

Week 8 – part 1 :Variation of membrane potential



Biological Modeling of Neural Networks

Week 8 – Noisy input models: Barrage of spike arrivals

Wulfram Gerstner

EPFL, Lausanne, Switzerland

8.1 Variation of membrane potential

- white noise approximation

8.2 Autocorrelation of Poisson

8.3 Noisy integrate-and-fire

- superthreshold and subthreshold

8.4 Escape noise

- stochastic intensity

8.5 Renewal models

8.6 Comparison of noise models

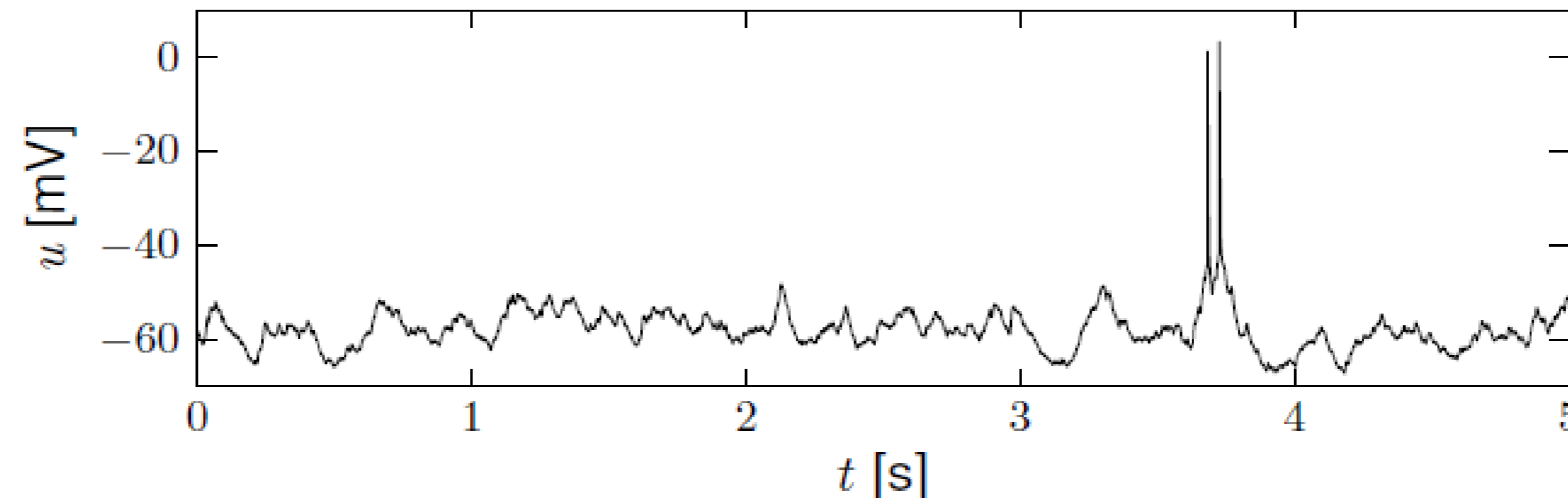
Neuronal Dynamics – 8.1 Review: Variability in vivo

Spontaneous activity *in vivo*

Variability

- of membrane potential?
- of spike timing?

awake mouse, cortex, freely whisking,



Crochet et al., 2011

Neuronal Dynamics – 8.1 Review. Variability

In vivo data

→ looks 'noisy'

In vitro data

→ fluctuations

Fluctuations

-of membrane potential

-of spike times

fluctuations=noise?

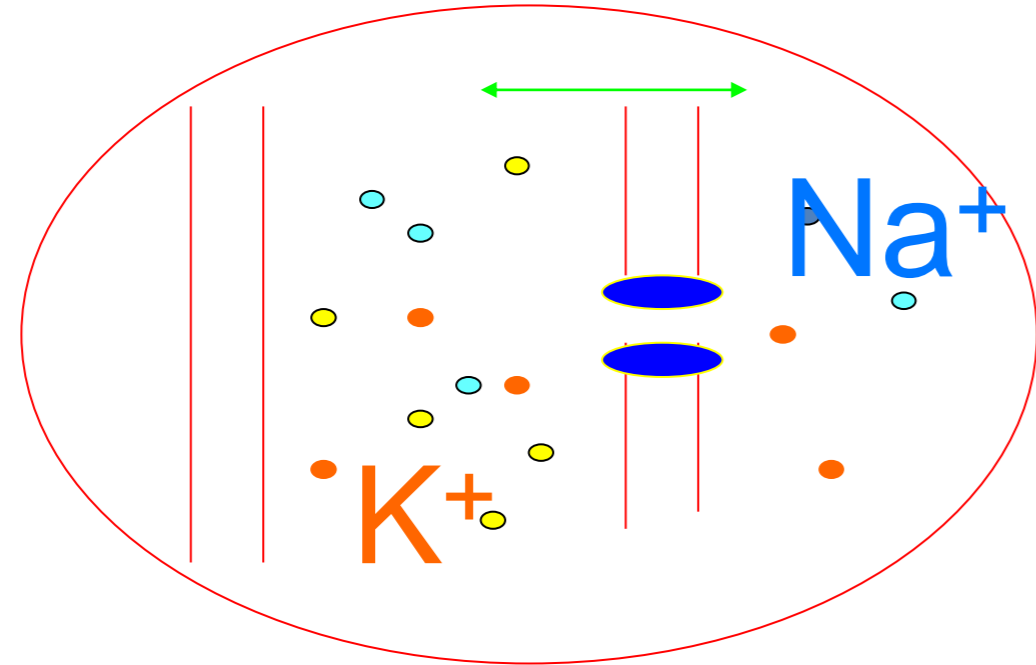
relevance for coding?

source of fluctuations?

model of fluctuations?

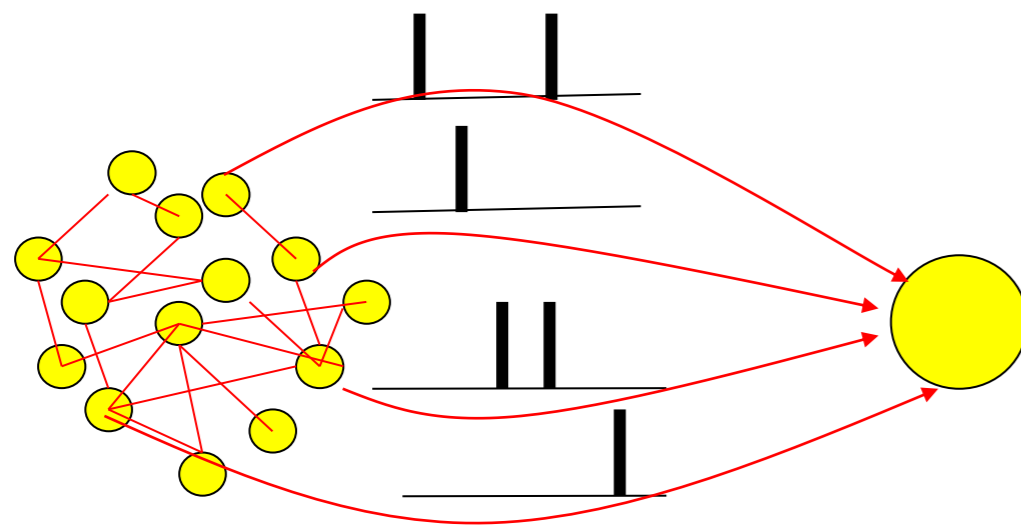
Neuronal Dynamics – 8.1. Review Sources of Variability

- 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 – 8.1. Review: Sources of Variability

In vivo data

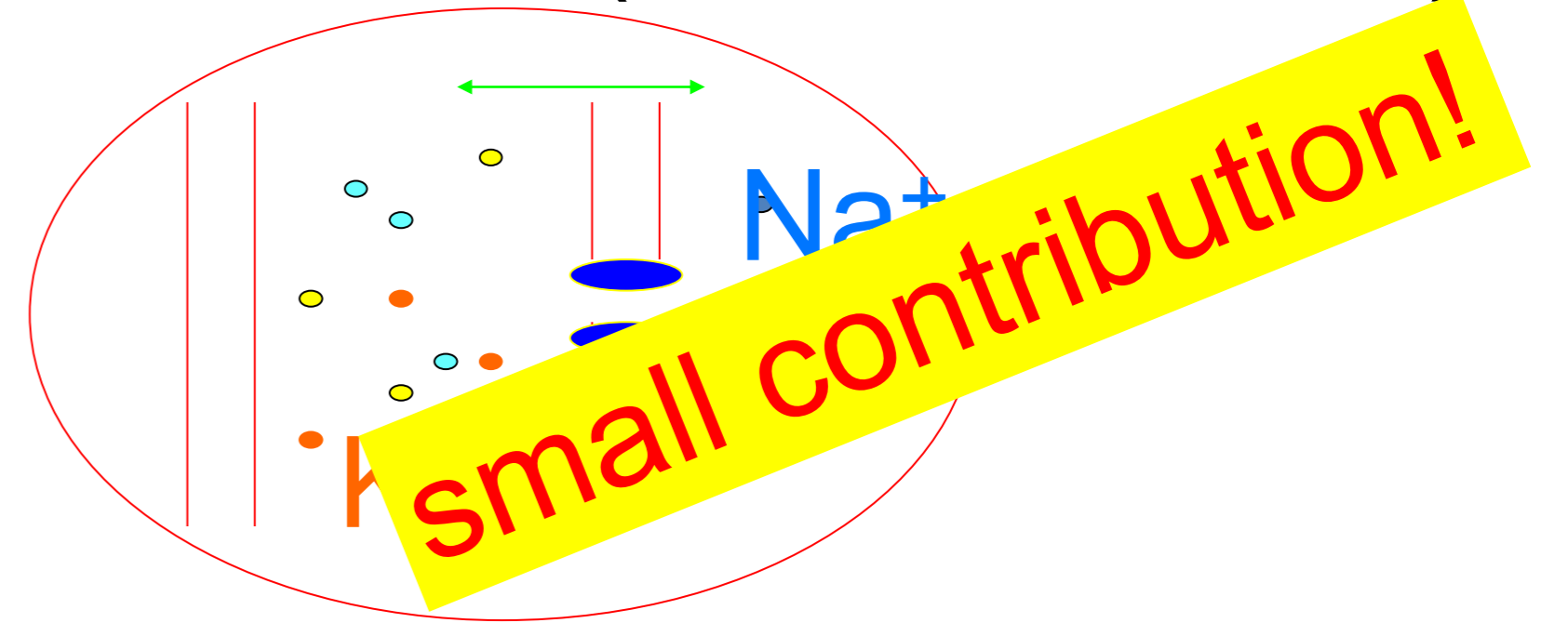
→ looks 'noisy'

In vitro data

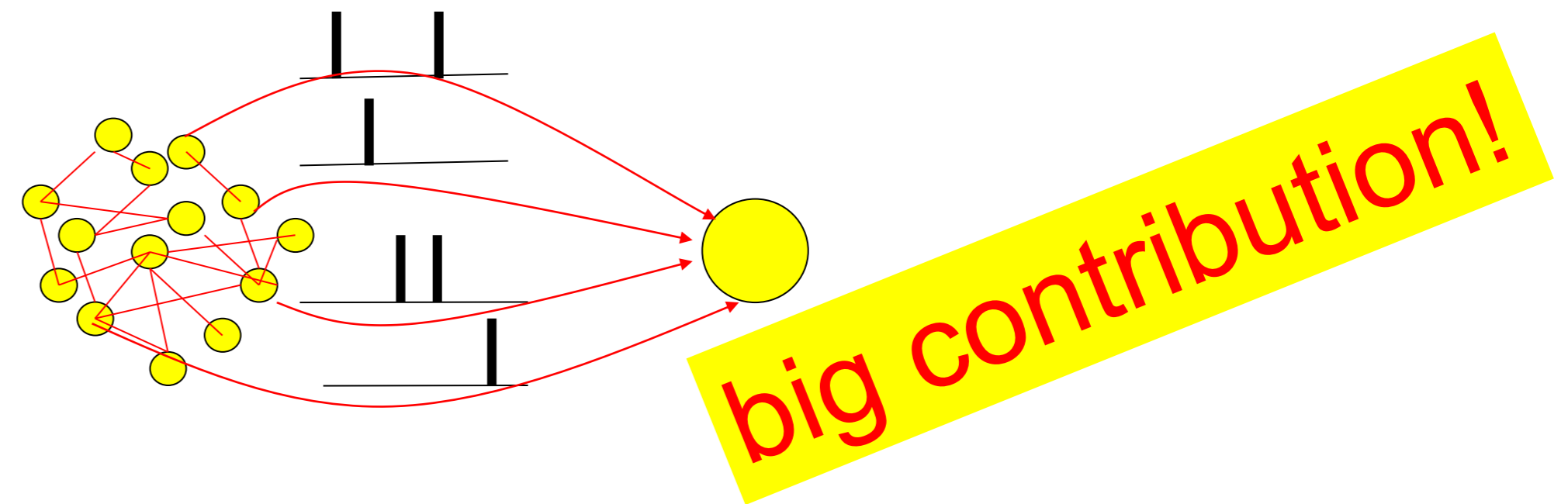
→ small fluctuations

→ nearly deterministic

- Intrinsic noise (ion channels)

