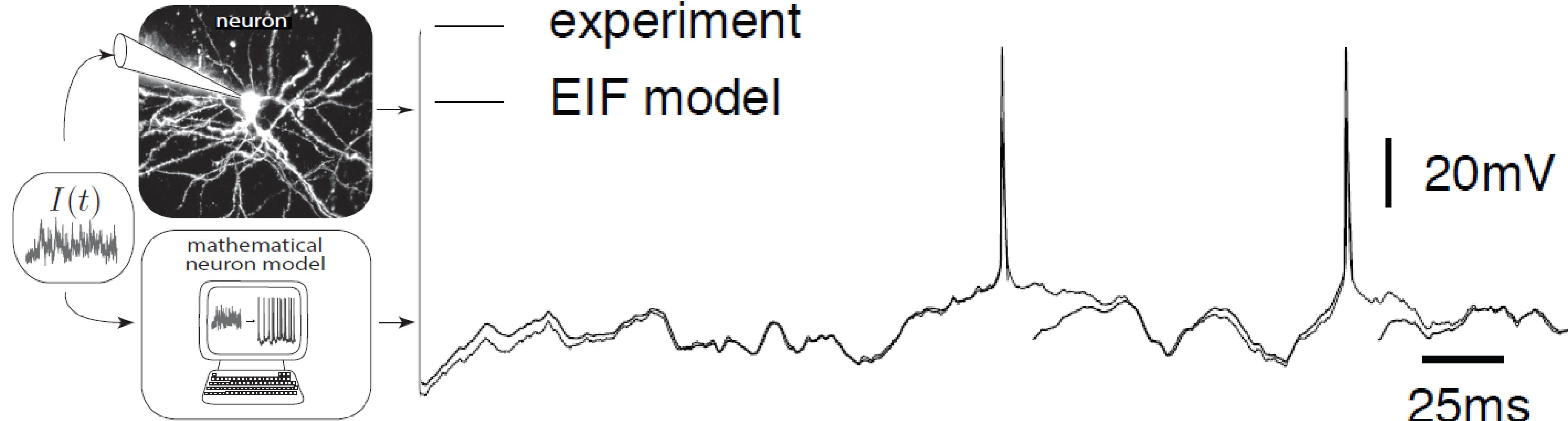
Neuronal Dynamics – 5.2 Variability in vitro



neurons are fairly reliable

*Image adapted from
Mainen&Sejnowski 1995*

REVIEW from 4.5: How good are integrate-and-fire models?



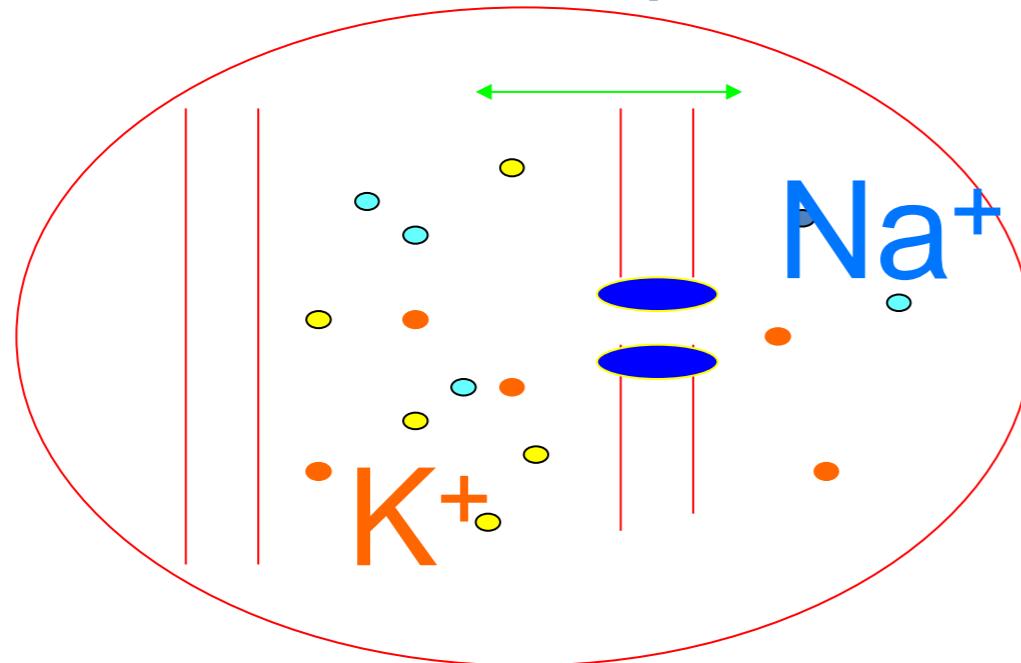
Badel et al., 2008

Aims: - predict spike initiation times
- predict subthreshold voltage

*only possible, because
neurons are fairly reliable*

Neuronal Dynamics – 5.2. Sources of Variability

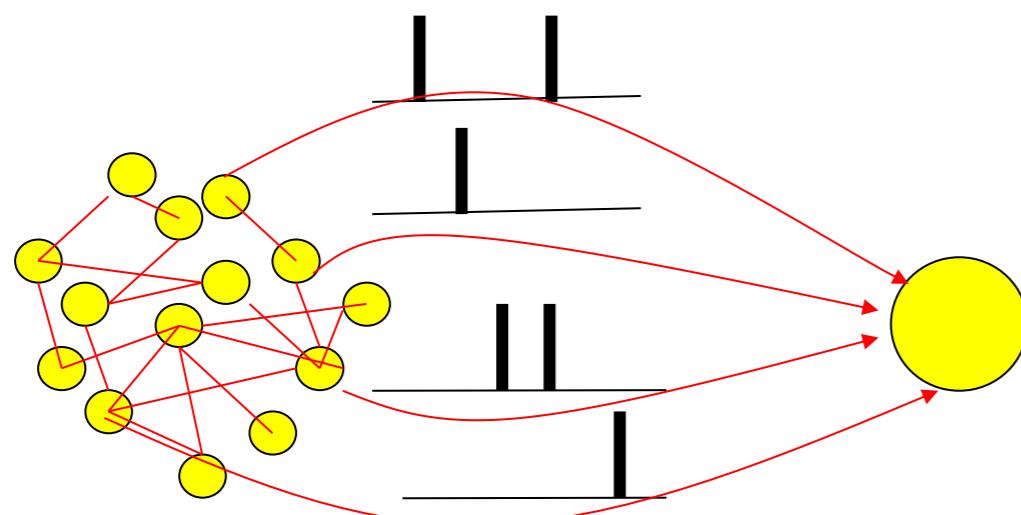
- Intrinsic noise (ion channels)



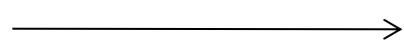
- Finite number of channels
- Finite temperature

small contribution!

- Network noise (background activity)

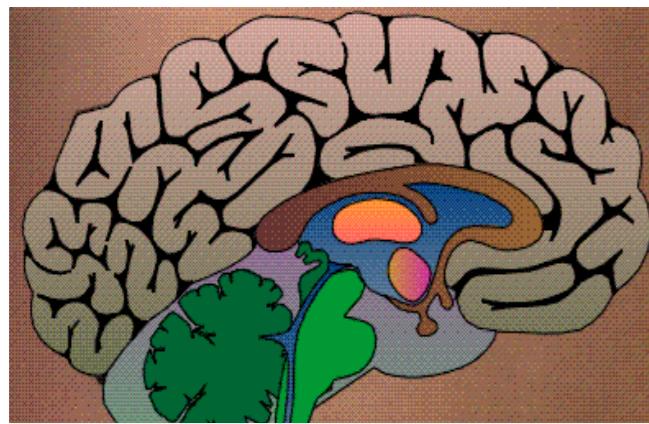


- Spike arrival from other neurons
- Beyond control of experimentalist

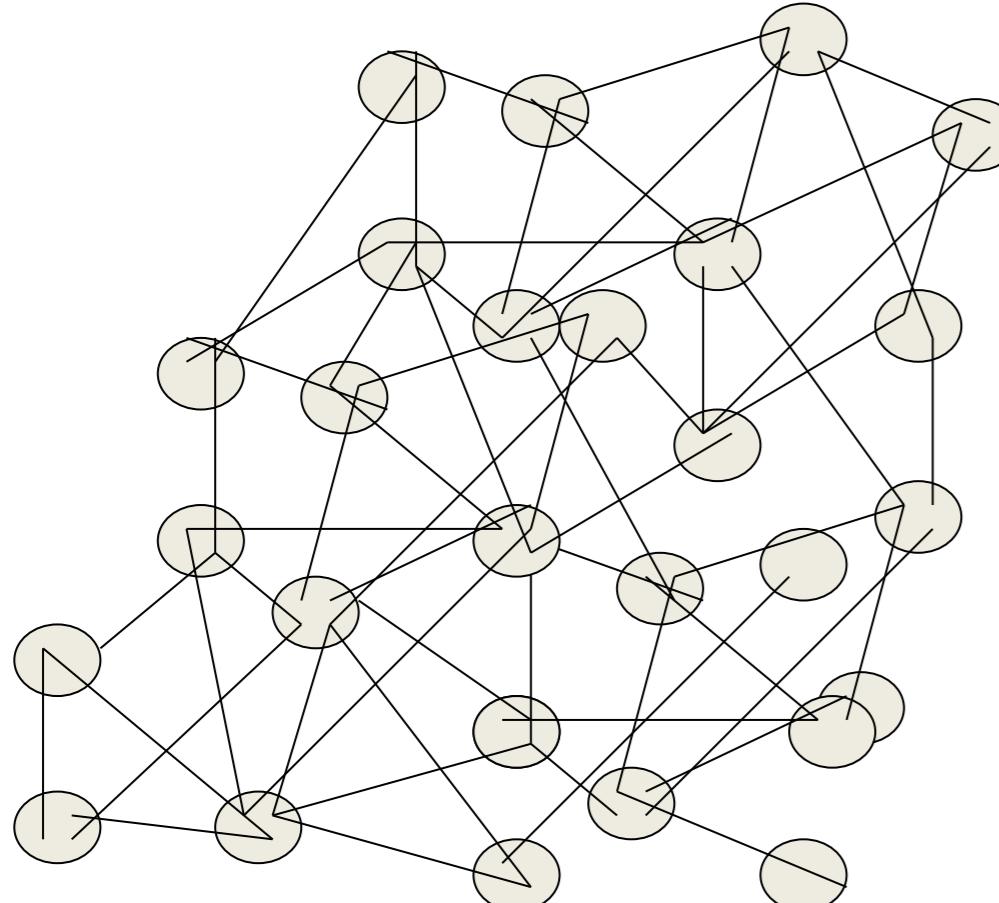


Check network noise by simulation!

Neuronal Dynamics – 5.2 Sources of Variability



Brain

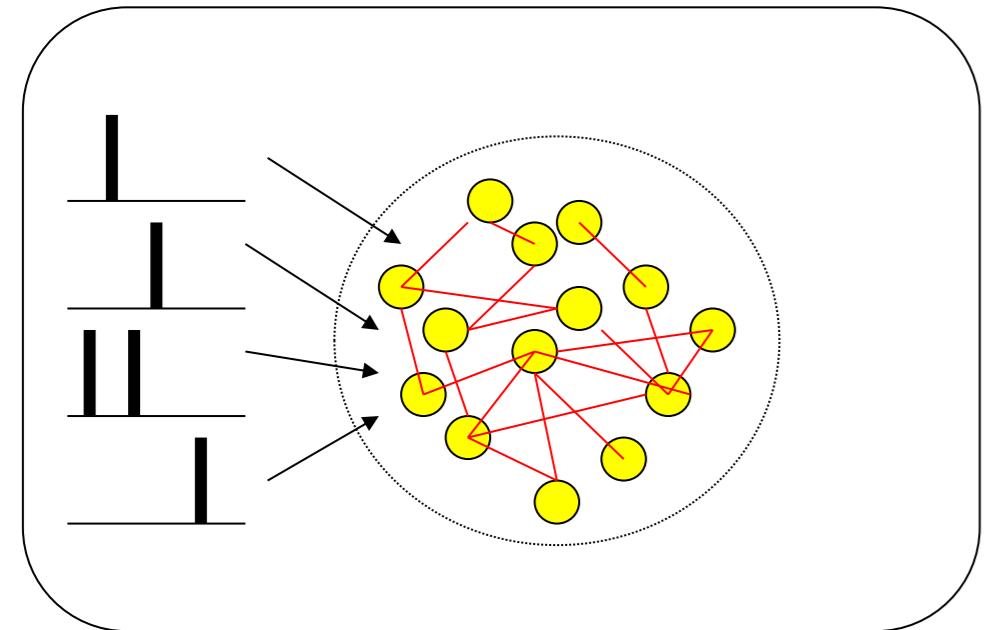


The Brain: a highly connected system

High connectivity:
systematic, organized in local populations
but **seemingly random**

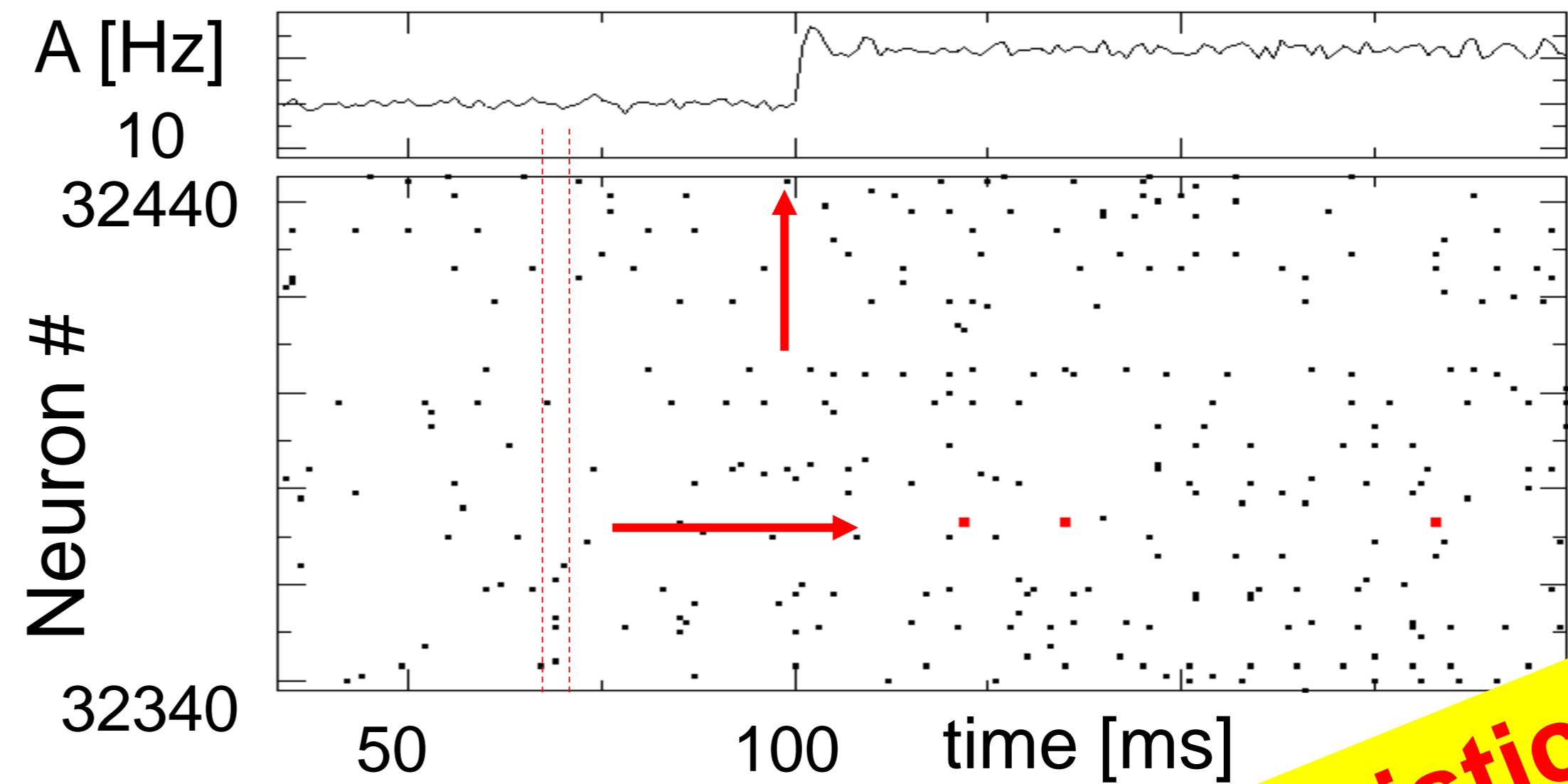
Distributed architecture
 10^{10} neurons
 10^4 connections/neurons

Random firing in a population of LIF neurons



input {
low rate
-high rate

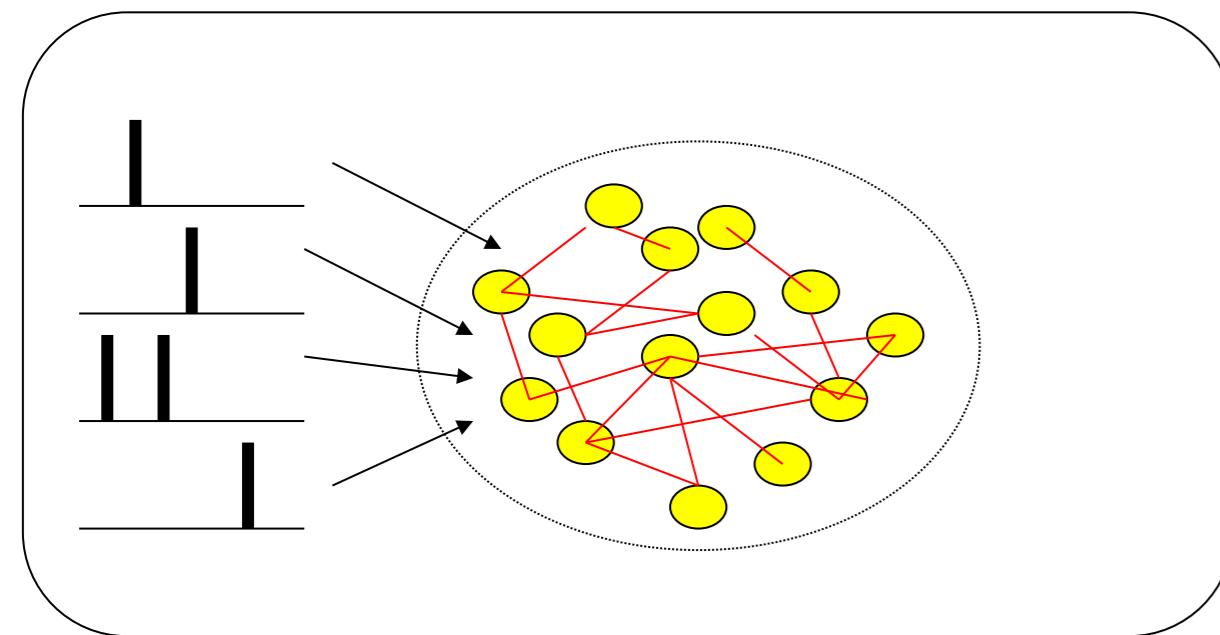
Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected



Brunel, J. Comput. Neurosc. 2000
Mayor and Gerstner, Phys. Rev E. 2000
Vogels et al., 2005

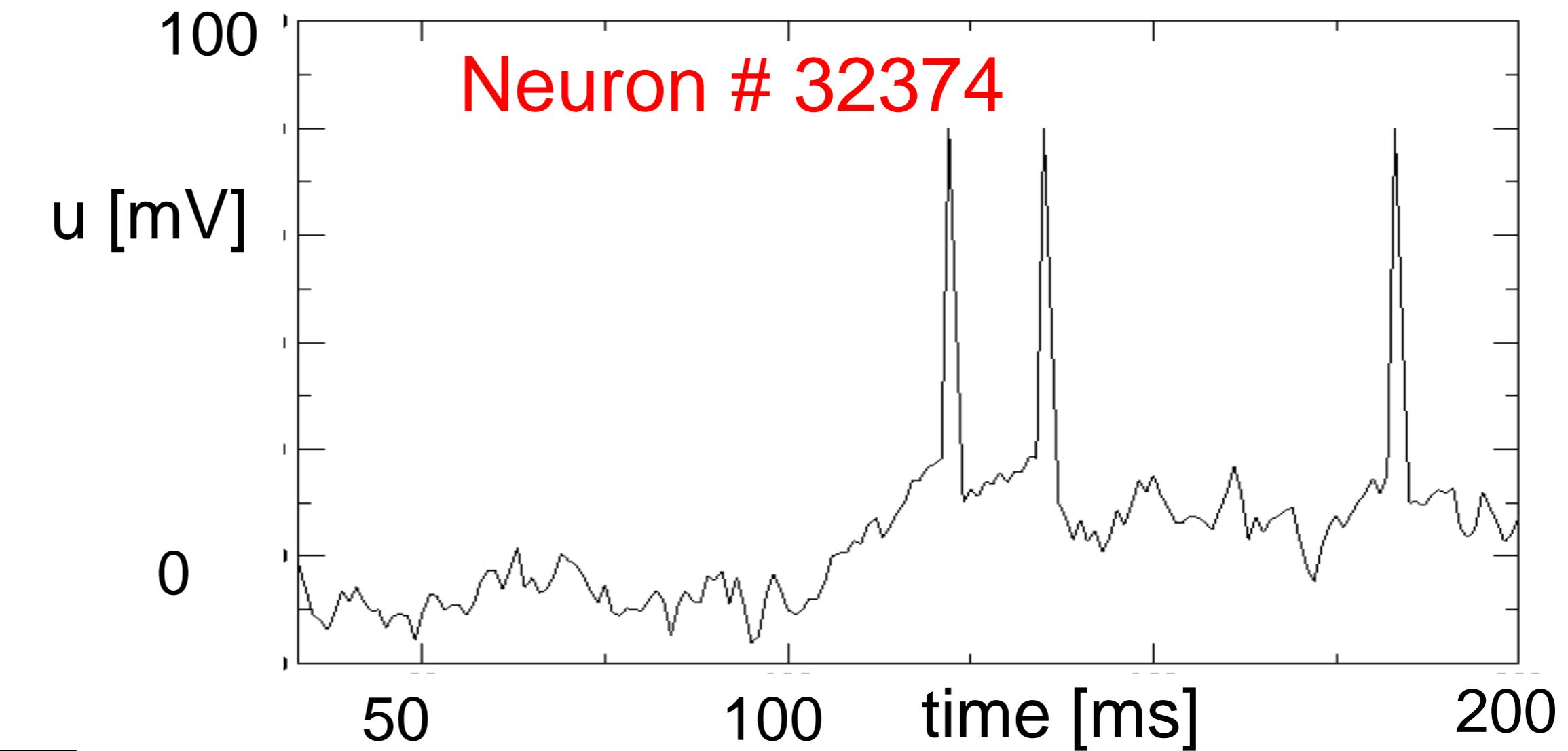
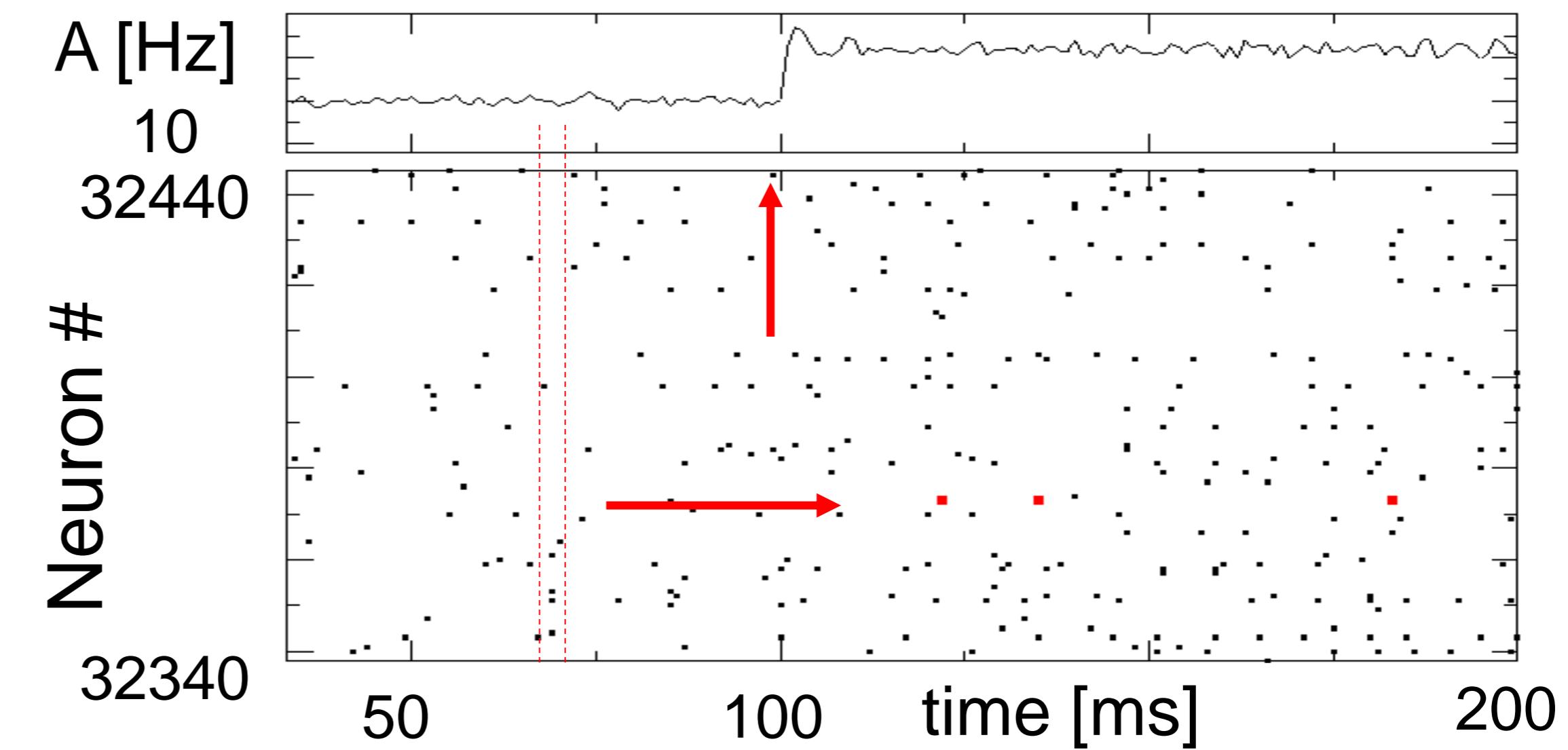
Network of deterministic
leaky integrate-and-fire:
'fluctuations'

