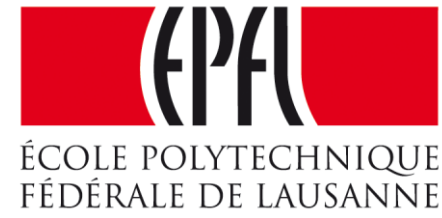


Week 5 – part 1 :Variability



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

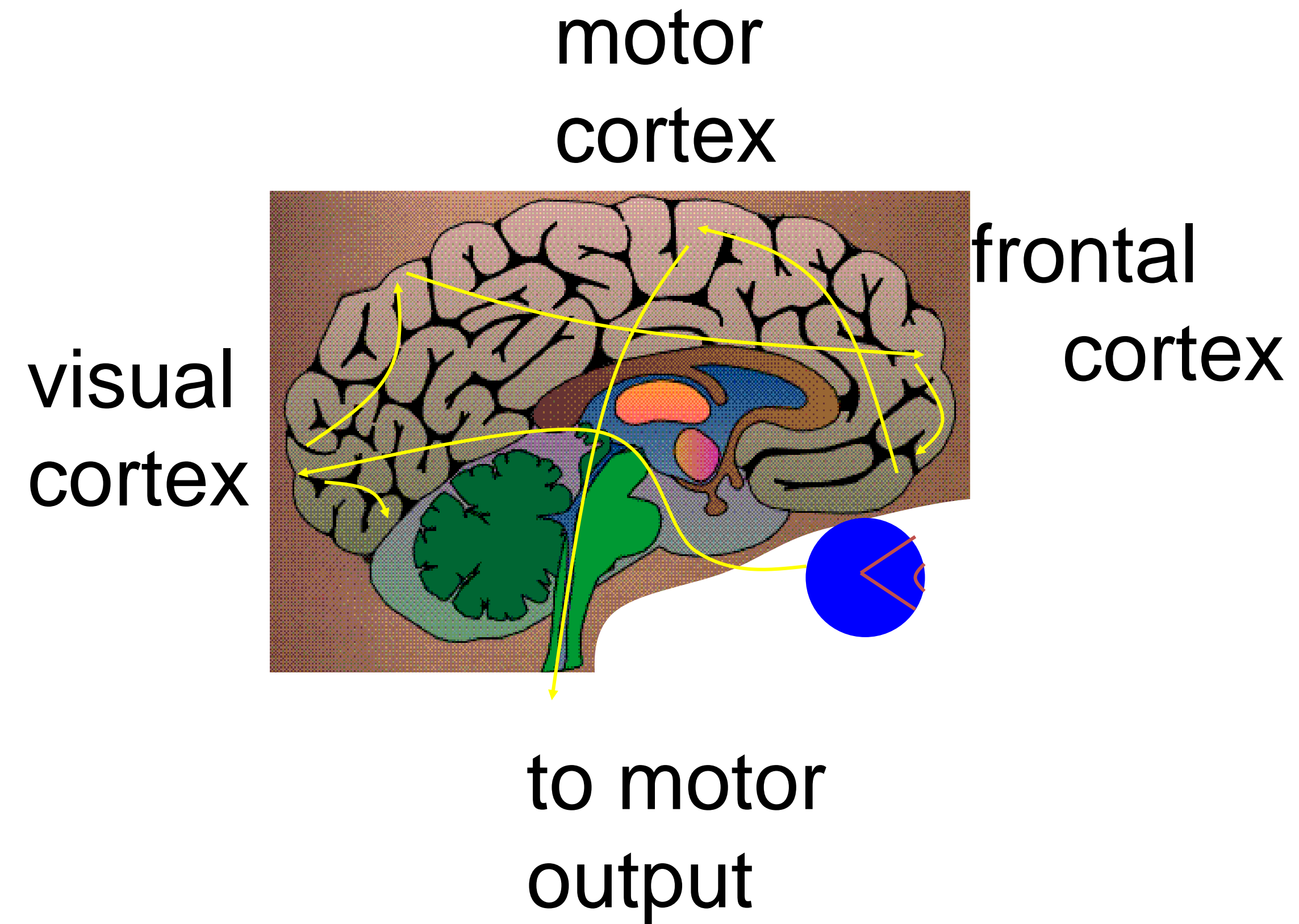
5.4 Stochastic spike arrival

- Membrane potential fluctuations

5.5. Stochastic spike firing

- subthreshold and superthreshold

Neuronal Dynamics – 5.1. Variability



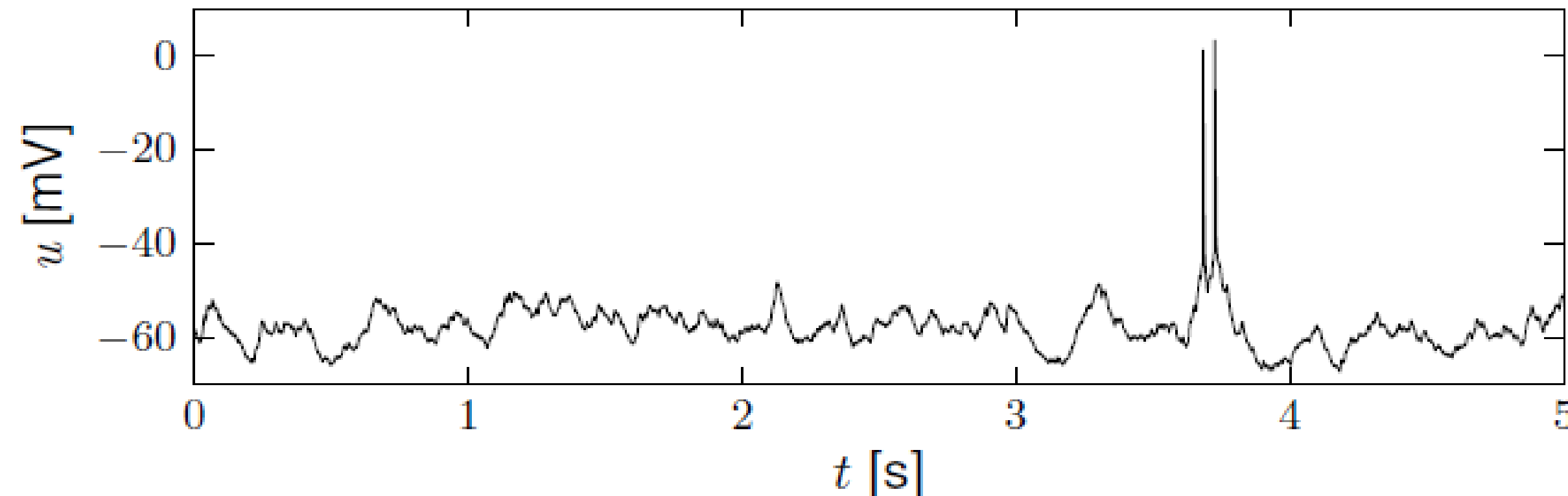
Neuronal Dynamics – 5.1 Variability in vivo

Spontaneous activity *in vivo*

Variability

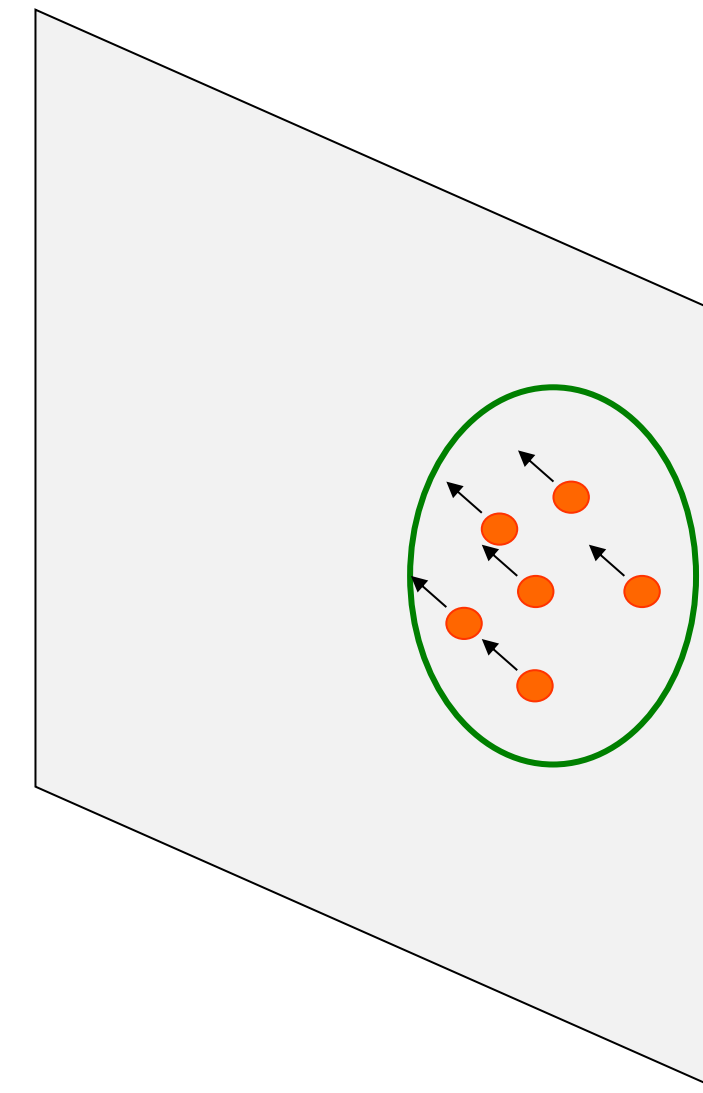
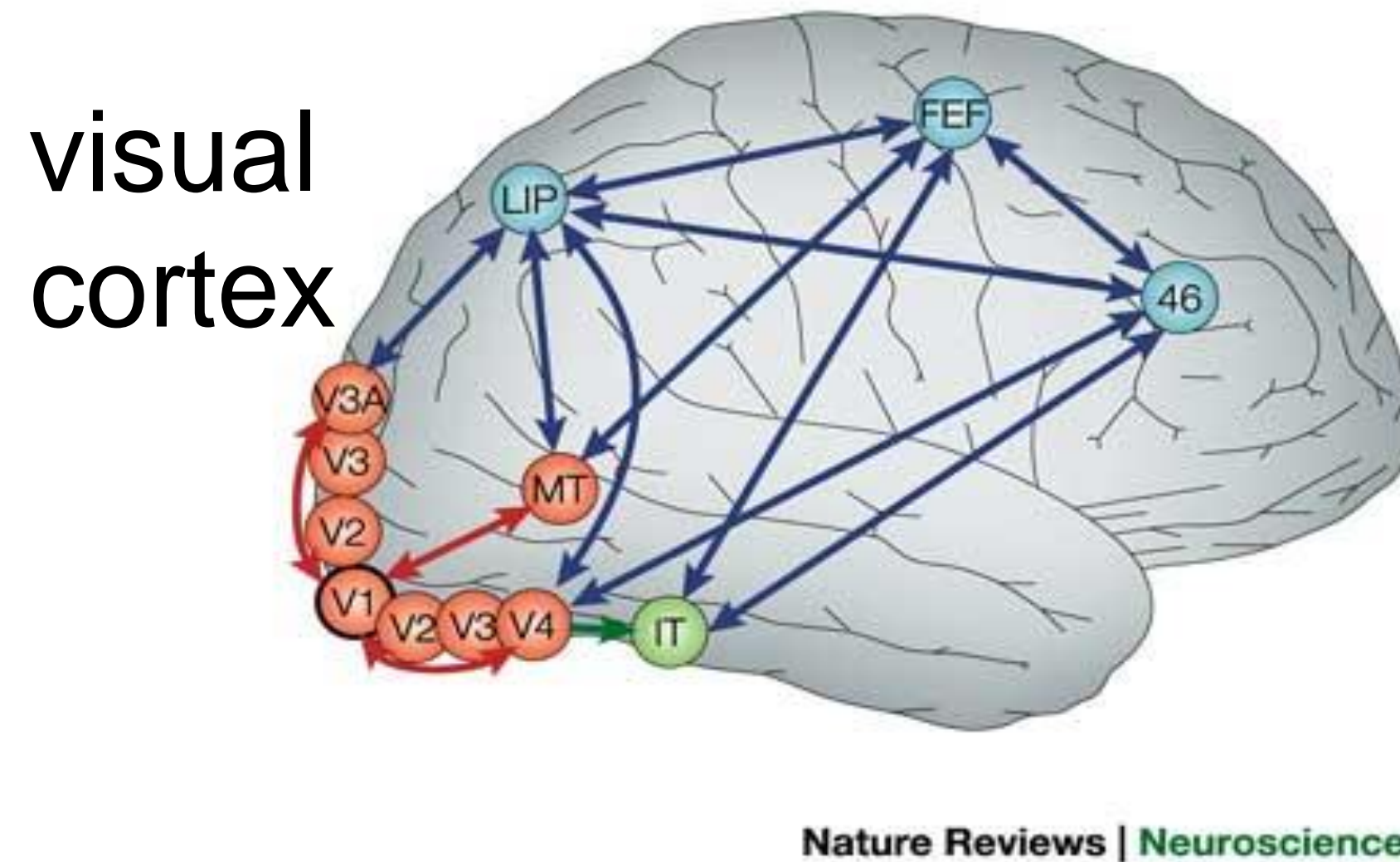
- of membrane potential?
- of spike timing?

awake mouse, cortex, freely whisking,



Crochet et al., 2011

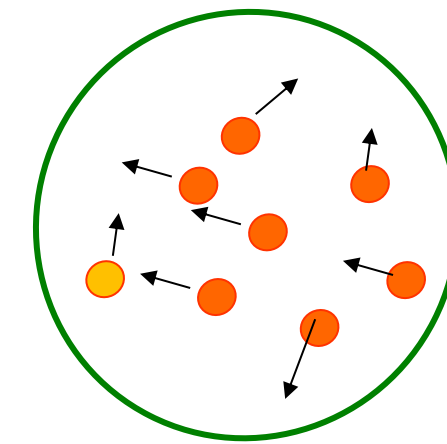
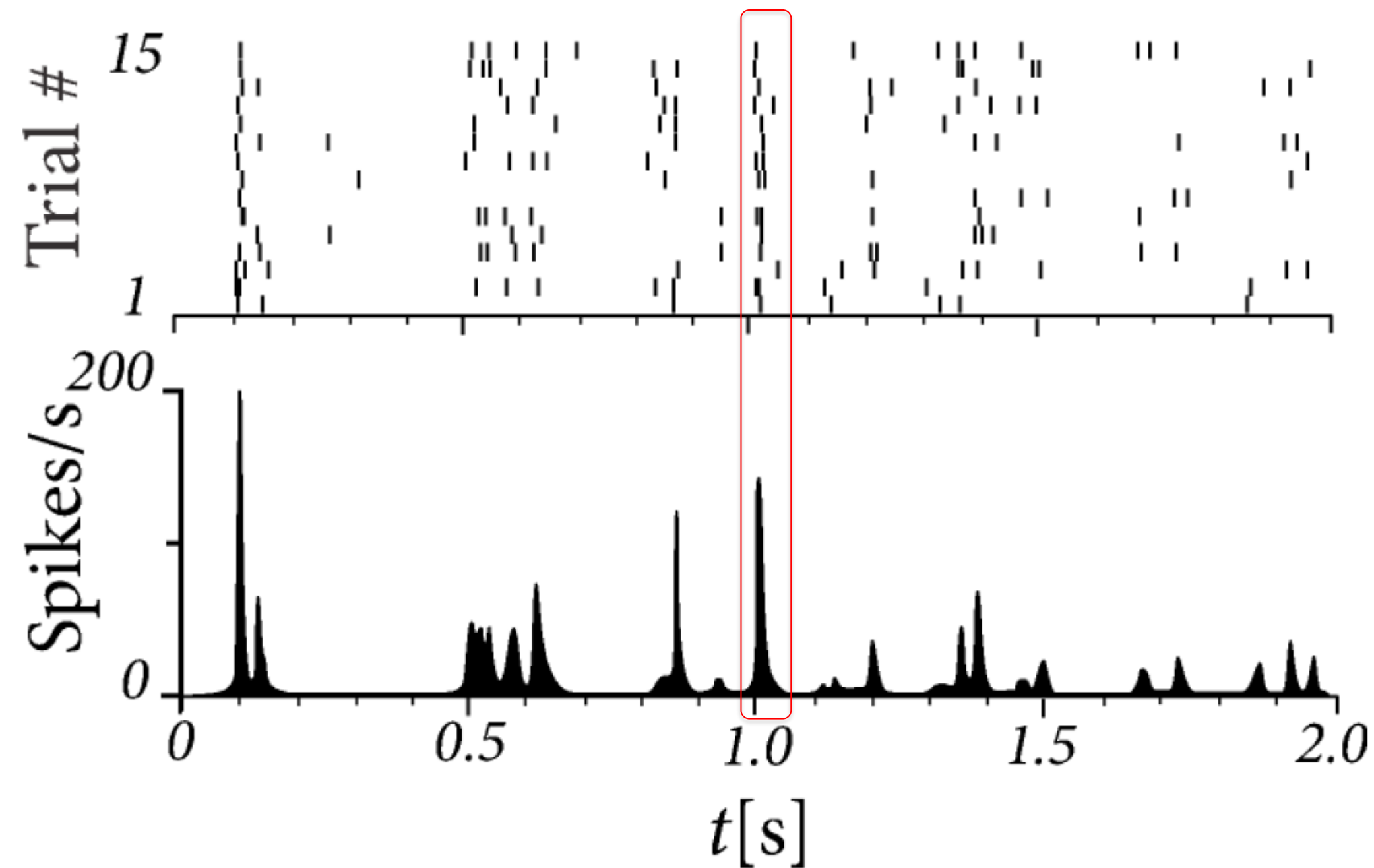
Detour: Receptive fields in V5/MT



cells in visual cortex MT/V5
respond to motion stimuli

Neuronal Dynamics – 5.1 Variability in vivo

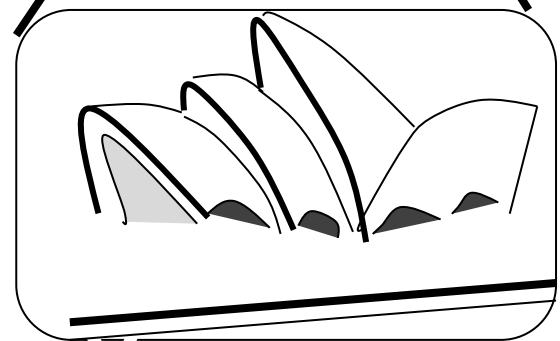
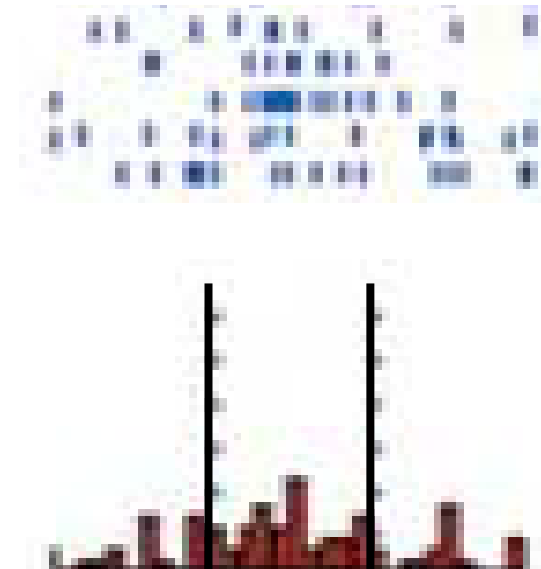
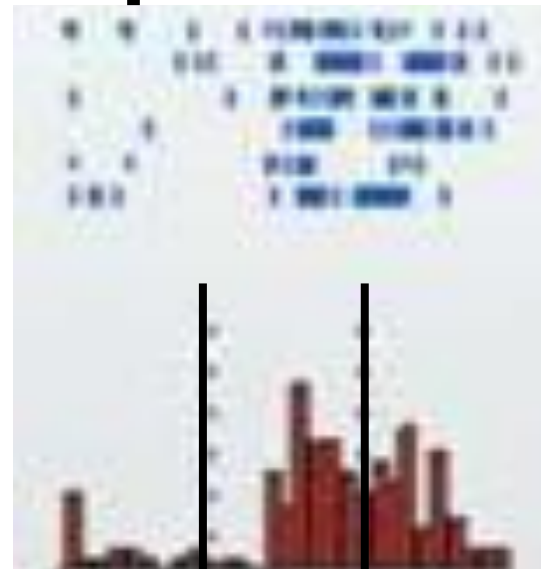
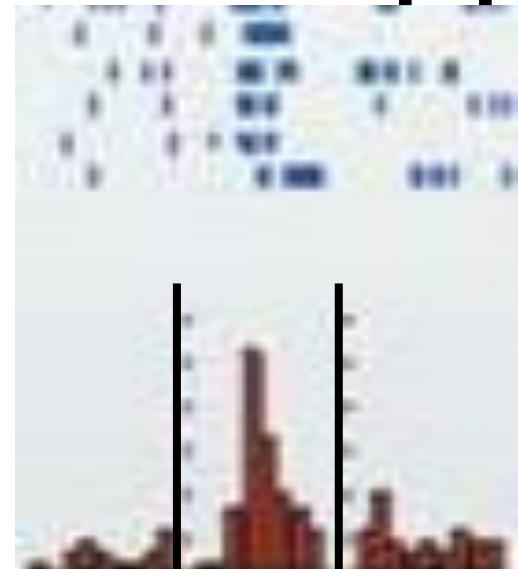
15 repetitions of the **same** random dot motion pattern



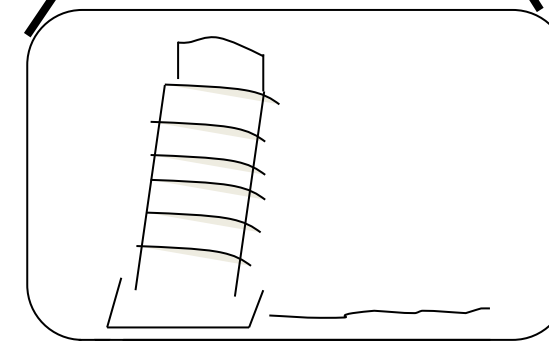
*adapted from Bair and Koch 1996;
data from Newsome 1989*

Neuronal Dynamics – 5.1 Variability in vivo

Human Hippocampus



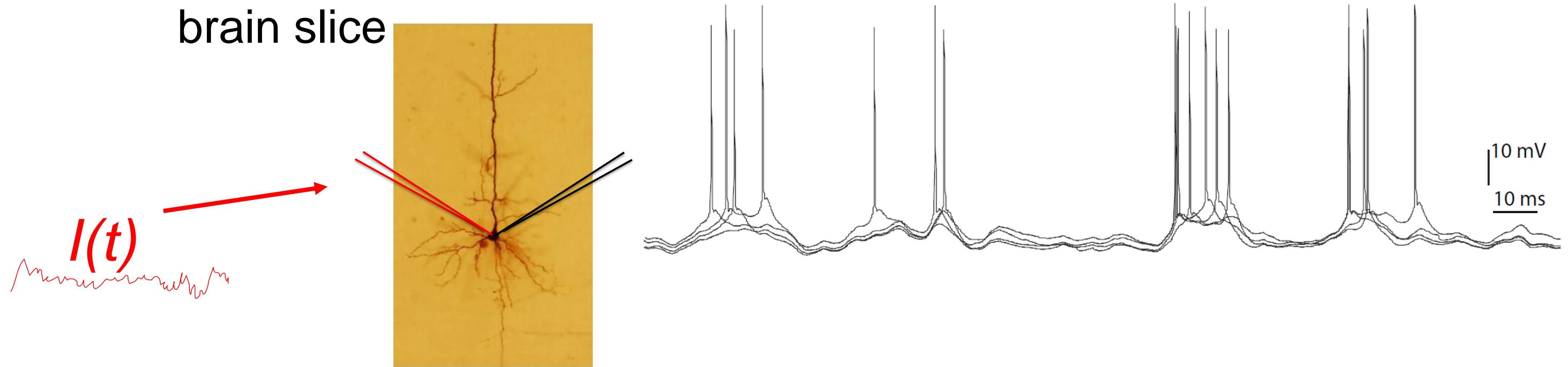
Sidney
opera



*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

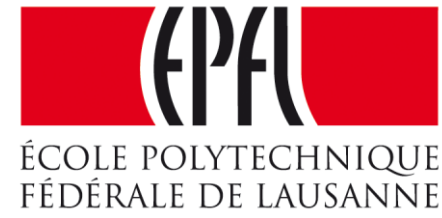
fluctuations=noise?

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

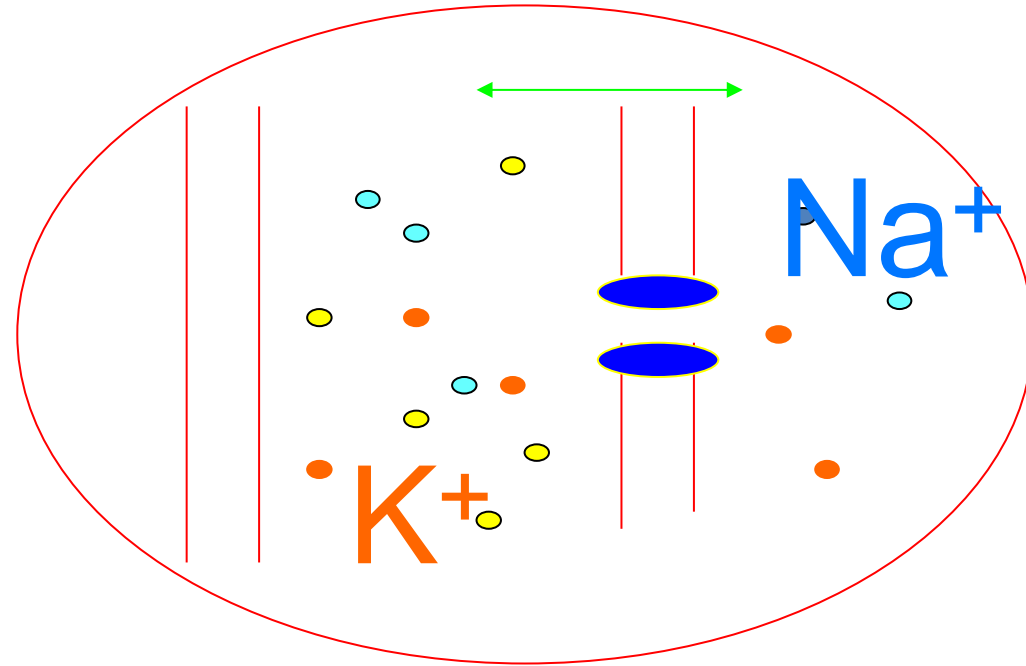
- Membrane potential fluctuations

5.5. Stochastic spike firing

- subthreshold and superthreshold

Neuronal Dynamics – 5.2. Sources of Variability

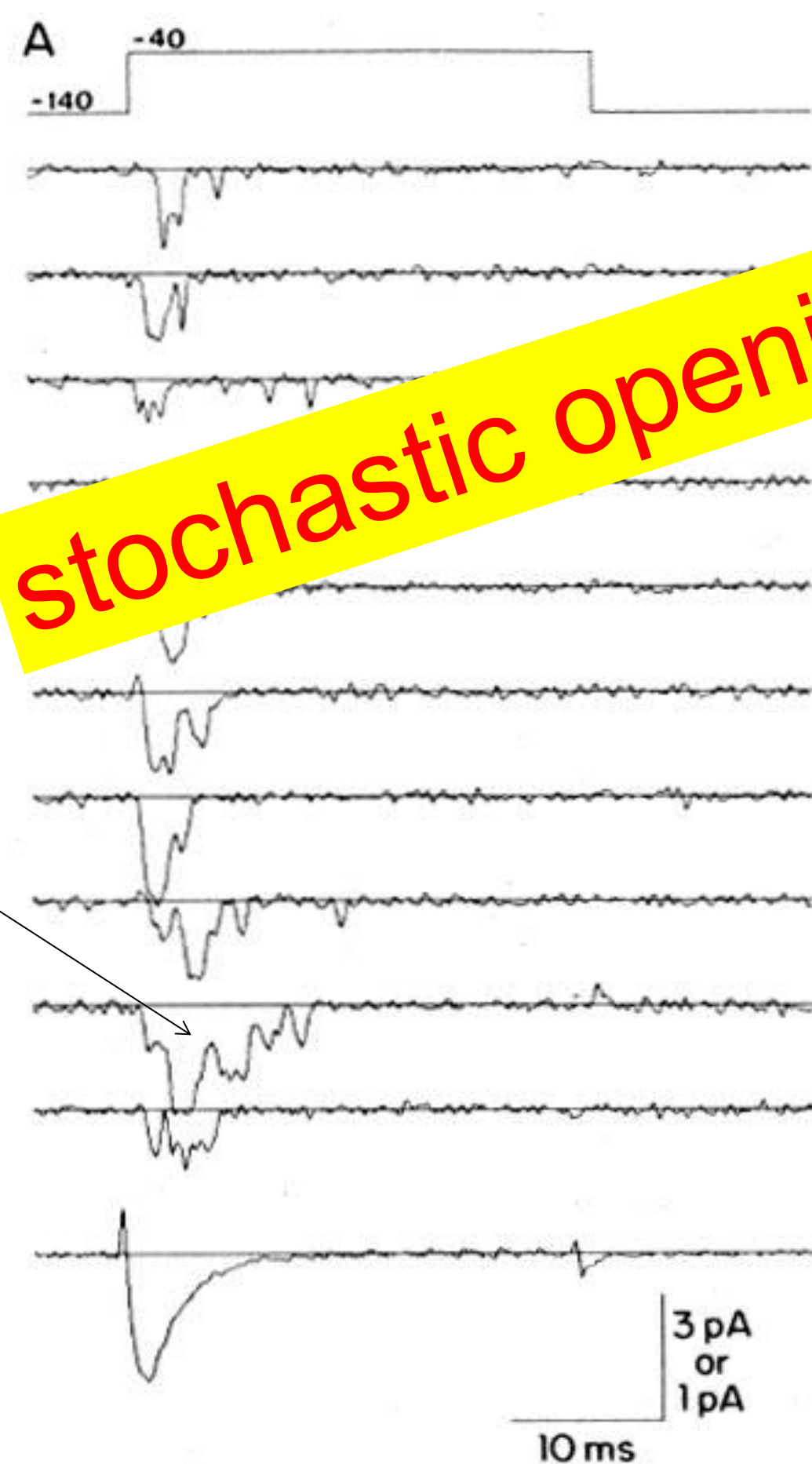
- Intrinsic noise (ion channels)



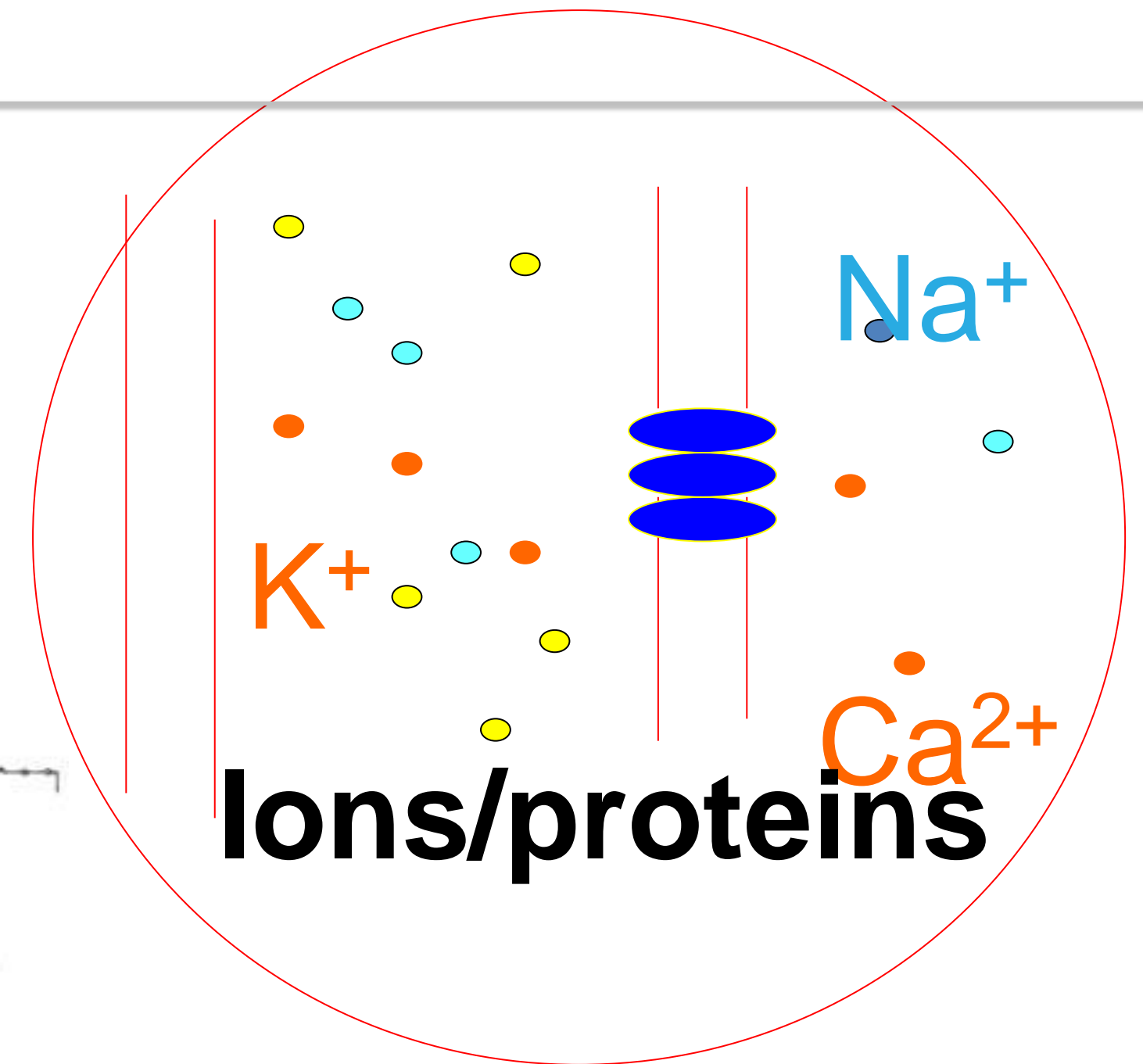
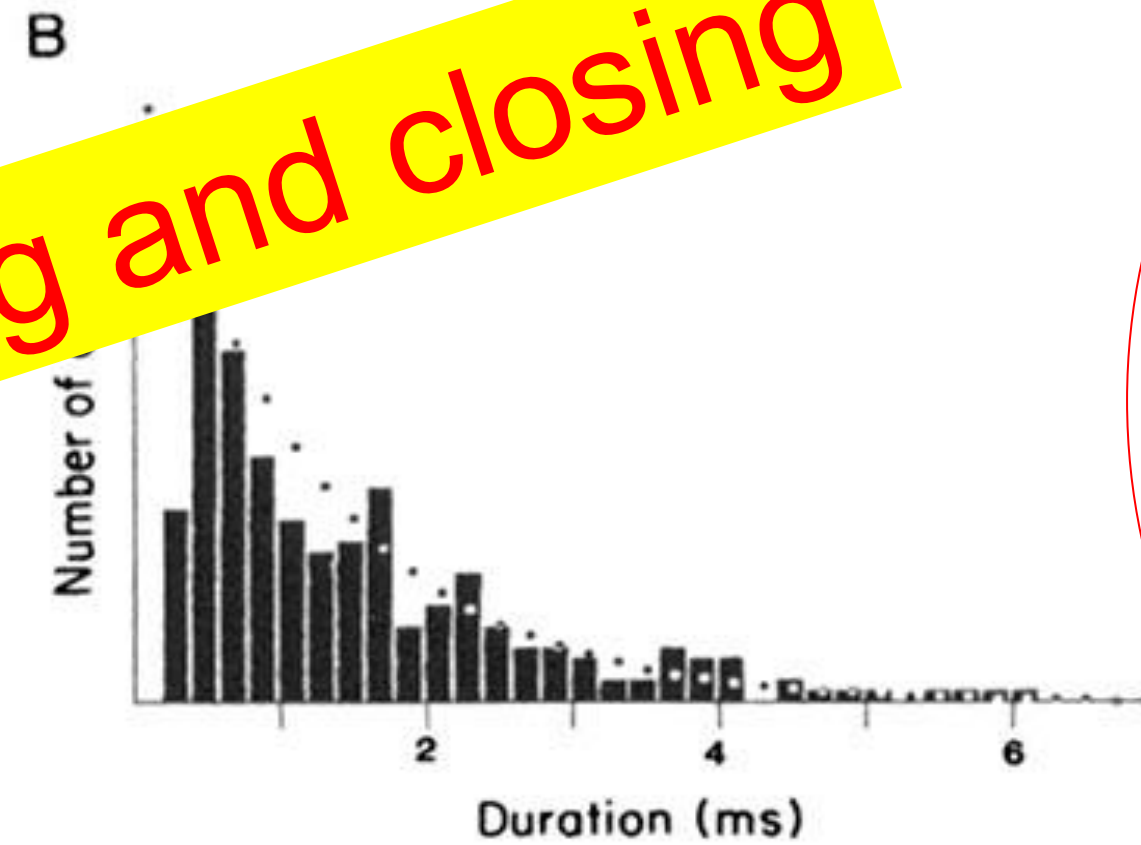
- Finite number of channels
- Finite temperature

