Biological Modeling of Neural Networks

EPFL

Week 11 – Variability and Noise: Autocorrelation

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11.1 Variation of membrane potential
- white noise approximation

11.2 Autocorrelation of Poisson

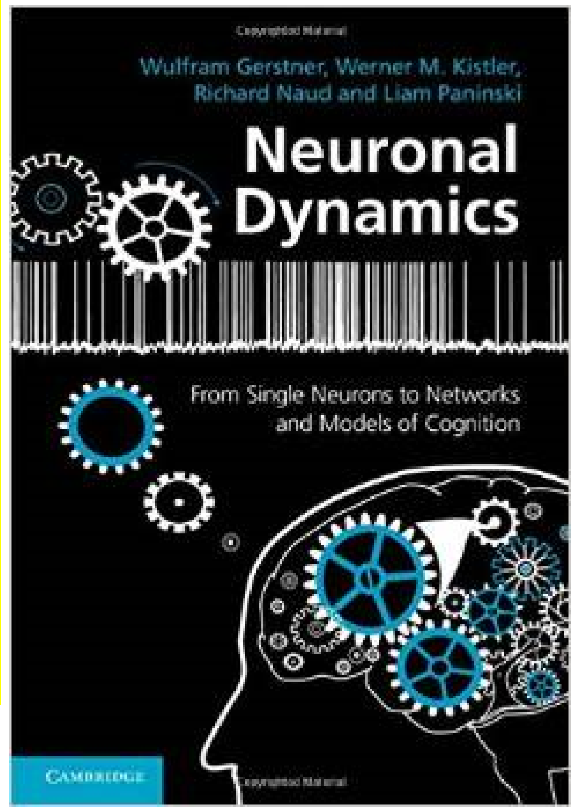
11.3 Noisy integrate-and-fire
- superthreshold and subthreshold

11.4 Escape noise
- stochastic intensity

11.5 Renewal models

Reading for week 11:
NEURONAL DYNAMICS
Ch. 7.4-7.5.1
Ch. 8.1-8.3 + Ch. 9.1

Cambridge Univ. Press

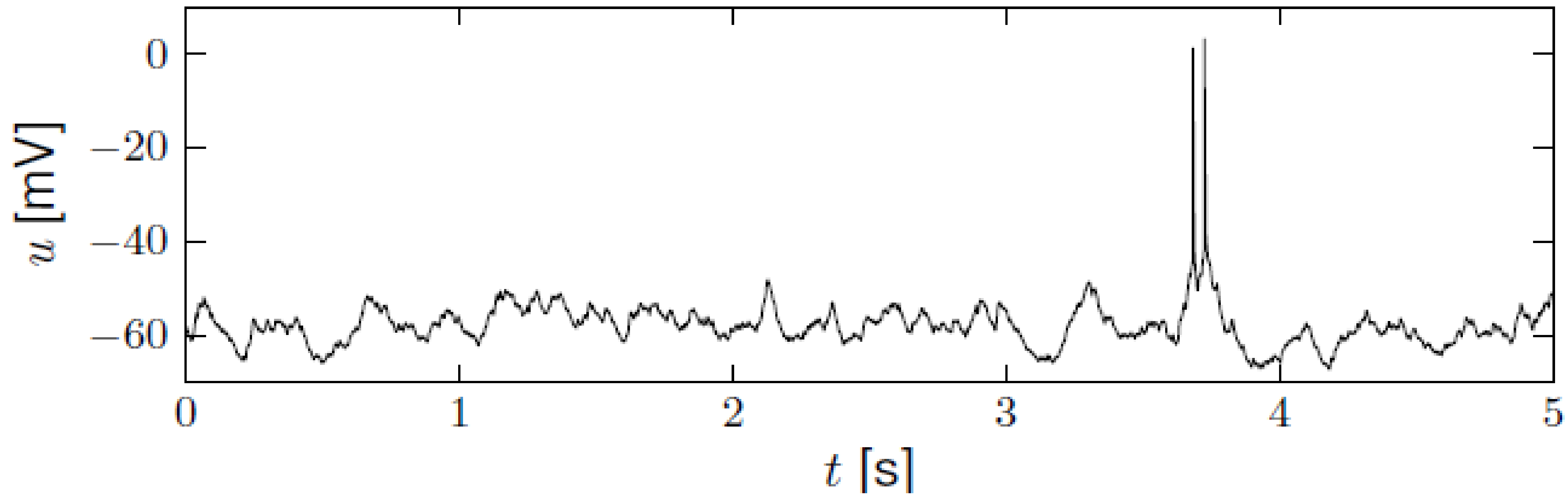


11.1 Review from week 10

Spontaneous activity *in vivo*

Variability
- of membrane potential?
- of spike timing?

awake mouse, cortex, freely whisking,



Crochet et al., 2011

11.1 Review from week 10

In vivo data
→ looks ‘noisy’

In vitro data
→ fluctuations

Fluctuations
-of membrane potential
-of spike times

fluctuations=noise?

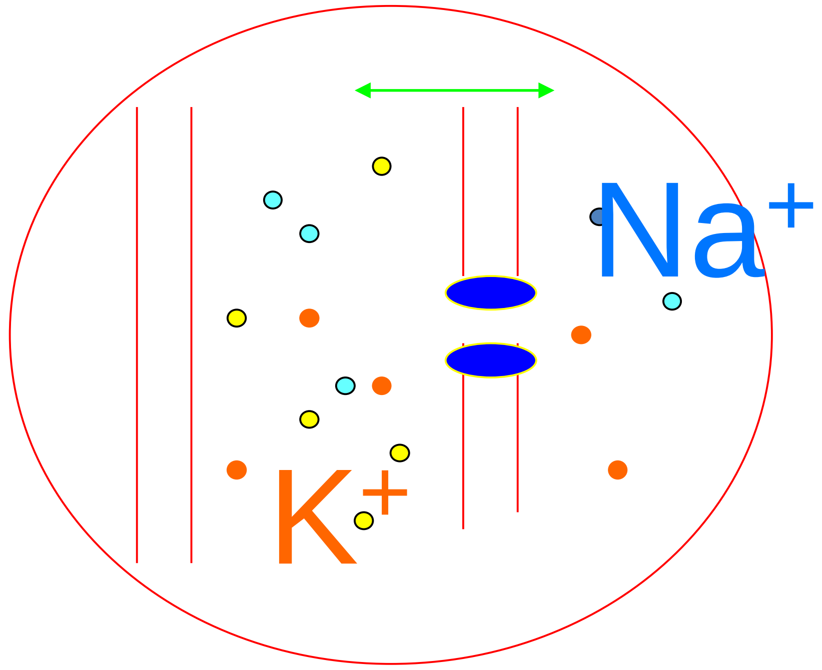
relevance for coding?

source of fluctuations?

model of fluctuations?

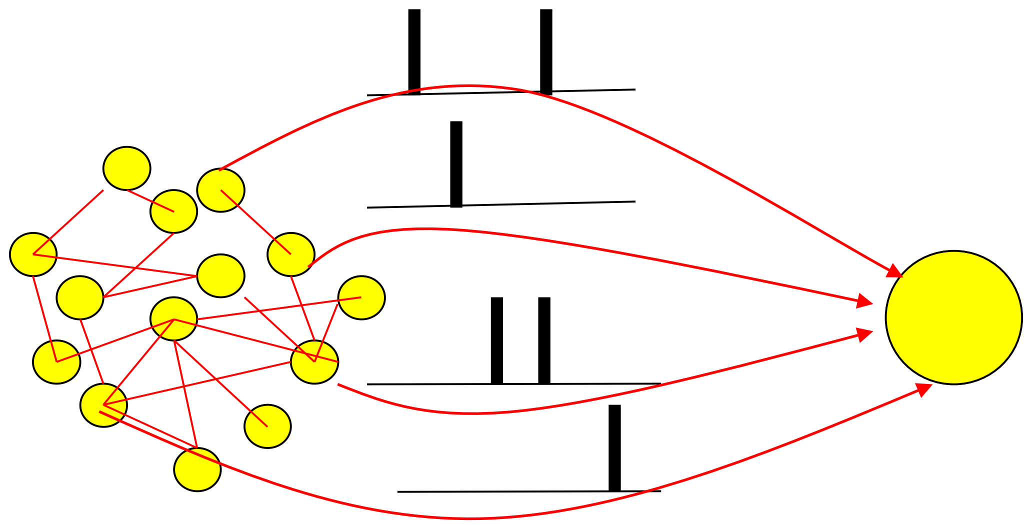
11.1. Review from week 10

- Intrinsic noise (ion channels)



-Finite number of channels
-Finite temperature

-Network noise (background activity)



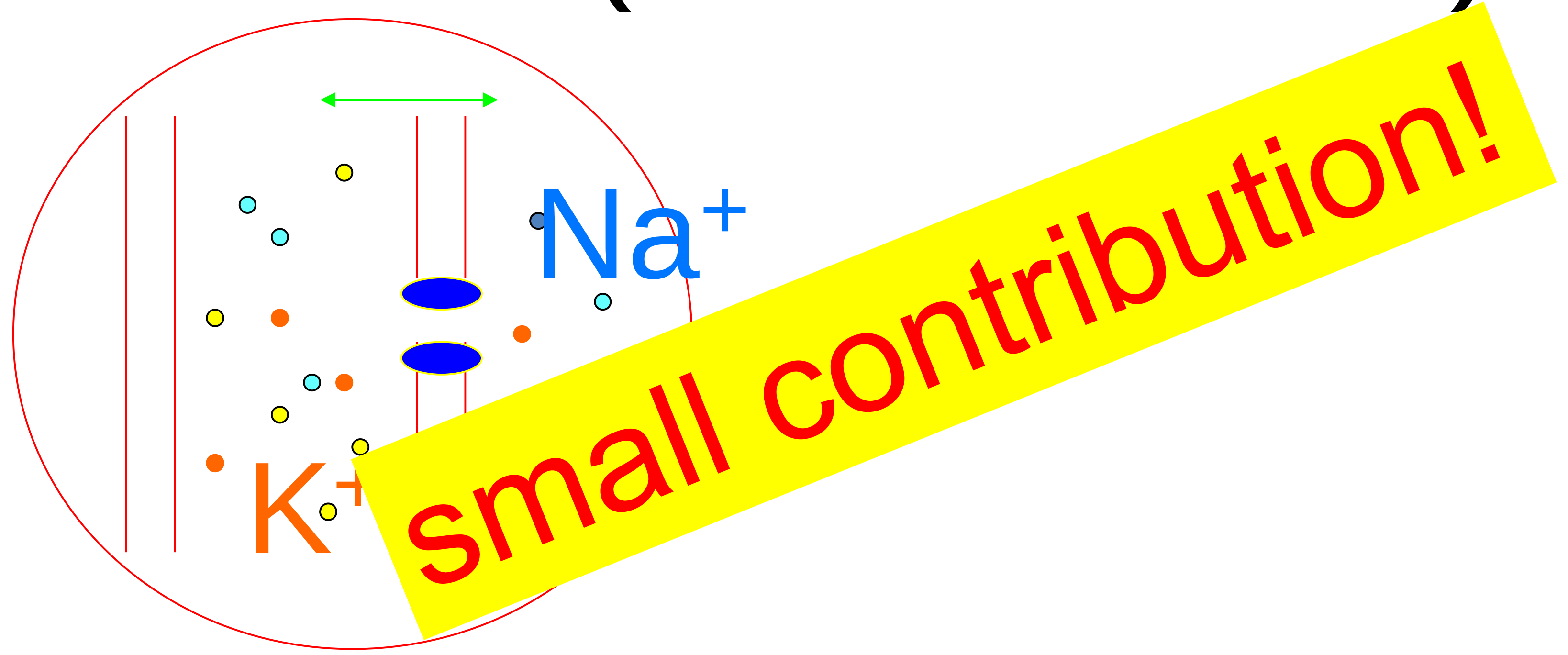
-Spike arrival from other neurons
-Beyond control of experimentalist

11.1. Review from week 10

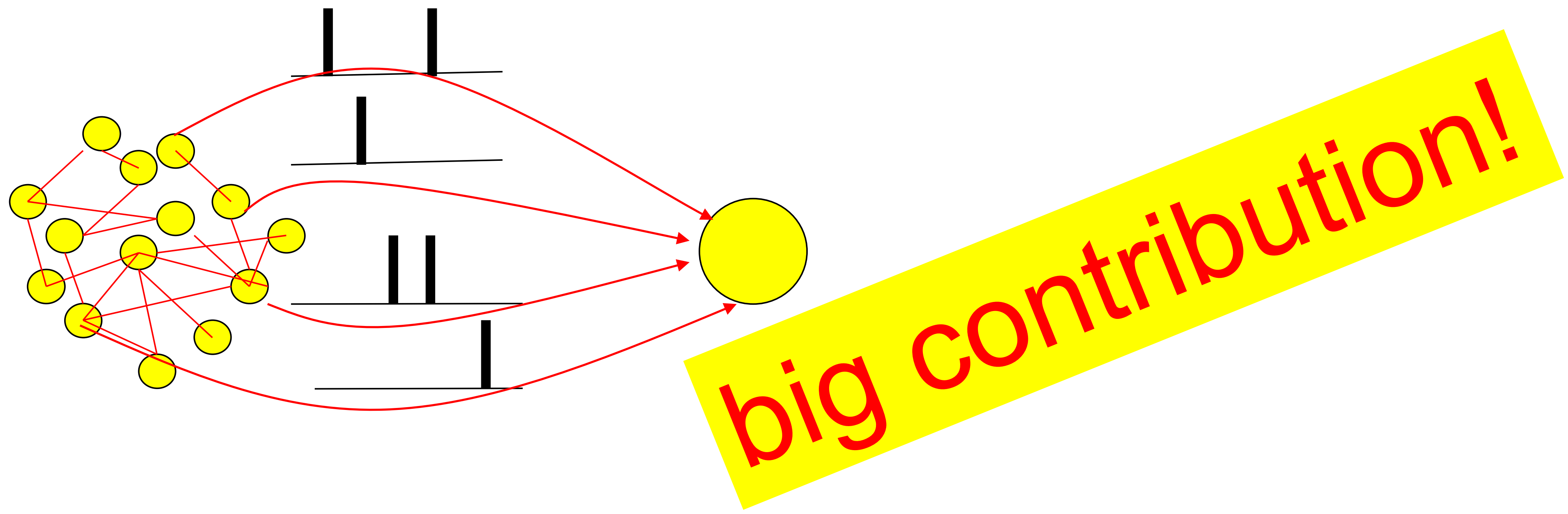
In vivo data
→ looks 'noisy'

In vitro data
→small fluctuations
→nearly deterministic

- Intrinsic noise (ion channels)

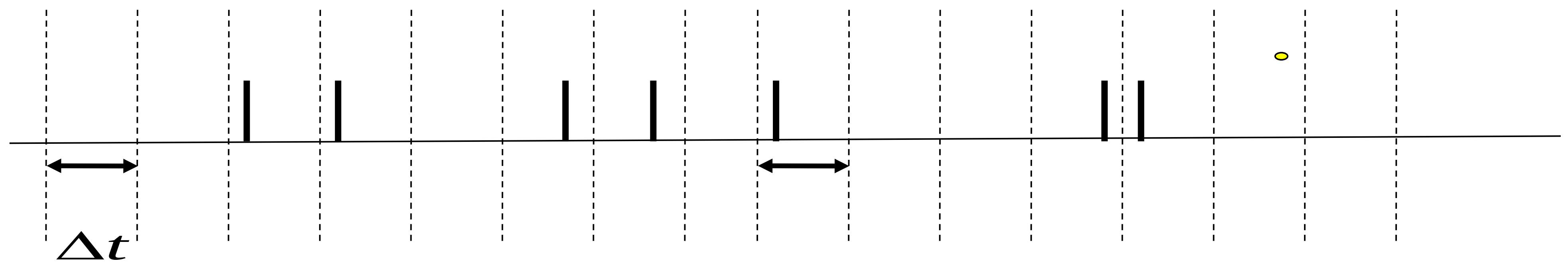


-Network noise



11.1 Review from week 10: 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

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

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

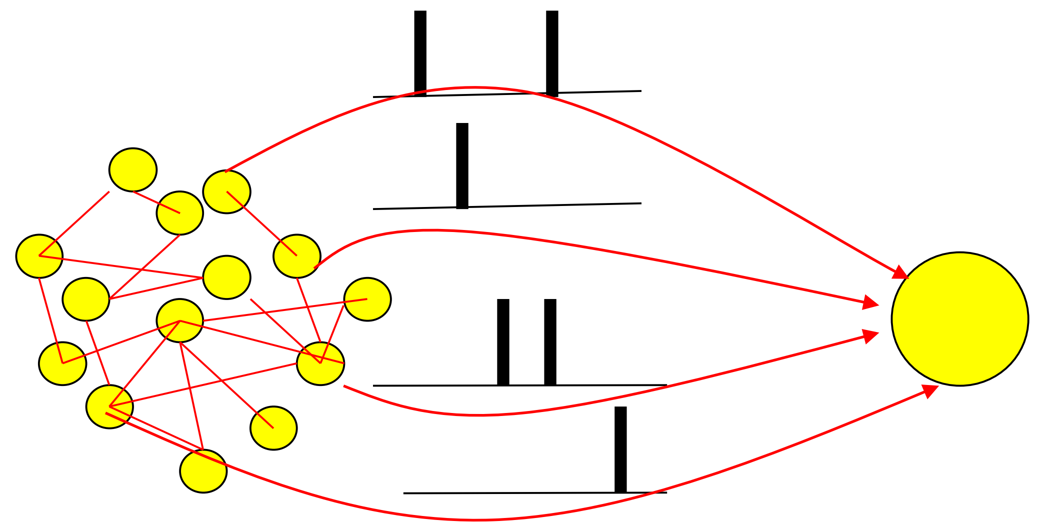
$$\langle x(t)\rangle = \int dt'\, f(t-t')\; \rho(t')$$

rate of inhomogeneous Poisson process

use for exercises
use for next slides

11.1. Fluctuation of potential

for a passive membrane, predict
-mean
-variance
of membrane potential fluctuations

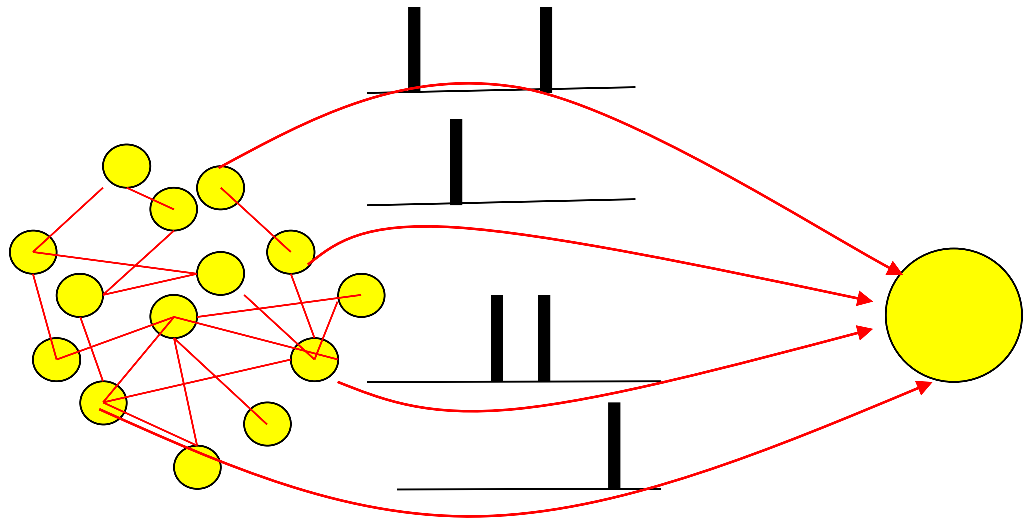


Passive membrane

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

Passive membrane
=Leaky integrate-and-fire
without threshold

11.1. Fluctuation of current/potential



Synaptic current pulses of shape α

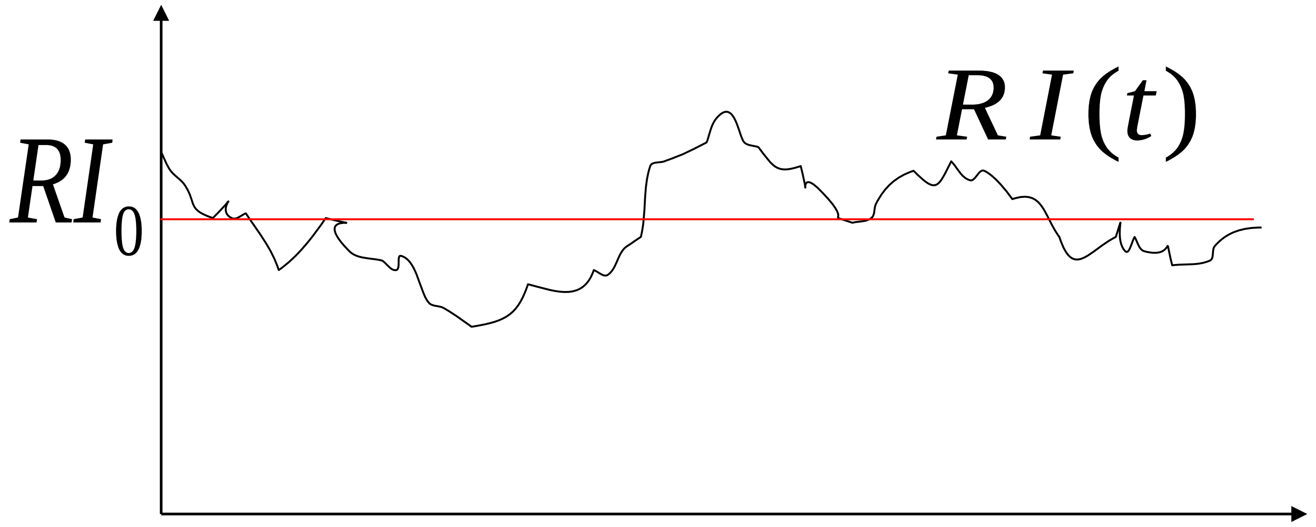
$$RI^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$