Random firing in a population of LIF neurons



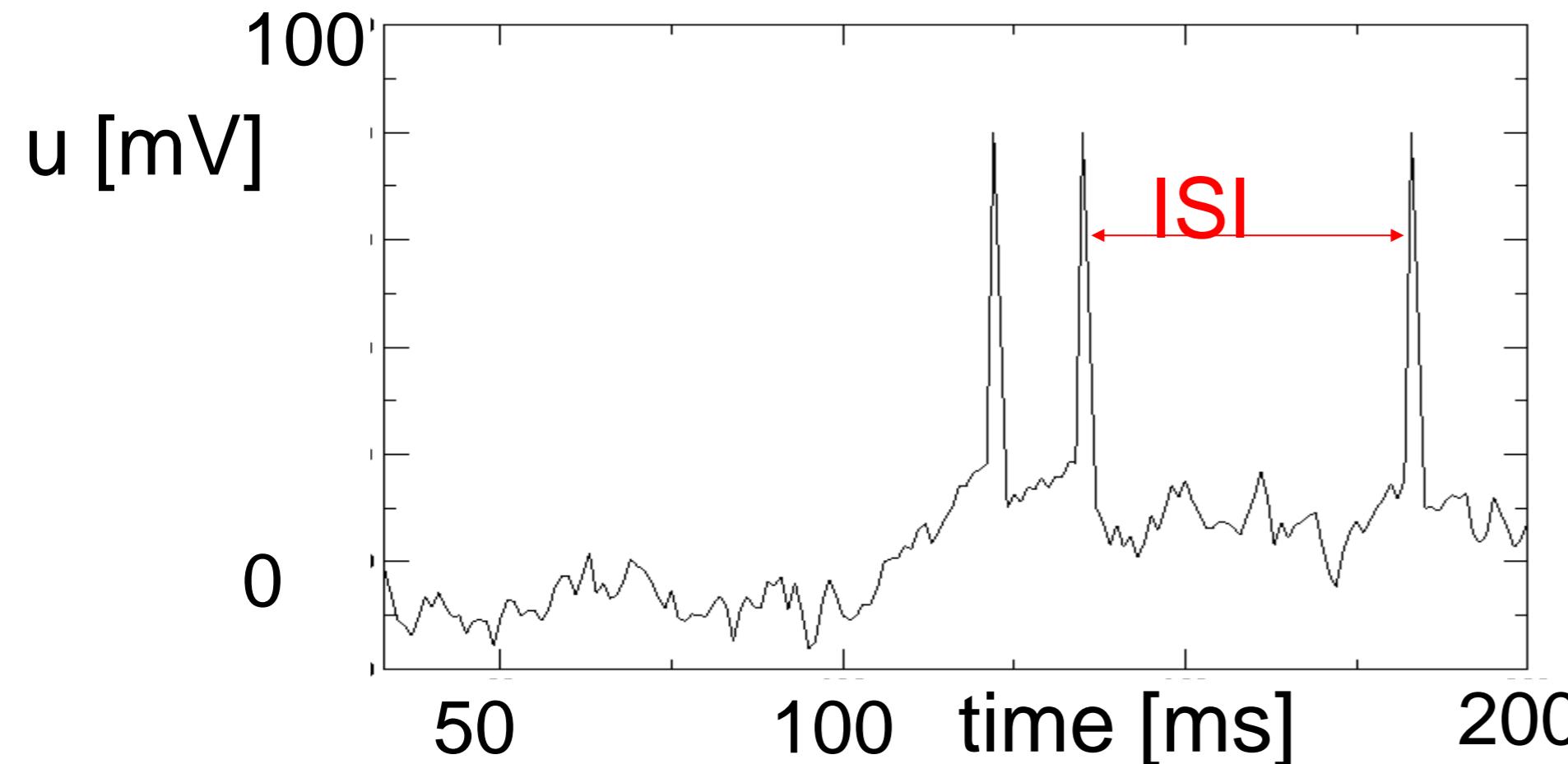
input {
low rate
- high rate

Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected

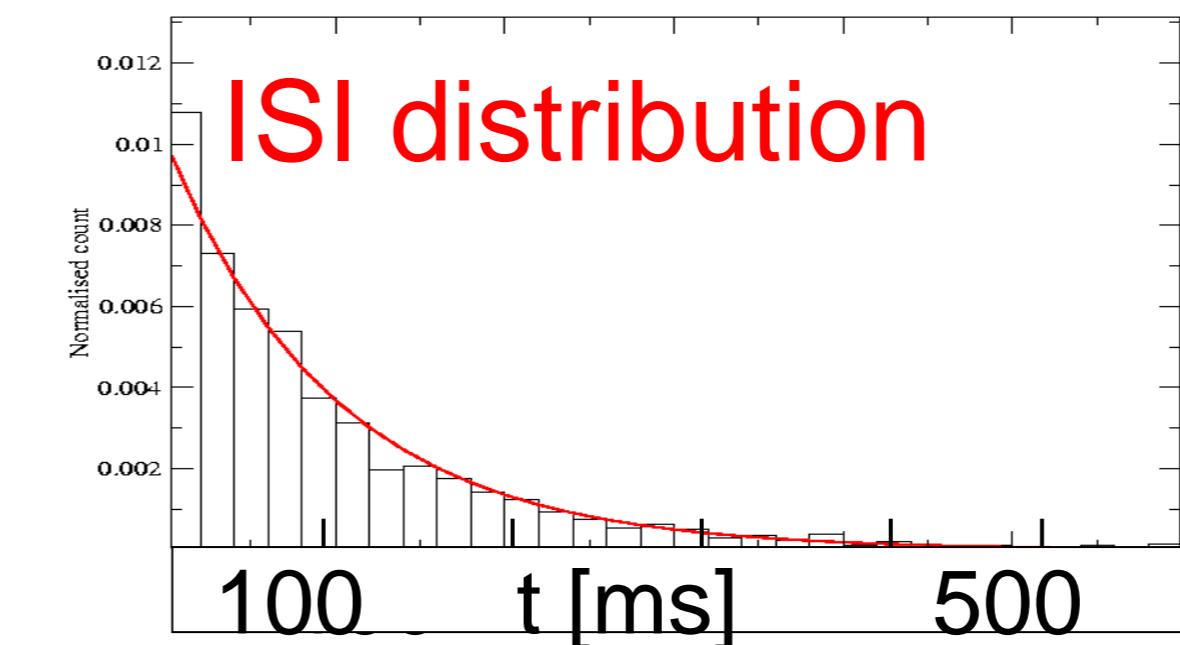


Neuronal Dynamics – 5.2. Interspike interval distribution

- Variability of interspike intervals (ISI)



here in simulations,
but also *in vivo*

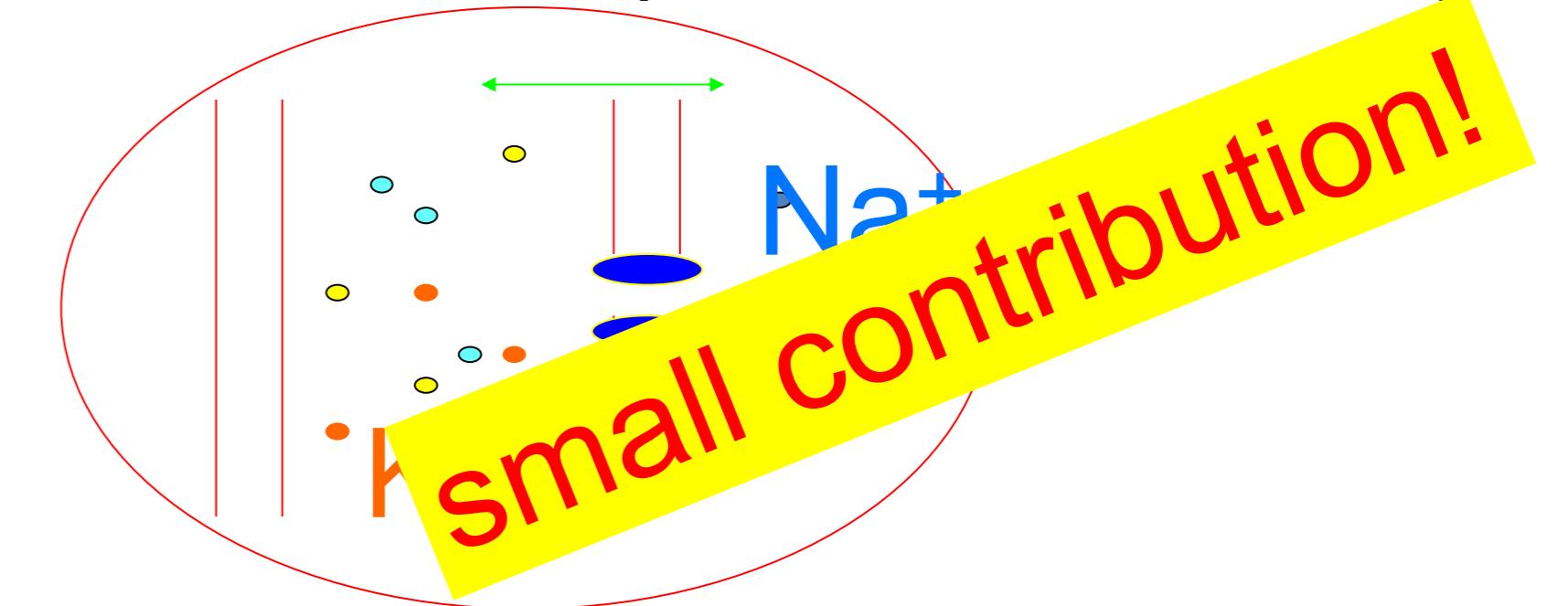


Variability of spike trains:
broad ISI distribution

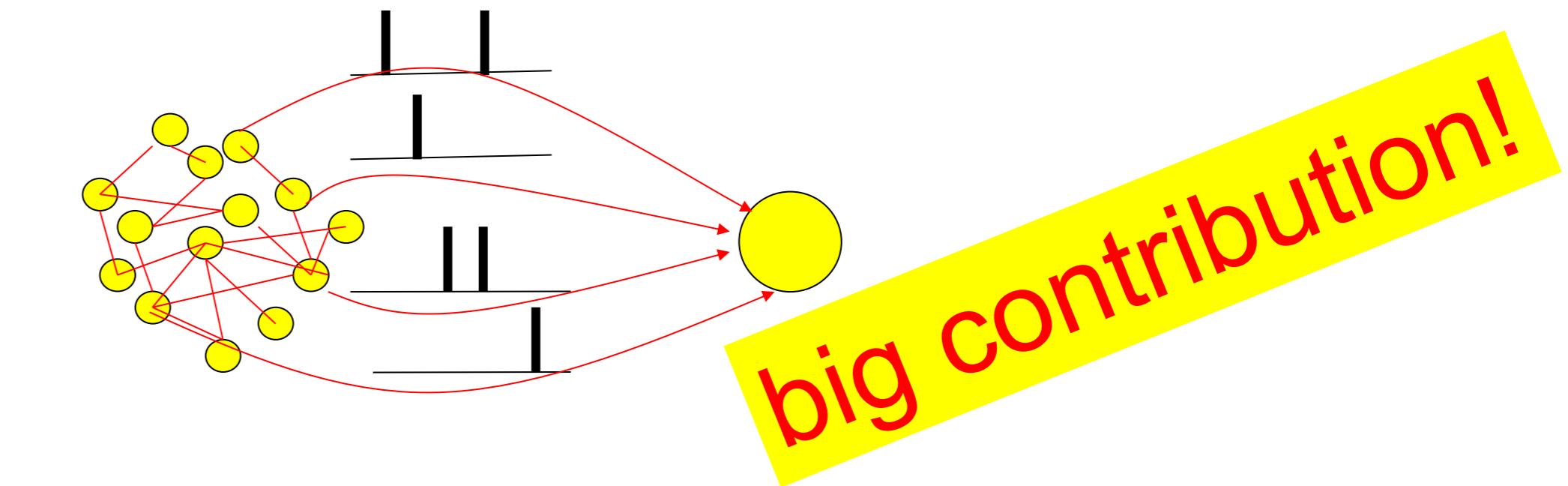
Brunel,
J. Comput. Neurosc. 2000
Mayor and Gerstner,
Phys. Rev E. 2005
Vogels and Abbott,
J. Neuroscience, 2005

Neuronal Dynamics – 5.2. Sources of Variability

- Intrinsic noise (ion channels)



- Network noise



Neuronal Dynamics – Quiz 5.1.

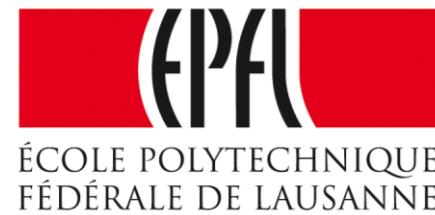
A- Spike timing in vitro and in vivo

- [] Reliability of spike timing can be assessed by repeating several times the same stimulus
- [] Spike timing in vitro is more reliable under injection of constant current than with fluctuating current
- [] Spike timing in vitro is less reliable under injection of constant current than with fluctuating current
- [] Spike timing in vitro is more reliable than spike timing in vivo
- [] Nothing is known about spike timing in humans in vivo

B – Interspike Interval Distribution (ISI)

- [] An isolated deterministic leaky integrate-and-fire neuron driven by a constant current can have a broad ISI
- [] A deterministic leaky integrate-and-fire neuron embedded into a randomly connected network of integrate-and-fire neurons can have a broad ISI
- [] An isolated deterministic Hodgkin-Huxley model as in week 2 driven by a constant current can have a broad ISI

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

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EPFL, Lausanne, Switzerland

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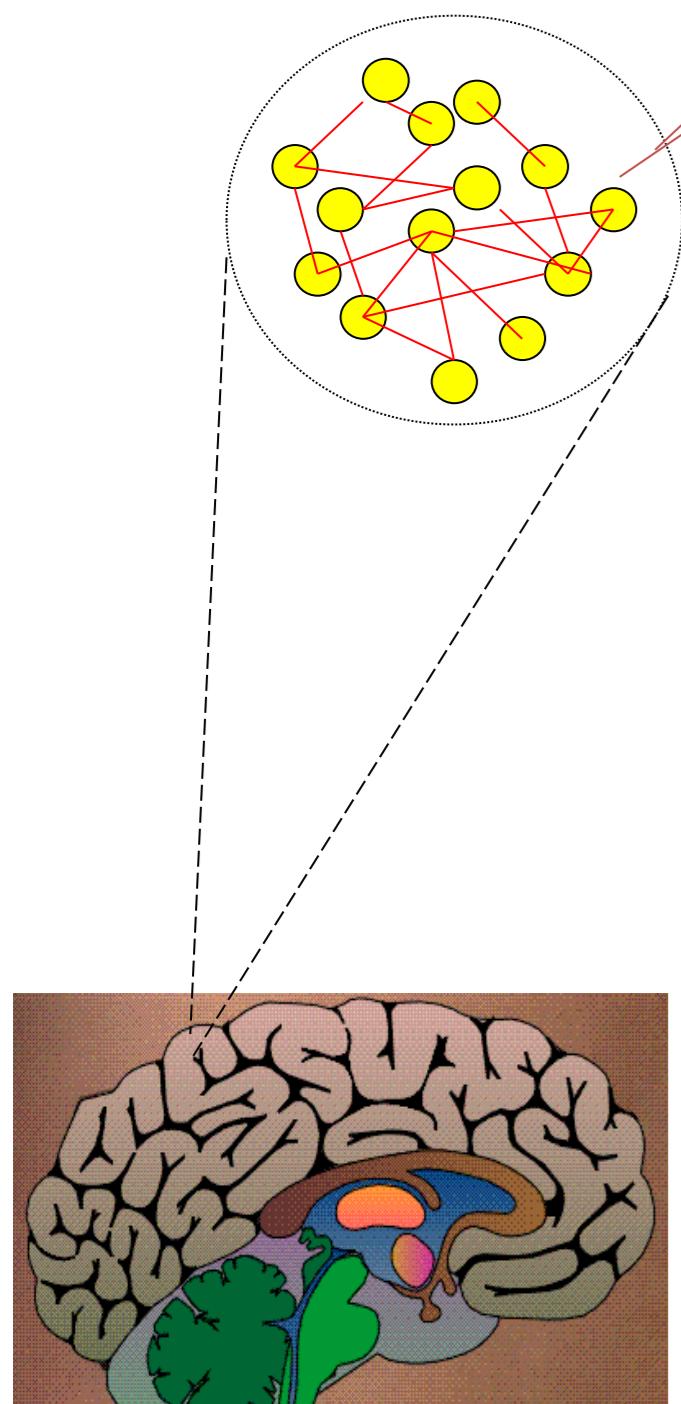
Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

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

Neuronal Dynamics – 5.3. Rate codes: spike count

Variability of spike timing

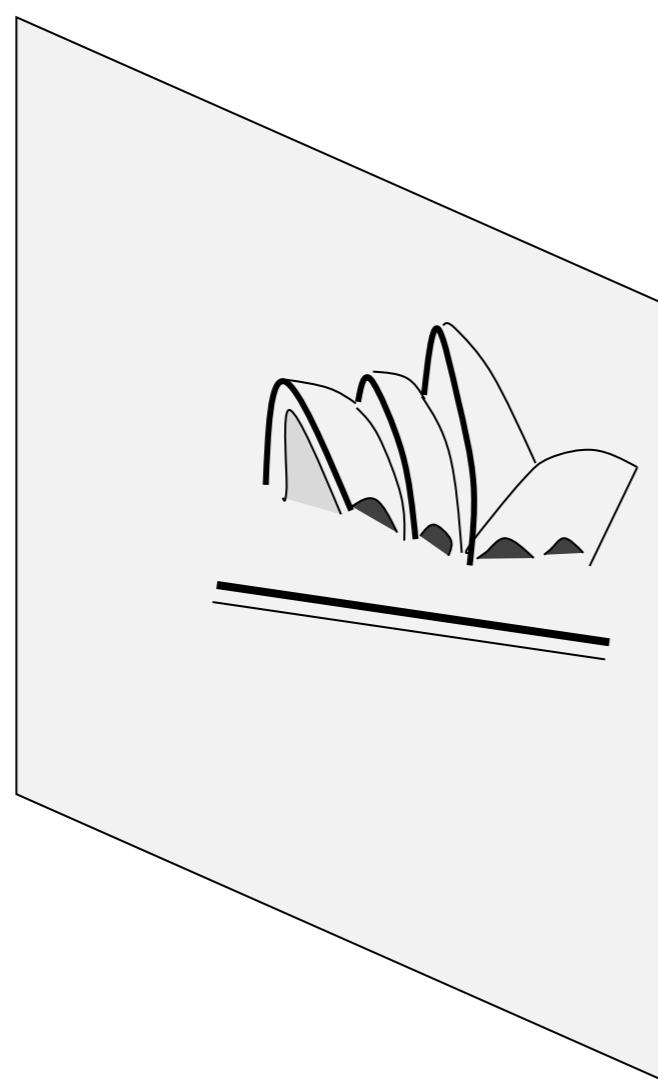


rate as a (normalized) spike count:

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

single neuron/single trial:
temporal average

Brain



stim

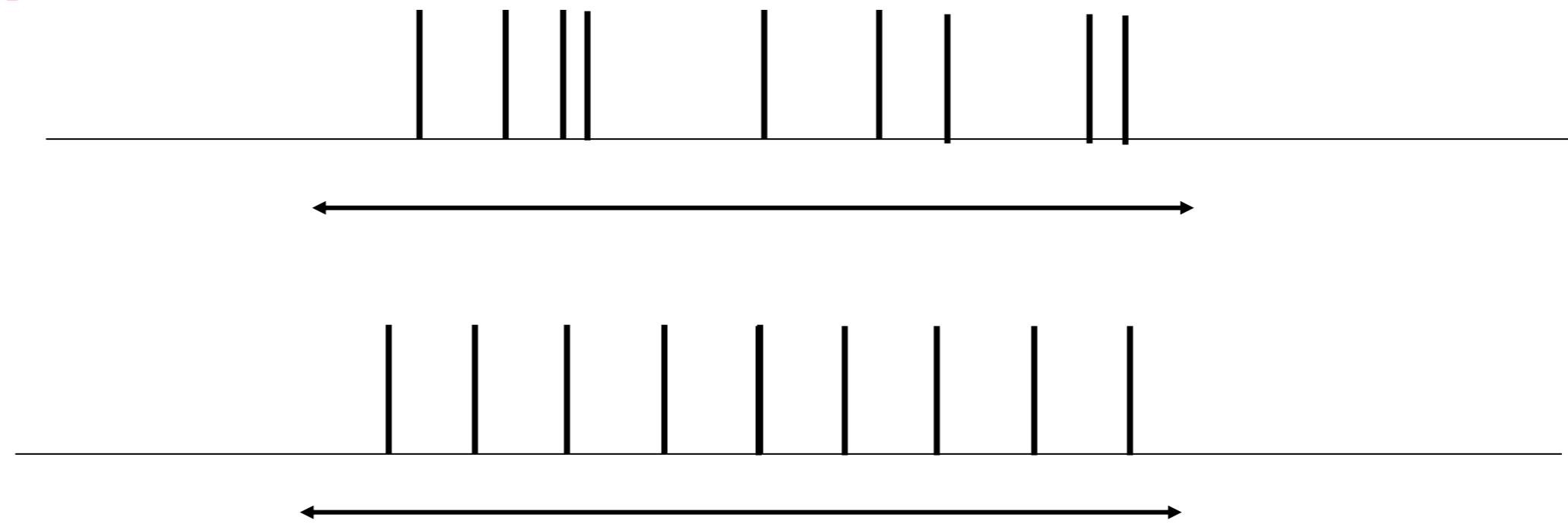
$T=1s$

trial 1

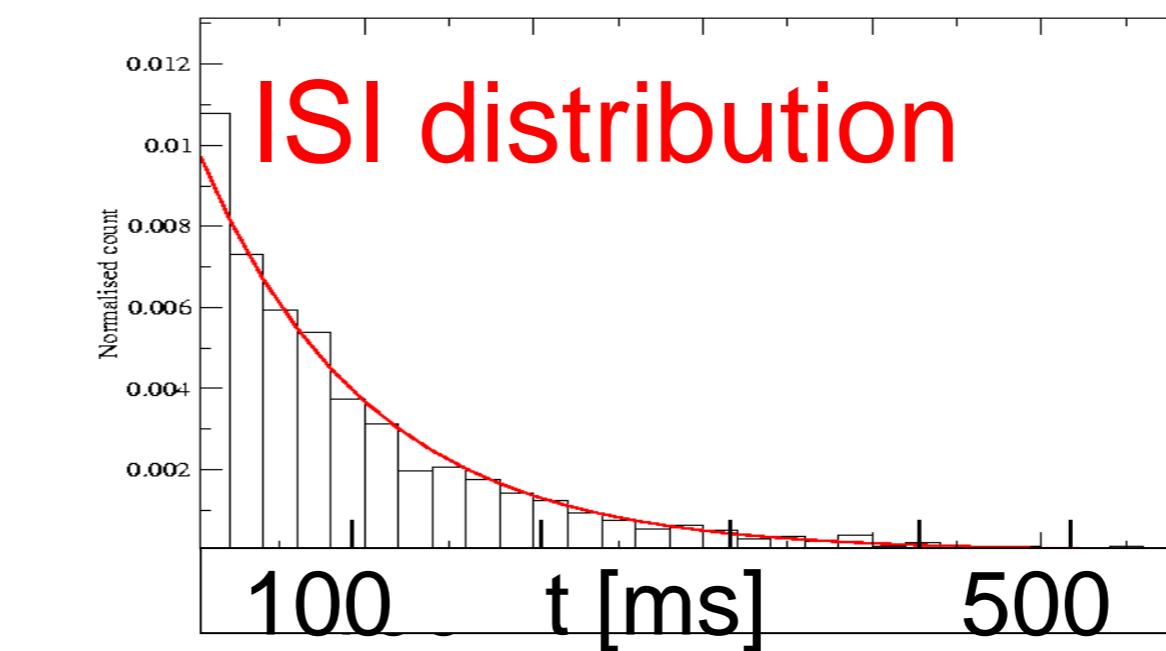
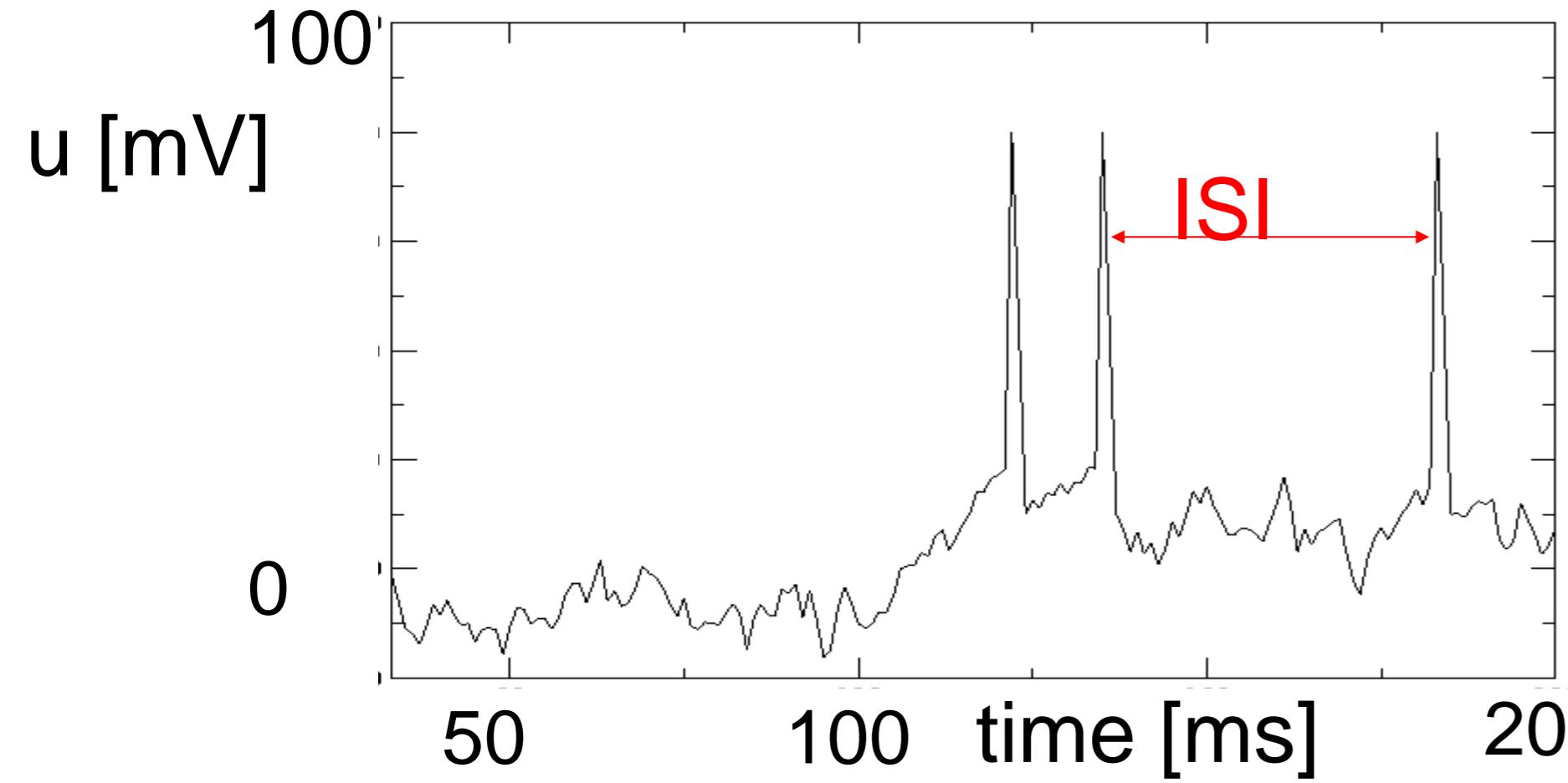
Neuronal Dynamics – 5.3. Rate codes: spike count

single neuron/single trial:
temporal average

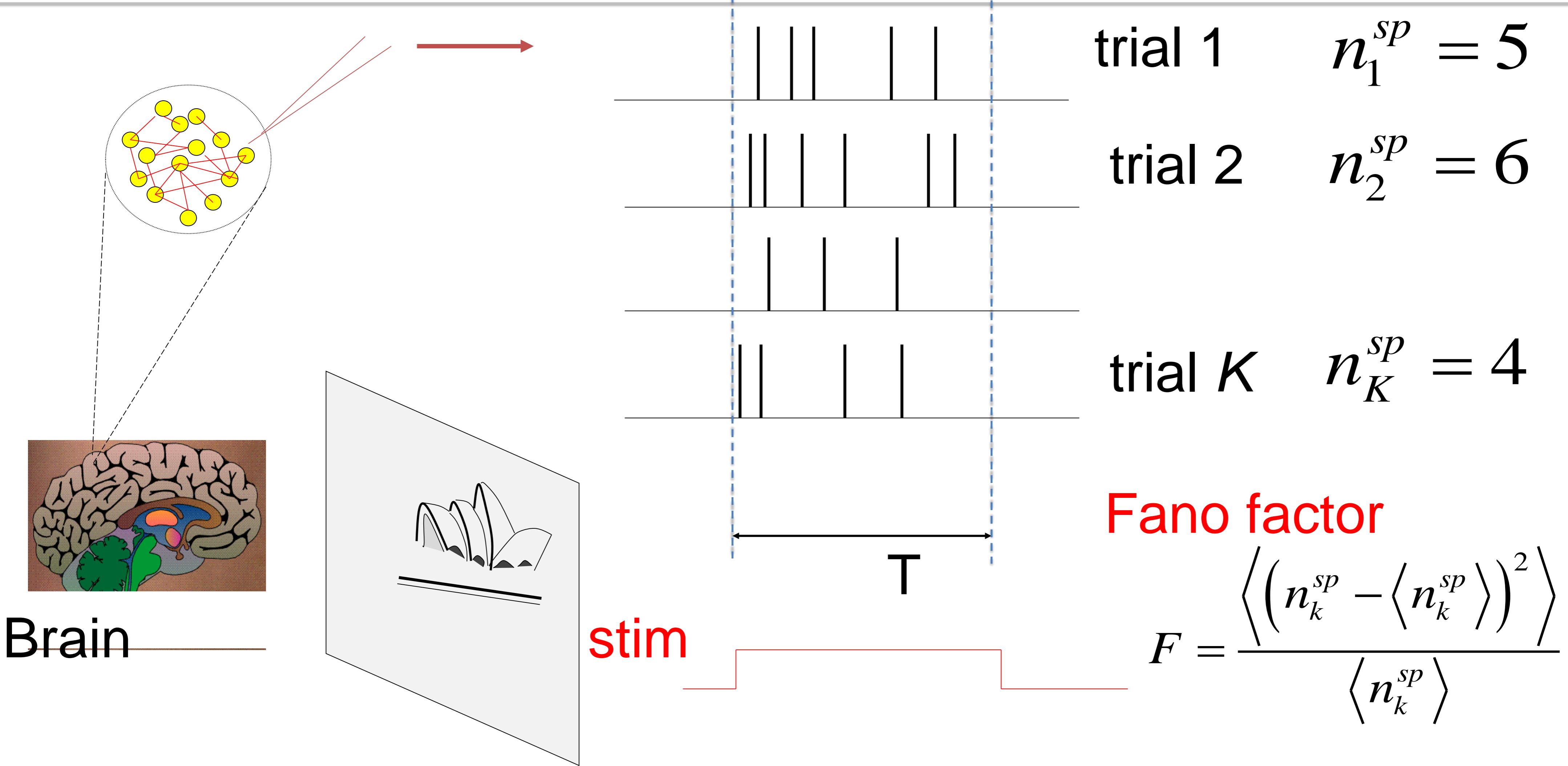
$$\nu(t) = \frac{n^{sp}}{T}$$



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



Neuronal Dynamics – 5.3. Spike count: FANO factor



Neuronal Dynamics – 5.3. Three definitions of Rate Codes

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

3 definitions

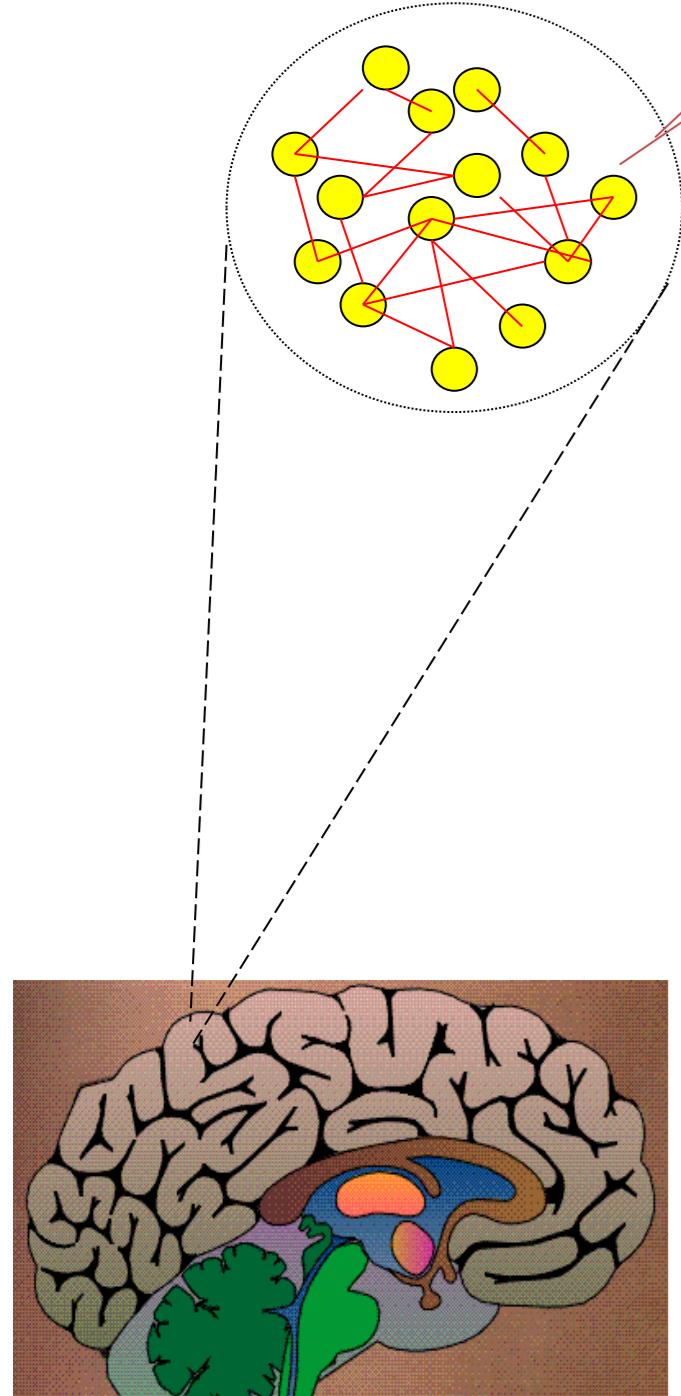
- ✓ - Temporal averaging

Problem: slow!!!