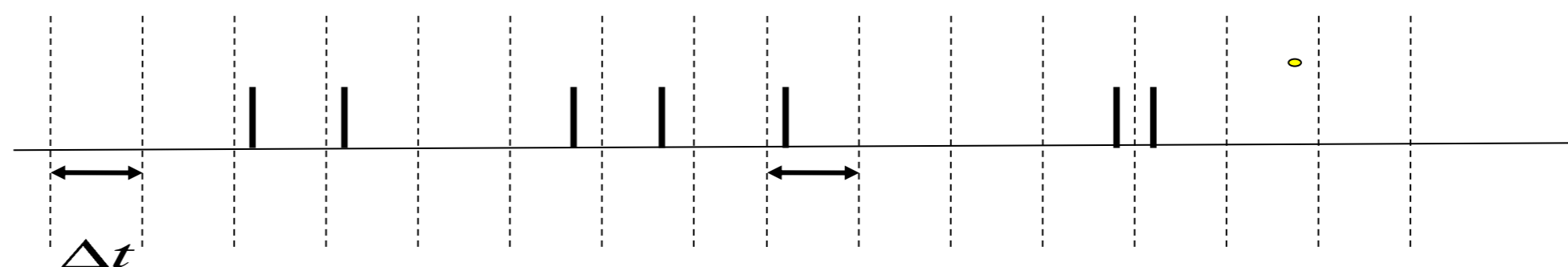


-Network noise



Neuronal Dynamics – 8.1 Review: 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

use for exercises

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

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

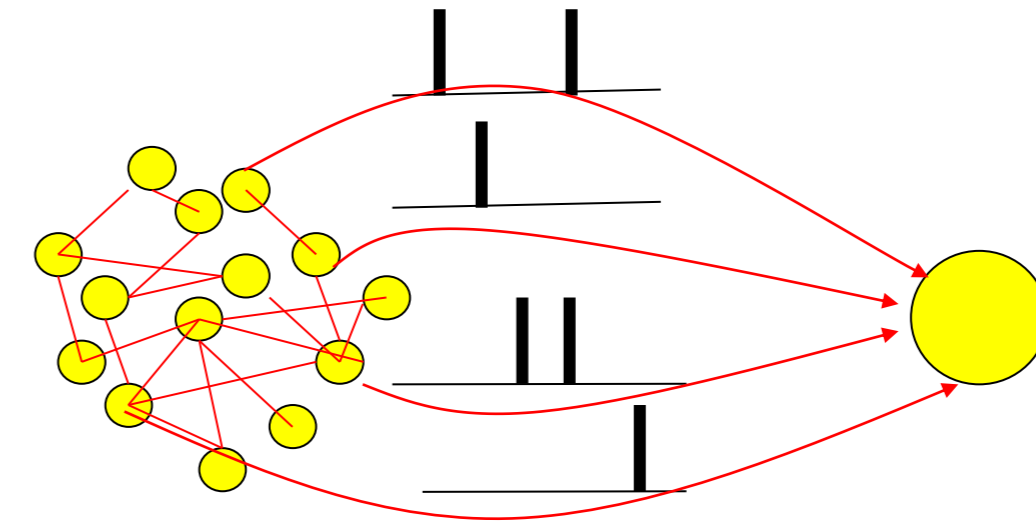
$$I_0 = \frac{1}{R} \sum_k w_k \int dt' \alpha(t - t') \nu_k$$

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

rate of inhomogeneous Poisson process

Neuronal Dynamics – 8.1. Fluctuation of potential

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

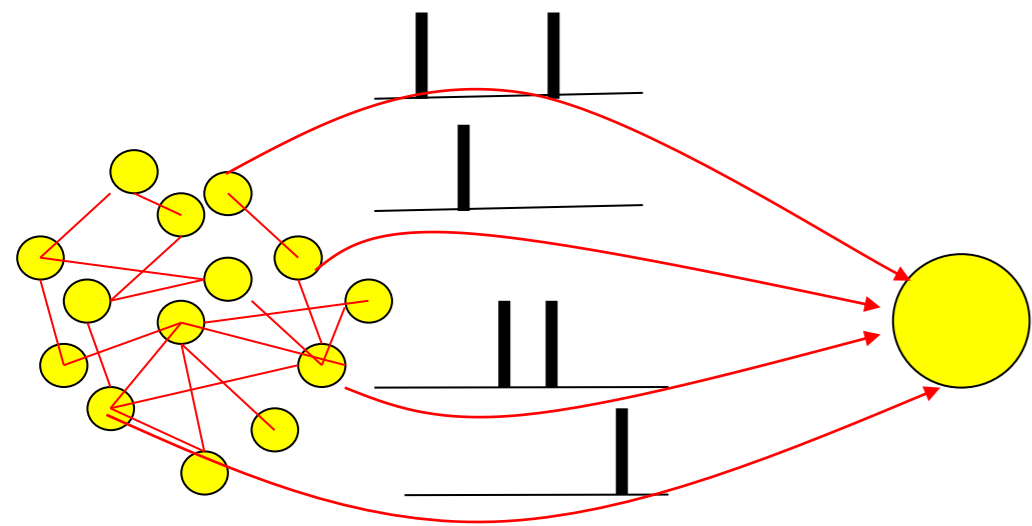


Passive membrane

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

Passive membrane
=Leaky integrate-and-fire
without threshold

Neuronal Dynamics – 8.1. Fluctuation of current/potential



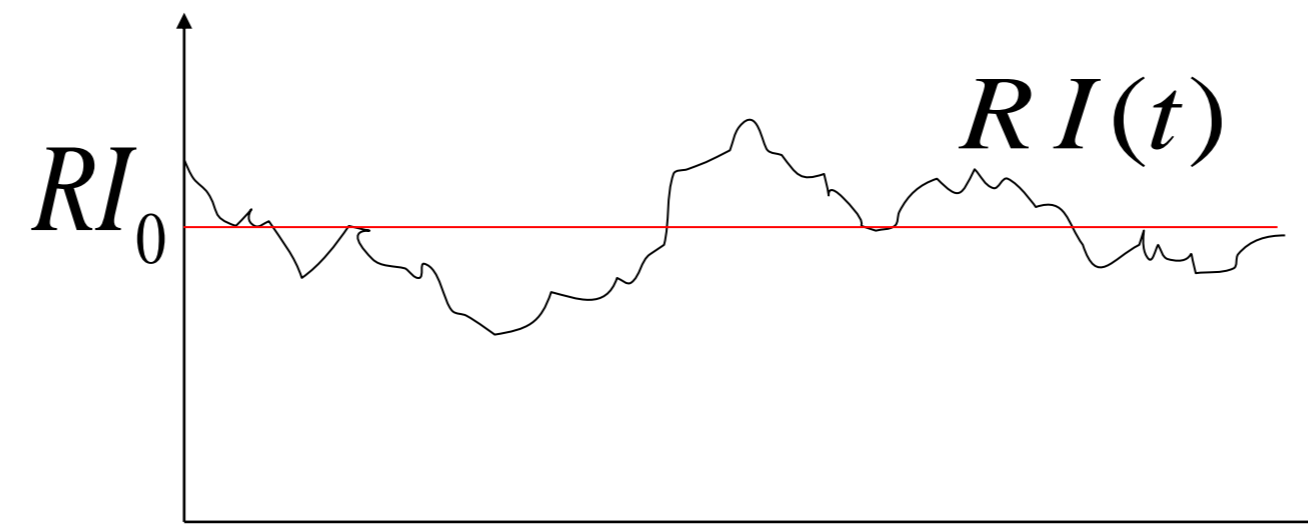
Synaptic current pulses of shape α

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

EPSC

Passive membrane

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



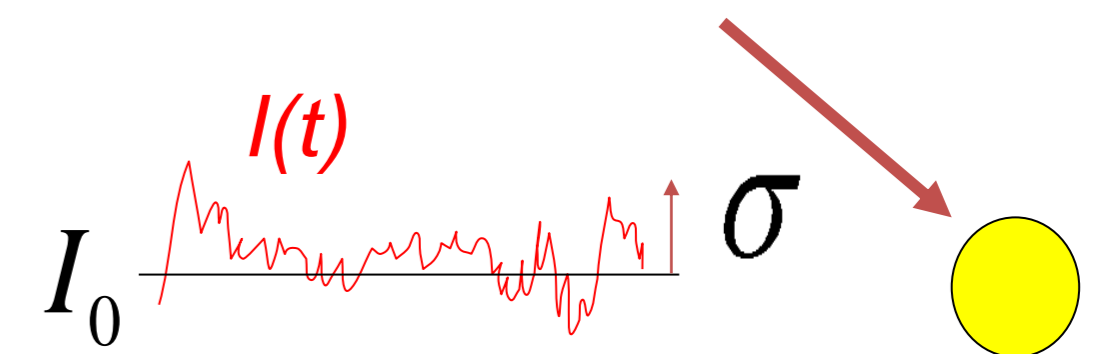
Blackboard,
Math detour:
White noise

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

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

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

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



Fluctuating input current

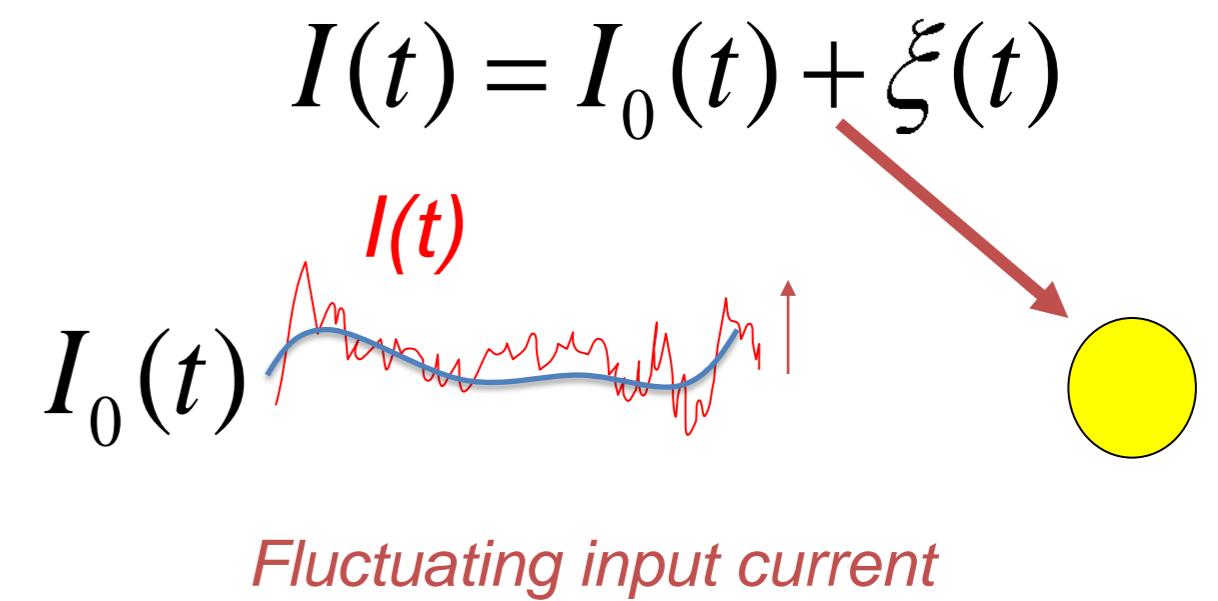
Neuronal Dynamics – 8.1 Calculating autocorrelations

Autocorrelation

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

Blackboard,
Math detour

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



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

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

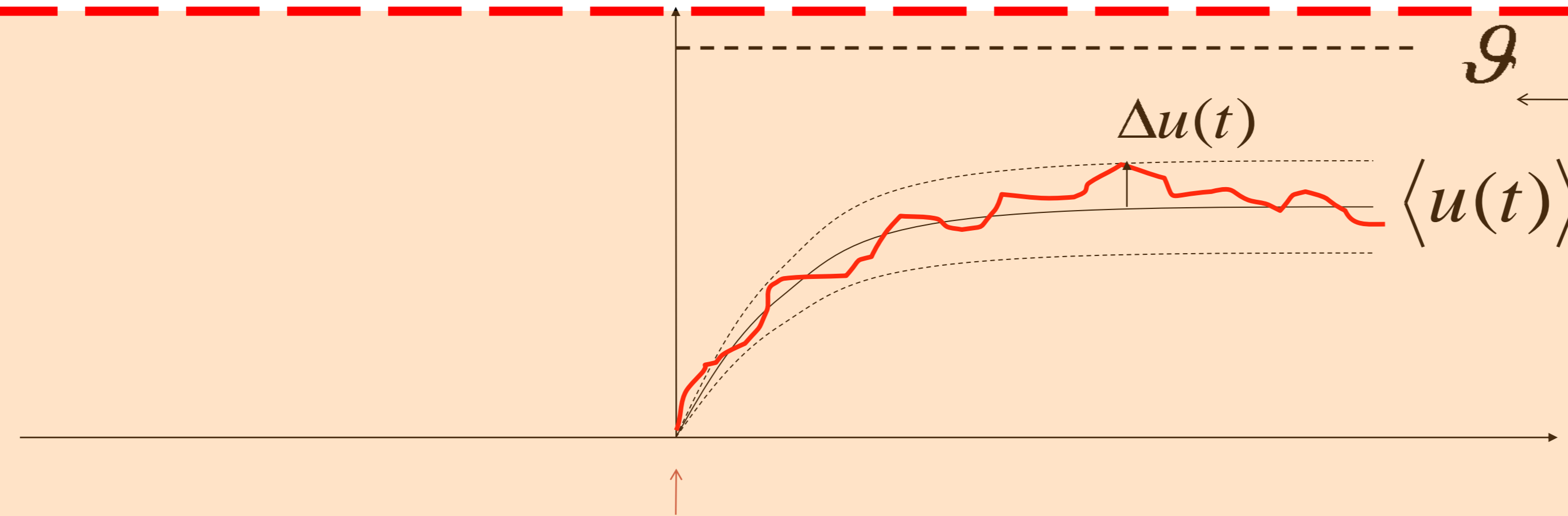
Mean:

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

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

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

White noise: Exercise 1.1-1.2 now



Assumption:
far away from theshold

Input starts here

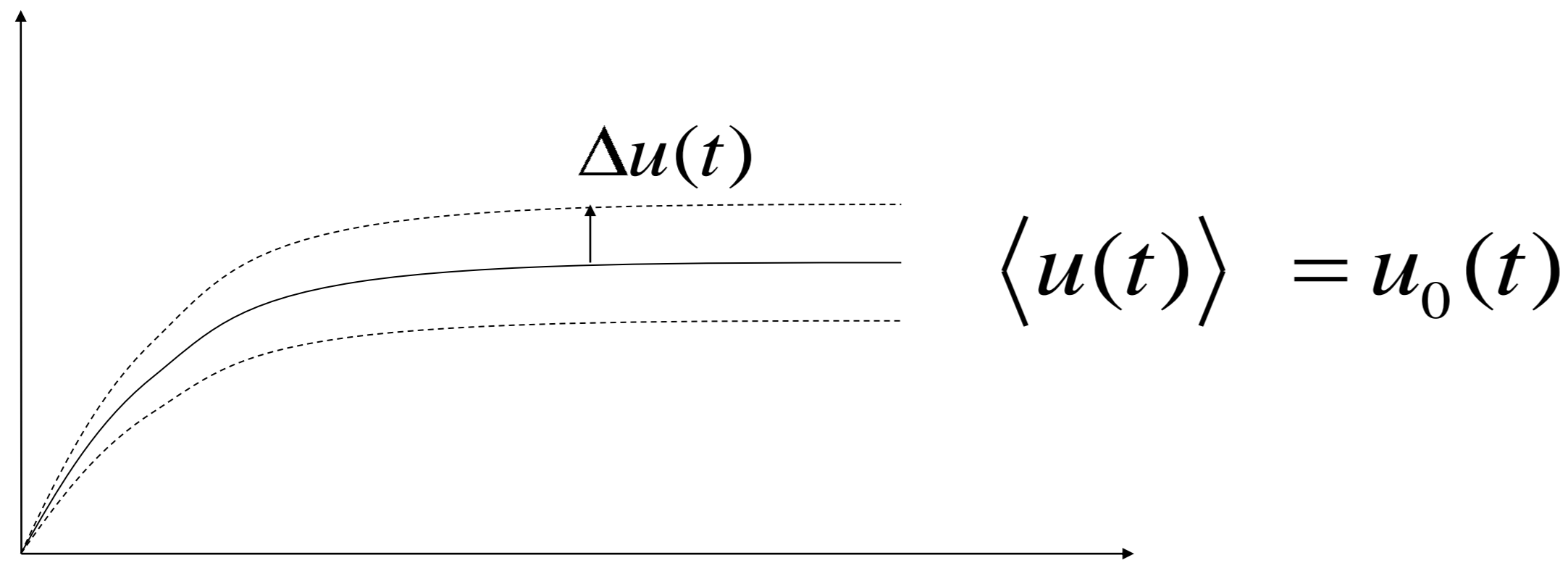
Expected voltage at time t $\langle u(t) \rangle = ?$

Variance of voltage at time t

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

Next lecture:
9:56

Diffusive noise (stochastic spike arrival)



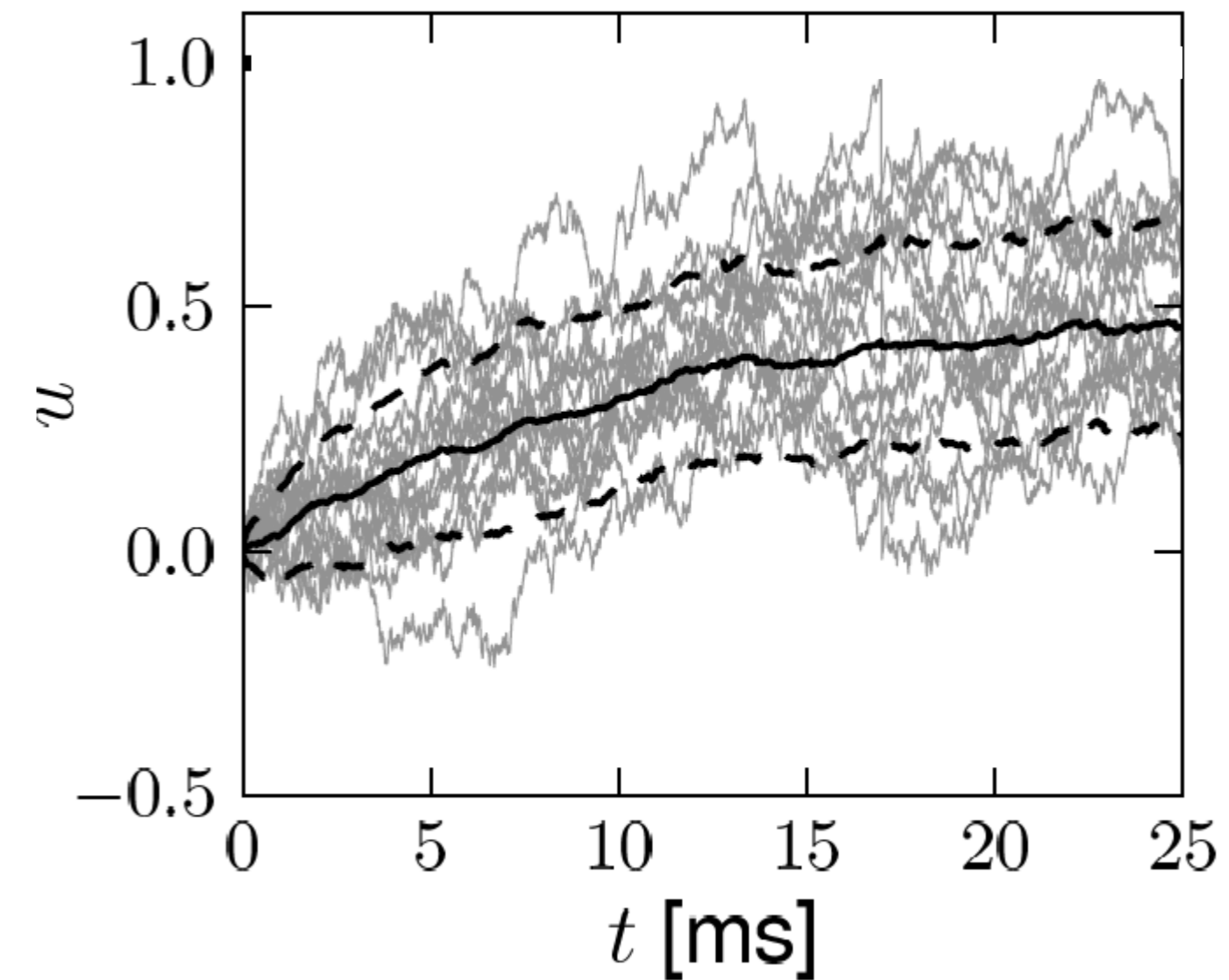
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t)u(t) \rangle - \langle u(t) \rangle^2 =$$

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

Math argument

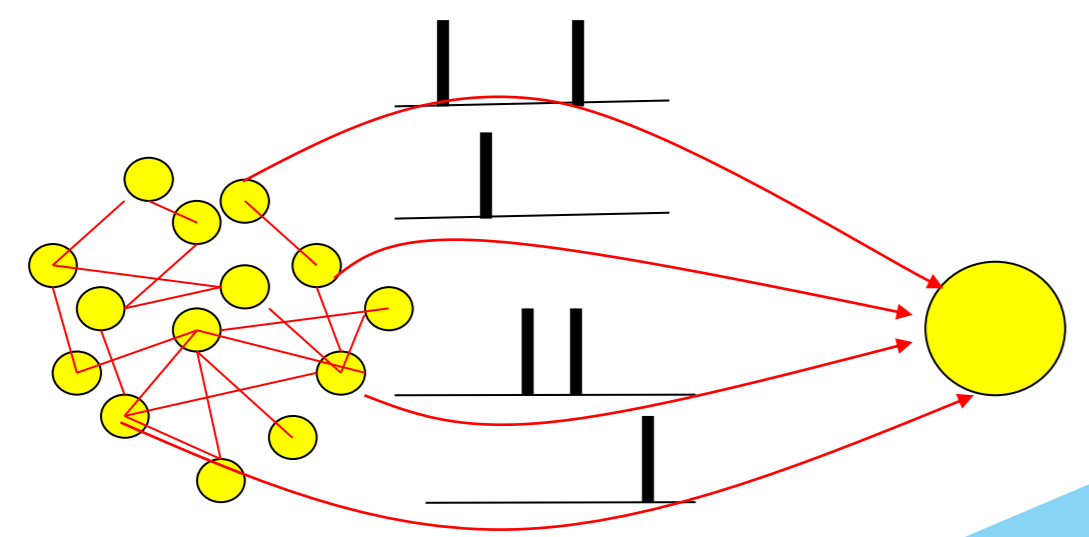
$$p(u, t) = \frac{1}{\sqrt{2\pi} \langle \Delta u^2(t) \rangle} \exp \left\{ -\frac{[u(t|\hat{t}) - u_0(t)]^2}{2 \langle \Delta u^2(t) \rangle} \right\}$$

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

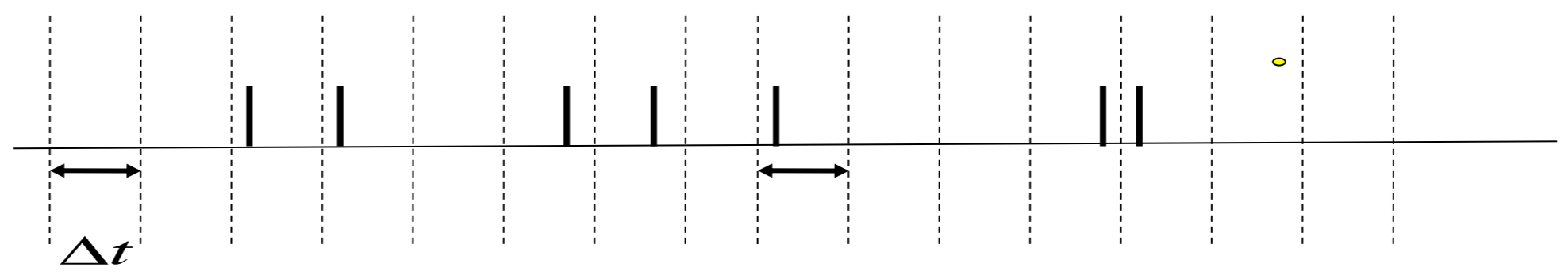


$$\langle [\Delta u(t)]^2 \rangle = \sigma_u^2 [1 - \exp(-2t / \tau)]$$

Neuronal Dynamics – 8.1 Calculating autocorrelations



**Blackboard,
Math detour**



Autocorrelation

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

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

Mean:

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

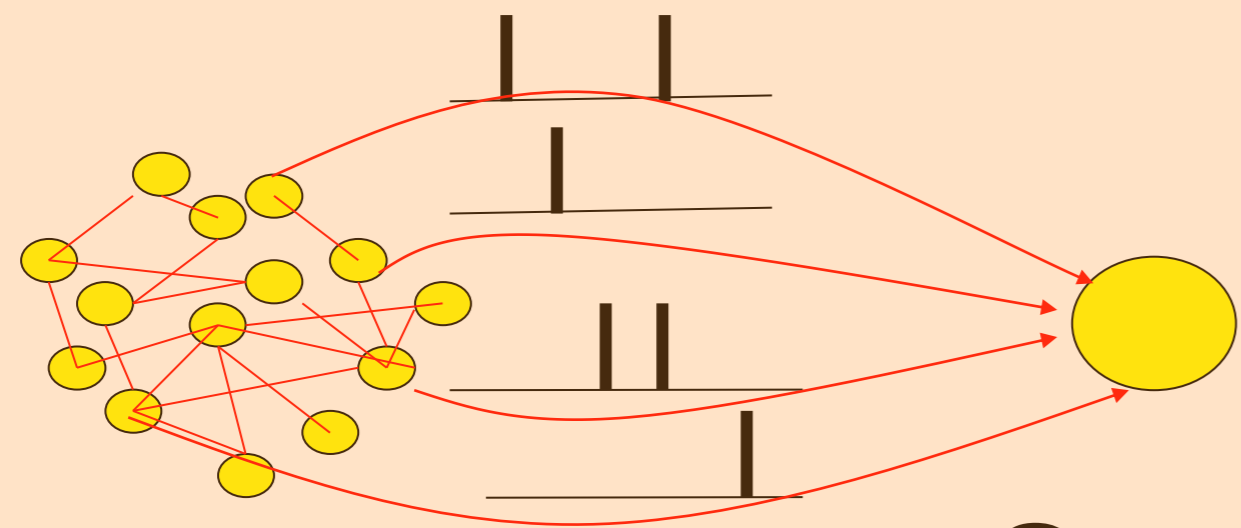
$$\langle x(t) \rangle = \int ds f(s) \nu(t-s)$$