Review from 2.5 Ion channels

Steps:
Different number
of channels



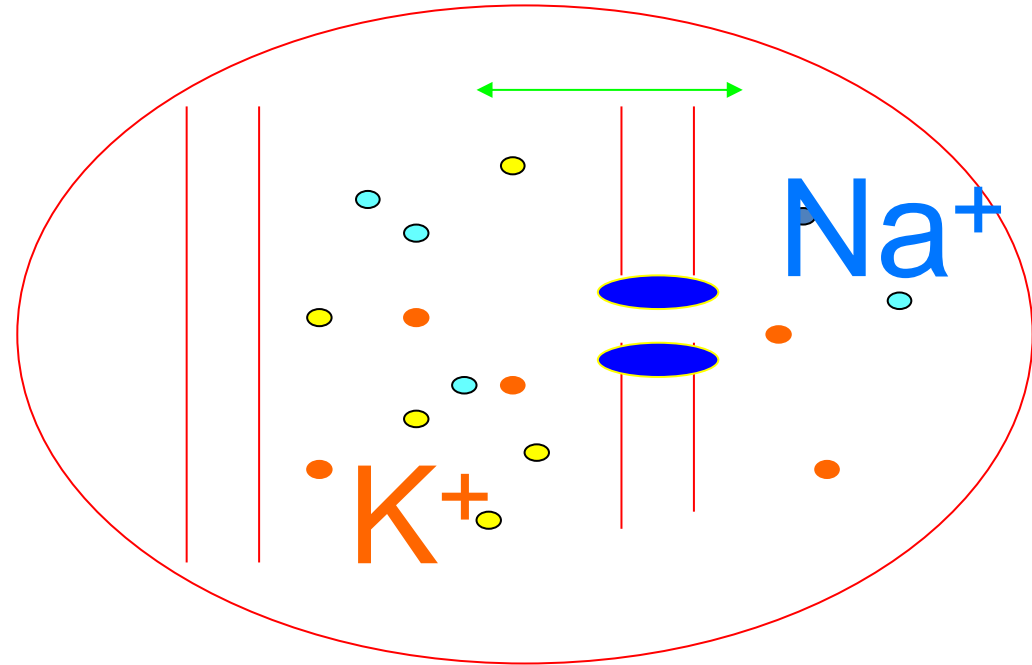
stochastic opening and closing



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

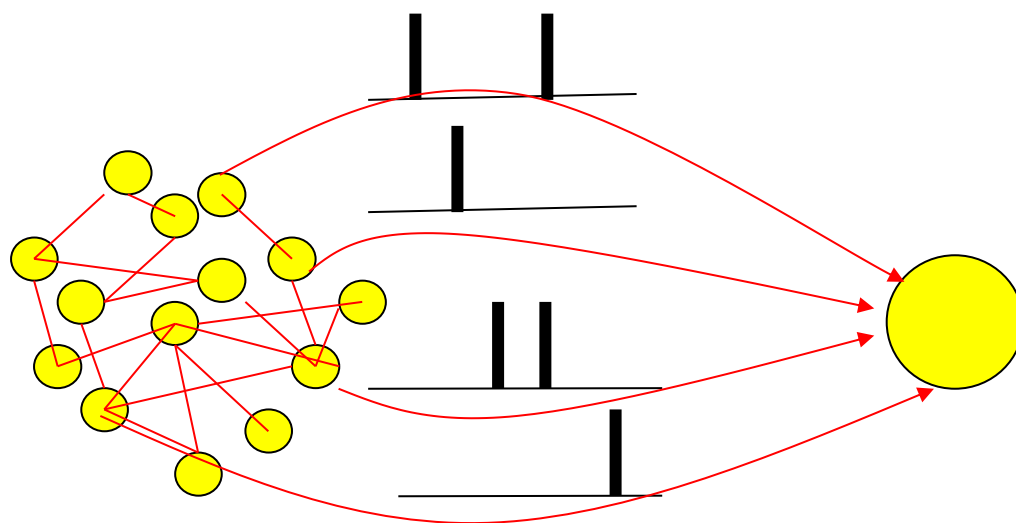
Neuronal Dynamics – 5.2. Sources of Variability

- Intrinsic noise (ion channels)



- Finite number of channels
- Finite temperature

- Network noise (background activity)

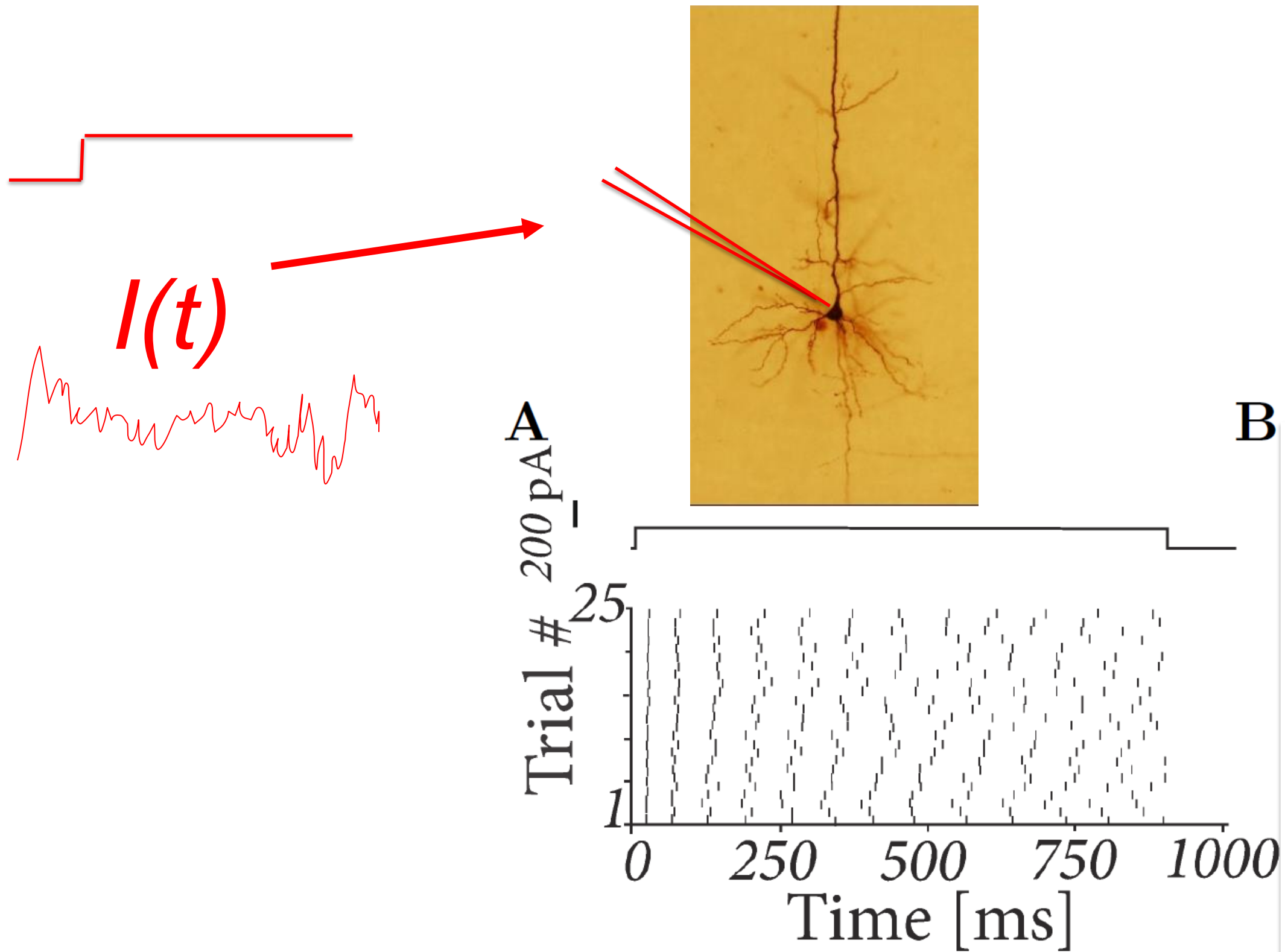


- Spike arrival from other neurons
- Beyond control of experimentalist

—————> Check intrinsic noise by removing the network

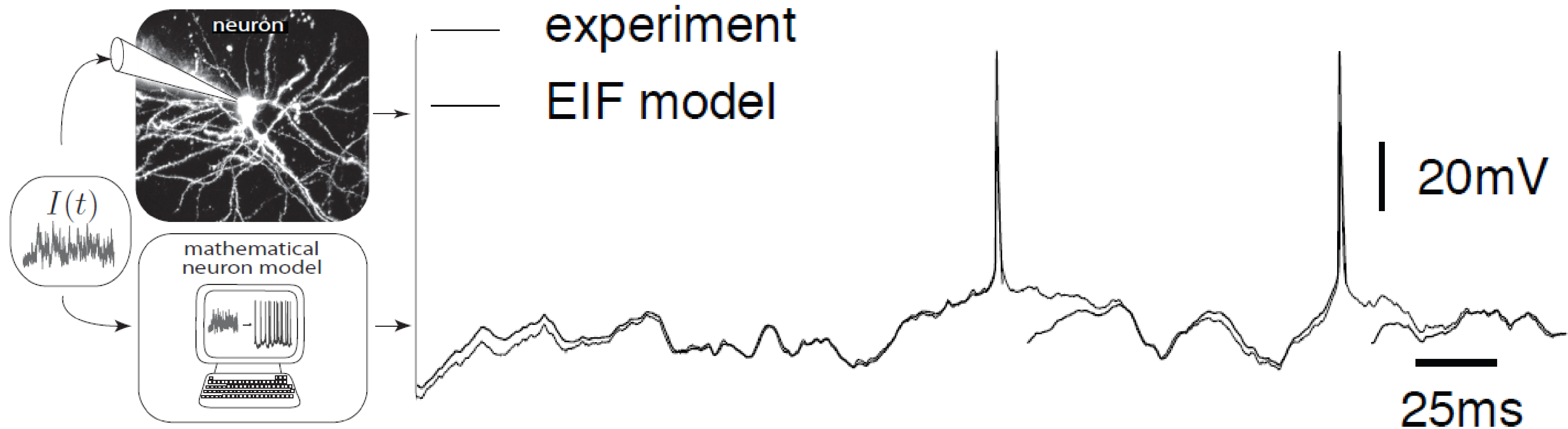
Neuronal Dynamics – 5.2 Variability in vitro

neurons are fairly reliable



*Image adapted from
Mainen&Sejnowski 1995*

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



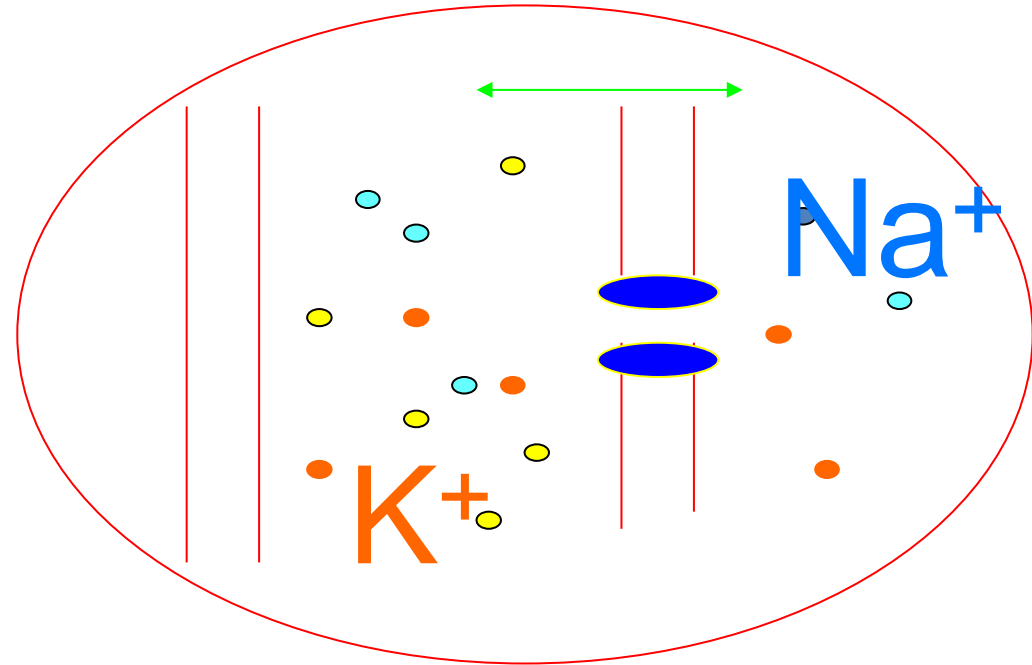
Badel et al., 2008

Aims: - predict spike initiation times
- predict subthreshold voltage

*only possible, because
neurons are fairly reliable*

Neuronal Dynamics – 5.2. Sources of Variability

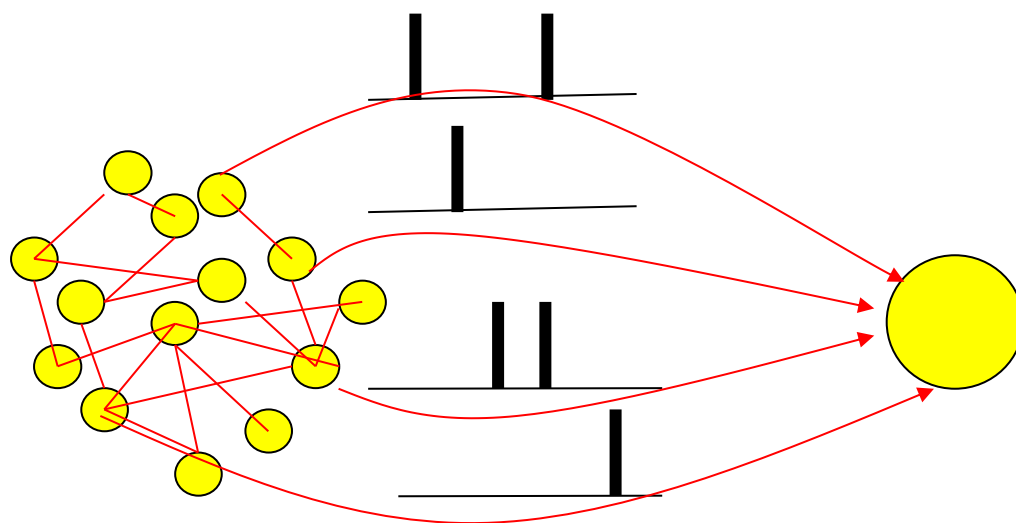
- Intrinsic noise (ion channels)



- Finite number of channels
- Finite temperature

small contribution!

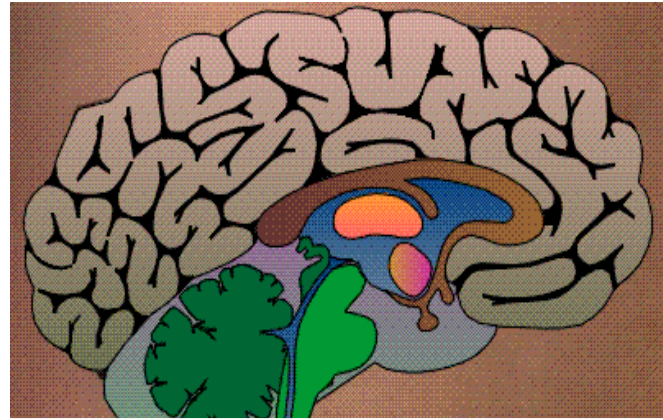
- Network noise (background activity)



- Spike arrival from other neurons
- Beyond control of experimentalist

→ Check network noise by simulation!

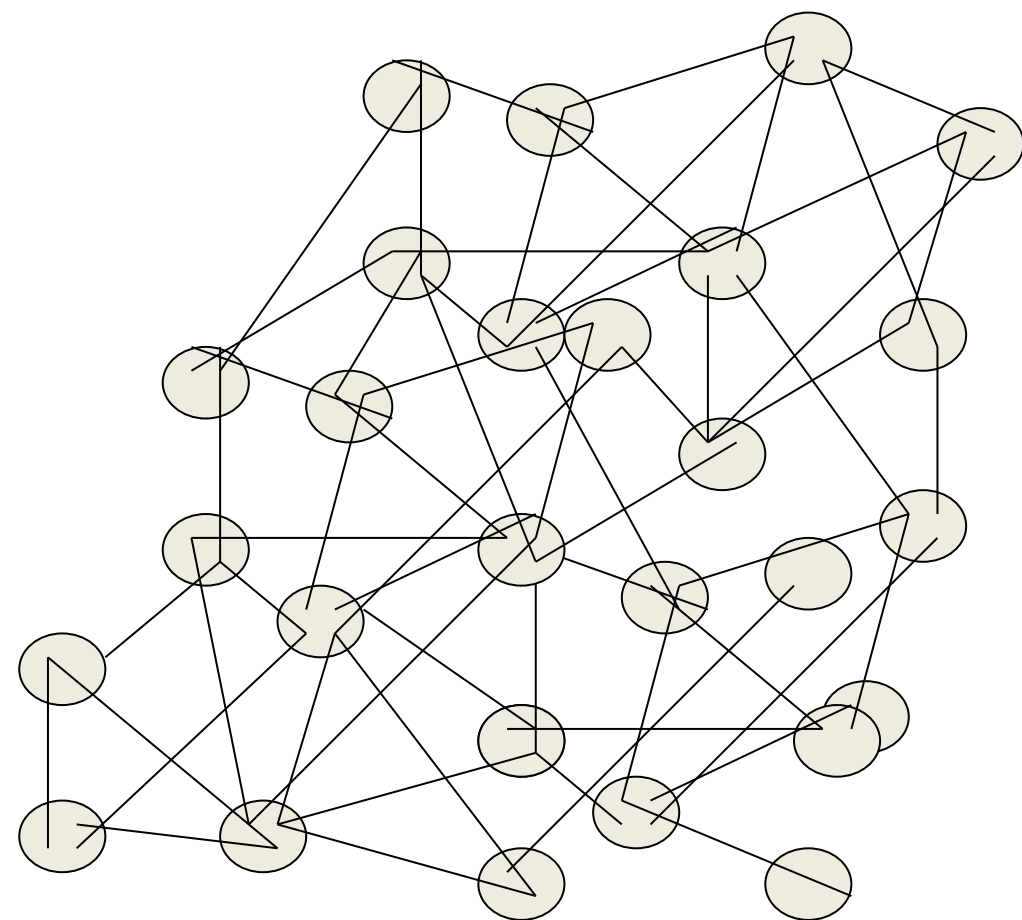
Neuronal Dynamics – 5.2 Sources of Variability



Brain

The Brain: a highly connected system

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

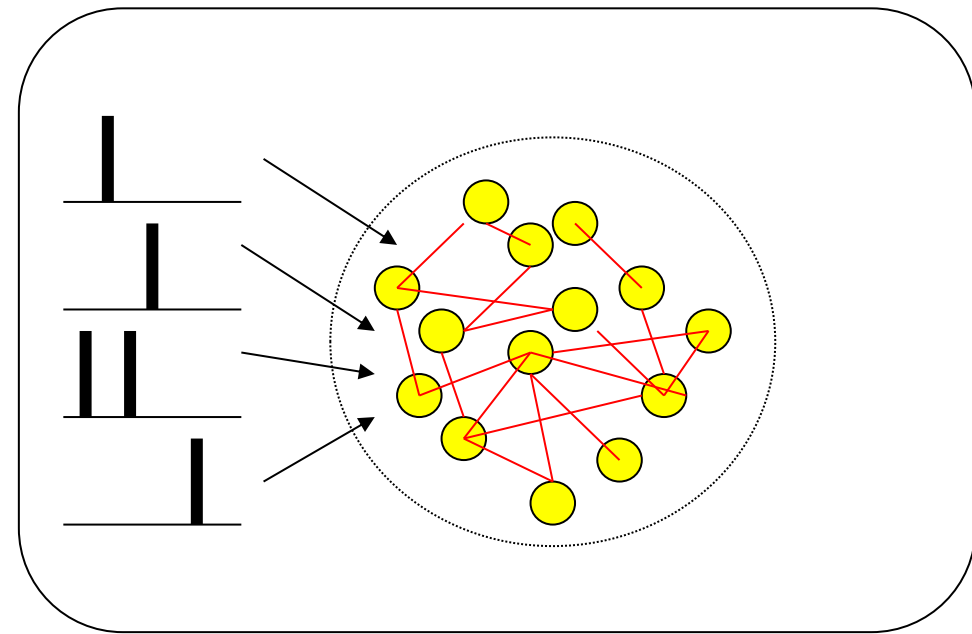


Distributed architecture

10^{10} neurons

10^4 connections/neurons

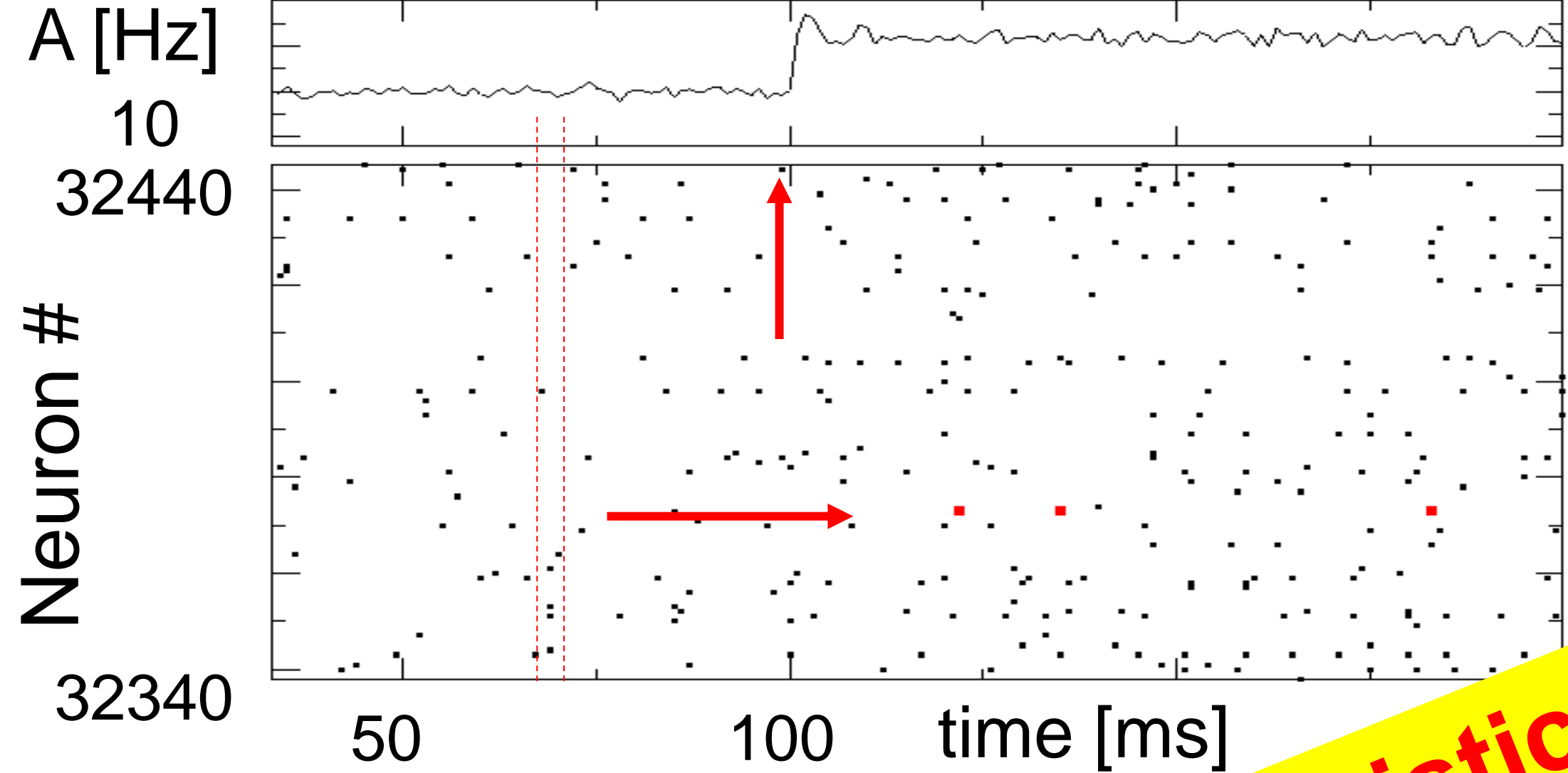
Random firing in a population of LIF neurons