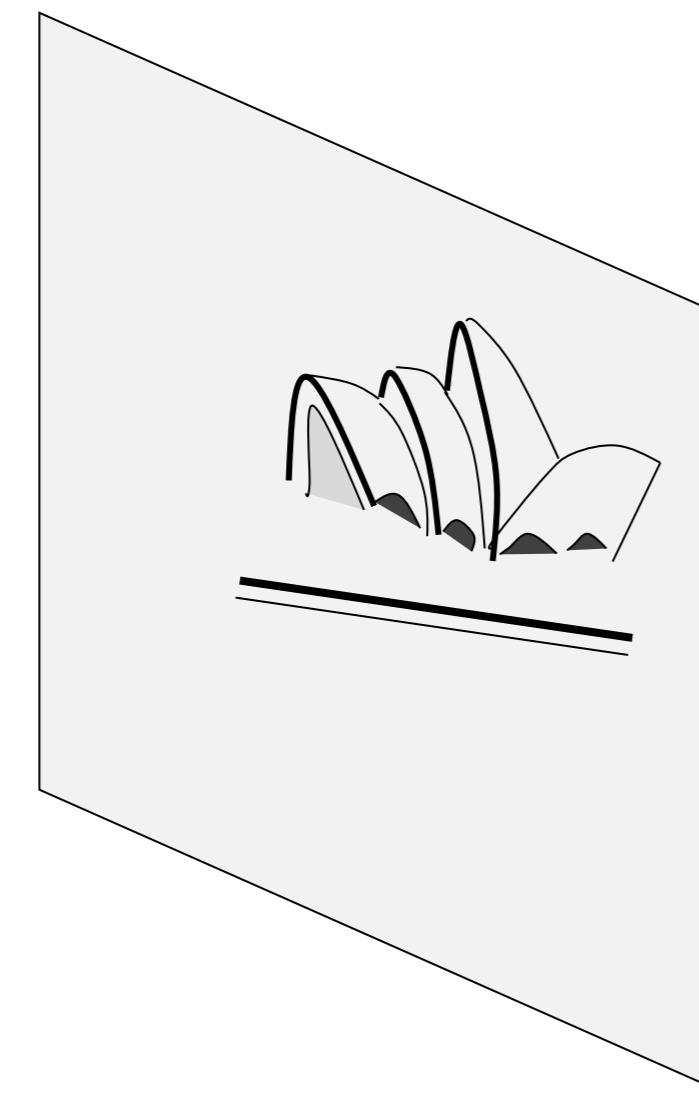
- Averaging across repetitions
- Population averaging

Neuronal Dynamics – 5.3. Rate codes: PSTH

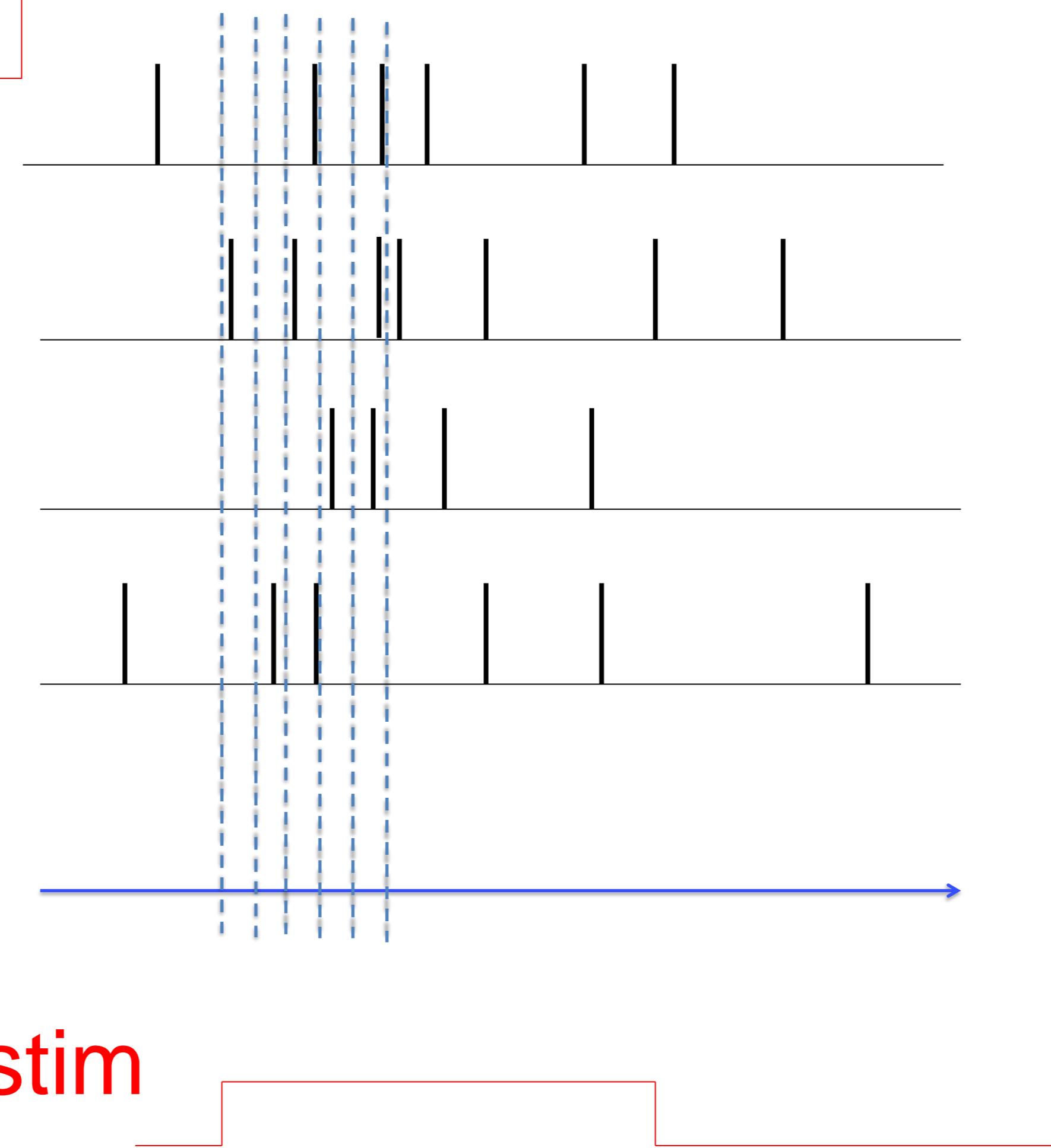
Variability of spike timing



Brain



stim



trial 1

trial 2

trial K

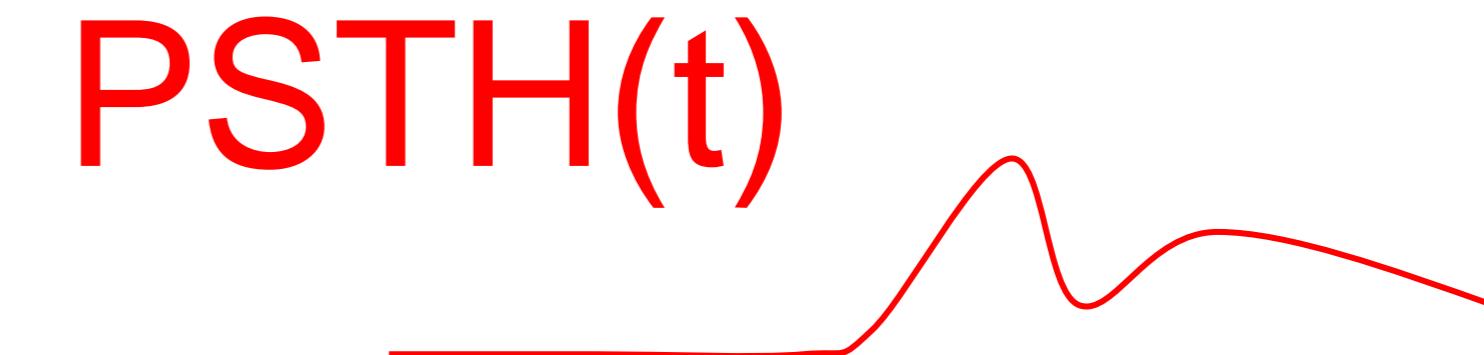
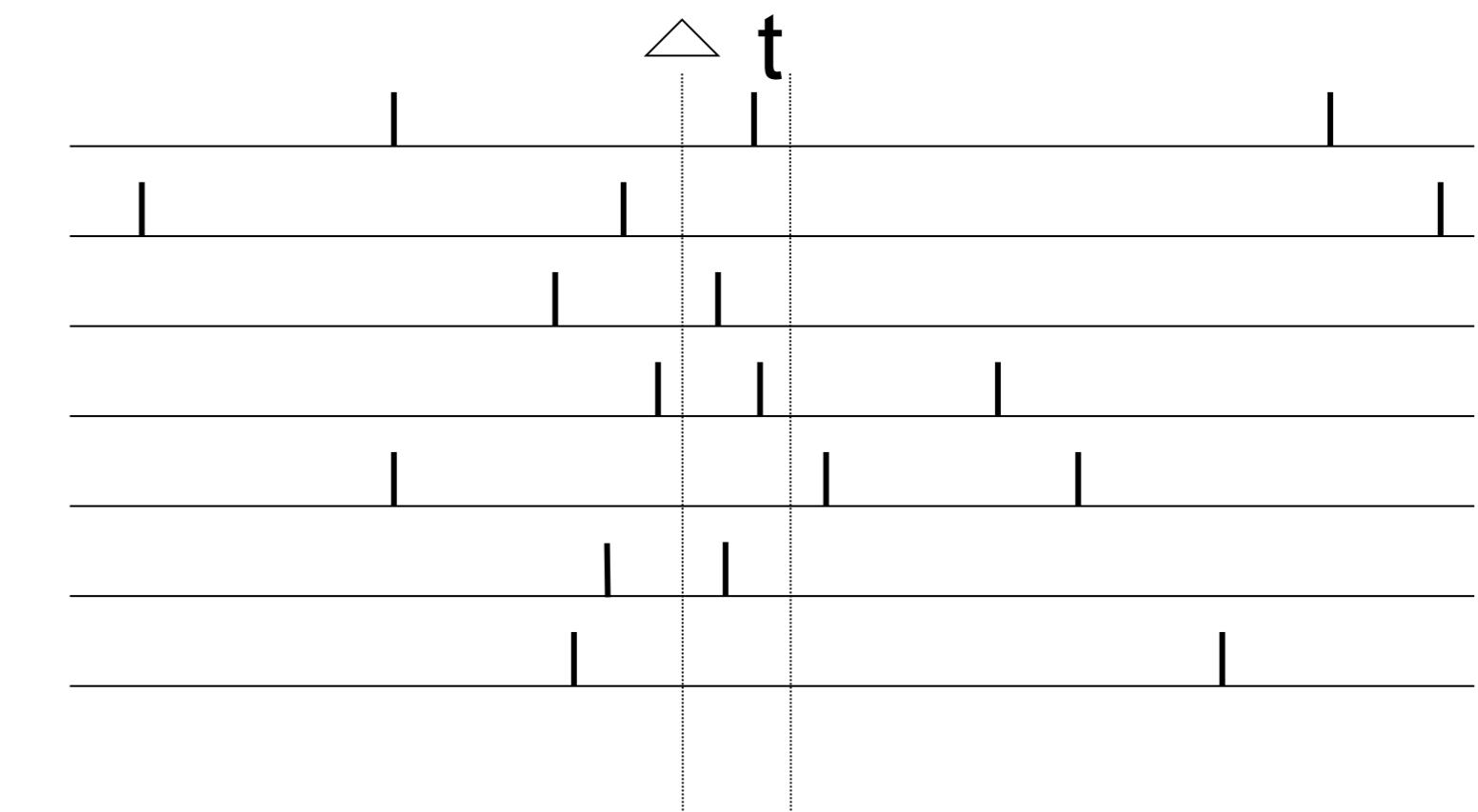
Neuronal Dynamics – 5.3. Rate codes: PSTH

Averaging across repetitions

single neuron/many trials:
average across trials

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

K repetitions



Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

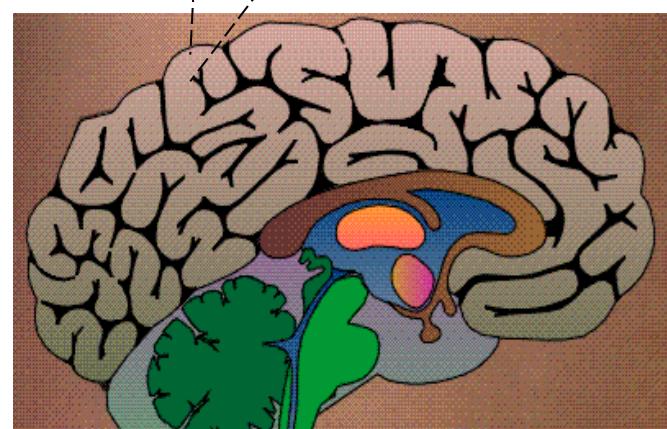
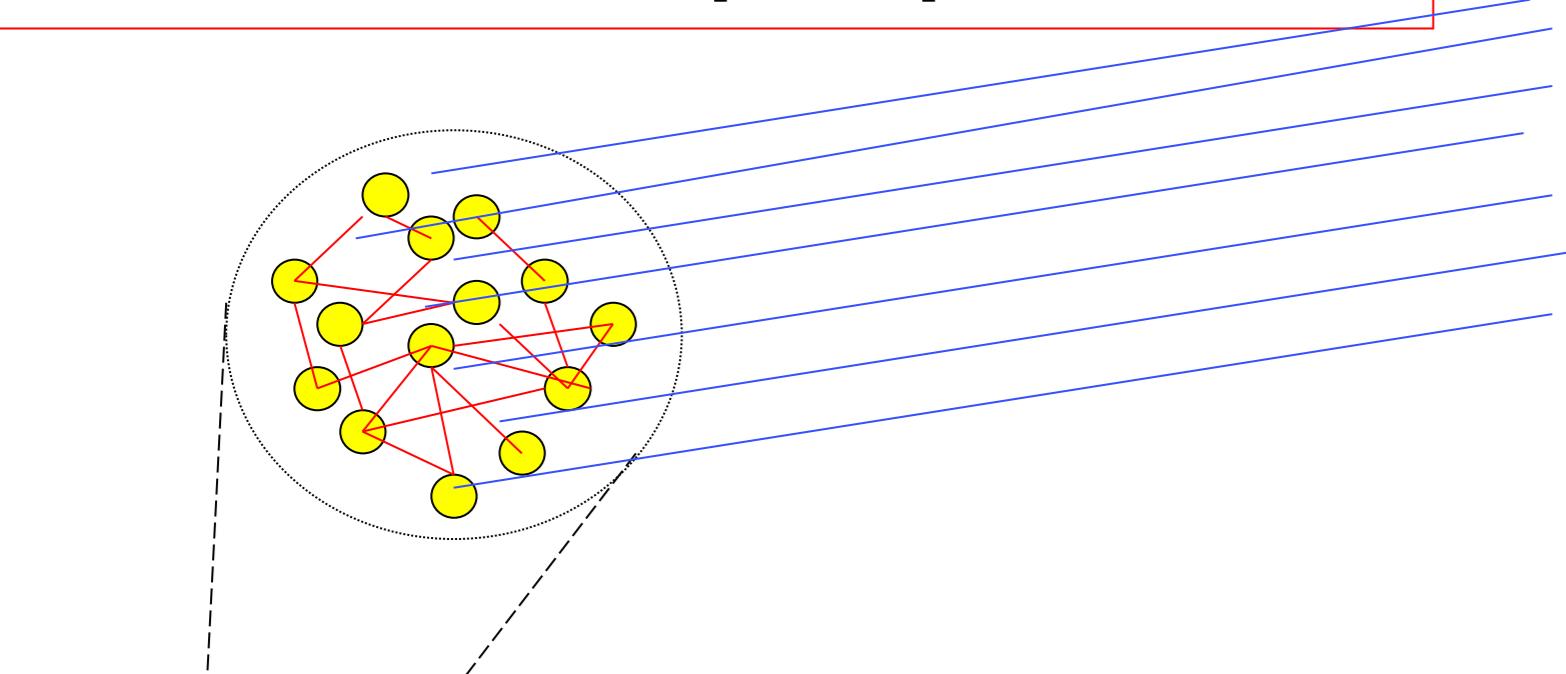
- ✓ -Temporal averaging
- ✓ - Averaging across repetitions

Problem: not useful
for animal!!!

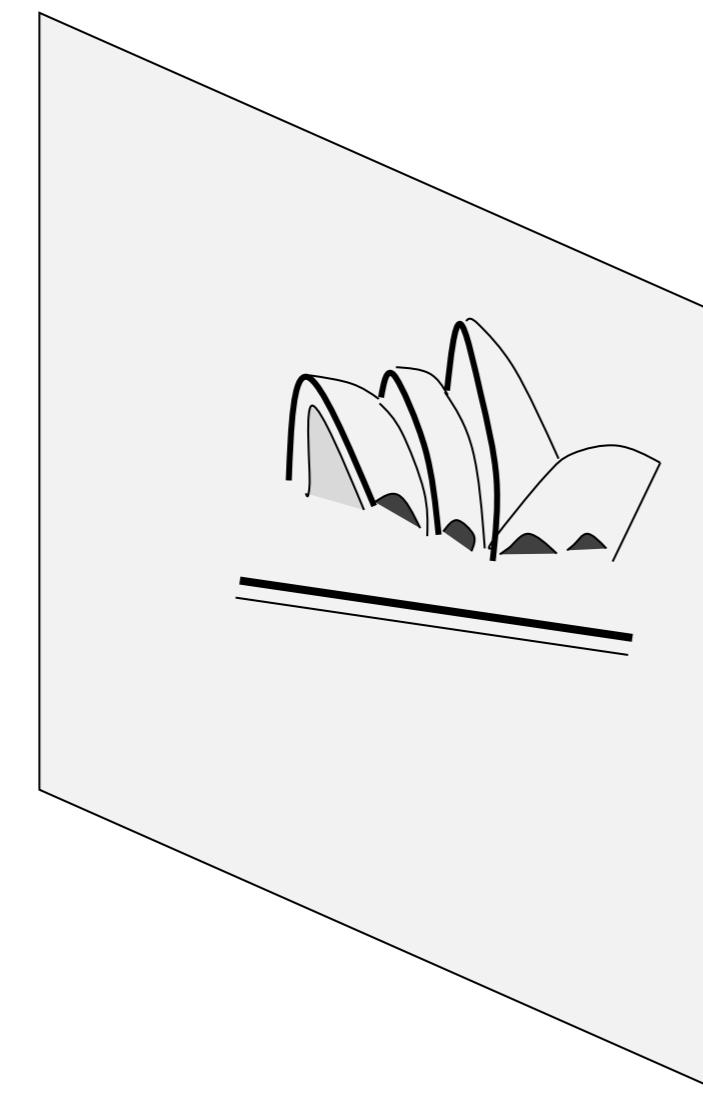
- Population averaging

Neuronal Dynamics – 5.3. Rate codes: population activity

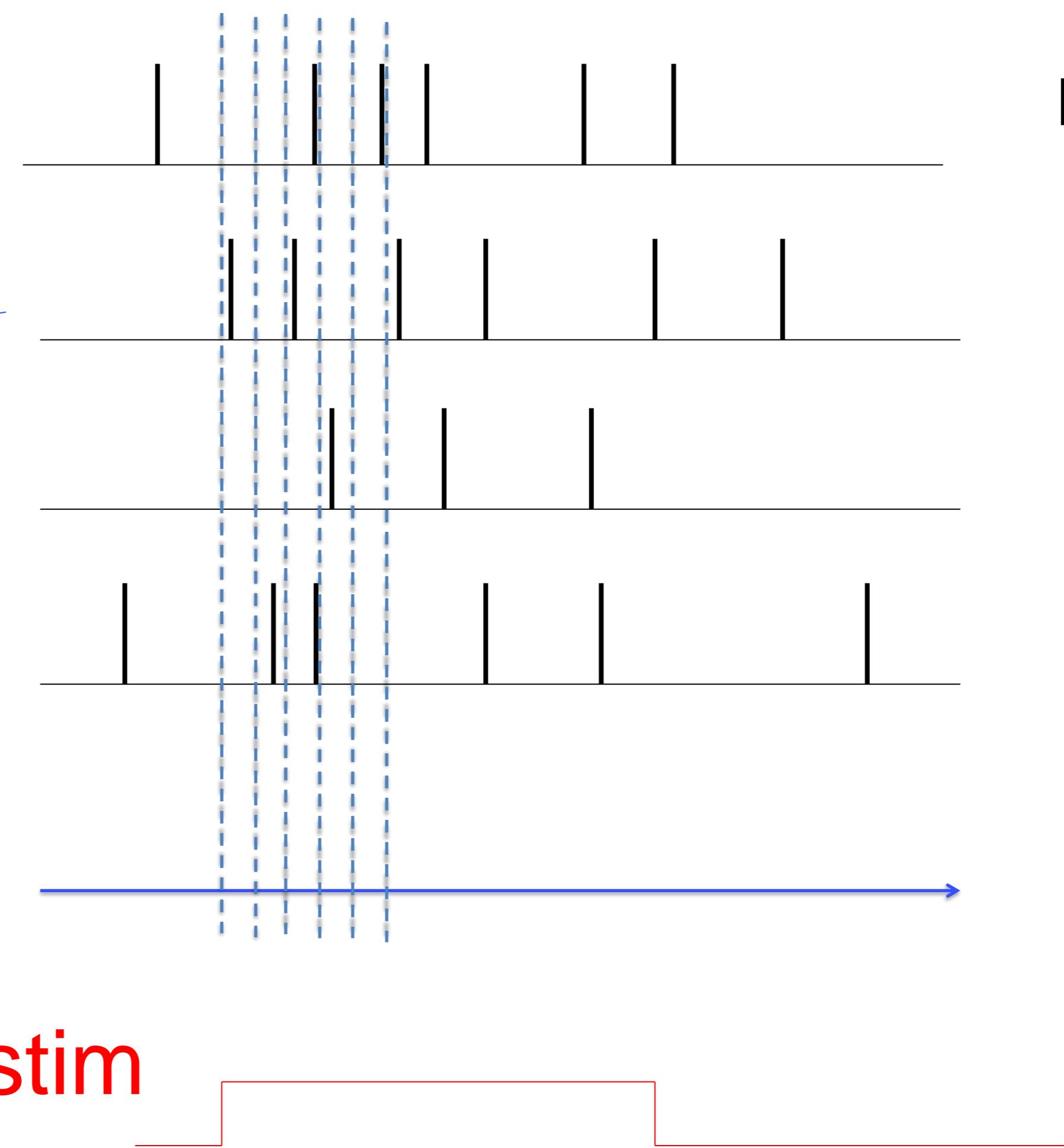
population of neurons
with similar properties



Brain



stim



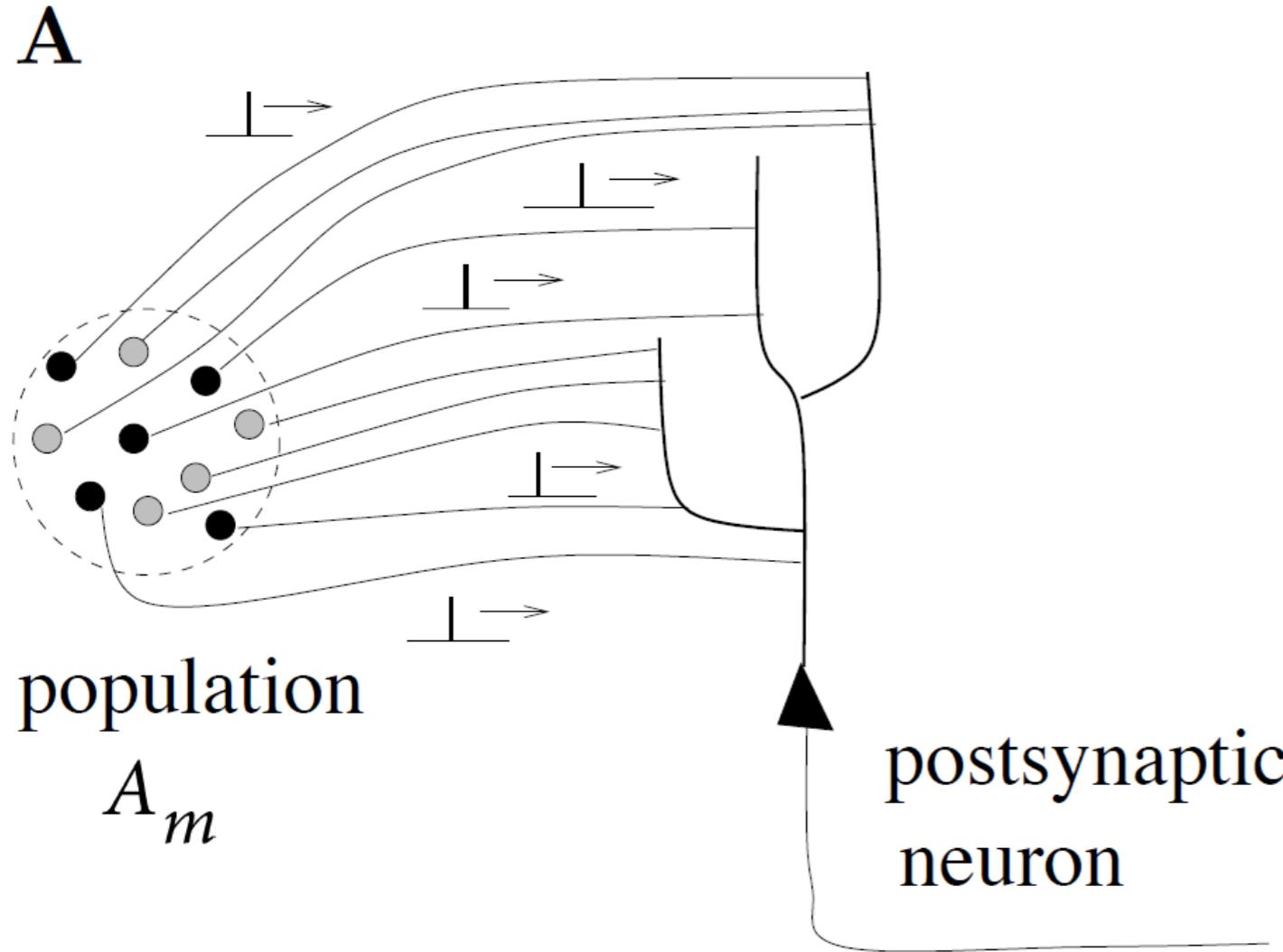
neuron 1

neuron 2

Neuron K

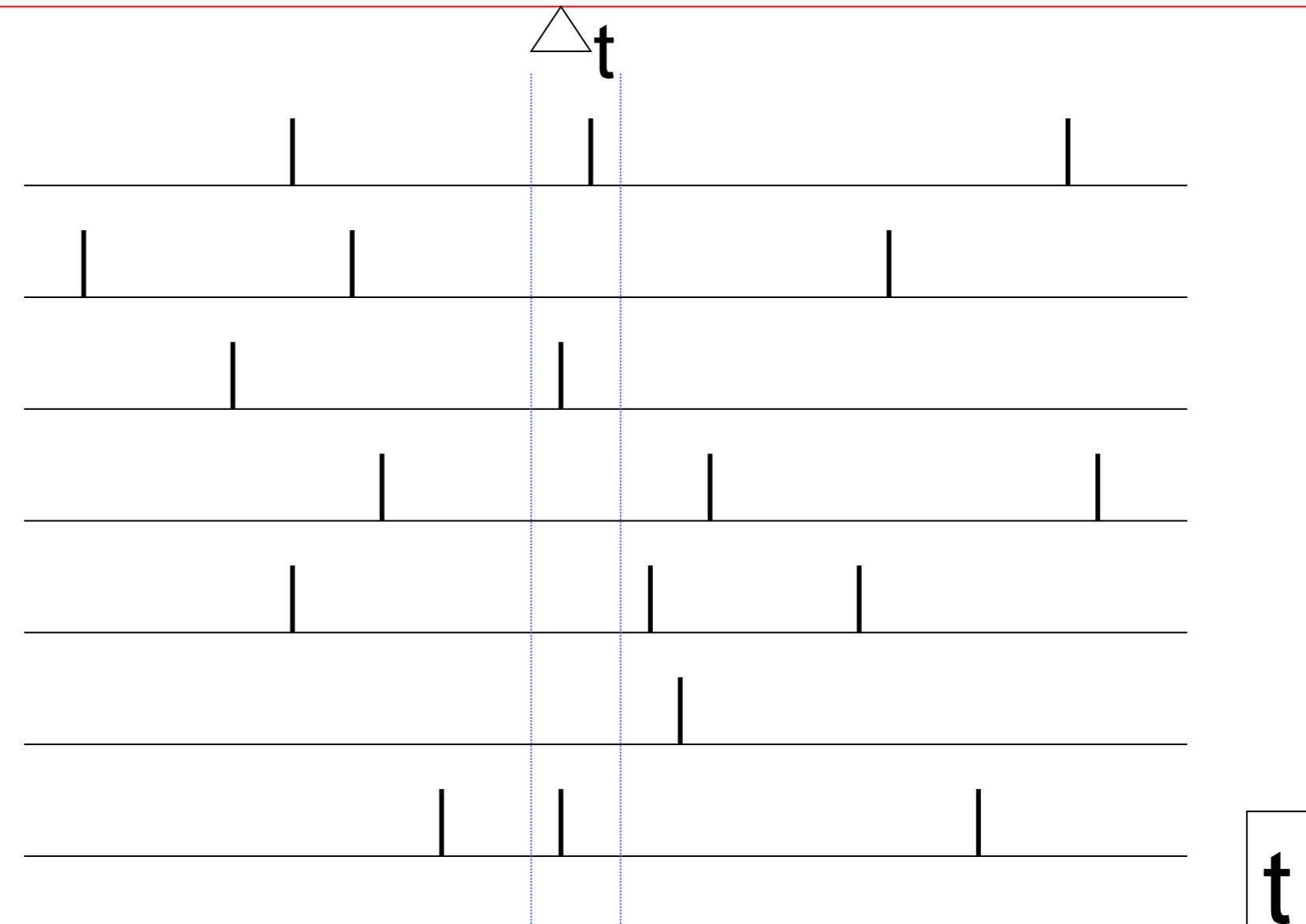
Neuronal Dynamics – 5.3. Rate codes: population activity

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

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.