**rate of inhomogeneous
Poisson process**

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

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

Exercise 2.1-2.3 now: Diffusive noise (stochastic spike arrival)



Stochastic spike arrival:

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

Synaptic current pulses

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

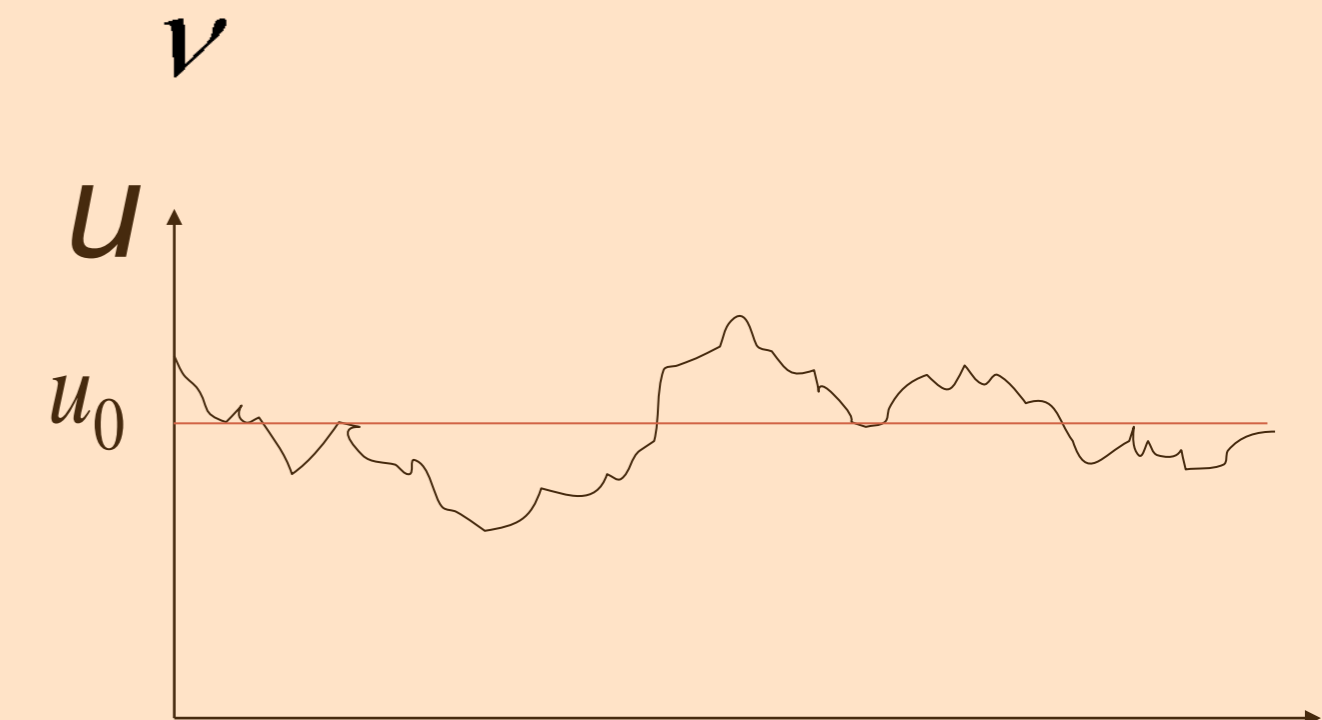
$$S(t) = q_e \sum_f \delta(t - t^f)$$

**Next lecture:
9h58**

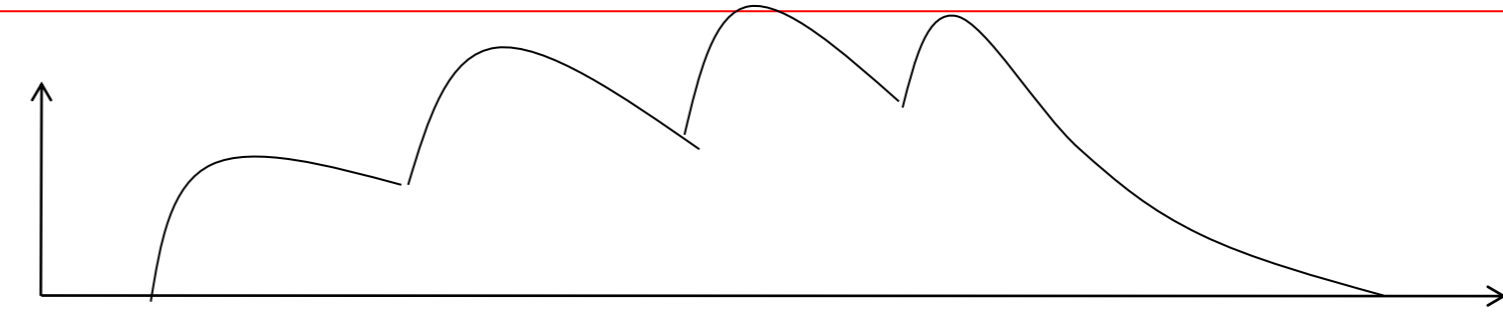
1. Assume that for $t > 0$ spikes arrive stochastically with rate ν
 - Calculate mean voltage

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

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



Poisson spike arrival: Mean and autocorrelation of filtered signal



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

$$F(s)$$

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

Filter

Assumption:
stochastic spiking
rate $\nu(t)$

mean

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

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

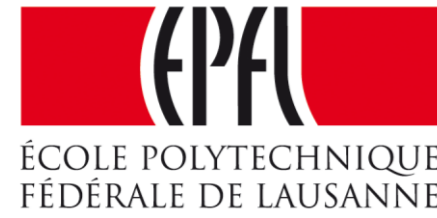
Autocorrelation of output

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

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

Autocorrelation of input

Week 8 – part 2 : Autocorrelation of Poisson Process



Biological Modeling of Neural Networks

Week 8 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

8.1 Variation of membrane potential
- white noise approximation

8.2 Autocorrelation of Poisson

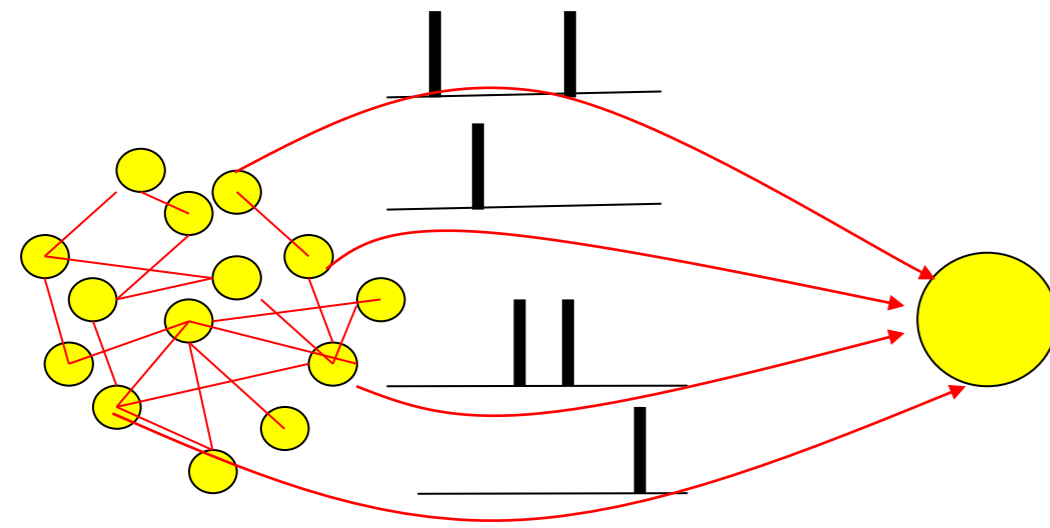
8.3 Noisy integrate-and-fire

- superthreshold and subthreshold

8.4 Escape noise

-renewal model

Justify autocorrelation of spike input: Poisson process in discrete time



Stochastic spike arrival:

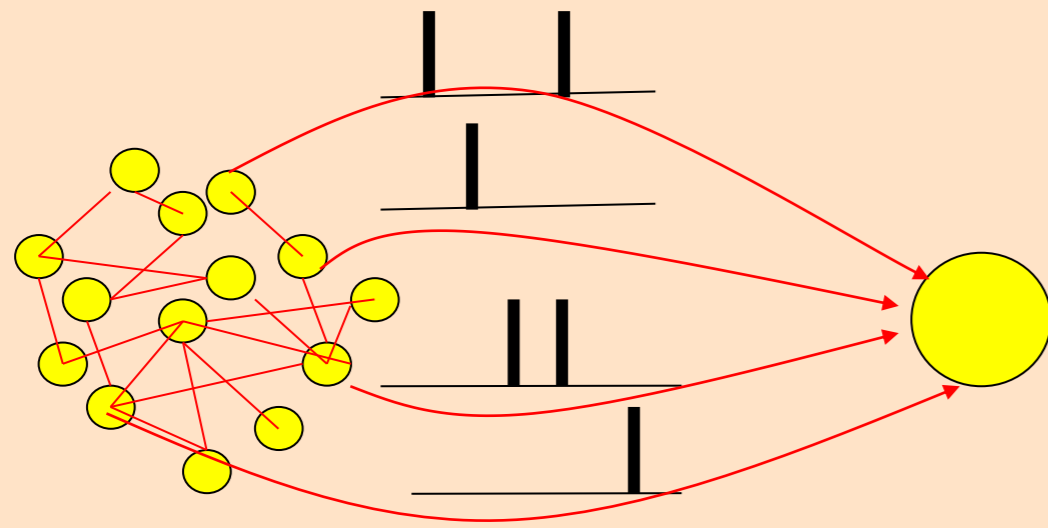
Blackboard

In each small time step Δt

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

Firing independent between one time step and the next

Exercise 2 now: Poisson process in discrete time



Stochastic spike arrival:
excitation, total rate

Next lecture:
10:46

In each small time step Δt
Prob. Of firing $p = \nu \Delta t$

Firing independent between one time step and the next

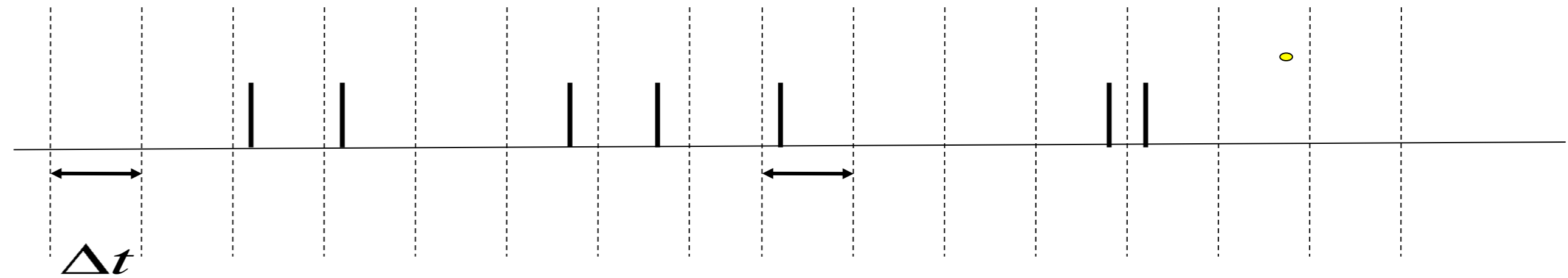
Show that autocorrelation $\langle S(t)S(t') \rangle = \nu \delta(t - t') + \nu^2$
for $\Delta t \rightarrow 0$

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

Neuronal Dynamics – 8.2. Autocorrelation of Poisson

math detour
now!