EPSC

Blackboard1, Math detour: White noise

Passive membrane

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

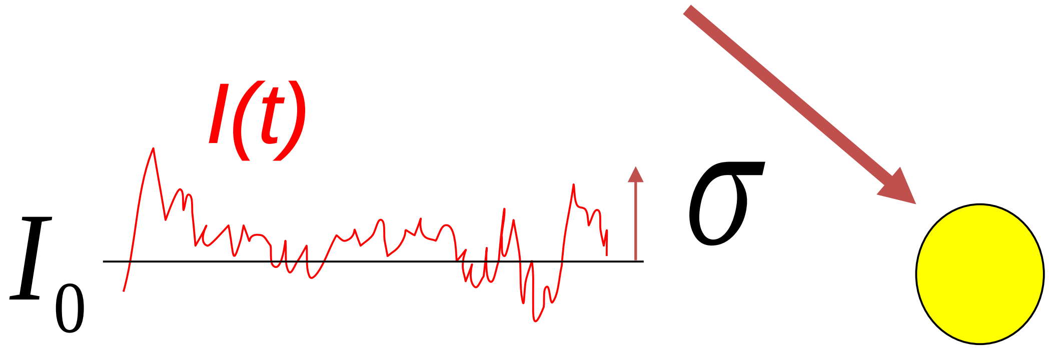


$$I^{syn}(t) = I_0 + I^{fluct}(t)$$

$$RI^{syn}(t) = RI_0(t) + \xi(t)$$

$$\langle \xi(t) \rangle = 0$$

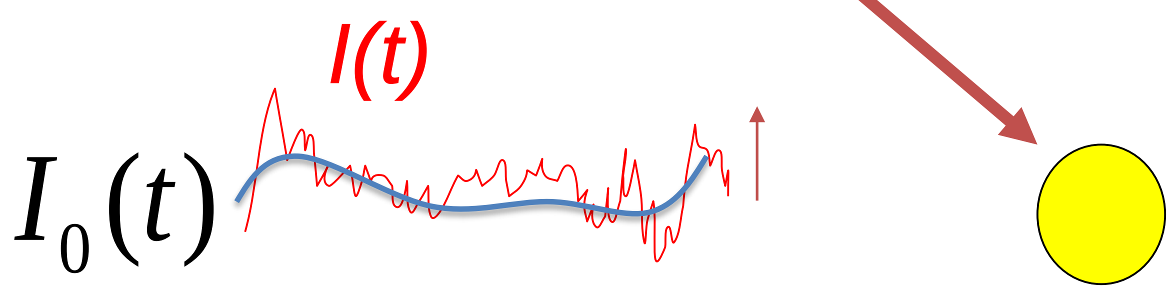
$$\langle \xi(t)\xi(t') \rangle = a^2 \tau\, \delta(t - t')$$



Fluctuating input current

11.1 Calculating autocorrelations

$$I(t) = I_0(t) + \xi(t)$$



Fluctuating input current

Autocorrelation

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

$$x(t) \;=\; \int dt'\, f(t-t')\, I(t)'$$

$$x(t) \;=\; \int ds\, f(s)\, I(t-s)$$

Mean:

$$\langle x(t)\rangle = \int ds\, f(s) \langle I(t-s)\rangle$$

$$\langle x(t)\rangle \;=\; \int ds\, f(s)\; [I_0(t-s) + \langle \xi(t-s)\rangle]$$

$$\langle x(t)\rangle \;=\; \int ds\, f(s)\;\; I_0(t-s)$$

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

use - $I(t') = I_0(t') + \xi(t')$

- $\langle \xi(t')\xi(t'')\rangle$

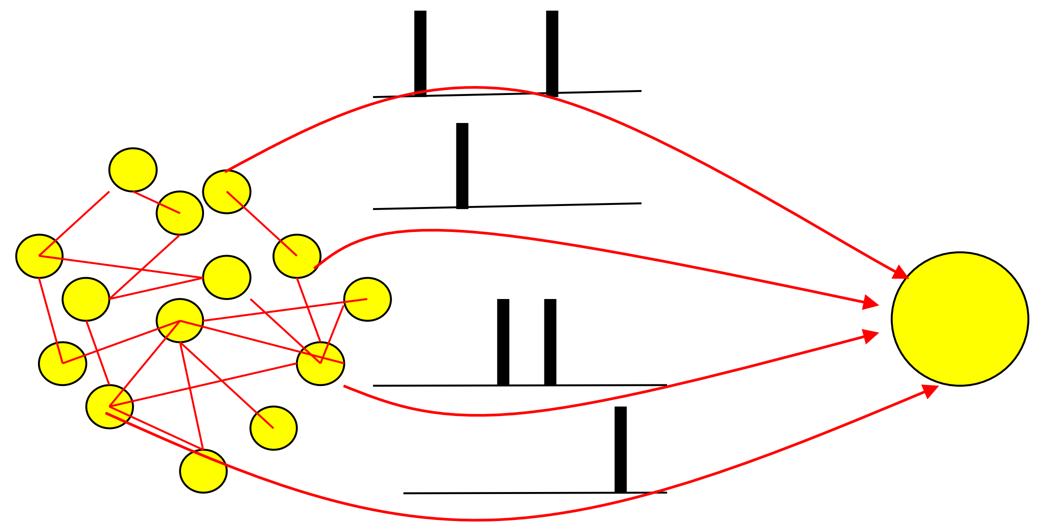
11.1. Fluctuation of potential

for a passive membrane, predict

-mean

-variance

of membrane potential fluctuations



Blackboard2, Math detour

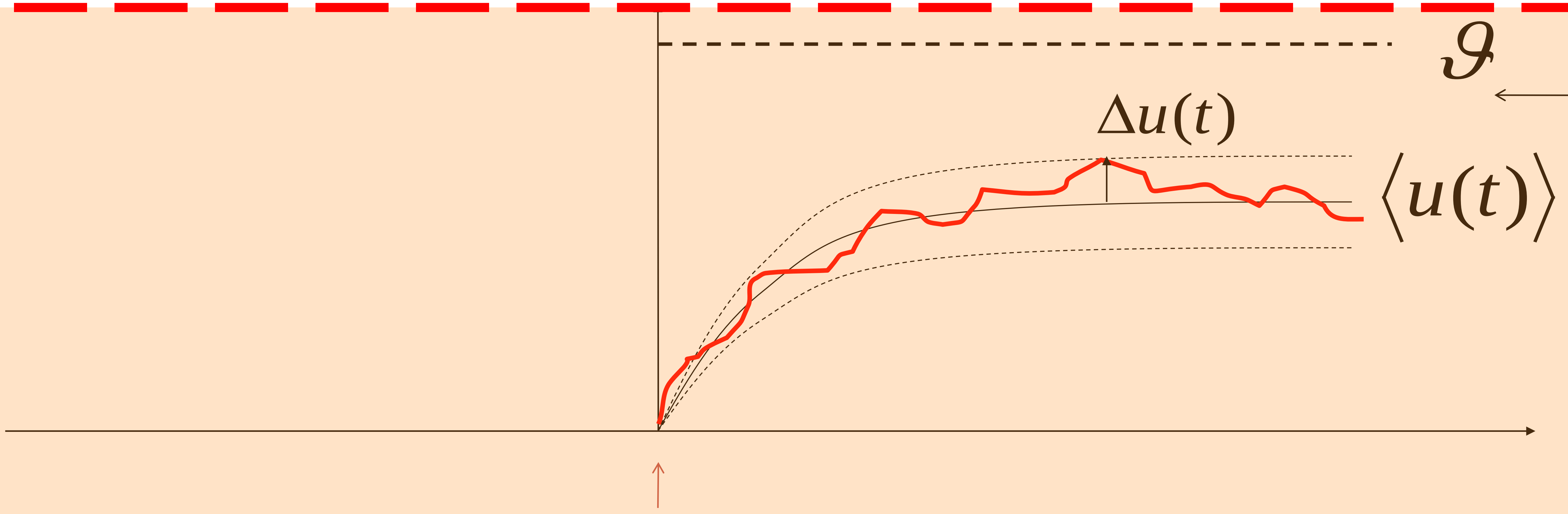
Passive membrane

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

$$u(t) = u_{rest} \quad + \frac{R}{\tau} \int \exp(-s/\tau)\, I^{syn}(t-s)\, ds$$

$$u(t) = u_{rest} \quad + \frac{1}{\tau} \int \exp(-s/\tau)[\langle RI(t-s) \rangle + \xi(t-s)]\, ds$$

White noise: Exercise 1.1-1.2 now



Assumption:
far away from theshold

Input starts here

Next lecture:
10:15

Expected voltage at time *t* $\langle u(t) \rangle = ?$

Variance of voltage at time *t*

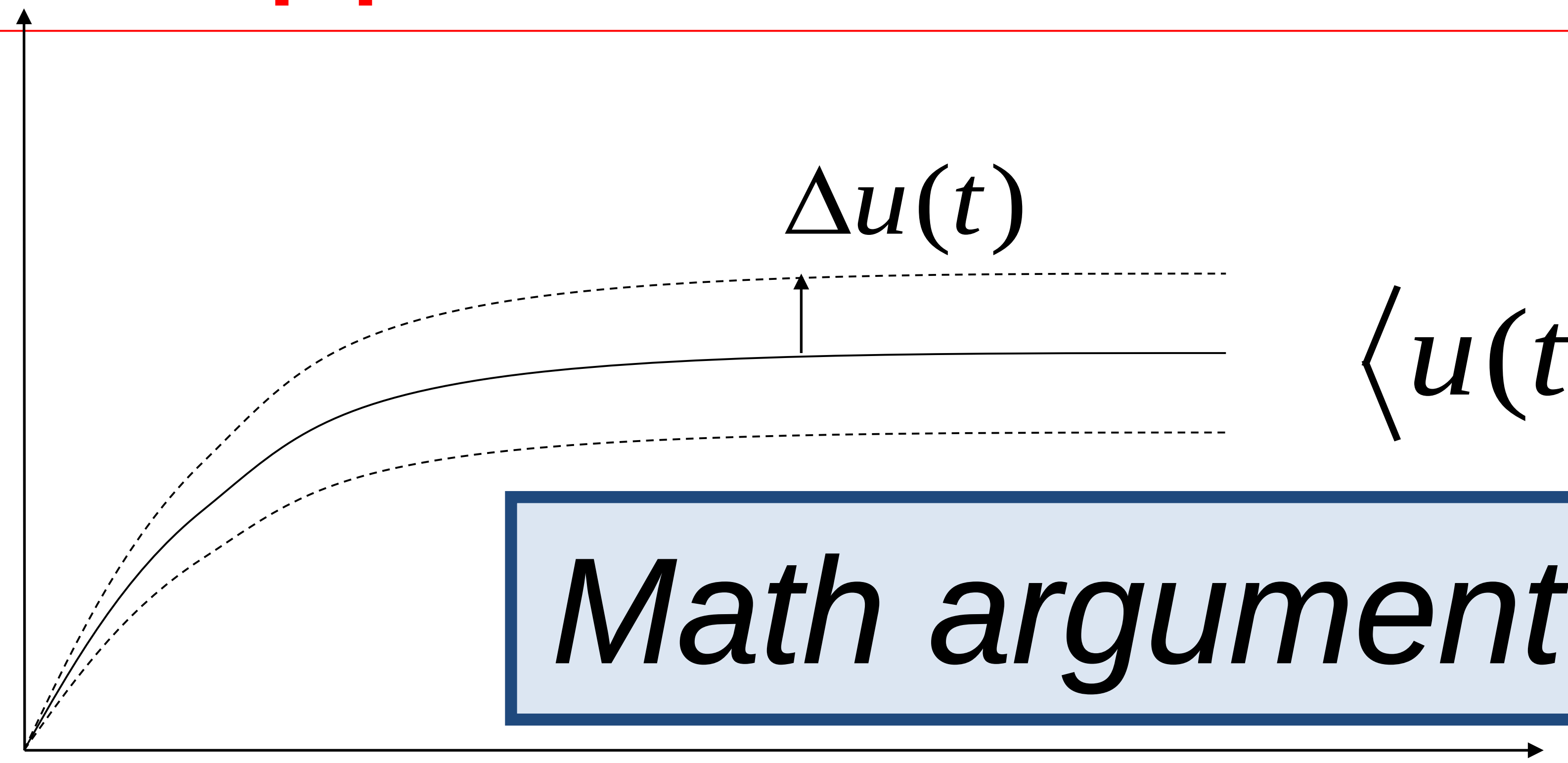
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

Report variance as function of time!

11.1 Calculating autocorrelations for stochastic spike arrival

First approach: white noise (to mimic stochastic spike arrival)

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



$$\langle u(t) \rangle = u_0(t)$$

Math argument

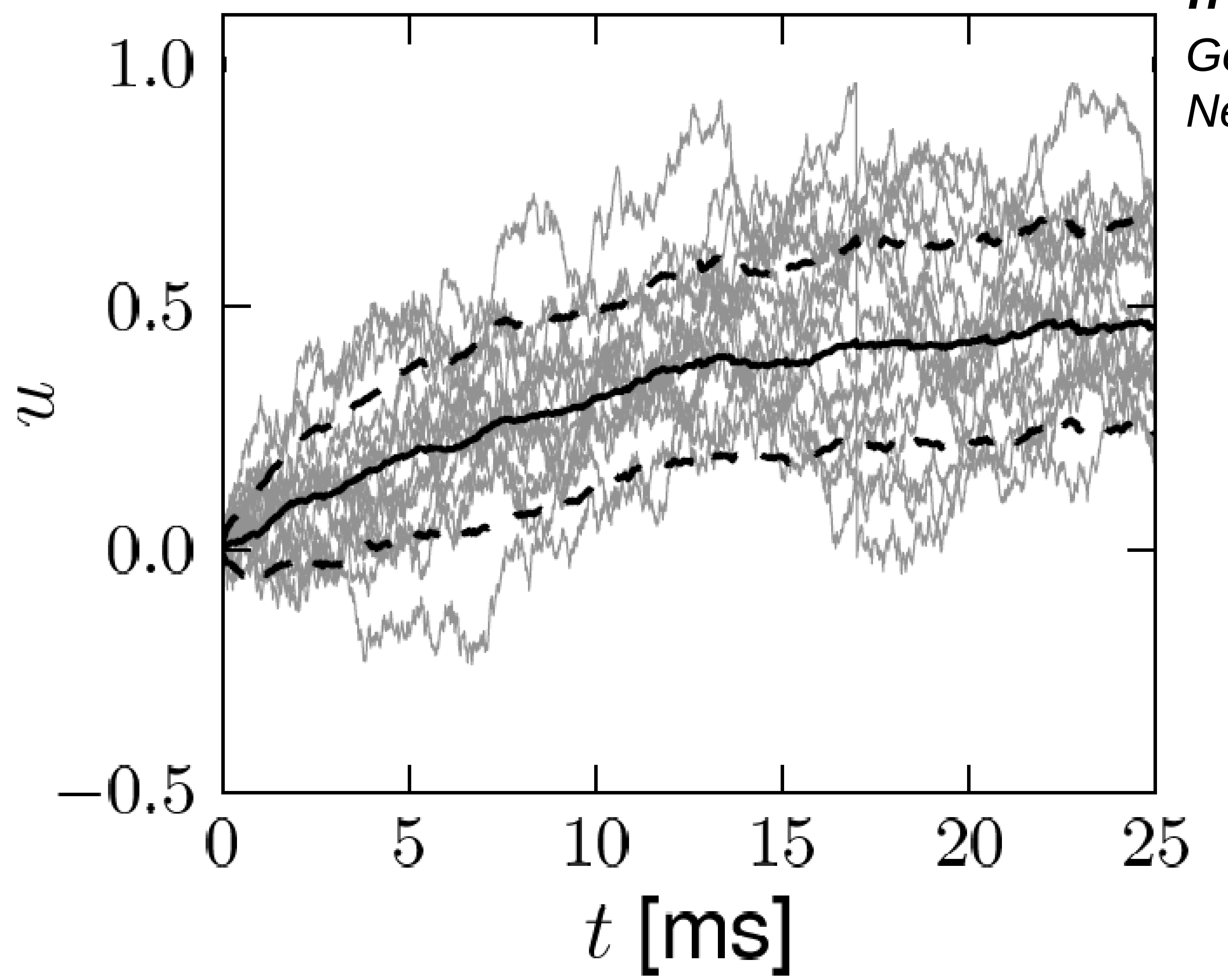


Image: *Gerstner et al. (2014), Neuronal Dynamics*

variance

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

$$\langle \Delta u(t') \Delta u(t) \rangle = \langle u(t) u(t') \rangle - \langle u(t) \rangle \langle u(t') \rangle =$$

Autocorrelation of membrane potential

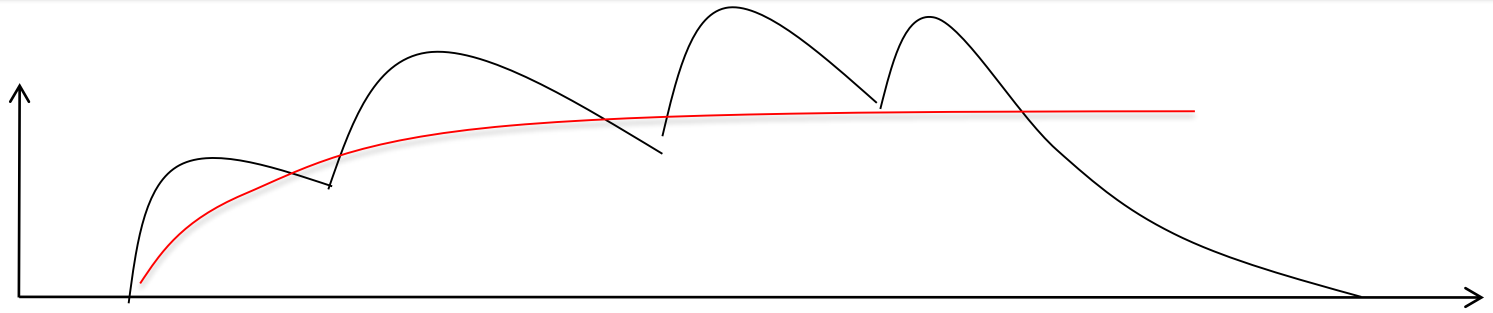
$$\langle [\Delta u(t)]^2 \rangle = \sigma_u^2 [1 - \exp(-2t/\tau)]$$

later

$$p(u,t) = \frac{1}{\sqrt{2\pi \langle \Delta u^2(t) \rangle}} \exp\left\{ -\frac{[u(t|\hat{t}) - u_0(t)]^2}{2 \langle \Delta u^2(t) \rangle} \right\}$$

11.1 Conclusion: Mean and autocorrelation of the membrane potential

S(t) 

u(t) 

First approach to calculate autocorrelations.

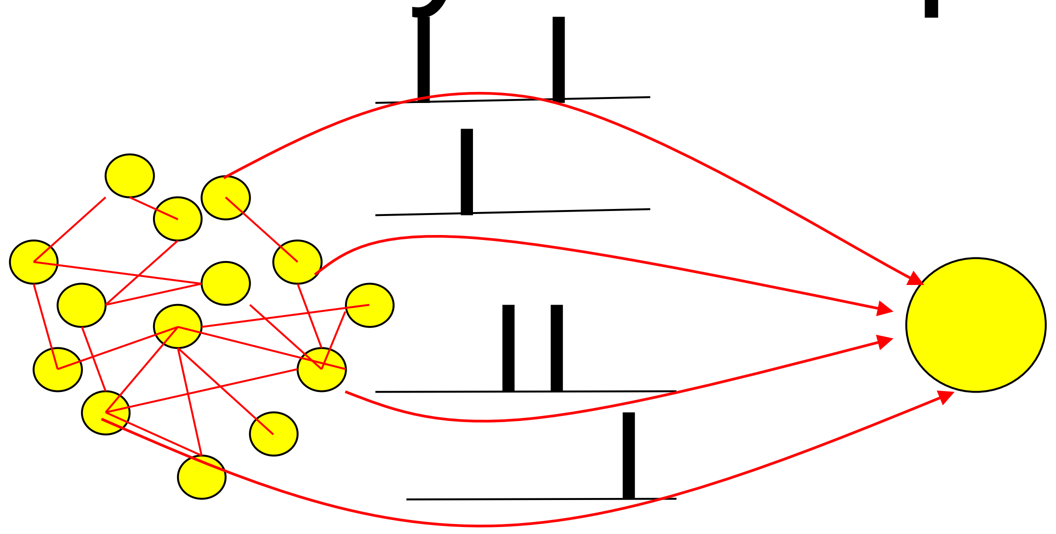
A spike train *S(t)* causes a fluctuating current *I(t)*.
We separate the fluctuating current into a mean current $\langle I(t) \rangle$ and a noise component $\xi(t)$.
By definition the mean of the noise vanishes: $\langle \xi(t) \rangle = 0$ at any moment in time.

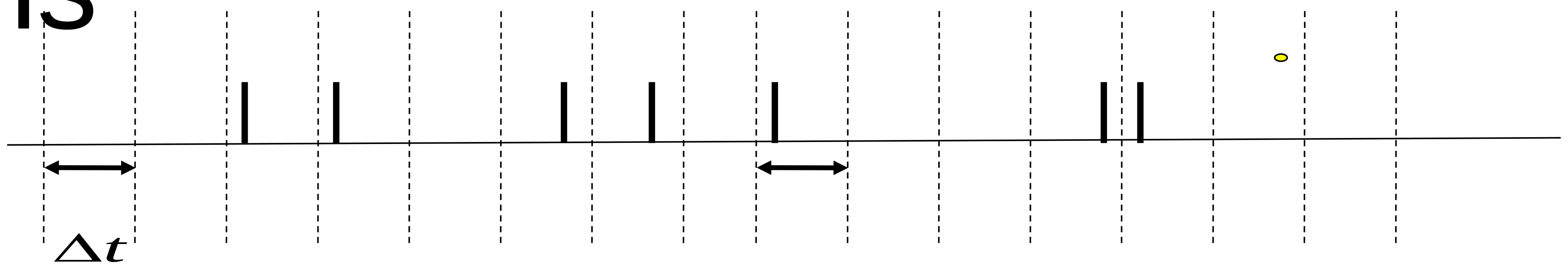
If the time constant of the synapse is extremely short, we can formulate the noise component as white noise. White noise has a vanishing autocorrelation,
$\langle \xi(t)\, \xi(t') \rangle = 0$ whenever t' is different from t, and a delta-peak for t=t'.

For a passive membrane model with time constant τ, we can calculate the mean $\langle u(t) \rangle$ of the membrane potential and its autocorrelation at times t and t' . The variance of the membrane potential is derived from its autocorrelation for t=t' by subtracting the mean.
Actual realizations are trajectories with a (Gaussian) distribution around the mean $\langle u(t) \rangle$,
The fact that the distribution is Gaussian has not been shown in the lecture today.