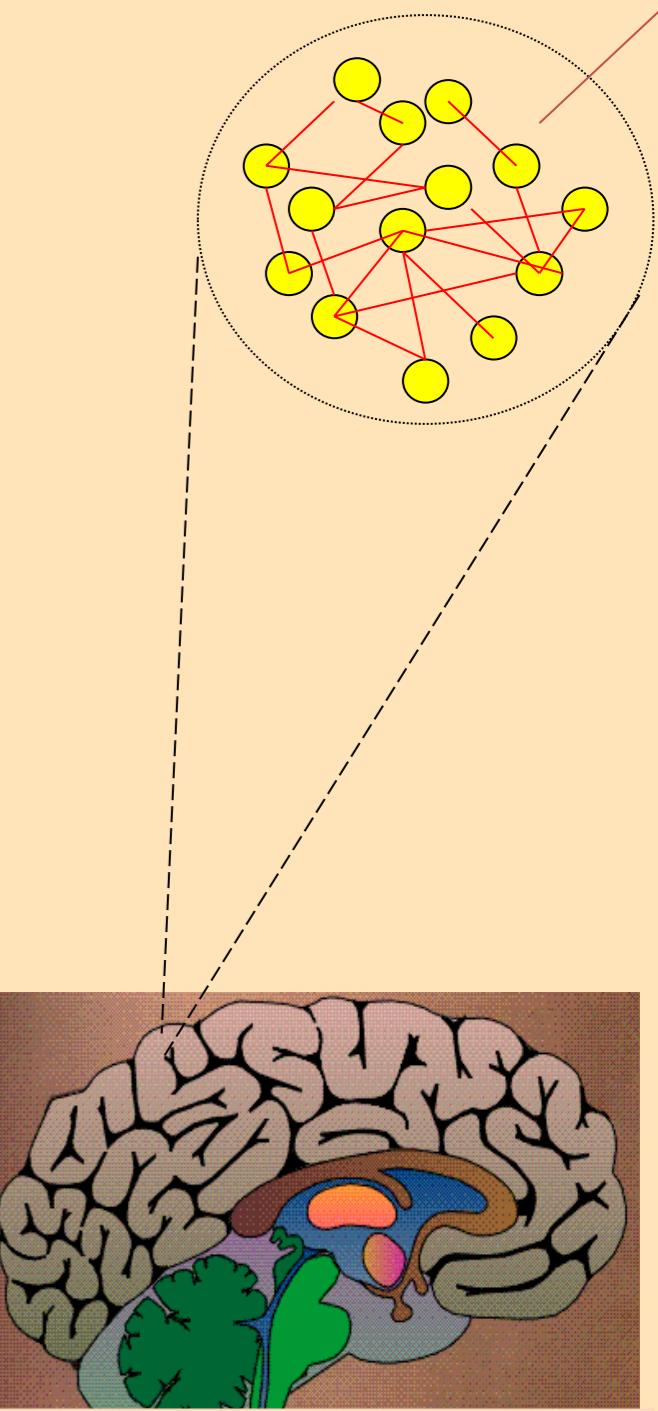
Experimentalist A makes a measurement in a single trial on all 500 neurons using a multi-electrode array, during a period of sensory stimulation.

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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↓ 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

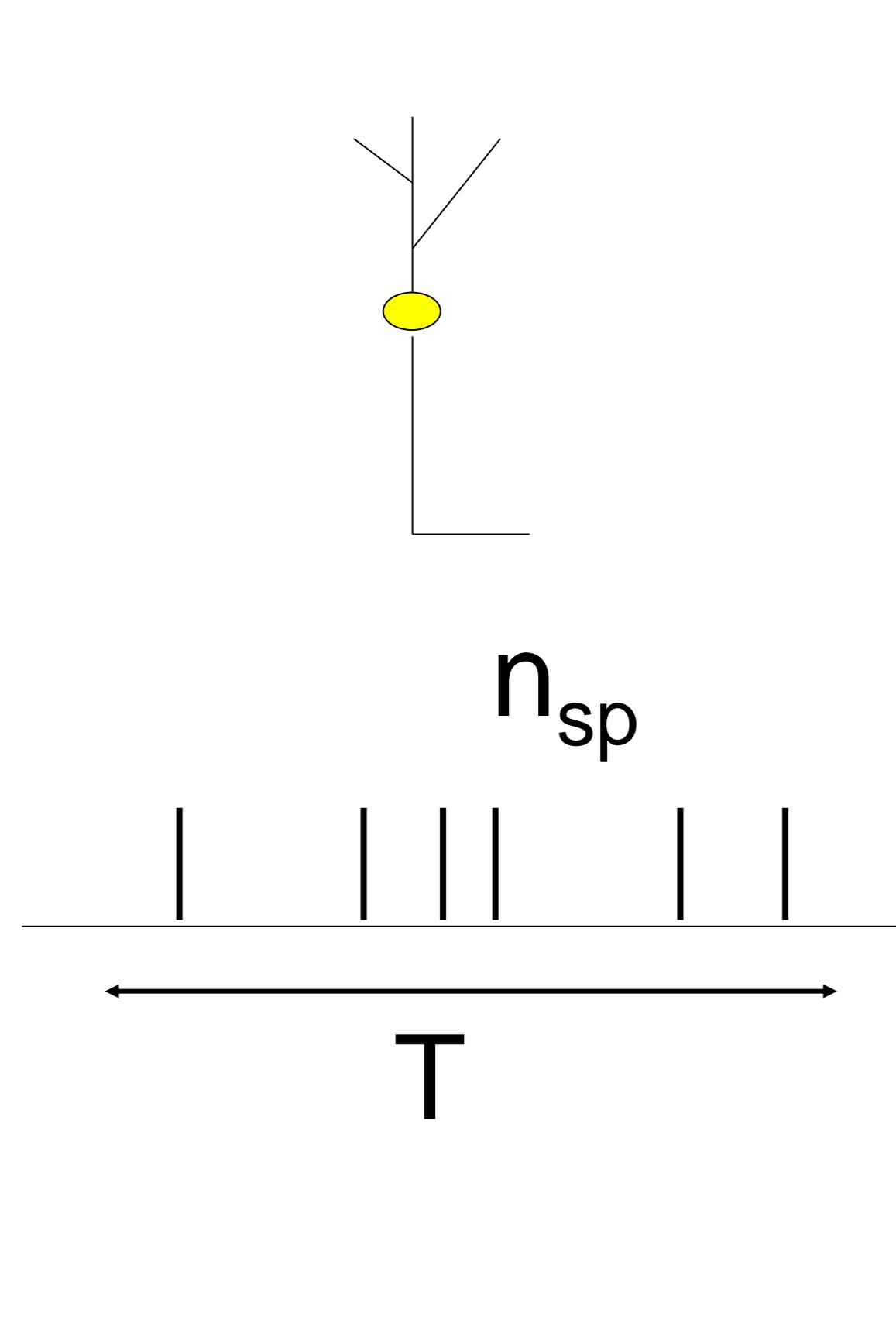
5.4 Stochastic spike arrival

- Membrane potential fluctuations

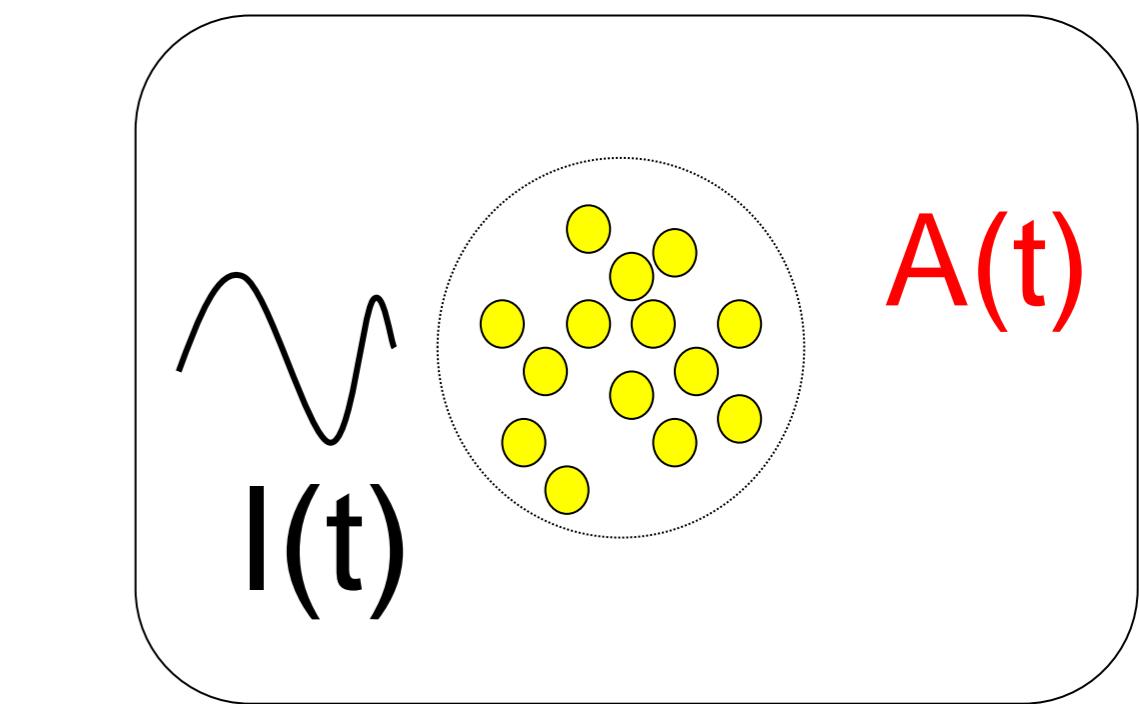
5.5. Stochastic spike firing

- subthreshold and superthreshold

Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process



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



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

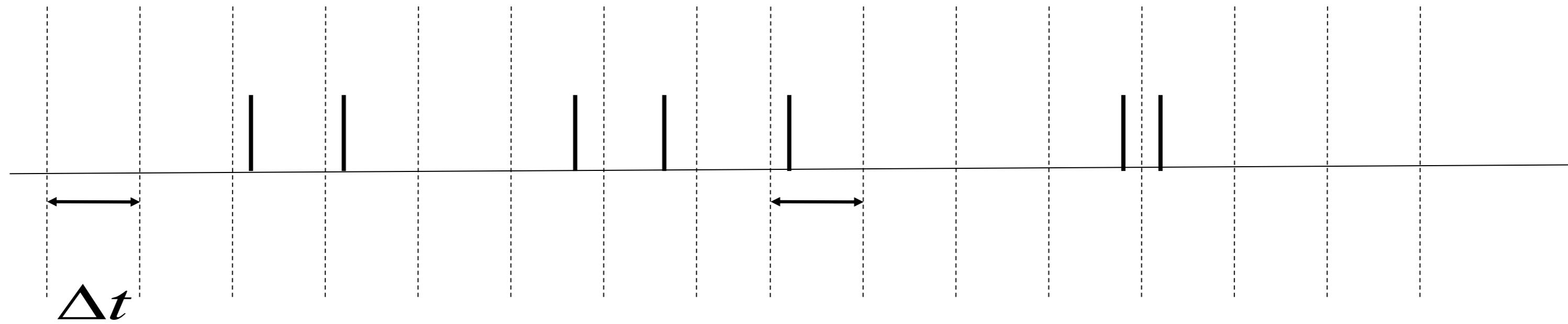
population
activity

Pure rate code = stochastic spiking → Poisson model

Neuronal Dynamics – 5.3b. Poisson Model

Homogeneous Poisson model: constant rate

*Math detour:
Poisson model*



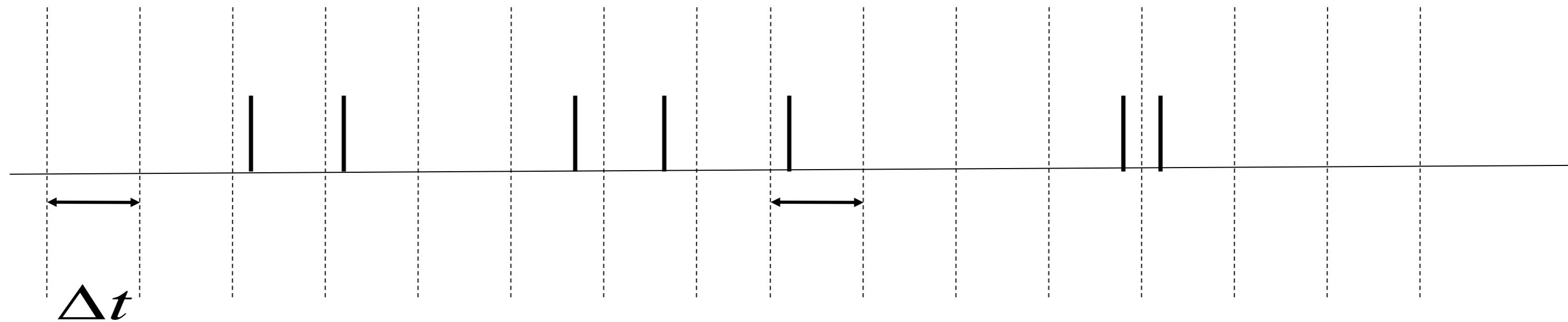
Probability of finding a spike $P_F = \rho_0 \Delta t$

Pure rate code = stochastic spiking → Poisson model

Neuronal Dynamics – 5.3b. Poisson Model

Probability of firing:

$$P_F = \rho_0 \Delta t$$



Take $\Delta t \rightarrow 0$

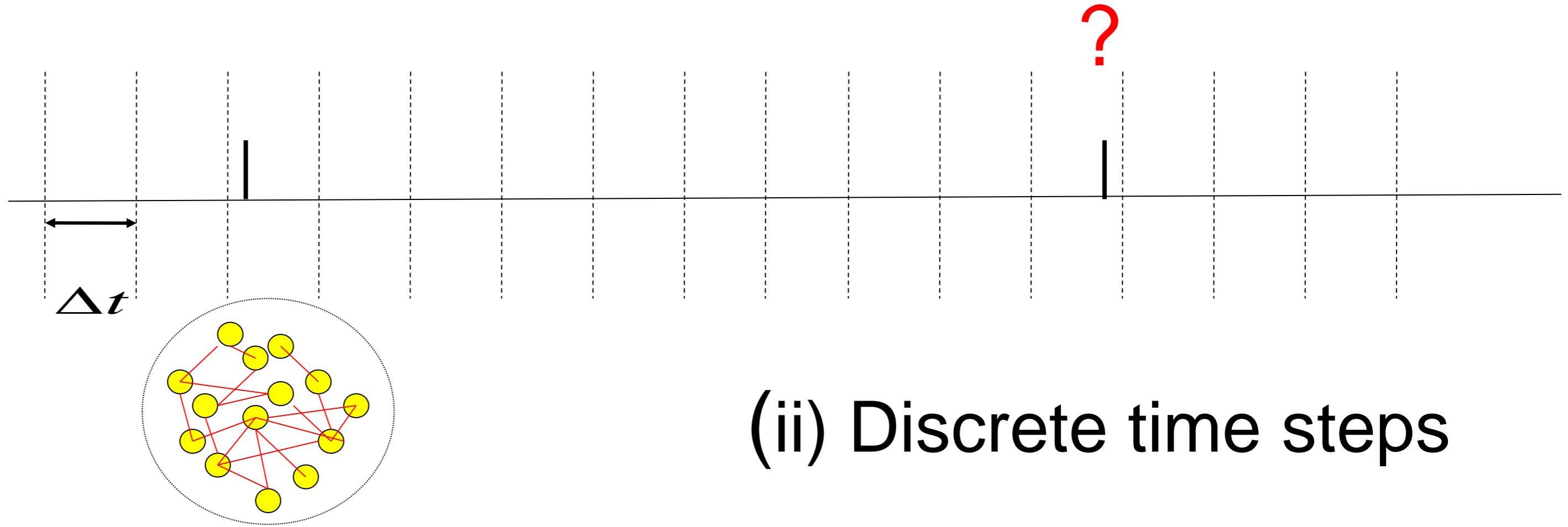
Neuronal Dynamics – 5.3b. Interval distribution

Probability of firing:

$$P_F = \rho_0 \Delta t$$

(i) Continuous time

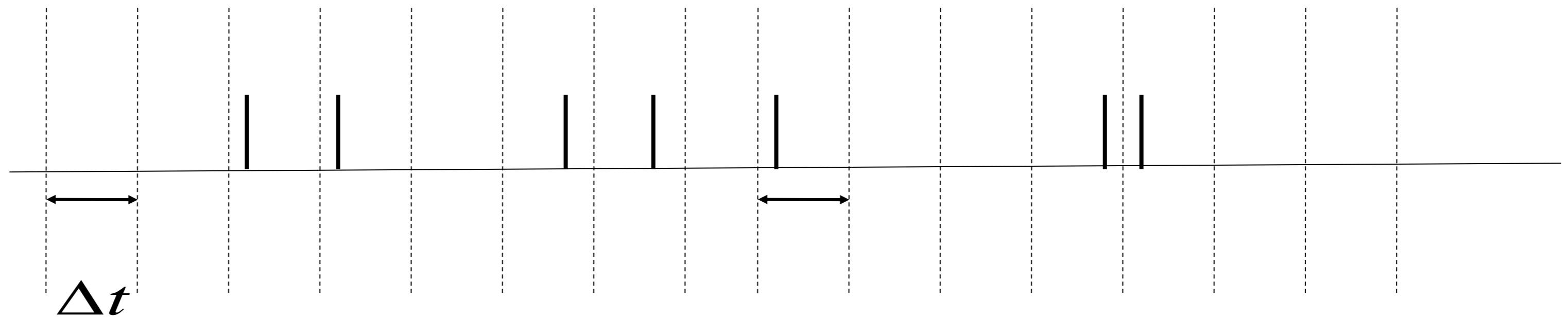
prob to ‘survive’



$$\Delta t \rightarrow 0$$

Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process

rate changes

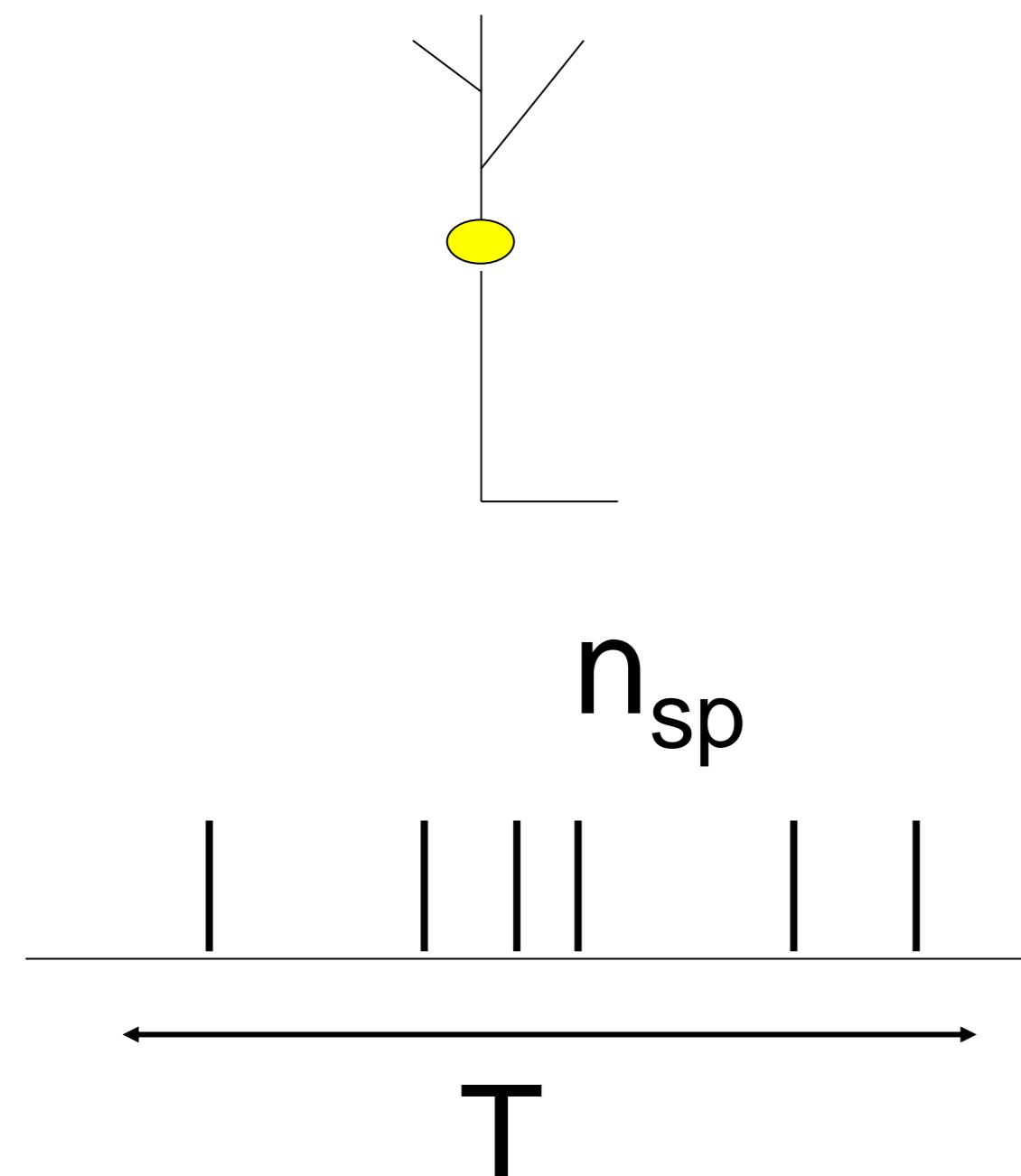


Probability of firing $P_F = \rho(t) \Delta t$

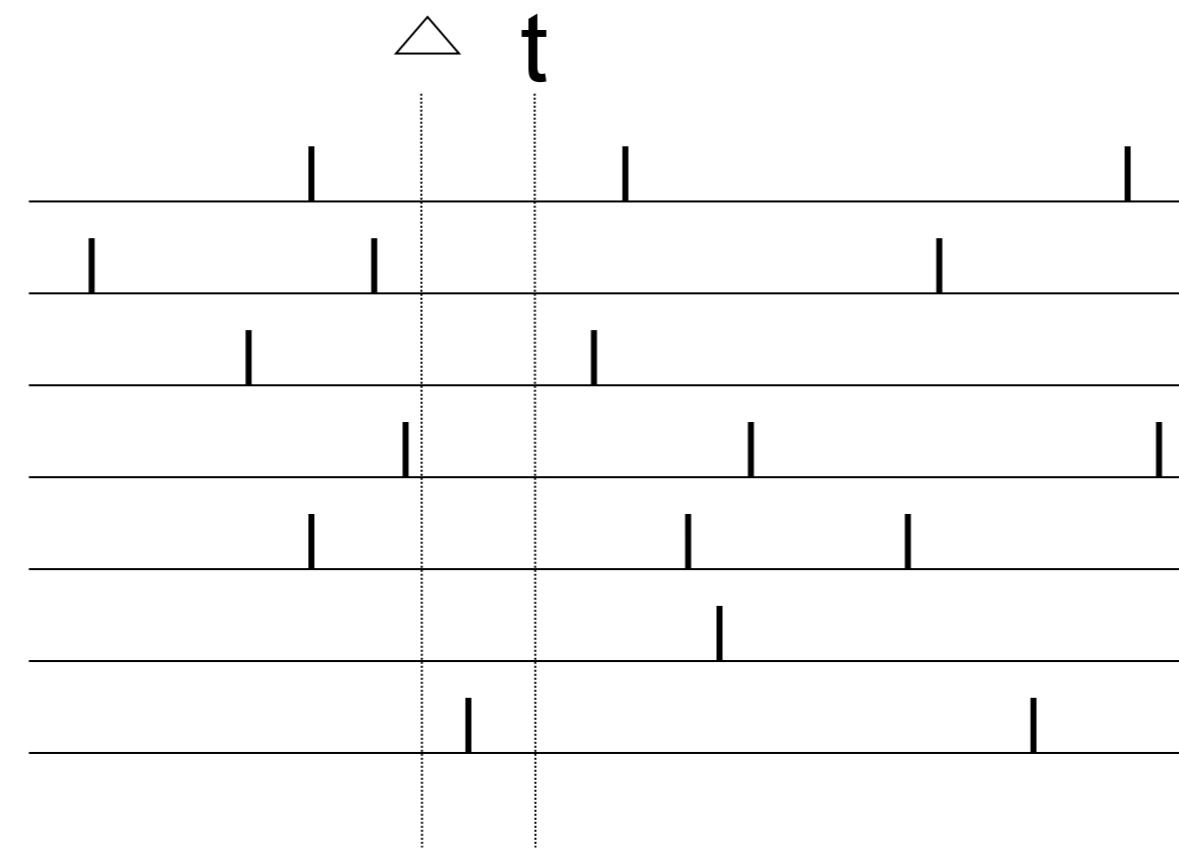
Survivor function $S(t | \hat{t}) = \exp\left(-\int_{\hat{t}}^t \rho(t') dt'\right)$

Interval distribution

Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process

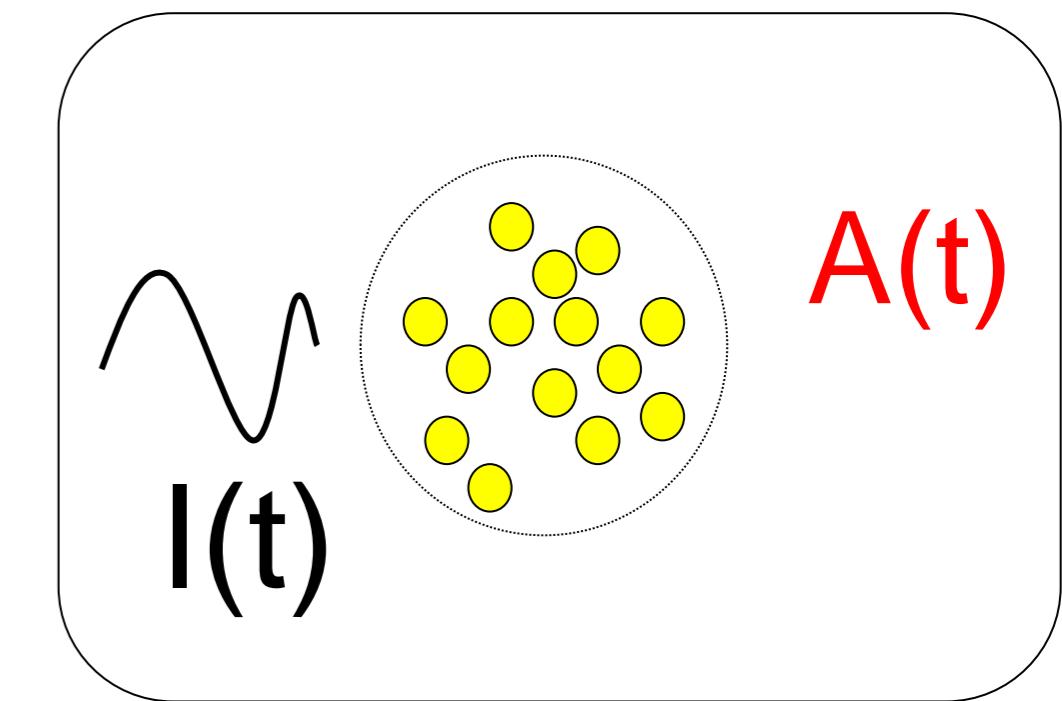


$$PSTH(t) = \frac{n(t; t + \Delta t)}{K \Delta t}$$



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

population
activity



inhomogeneous Poisson model consistent with rate coding

Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process

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.

Poisson Processes: A modern approach

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading:

[1] A.W. Lewis, G.S. Shedler (1979), Simulation of nonhomogeneous Poisson processes by thinning, Naval Res. Logist. Q. 26: 403–413.