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



spike train

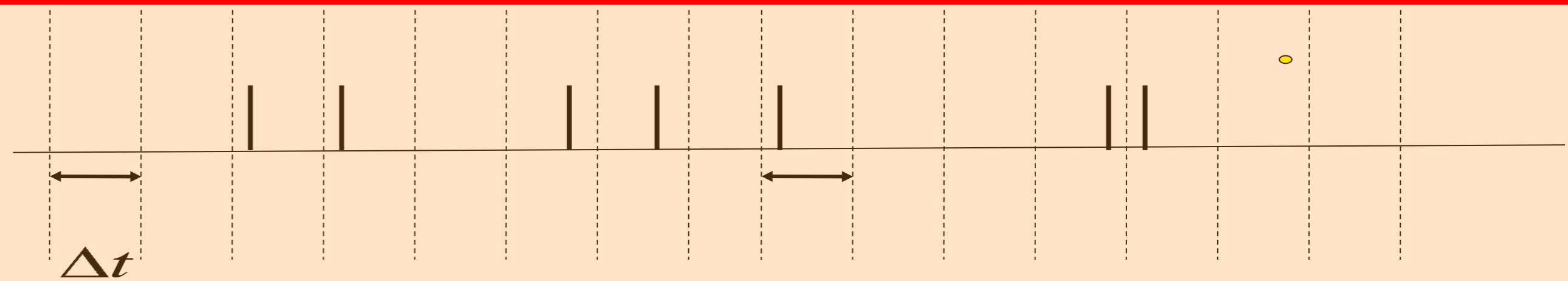
Probability of spike in time step:

$$P_F = \nu_0 \Delta t$$

Autocorrelation (continuous time)

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

Quiz – 8.1. Autocorrelation of Poisson



The Autocorrelation (continuous time)

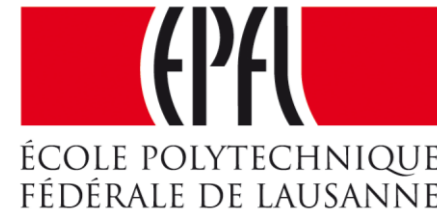
spike train

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

Has units

- probability (unit-free)
- probability squared (unit-free)
- rate (1 over time)
- (1 over time)-squared

Week 8 – part 3 : Noisy Integrate-and-fire



Biological Modeling of Neural Networks

Week 8 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

8.1 Variation of membrane potential

- white noise approximation

8.2 Autocorrelation of Poisson

8.3 Noisy integrate-and-fire

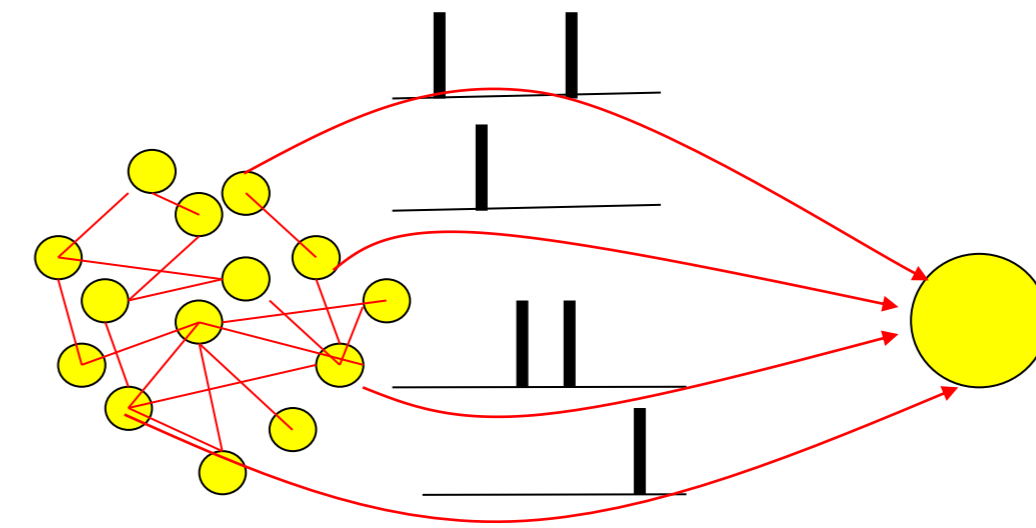
- superthreshold and subthreshold

8.4 Escape noise

-renewal model

Neuronal Dynamics – 8.3 Noisy Integrate-and-fire

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



Passive membrane

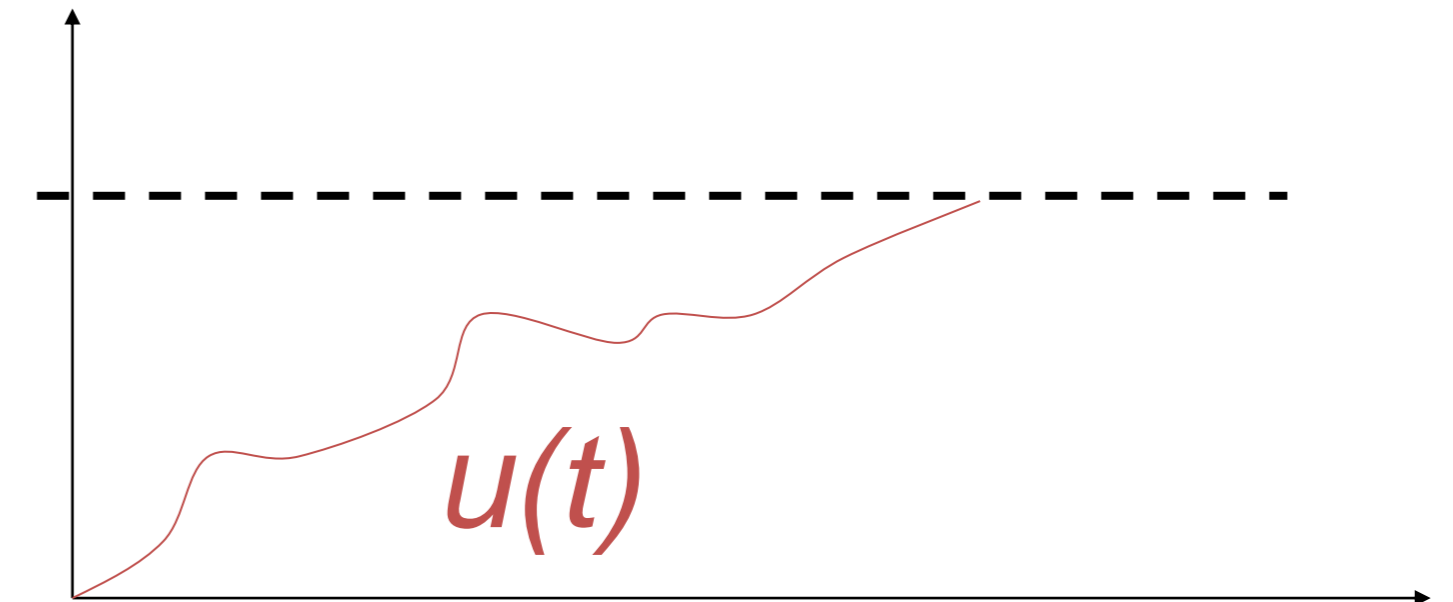
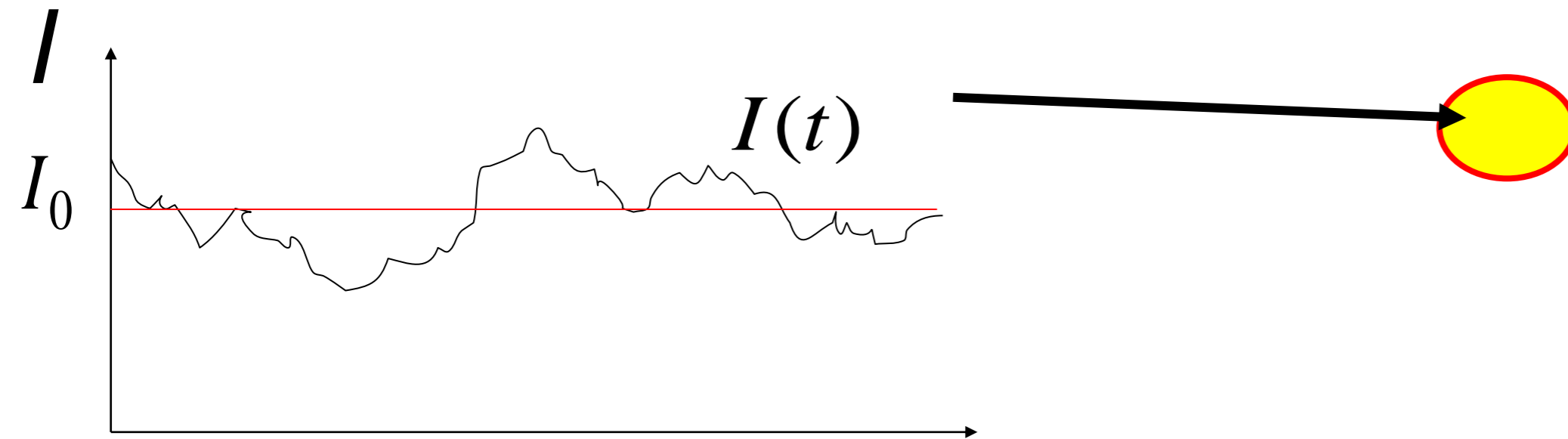
$$\tau \frac{d}{dt} u = -(u - u_{rest}) + R I^{syn}(t)$$

Passive membrane
=Leaky integrate-and-fire
without threshold

ADD THRESHOLD
→ Leaky Integrate-and-Fire

Neuronal Dynamics – 8.3 Noisy Integrate-and-fire

effective noise current



LIF

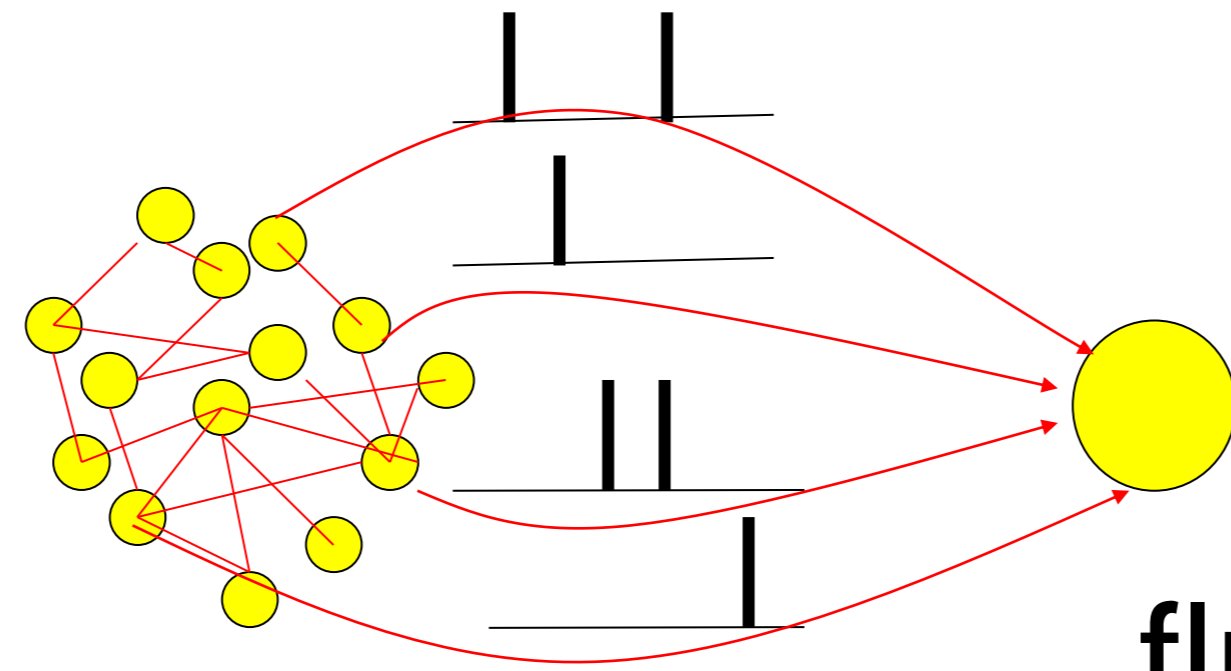
$$\tau \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

$$I(t) = I_0 + I_{noise}$$

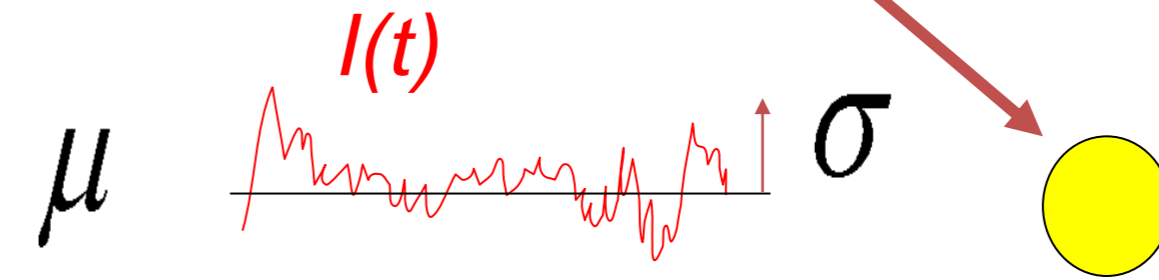
$$IF \ u(t) = \mathcal{G} \ THEN \ u(t + \Delta) = u_r$$