input { low rate
high rate

Population

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



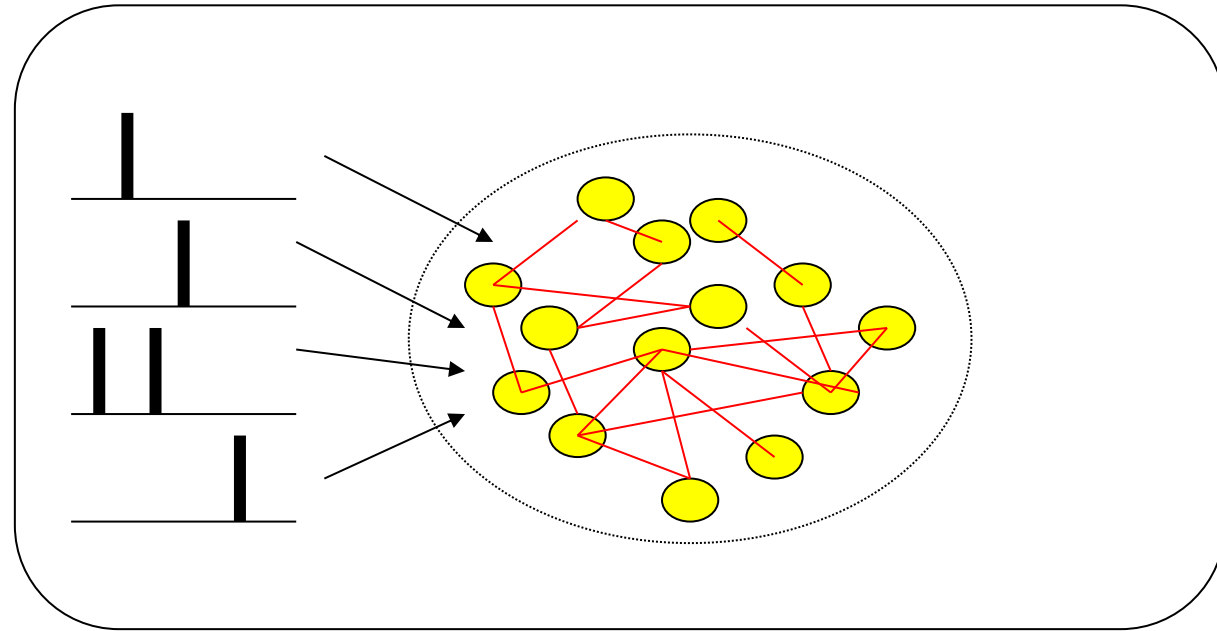
Brunel, J. Comput. Neurosc. 2000

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



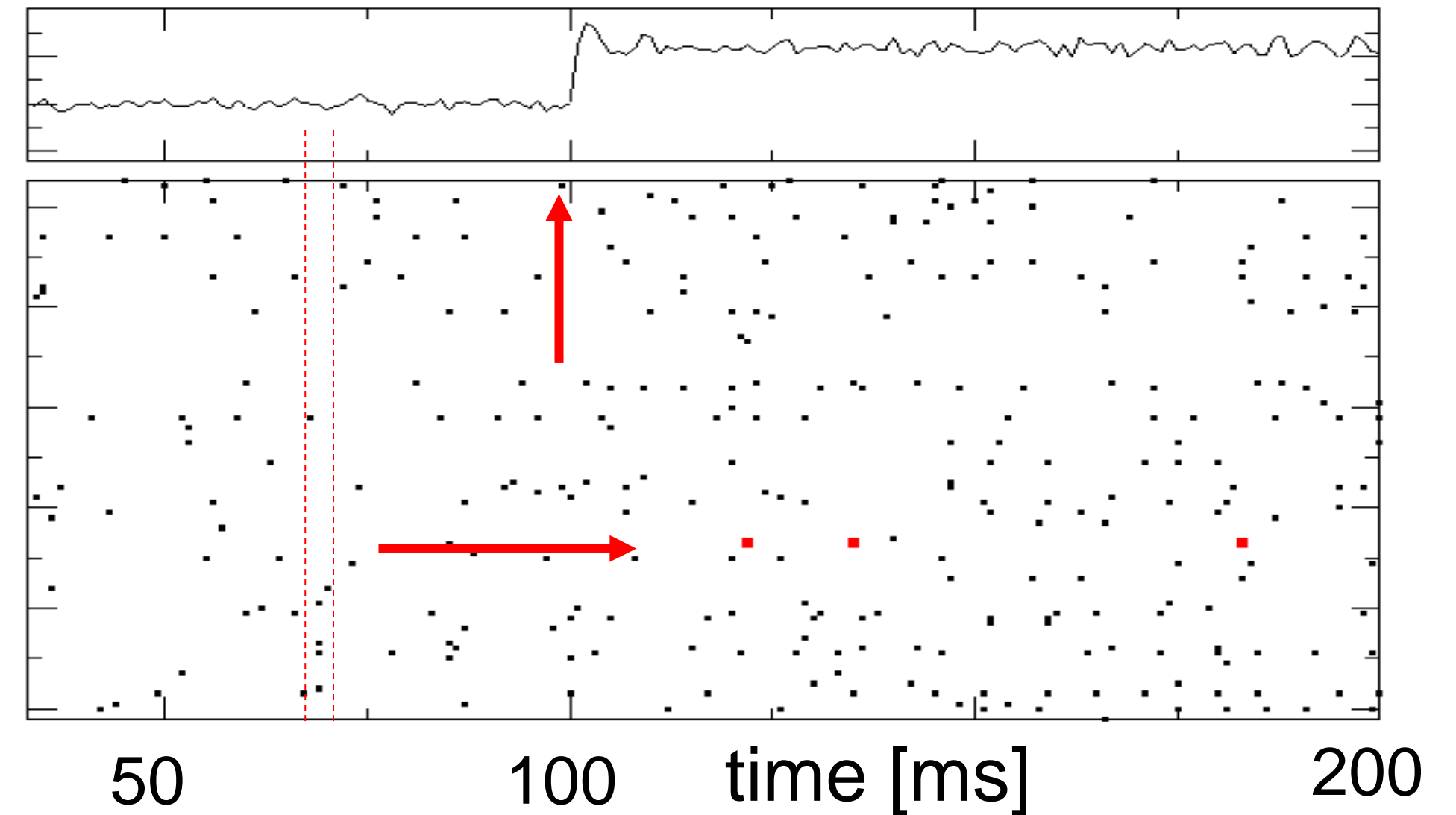
input { low rate
high rate

Population

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

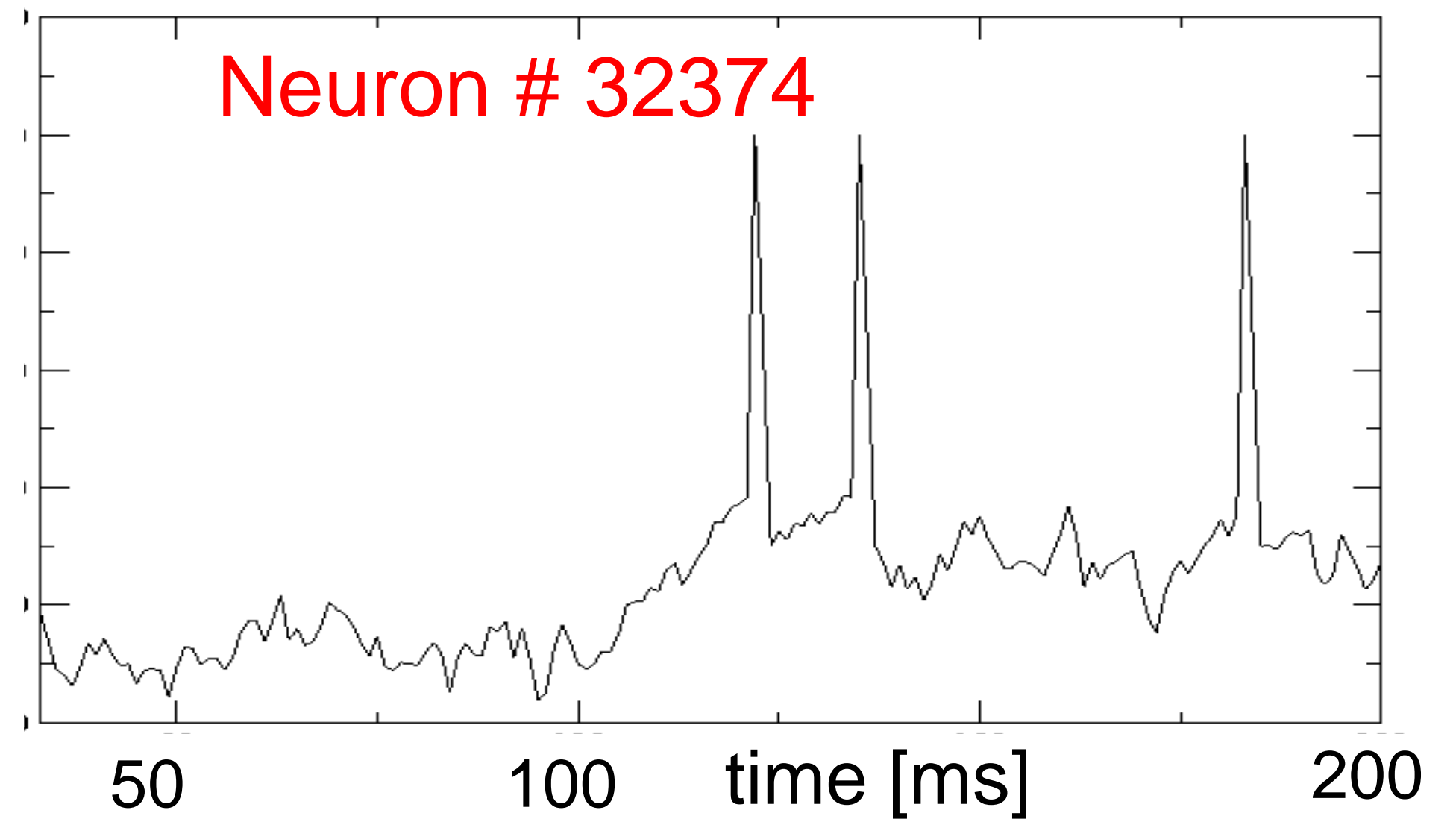
A [Hz]
10
32440

Neuron #
32340



u [mV]
100
0

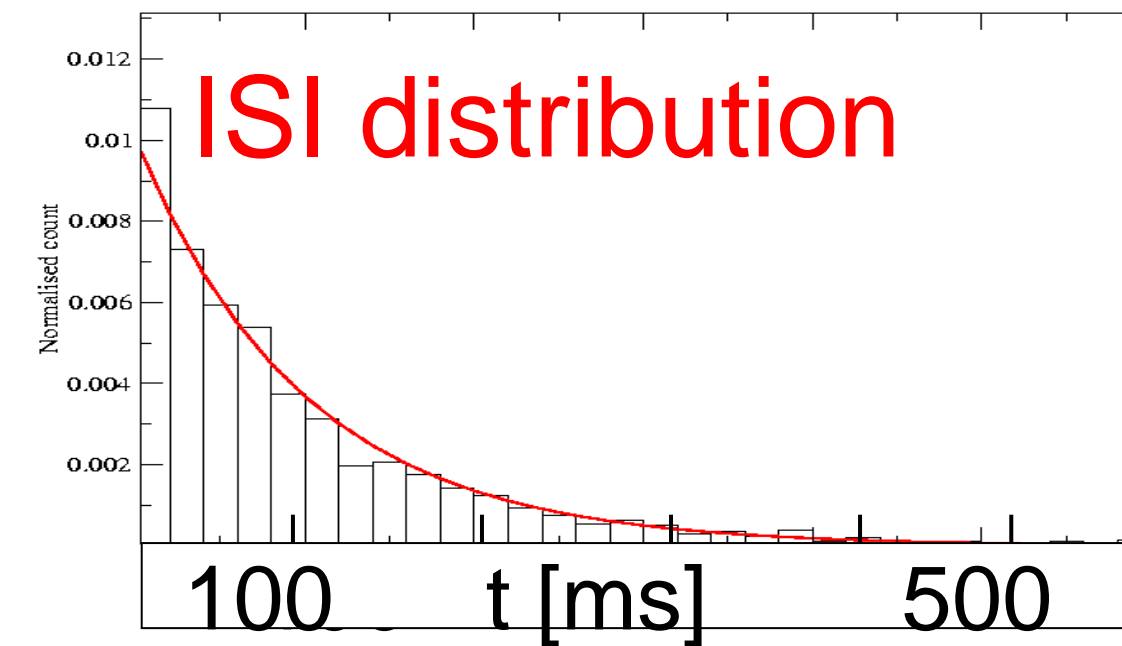
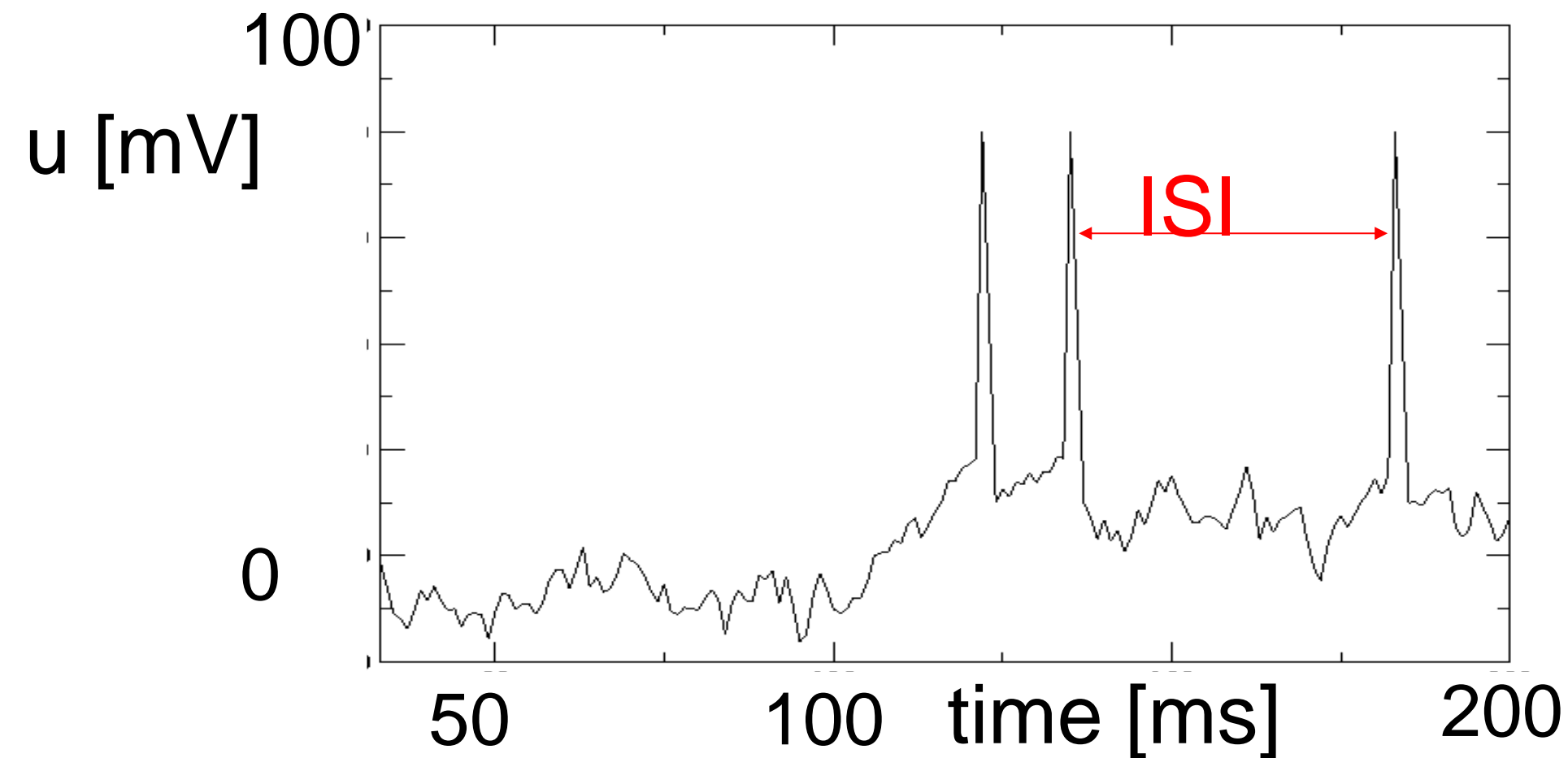
Neuron # 32374



Neuronal Dynamics – 5.2. Interspike interval distribution

- Variability of interspike intervals (ISI)

here in simulations,
but also *in vivo*

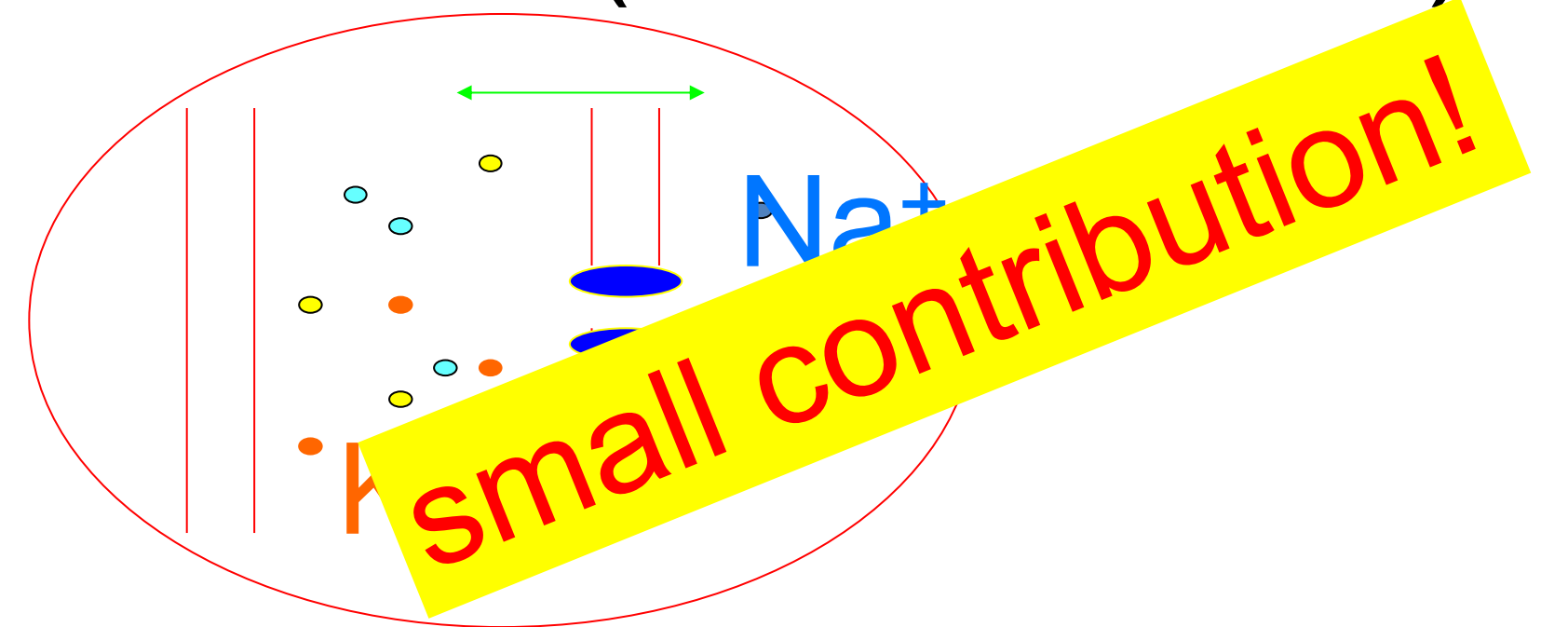


Variability of spike trains:
broad ISI distribution

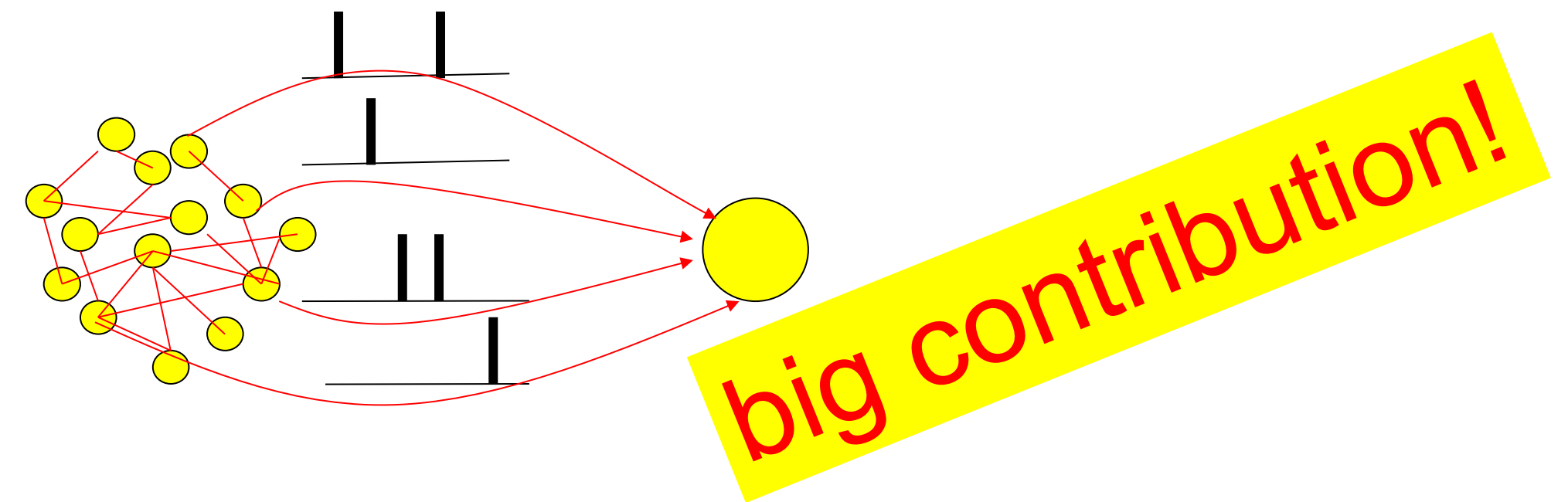
Brunel,
J. Comput. Neurosc. 2000
Mayor and Gerstner,
Phys. Rev E. 2005
Vogels and Abbott,
J. Neuroscience, 2005

Neuronal Dynamics – 5.2. Sources of Variability

- Intrinsic noise (ion channels)



- Network noise



Neuronal Dynamics – Quiz 5.1.

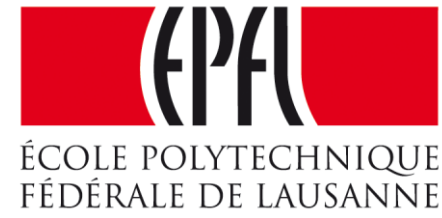
A- Spike timing in vitro and in vivo

- ☐ 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

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

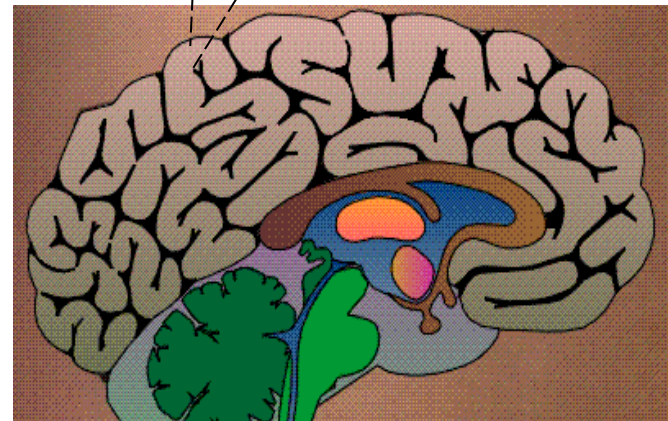
Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

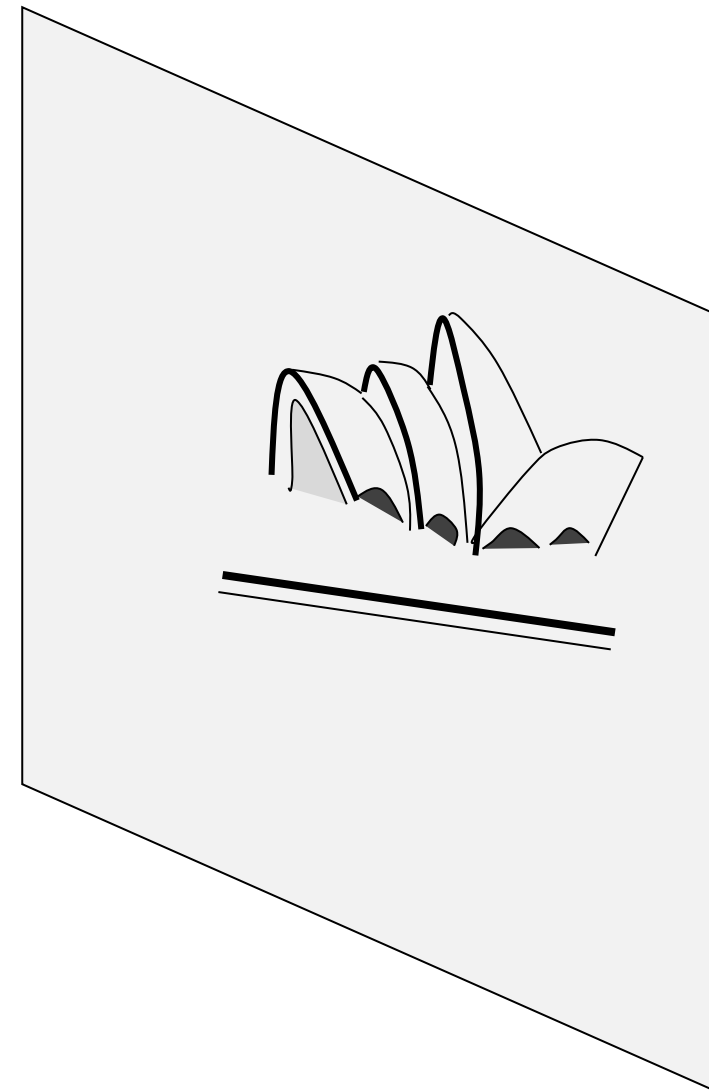
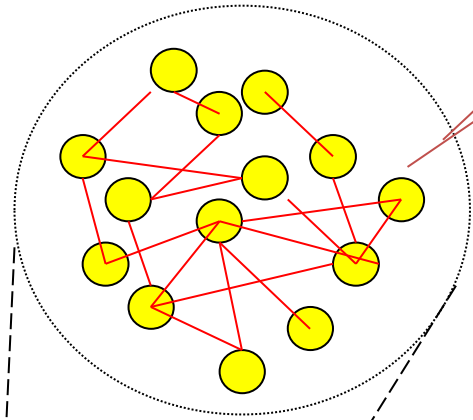
- Temporal averaging
- Averaging across repetitions
- Population averaging ('spatial' averaging)

Neuronal Dynamics – 5.3. Rate codes: spike count

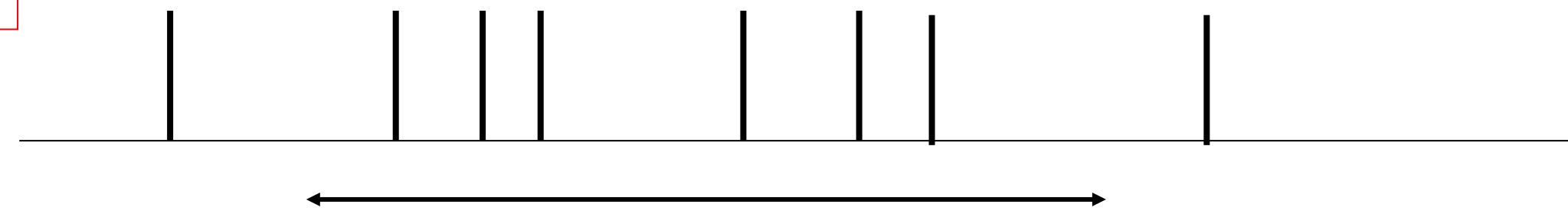
Variability of spike timing



Brain



stim



trial 1

rate as a (normalized) spike count:

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

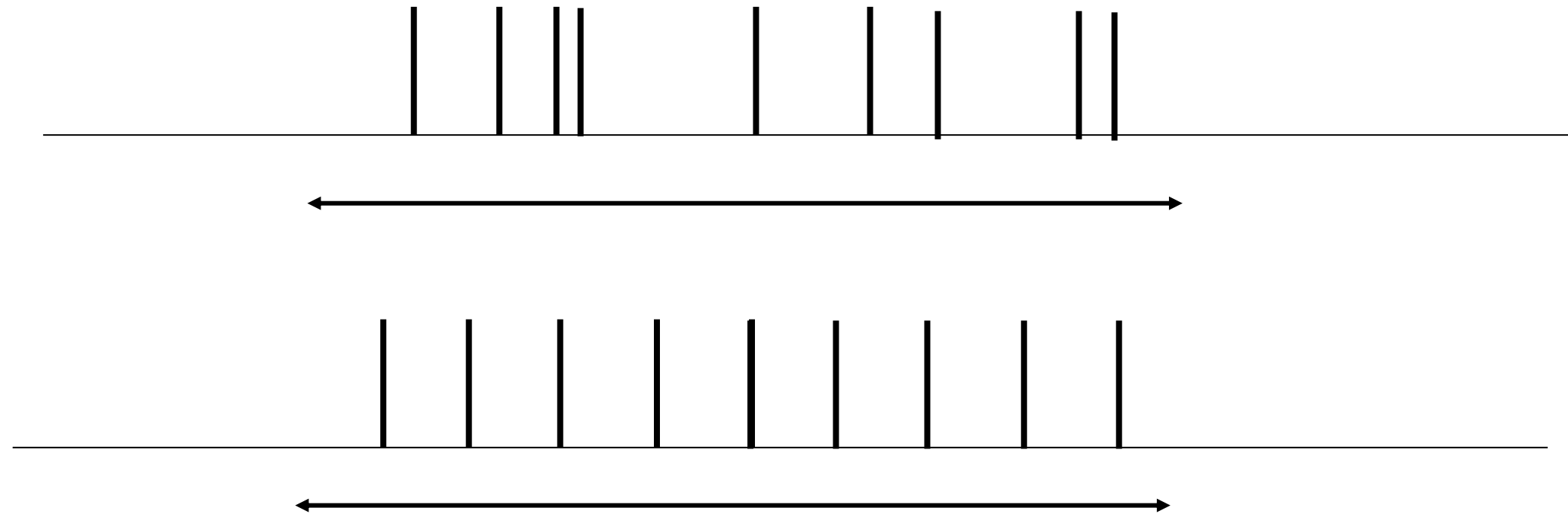
single neuron/single trial:
temporal average

T=1s

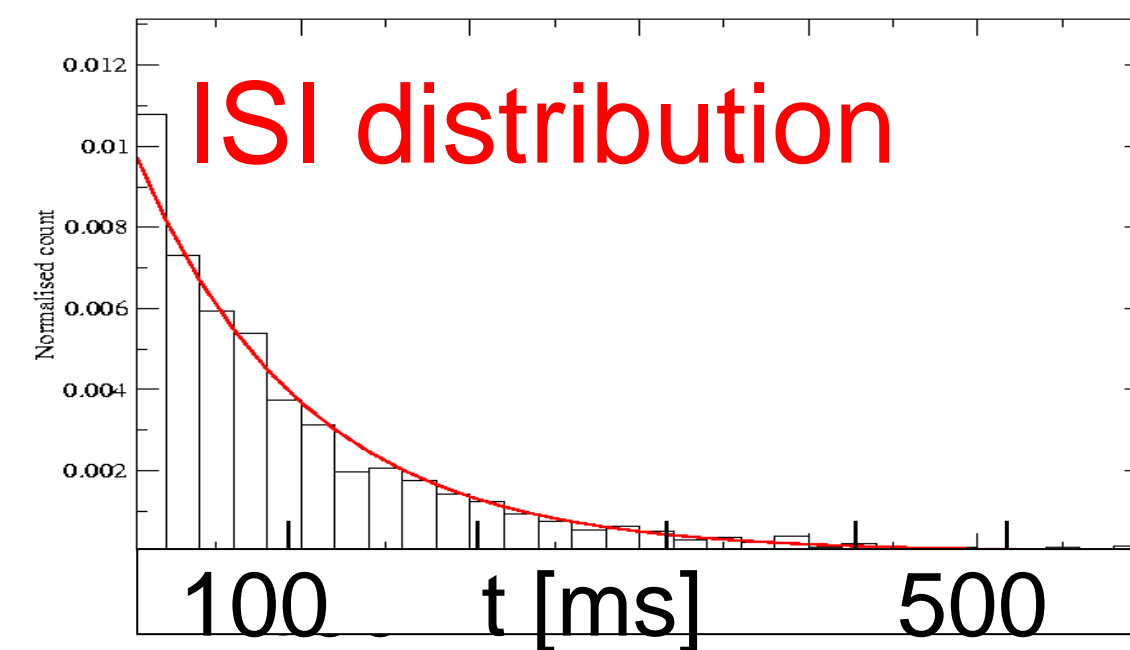
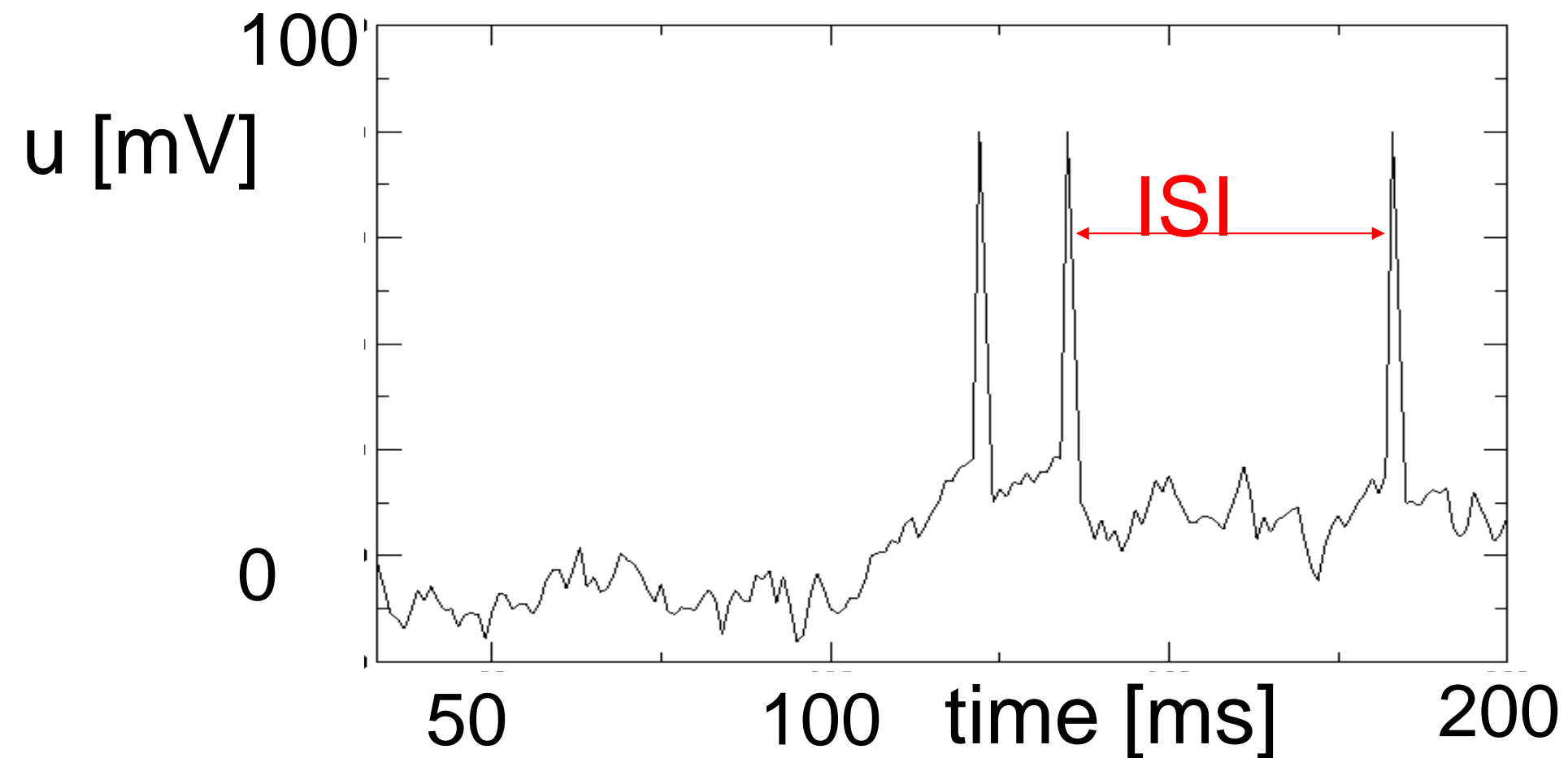
Neuronal Dynamics – 5.3. Rate codes: spike count

single neuron/single trial:
temporal average

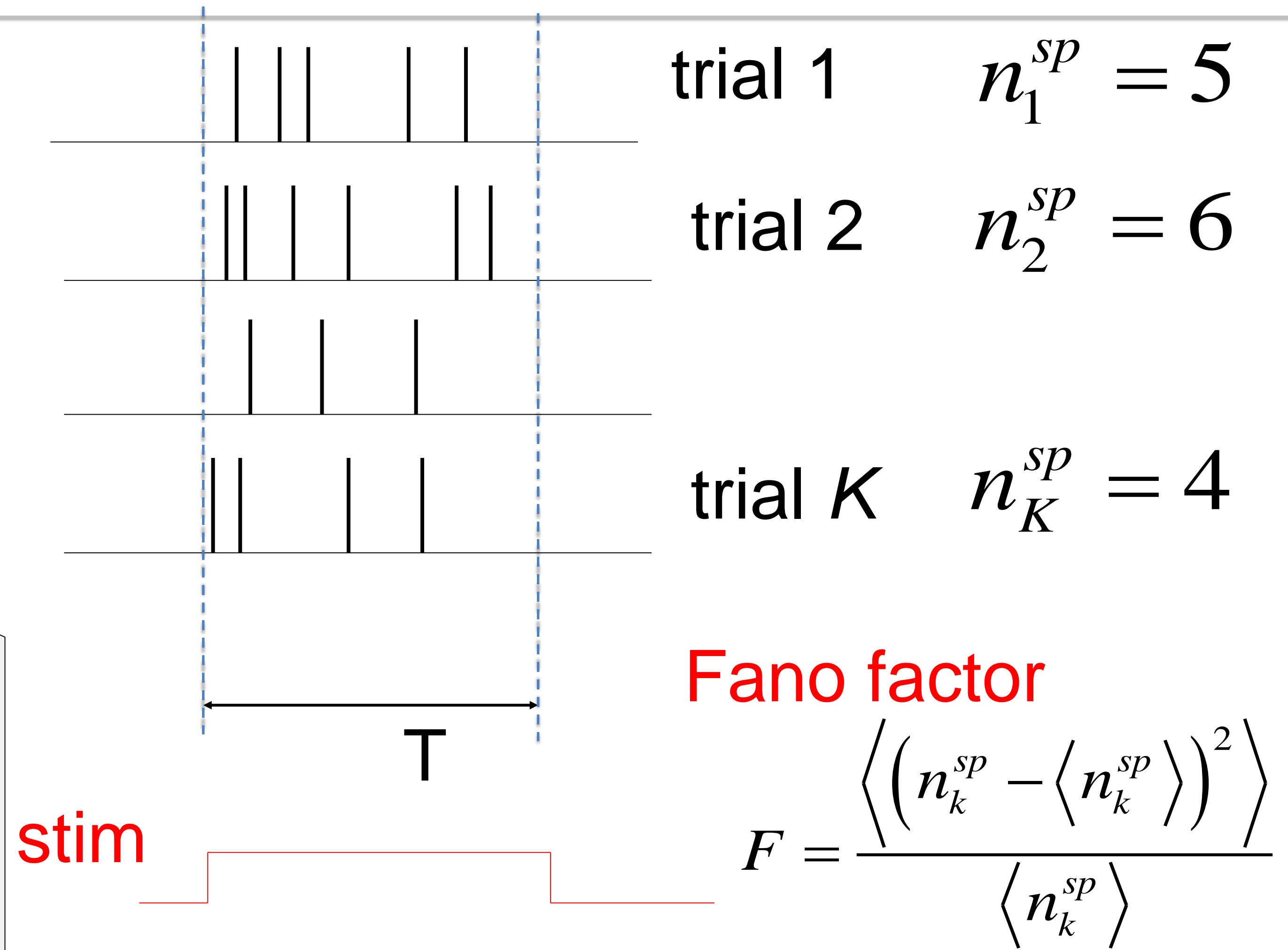
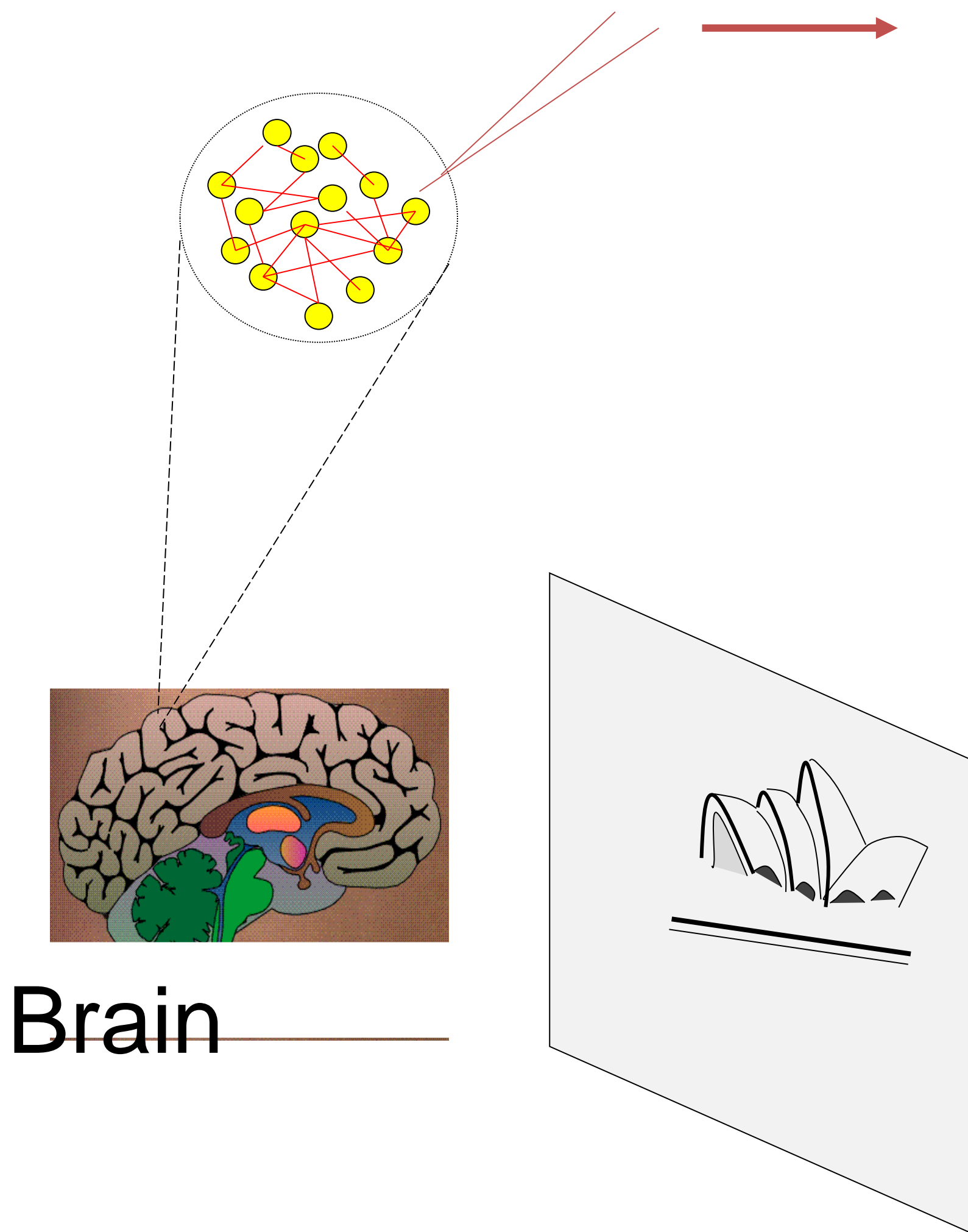
$$\nu(t) = \frac{n^{sp}}{T}$$



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

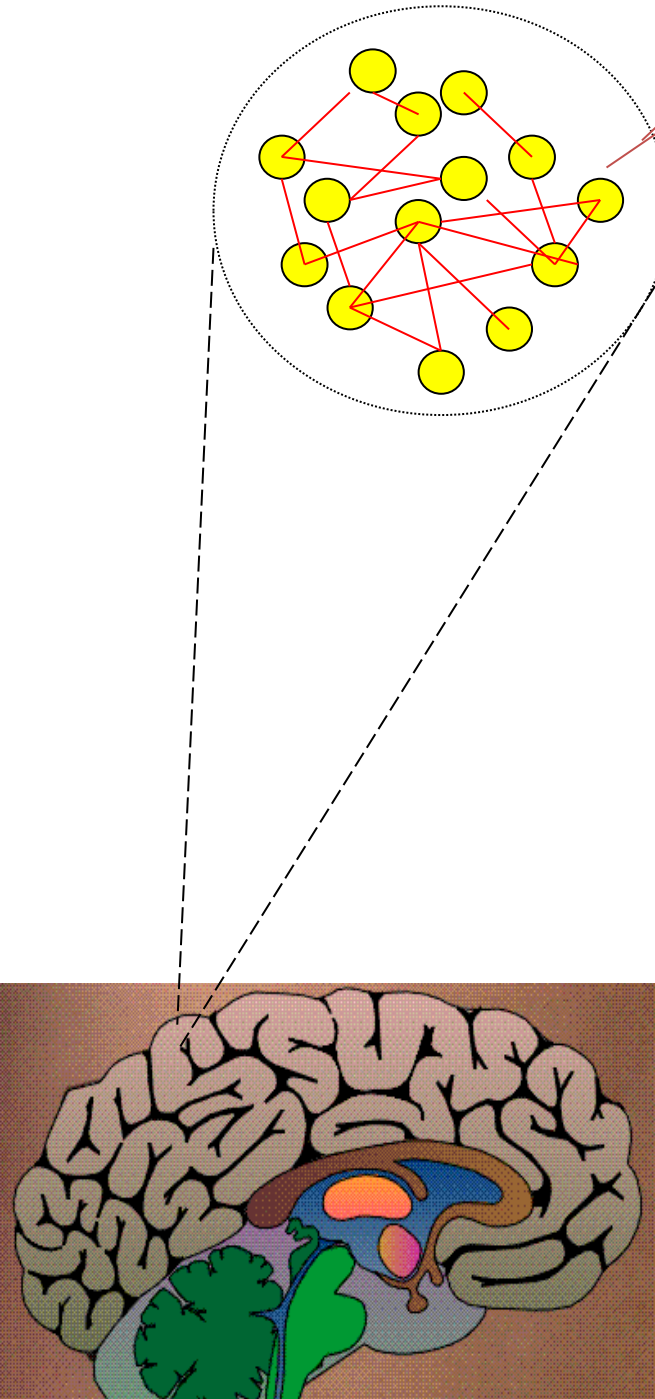
- ✓ -Temporal averaging

Problem: slow!!!