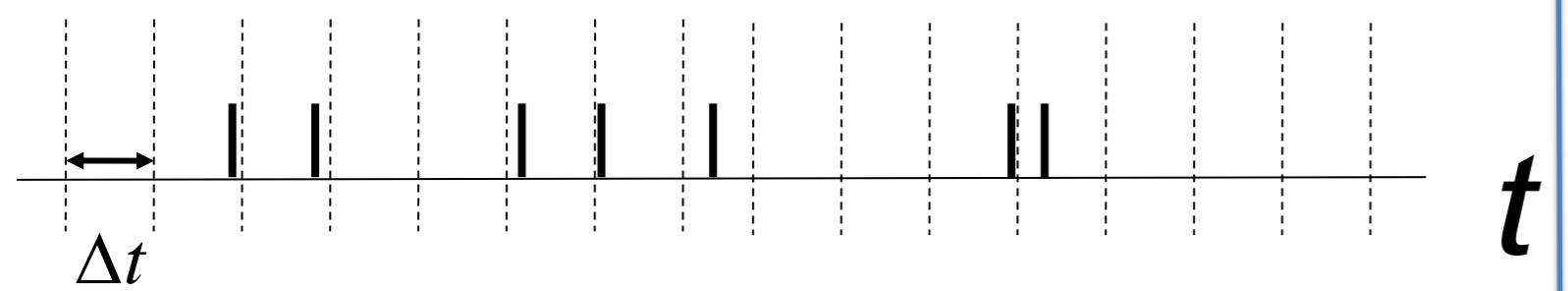
[2] V. Schmutz (2022), Mean-field limit of age and leaky memory dependent Hawkes processes. Stochastic Process. Appl., 149:39-59
<https://doi.org/10.1016/j.spa.2022.03.006>

[3] N. Fournier and E. Löcherbach (2016), On a toy model of interacting neurons. Annals Inst. H. Poincare, 52: 1844-1876
DOI: 10.1214/15-AIHP701

[4] J. Chevallier, Mean-field limit of generalized Hawkes processes (2017), Stochastic Process. Appl., 127:3870--3912. <http://dx.doi.org/10.1016/j.spa.2017.02.012>

Poisson Process (PP): 2 constructive procedures

classic procedure



Probability of generating an event

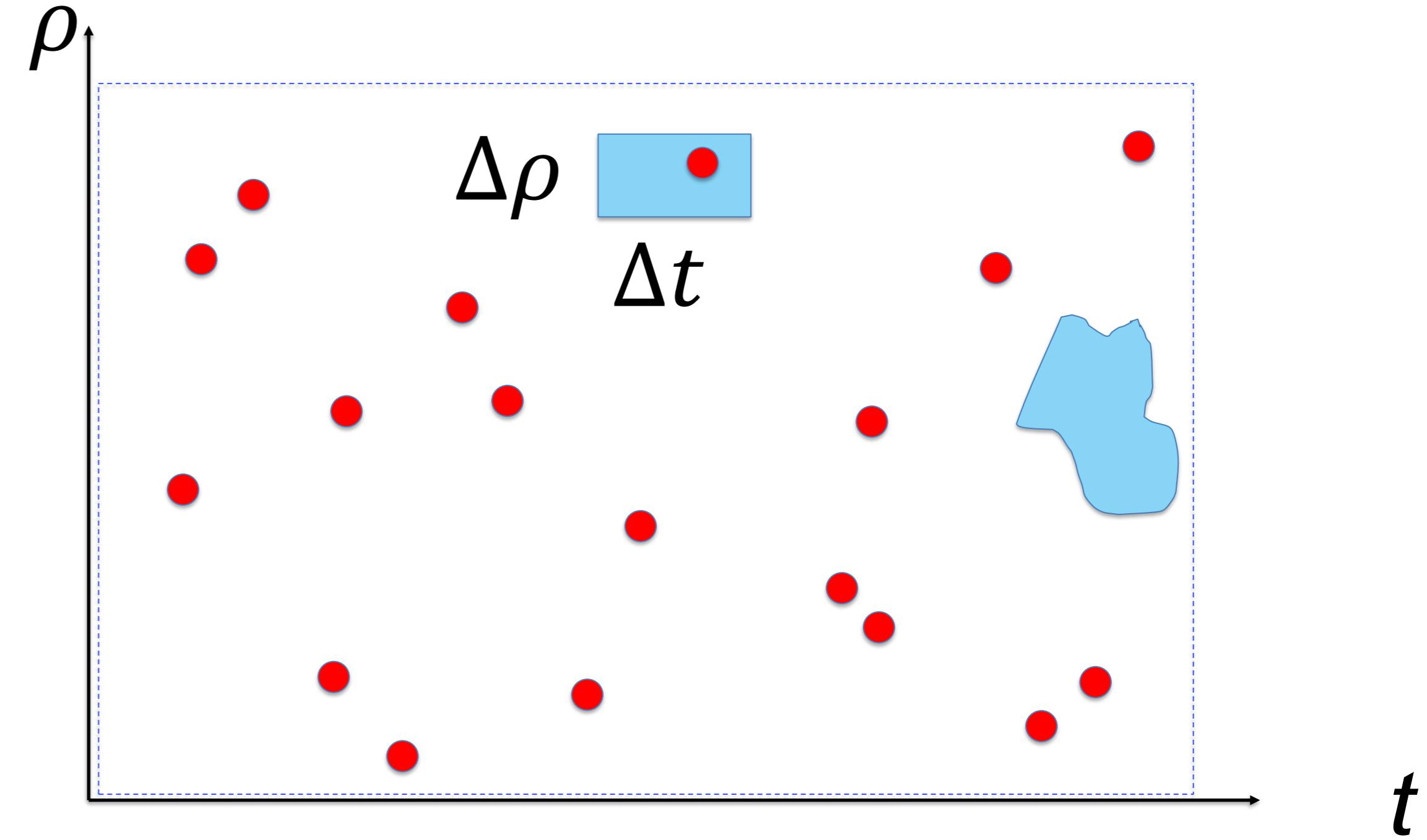
$$P_F = \rho_0 \Delta t$$

time step $\Delta t \rightarrow 0$

Inhomogeneous PP

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

call random number every time step



Probability of generating event:
uniform in 2 dimensions:
 $E(\text{number of events} / \text{area}) = \text{area}$

- choose number of events | total area
- call random number twice per event

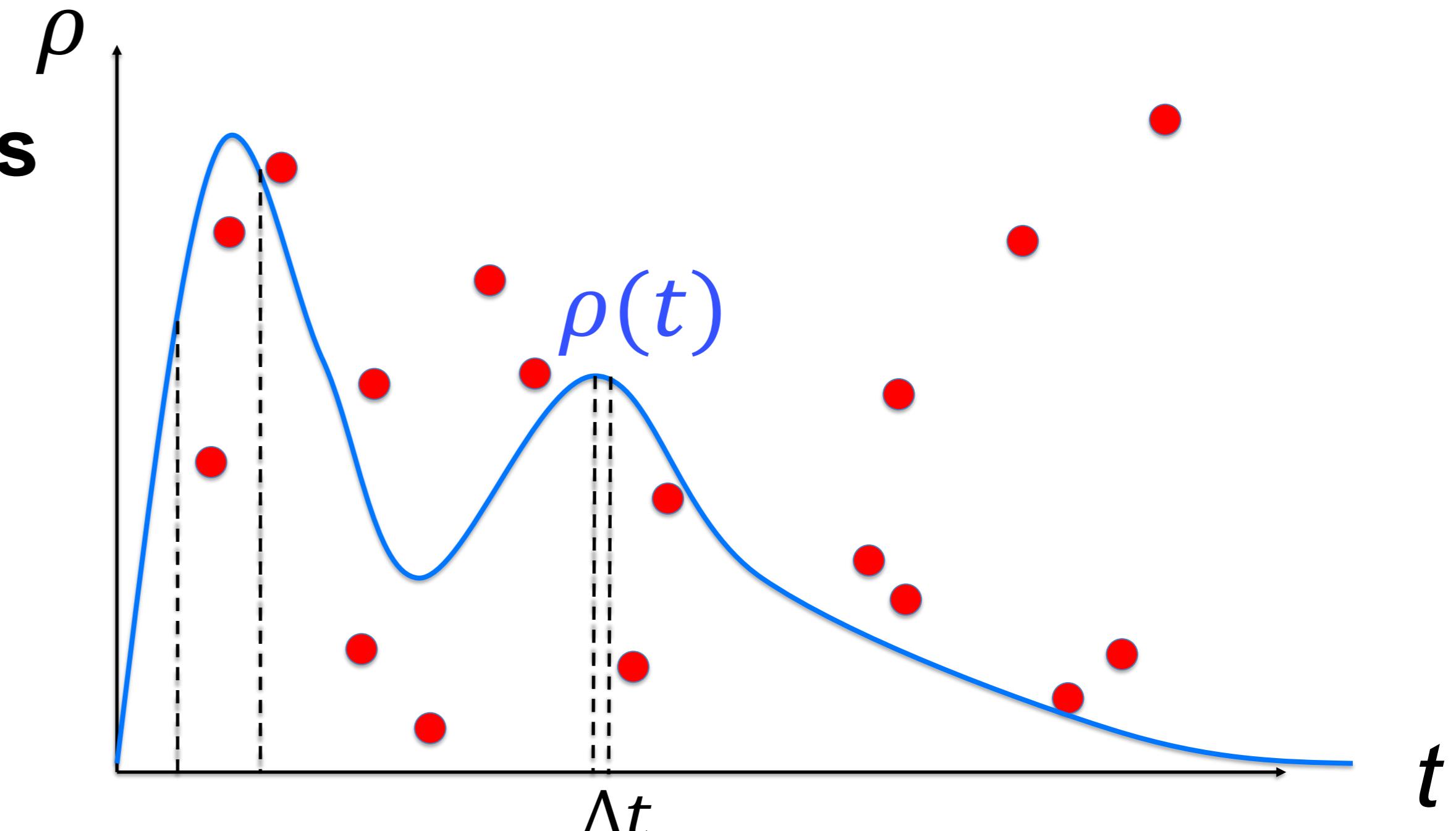
Efficient constructive procedure

Example:
inhomogeneous Poisson Process

rate (stochastic intensity):

$$\rho(t) = f(h(t))$$

- (i) create events in total area
- (ii) visualize $\rho(t)$
- (iii) project 'events below line' to t -axis
- (iv) read-off event times
- [(v) you may discretize]



Probability of generating event:
uniform in 2 dimensions:

$$E(\text{number of events} / \text{area}) = \text{area}$$

- choose number of events | total area
- call random number twice per event

From 2 dimensions to spike trains $S(t)$ and counts $N(t)$

points in time yield:

(i) a pulse train

$$S_k(t) = \sum_f \delta(t - t_k^f)$$

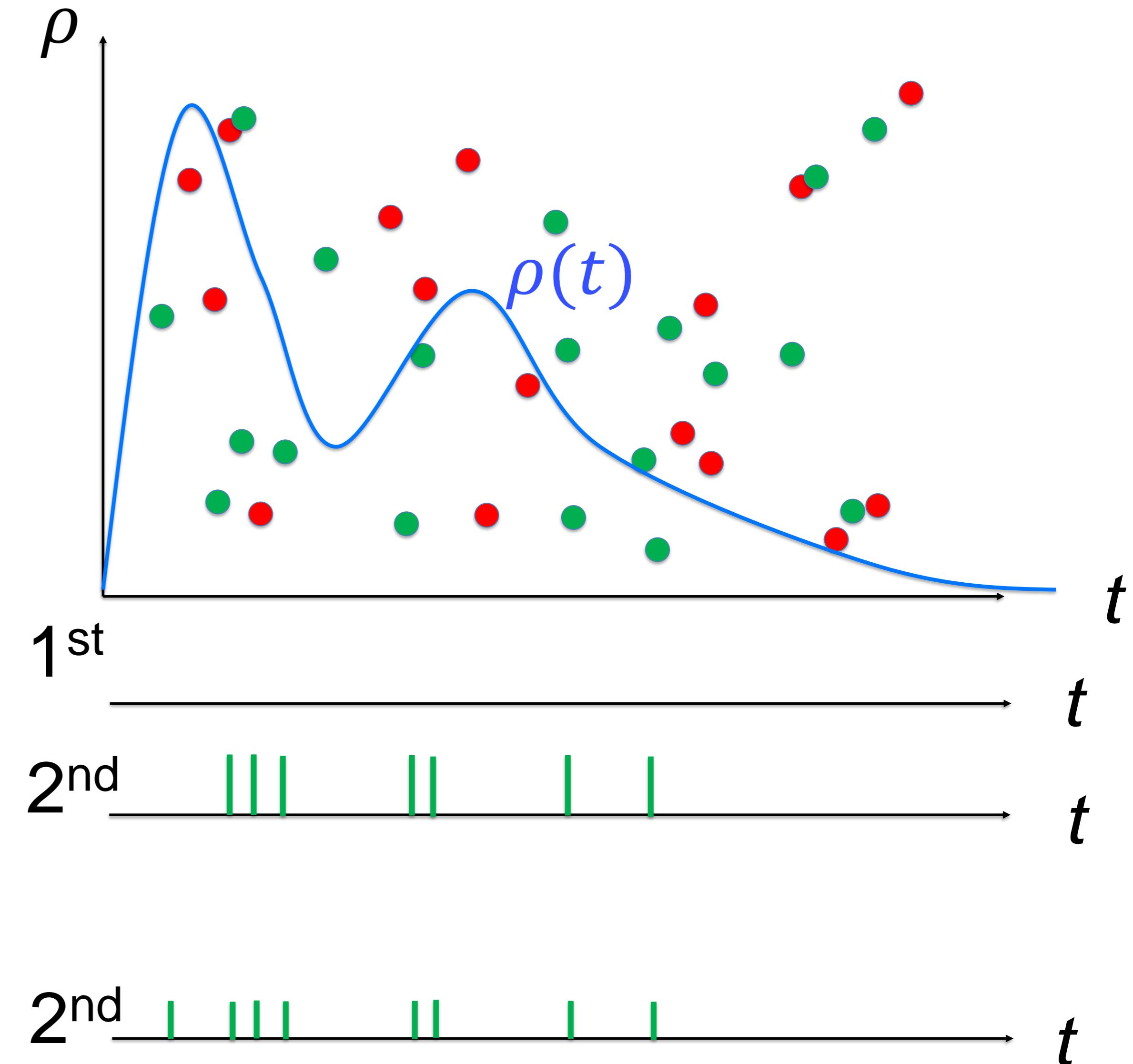
(ii) a counting process

$$N_k(t) = \int_0^t S_k(t') dt'$$

Expectation at time t :

$$\langle N(t) \rangle = E_k[N_k] = \int_0^t \rho(t') dt'$$

$$\langle S(t) \rangle = E_k [S_k(t)] = \rho(t)$$



Poisson process: a modern view

- Realization can be generated **before** the start of the simulation
- Realization = points in 2 dimension:
area of 2-dim surface = expected number of events
- Advantage:
no need to know the time-dependent intensity $\rho(t)$ beforehand
→ could depend on what happens in other parts of an interacting network
- Number of actual events in interval $[t_0, t_1]$ generated by this realization = ‘points below the curve $\rho(t)$ ’

$$E[\text{events in } [t_0, t_1]] = \int_{t_0}^{t_1} \int_0^{\rho(t)} dz \ dt$$

- in particular

$$\langle S(t) \rangle := E[S(t)] = \rho(t) = \left\langle \sum_f \delta(t - t^f) \right\rangle$$

Poisson Processes: A modern approach

Interested in using this method?
Please cite for applications in the neurosciences

[1] V. Schmutz (2022), Mean-field limit of age and leaky memory dependent Hawkes processes.

Stochastic Processes and their Applications, 149:39-59

<https://doi.org/10.1016/j.spa.2022.03.006>

[2] N Fournier and E. Löcherbach (2016), On a toy model of interacting neurons.

Annals Inst. H. Poincaré, 52: 1844-1876

DOI: 10.1214/15-AIHP701

The classical reference for the 2-dimensional approach is

[3] A.W. Lewis, G.S. Shedler (1979),

Simulation of nonhomogeneous Poisson processes by thinning,

Naval Res. Logist. Q. 26: 403–413.

Week 5 – part 4 :Stochastic spike arrival



Neuronal Dynamics: Computational Neuroscience of Single Neurons

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

Wulfram Gerstner

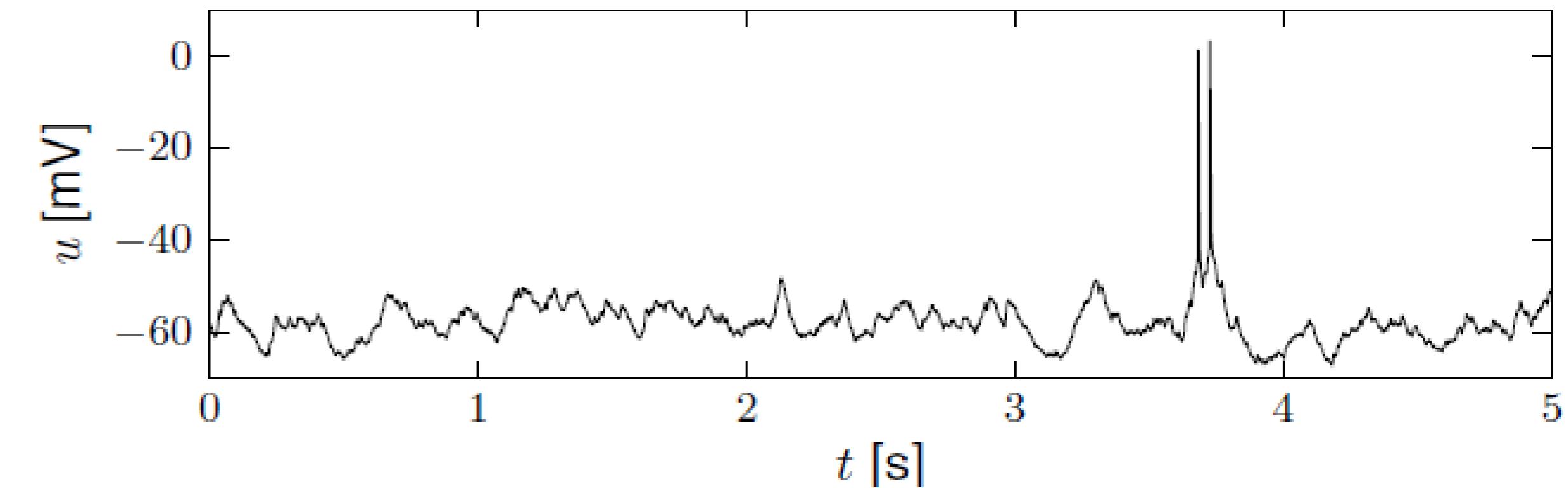
EPFL, Lausanne, Switzerland

- ↓ 5.1 Variability of spike trains
 - experiments
- ↓ 5.2 Sources of Variability?
 - Is variability equal to noise?
- ↓ 5.3 Three definitions of Rate code
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- 5.5. Stochastic spike firing
 - subthreshold and superthreshold

Neuronal Dynamics – 5.4 Variability *in vivo*

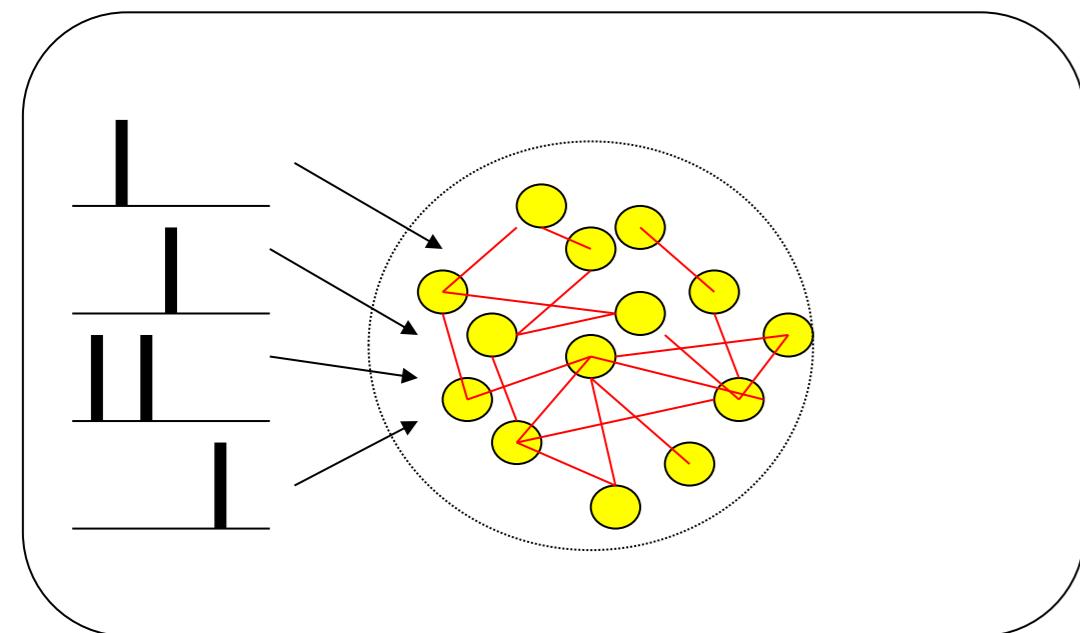
Spontaneous activity *in vivo*

Variability
of membrane potential?
awake mouse, freely whisking,



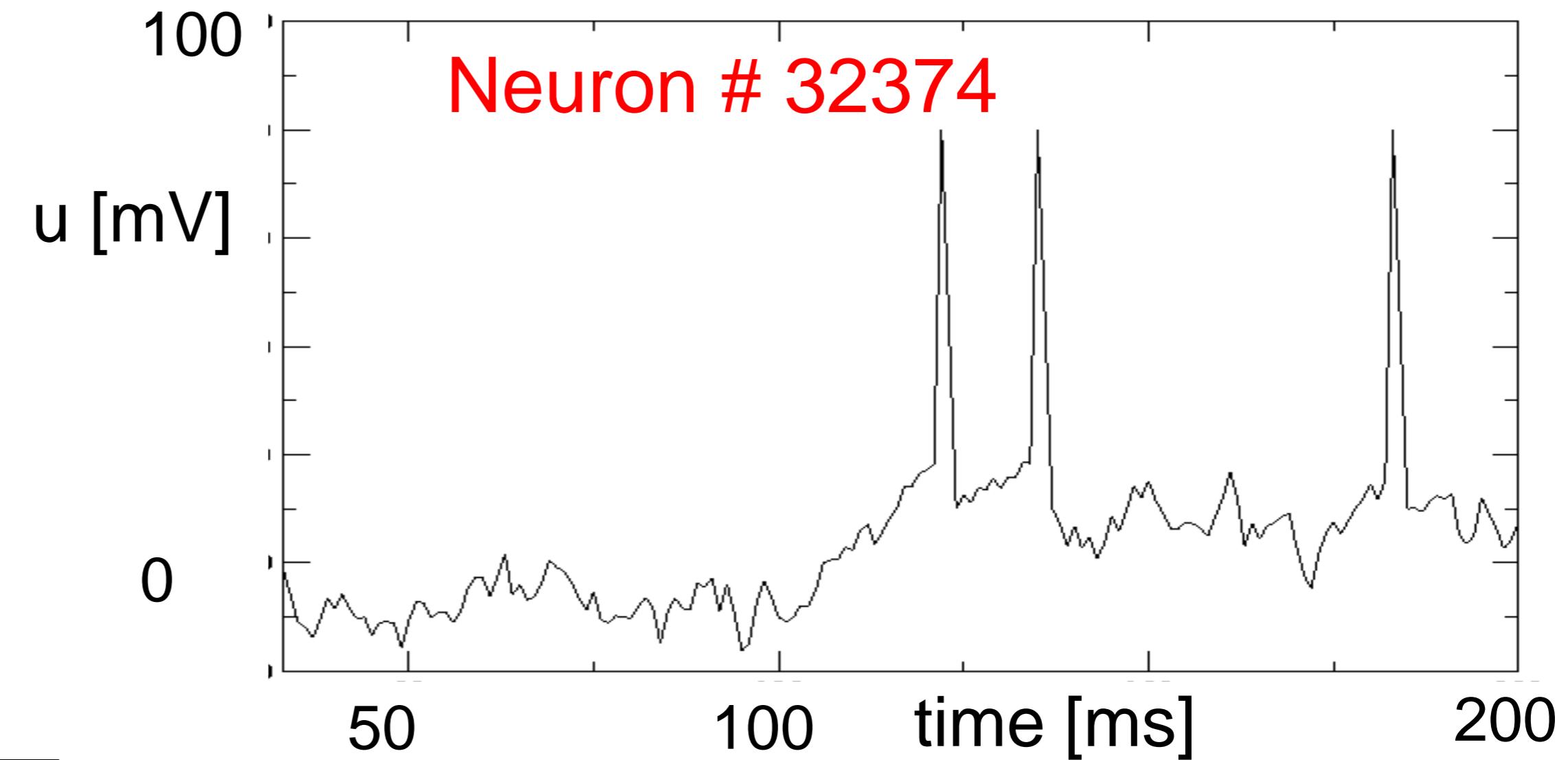
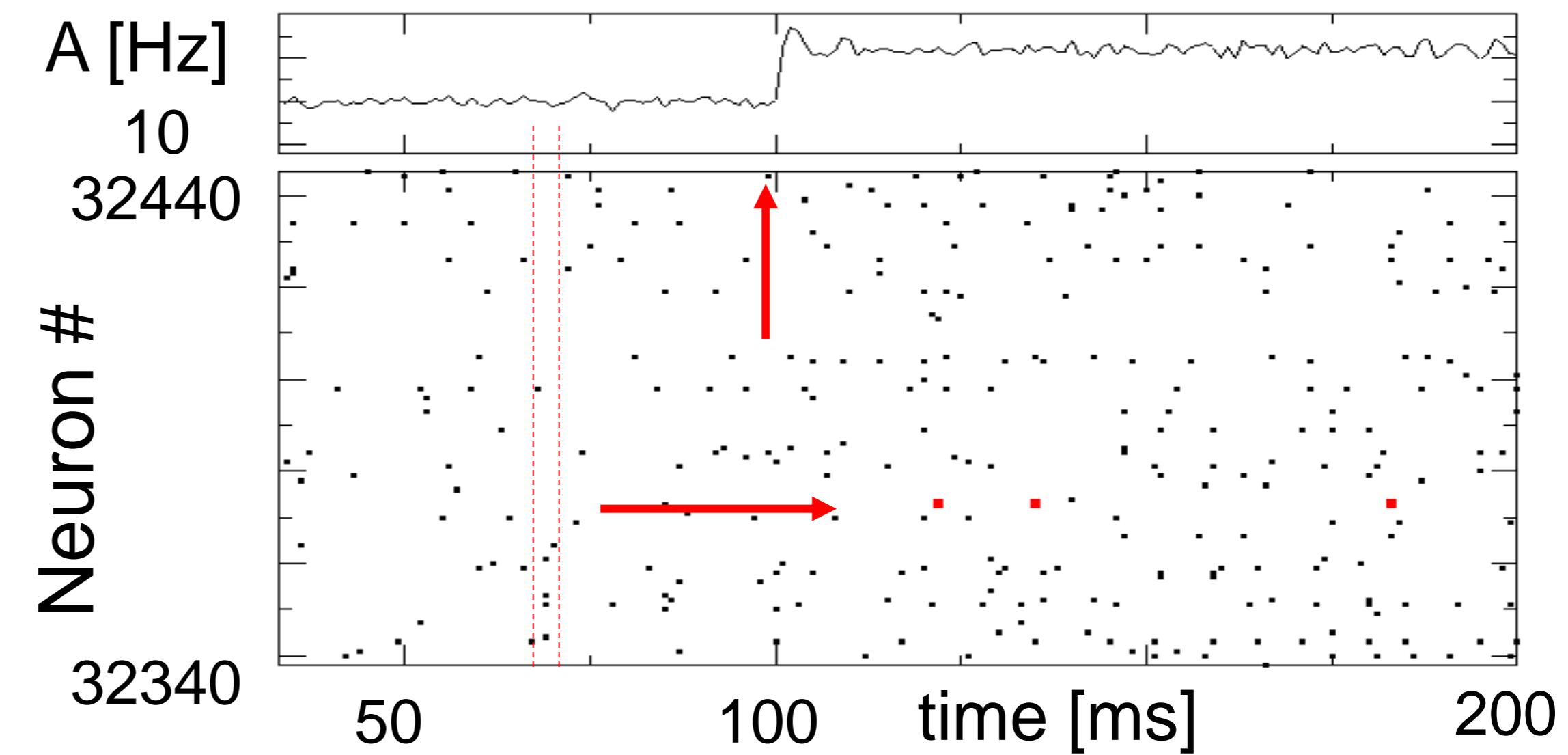
Crochet et al., 2011

Random firing in a population of LIF neurons

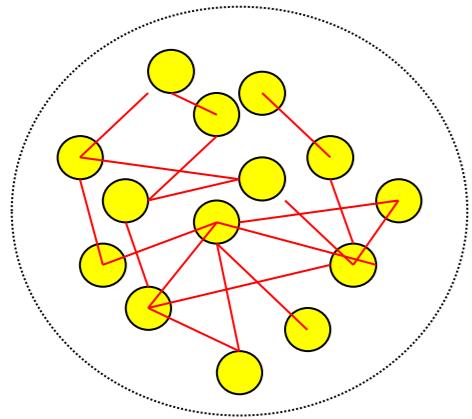


input {
low rate
- high rate

Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected



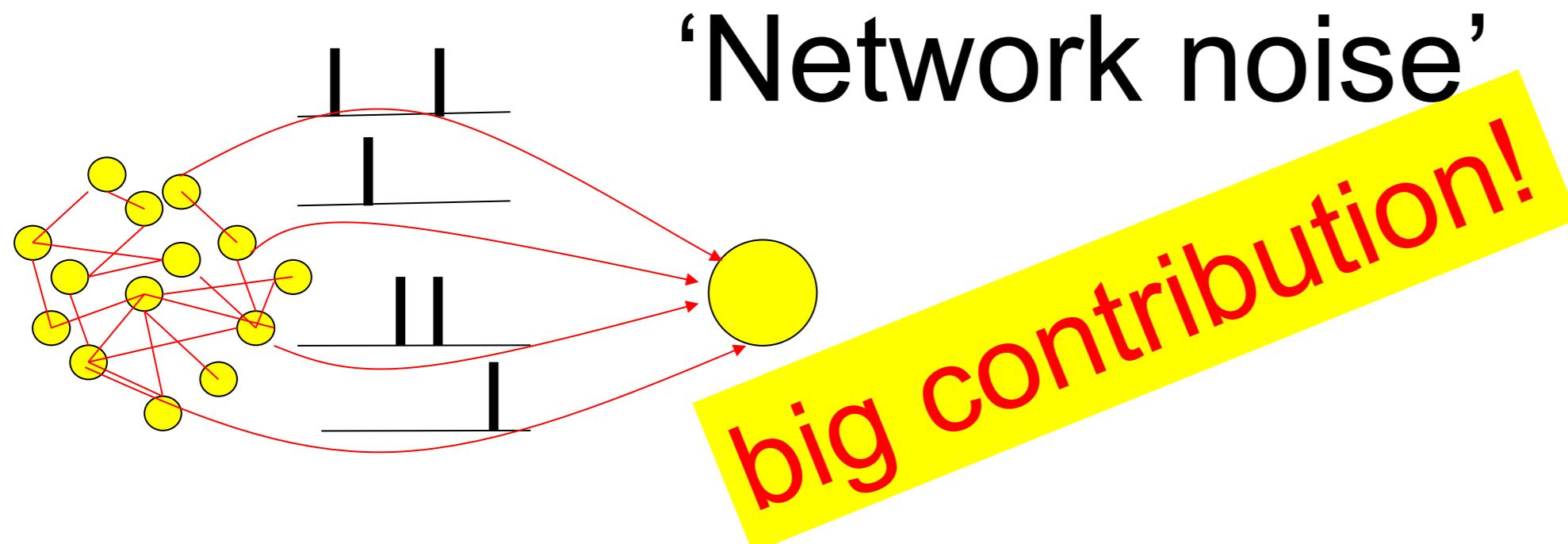
Neuronal Dynamics – 5.4 Membrane potential fluctuations



from neuron's point
of view:

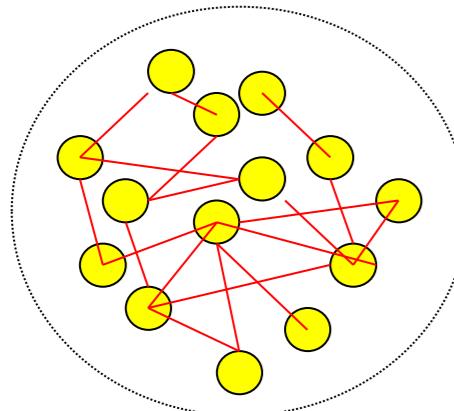
stochastic spike arrival

Pull out one neuron

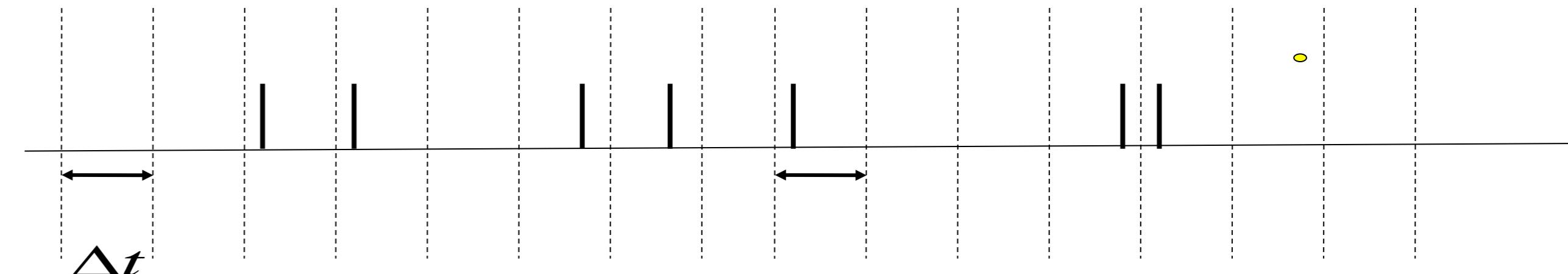


Neuronal Dynamics – 5.4. Stochastic Spike Arrival

math detour
now!