11.1 Calculating autocorrelations: second approach

work directly with spike trains





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

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

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

$$\langle x(t) \rangle = \int ds \, f(s) \;\; \nu(t-s)$$

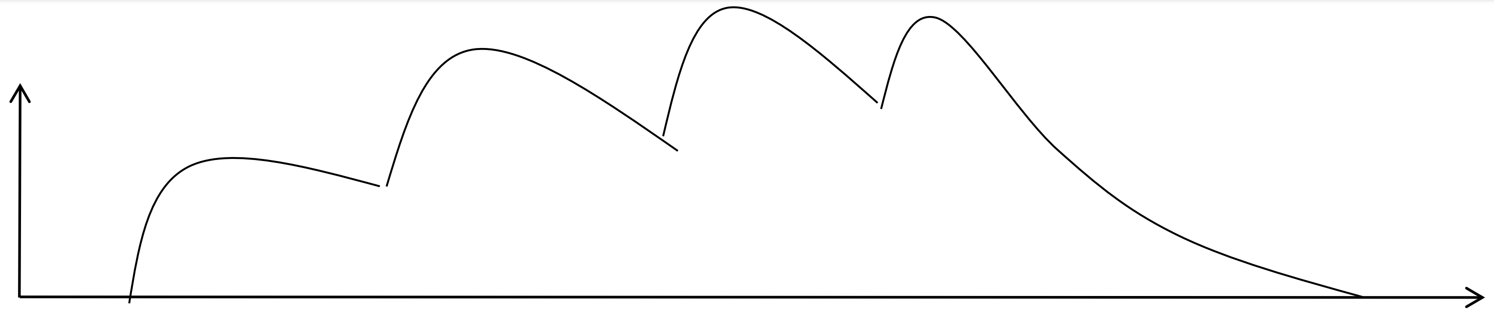
rate of inhomogeneous Poisson process

Autocorrelation

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

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

11.1 Mean and autocorrelation of filtered spike signal



$$S(t) = \sum_f \delta(t - t^f)$$

$$F(s)$$

Filter

$$x(t) = \int F(s) S(t-s) ds$$

Assumption: stochastic spiking

rate $\nu(t)$

$$\langle x(t) \rangle = \int F(s) \langle S(t-s) \rangle ds$$

mean

$$\langle x(t) \rangle = \int F(s) \langle \nu(t-s) \rangle ds$$

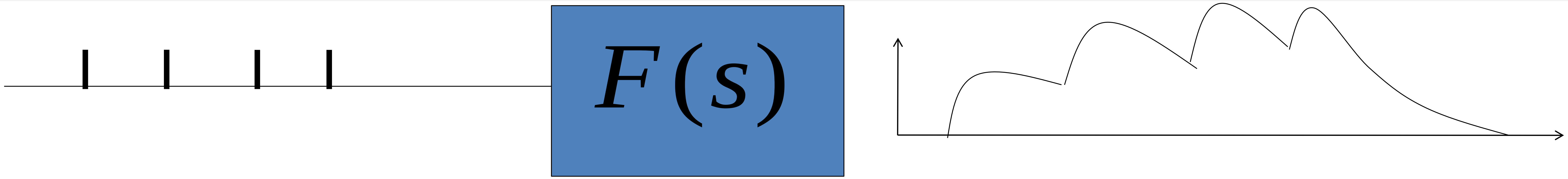
Autocorrelation of output

$$\langle x(t) x(t') \rangle = \left\langle \int F(s) S(t-s) ds \int F(s') S(t'-s') ds' \right\rangle$$

$$\langle x(t) x(t') \rangle = \int F(s) F(s') \underline{\langle S(t-s) S(t'-s') \rangle} ds ds'$$

Autocorrelation of input

11.1 Conclusion: Mean and autocorrelation of filtered spike train



Second approach to calculate autocorrelations.

A spike train S(t) is formulated as a sequence of delta functions.
  The expectation <S(t)> of S(t) at time t is the instantaneous 'rate' ν(t).
  The auto-correlation of S(t) with S(t') is <S(t)S(t')>

After filtering with a filter F(s) we get a variable x(t).
The mean and autocorrelation of x can be calculated.
The formulas will be used a lot in this and the next lectures.

Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Week 11 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

11.1 Variation of membrane potential
- white noise approximation

11.2 Autocorrelation of Poisson

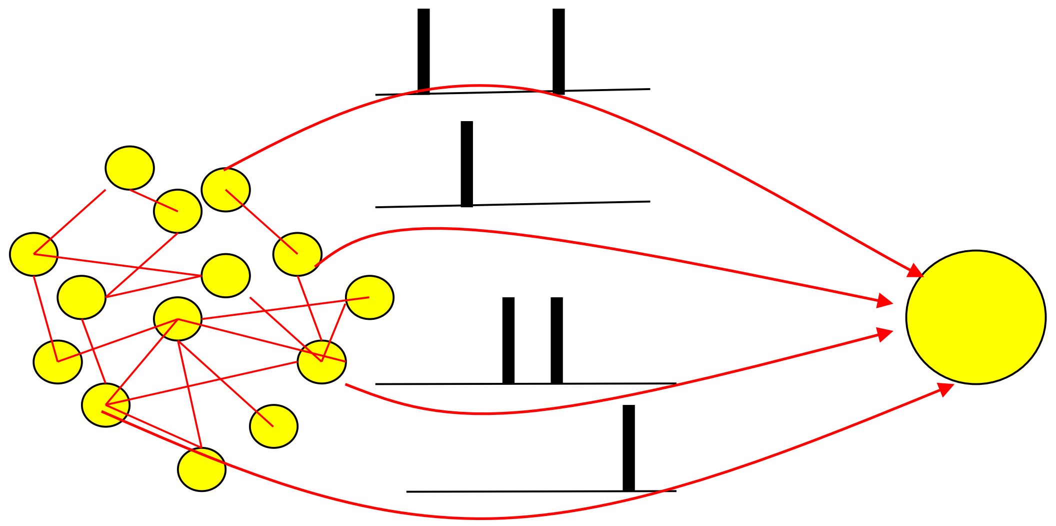
11.3 Noisy integrate-and-fire
- superthreshold and subthreshold

11.4 Escape noise
- stochastic intensity

11.5 Renewal models

11.2 Autocorrelation of Poisson (preparation)

Justify autocorrelation of spike input:
Poisson process in discrete time



Stochastic spike arrival:

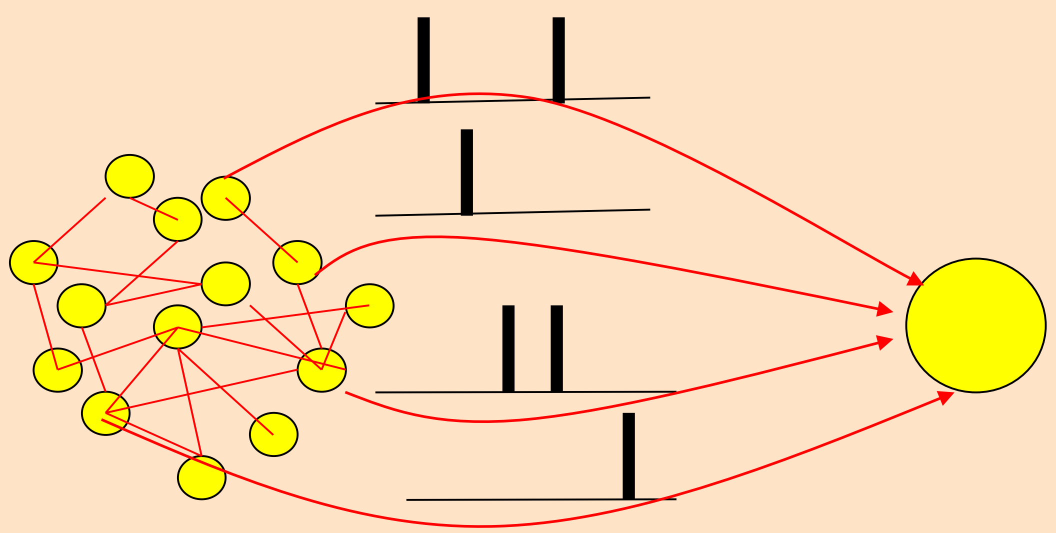
Blackboard3

In each small time step Δt

Prob. Of firing $p = \nu \Delta t$

Firing independent between one time step and the next

Exercise 3 now: Poisson process in continuous time



Stochastic spike arrival:
excitation, total rate

Next lecture: 10:57

In each small time step Δt

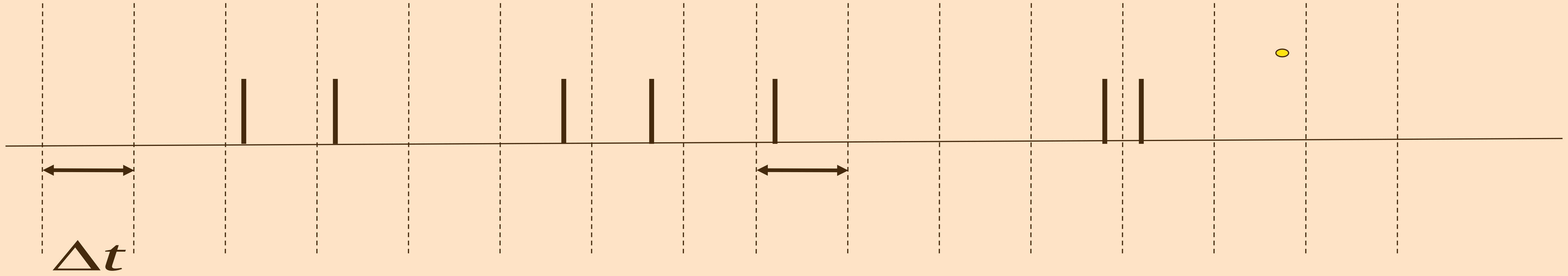
Prob. Of firing $p = \nu \, \Delta t$

Firing independent between one time step and the next

Show that autocorrelation for $\Delta t \to 0$ $$\langle S(t) S(t') \rangle = \nu \, \delta(t - t') + \nu^2$$

Show that in a a long interval of duration T, the expected number of spikes is $$\langle N(T) \rangle = \nu \, T$$

Quiz – 1. Autocorrelation of Poisson



The Autocorrelation (continuous time)

spike train

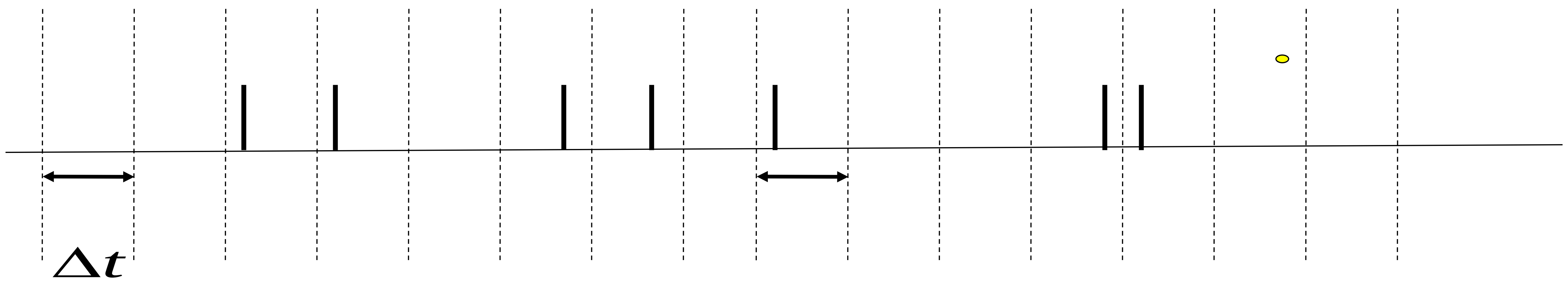
$$\langle S(t)S(t')\rangle$$

Has units

[ ] probability (unit-free)
[ ] probability squared (unit-free)
[ ] rate (1 over time)
[ ] (1 over time)-squred

11.2. Autocorrelation of Poisson

math detour now!



Probability of spike
in step *n* **AND** step *k*

spike train

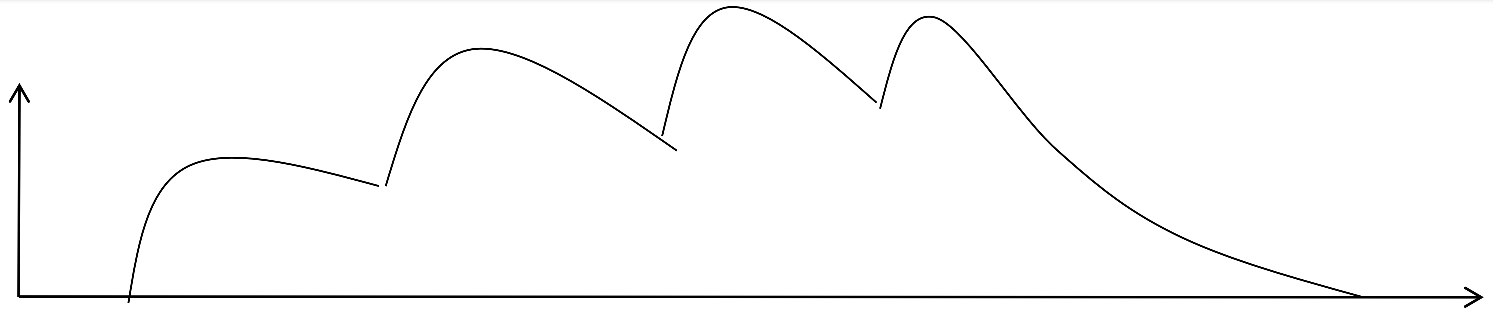
Probability of spike in time step:

$$P_F = \nu_0 \,\Delta t$$

Autocorrelation (continuous time)

$$\langle S(t)S(t')\rangle = \nu_0\,\delta(t-t') + [\nu_0]^2$$

11.2. Autocorrelation of Poisson: units



$$S(t) = \sum_f \delta(t - t^f)$$

$$F(s)$$

$$x(t) = \int F(s) S(t-s) ds$$

Assumption: stochastic spiking (Poisson)

rate $\nu(t)$

Autocorrelation of output

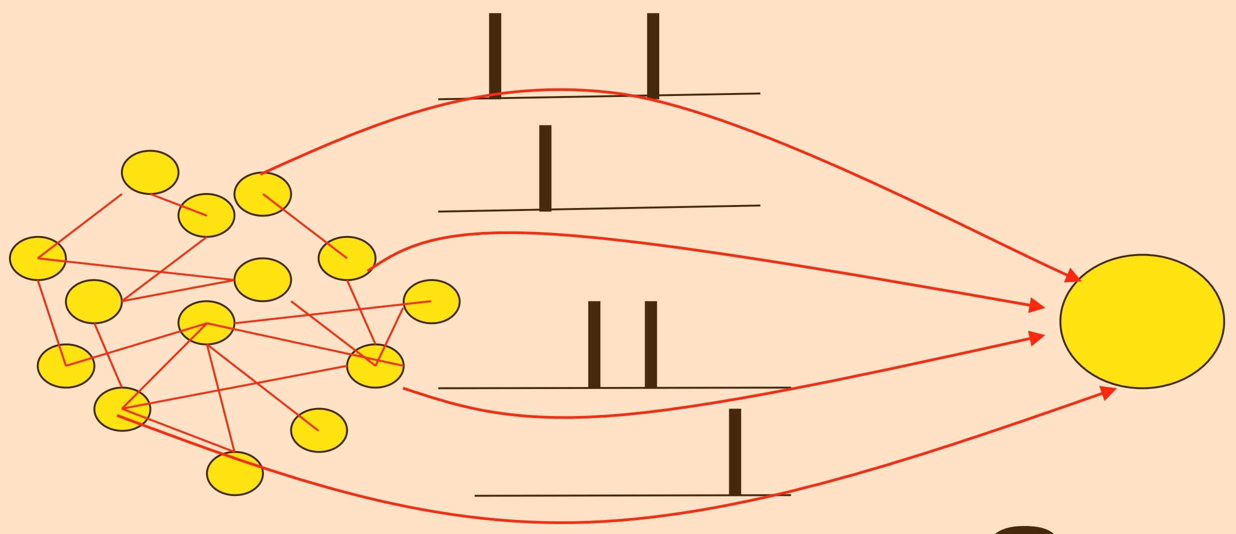
$$\langle x(t) x(t') \rangle = \left\langle \int F(s) S(t-s) ds \int F(s') S(t'-s') ds' \right\rangle$$

$$\langle x(t) x(t') \rangle = \int \int F(s) F(s') \langle S(t-s) S(t'-s') \rangle ds ds'$$

Autocorrelation of input (Poisson)

We integrate twice!

Exercise 2 **Homework:** stochastic spike arrival



Stochastic spike arrival:

excitation, total rate $\langle S(t) \rangle = \nu$

Synaptic current pulses

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

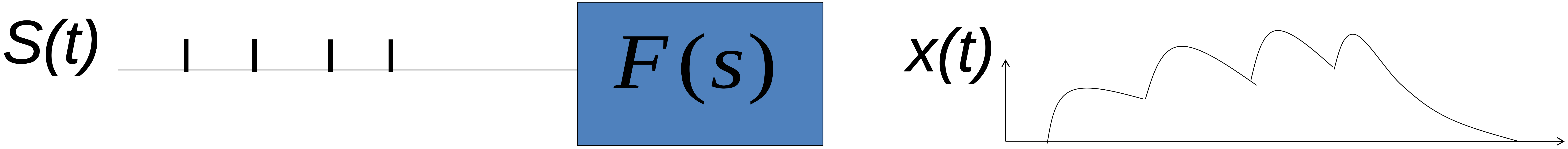
$$S(t) = q_e \sum_f \delta(t - t^f)$$

1. Assume that for t>0 spikes arrive stochastically with rate ν
   - Calculate mean voltage

2. Assume autocorrelation $\langle S(t) S(t') \rangle = \nu\, \delta(t - t') + \nu^2$

   - Calculate $\langle u(t) u(t) \rangle = ?$

11.2 Conclusion: Mean and autocorrelation of the Poisson Process.



Second approach to calculate autocorrelations.

A spike train *S(t)* is formulated as a sequence of delta functions generated by a Poisson process

The expectation $\langle S(t) \rangle$ of *S(t)* at time t is the instantaneous 'rate' $\nu(t)$, given by the rate $\rho(t)$ of the Poisson process.

The auto-correlation of the Poisson Process $\langle S(t)S(t') \rangle$ is

$$\langle S(t)S(t') \rangle = \nu(t)\,\nu(t') + \nu(t)\,\delta(t-t')$$

Note1: if the variable *x* is a filtered version of the spike train with a filter F, we insert the autocorrelation of the Poisson process, to get the autocorrelation and variance of *x* (see Section 11.1).

Note2: stochastic pulses such as a Poissone spike train is also called 'shot noise'.

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Week 11 – Variability and Noise: Autocorrelation

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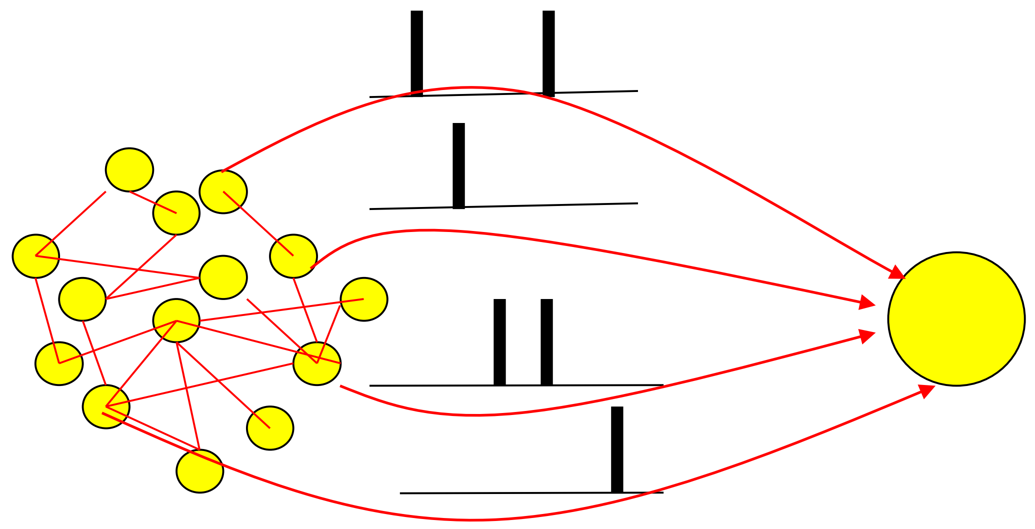
EPFL, Lausanne, Switzerland

11.3 Noisy Integrate-and-fire



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

Passive membrane

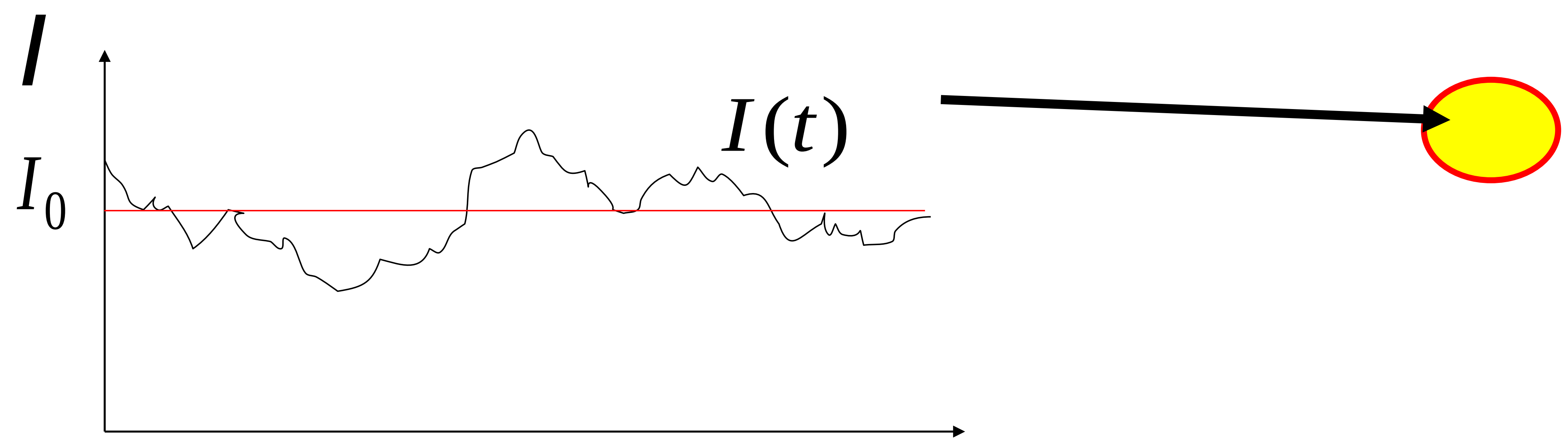
$$\tau \frac{d}{dt} u = -(u - u_{rest}) \quad + R I^{syn}(t)$$