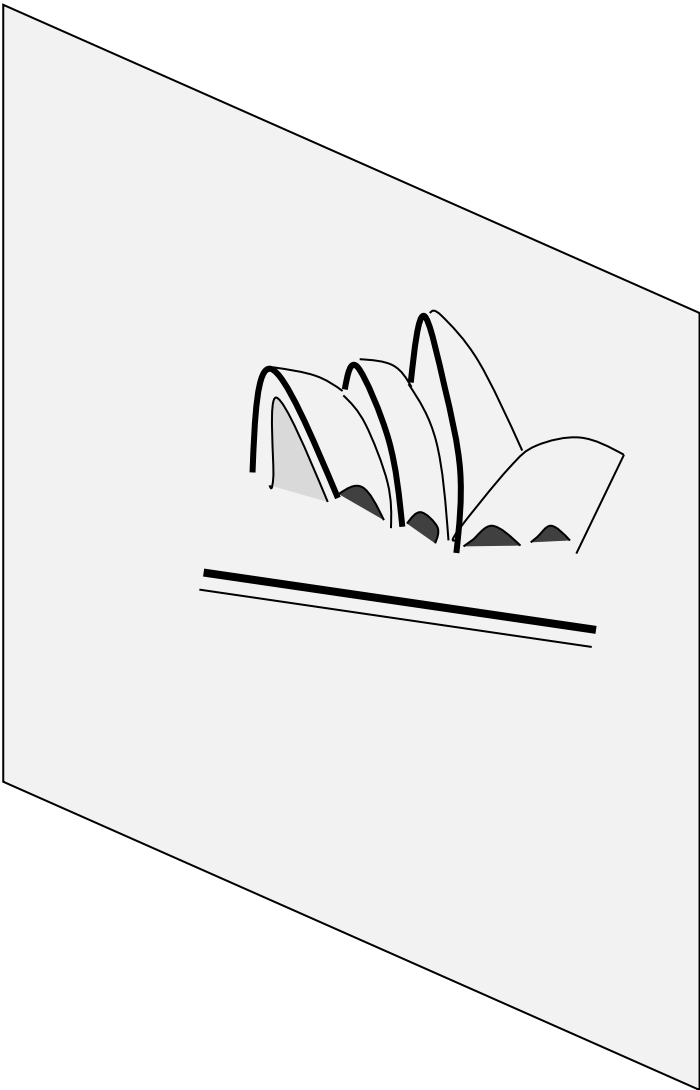
- Averaging across repetitions
- Population averaging

Neuronal Dynamics – 5.3. Rate codes: PSTH

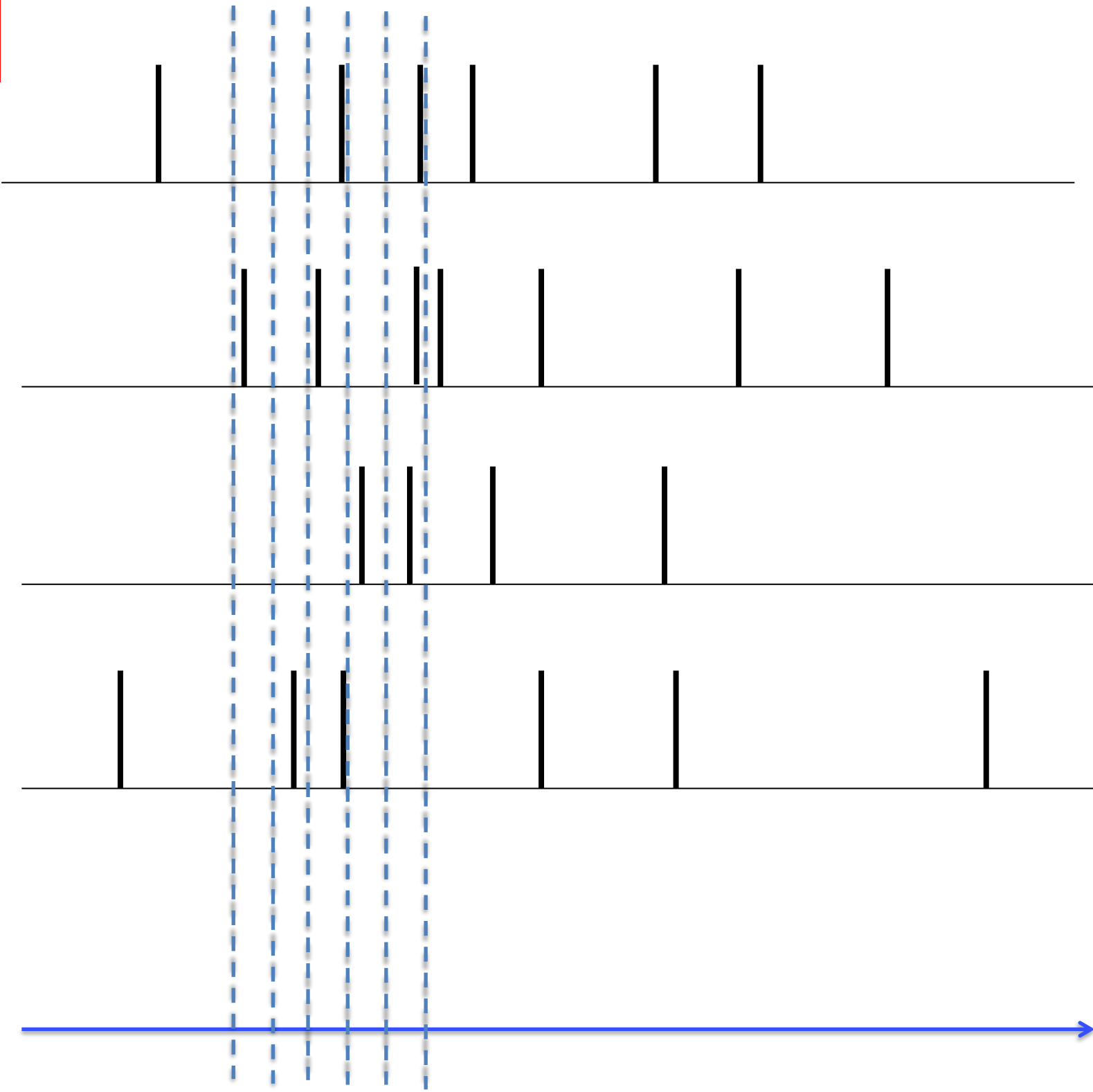
Variability of spike timing



Brain



stim



trial 1

trial 2

trial K

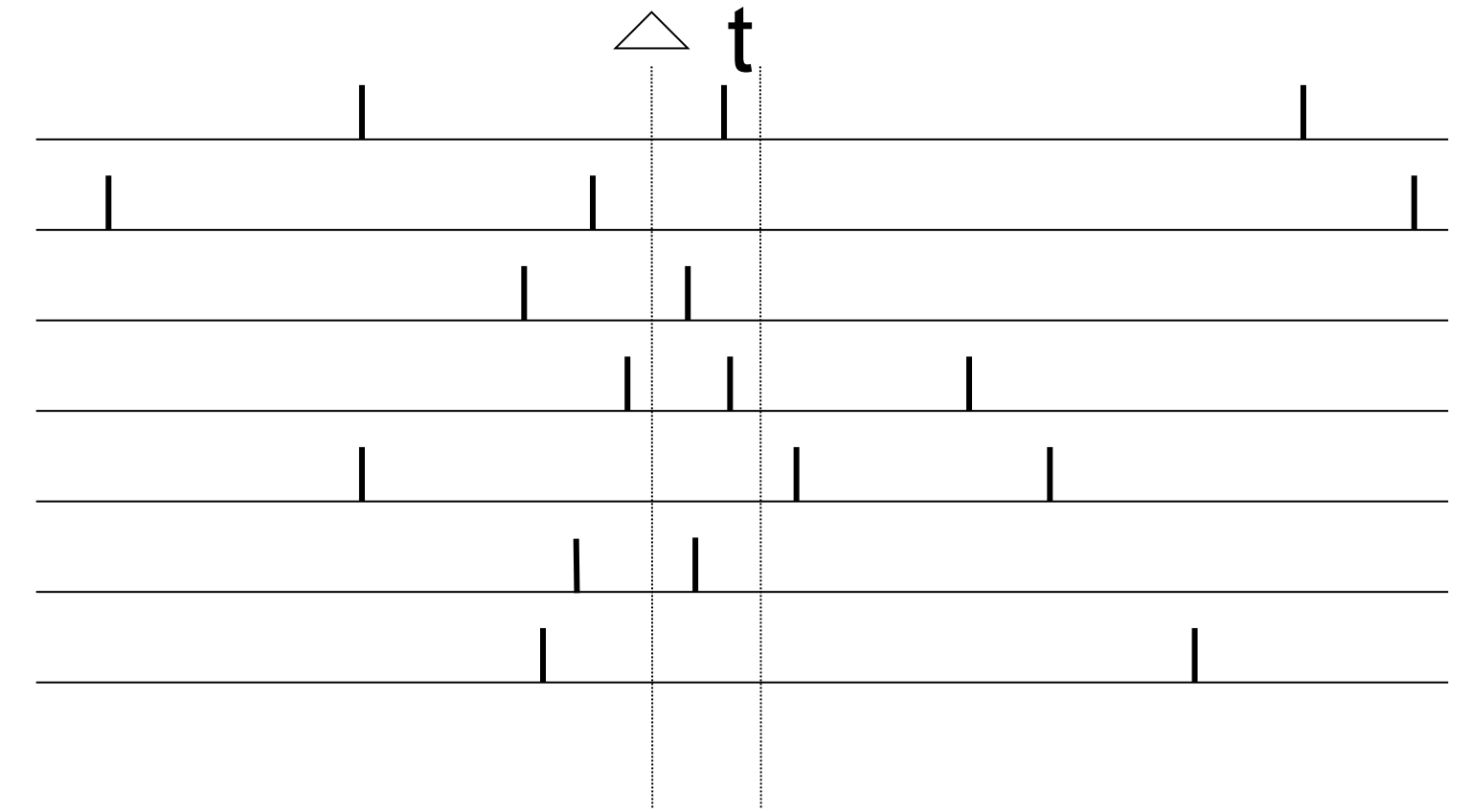
Neuronal Dynamics – 5.3. Rate codes: PSTH

Averaging across repetitions

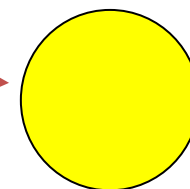
single neuron/many trials:
average across trials

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

K repetitions

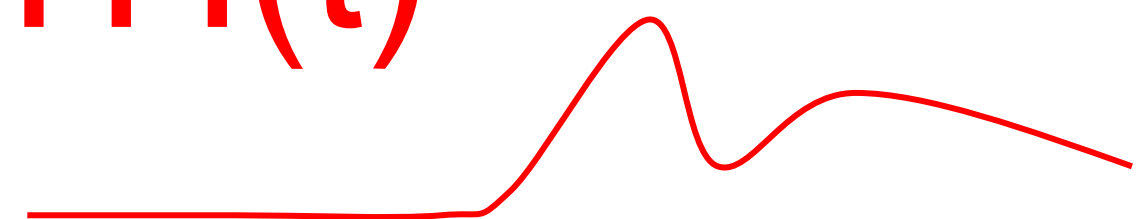


Stim(t)



$K=50$ trials

PSTH(t)



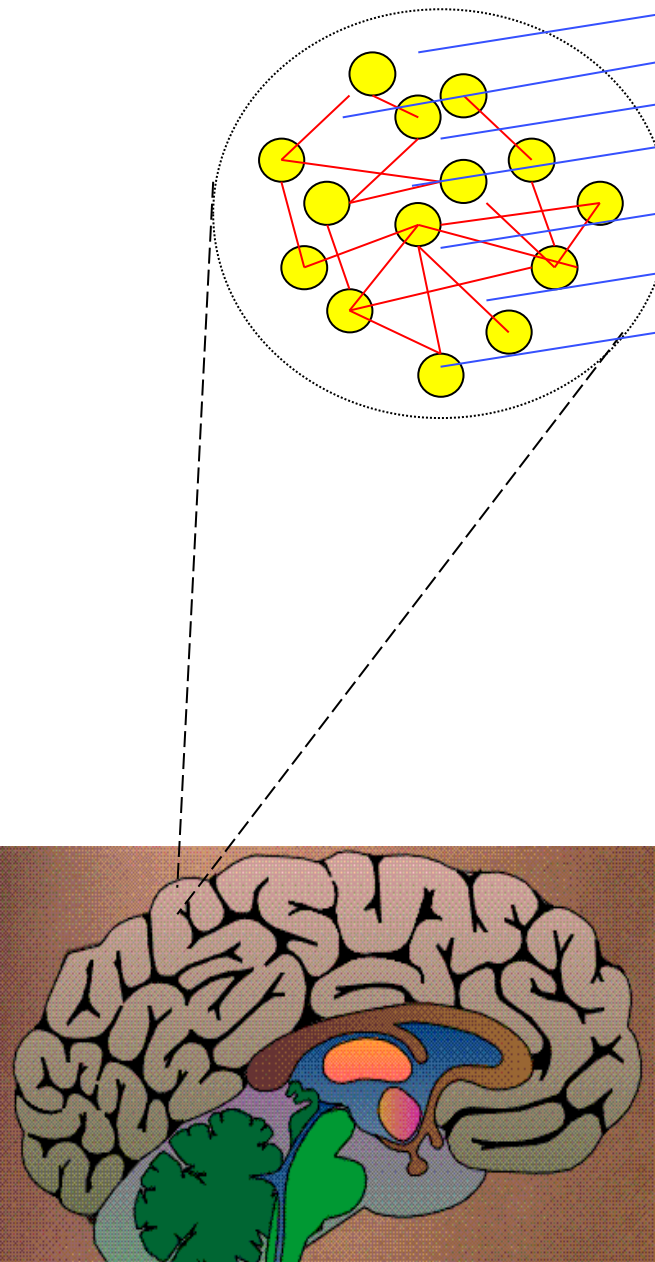
Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

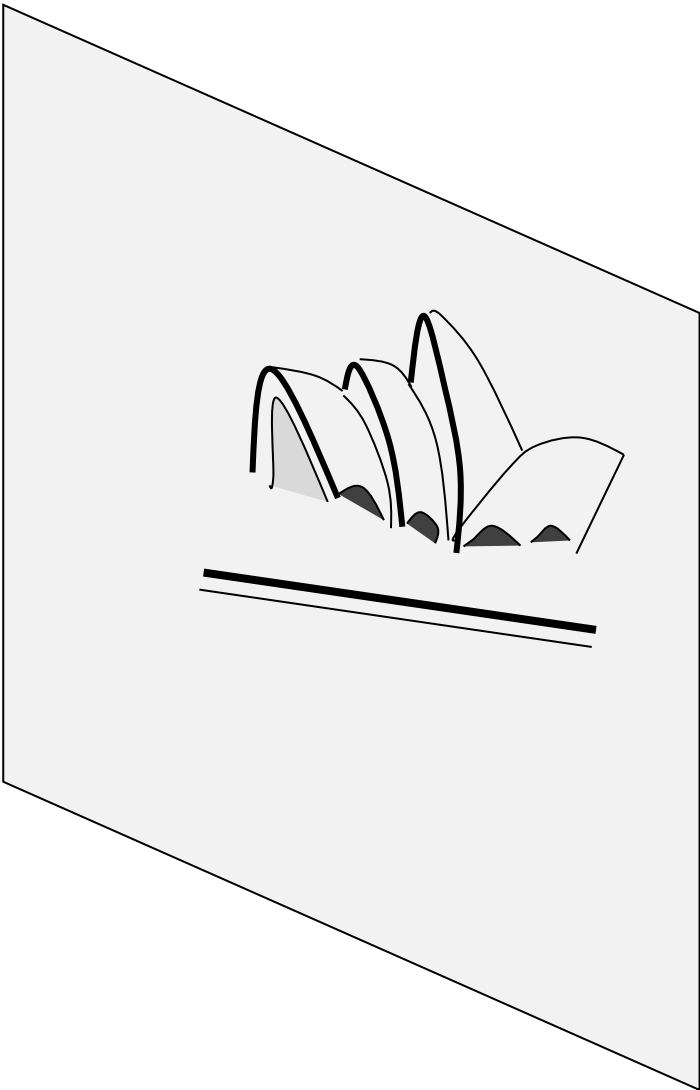
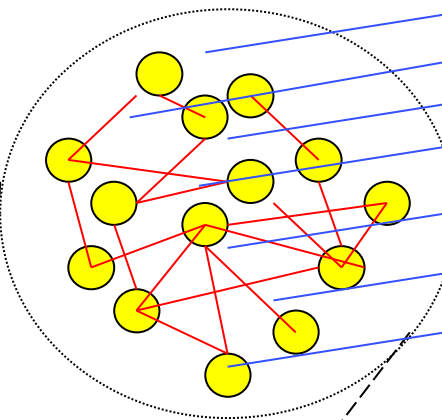
- ✓ -Temporal averaging
- ✓ - Averaging across repetitions
 - Problem: not useful for animal!!!
- Population averaging

Neuronal Dynamics – 5.3. Rate codes: population activity

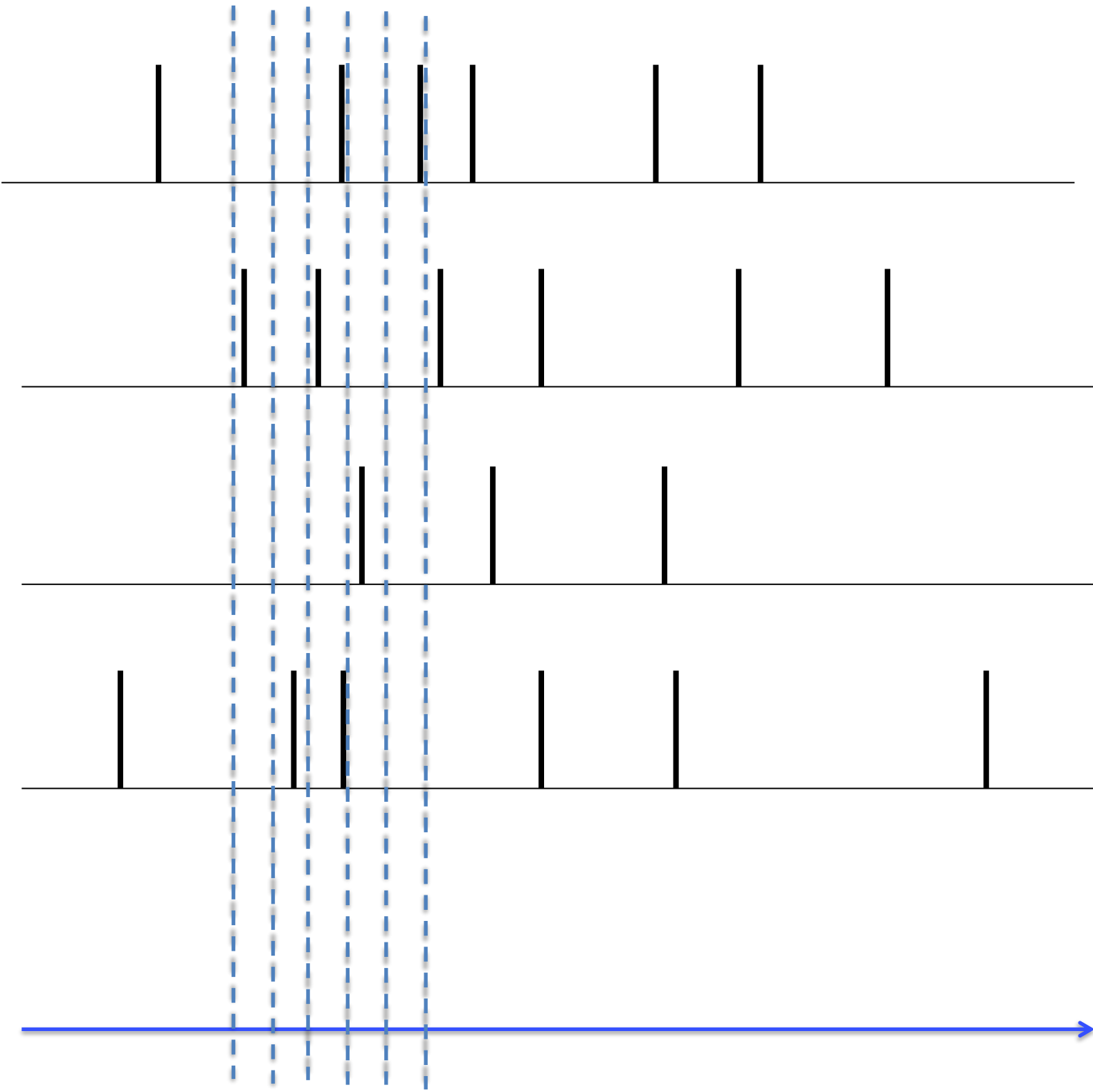
population of neurons
with similar properties



Brain



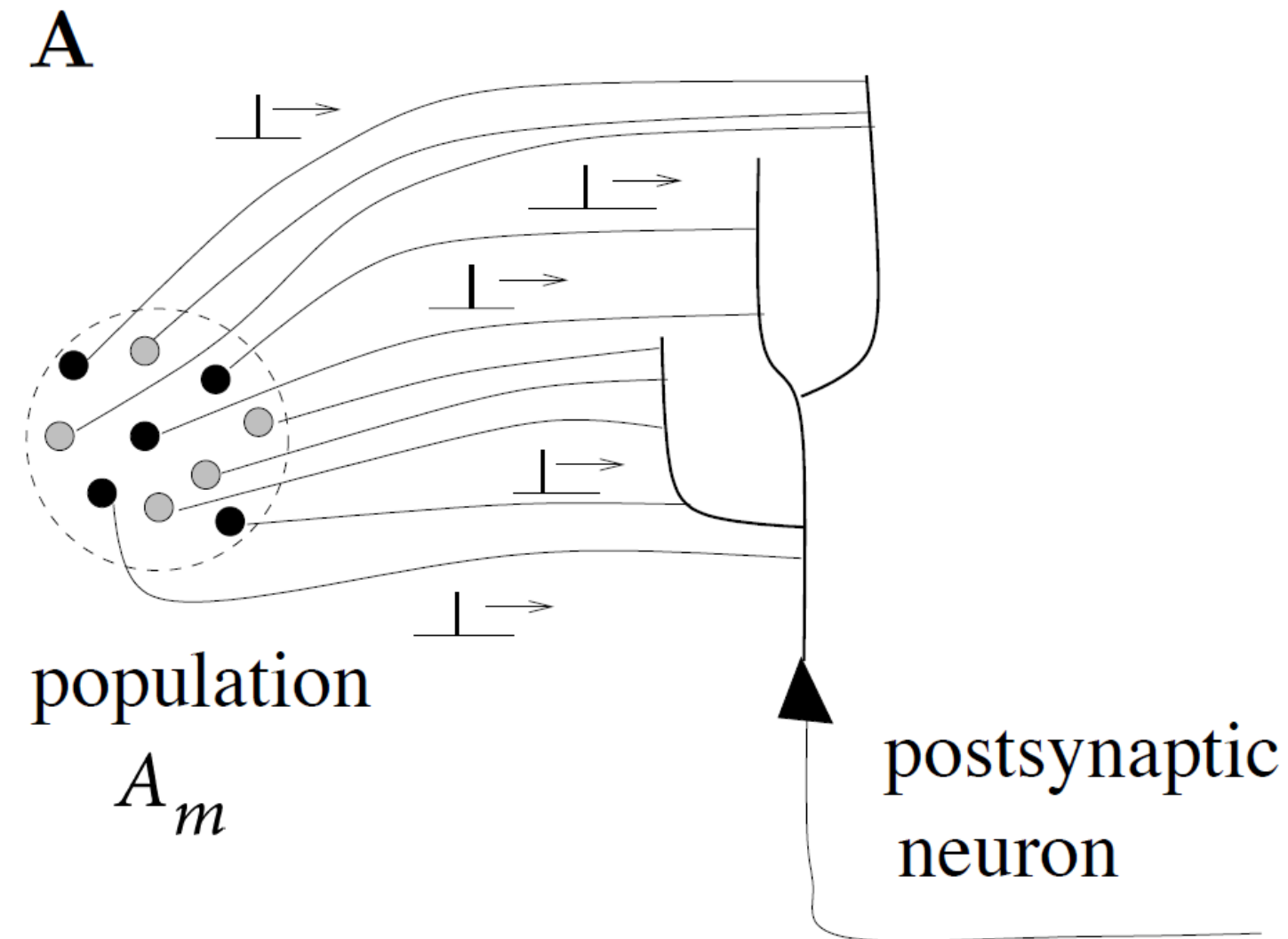
stim



neuron 1
neuron 2
Neuron K

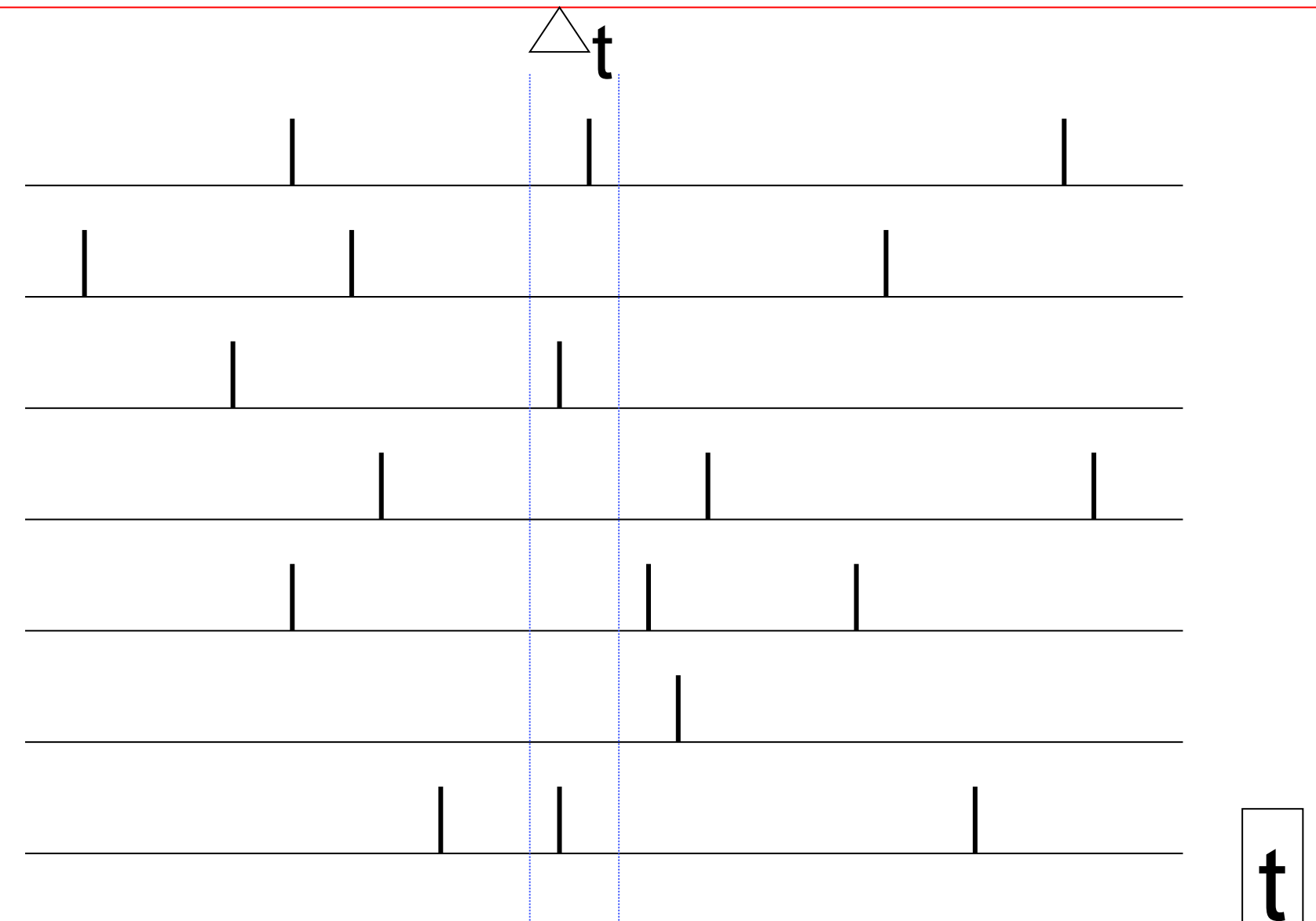
Neuronal Dynamics – 5.3. Rate codes: population activity

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).

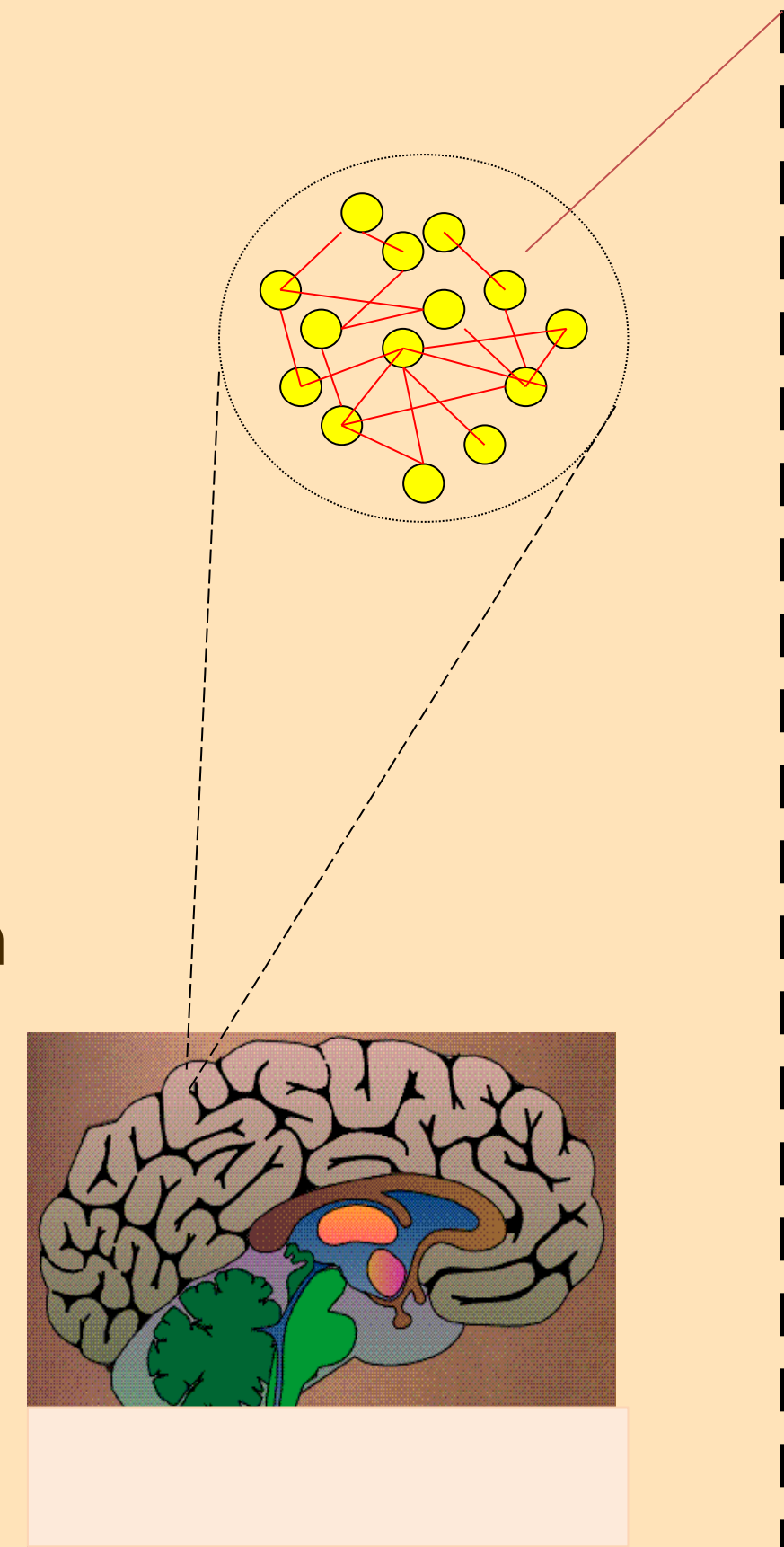
All three determine the time-dependent firing rate.

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

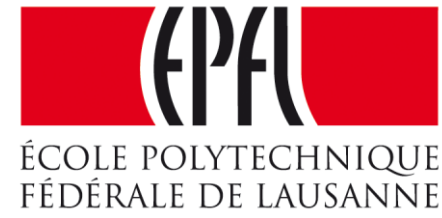
☐ A and B are expected to find the same result, but that of C is expected to be different.