noisy input/
diffusive noise/
stochastic spike
arrival

Neuronal Dynamics – 8.3 Noisy Integrate-and-fire



fluctuating input current

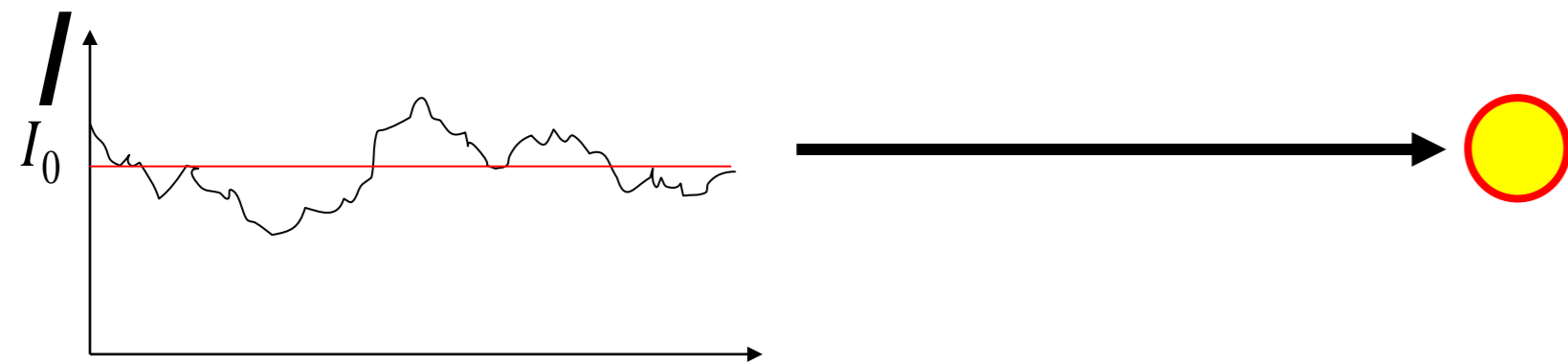


Random spike arrival

fluctuating potential

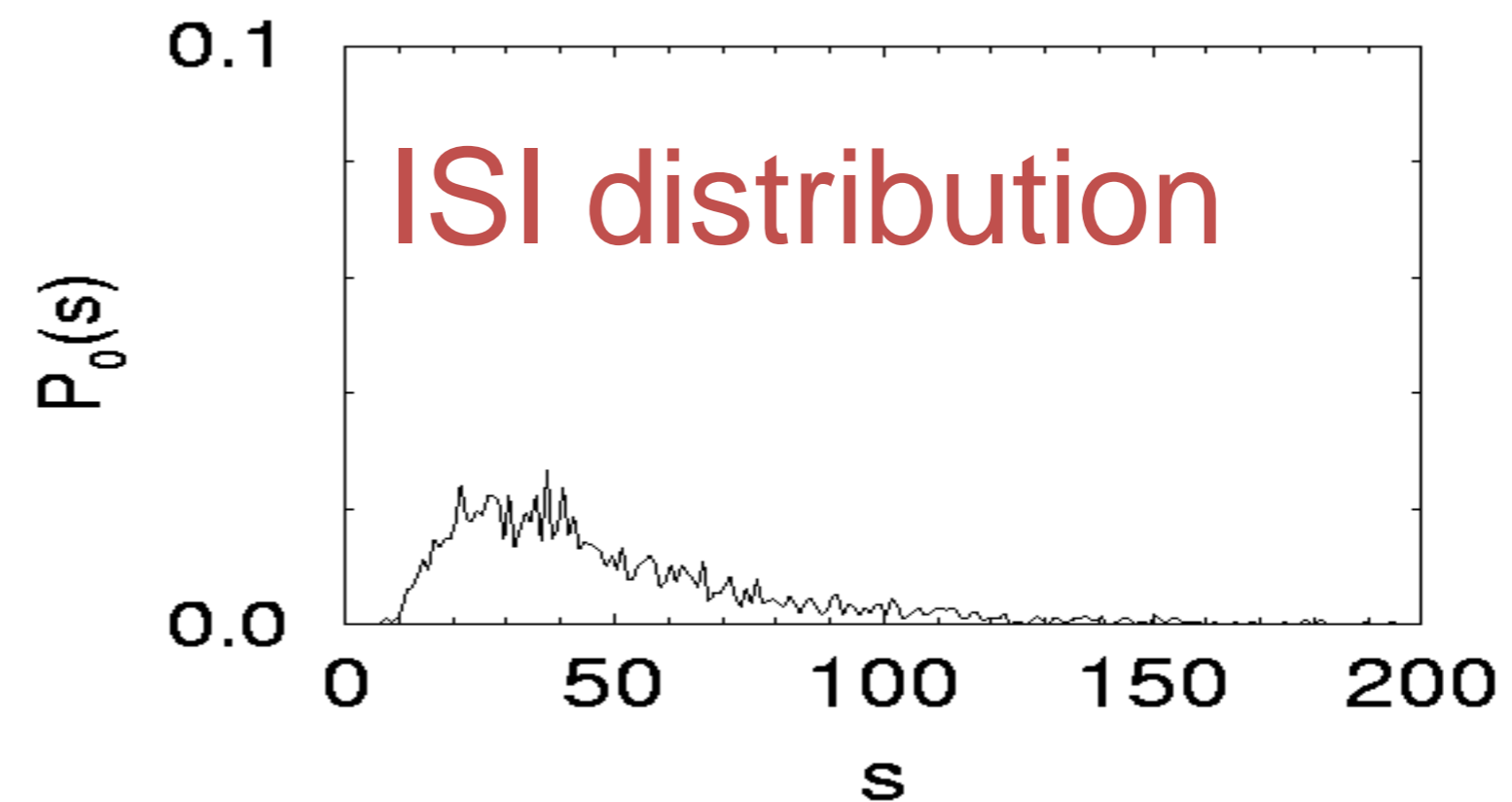
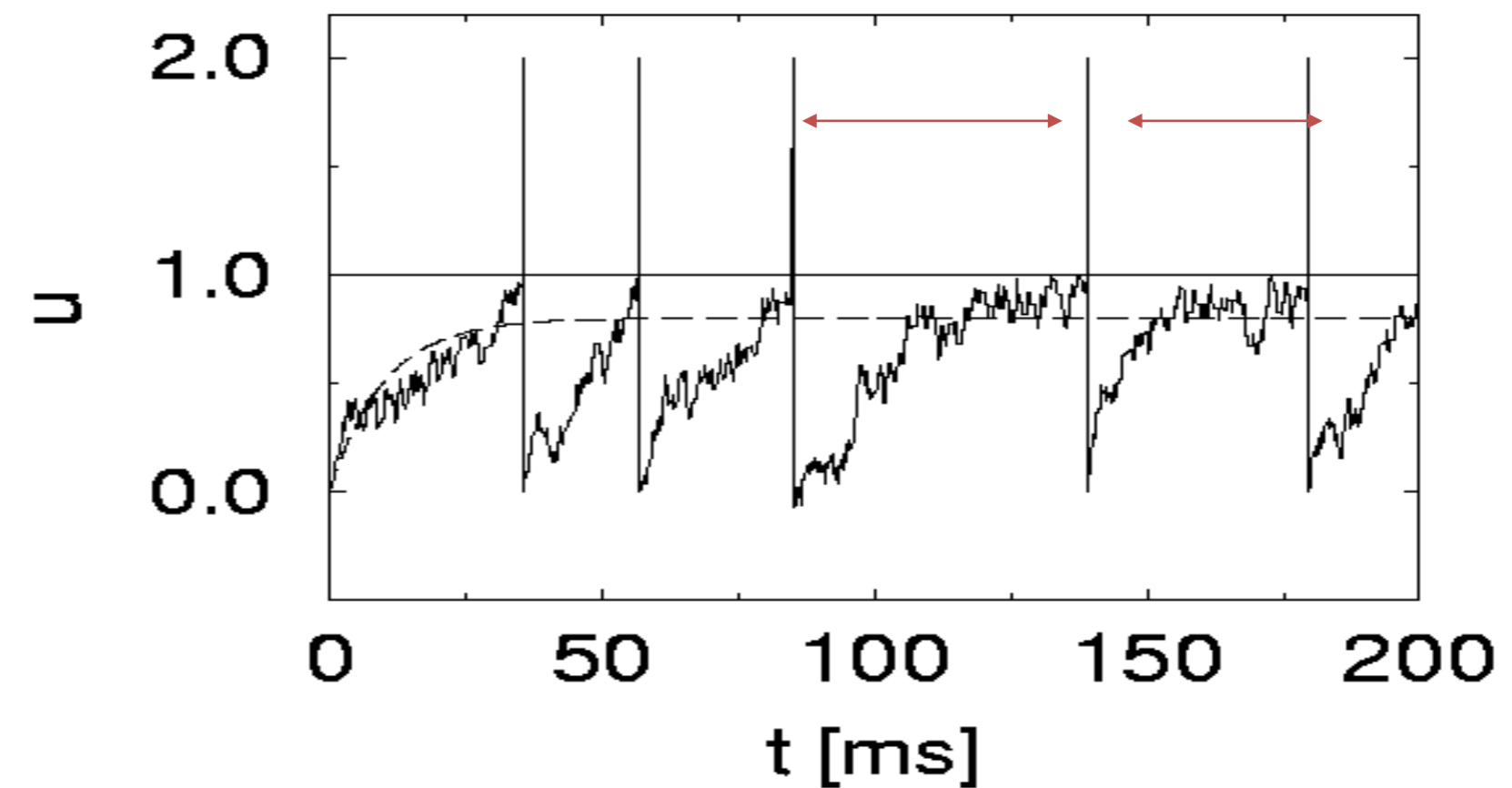
Neuronal Dynamics – 8.3 Noisy Integrate-and-fire