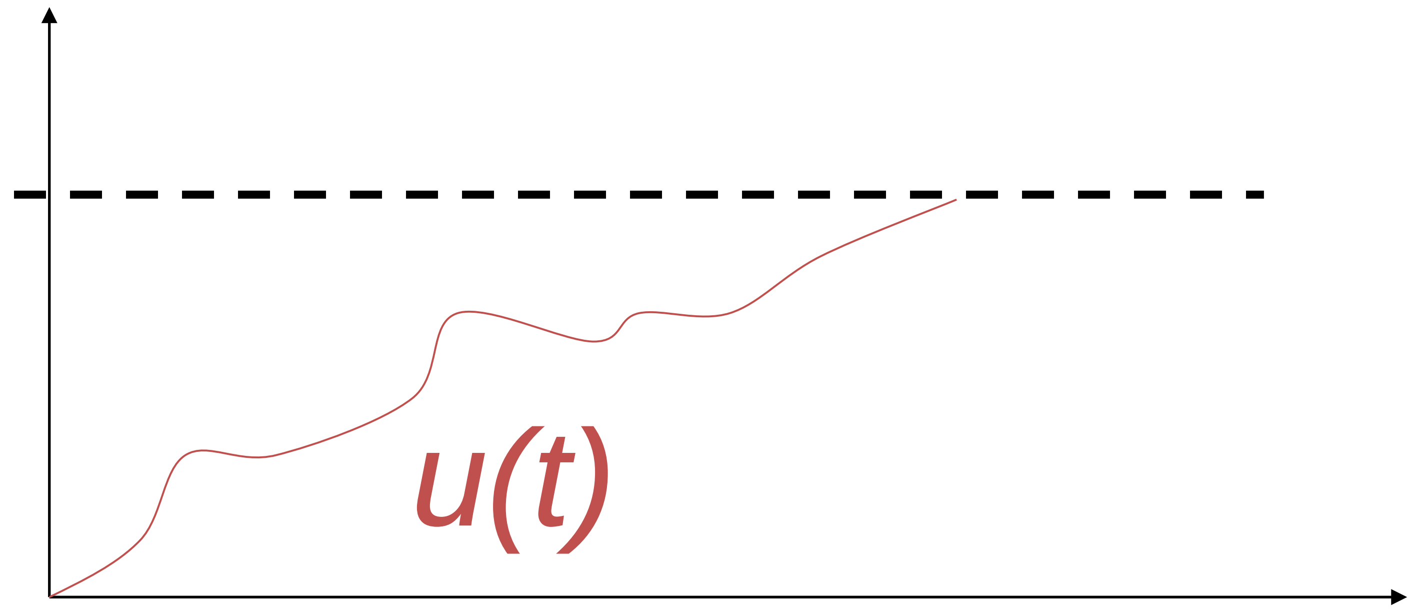
Passive membrane =Leaky integrate-and-fire without threshold

ADD THRESHOLD
→ Leaky Integrate-and-Fire

11.3 Noisy Integrate-and-fire

effective noise current





LIF

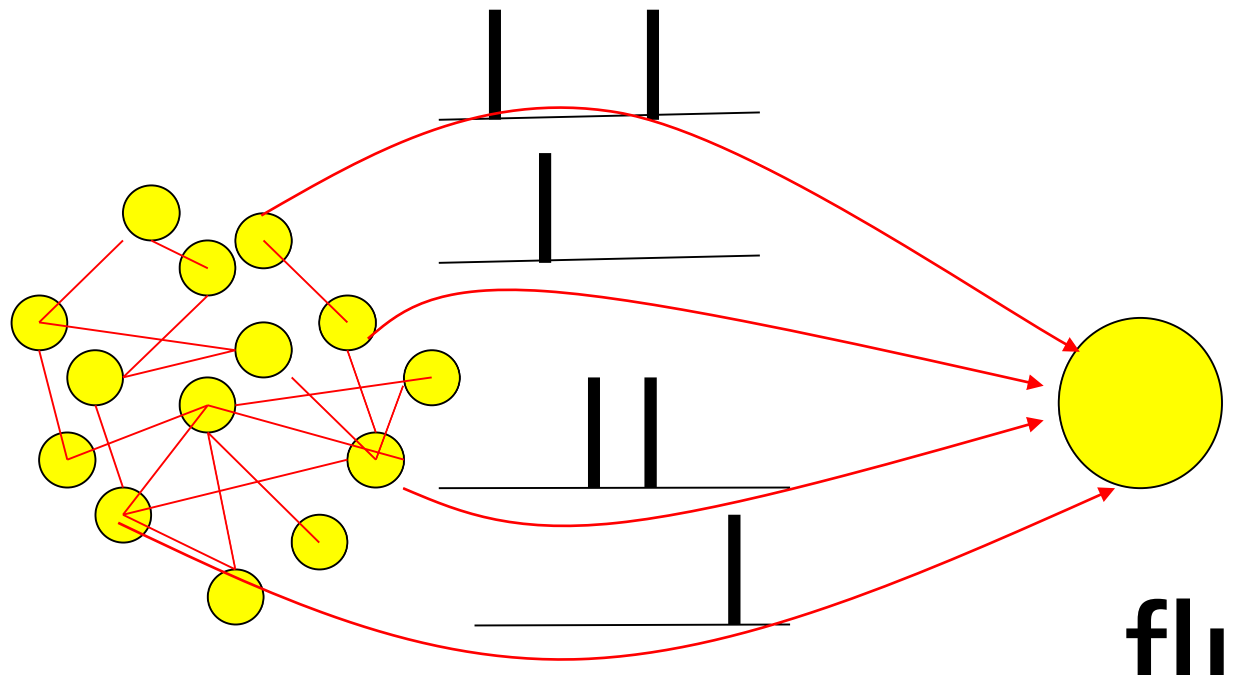
$$\tau \frac{d}{dt} u = -(u - u_{rest}) \quad + R\, I(t)$$

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

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

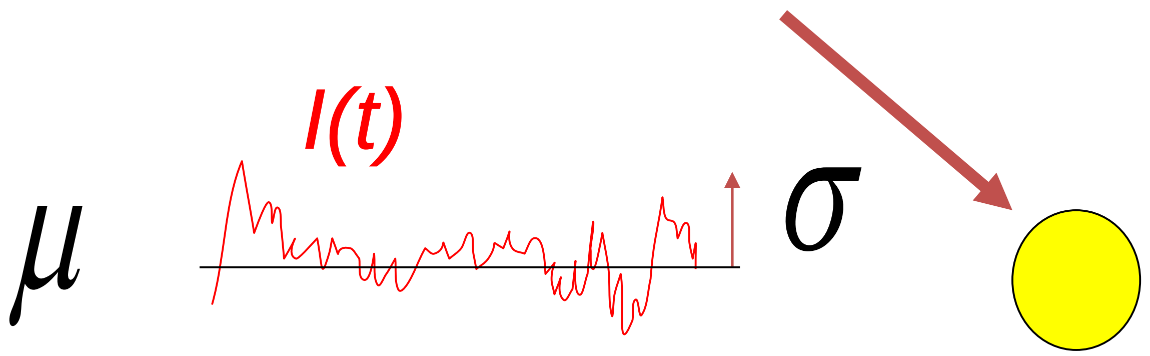
noisy input/
diffusive noise/
stochastic spike
arrival

11.3 Noisy Integrate-and-fire



Random spike arrival

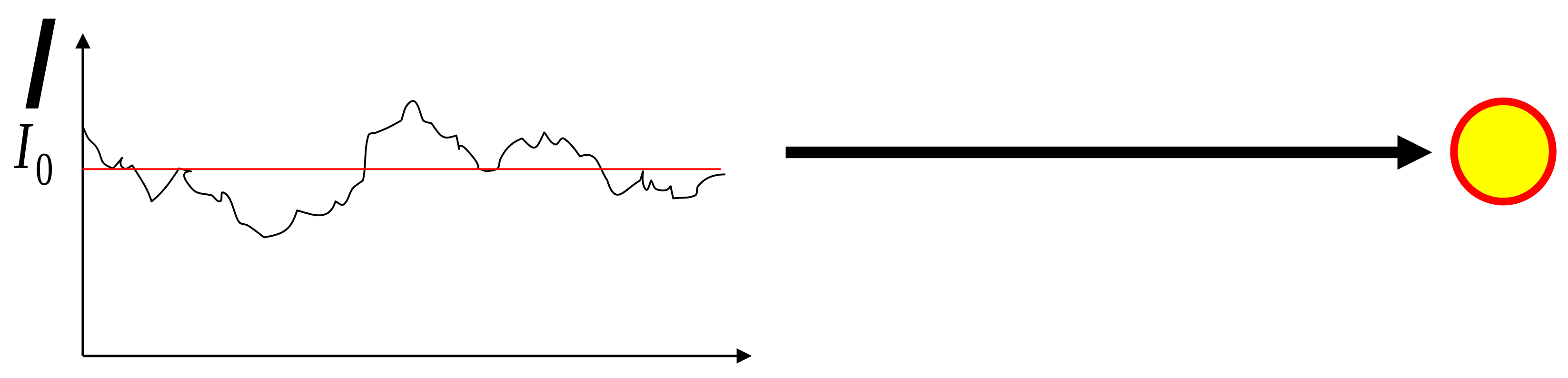
fluctuating input current



fluctuating potential

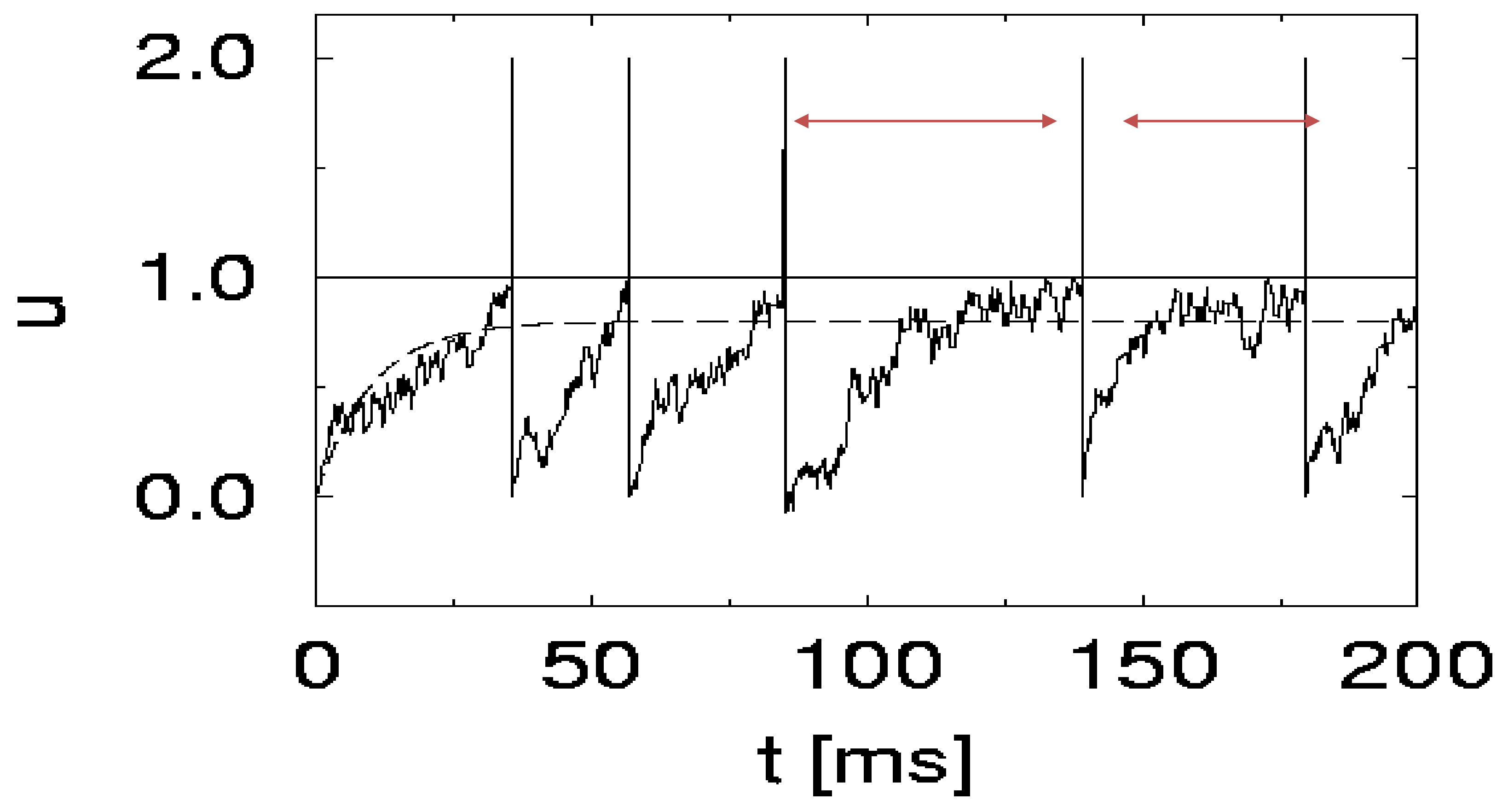
11.3 Noisy Integrate-and-fire (noisy input)

stochastic spike arrival in I&F – interspike intervals



$$RI^{syn}(t) = RI_0(t) + \xi(t)$$

white noise



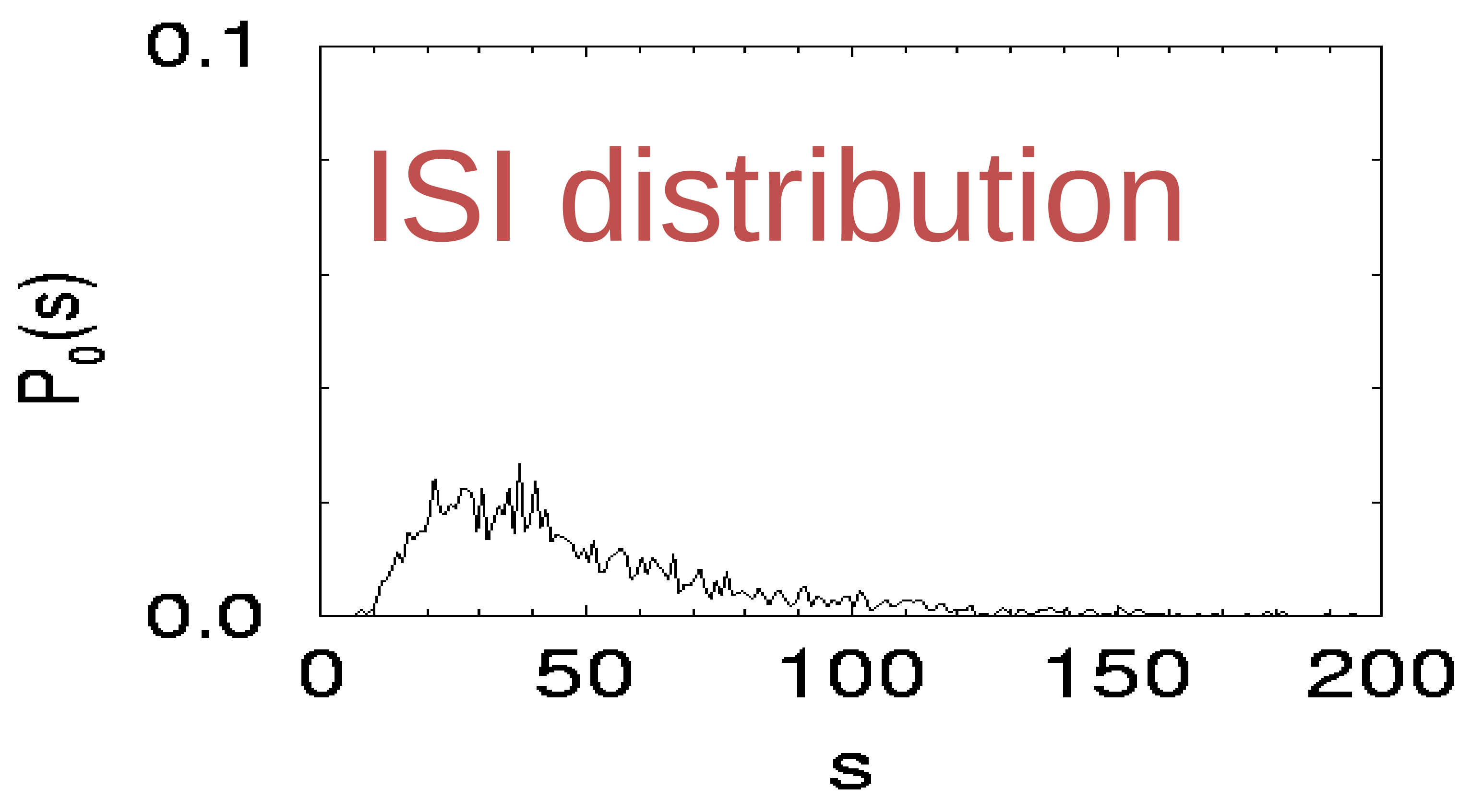


Image:
Gerstner et al. (2014),
Neuronal Dynamics,

11.3 Noisy Integrate-and-fire (noisy input)

Superthreshold vs. Subthreshold regime

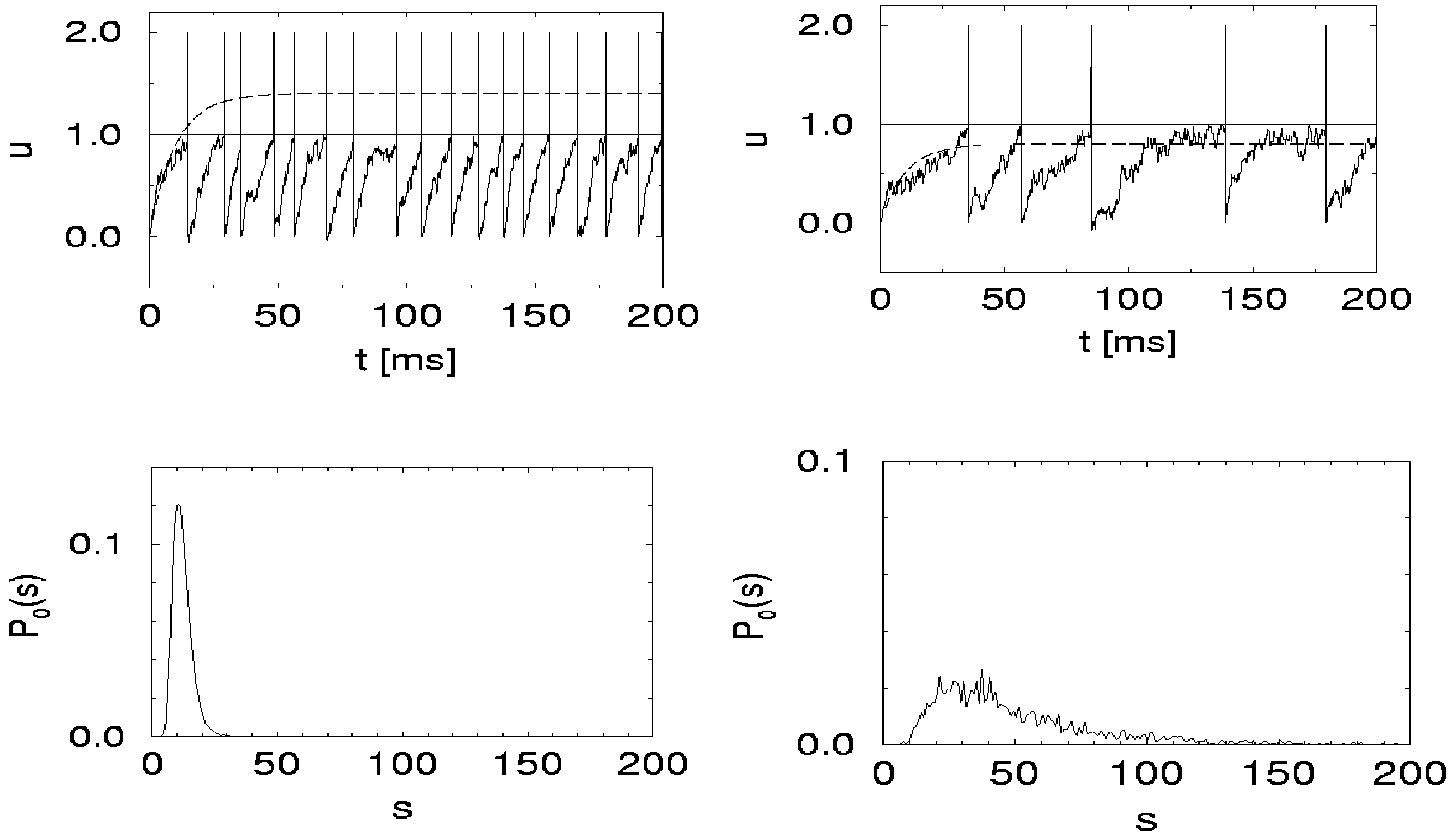
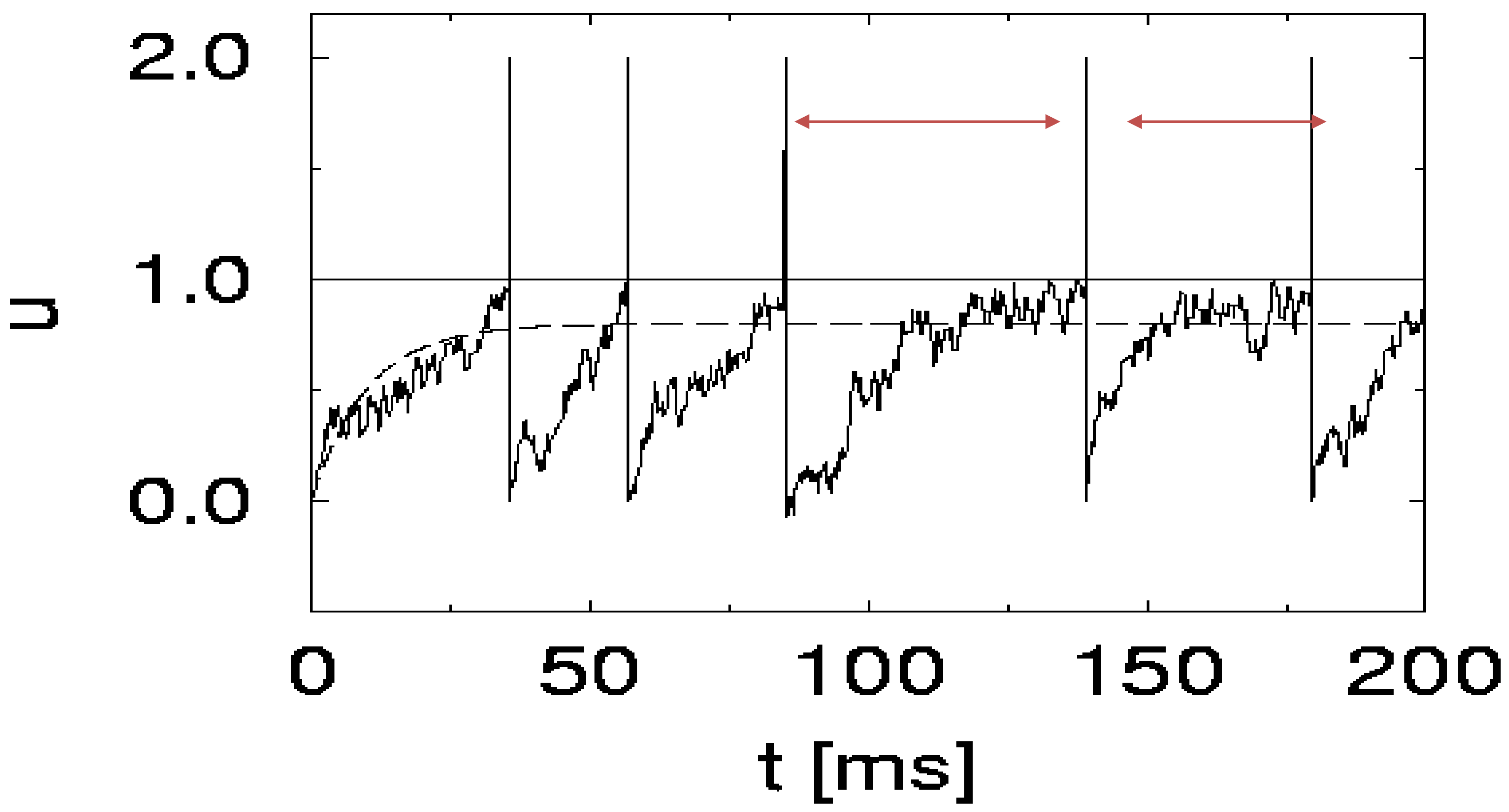