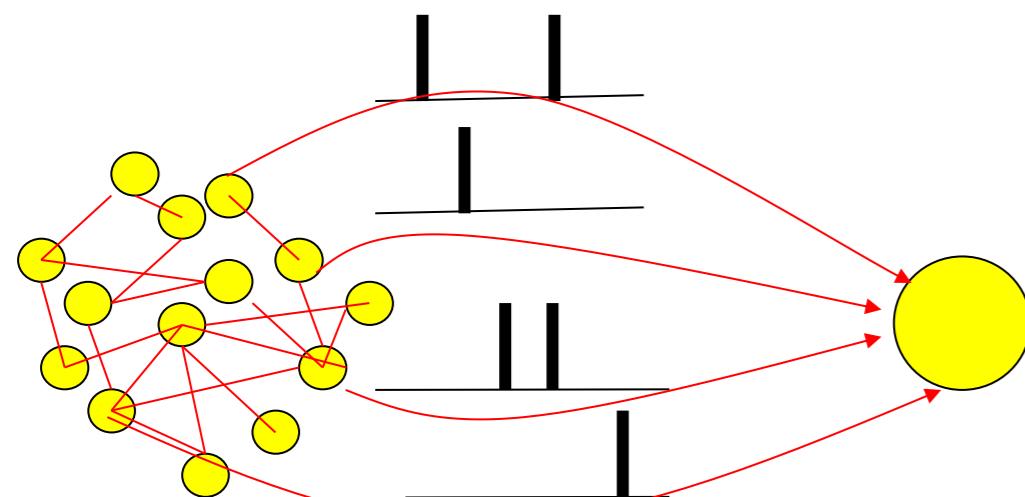


Total spike train of K presynaptic neurons



spike train

Pull out one neuron



Probability of spike arrival:

$$P_F = K \rho_0 \Delta t$$

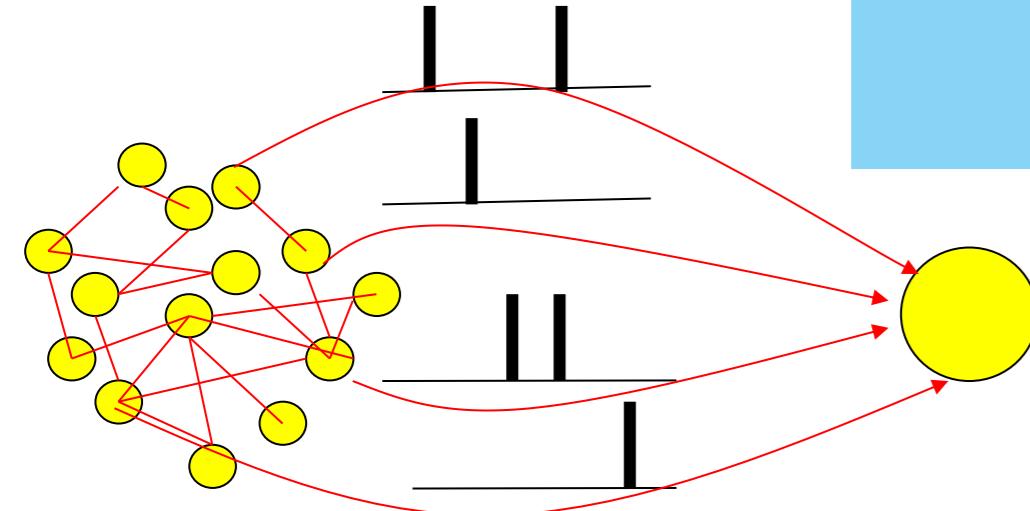
Take $\Delta t \rightarrow 0$

expectation

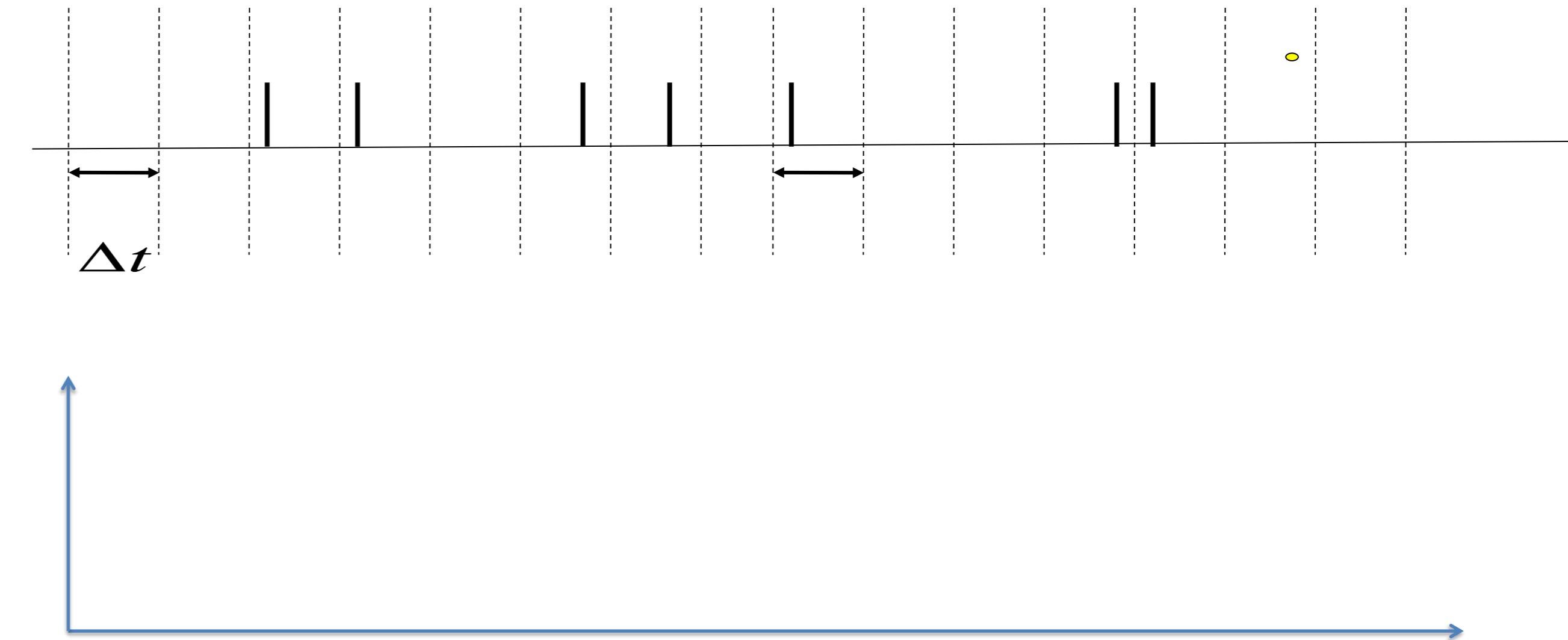
$$S(t) = \sum_{k=1}^K \sum_f \delta(t - t_k^f)$$

Neuronal Dynamics – 5.4. Fluctuation of input current

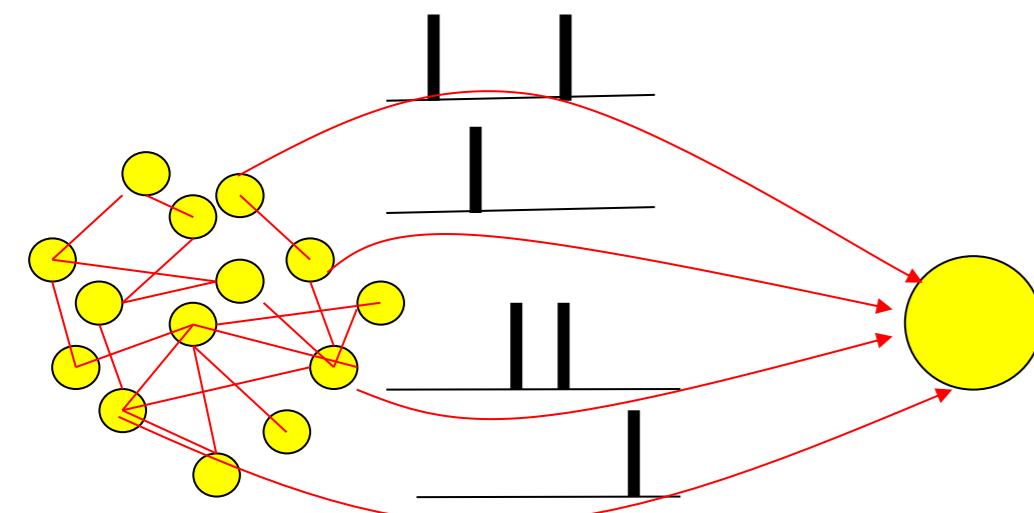
math detour
now!



Total spike train of K presynaptic neurons



Neuronal Dynamics – 5.4. Fluctuation of current/potential



Passive membrane

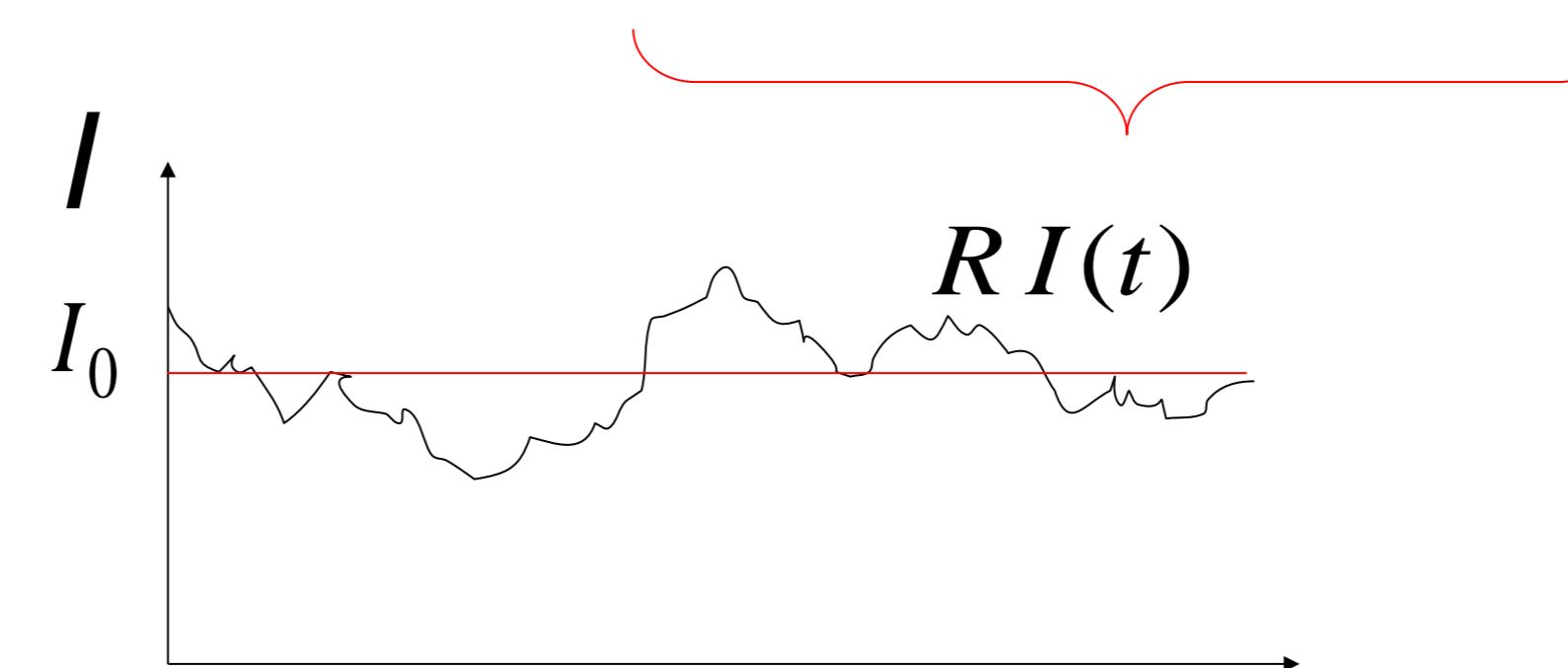
$$\tau \frac{d}{dt}u = -(u - u_{rest}) + RI^{syn}(t)$$

→ Fluctuating potential

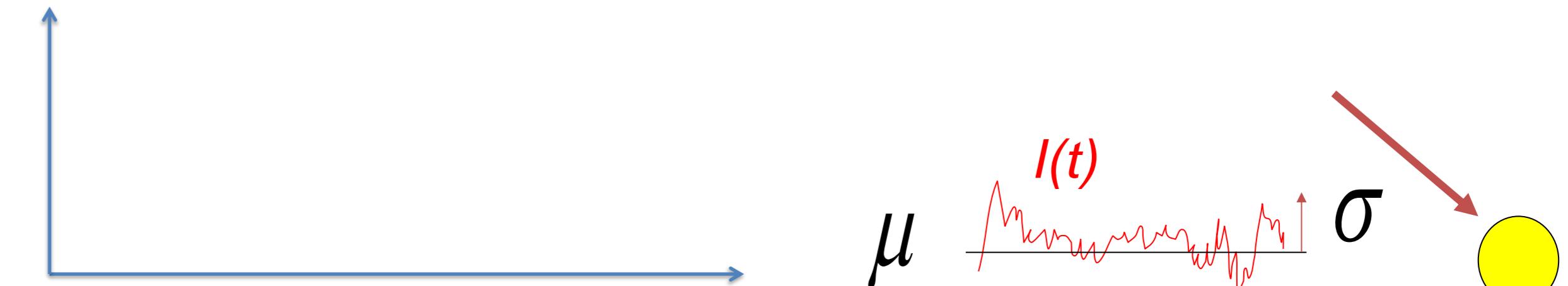
Synaptic current pulses of shape α

$$RI^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$

EPSC



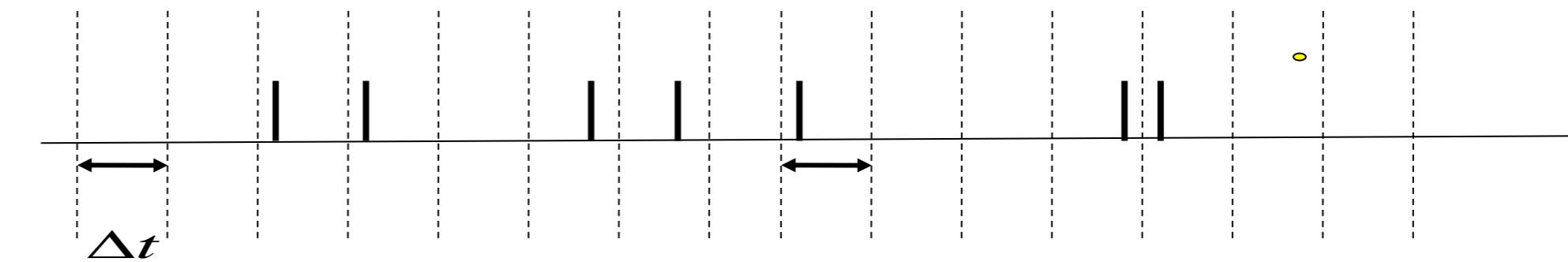
$$I^{syn}(t) = I_0 + I^{fluct}(t)$$



Fluctuating input current

Neuronal Dynamics – 5.4. Calculating the mean

$$RI^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$



$$I^{syn}(t) = \frac{1}{R} \sum_k w_k \sum_f \int dt' \alpha(t - t') \delta(t' - t_k^f)$$

$$x(t) = \sum_f \int dt' f(t - t') \delta(t' - t_k^f)$$

mean: assume Poisson process

$$I_0 = \langle I^{syn}(t) \rangle = \frac{1}{R} \sum_k w_k \int dt' \alpha(t - t')$$

use for assignment/
homework!

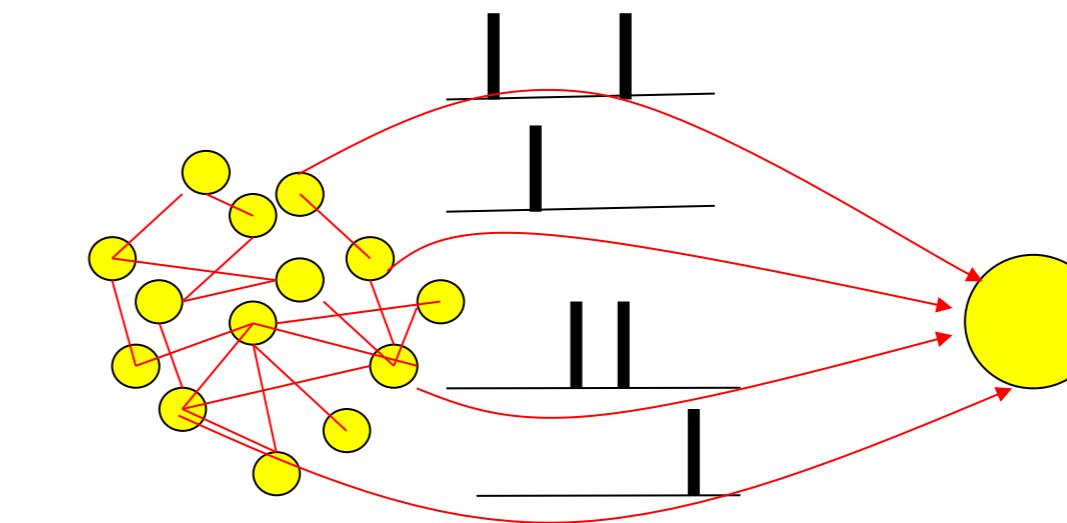
$$I_0 = \frac{1}{R} \sum_k w_k \int dt' \alpha(t - t') v_k$$

$$\langle x(t) \rangle = \int dt' f(t - t') \left\langle \sum_f \delta(t' - t_k^f) \right\rangle$$

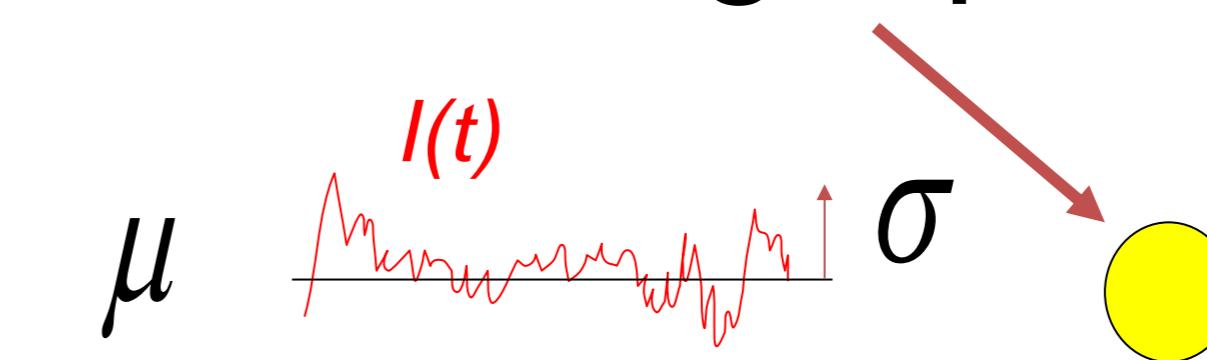
$$\langle x(t) \rangle = \int dt' f(t - t') \rho(t')$$

rate of inhomogeneous
Poisson process

Neuronal Dynamics – 5.4. Fluctuation of current/potential

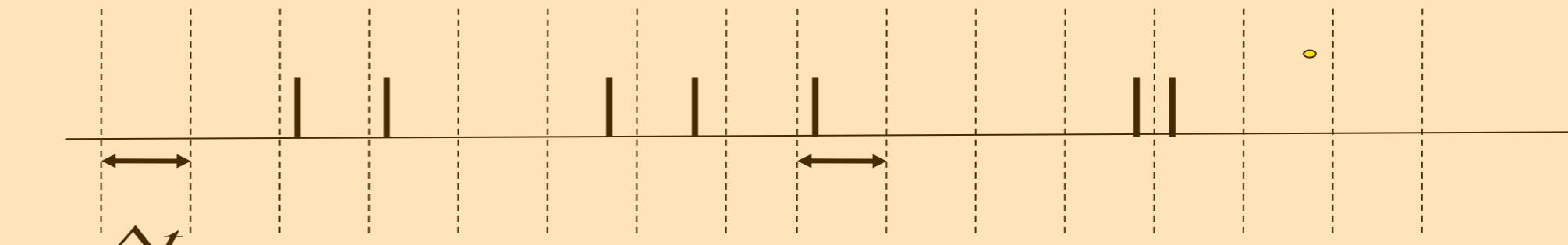
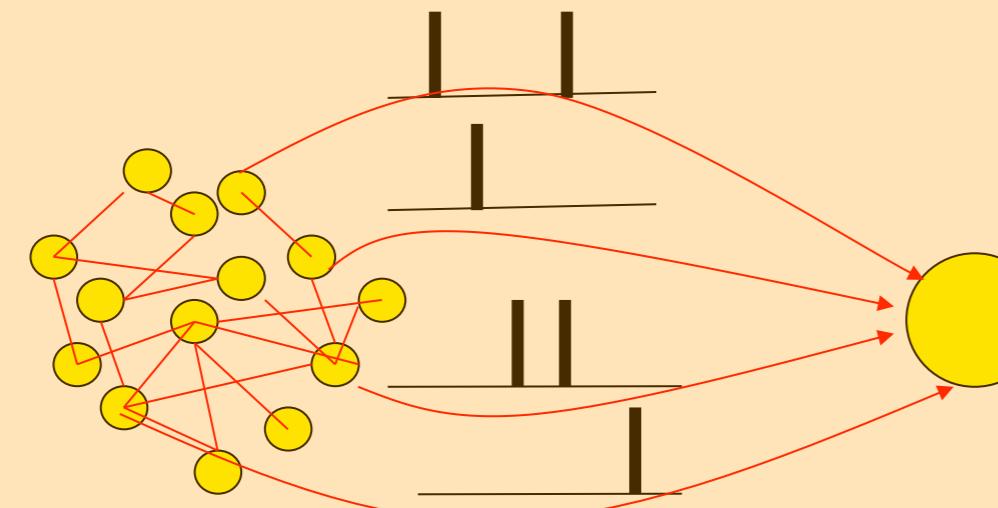


fluctuating input current



fluctuating potential

Neuronal Dynamics – Assignment/homework

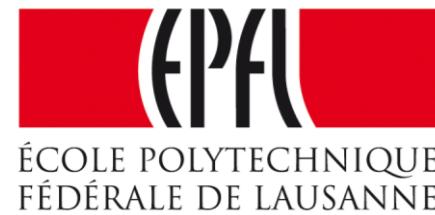


$$u(t) = \sum_f \int dt' f(t-t') \delta(t-t_k^f)$$

A leaky integrate-and-fire neuron receives stochastic spike arrival, described as a homogeneous Poisson process.

Calculate the mean membrane potential. To do so, use the above formula.

Week 5 – part 4b : Membrane potential fluctuations



Neuronal Dynamics: Computational Neuroscience of Single Neurons

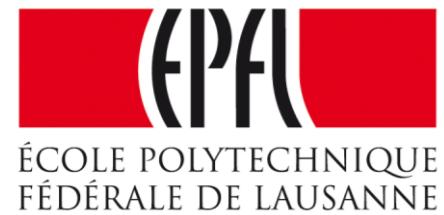
Week 5 – Variability and Noise: The question of the neural code

Wulfram Gerstner

EPFL, Lausanne, Switzerland

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 - experiments
- ↓ 5.2 Sources of Variability?
 - Is variability equal to noise?
- ↓ 5.3 Three definitions of Rate code
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 - subthreshold and superthreshold

Week 5 – part 4b : Membrane potential fluctuations

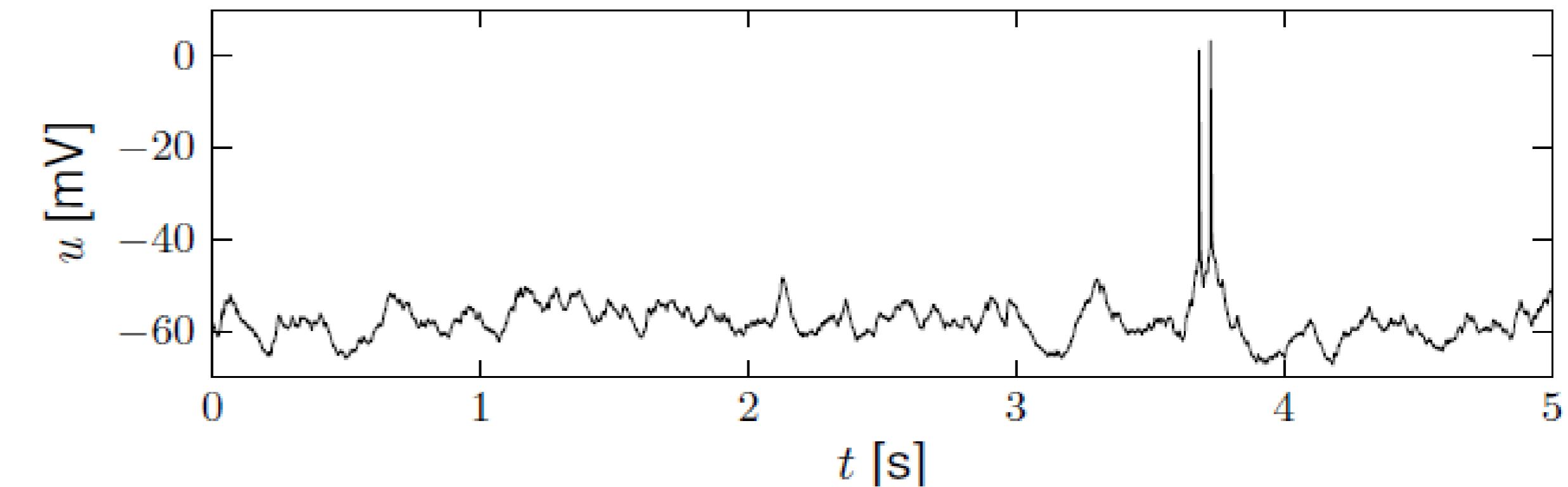


- ↓ **5.1 Variability of spike trains**
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- 5.5. Stochastic spike firing**
 - subthreshold and superthreshold