stochastic spike arrival in I&F – interspike intervals



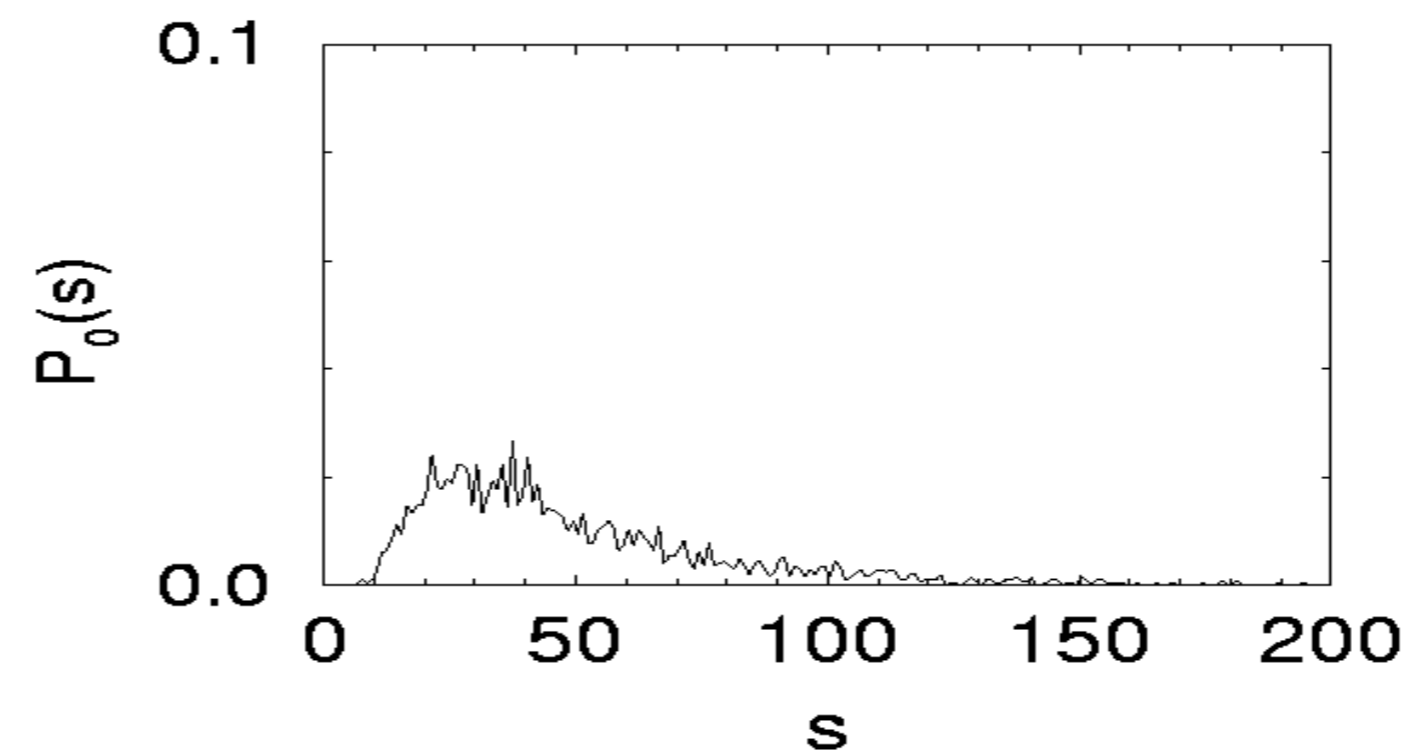
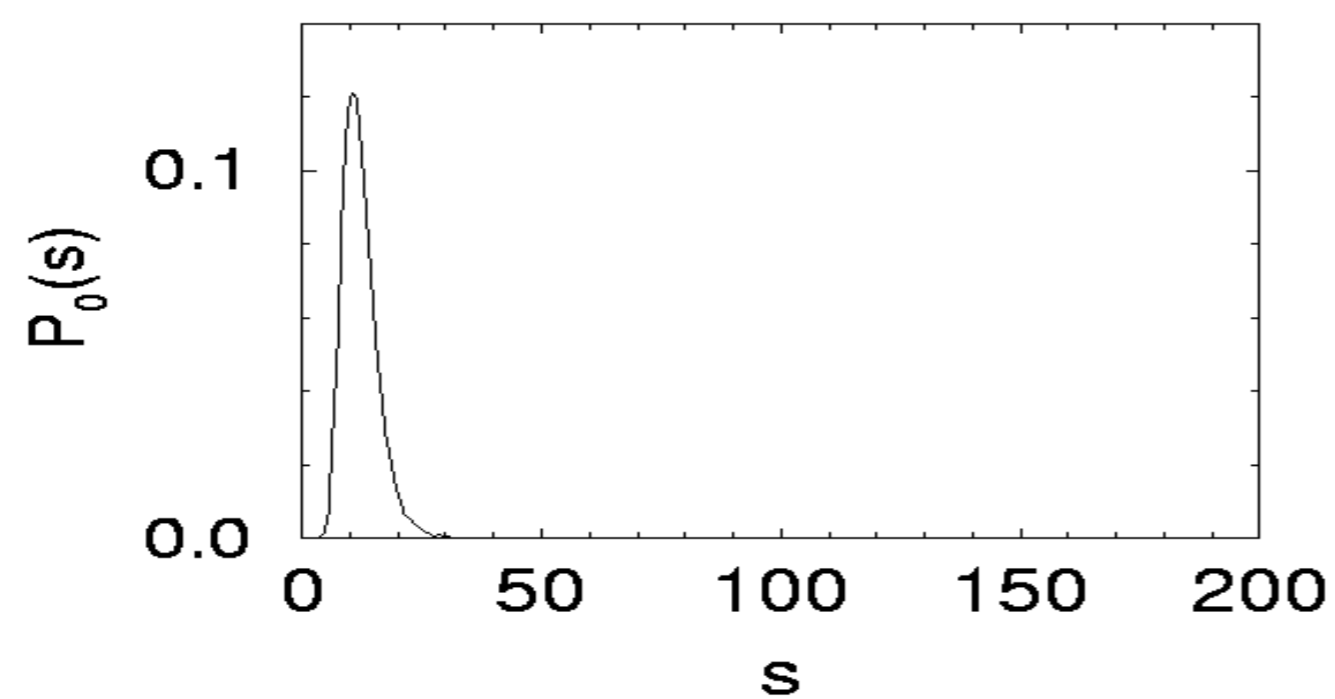
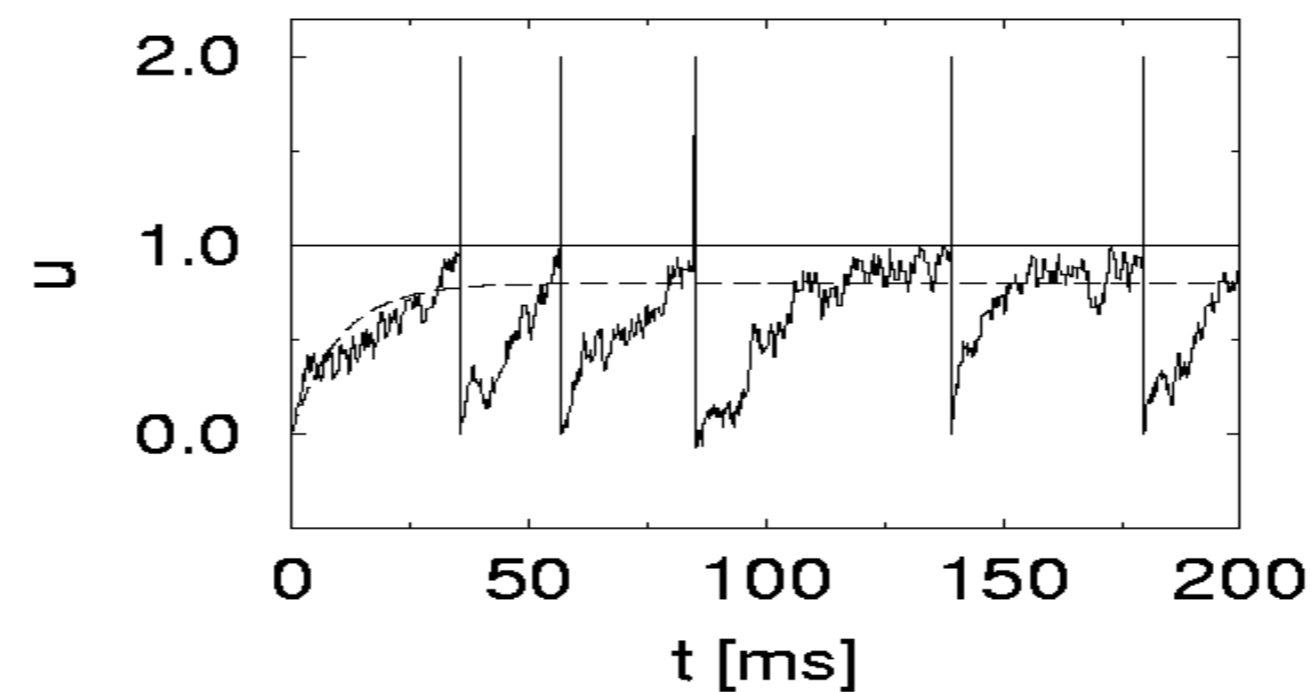
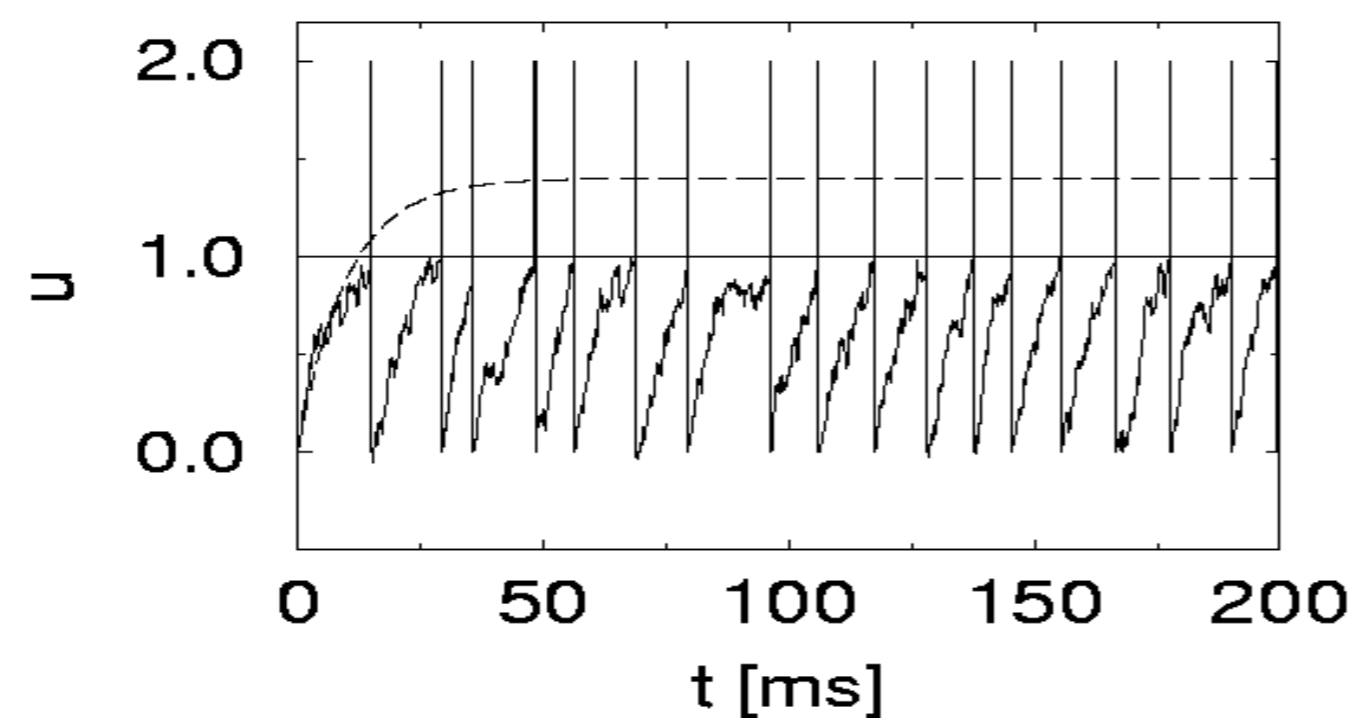
$$RI^{syn}(t) = RI_0(t) + \xi(t)$$