Image:
Gerstner et al. (2014), Neuronal Dynamics, Cambridge Univ. Press;
See: Konig et al. (1996)

11.3. Noisy integrate-and-fire (noisy input)



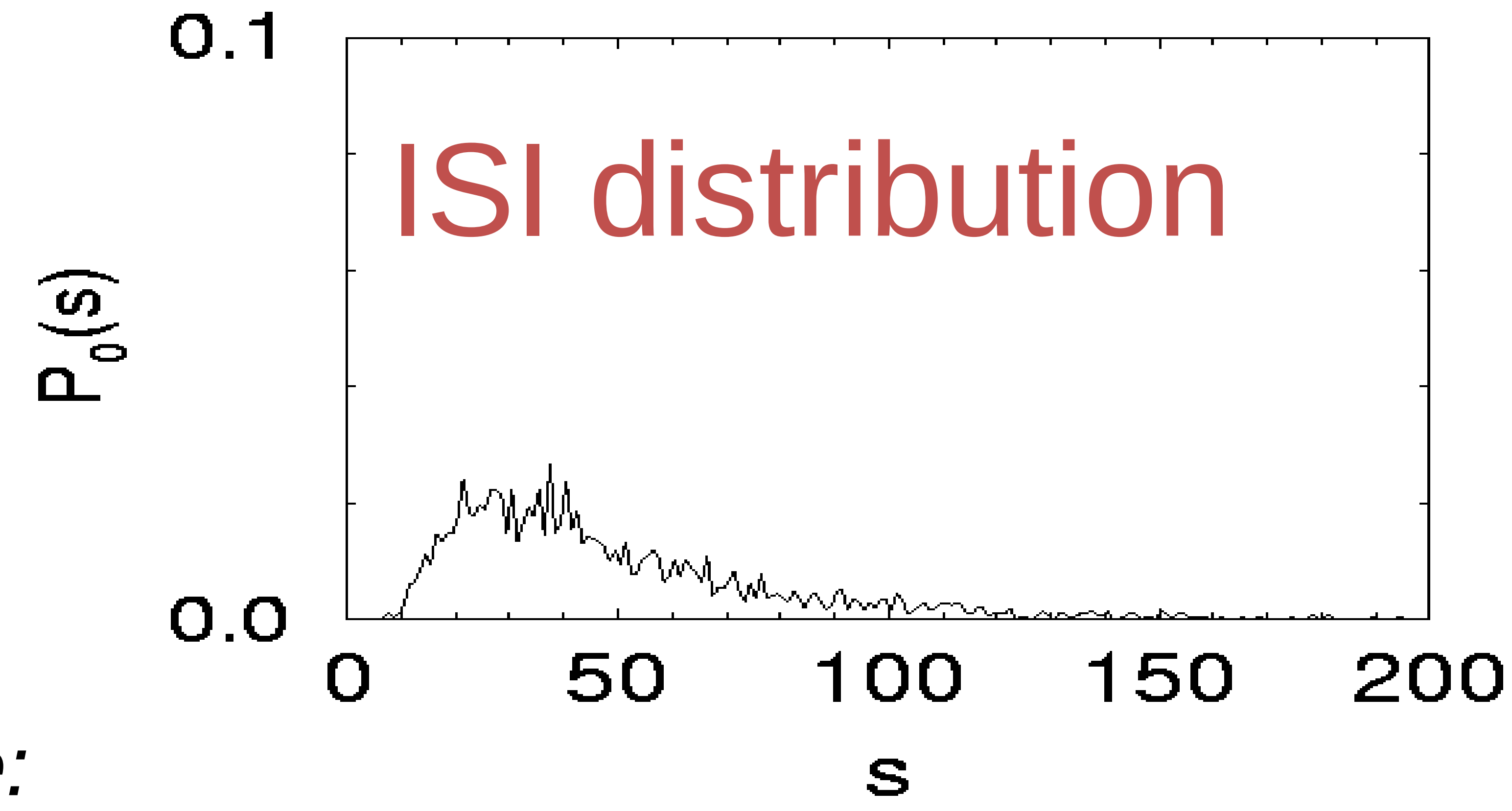
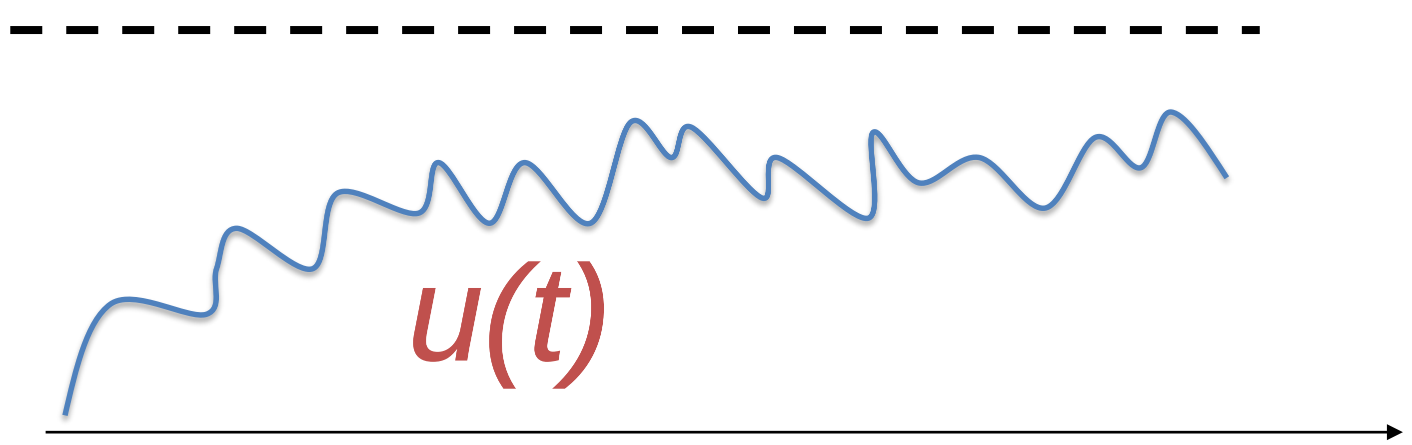


Image:
Gerstner et al. (2014),
Neuronal Dynamics,

noisy input/ diffusive noise/ stochastic spike arrival



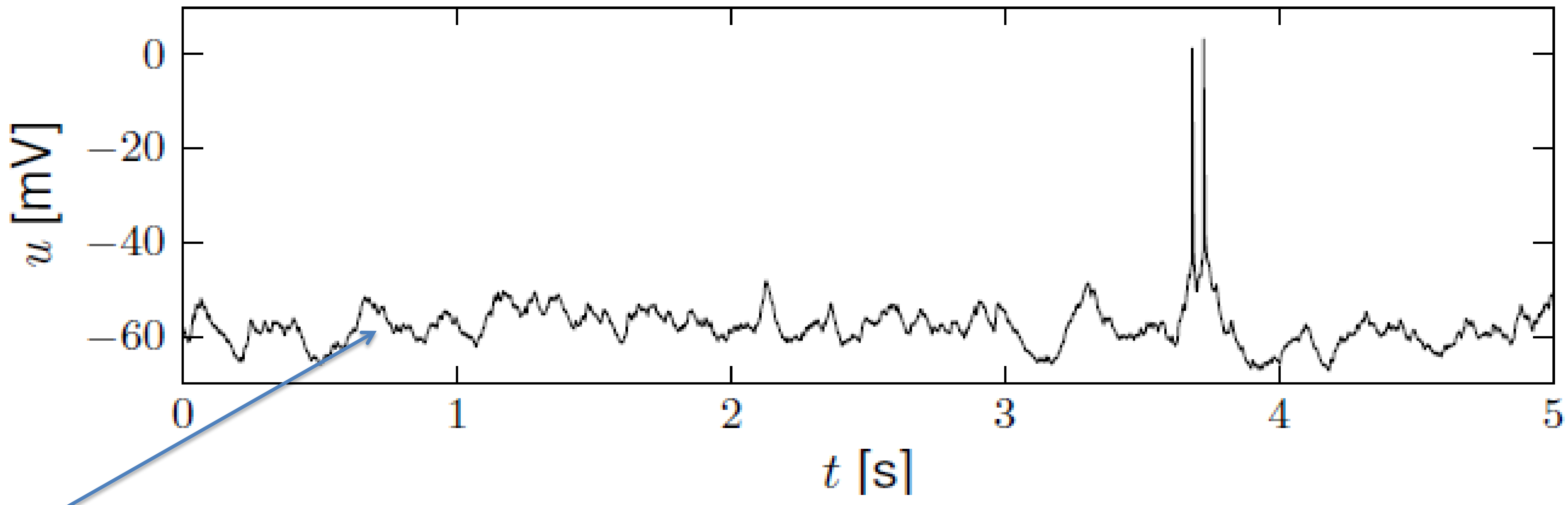
subthreshold regime:

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

Spontaneous activity *in vivo*

Variability
of membrane potential?

awake mouse, freely whisking,

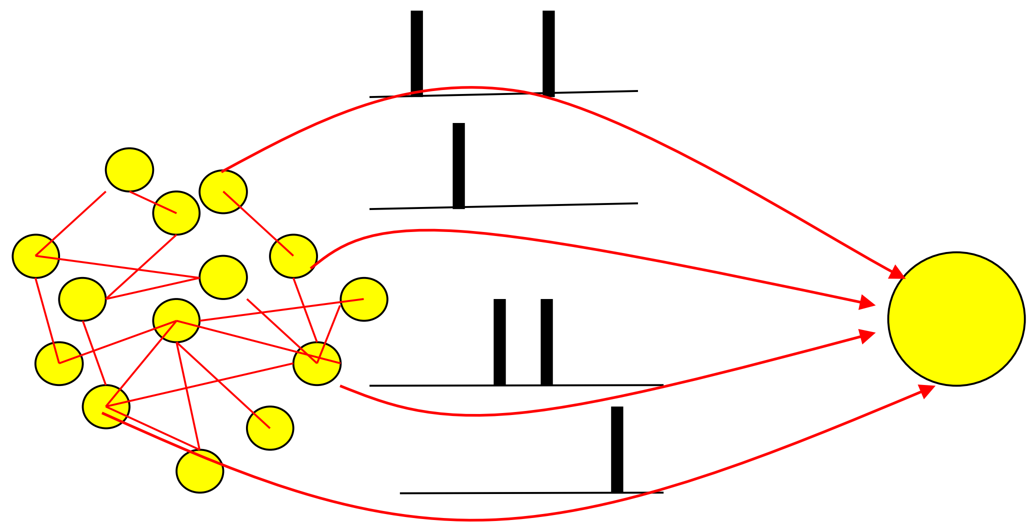


Subthreshold regime

Crochet et al., 2011

Image:
Gerstner et al. (2014),
Neuronal Dynamics,
Cambridge Univ. Press;
Courtesy of: Crochet et al. (2011)

11.3 Noisy Integrate-and-fire (noisy input)



Stochastic spike arrival:

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

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

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

Leaky integrate-and-fire
in ***subthreshold*** *regime*
can explain variations
of membrane potential and ISI

11.3 Conclusion: Leaky integrate-and-fire with noisy input.

The leaky integrate-and-fire model (LIF) is a passive membrane model together with a threshold.
When driven with a constant mean current plus a white noise, two regimes emerge:
(i) Superthreshold regime. The mean current alone would be sufficient to fire spikes. In this case the interspike interval distribution (ISI) is fairly regular, visible as a sharp peak around the noise-free interspike-interval.
(ii) Subtrheshold regime. The mean current alone would not be sufficient to fire spikes. Noise is essential to make the neuron fire. In this case, the ISI is very broad and extends to very long intervals.

In the subthreshold regime we observe fluctuations of the membrane potential in a regime below threshold and rare spiking, consistent with typical experimental results in vivo.

Biological Modeling of Neural Networks

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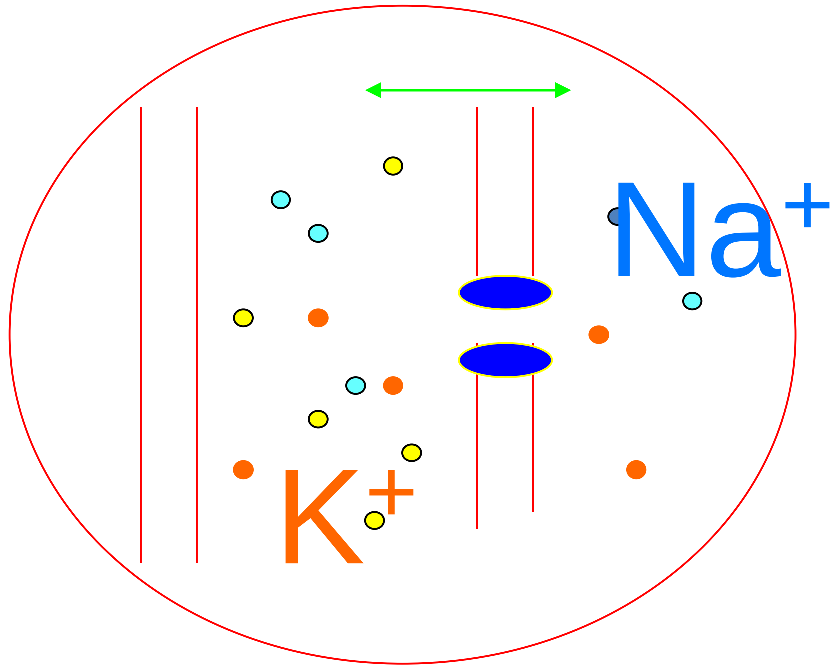
Week 11 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Review: Sources of Variability

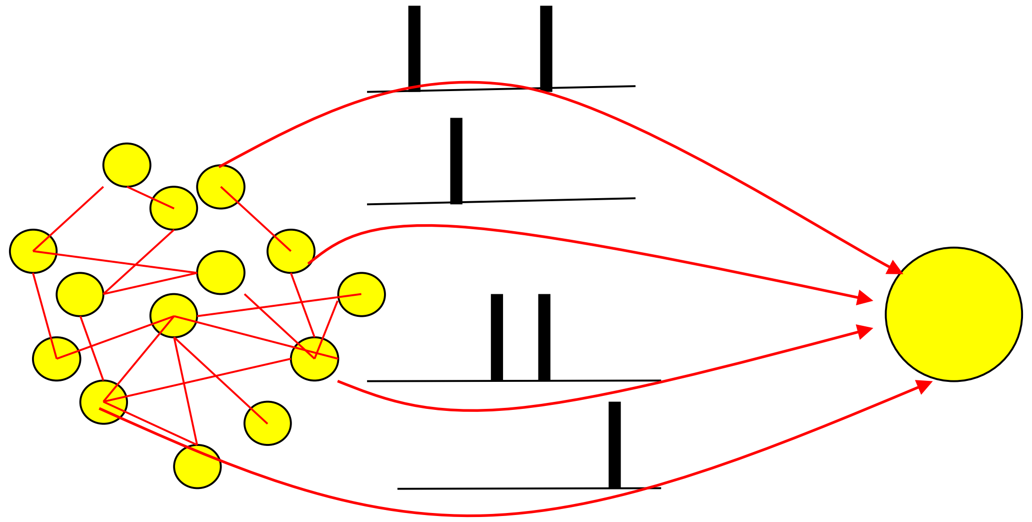
- Intrinsic noise (ion channels)



-Finite number of channels
-Finite temperature

small contribution!

-Network noise (background activity)



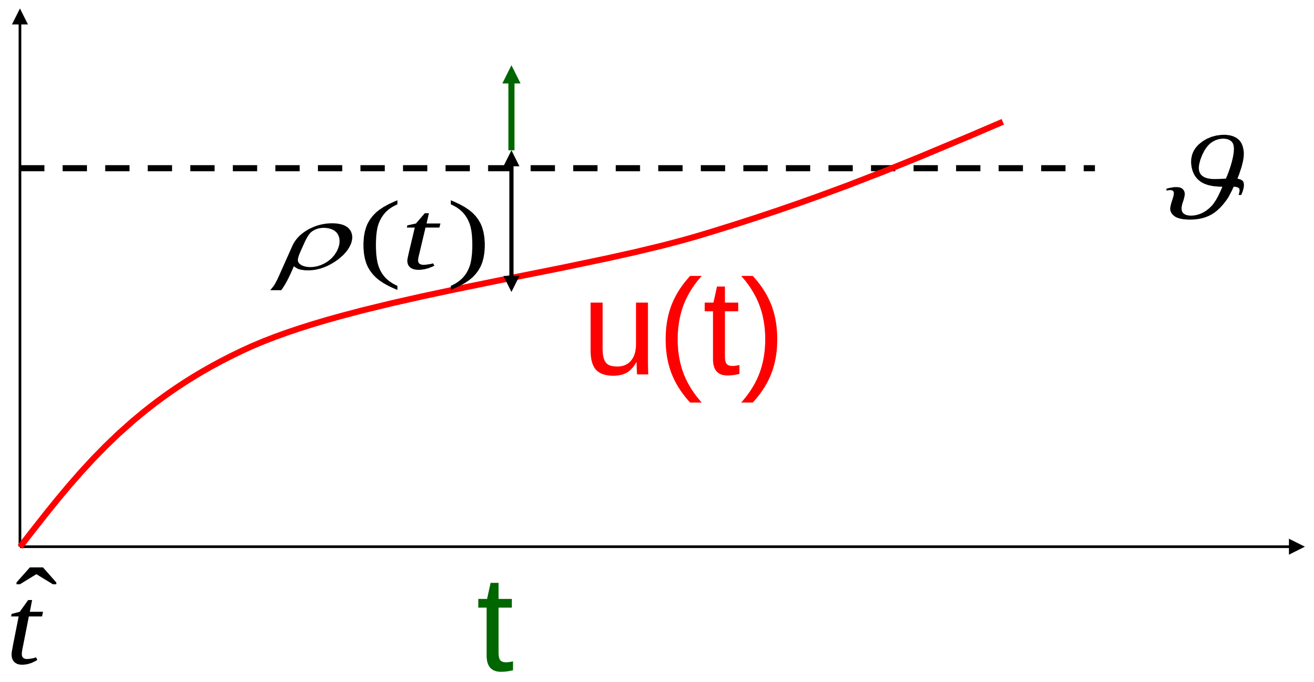
-Spike arrival from other neurons
-Beyond control of experimentalist

big contribution!

Noise models?

11.4 Noise models: Escape noise vs. input noise

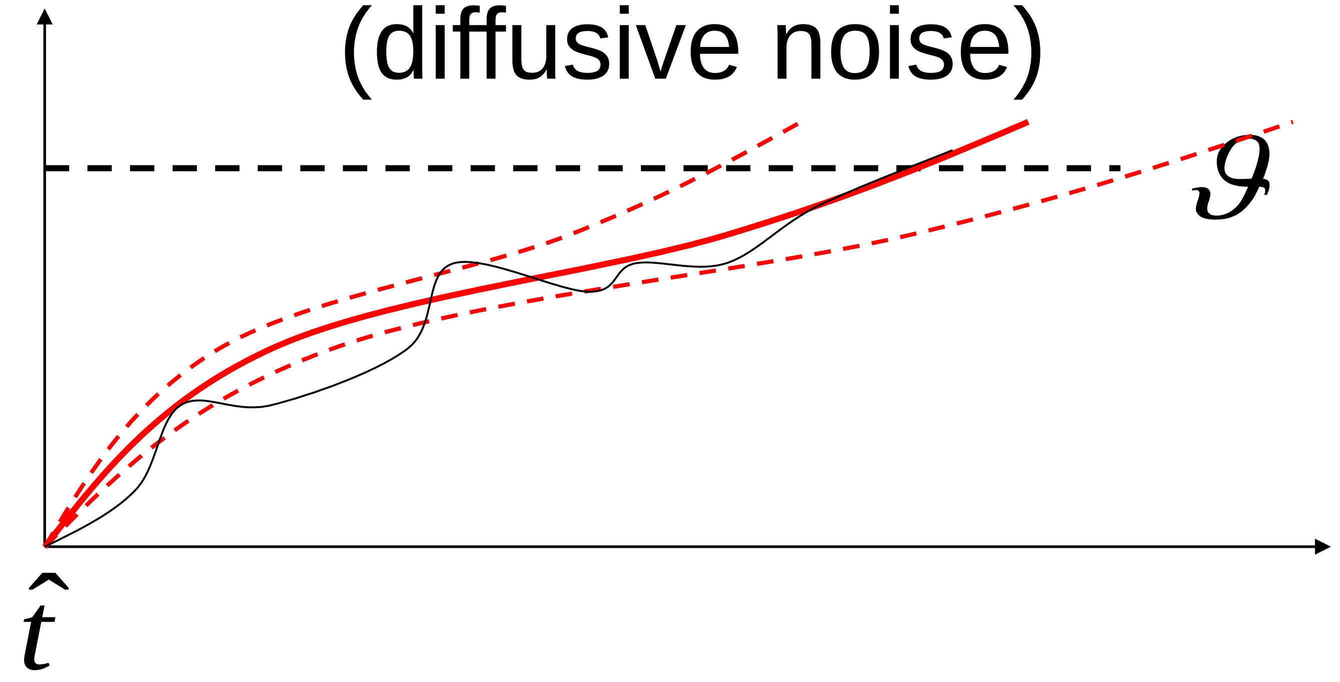
escape process,
stochastic intensity



escape rate

$$\rho(t) = f(u(t) - \vartheta)$$

stochastic spike arrival
(diffusive noise)



noisy integration

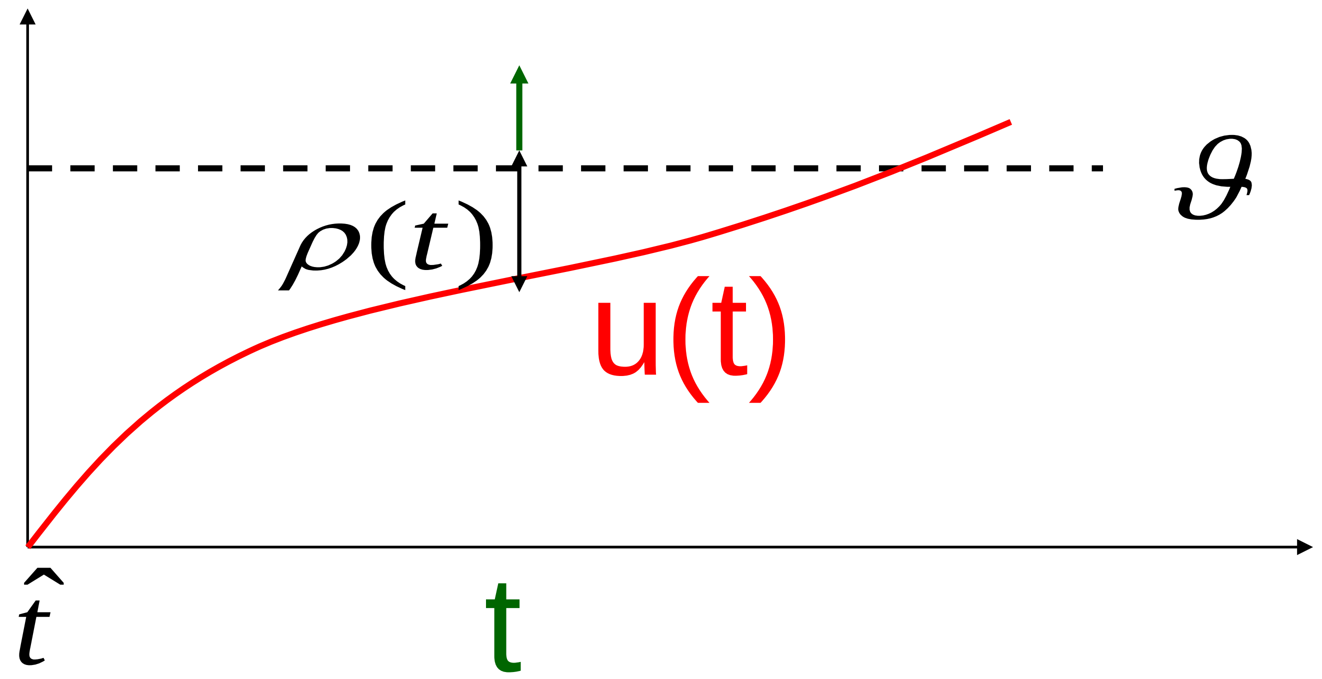
$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$

Now:
Escape noise!