Neuronal Dynamics – 5.4 Variability *in vivo*

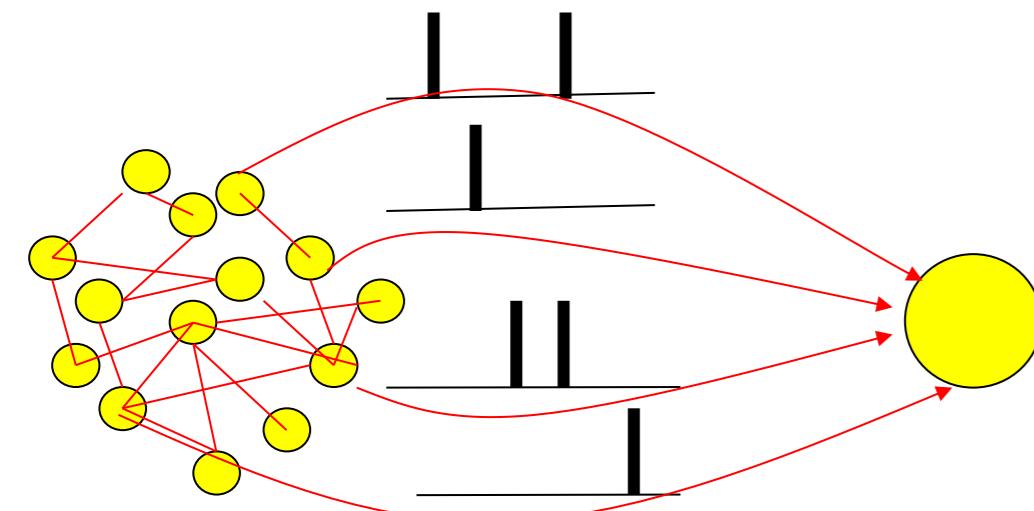
Spontaneous activity *in vivo*

Variability
of membrane potential?
awake mouse, freely whisking,



Crochet et al., 2011

Neuronal Dynamics – 5.4b. Fluctuations of potential



Passive membrane

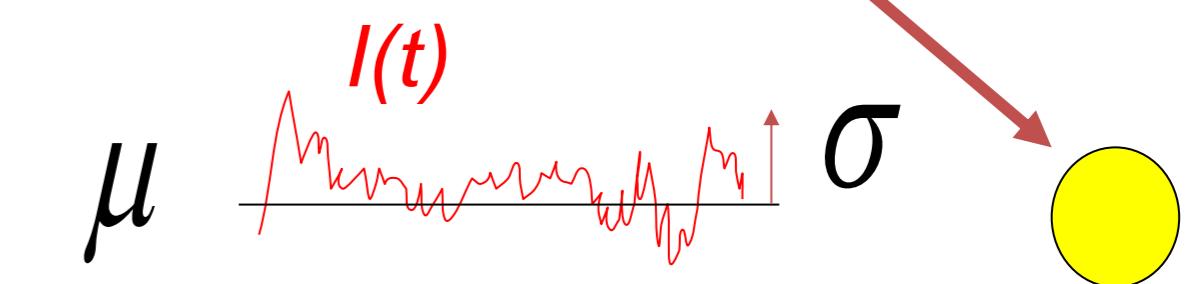
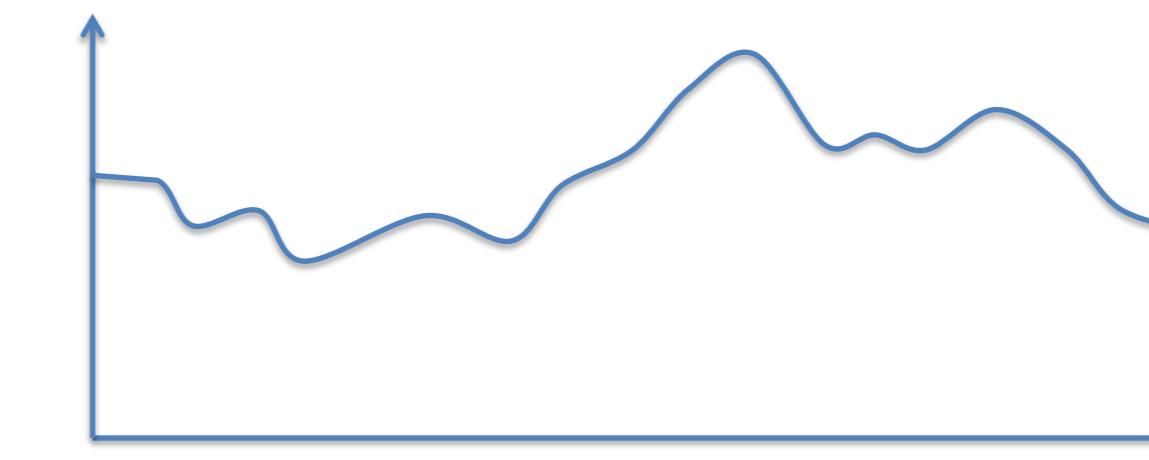
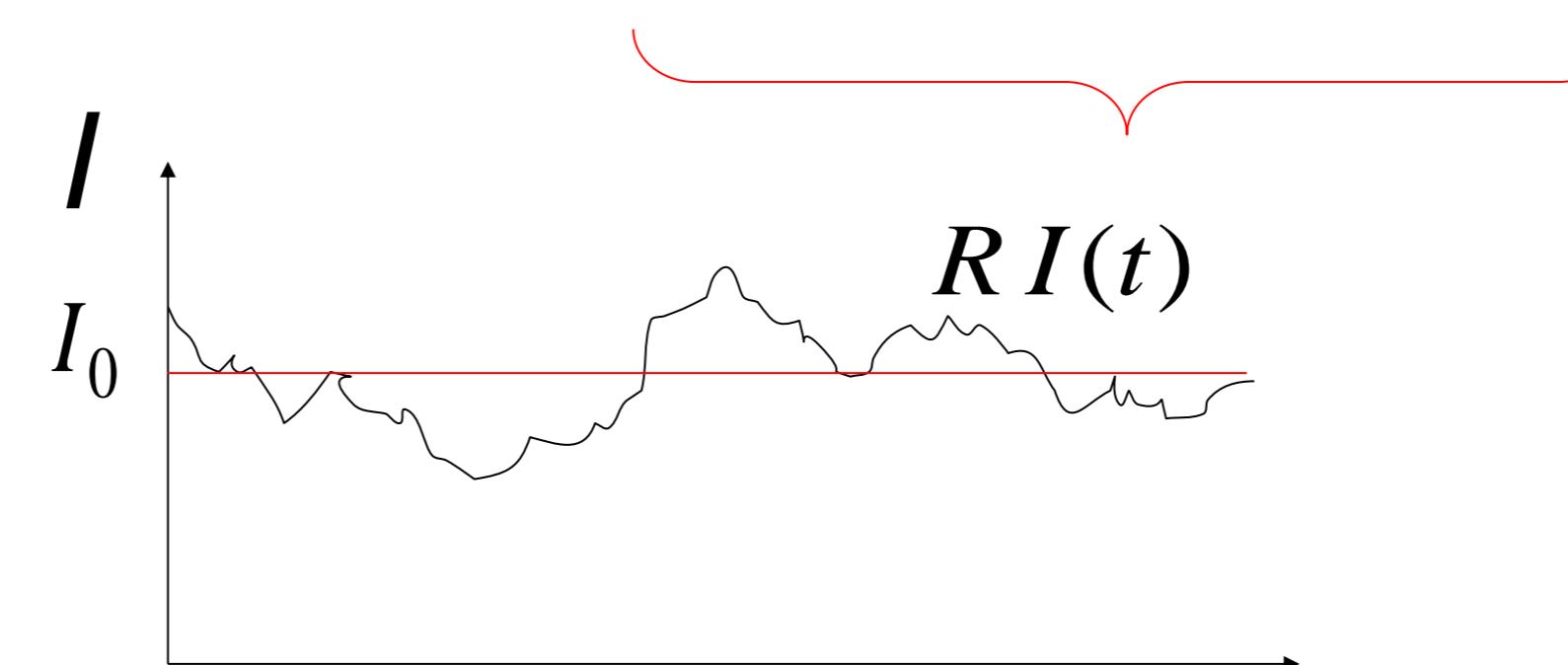
$$\tau \frac{d}{dt}u = -(u - u_{rest}) + RI^{syn}(t)$$

→ Fluctuating potential

Synaptic current pulses of shape α

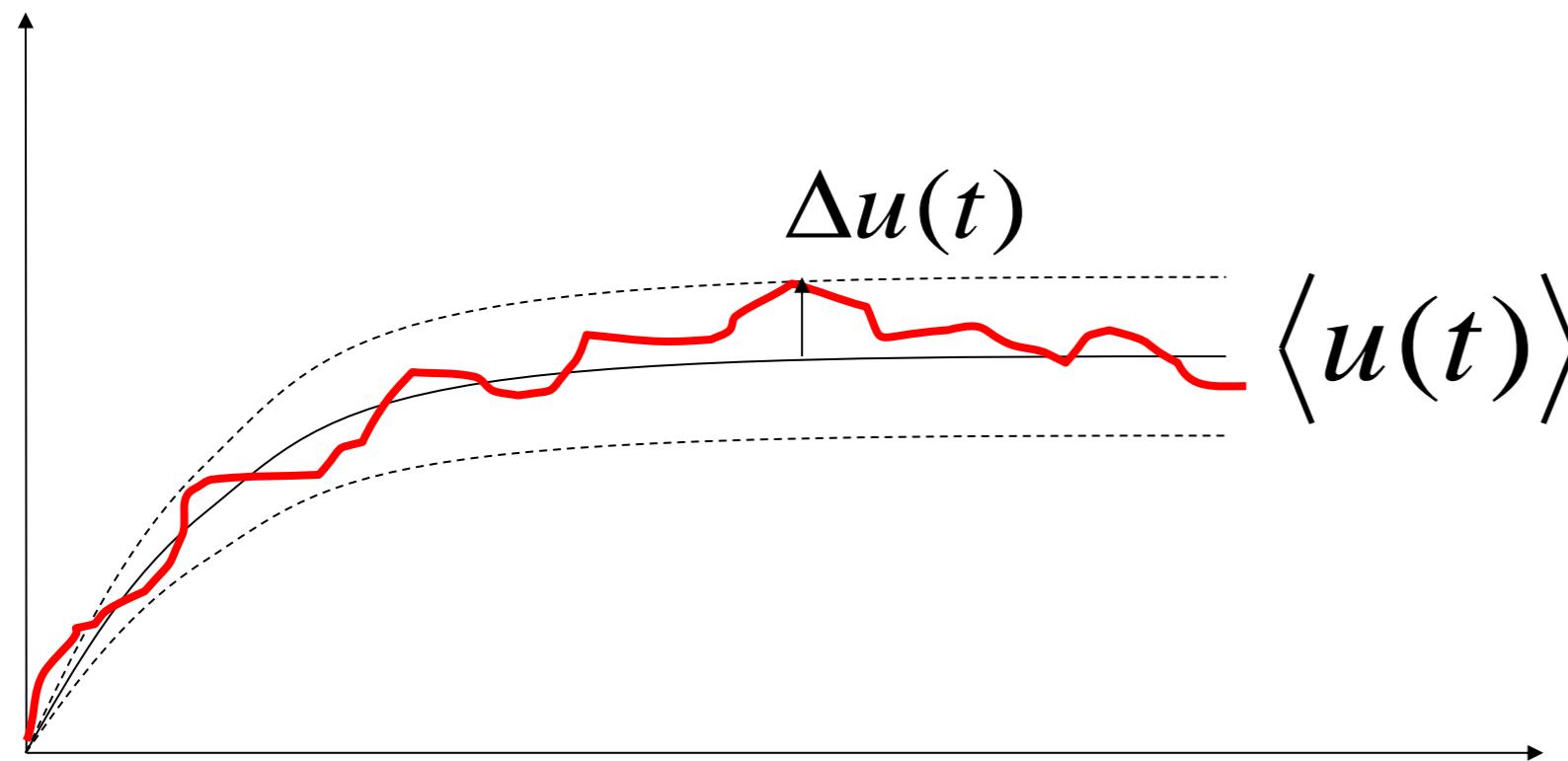
$$RI^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$

EPSC



Fluctuating input current

Neuronal Dynamics – 5.4b. Fluctuations of potential



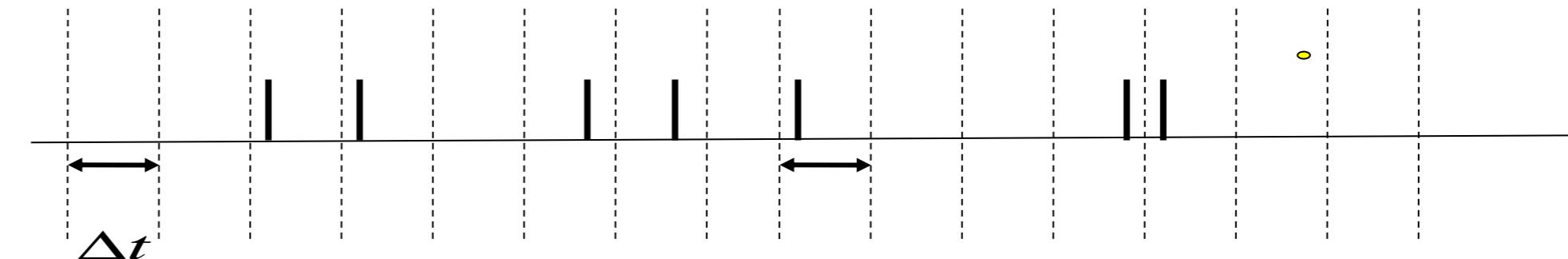
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

Input: step + fluctuations

Neuronal Dynamics – 5.4b. Calculating autocorrelations

Autocorrelation

$$\langle x(t)x(t') \rangle =$$



$$\begin{aligned} x(t) &= \sum_f \int dt' f(t-t') \delta(t'-t_k^f) \\ &= \int dt' f(t-t') S(t') \end{aligned}$$

Mean:

$$\langle x(t) \rangle = \int dt' f(t-t') \langle S(t') \rangle$$

$$\langle x(t) \rangle = \int ds f(s) \rho_0$$

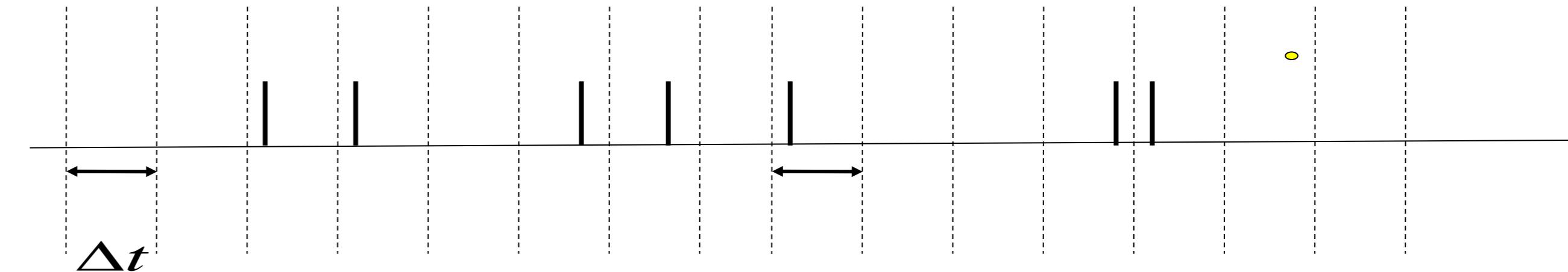
rate of homogeneous
Poisson process

$$\langle x(t)x(\hat{t}) \rangle = \int dt' \int dt'' f(t-t') f(\hat{t}-t'') \langle S(t')S(t'') \rangle$$

Neuronal Dynamics – 5.4b. Autocorrelation of Poisson

math detour
now!

Probability of spike
in step n AND step k



spike train

Probability of spike in time step:

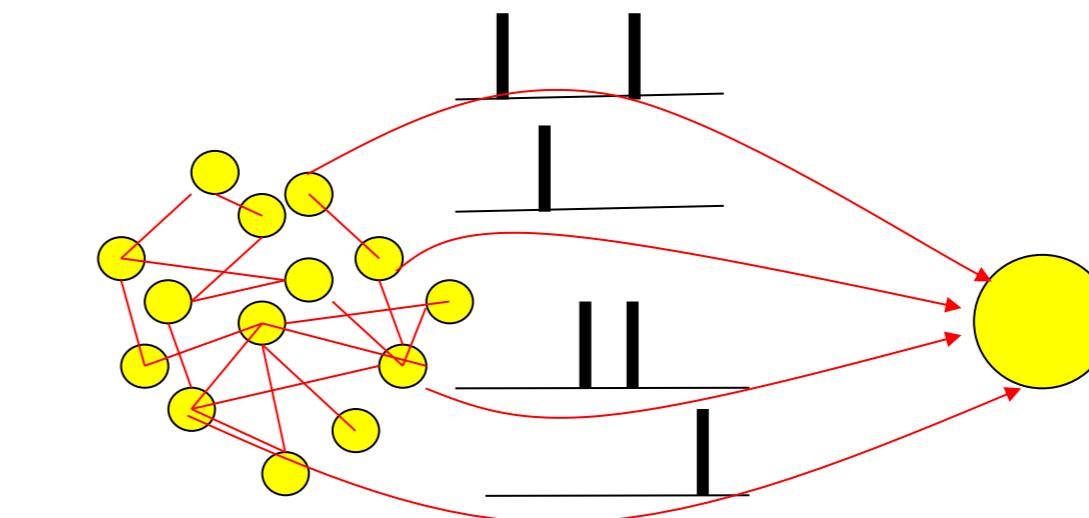
$$P_F = \rho_0 \Delta t$$

Autocorrelation (continuous time)
 $\langle S(t)S(t') \rangle = \rho_0 \delta(t - t') + [\rho_0]^2$

Neuronal Dynamics – 5.4b. Fluctuation of potential

for a passive membrane, we can analytically predict the amplitude of membrane potential fluctuations

Leaky integrate-and-fire in subthreshold regime



Passive membrane

$$u(t) = \sum_k w_k \sum_f \varepsilon(t - t_k^f)$$

$$= \sum_k w_k \int dt' \varepsilon(t - t') S_k(t')$$

fluctuating potential

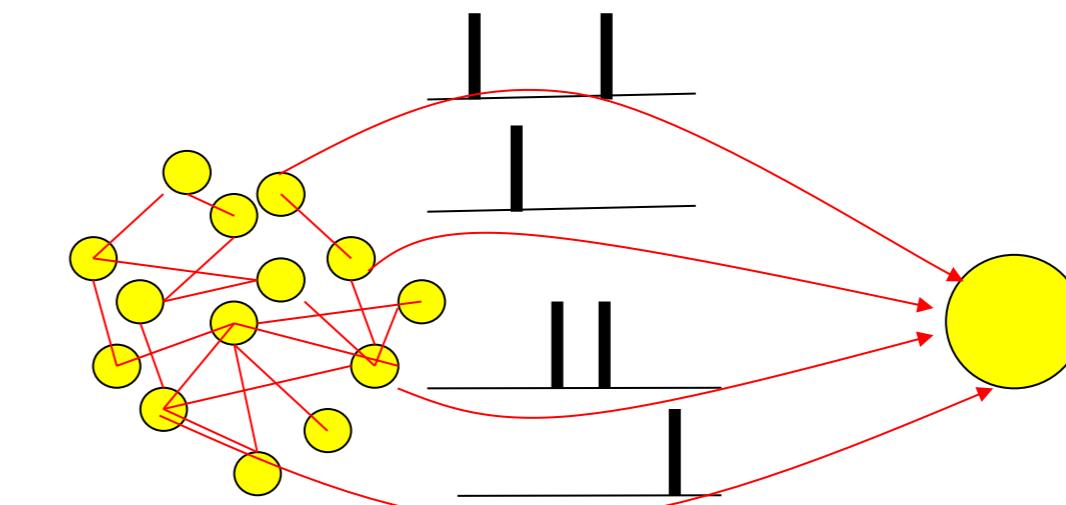
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle [u(t)]^2 \rangle - \langle u(t) \rangle^2$$

Neuronal Dynamics – 5.4b. Fluctuation of potential

Stochastic spike arrival:

for a passive membrane, we can analytically predict the amplitude of membrane potential fluctuations

*Leaky integrate-and-fire
in subthreshold regime*



Passive membrane

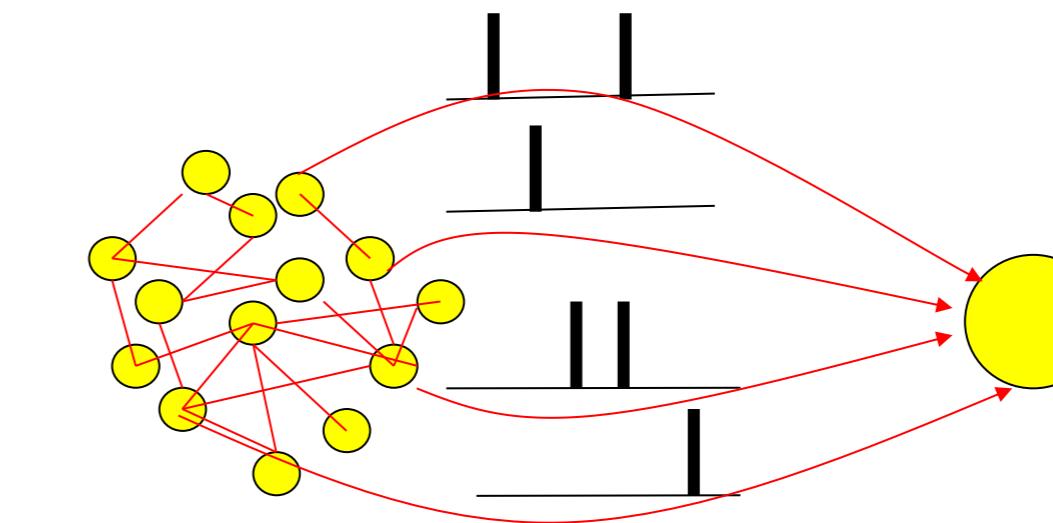
$$u(t) = \sum_k w_k \sum_f \varepsilon(t - t_k^f)$$

$$= \sum_k w_k \int dt' \varepsilon(t - t') S_k(t')$$

fluctuating potential

$$\langle \Delta u(t) \Delta u(t) \rangle = \langle [u(t)]^2 \rangle - \langle u(t) \rangle^2$$

Neuronal Dynamics – 5.4b. Fluctuation of potential



Passive membrane

$$u(t) = \sum_k w_k \sum_f \varepsilon(t - t_k^f) \\ = \sum_k w_k \int dt' \varepsilon(t - t') S_k(t')$$

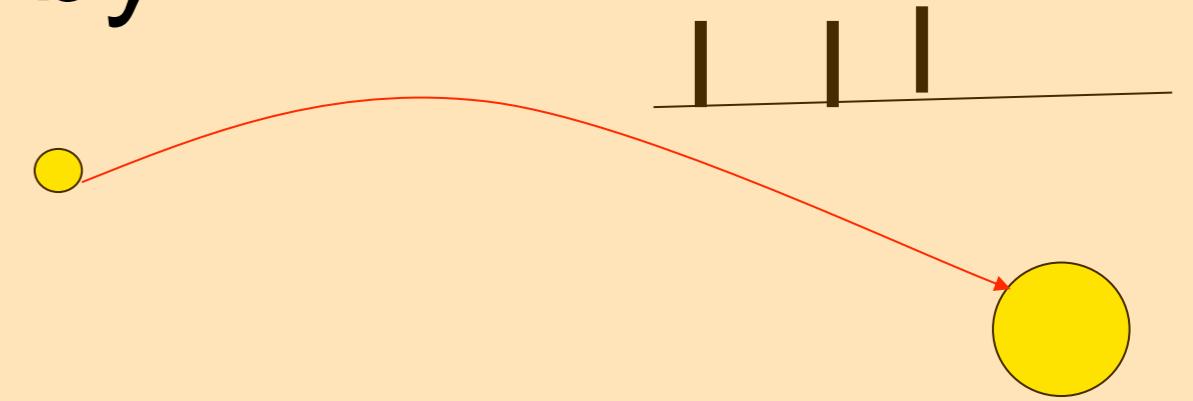
Fluctuations of potential

$$\langle [\Delta u(t)]^2 \rangle = \langle [u(t)]^2 \rangle - \langle u(t) \rangle^2$$

Neuronal Dynamics – Quiz 5.4

A linear (=passive) membrane has a potential given by

$$u(t) = \sum_f \int dt' f(t-t') \delta(t'-t_k^f) + a$$

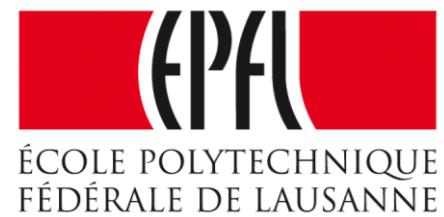


Suppose the neuronal dynamics are given by

$$\tau \frac{d}{dt} u = -(u - u_{rest}) + q \sum_f \delta(t - t_k^f)$$

- the filter f is exponential with time constant τ
- the constant a is equal to the time constant τ
- the constant a is equal to u_{rest}
- the amplitude of the filter f is q
- the amplitude of the filter f is u_{rest}

Week 5 – part 5 : Stochastic spike firing in integrate-and-fire models



Neuronal Dynamics: Computational Neuroscience of Single Neurons

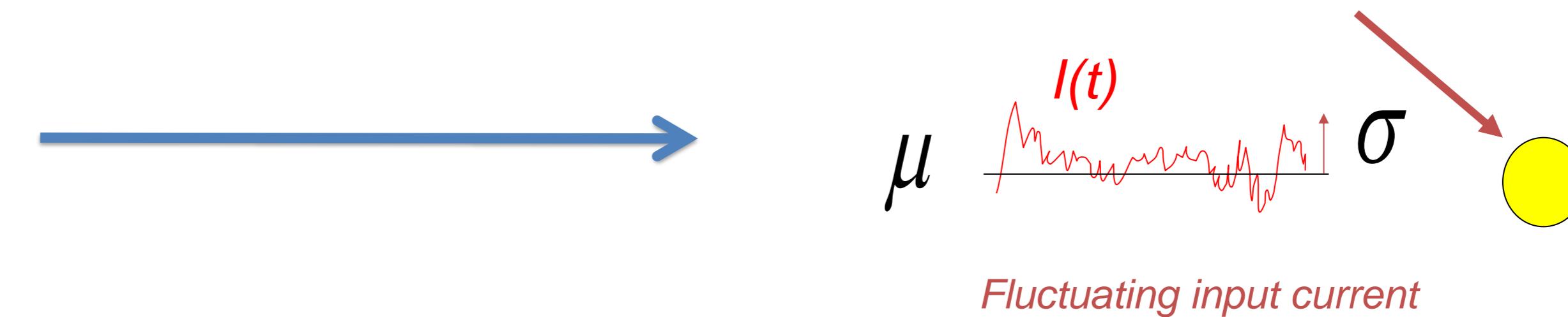
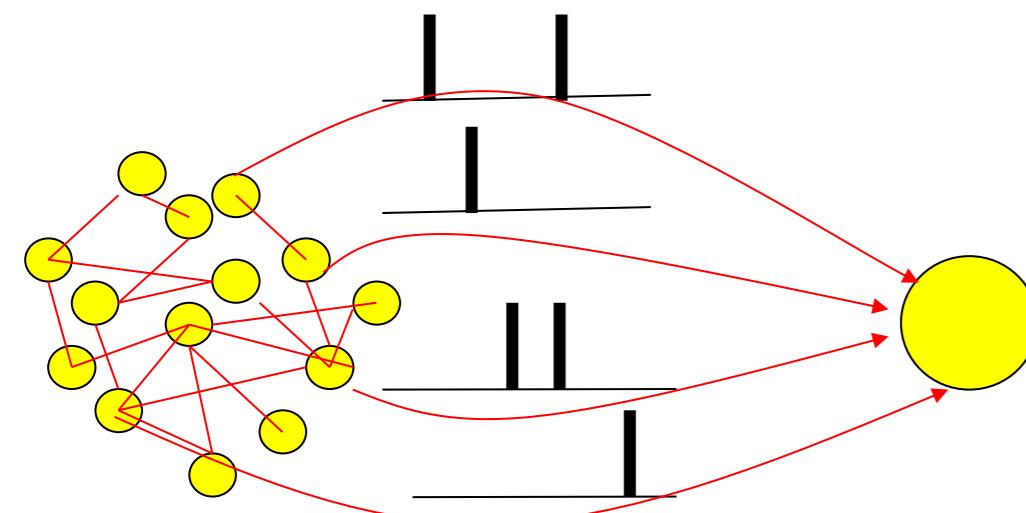
Week 5 – Variability and Noise: The question of the neural code

Wulfram Gerstner

EPFL, Lausanne, Switzerland

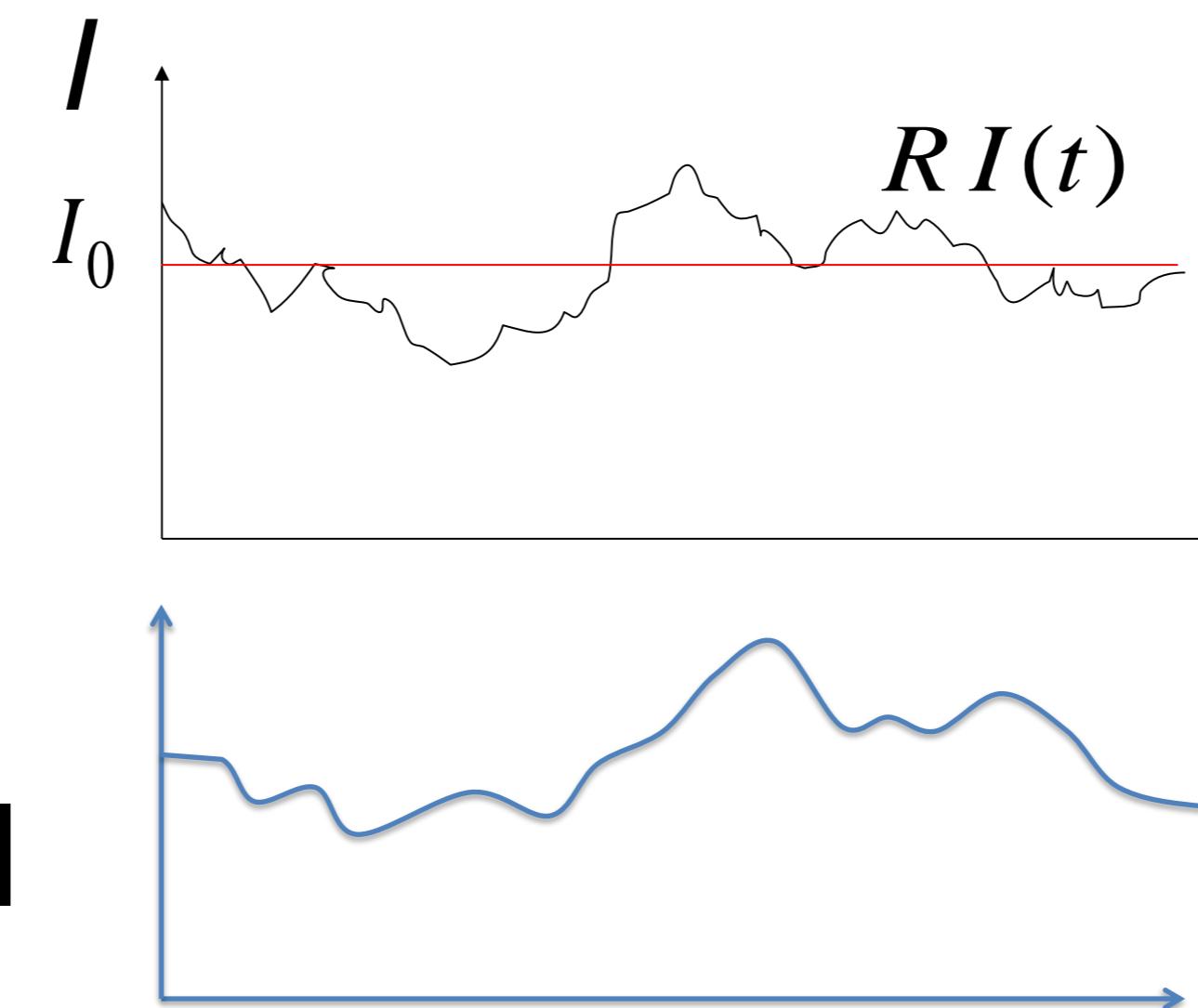
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Neuronal Dynamics – review: Fluctuations of potential