☐ 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

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

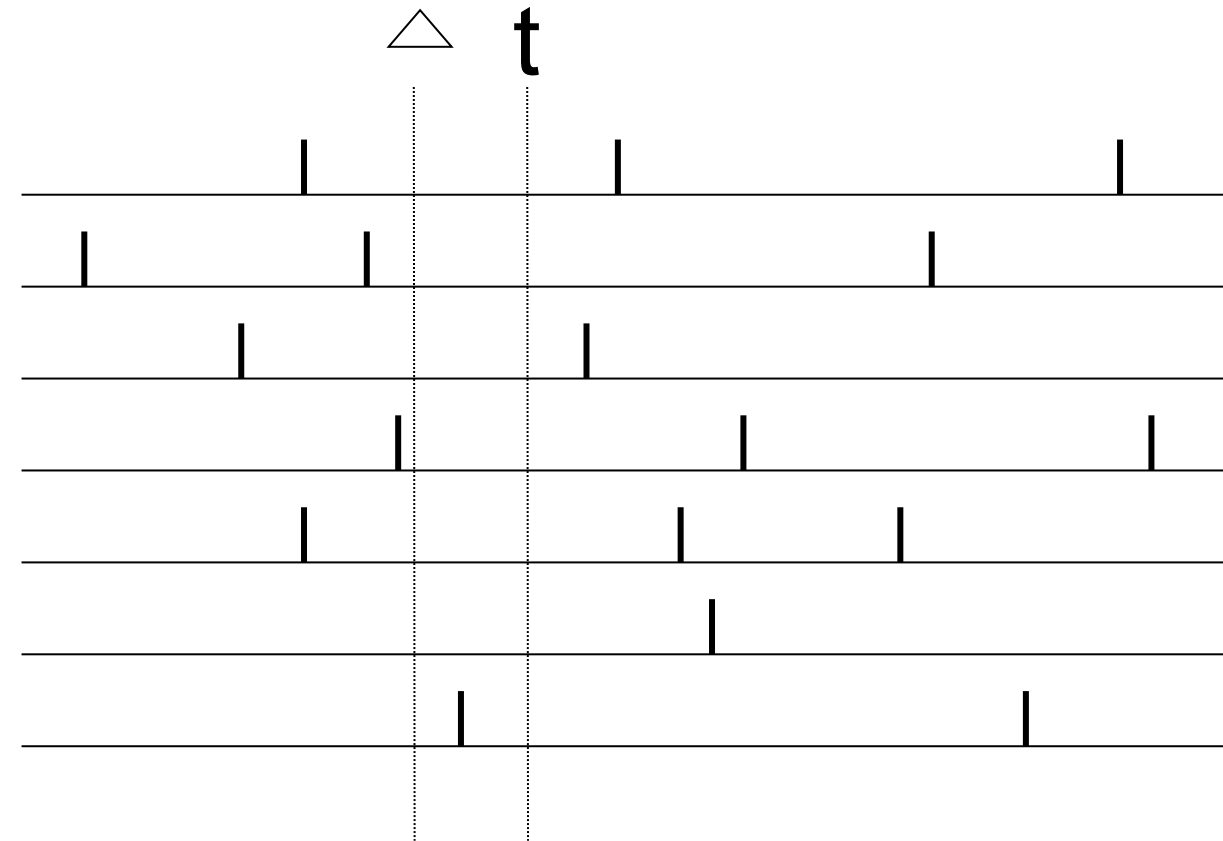
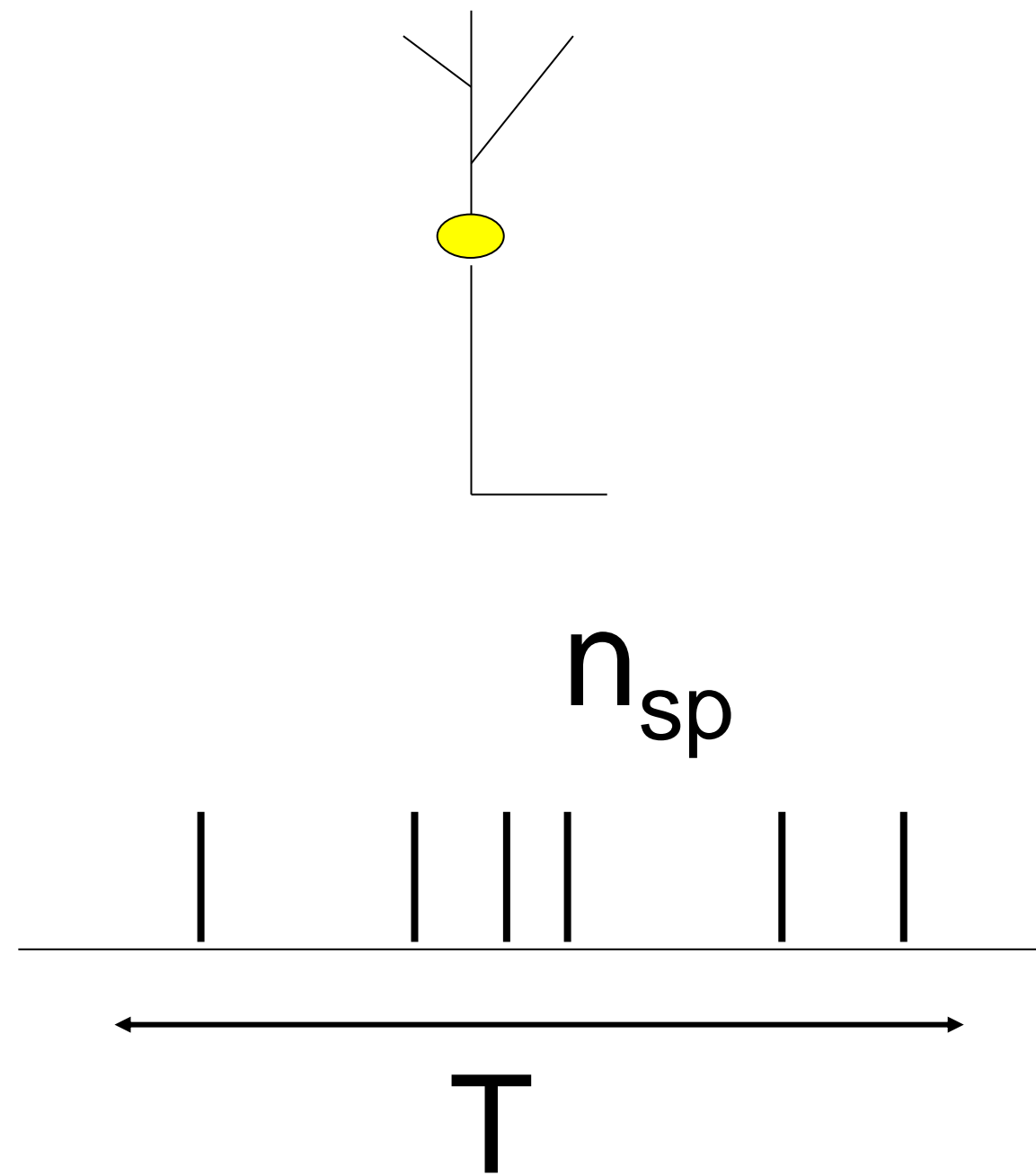
5.4 Stochastic spike arrival

- Membrane potential fluctuations

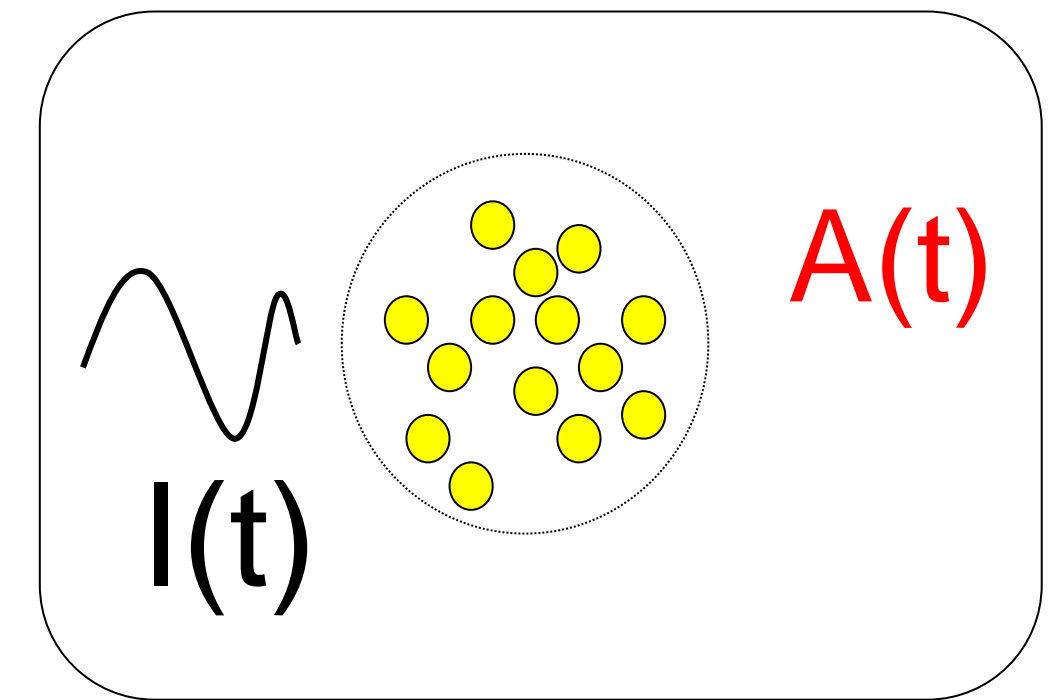
5.5. Stochastic spike firing

- subthreshold and superthreshold

Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process



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



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

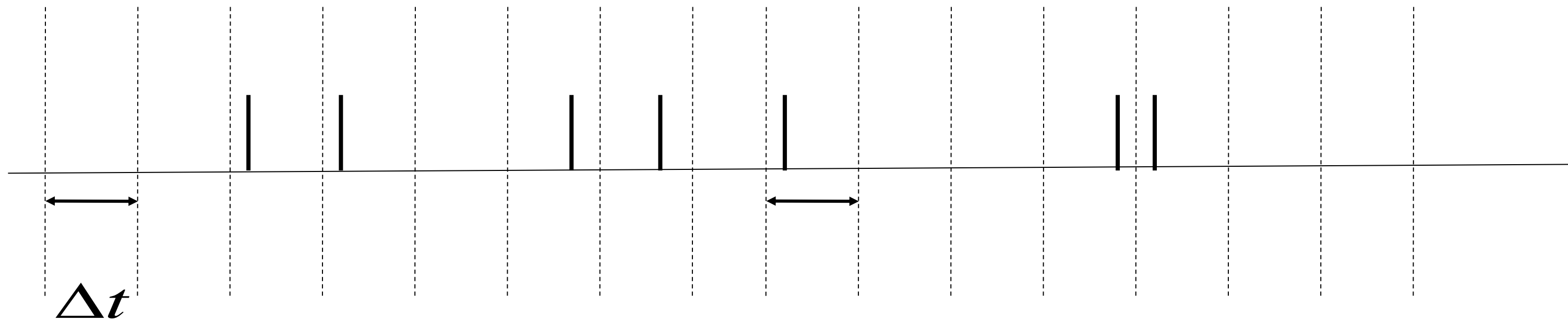
population
activity

Pure rate code = stochastic spiking \rightarrow Poisson model

Neuronal Dynamics – 5.3b. Poisson Model

Homogeneous Poisson model: constant rate

*Math detour:
Poisson model*



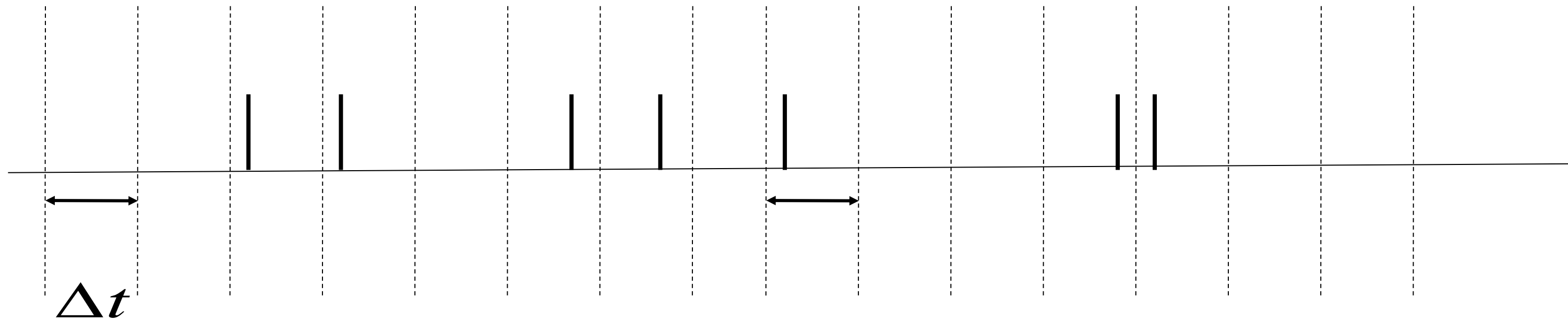
Probability of finding a spike $P_F = \rho_0 \Delta t$

Pure rate code = stochastic spiking \rightarrow Poisson model

Neuronal Dynamics – 5.3b. Poisson Model

Probability of firing:

$$P_F = \rho_0 \Delta t$$



Take $\Delta t \rightarrow 0$

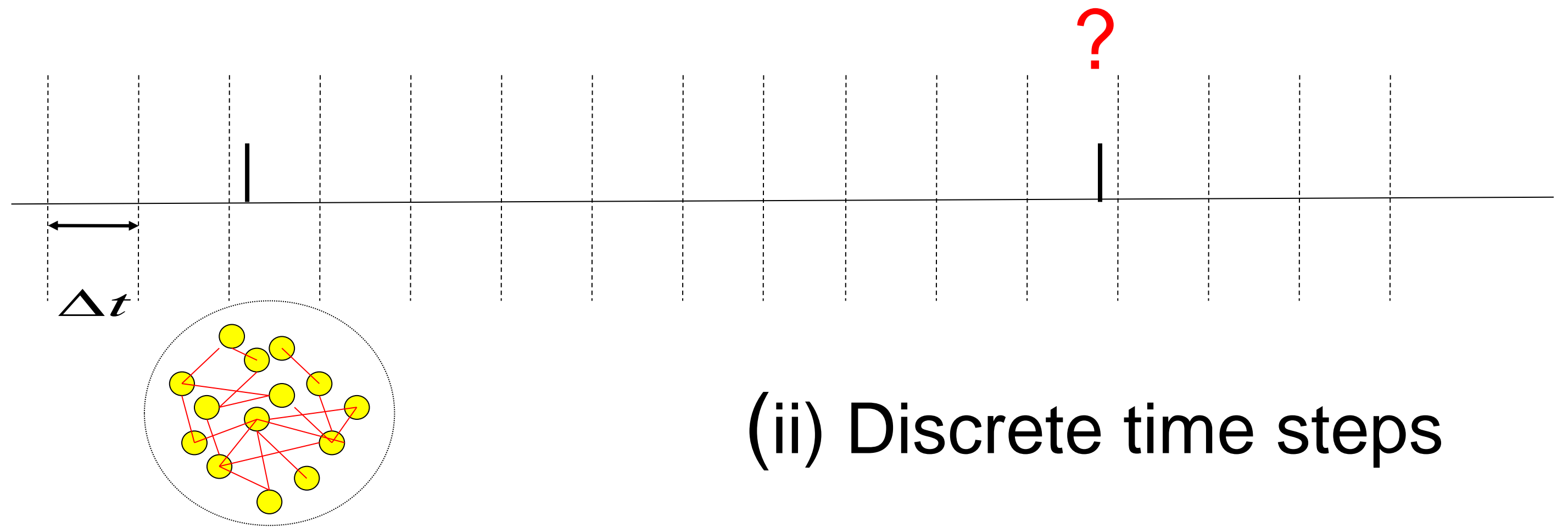
Neuronal Dynamics – 5.3b. Interval distribution

Probability of firing:

$$P_F = \rho_0 \Delta t$$

(i) Continuous time

prob to 'survive'

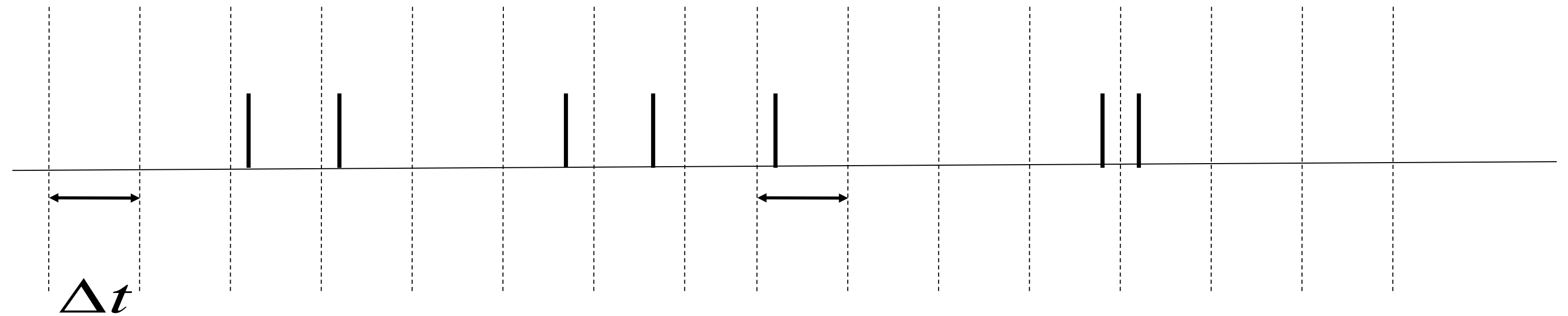


(ii) Discrete time steps

$$\Delta t \rightarrow 0$$

Neuronal Dynamics – 5.3b. Inhomogeneous Poisson Process

rate changes

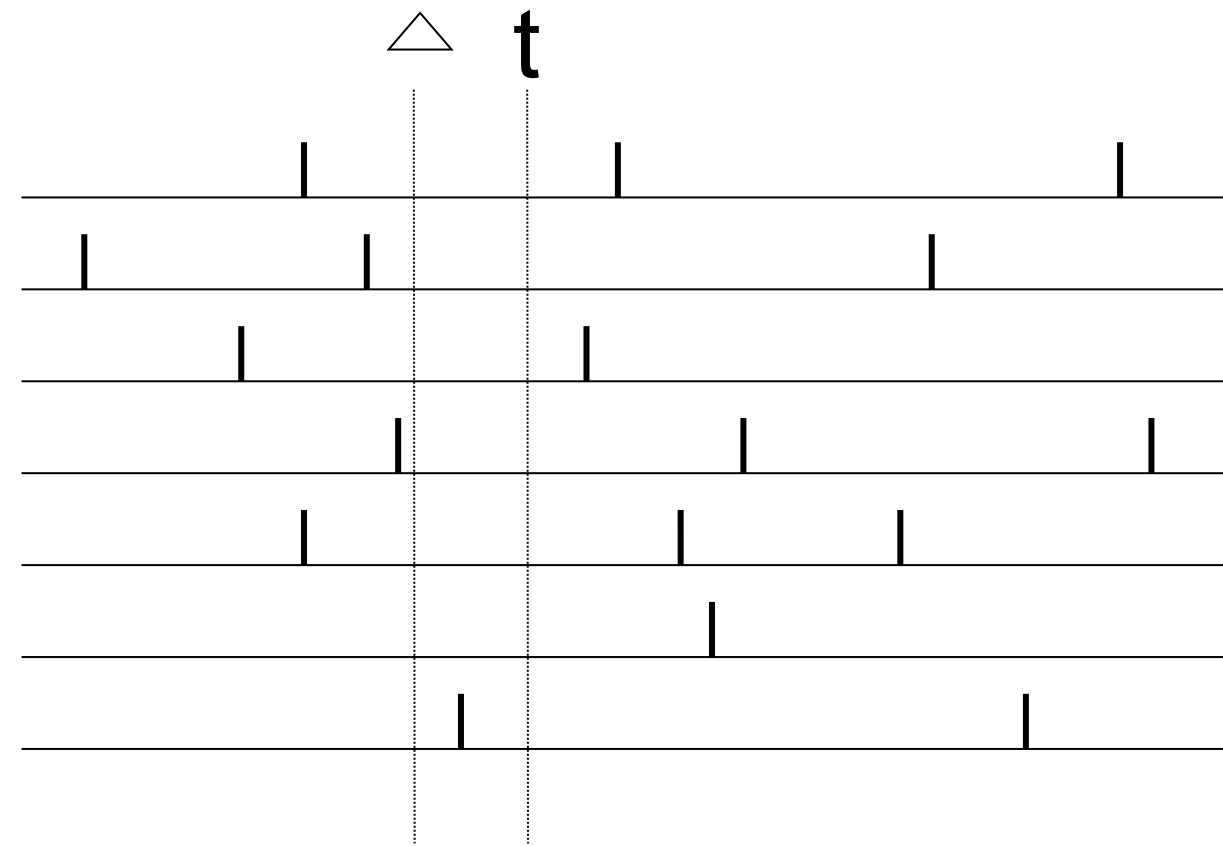
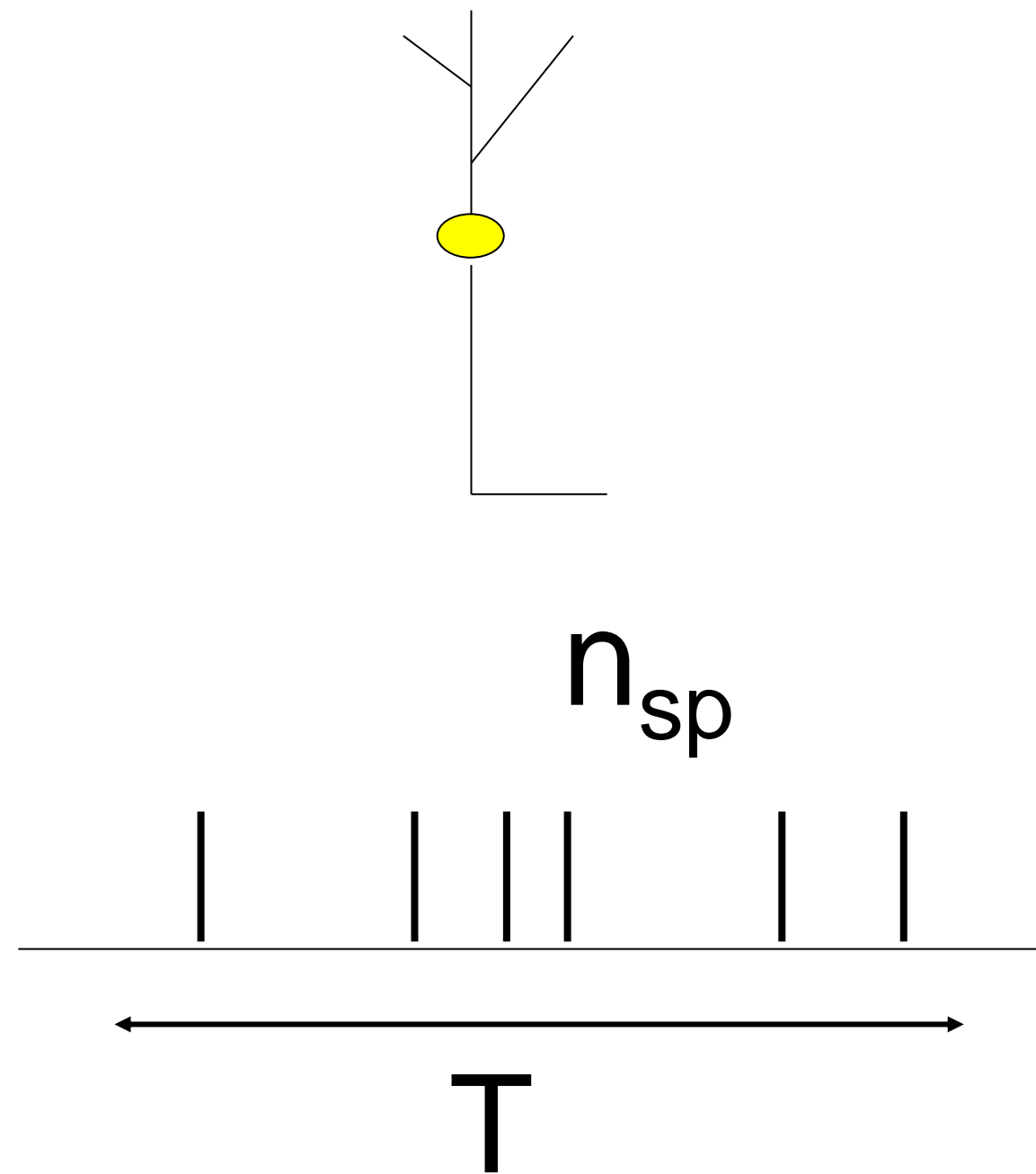


Probability of firing $P_F = \rho(t) \Delta t$

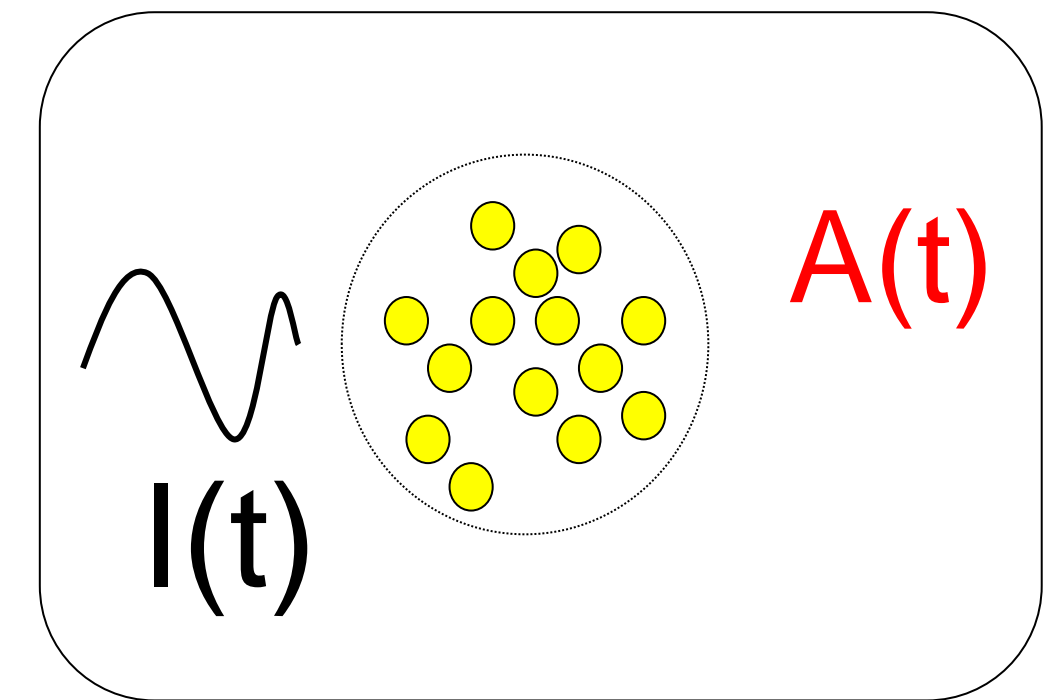
Survivor function $S(t | \hat{t}) = \exp\left(-\int_{\hat{t}}^t \rho(t') dt'\right)$

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

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.

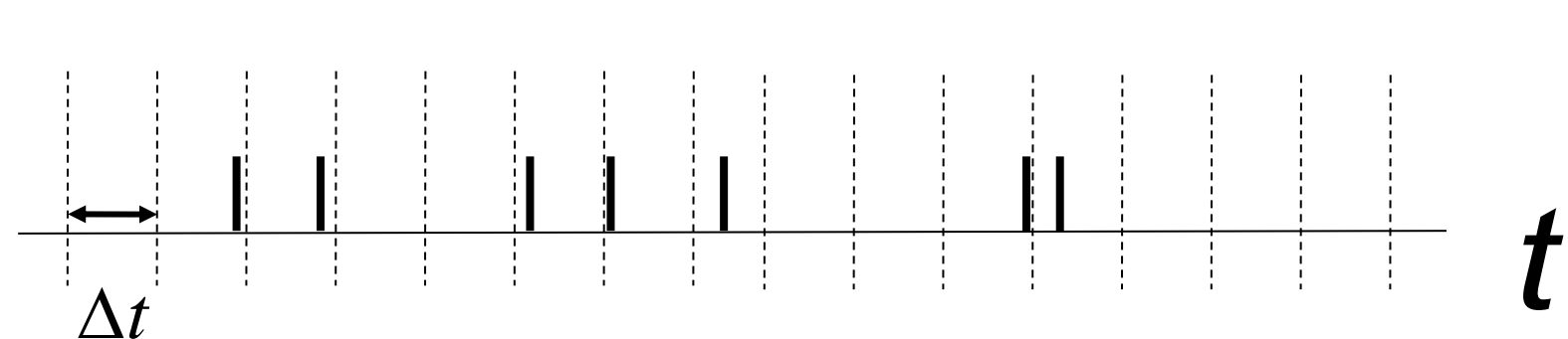
[2] V. **Schmutz** (2022), Mean-field limit of age and leaky memory dependent Hawkes processes. Stochastic Process. Appl., 149:39-59
<https://doi.org/10.1016/j.spa.2022.03.006>

[3] N. Fournier and E. **Löcherbach** (2016), On a toy model of interacting neurons. Annals Inst. H. Poincaré, 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

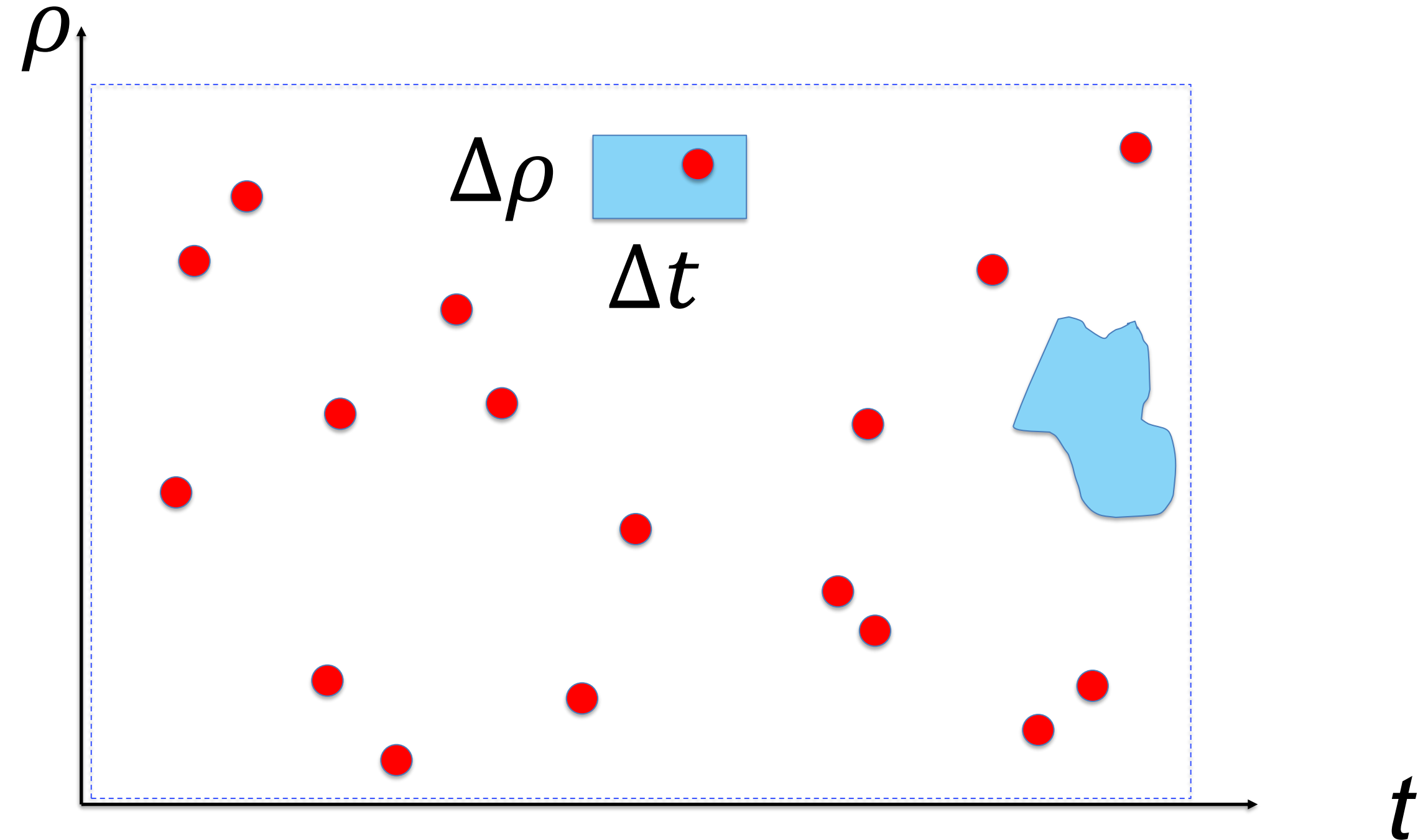
$$P_F = \rho_0 \Delta t$$

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

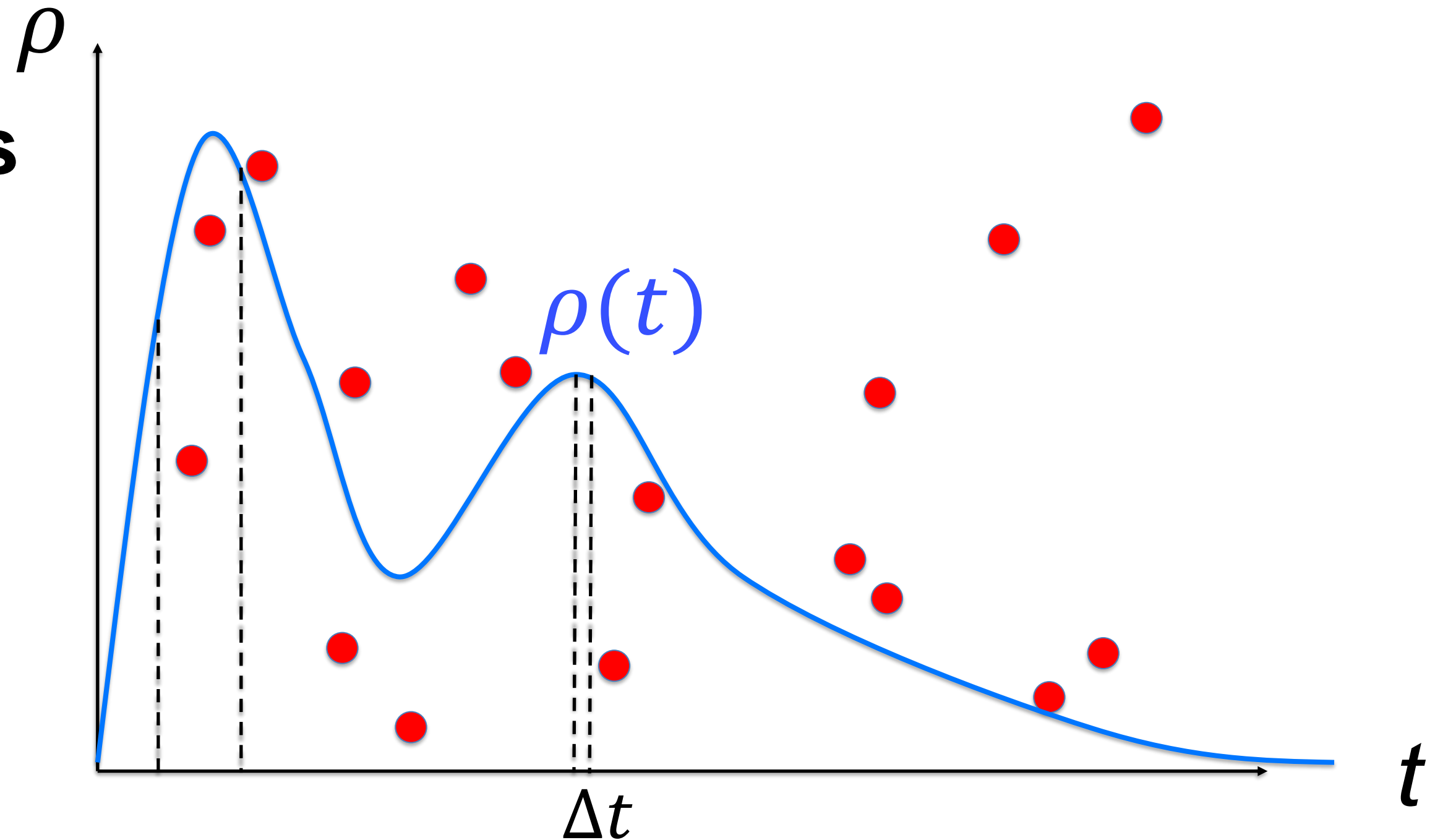
Efficient constructive procedure

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

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

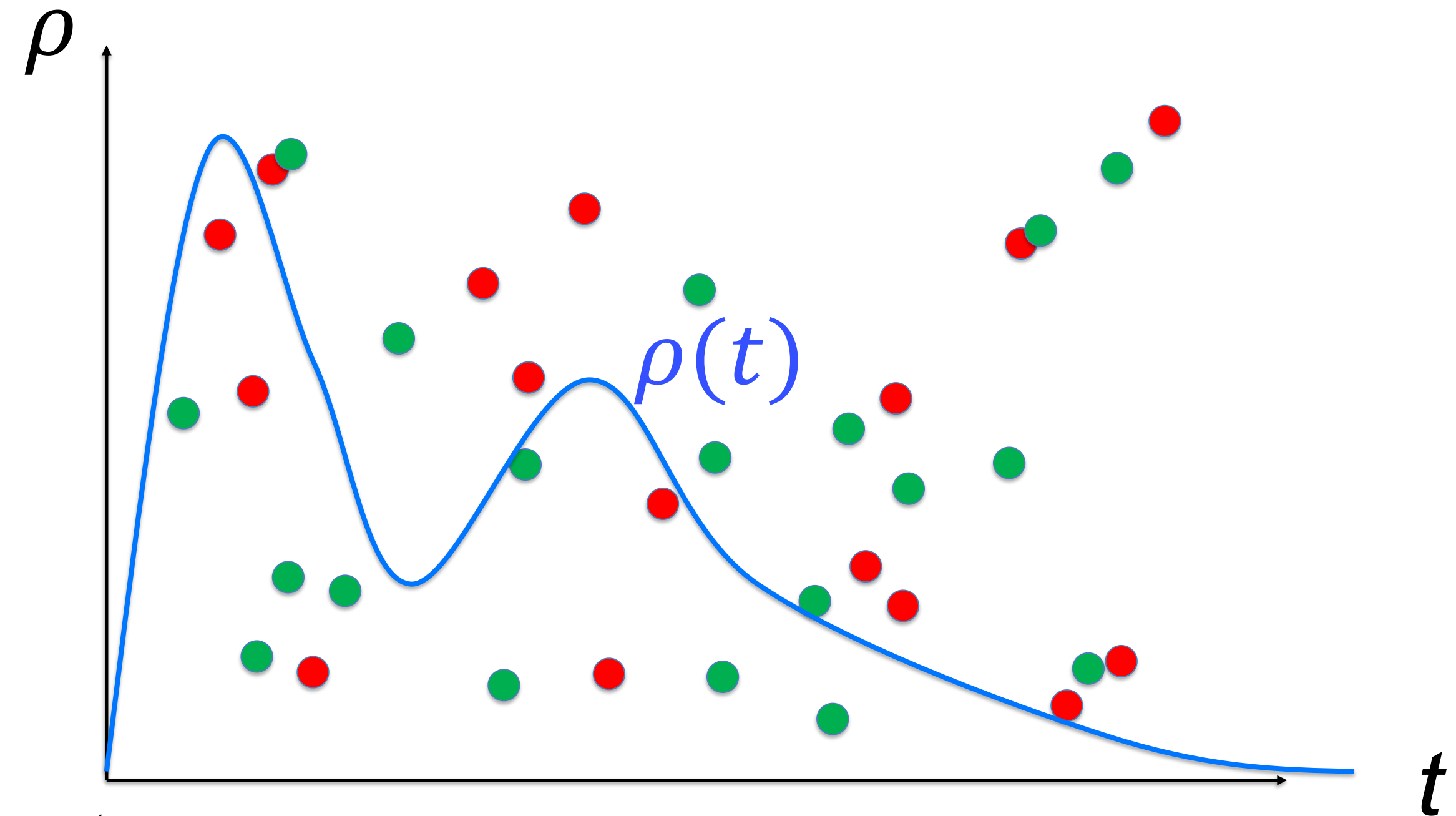
(ii) a counting process

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

Expectation at time t:

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

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



1st

2nd

2nd

2nd

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. Poincare, 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

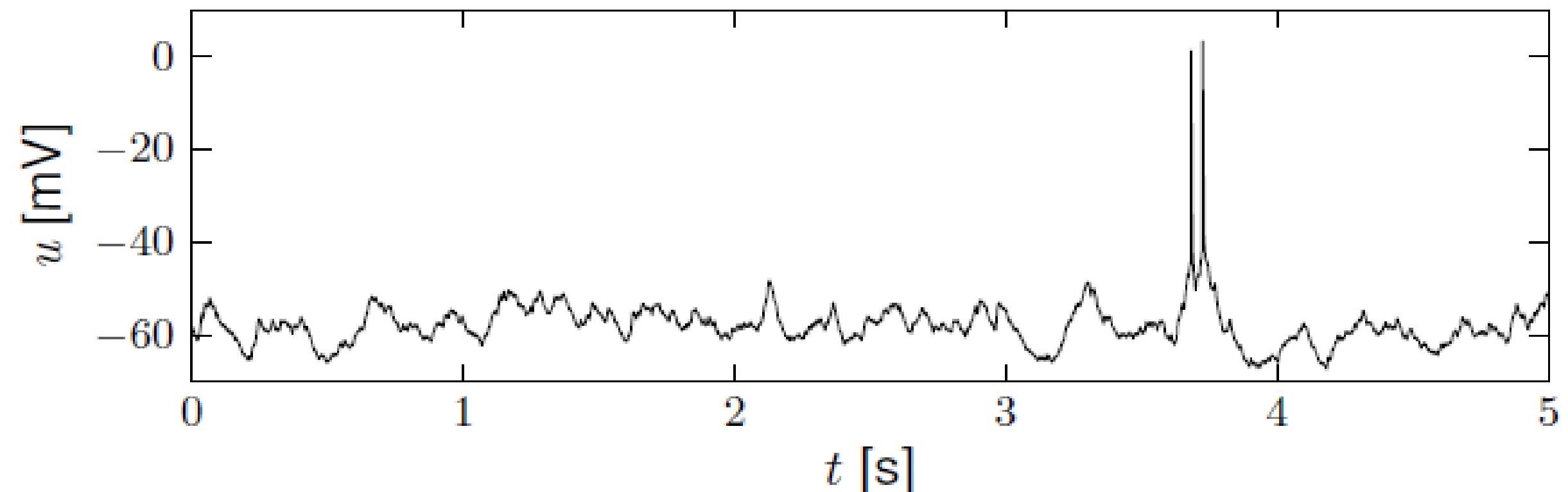
EPFL, Lausanne, Switzerland

- ✓ 5.1 Variability of spike trains
 - experiments
- ✓ 5.2 Sources of Variability?
 - Is variability equal to noise?
- ✓ 5.3 Three definitions of Rate code
 - Poisson Model
- 5.4 Stochastic spike arrival
 - Membrane potential fluctuations
- 5.5. Stochastic spike firing
 - subthreshold and superthreshold

Neuronal Dynamics – 5.4 Variability in vivo

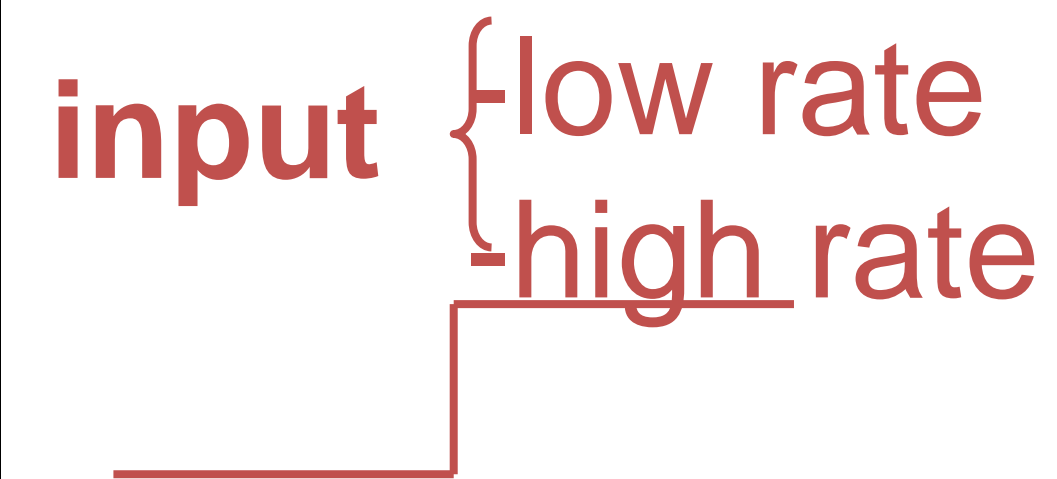
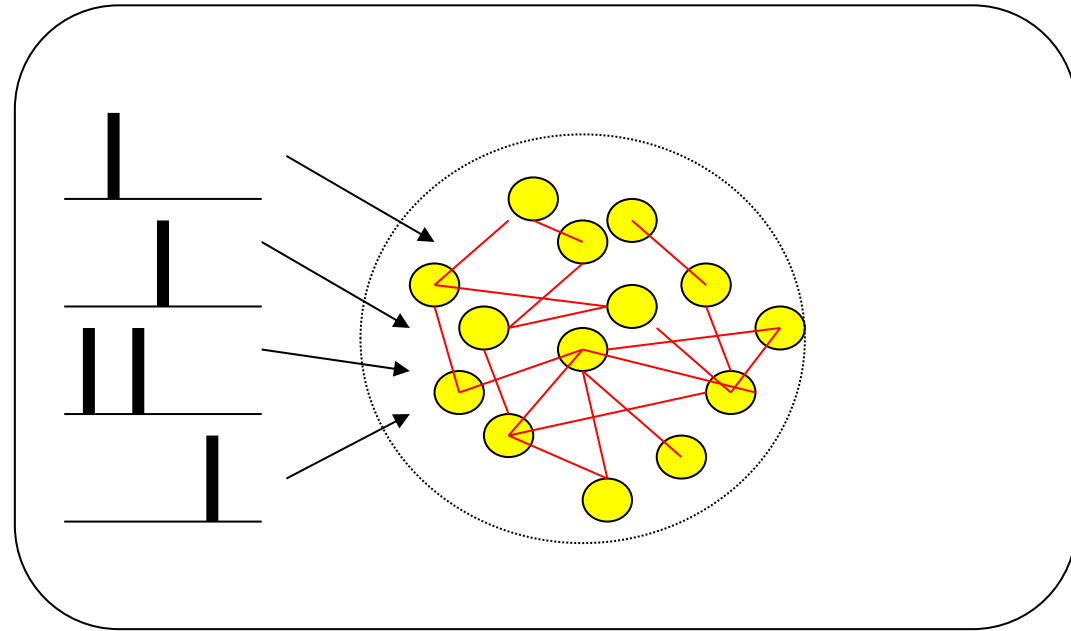
Spontaneous activity *in vivo*

Variability
of membrane potential?
awake mouse, freely whisking,



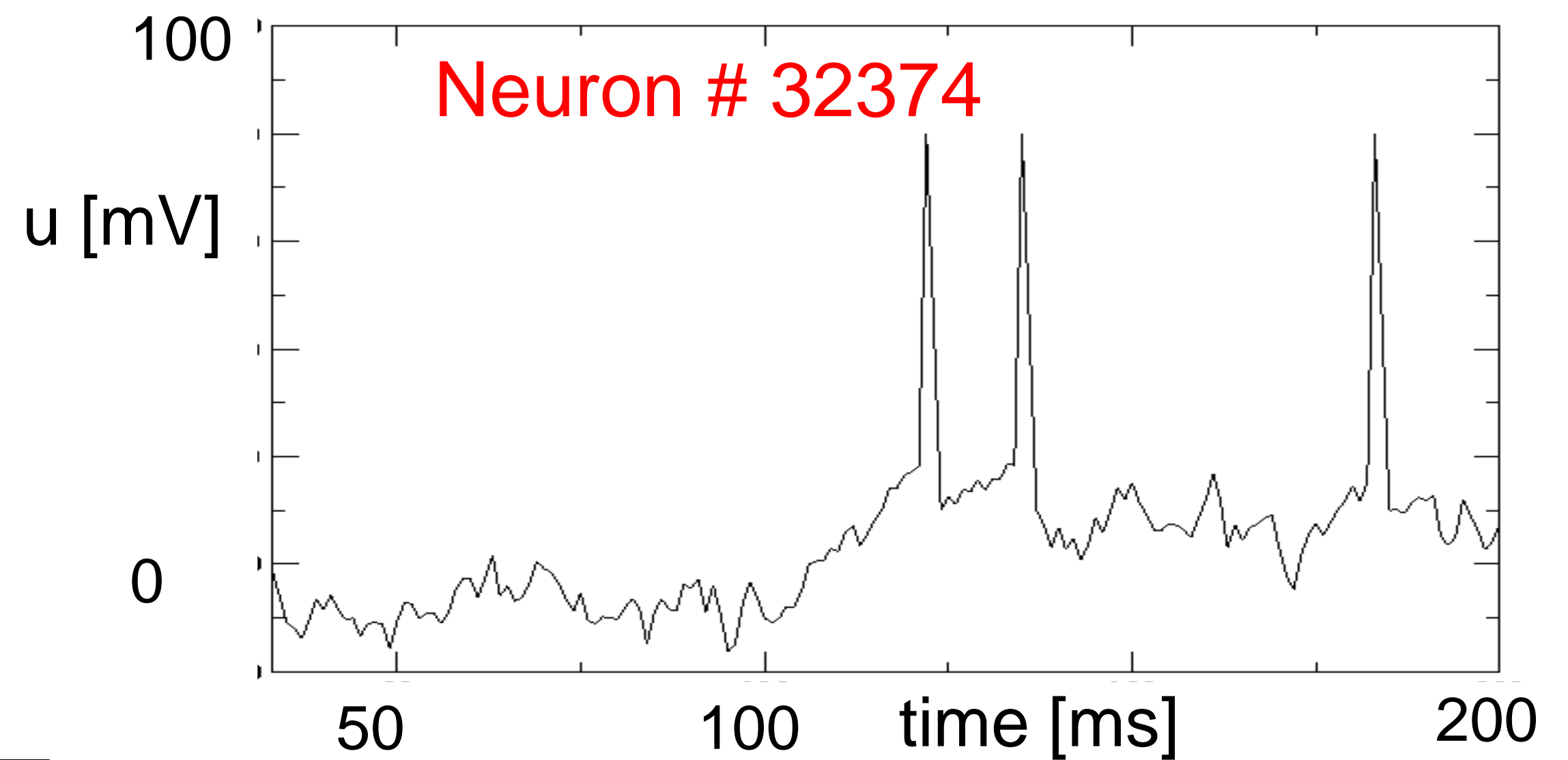
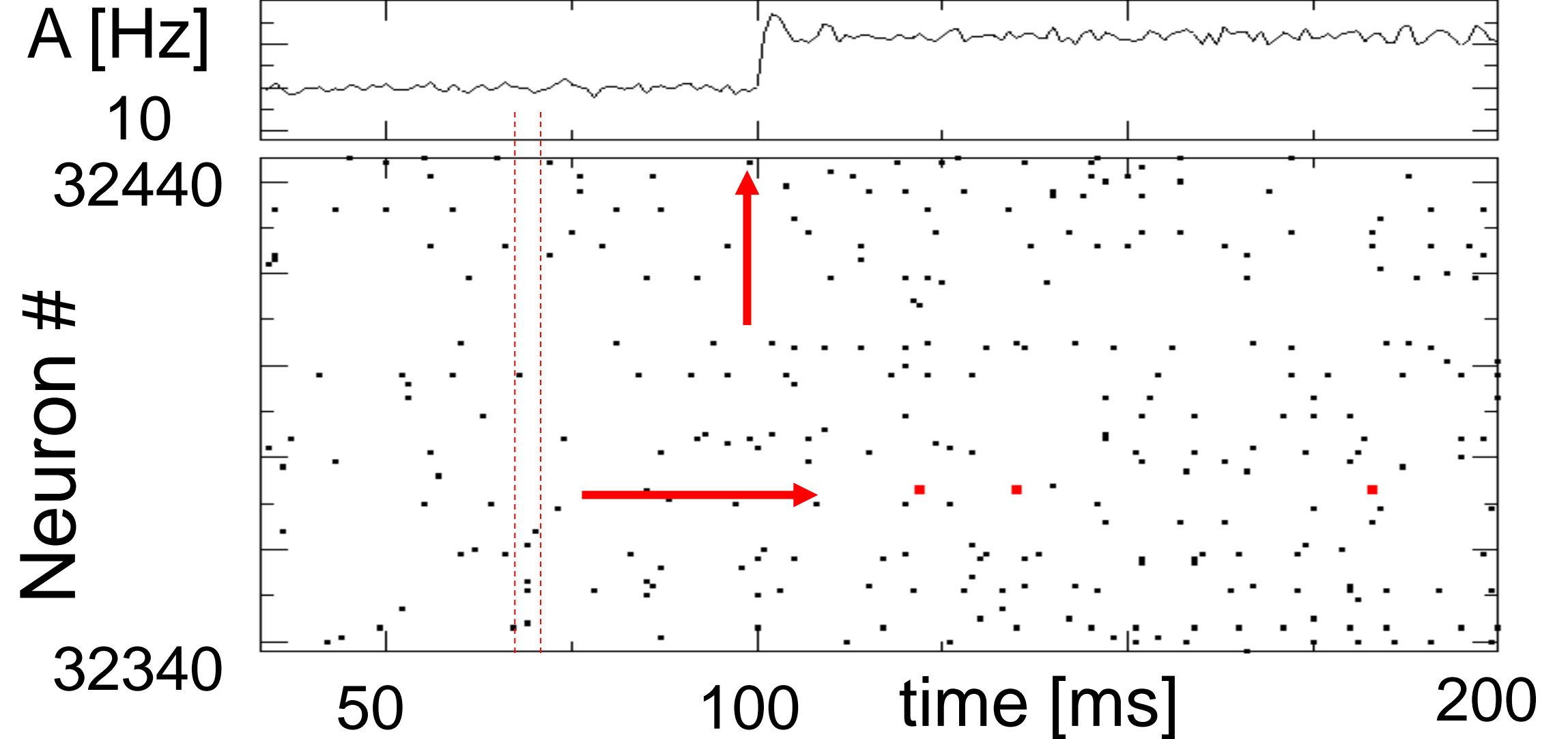
Crochet et al., 2011

Random firing in a population of LIF neurons

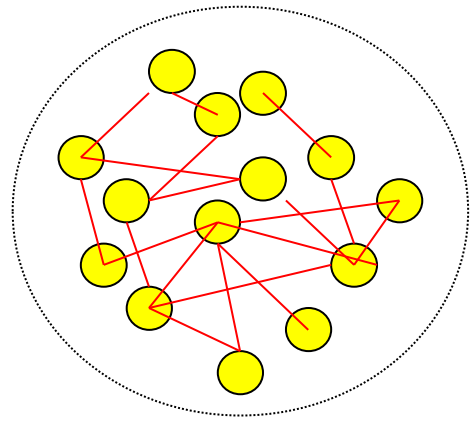


Population

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



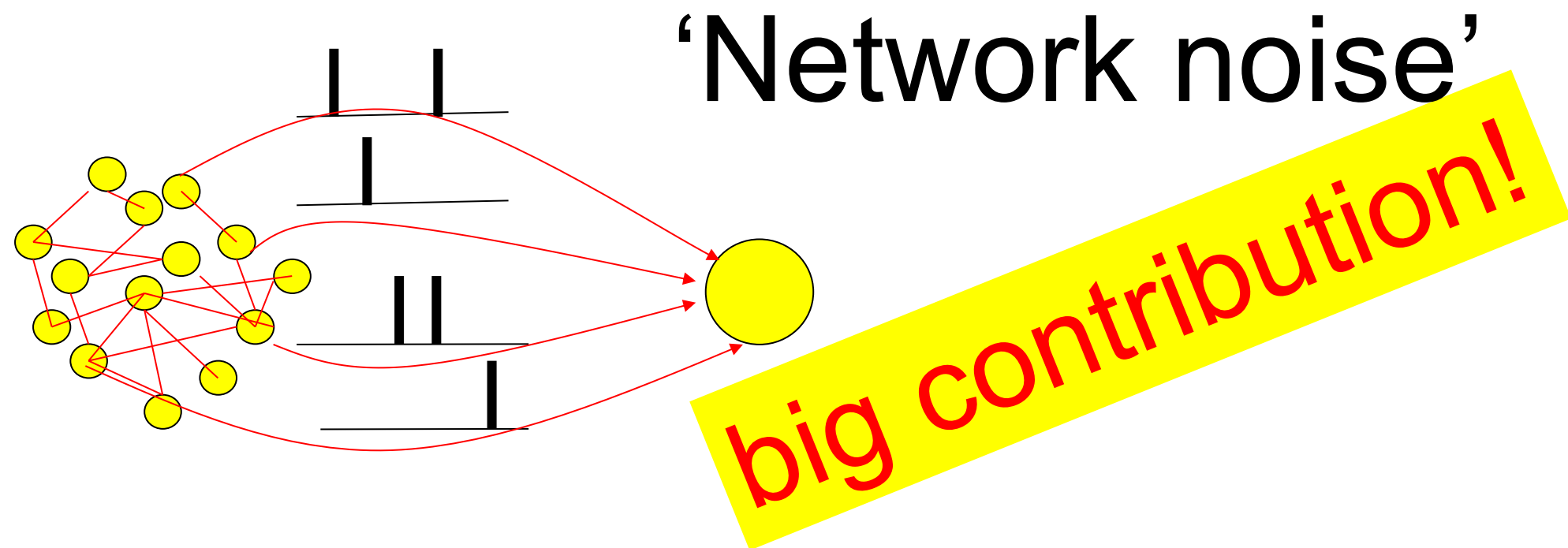
Neuronal Dynamics – 5.4 Membrane potential fluctuations



from neuron's point
of view:

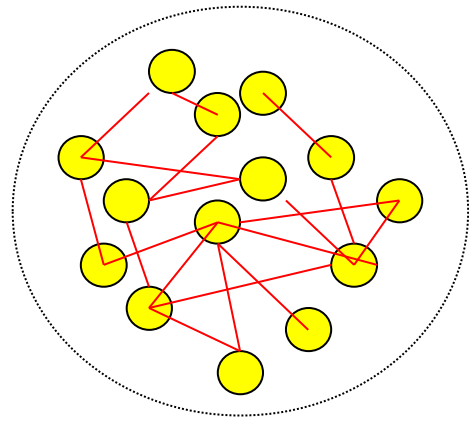
stochastic spike arrival

Pull out one neuron

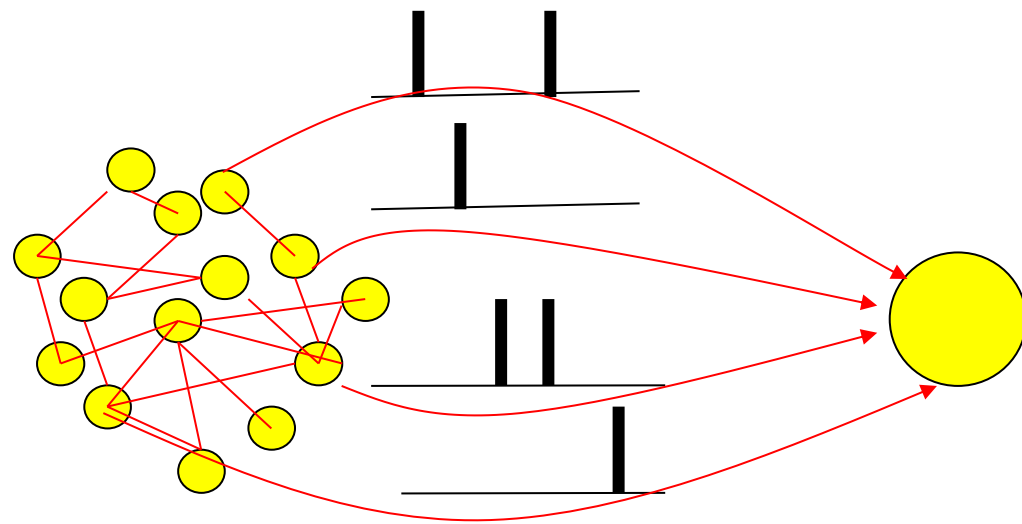


Neuronal Dynamics – 5.4. Stochastic Spike Arrival

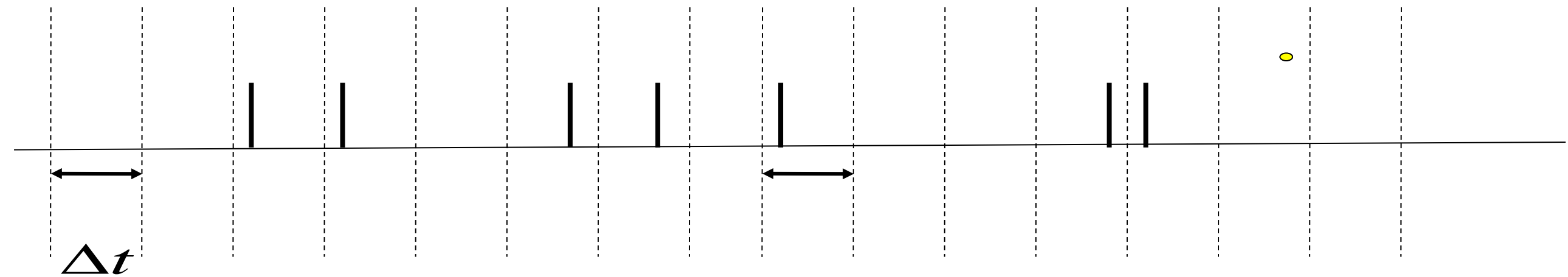
math detour
now!



Pull out one neuron



Total spike train of K presynaptic neurons



spike train

Probability of spike arrival:

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

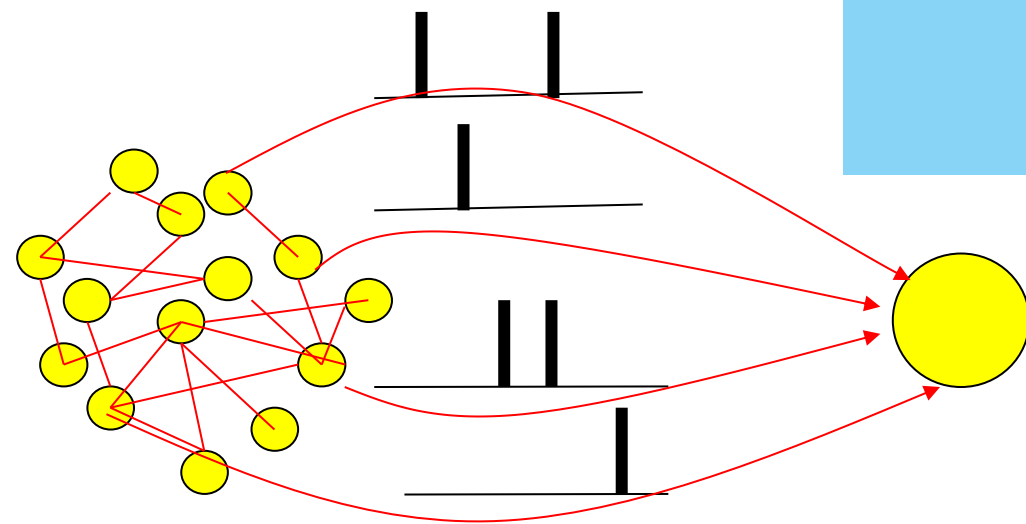
Take $\Delta t \rightarrow 0$

expectation

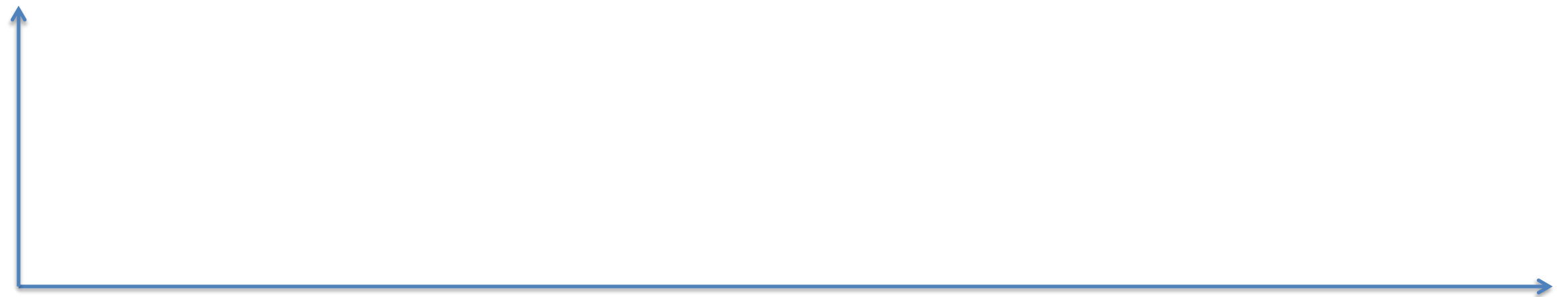
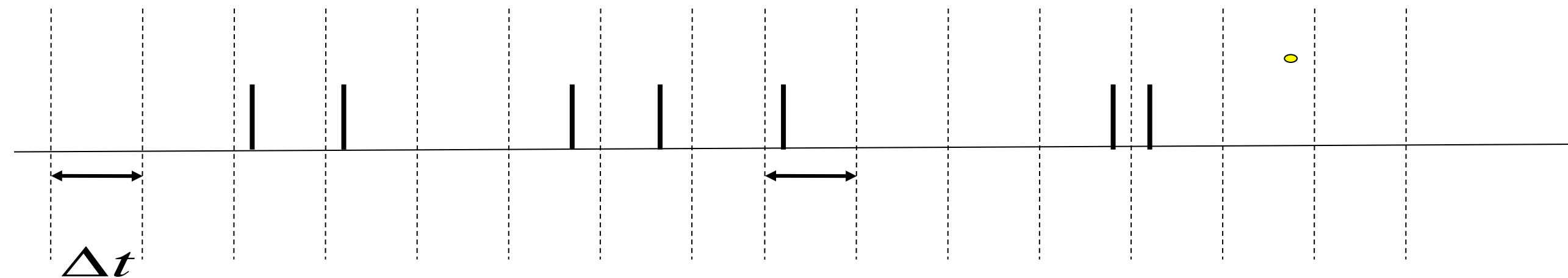
$$S(t) = \sum_{k=1}^K \sum_f \delta(t - t_k^f)$$

Neuronal Dynamics – 5.4. Fluctuation of input current

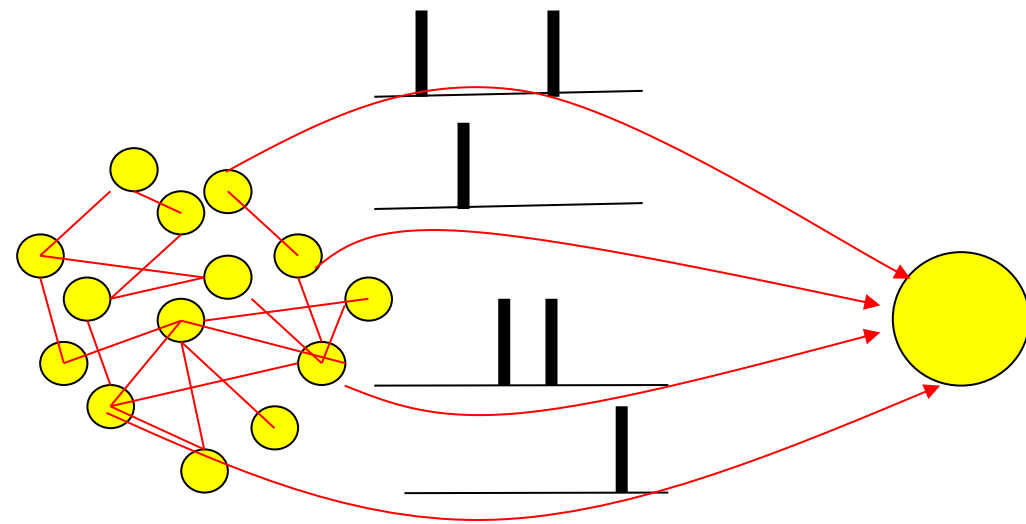
math detour
now!



Total spike train of K presynaptic neurons



Neuronal Dynamics – 5.4. Fluctuation of current/potential



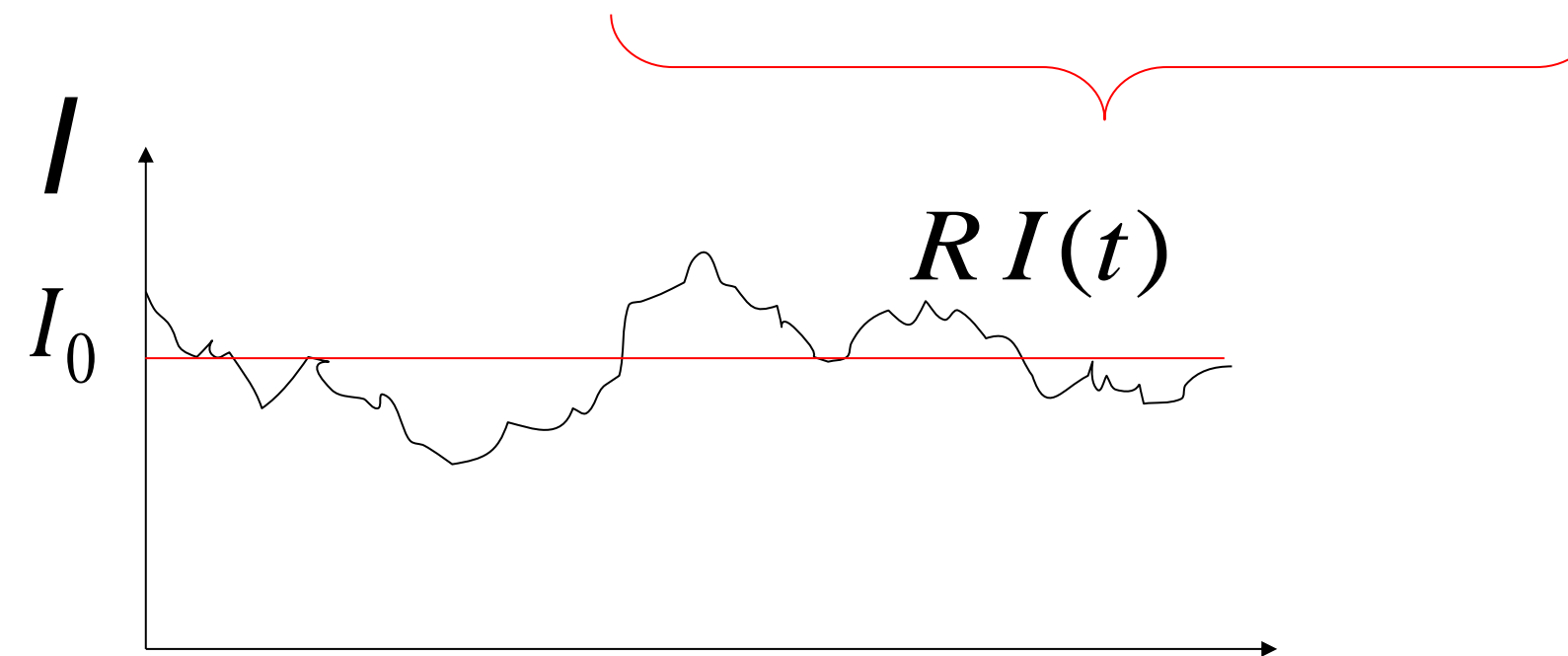
Synaptic current pulses of shape α

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

EPSC

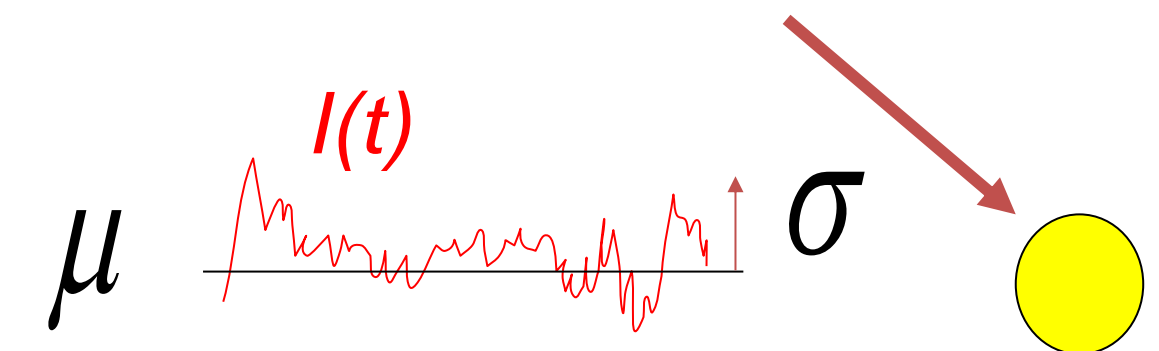
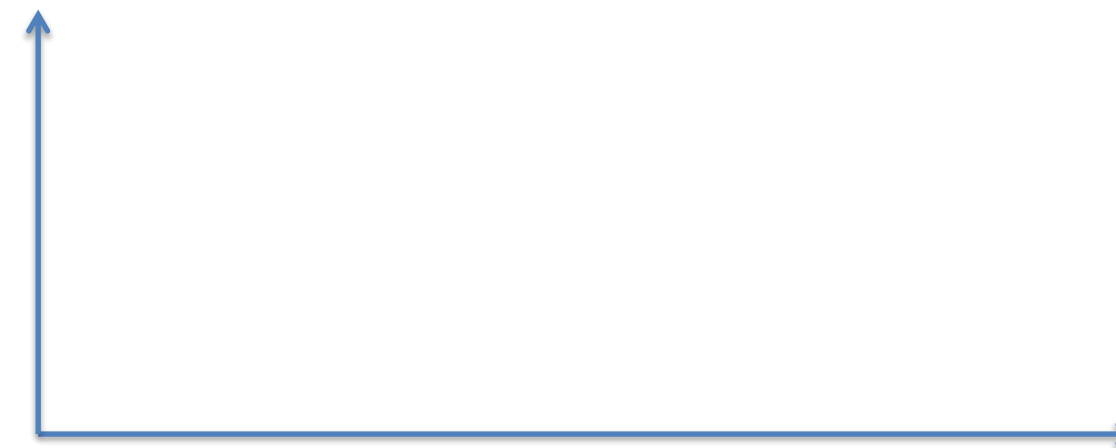
Passive membrane

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



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

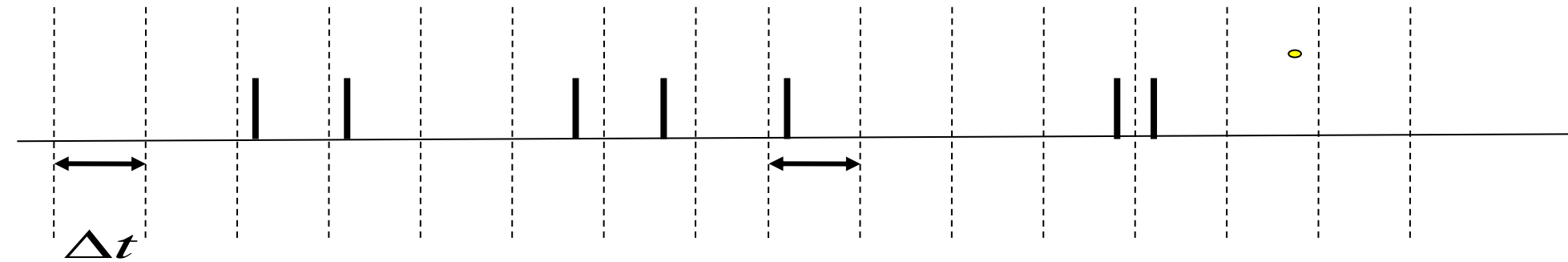
→ Fluctuating potential



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

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

use for assignment/
homework!