Relation between the two models:
see Ch. 9.4 of
Neuronal Dynamics

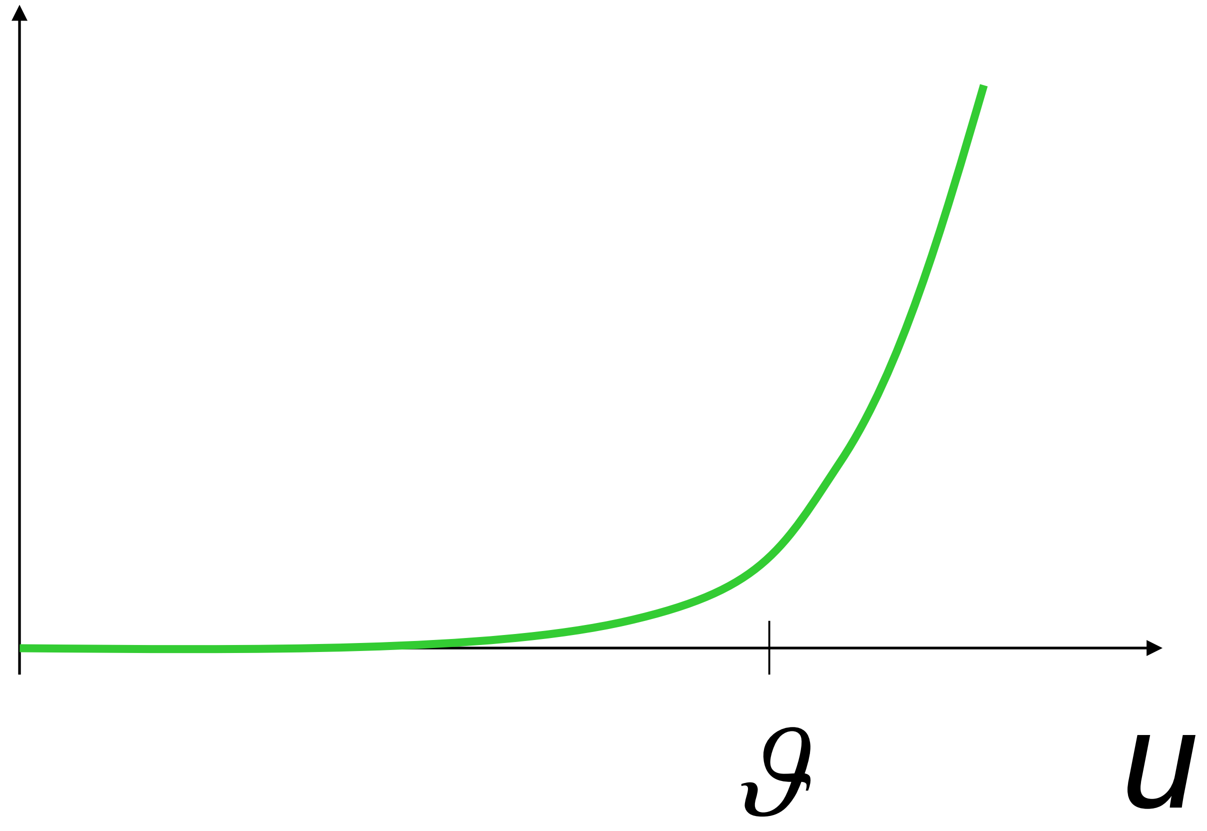
11.4 Escape noise

escape process



escape rate

$$\rho(t) = f(u(t) - \vartheta)$$



escape rate

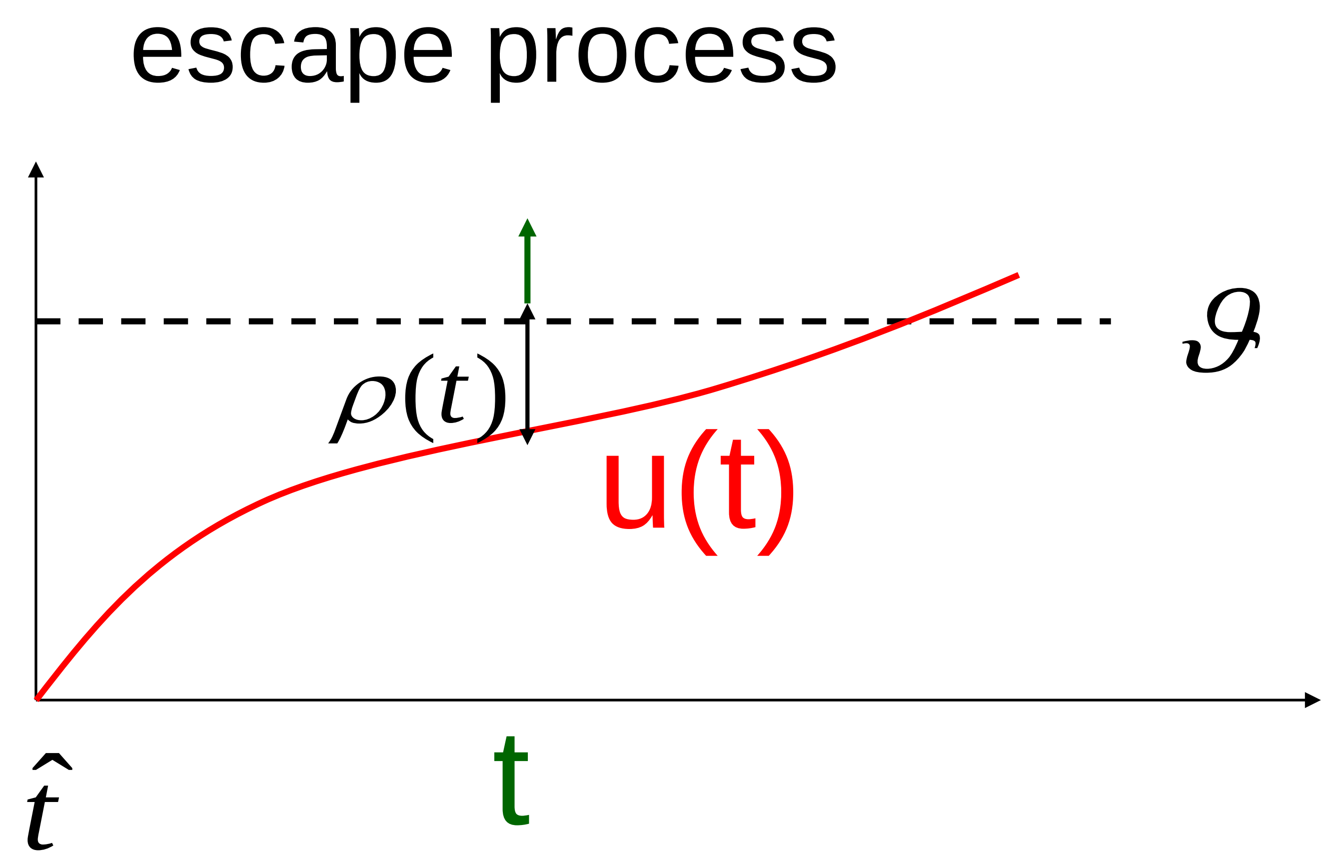
$$\rho(t) = \frac{1}{\Delta}\exp\left(\frac{u(t) - \vartheta}{\Delta}\right)$$

Example: leaky integrate-and-fire model

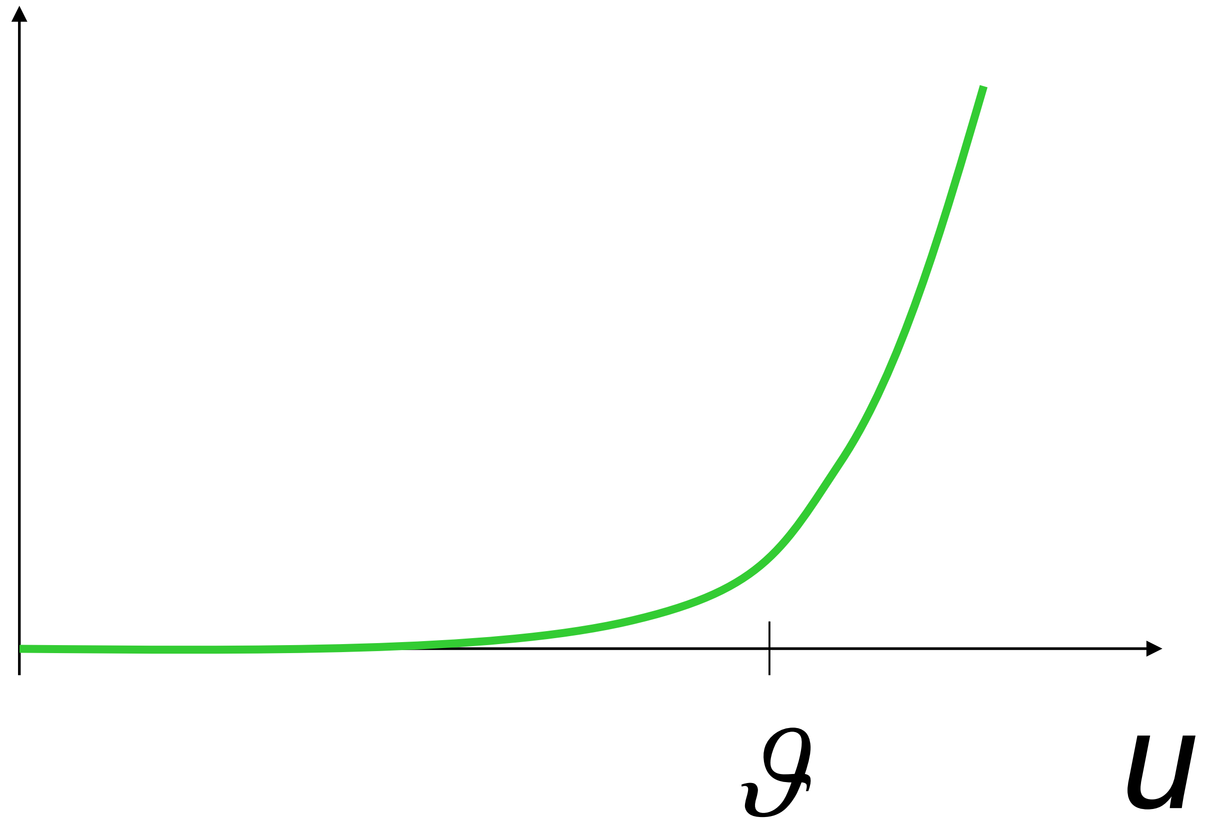
$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

$$\text{if spike at } t^f \Rightarrow u\left(t^f + \delta\right) = u_r$$

11.4 stochastic intensity



escape rate $\rho(t) = f(u(t) - \vartheta)$



Escape rate = stochastic intensity
of point process

$$\rho(t) = f(u(t) - \vartheta)$$

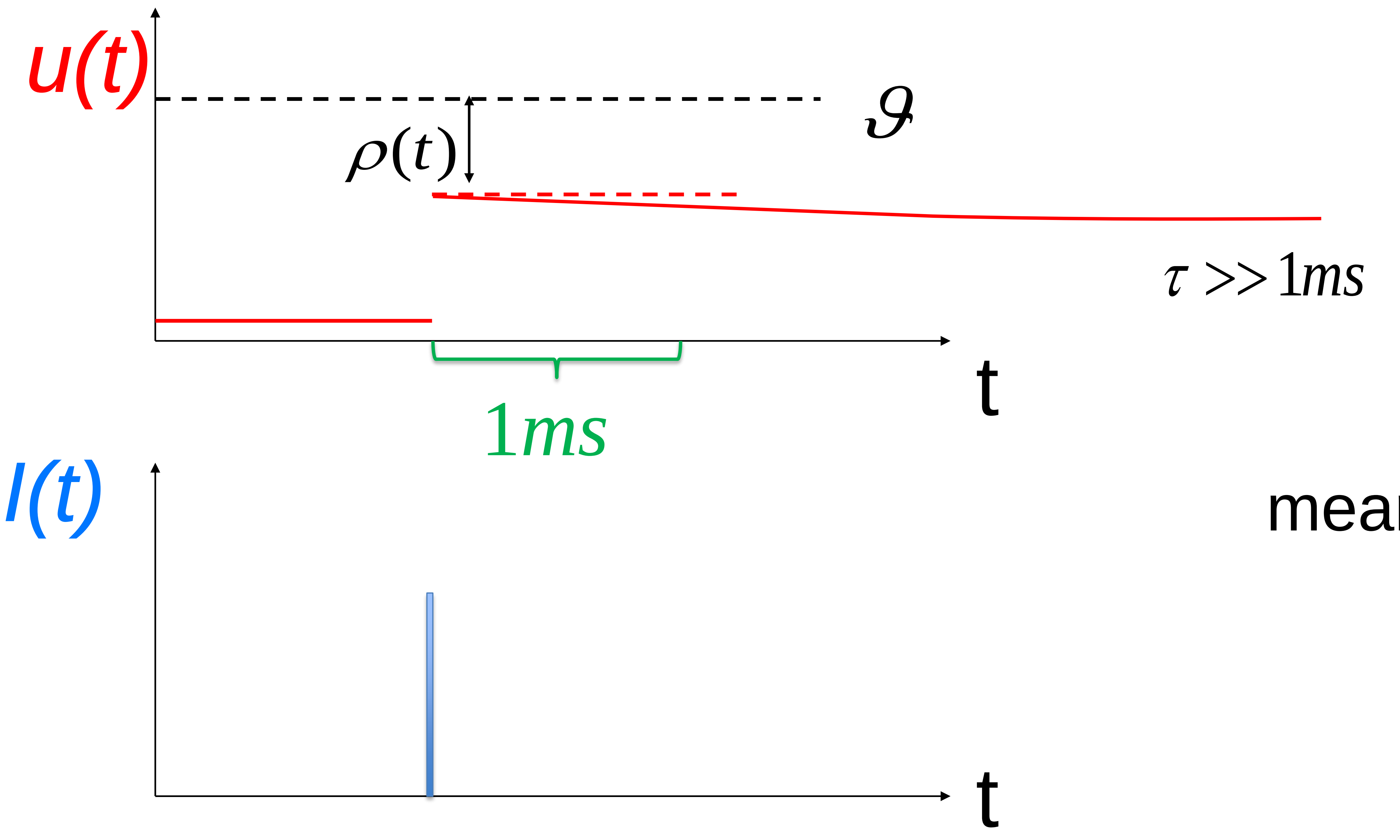
examples

$$\rho(t) = \frac{c}{\Delta} \exp\left(\frac{u(t) - \vartheta}{\Delta}\right)$$

$$\rho(t) =$$

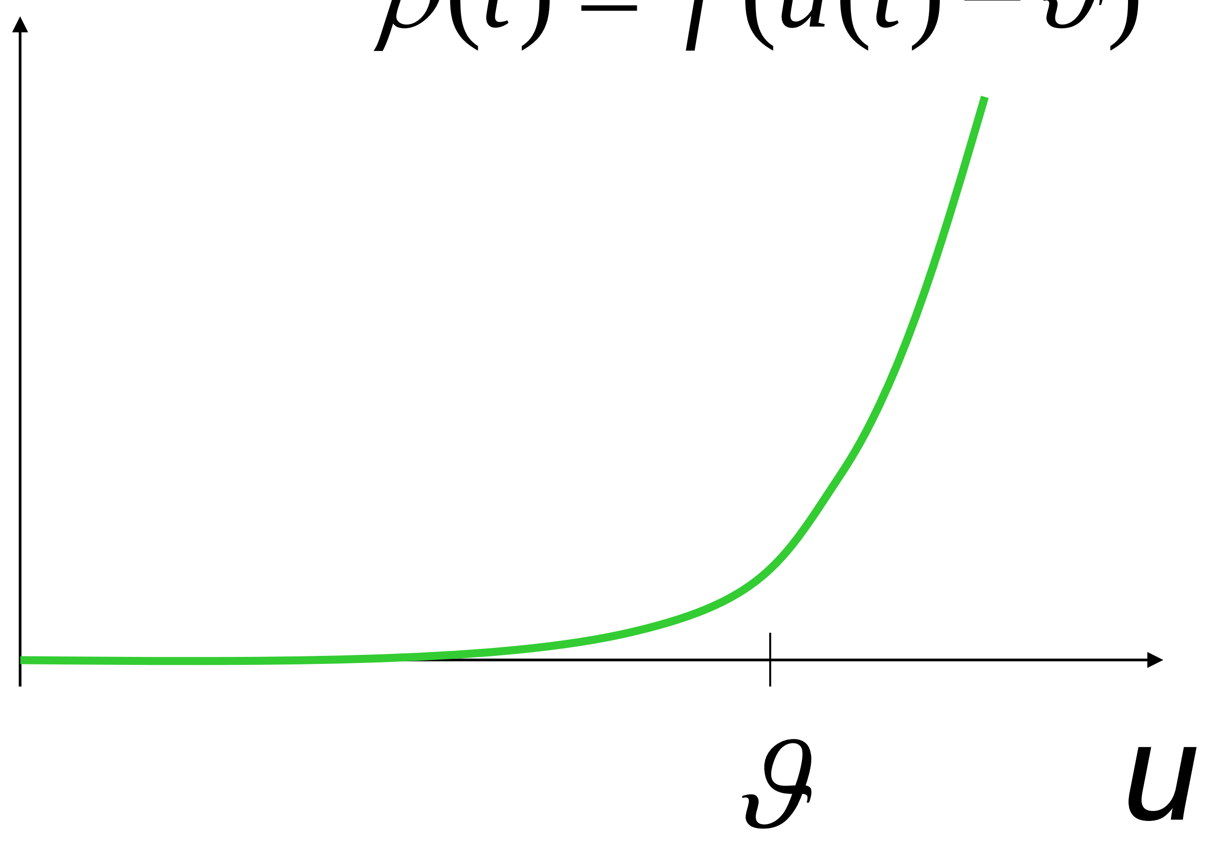
11.4 mean waiting time

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



escape rate

$$\rho(t) = f(u(t) - \vartheta)$$



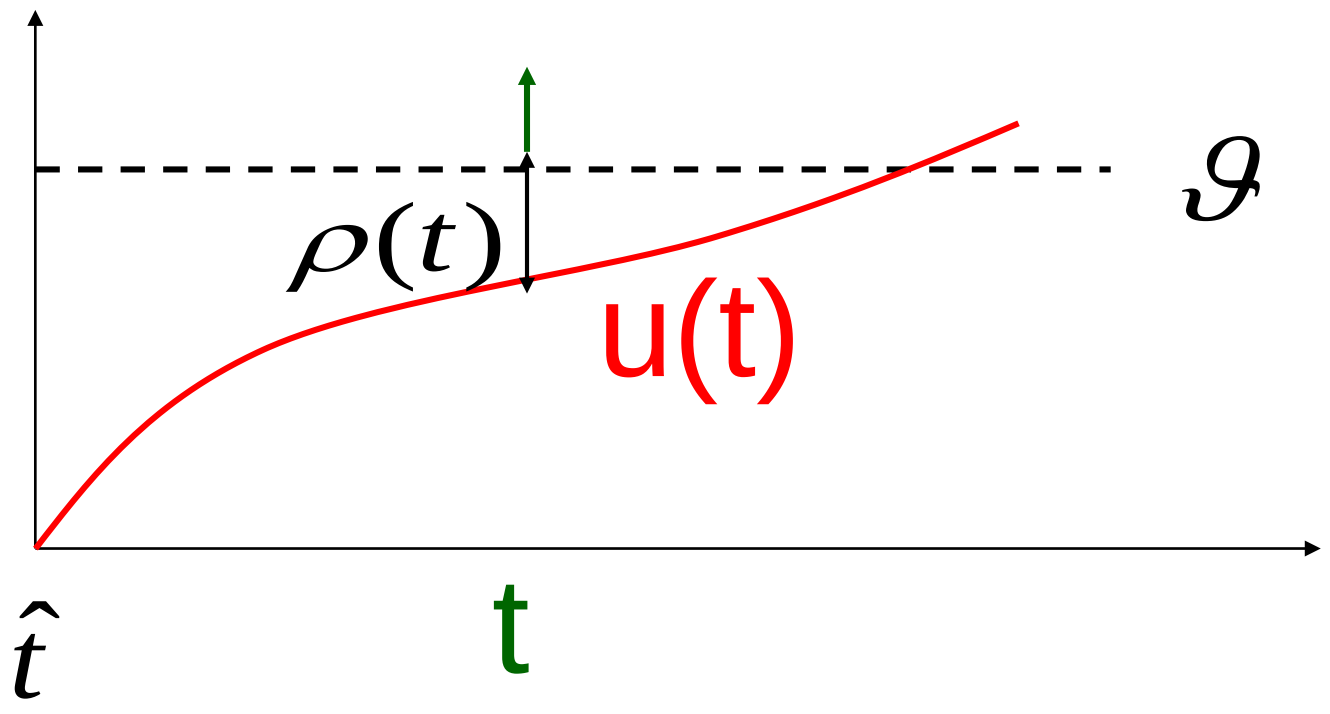
mean waiting time, after switch

Blackboard4,
Math detour

11.4 escape noise/stochastic intensity

Escape rate = stochastic intensity of point process

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



- Escape rate depends on momentary distance of u(t) to threshold

- u(t) depends on the inpu but also on previous spikes (because of the reset)

Quiz 4

Escape rate/stochastic intensity in neuron models

[ ] The escape rate of a neuron model has units one over time

[ ] The stochastic intensity of a point process has units one over time

[ ] For large voltages, the escape rate of a neuron model always saturates at some finite value

[ ] After a step in the membrane potential, the mean waiting time until a spike is fired is proportional to the escape rate

[ ] After a step in the membrane potential, the mean waiting time until a spike is fired is equal to the inverse of the escape rate

[ ] The stochastic intensity of a leaky integrate-and-fire model with reset only depends on the external input current but not on the time of the last reset

[ ] The stochastic intensity of a leaky integrate-and-fire model with reset depends on the external input current AND on the time of the last reset

11.4 Conclusion: Escape noise

All noise models are ad hoc. In part 11.1 we focused on white noise as an approximation of stochastic spike arrival. We can think of this as noise in the input.
In this section we focused on a different noise model that we call escape noise.
In discrete time, the probability to generate a spike with the escape noise model depends on the momentary distance between the membrane potential u(t) and the threshold θ.
In continuous time, this 'probability' corresponds to a stochastic intensity of spike firing $\rho(t) = f[u(t) - \theta]$. We can think of escape noise as a noise in the output.