Passive membrane

$$\tau \frac{d}{dt}u = -(u - u_{rest}) + RI(t)$$

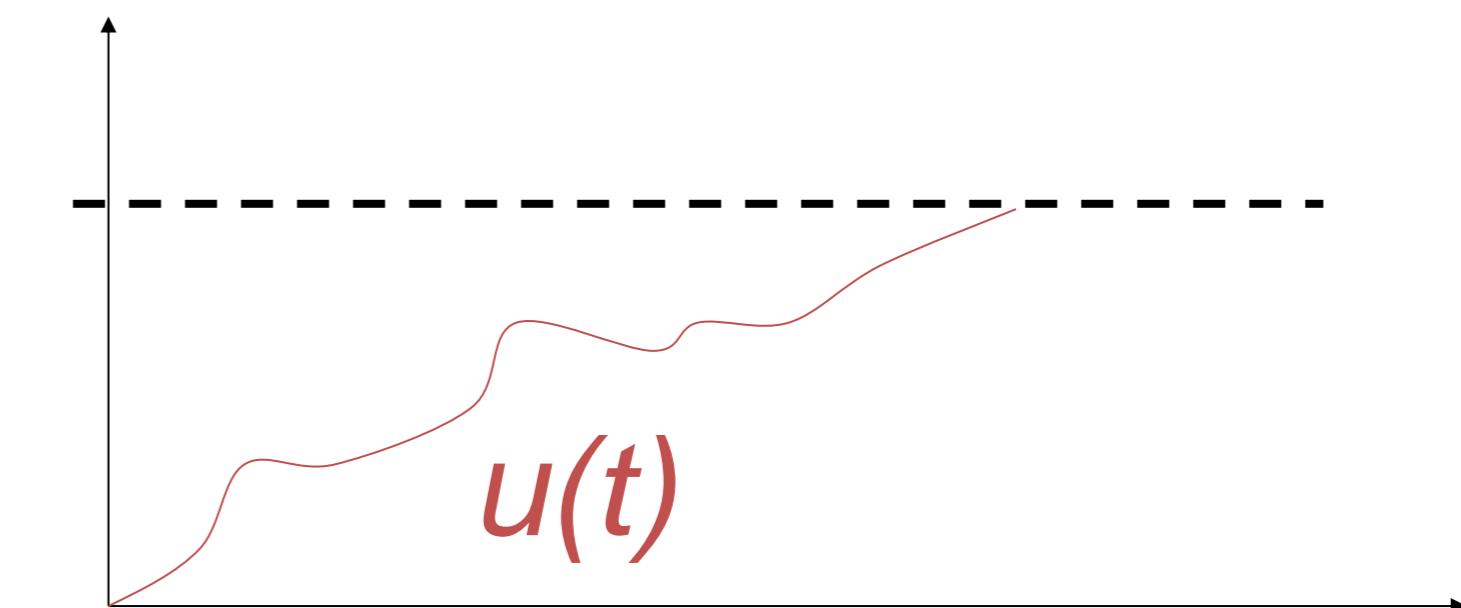
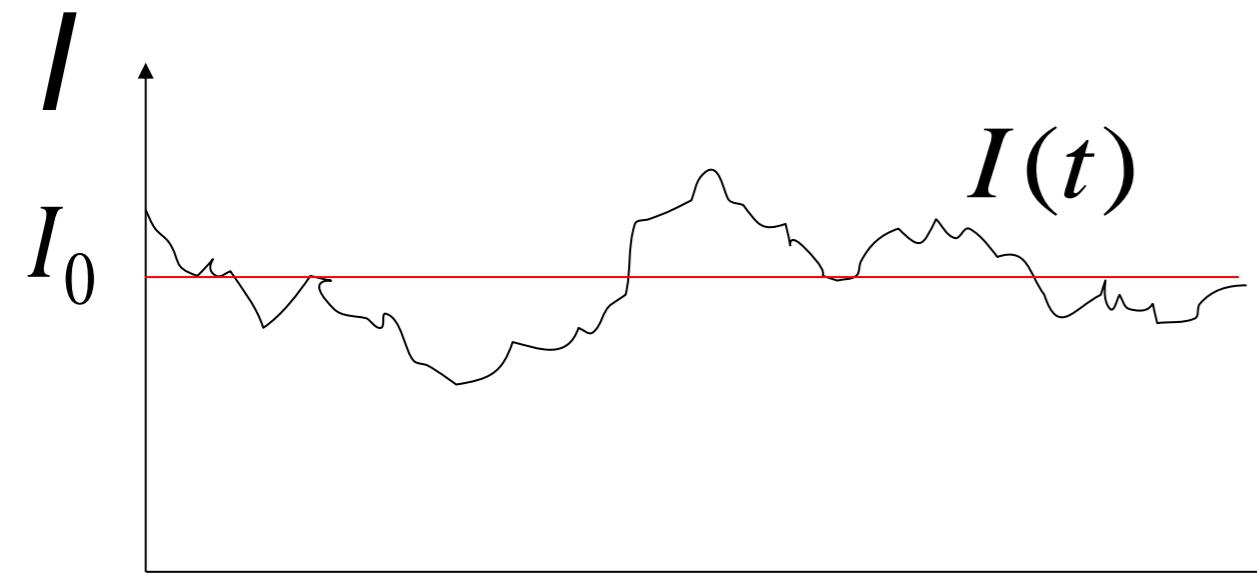


→ Fluctuating potential

$$I^{syn}(t) = I_0 + I^{fluct}(t)$$

Neuronal Dynamics – 5.5. Stochastic leaky integrate-and-fire

effective noise current



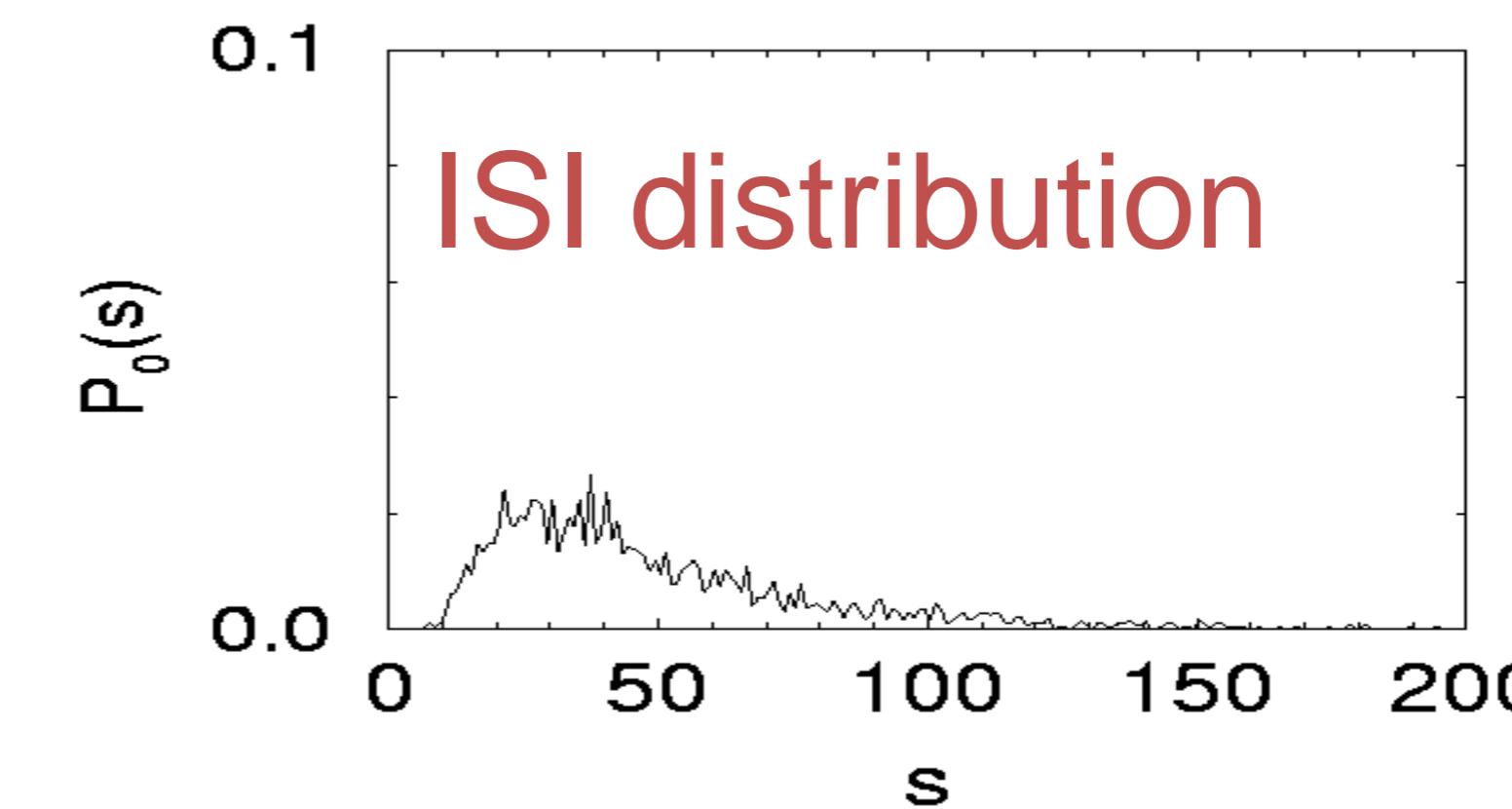
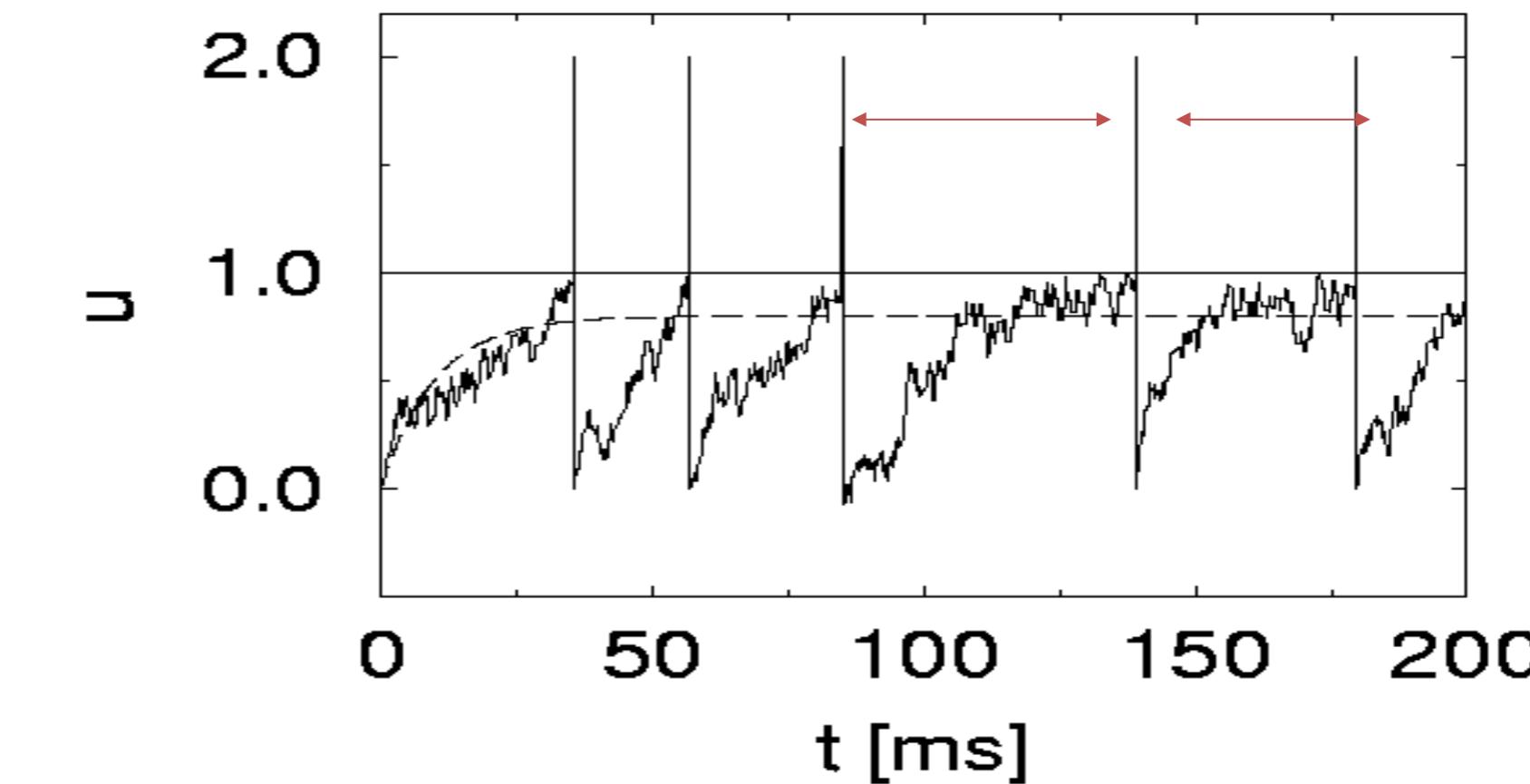
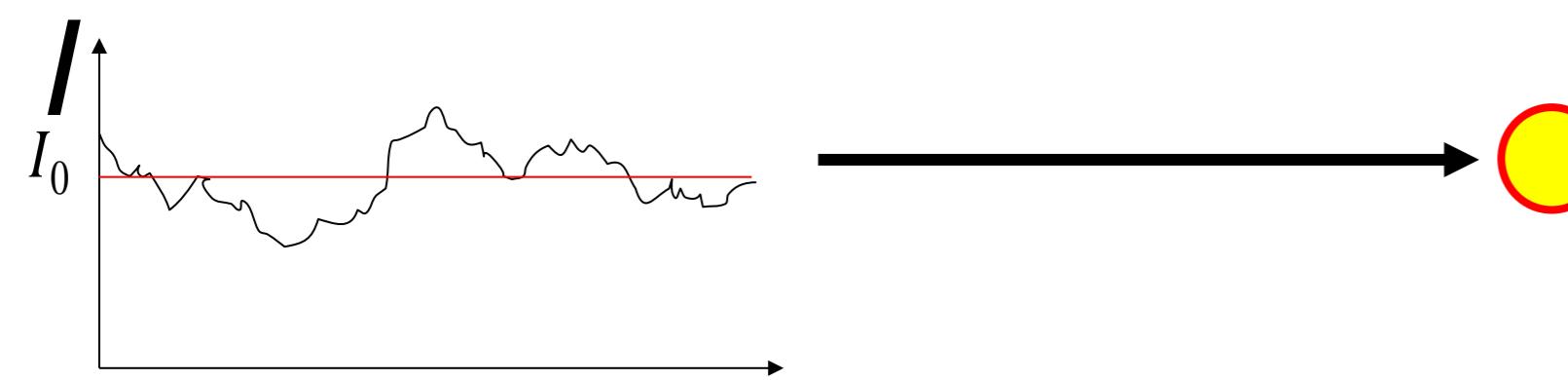
LIF

$$\tau \frac{d}{dt}u = -(u - u_{rest}) + RI(t)$$
$$I(t) = [I_o + I_{noise}]$$

IF $u(t) = \vartheta$ THEN $u(t + \Delta) = u_r$

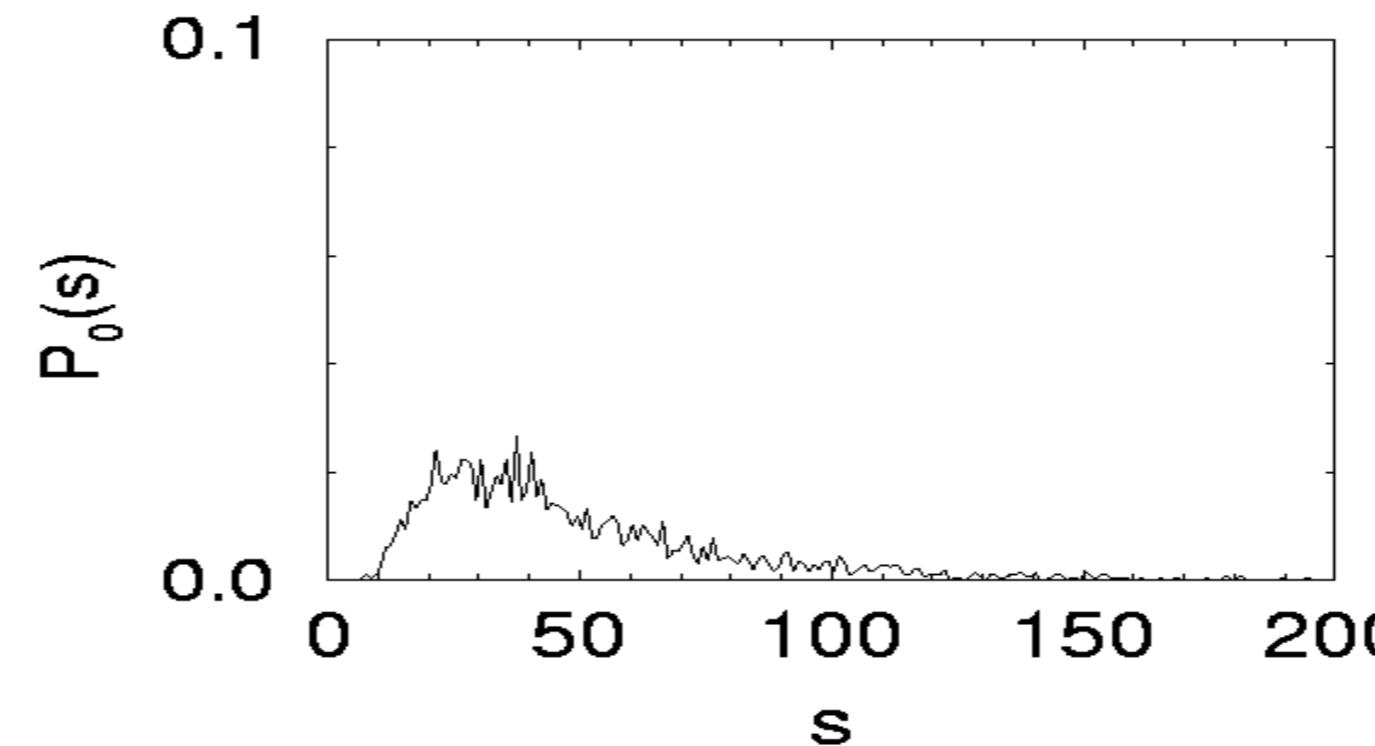
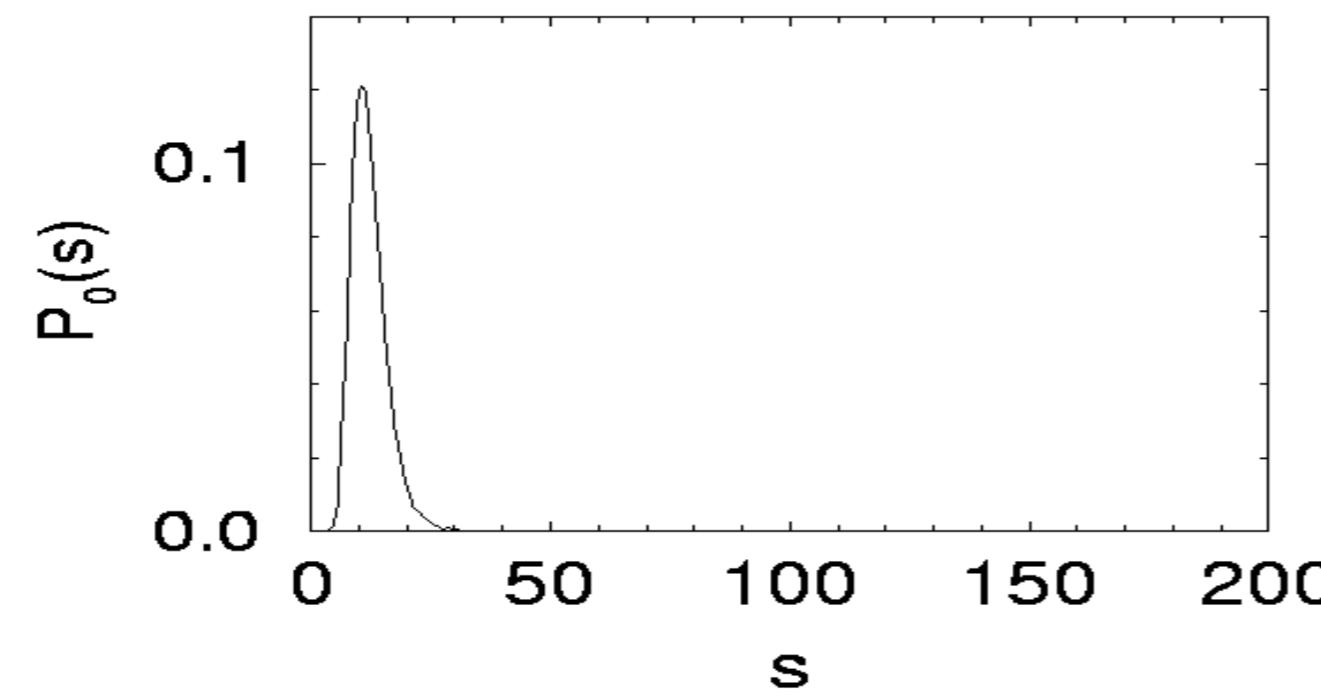
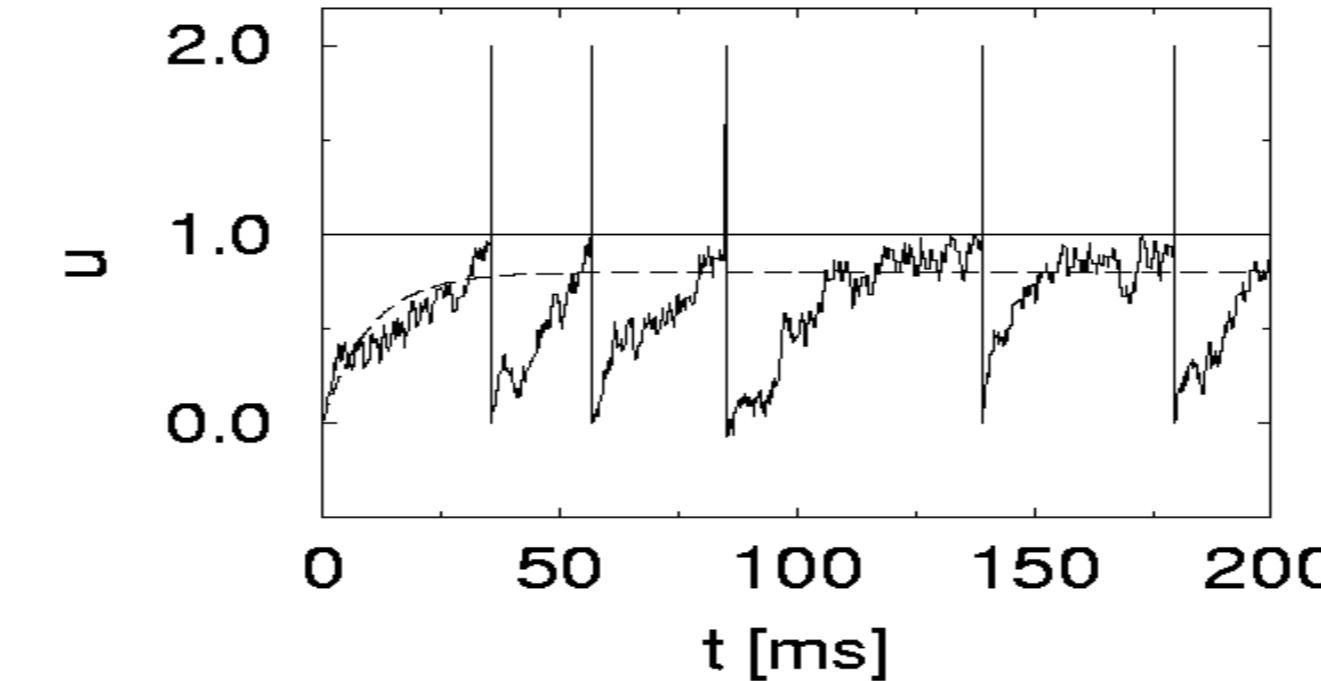
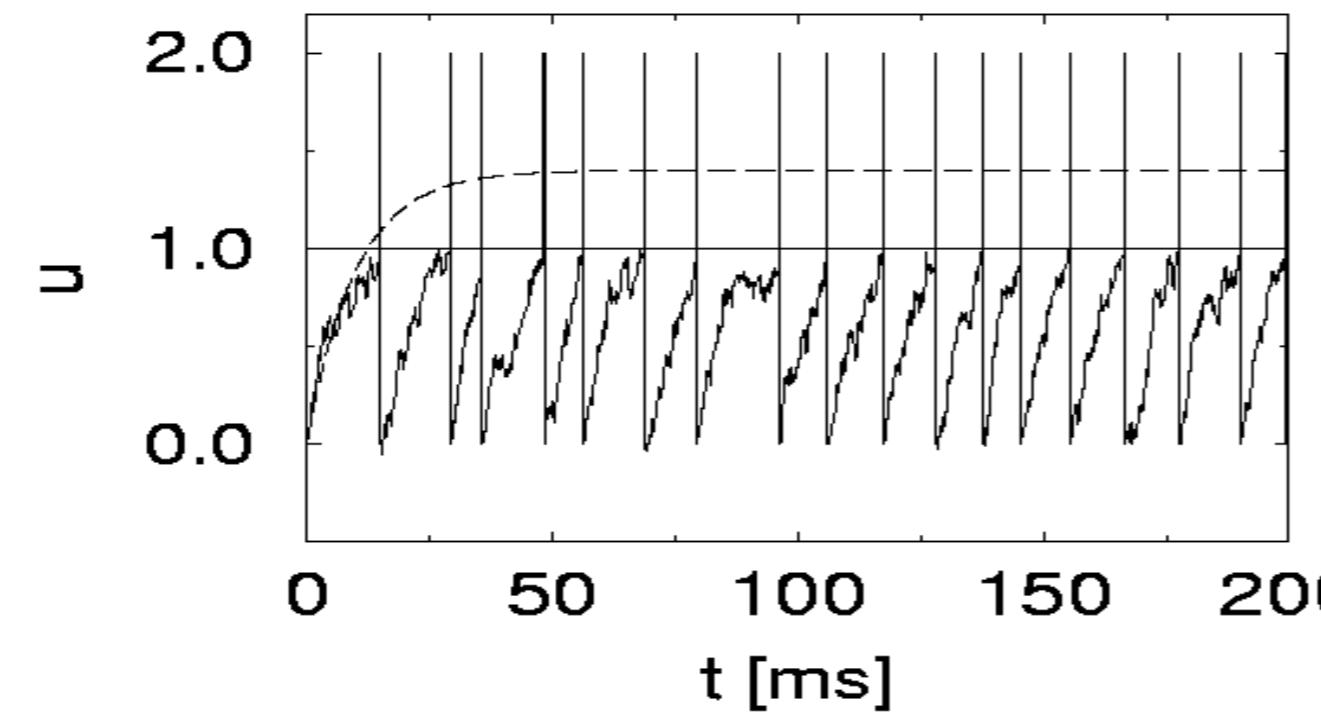
noisy input/
diffusive noise/
stochastic spike
arrival

stochastic spike arrival in I&F – interspike intervals



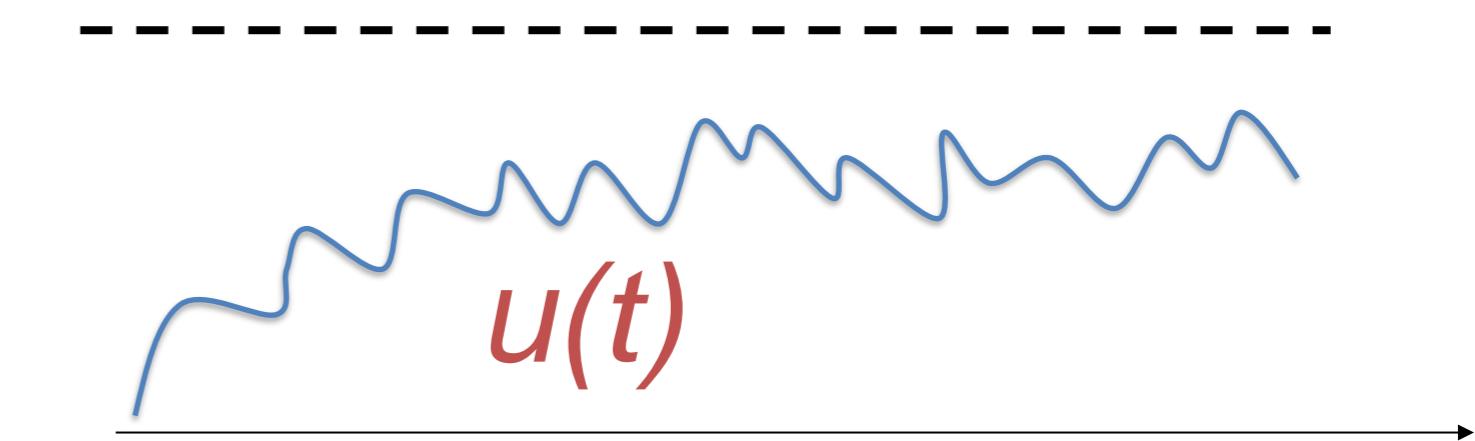
LIF with Diffusive noise (stochastic spike arrival)

Superthreshold vs. Subthreshold regime



Neuronal Dynamics – 5.5. Stochastic leaky integrate-and-fire

noisy input/ diffusive noise/
stochastic spike arrival



subthreshold regime:

- firing driven by fluctuations
- broad ISI distribution
- *in vivo* like

Neuronal Dynamics week 5– References and Suggested Reading

Reading: W. Gerstner, W.M. Kistler, R. Naud and L. Paninski,

Neuronal Dynamics: from single neurons to networks and models of cognition. Ch. 7,8: Cambridge, 2014

OR W. Gerstner and W. M. Kistler, Spiking Neuron Models, Chapter 5, Cambridge, 2002

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- Konig, P., et al. (1996). Integrator or coincidence detector? the role of the cortical neuron revisited. *Trends Neurosci*, 19(4):130-137.