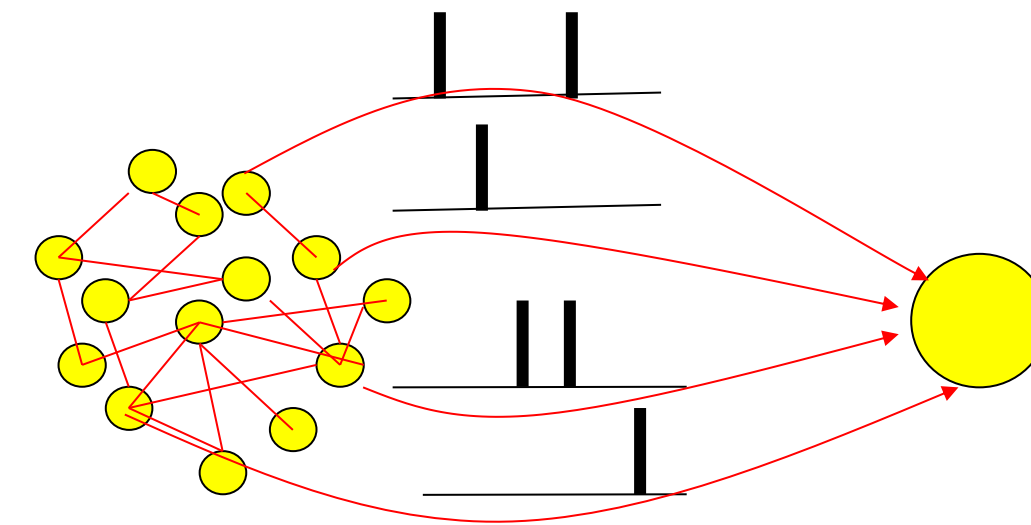
$$I_0 = \frac{1}{R} \sum_k w_k \int dt' \alpha(t - t') \nu_k$$

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

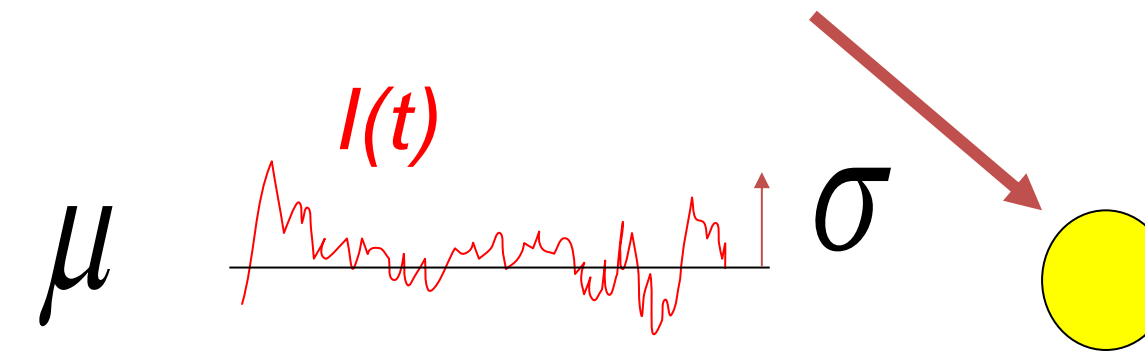
$$\langle x(t) \rangle = \int dt' f(t - t') \rho(t')$$

rate of inhomogeneous
Poisson process

Neuronal Dynamics – 5.4. Fluctuation of current/potential

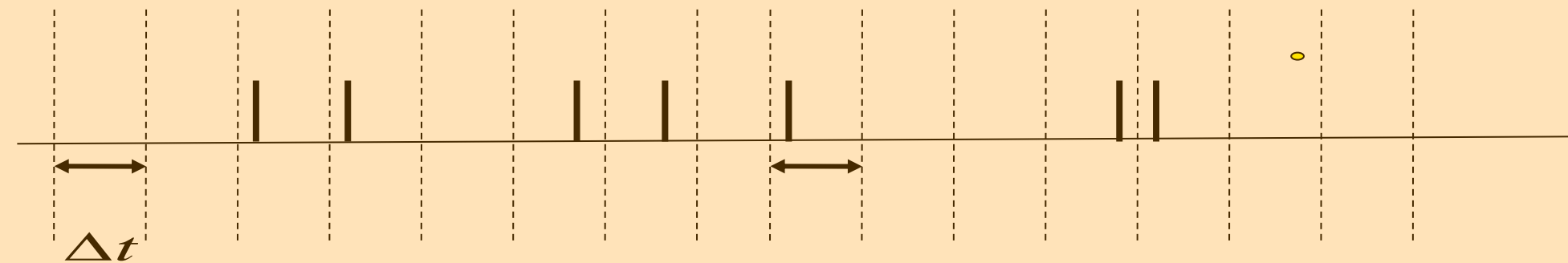
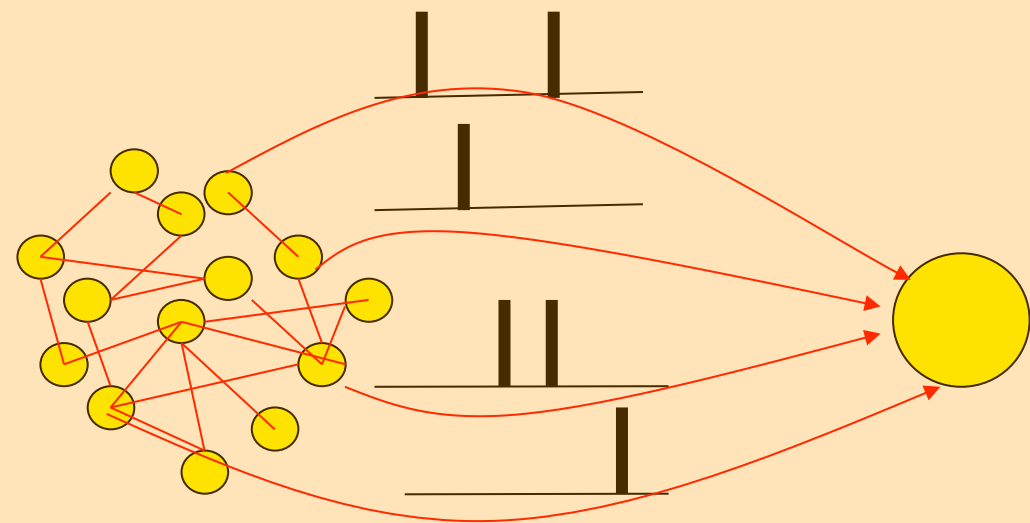


fluctuating input current



fluctuating potential

Neuronal Dynamics – Assignment/homework

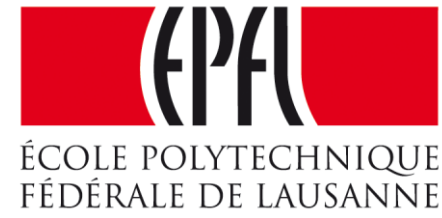


$$u(t) = \sum_f \int dt' f(t-t') \delta(t'-t_k^f)$$

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

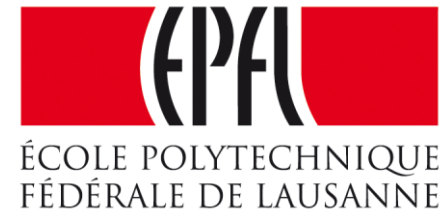
Week 5 – Variability and Noise: The question of the neural code

Wulfram Gerstner

EPFL, Lausanne, Switzerland

- ✓ 5.1 Variability of spike trains
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Week 5 – part 4b : Membrane potential fluctuations

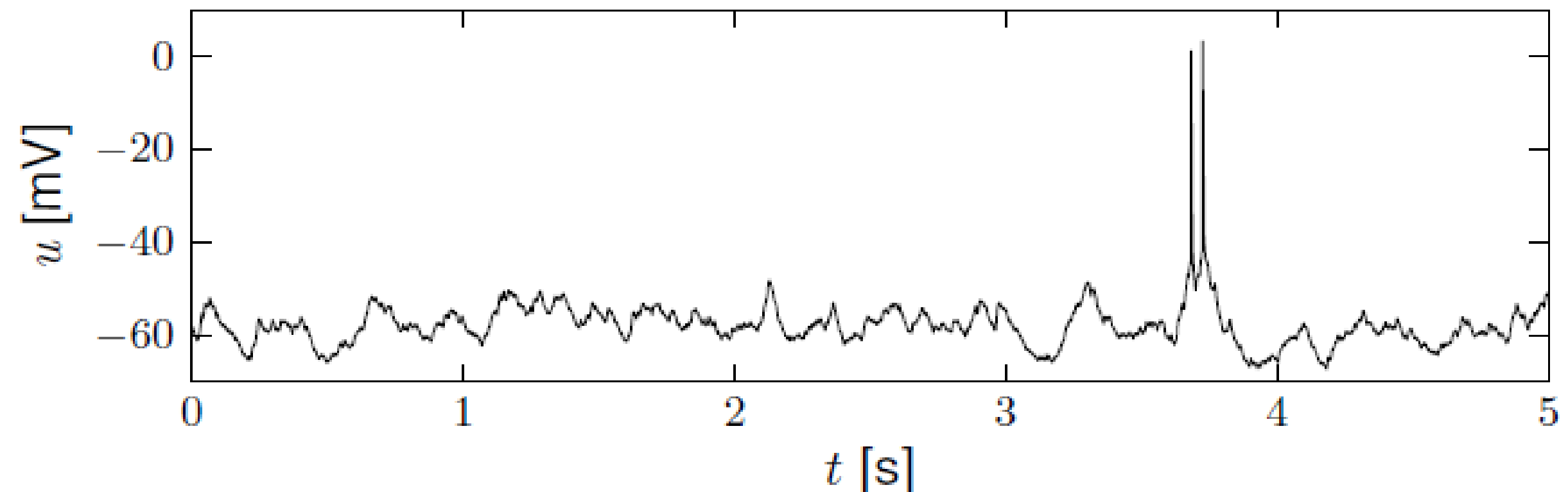


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Neuronal Dynamics – 5.4 Variability in vivo

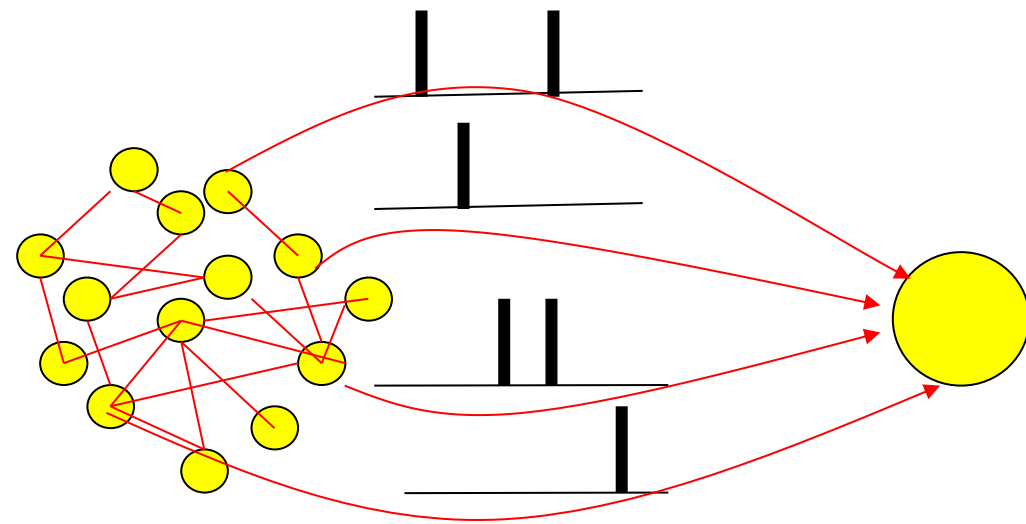
Spontaneous activity *in vivo*

Variability
of membrane potential?
awake mouse, freely whisking,



Crochet et al., 2011

Neuronal Dynamics – 5.4b. Fluctuations of potential



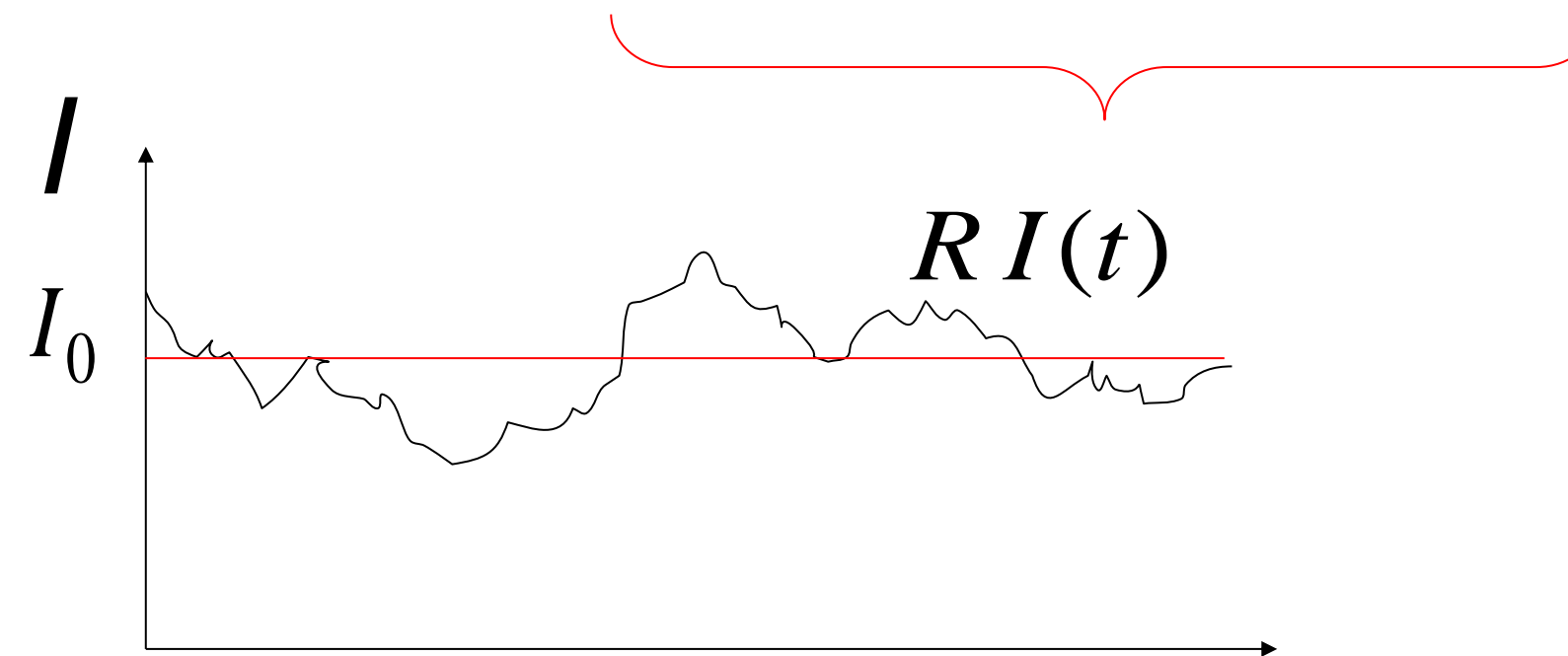
Synaptic current pulses of shape α

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

EPSC

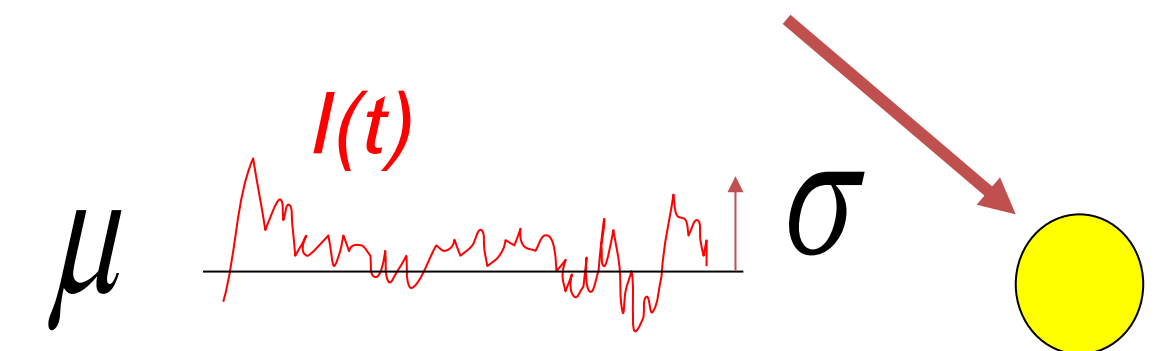
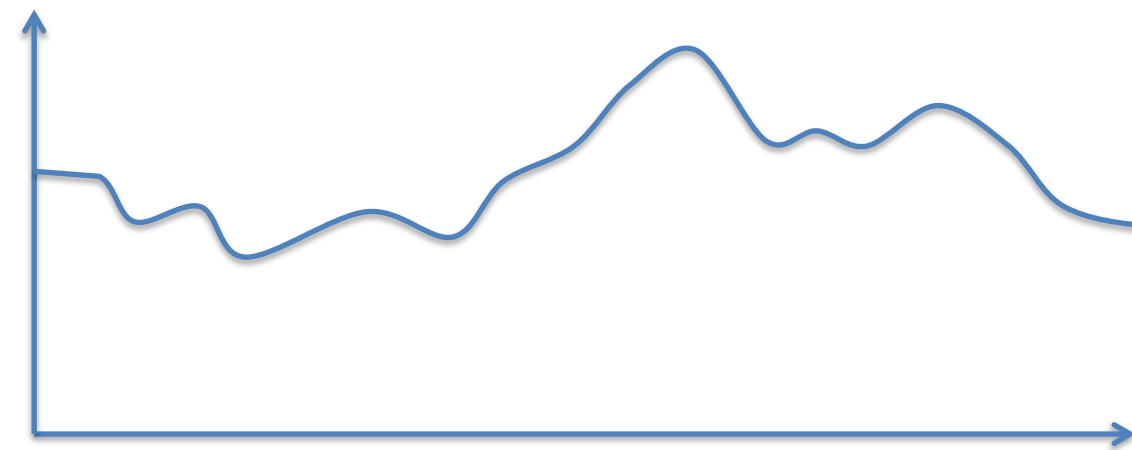
Passive membrane

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



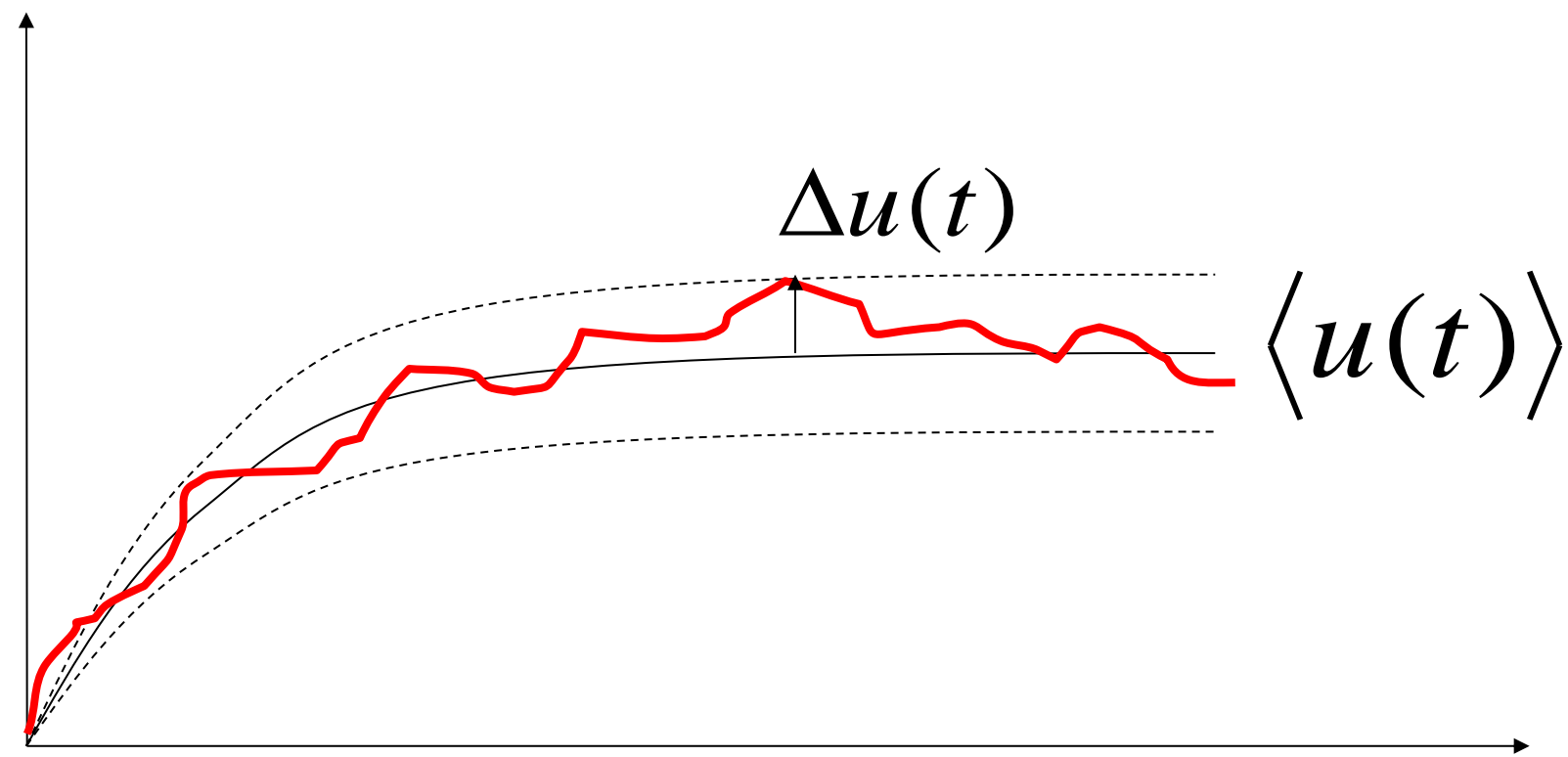
$$I^{syn}(t) = I_0 + I^{fluct}(t)$$

→ Fluctuating potential



Fluctuating input current

Neuronal Dynamics – 5.4b. Fluctuations of potential



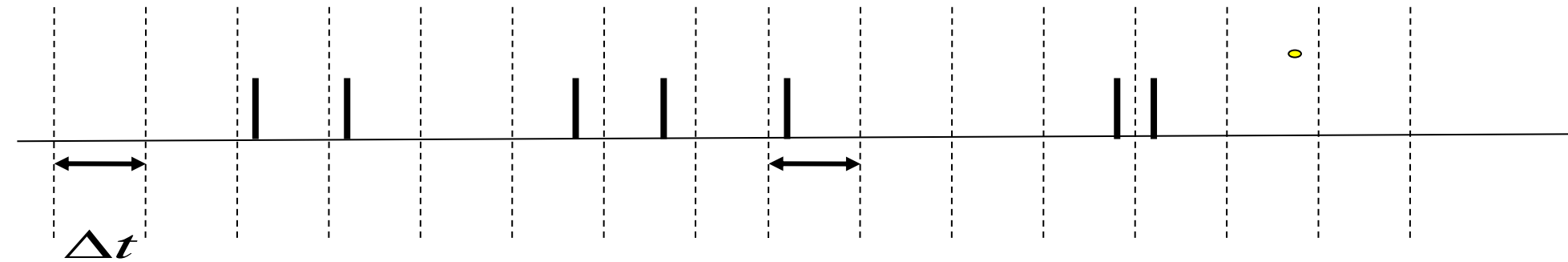
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

Input: step + fluctuations

Neuronal Dynamics – 5.4b. Calculating autocorrelations

Autocorrelation

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



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

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

Mean:

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

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

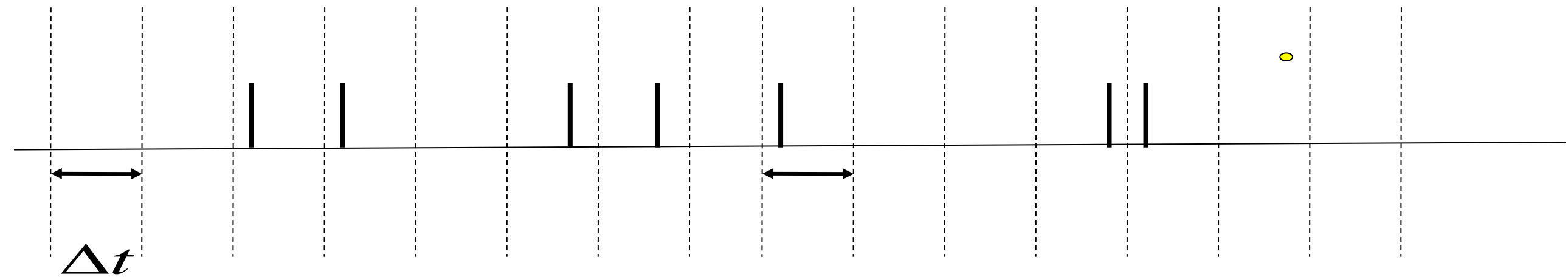
rate of homogeneous
Poisson process

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

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:

$$P_F = \rho_0 \Delta t$$

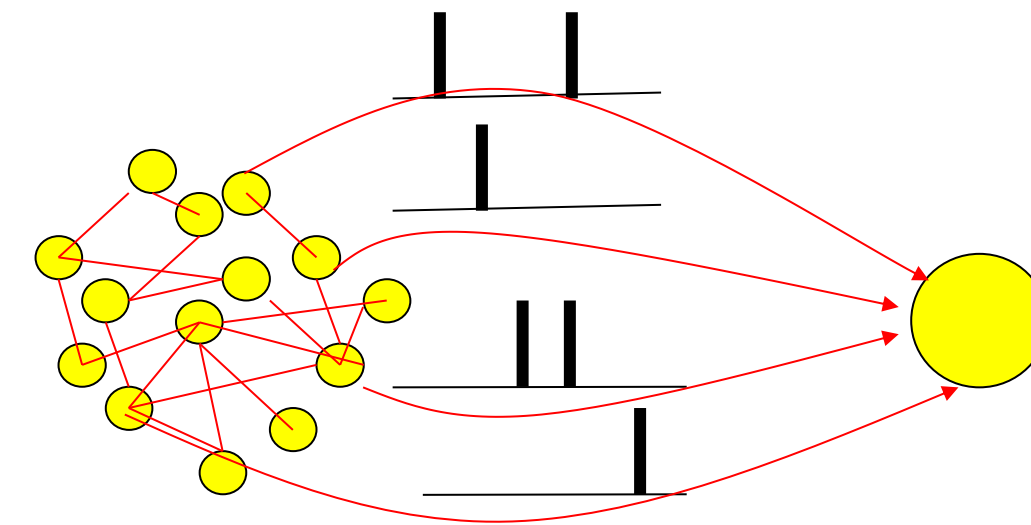
Autocorrelation (continuous time)

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

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

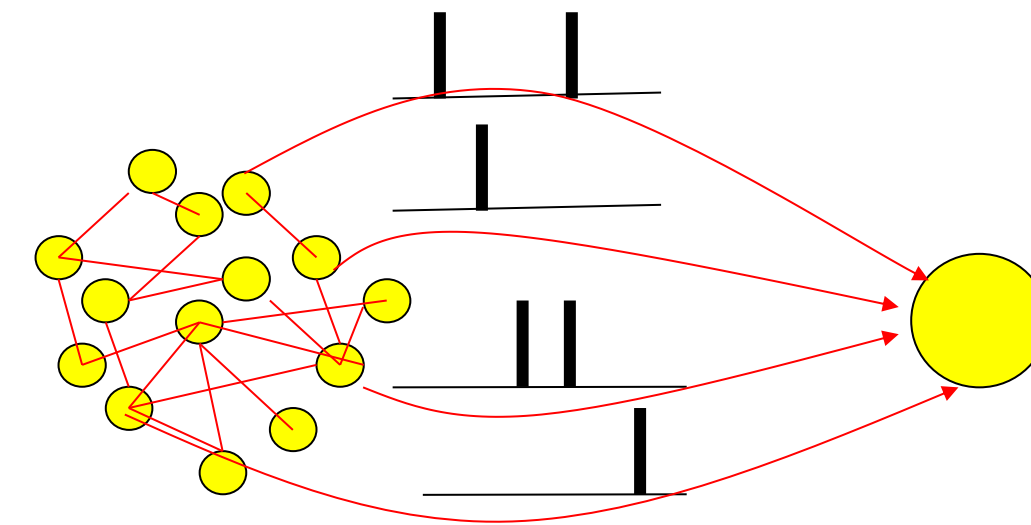
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle [u(t)]^2 \rangle - \langle u(t) \rangle^2$$

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*



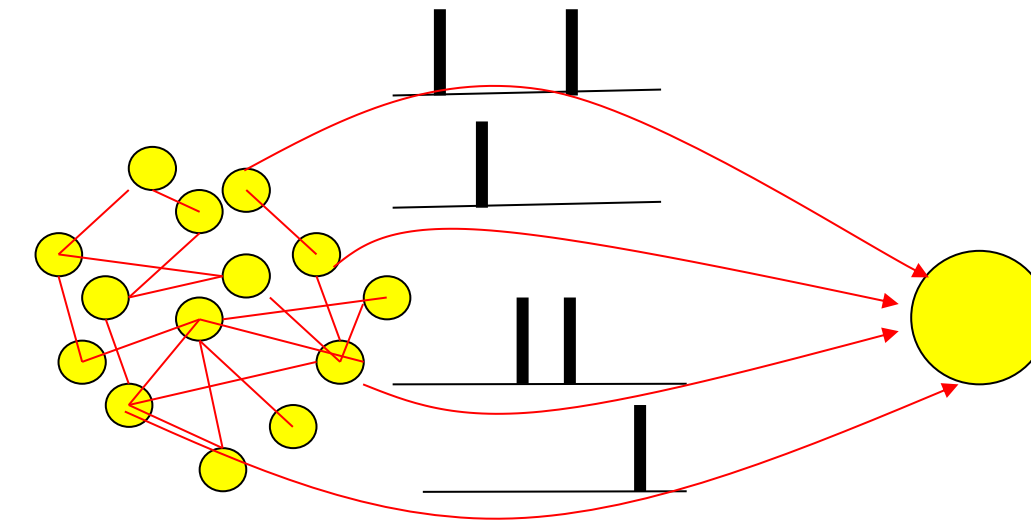
Passive membrane

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

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

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

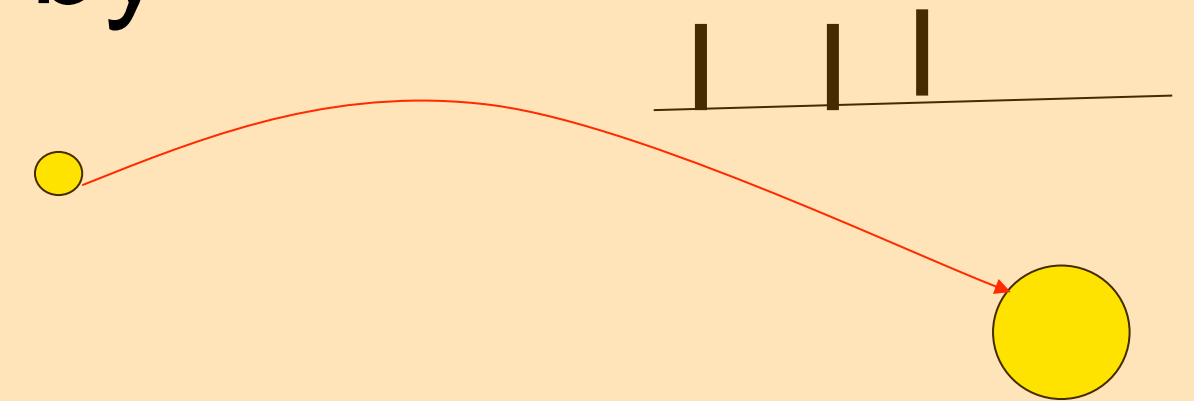
Fluctuations of potential

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

Neuronal Dynamics – Quiz 5.4

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

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

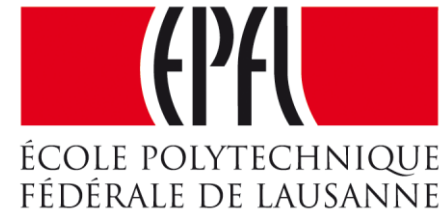


Suppose the neuronal dynamics are given by

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

- ☐ 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

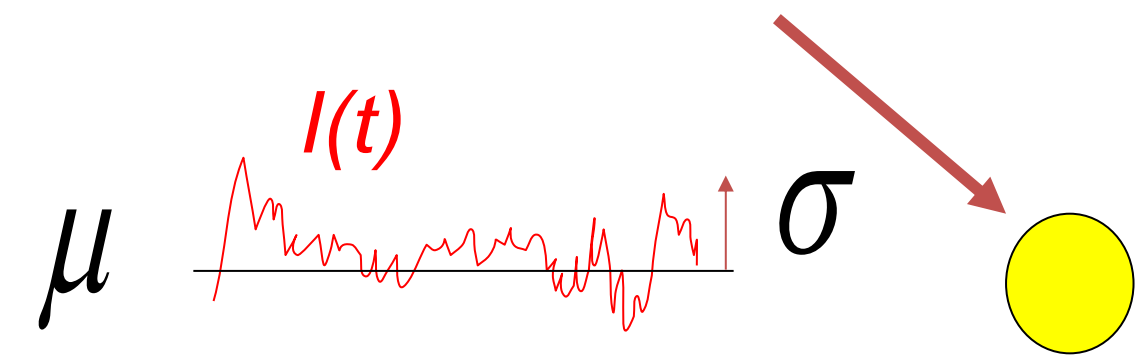
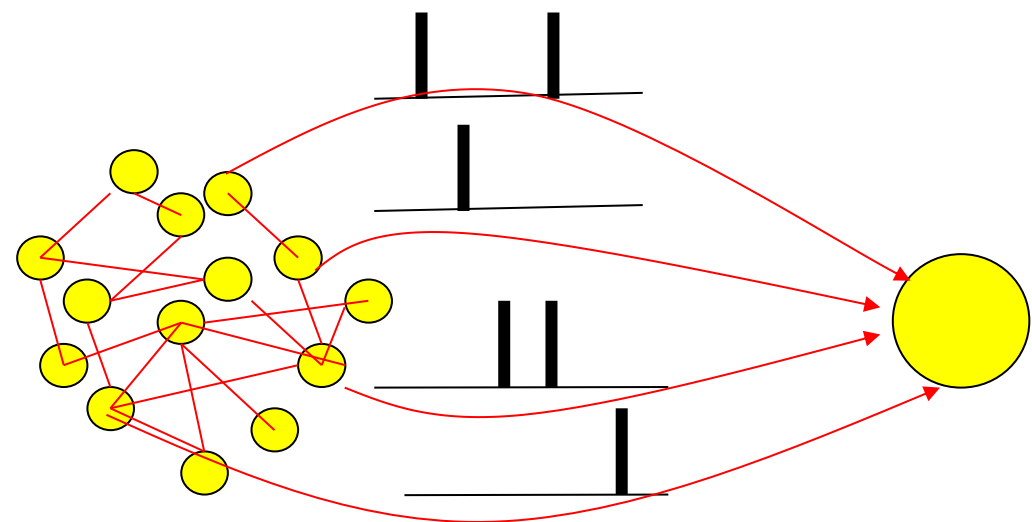
Week 5 – Variability and Noise: The question of the neural code