Escape noise can be combined with a leaky integrate-and-fire model: As soon as a spike is fired, the membrane potential is reset to a lower value so that a second spike becomes unlikely. In this case a good choice of the function f is an exponential.

$$\rho(t) = \frac{c}{\Delta}\exp\left(\frac{u(t)-\vartheta}{\Delta}\right)$$

$\rho_0 = c/\Delta$ is a constant the characterizes the mean firing rate at $u(t) = \theta$

Here the parameter Δ indicates how 'smooth' the threshold is. In practice, for $u(t) < \theta - 3\Delta$ the neuron is unlikely to fire and for $u(t) > \theta + 3\Delta$ it fires immediately.

Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Week 11 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

√11.1 Variation of membrane potential
- white noise approximation

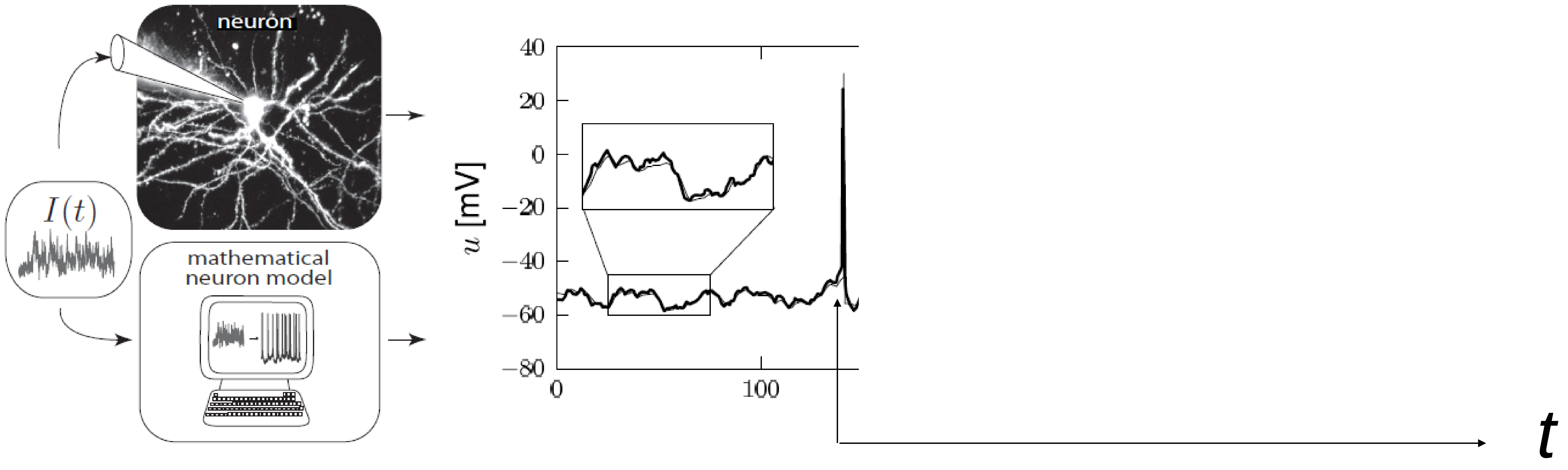
√11.2 Autocorrelation of Poisson

√11.3 Noisy integrate-and-fire
- superthreshold and subthreshold

√11.4 Escape noise
- stochastic intensity

11.5 Renewal models

11.5. Interspike Intervals for time-dependent input



deterministic part of input

$$I(t) \rightarrow u(t)$$

noisy part of input/intrinsic noise

→ *escape rate*

Example:
nonlinear integrate-and-fire model

$$\tau \cdot \frac{d}{dt} u = F(u) + RI(t)$$

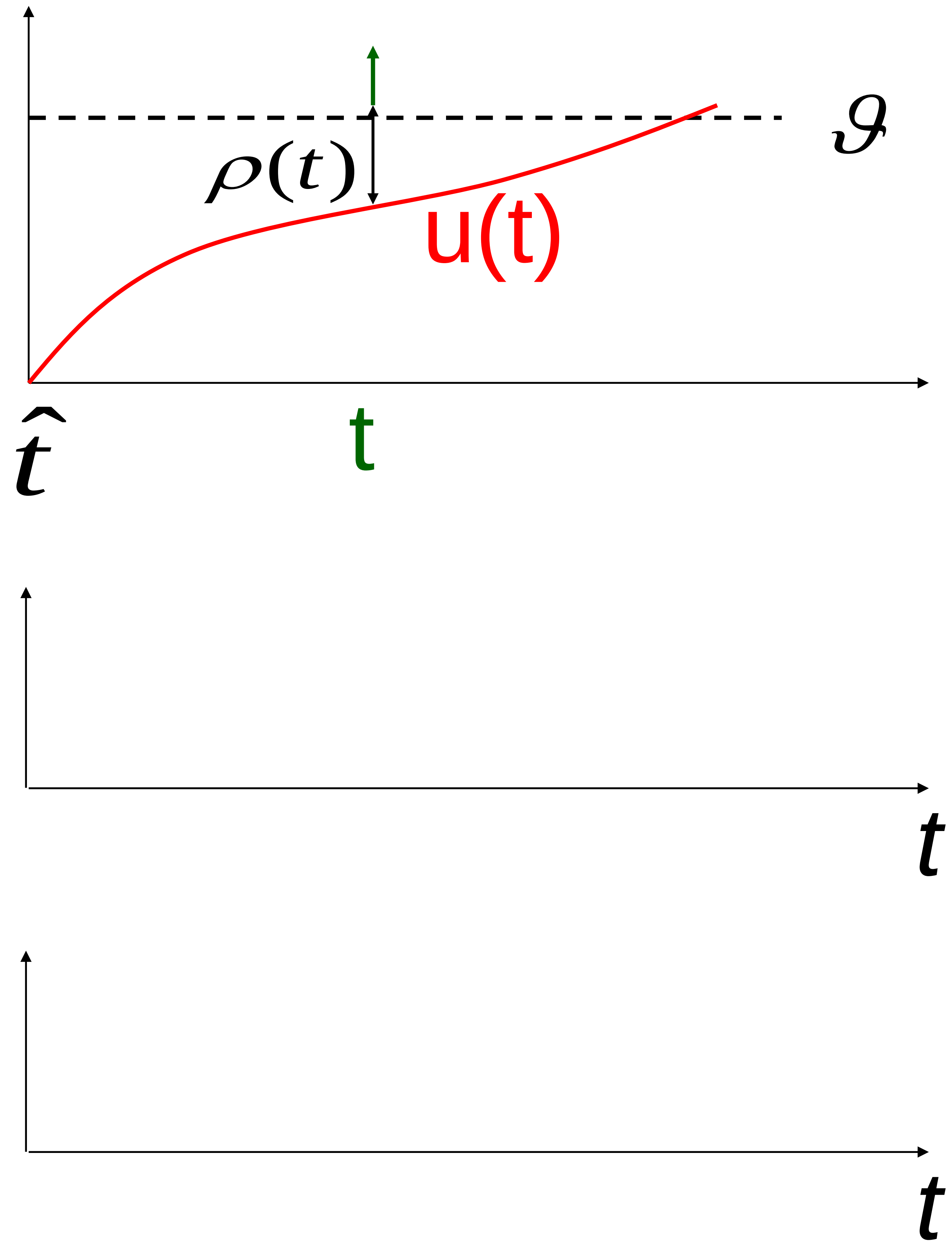
$$\text{if spike at } t^f \Rightarrow u\left(t^f + \delta\right) = u_r$$

Example:
exponential stochastic intensity

$$\rho(t) = f(u(t)) = \rho_\vartheta \exp(u(t) - \vartheta)$$

11.5. Interspike Interval distribution (time-dependent inp.)

escape process



Blackboard

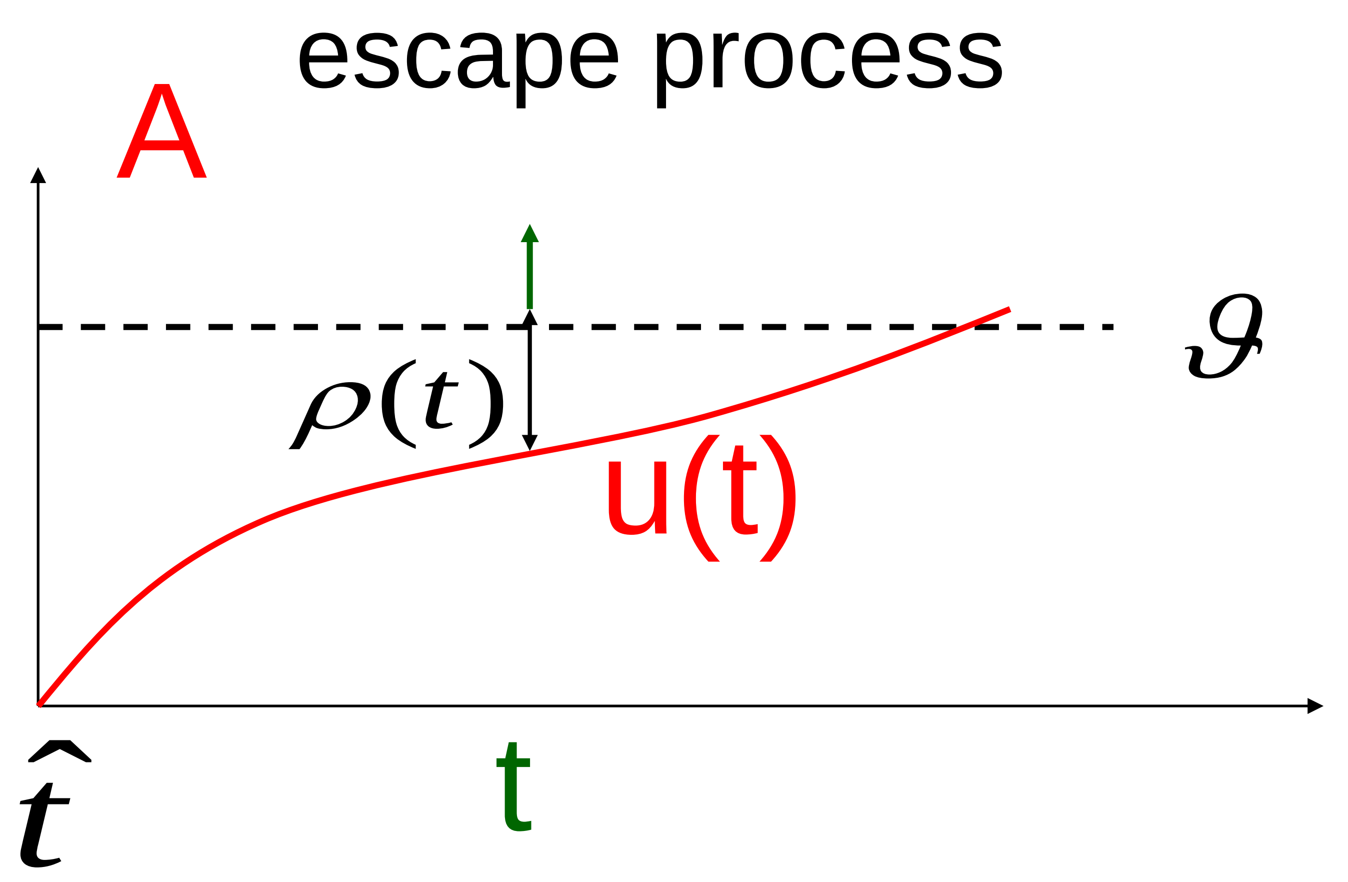
escape rate

$$\rho(t) = f(u(t) - \vartheta)$$

Survivor function

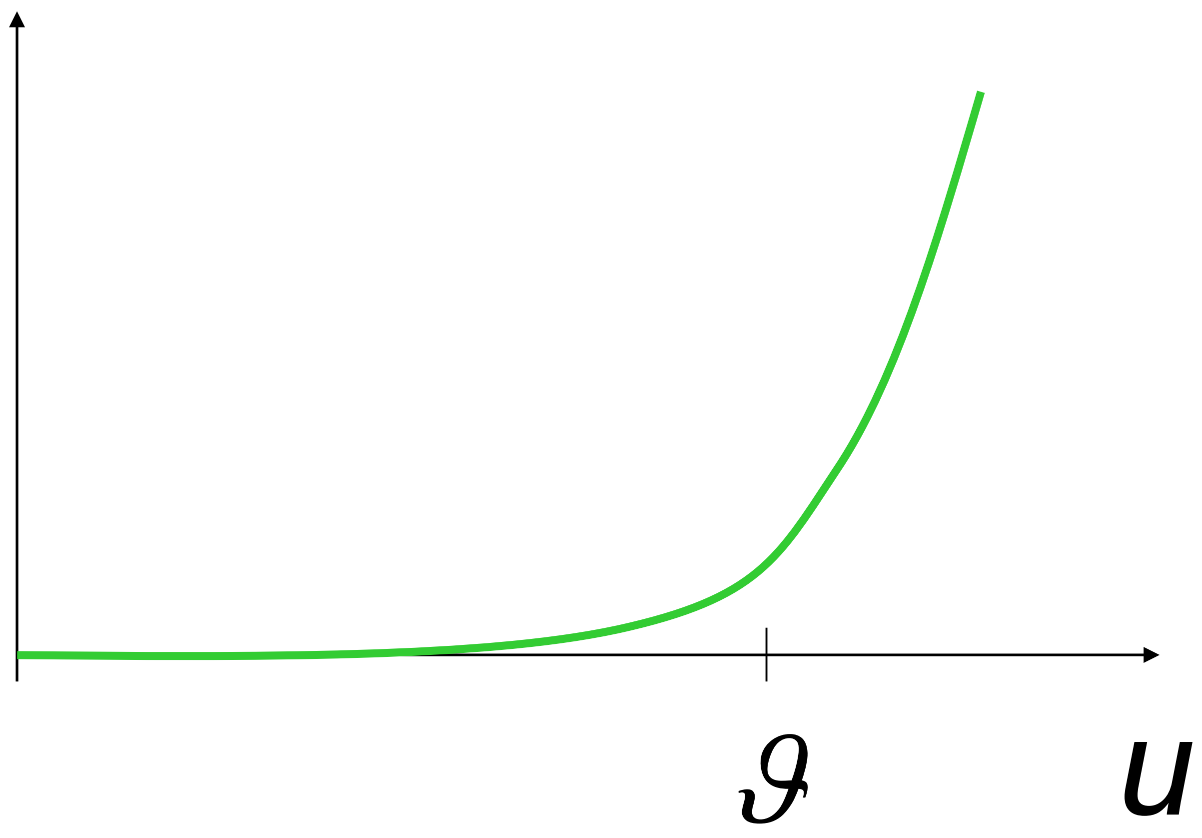
$$\frac{d}{dt} S_I(t|\hat{t}) = -\rho(t)\, S_I(t|\hat{t})$$

11.5. Interspike Intervals



escape rate

$$\rho(t) = f(u(t) - \vartheta)$$



Survivor function

Examples now

$$\frac{d}{dt} S_I(t|\hat{t}) = -\rho(t)\, S_I(t|\hat{t})$$

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

Interval distribution

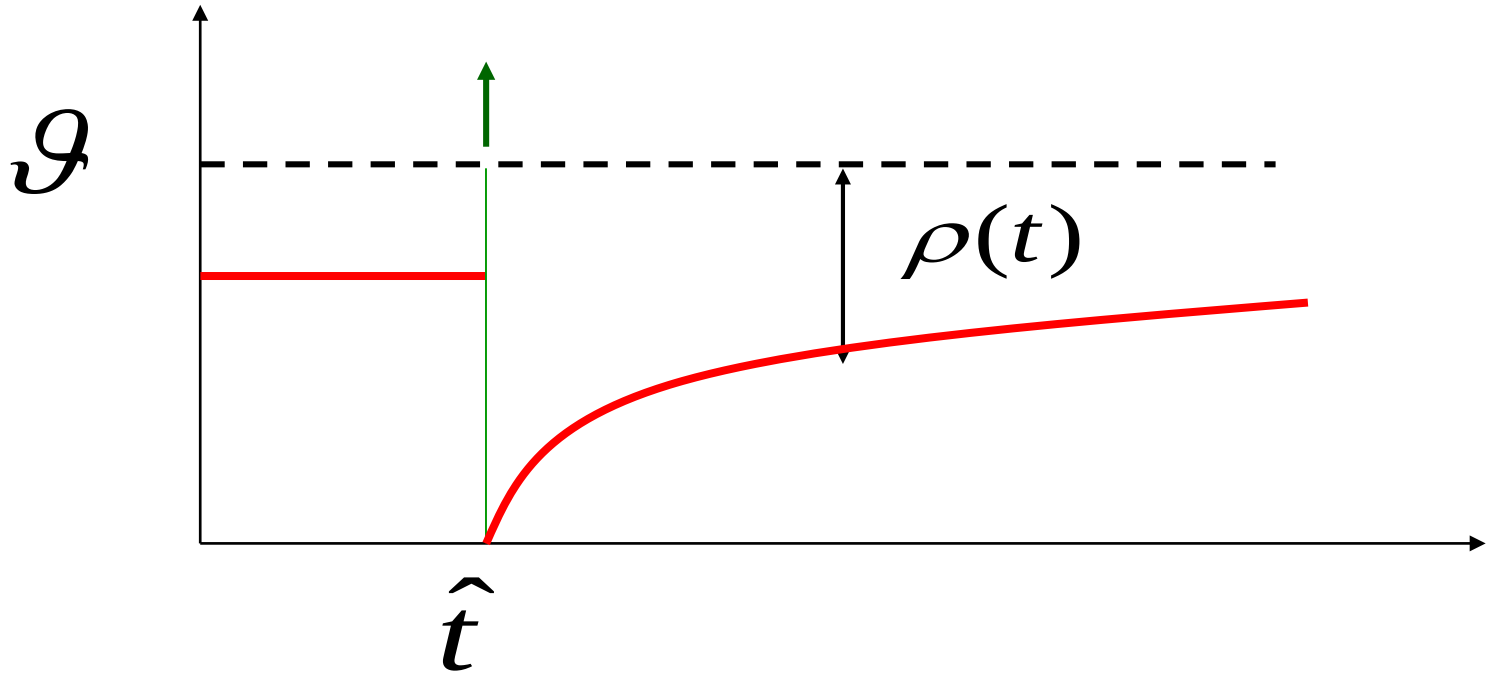
$$P_I(t|\hat{t}) = \rho(t) \cdot \exp\left(-\int_{\hat{t}}^{t} \rho(t')\,dt'\right)$$

escape rate

Survivor function

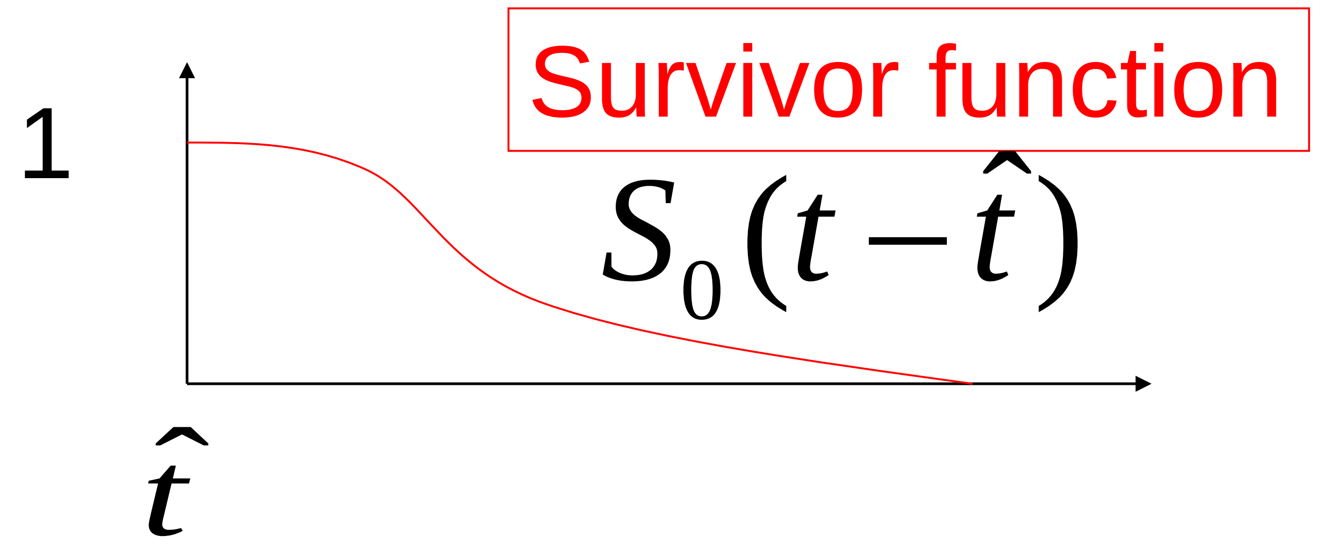
11.5. Renewal theory

Example: I&F with reset, **constant input**

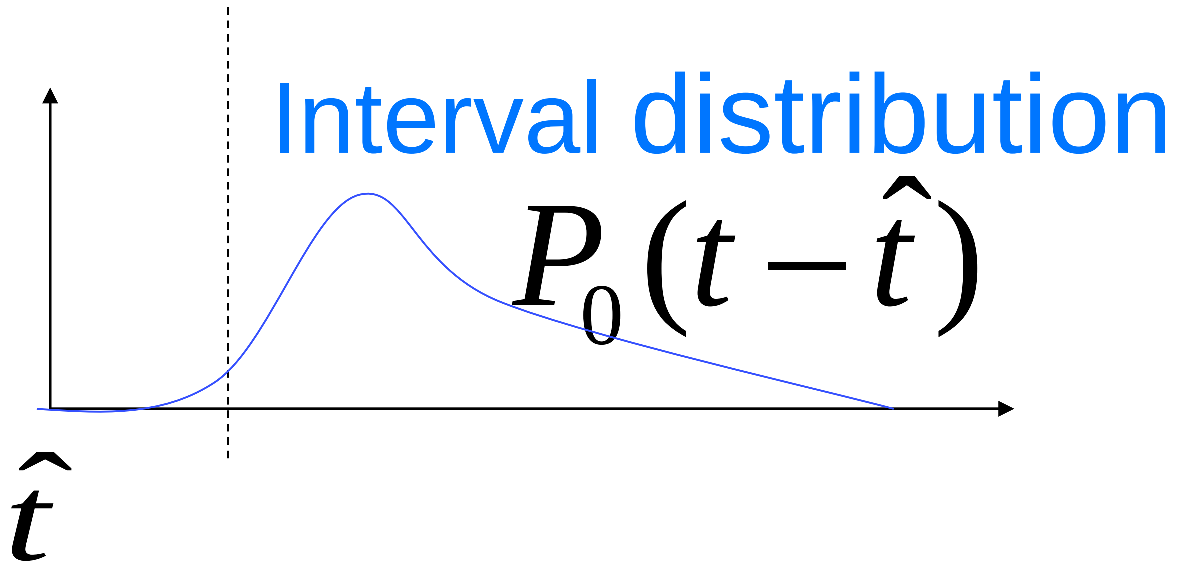


escape rate

$$\rho(t|\hat{t}) = f(u(t|\hat{t})) = \rho_\vartheta \exp(u(t|\hat{t}) - \vartheta)$$