Wulfram Gerstner

EPFL, Lausanne, Switzerland

- ✓ 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

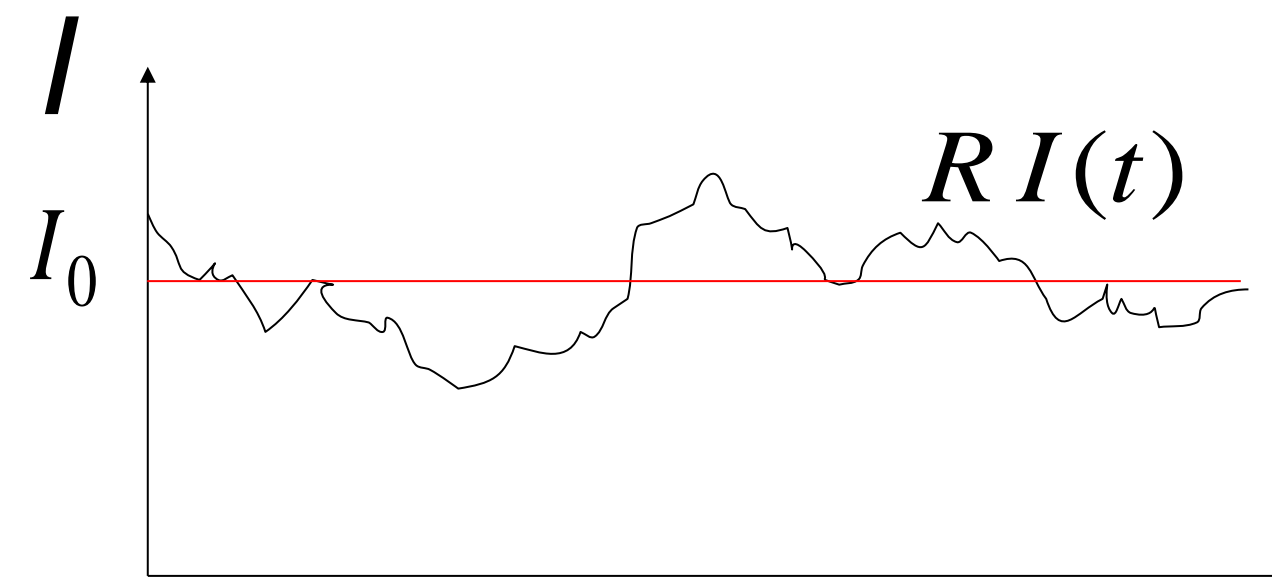
Neuronal Dynamics – review: Fluctuations of potential



Fluctuating input current

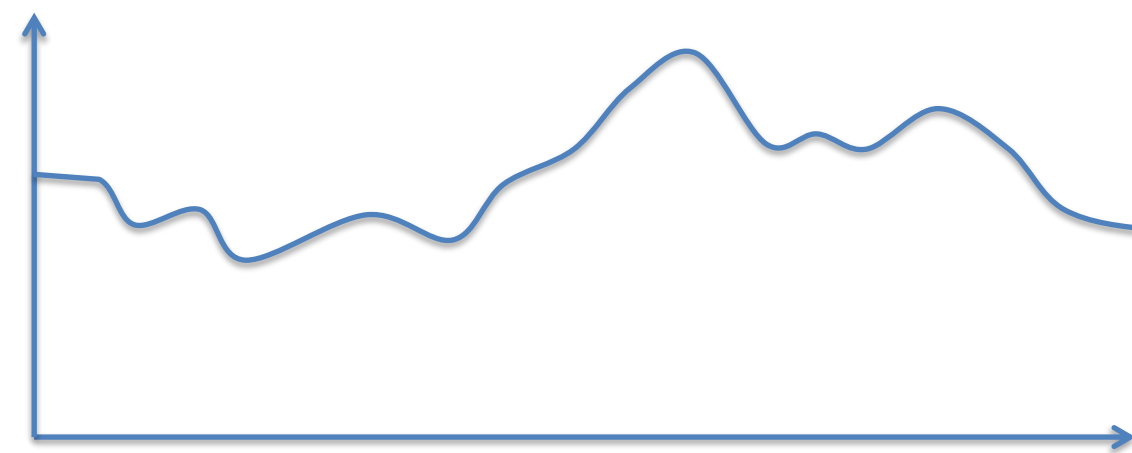
Passive membrane

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



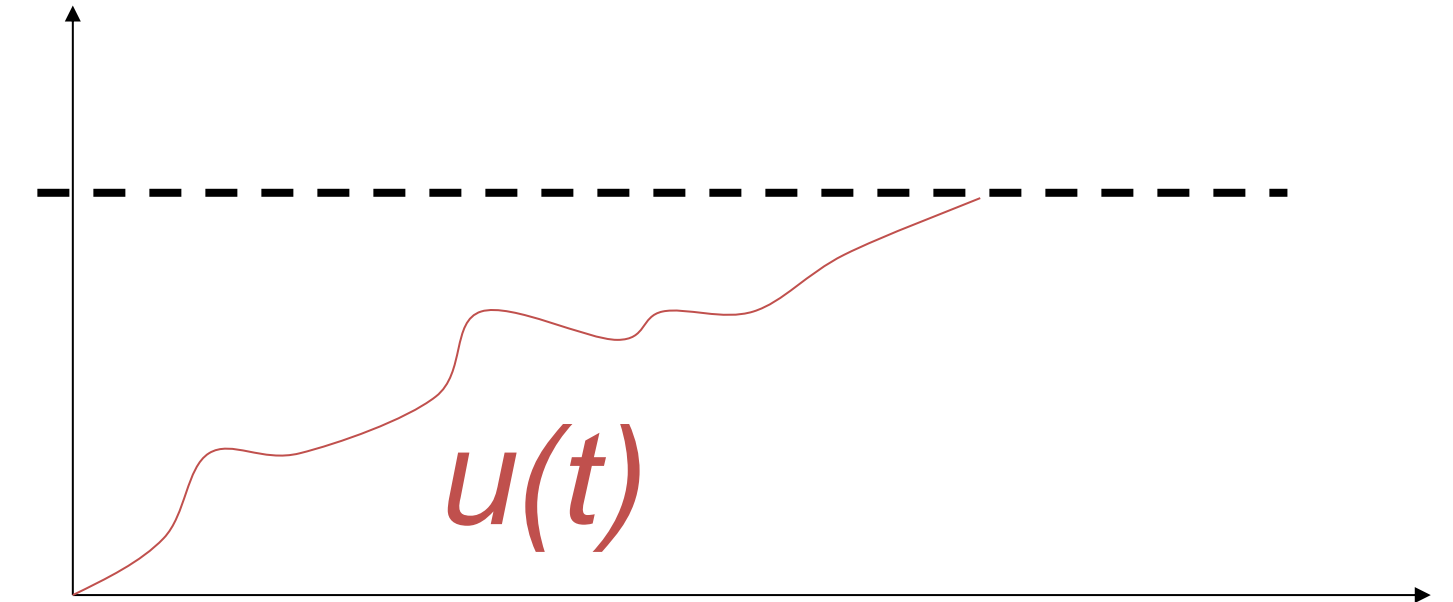
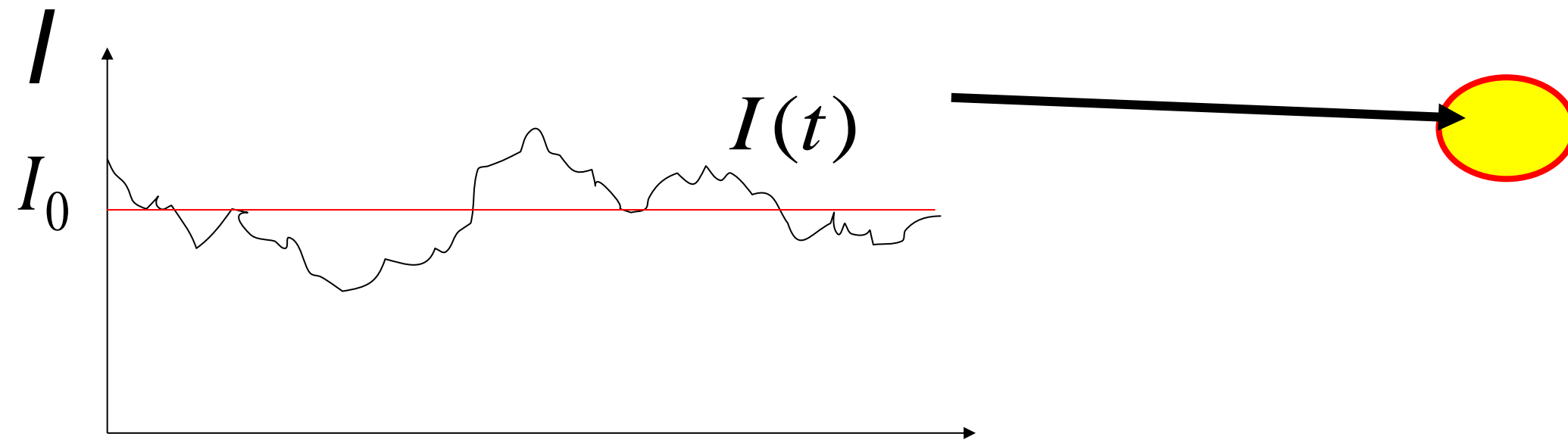
$$I^{syn}(t) = I_0 + I^{fluct}(t)$$

→ Fluctuating potential



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

effective noise current



LIF

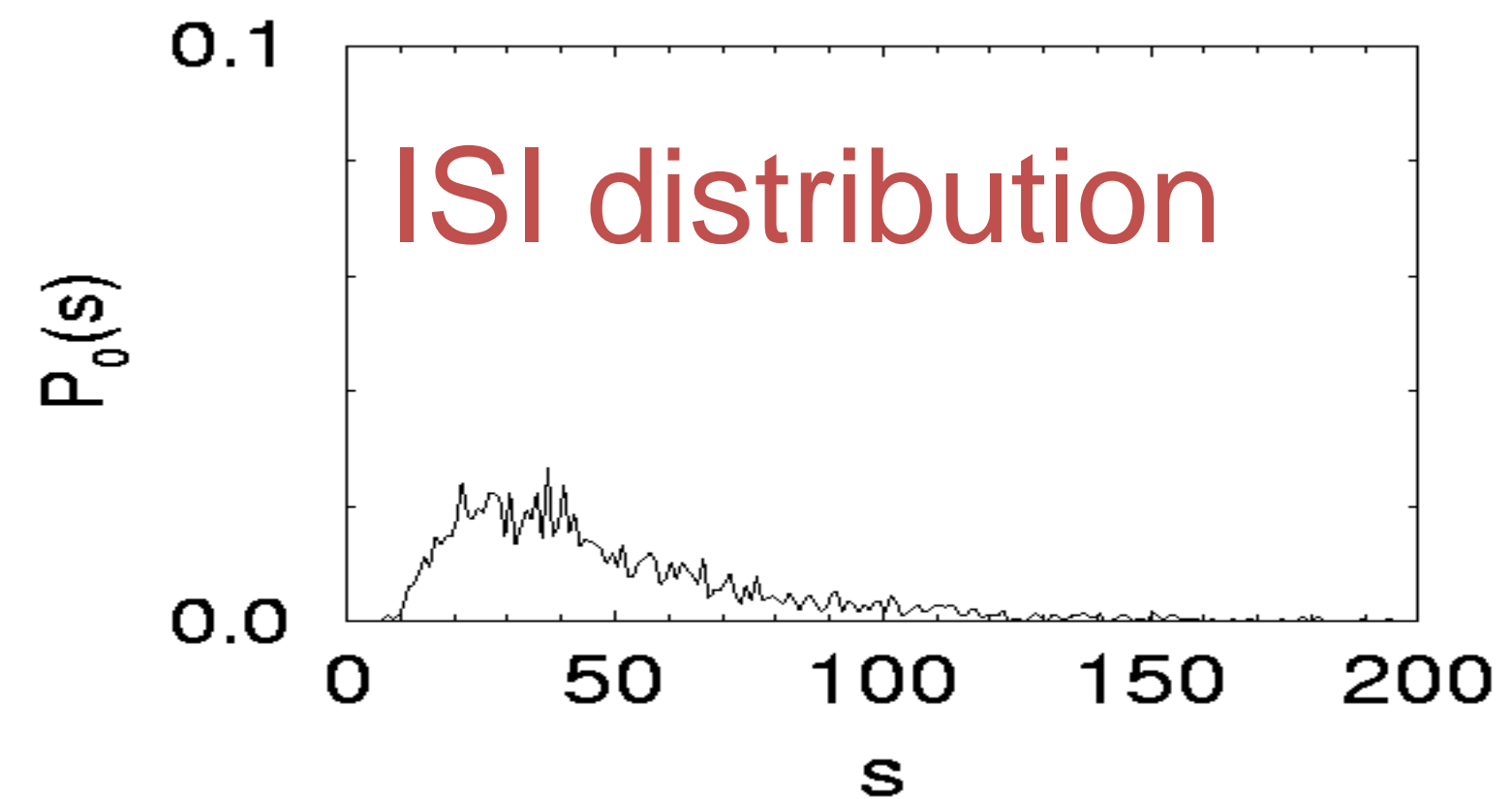
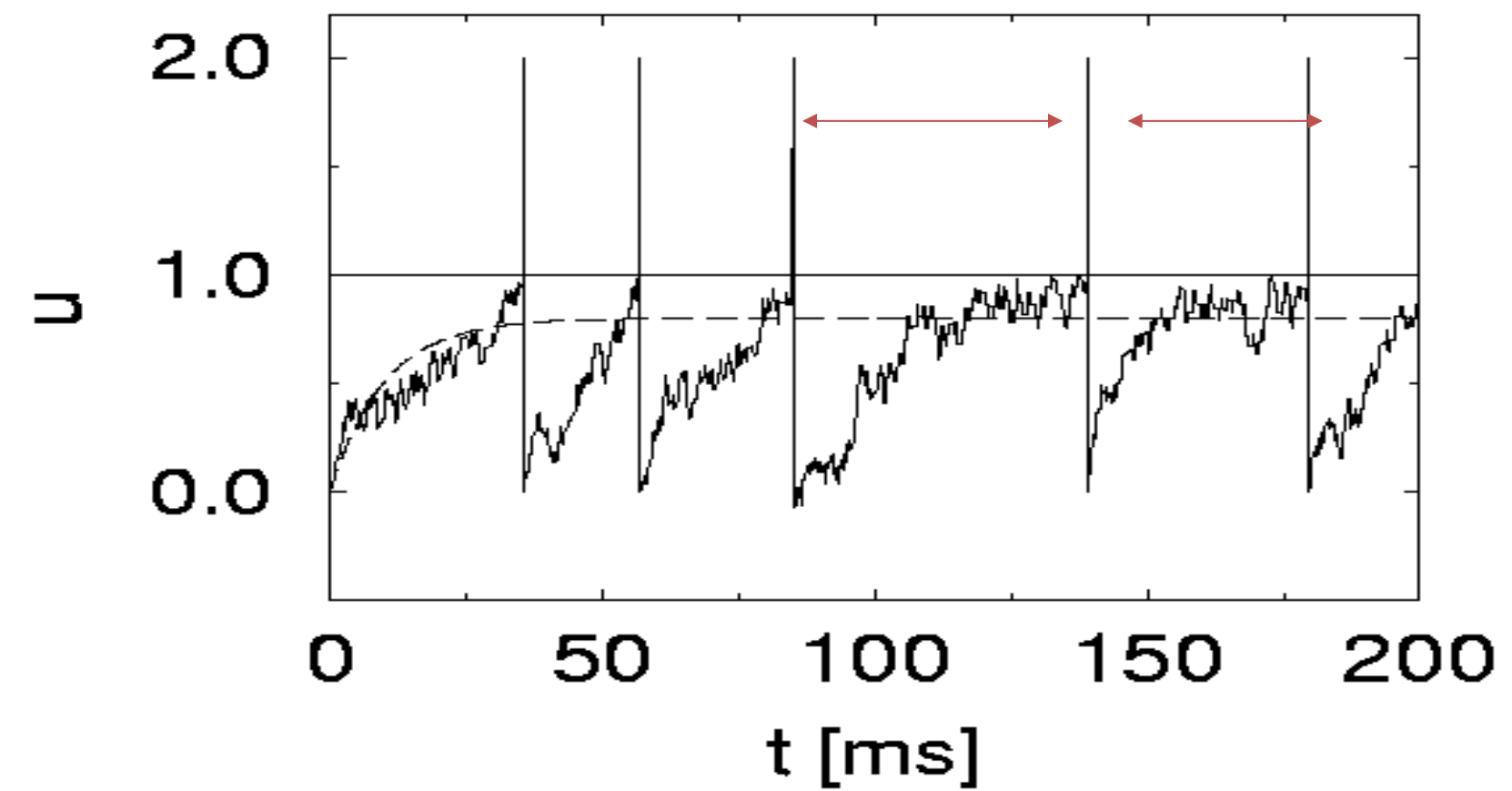
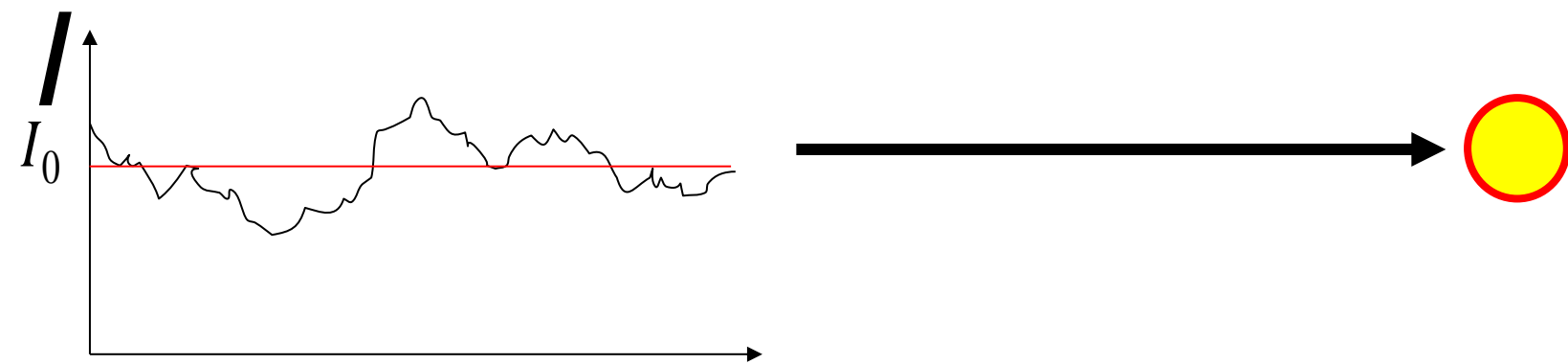
$$\tau \frac{d}{dt} u = -(u - u_{rest}) + R I(t)$$

$$I(t) = [I_o + I_{noise}]$$

$$IF \ u(t) = \mathcal{V} \ THEN \ u(t + \Delta) = u_r$$

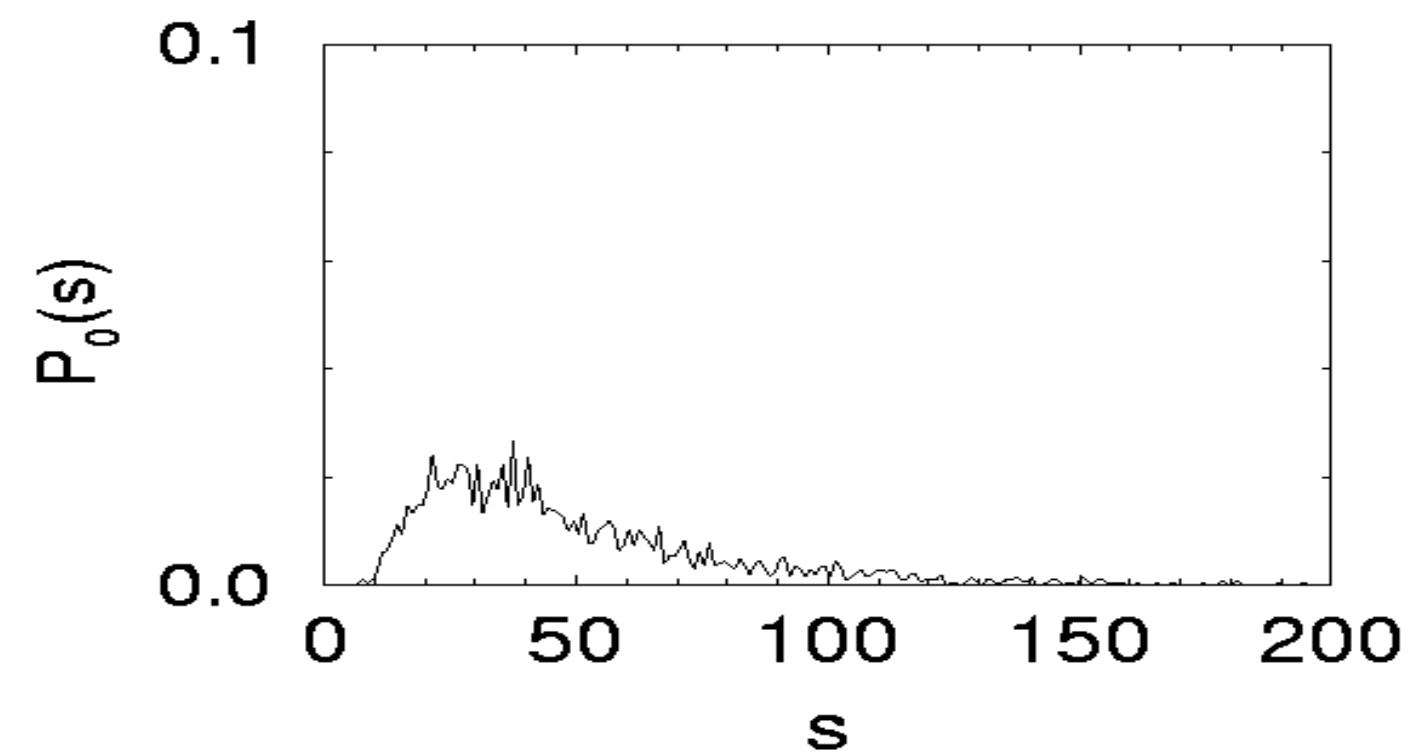
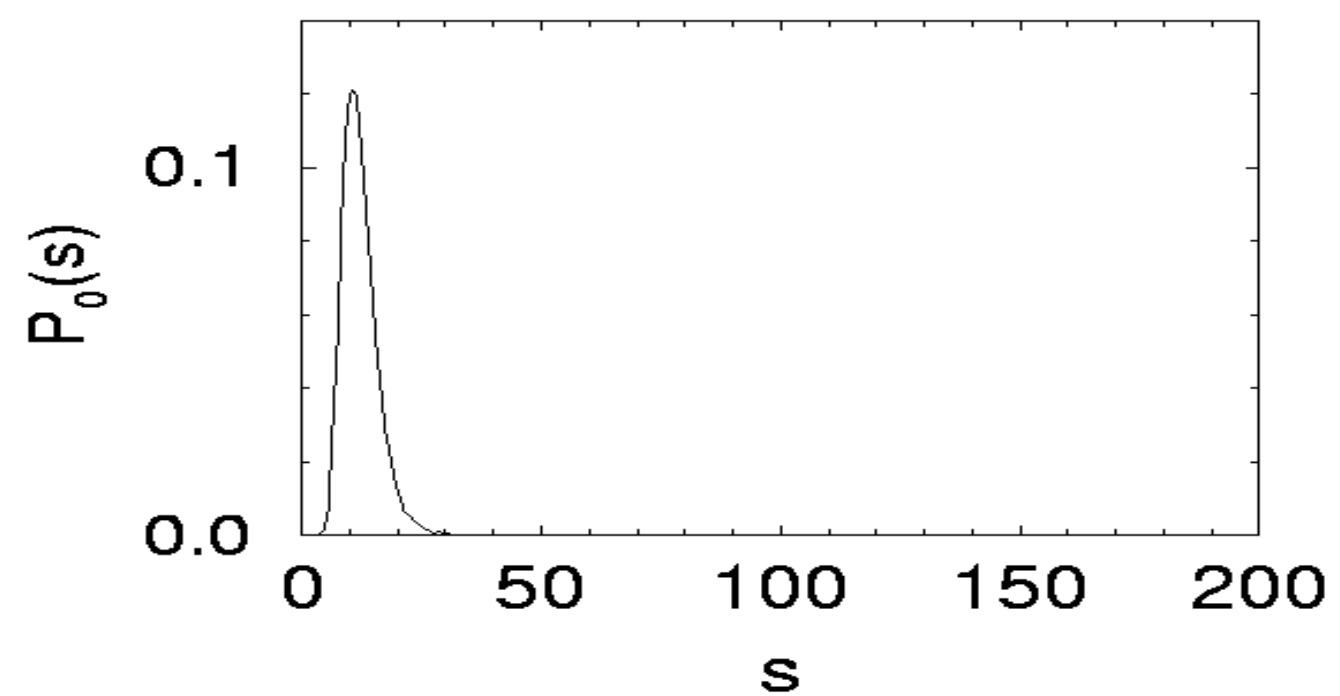
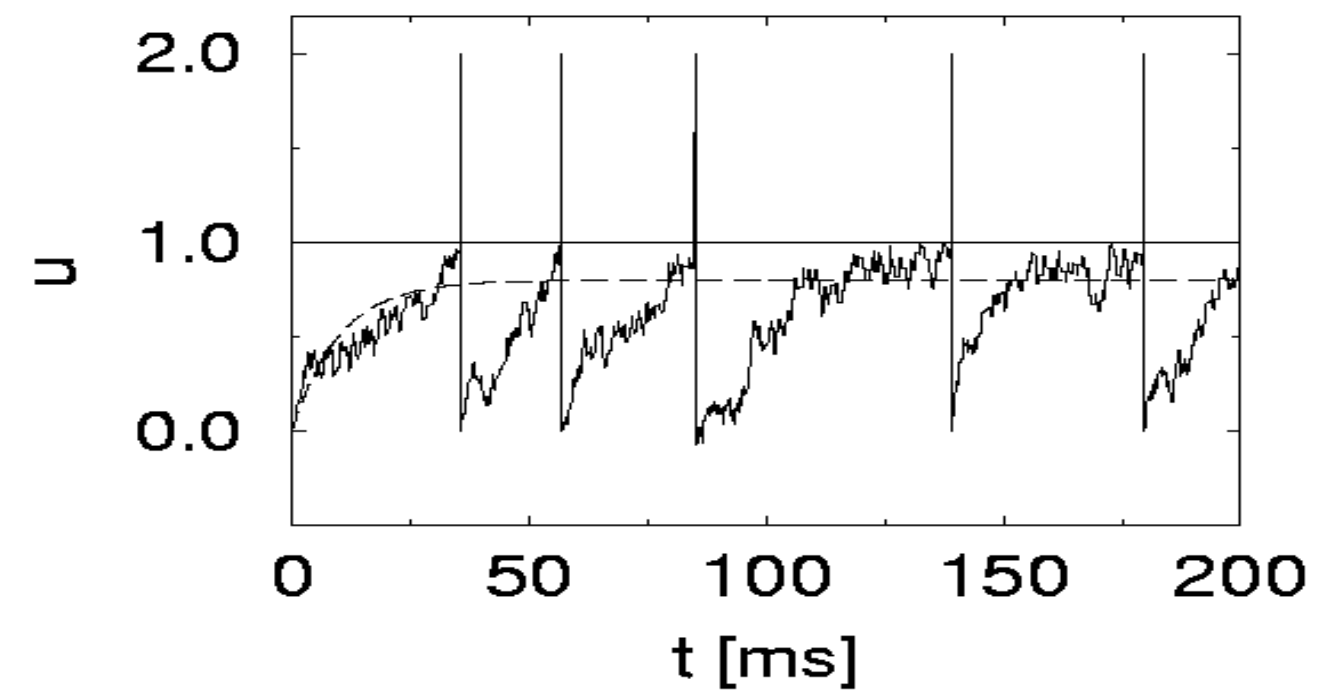
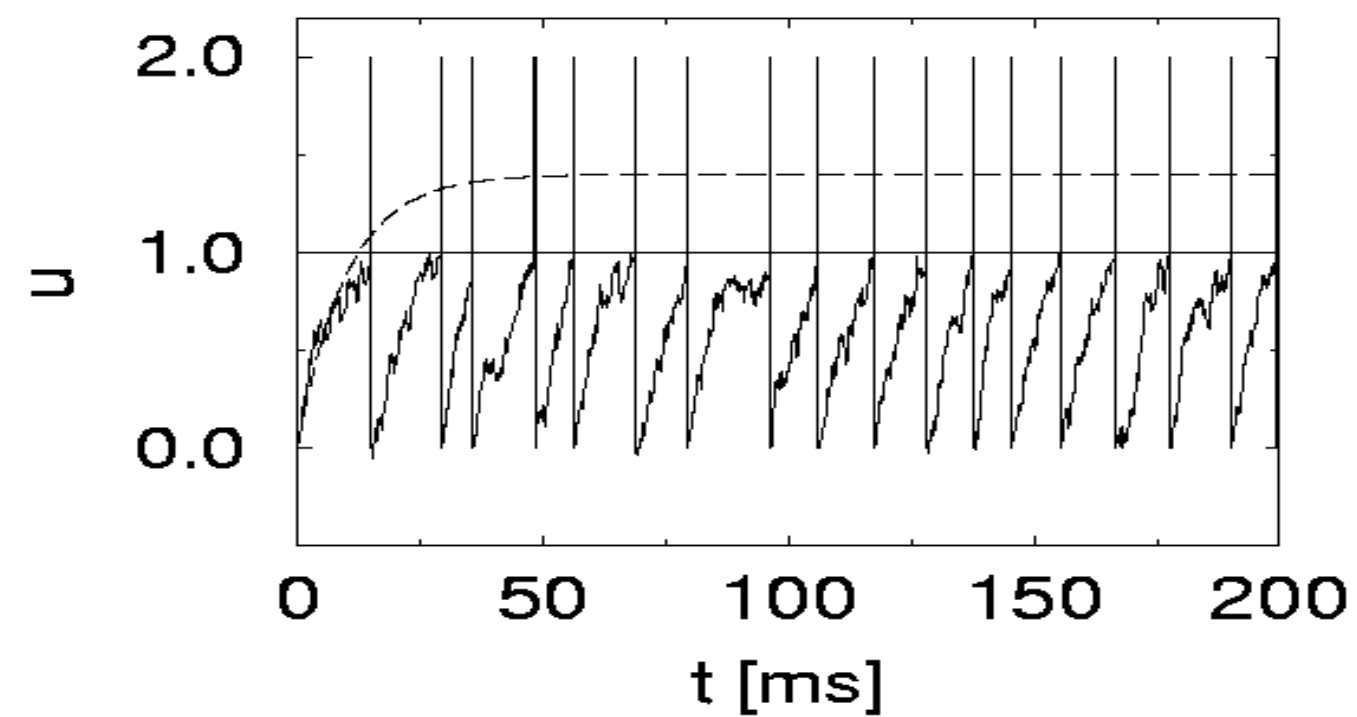
noisy input/
diffusive noise/
stochastic spike
arrival

stochastic spike arrival in I&F – interspike intervals



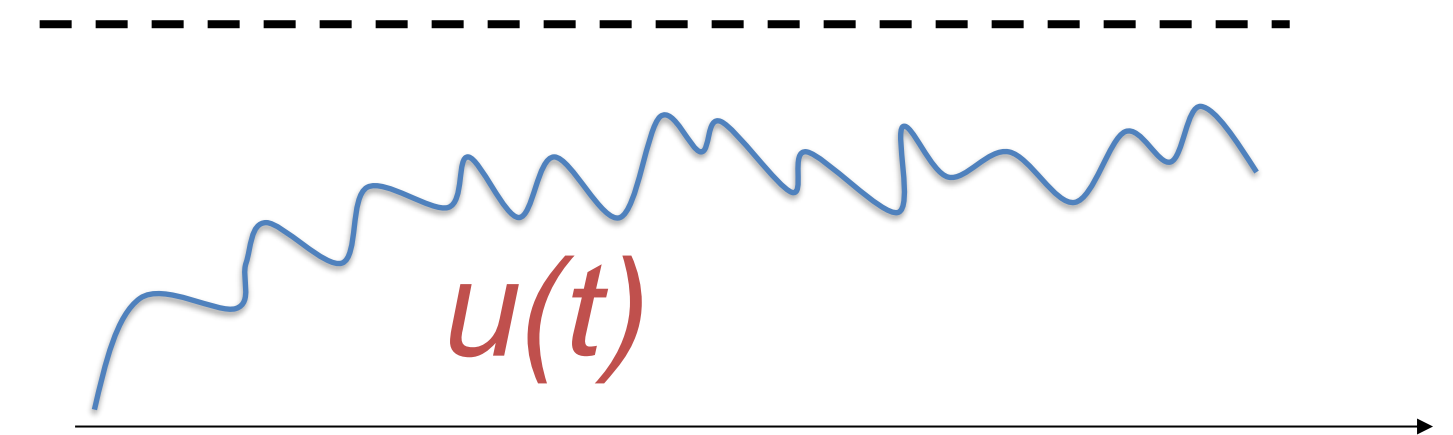
LIF with Diffusive noise (stochastic spike arrival)

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.