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

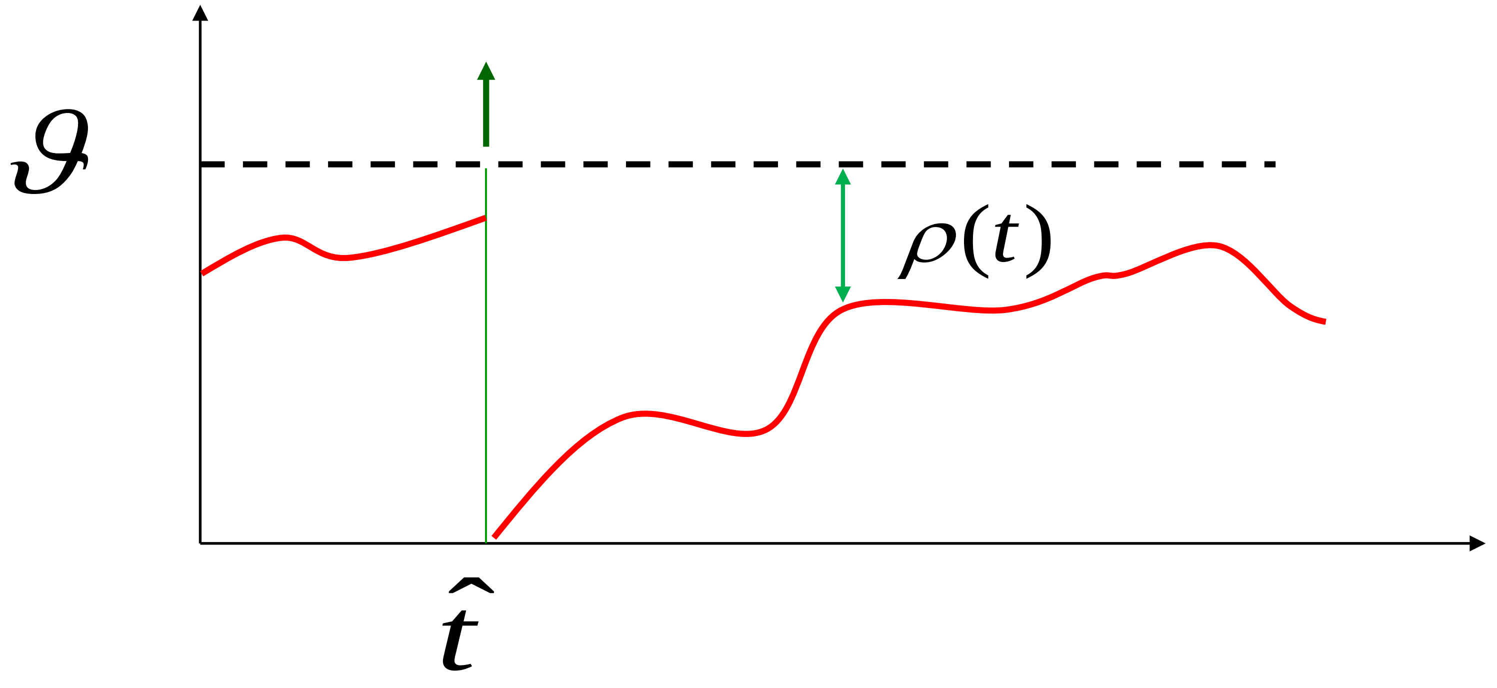


$$P(t|\hat{t}) = \rho(t|\hat{t}) \exp(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})dt')$$

$$= -\frac{d}{dt} S(t|\hat{t})$$

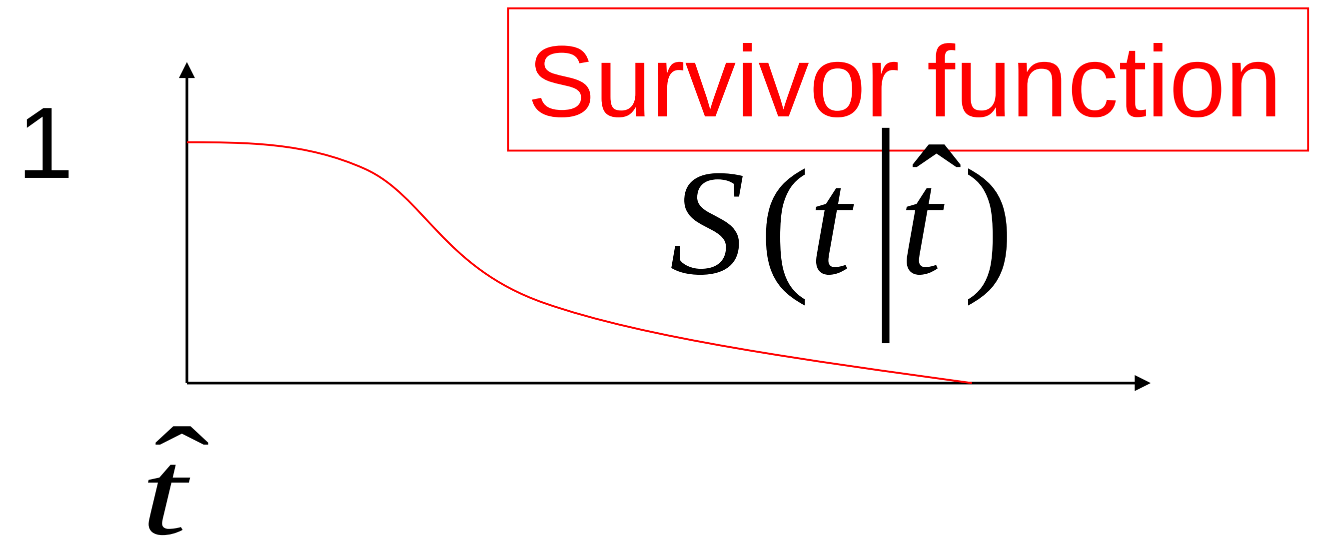
11.5. Time-dependent Renewal theory

Example: I&F with reset, **time-dependent input**,

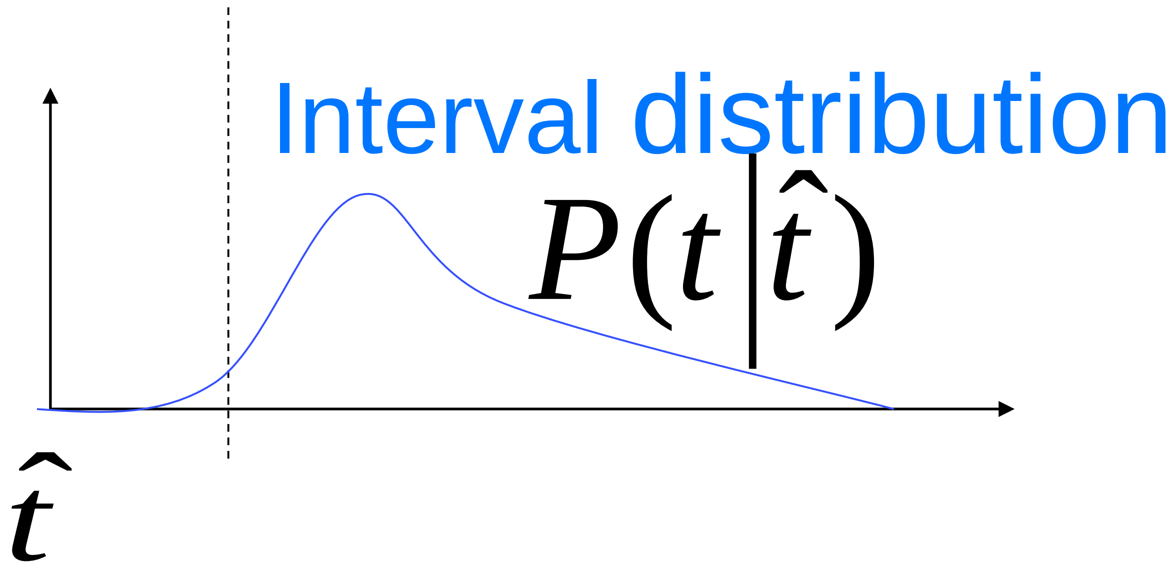


escape rate

$$\rho(t|\hat{t}) = f(u(t|\hat{t})) = \rho_{\vartheta} \exp(u(t|\hat{t}) - \vartheta)$$



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

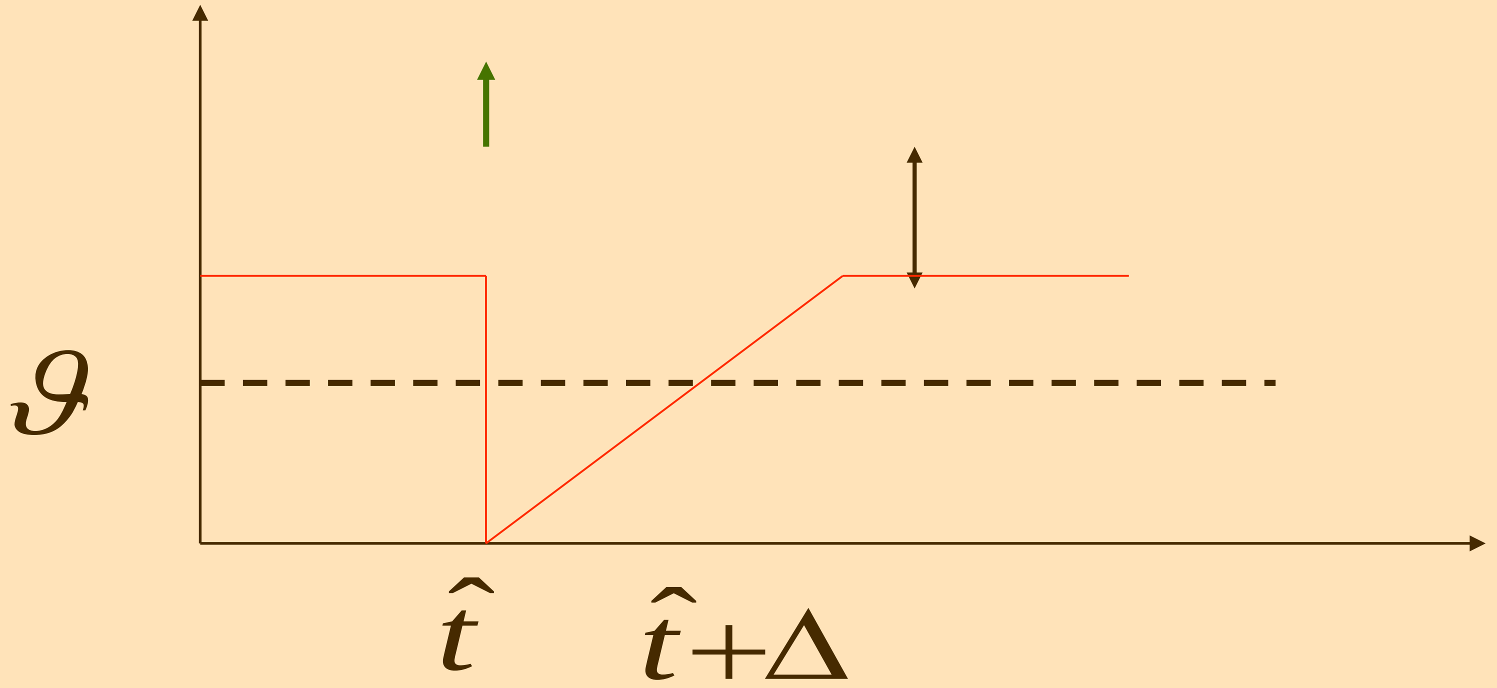


$$P(t|\hat{t}) = \rho(t|\hat{t}) \exp(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})dt')$$

$$= -\tfrac{d}{dt} S(t|\hat{t})$$

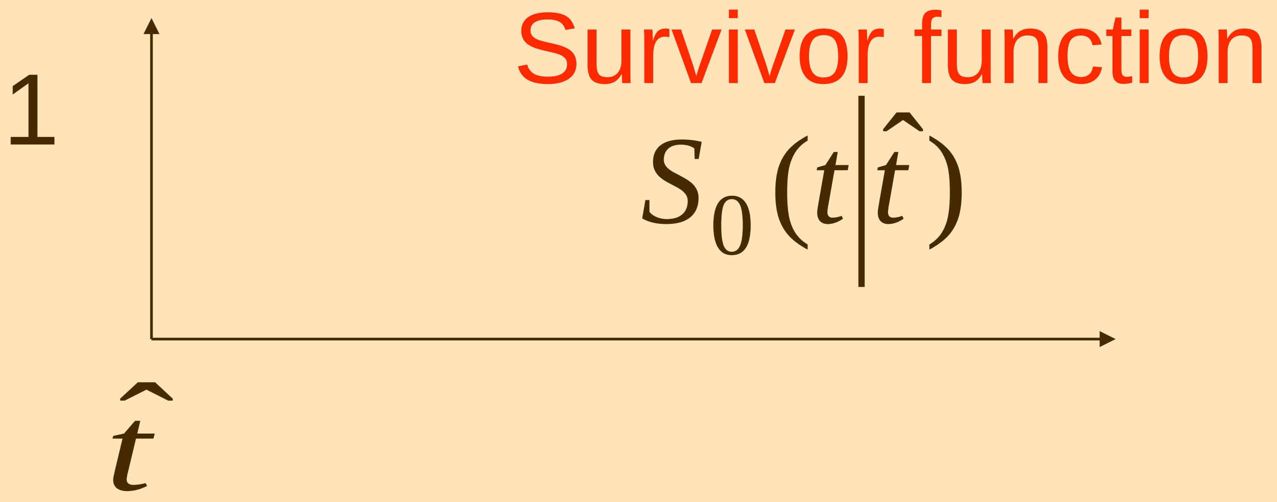
Homework assignement: Exercise 4

neuron with relative refractoriness, constant input

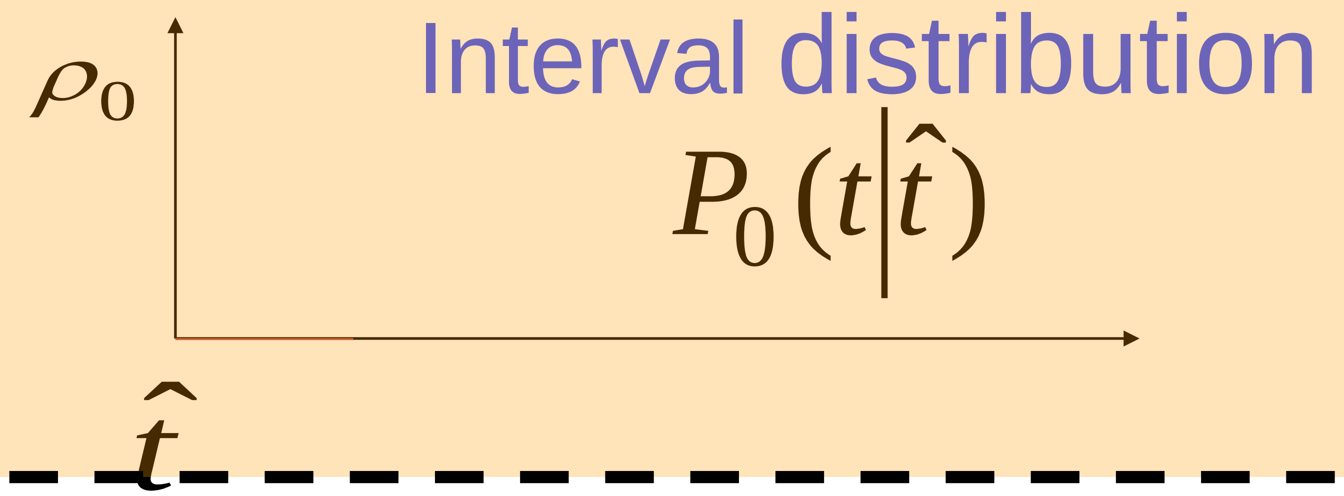


escape rate

$$\rho(t) = \rho_0 \frac{u}{\vartheta} \quad for \;\; u > \vartheta$$

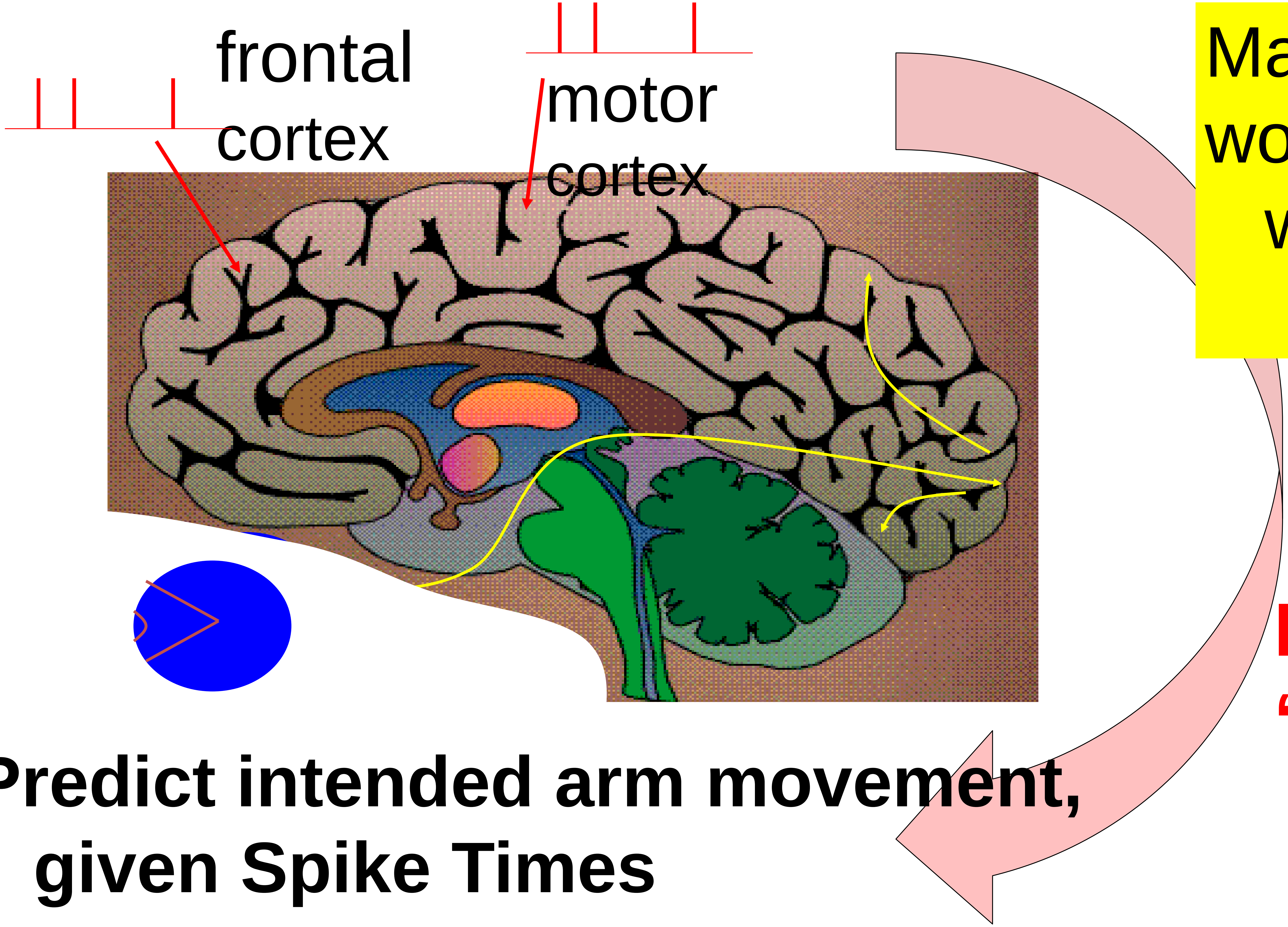


$$S_0(t|\hat{t}) = \{$$



$$P_0(t|\hat{t}) = \{$$

Application: Neuroprosthetics



Many groups world wide work on this problem!

Model of 'Decoding'

Predict intended arm movement, given Spike Times

11.5 Conclusion: Renewal models

Even though the interspike-interval-distribution is most often used for STATIONARY data, (or constant input), we can also define an interspike-interval distribution for time-dependent input: Given an observed spike at time t^, and given that we know the time-dependent input up to time t, we ask: what is the probability density that the next spike occurs at time t? The answer is given by the ISI distribution P(t|t^).

In the same way we can ask: Given an observed spike at time t^, and given that we know the time-dependent input up to time t, what is the probability that the neuron 'survives' without firing up to time t? The answer is given by the survivor function S(t|t^).
Similarly, given an observed spike at time t^, and given that we know the time-dependent input up to time t, what is the momentary rate of firing at time t? The answer is given by the stochastic intensity ρ(t|t^), also called the 'hazard'. The three functions are closely related to each other.

For constant input, all three functions only depend on the time difference t-t^. If the stochastic intensity (e.g., of a neuron model) only depends on the time difference t-t^ it is called a (stationary) renewal model. If it depends on t-t^ and the input (but not on earlier spikes), it is a generalized (or time-dependent) renewal model. The LIF with escape noise and constant input is a renewal model, with time-dependent input it is a generalized renewal model.

THE END

Escape noise = stochastic intensity

-Renewal theory
- hazard function
- survivor function
- interval distribution

-time-dependent renewal theory
-discrete-time firing probability
-Link to experiments

→ basis for modern methods of neuron model fitting