white noise

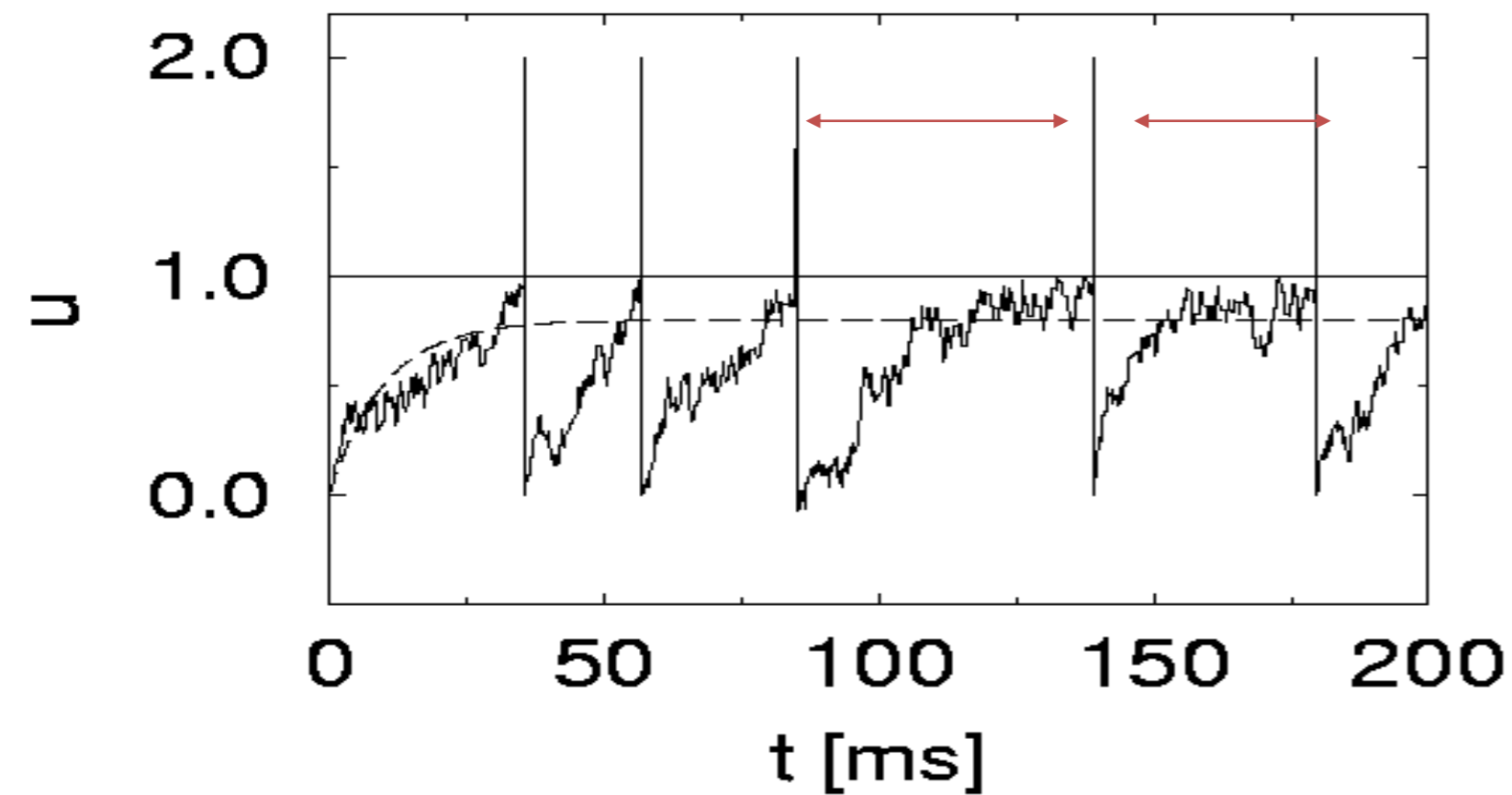


Neuronal Dynamics – 8.3 Noisy Integrate-and-fire

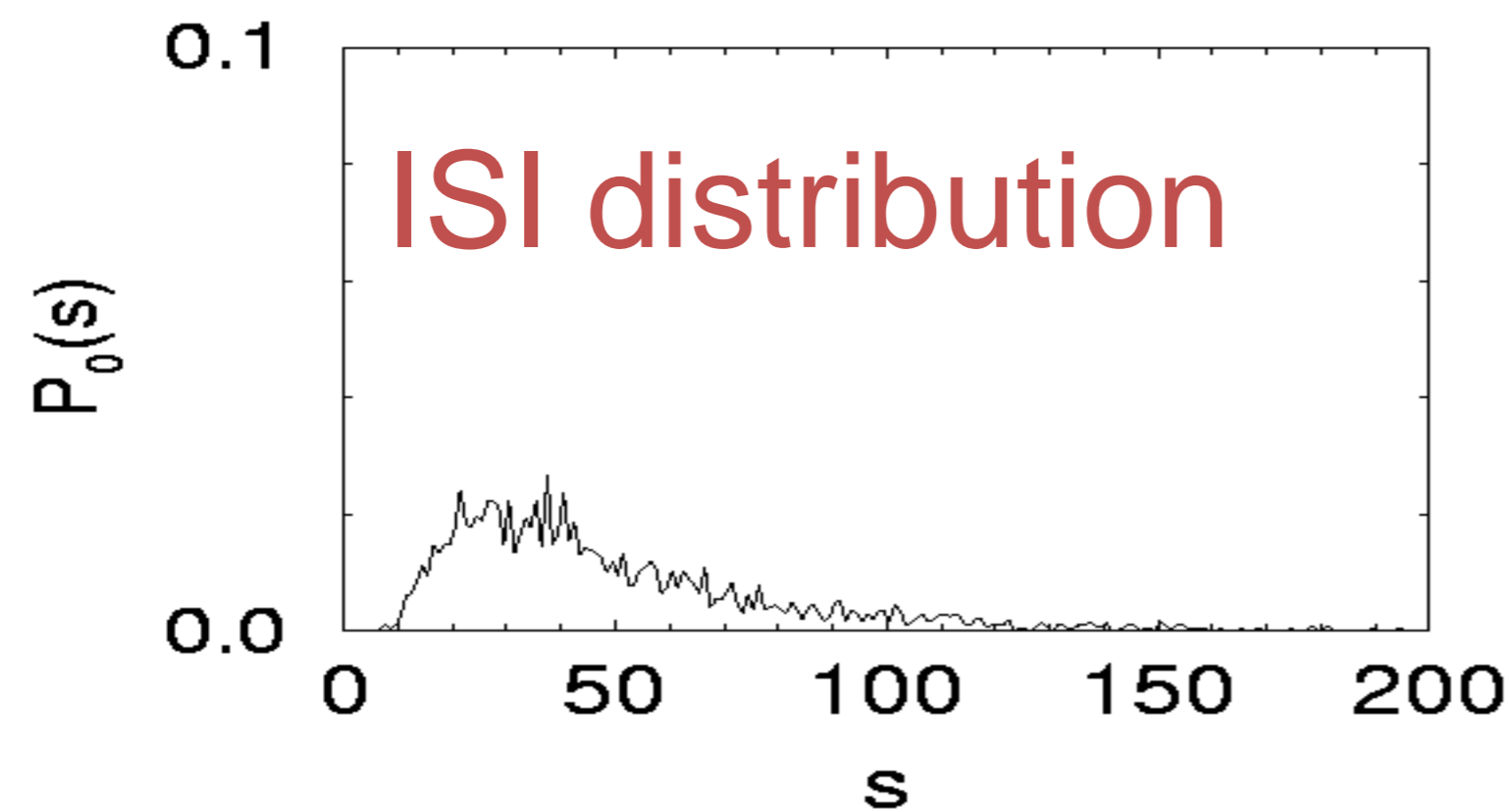
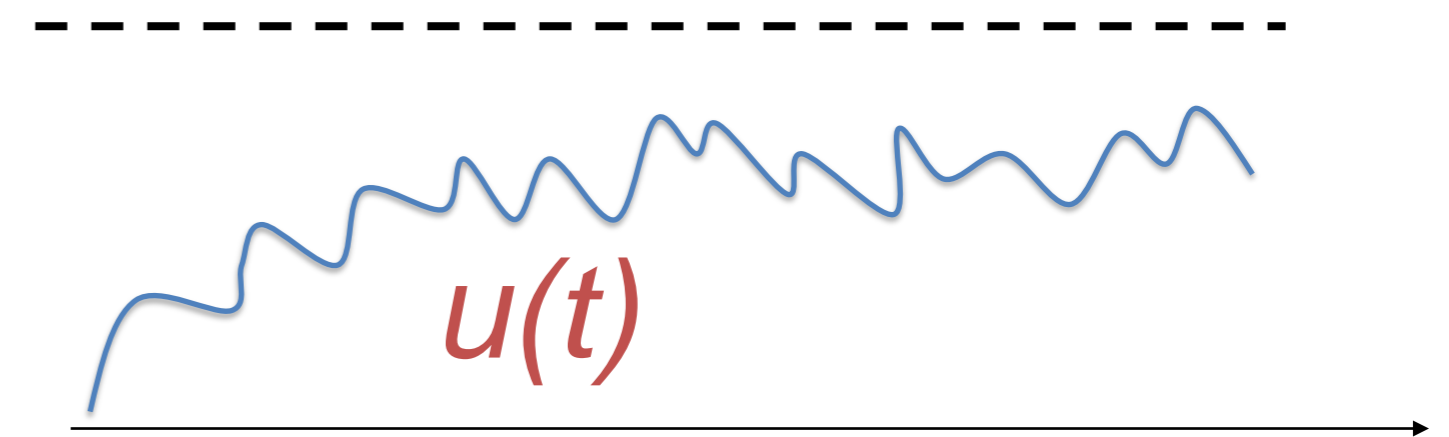
Superthreshold vs. Subthreshold regime



Neuronal Dynamics – 8.3. Stochastic leaky integrate-and-fire



noisy input/ diffusive noise/
stochastic spike arrival



subthreshold regime:

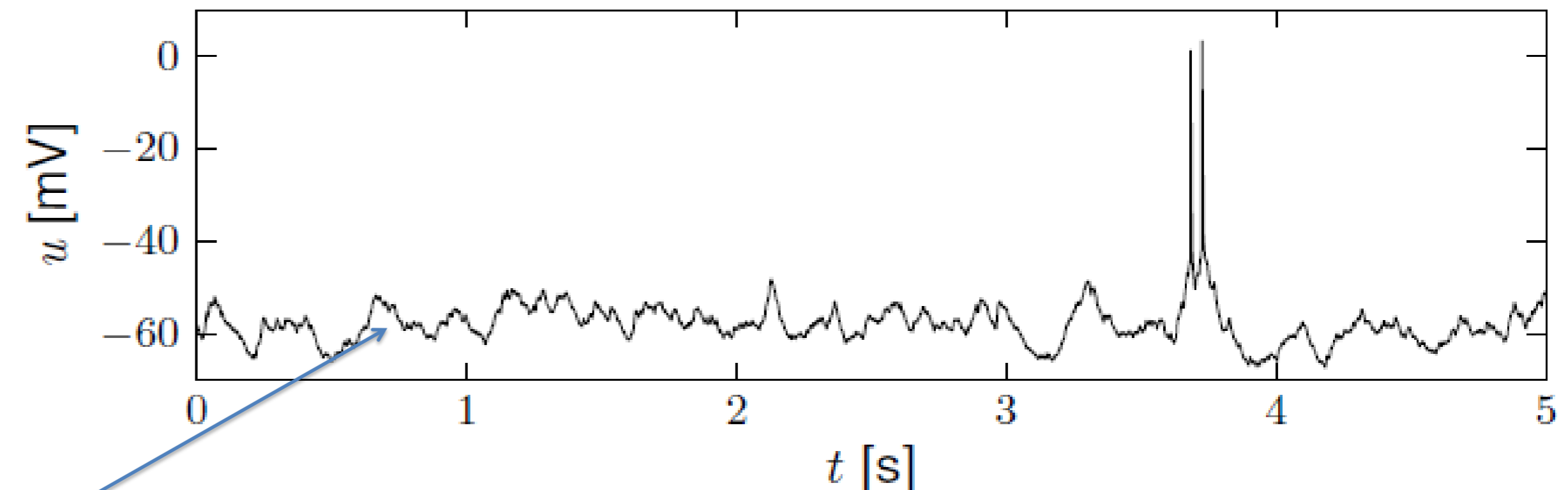
- firing driven by fluctuations
- **broad ISI distribution**
- *in vivo* like

Neuronal Dynamics – review- Variability in vivo

Spontaneous activity *in vivo*

Variability
of membrane potential?

awake mouse, freely whisking,



Crochet et al., 2011

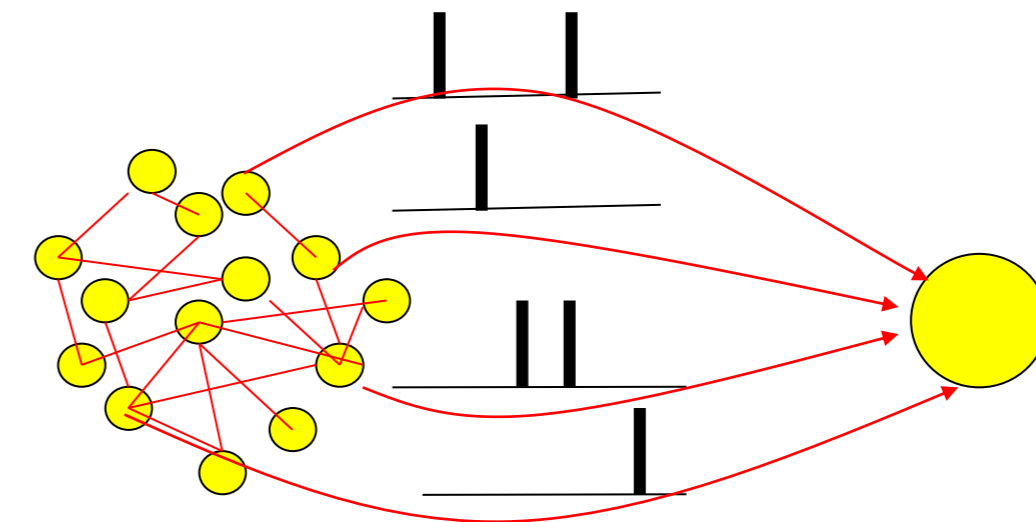
Subthreshold regime

Neuronal Dynamics – 8.3 Summary: Noisy Integrate-and-fire

Stochastic spike arrival:

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

*Leaky integrate-and-fire
in subthreshold regime
→ In vivo like*



Passive membrane

$$\begin{aligned} u(t) &= \sum_k w_k \sum_f \varepsilon(t' - t_k^f) \\ &= \sum_k w_k \int dt' \varepsilon(t - t') S_k(t') \end{aligned}$$

fluctuating potential

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

Week 8 – Noisy input models: barrage of spike arrivals



Biological Modeling of Neural Networks

8.1 Variation of membrane potential

- white noise approximation

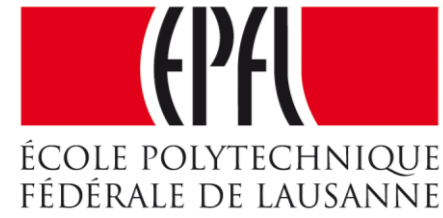
8.2 Autocorrelation of Poisson

8.3 Noisy integrate-and-fire

- superthreshold and subthreshold

THE END

Week 8 – part 4 : Escape noise



Biological Modeling of Neural Networks

Week 8 – Noisy input models: Barrage of spike arrivals

Wulfram Gerstner

EPFL, Lausanne, Switzerland

8.1 Variation of membrane potential

- white noise approximation

8.2 Autocorrelation of Poisson

8.3 Noisy integrate-and-fire

- superthreshold and subthreshold

8.4 Escape noise

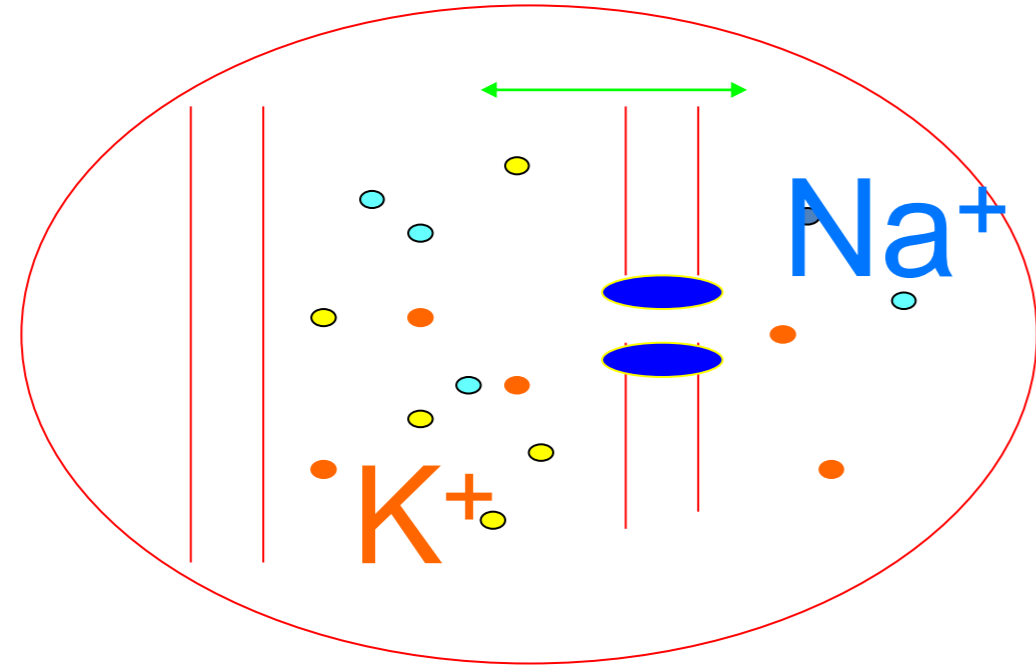
- stochastic intensity

8.5 Renewal models

8.6 Comparison of noise models

Neuronal Dynamics – Review: Sources of Variability

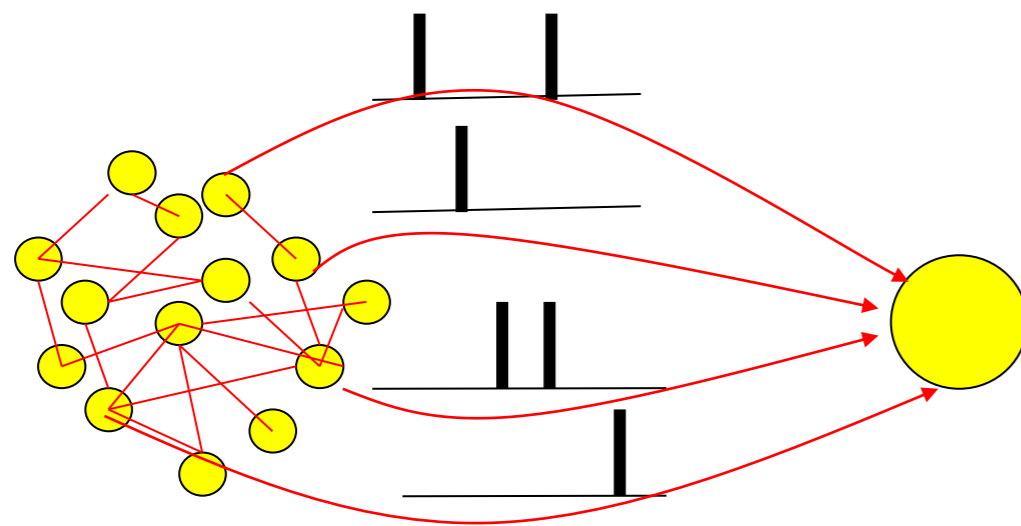
- Intrinsic noise (ion channels)



- Finite number of channels
- Finite temperature

small contribution!

- Network noise (background activity)



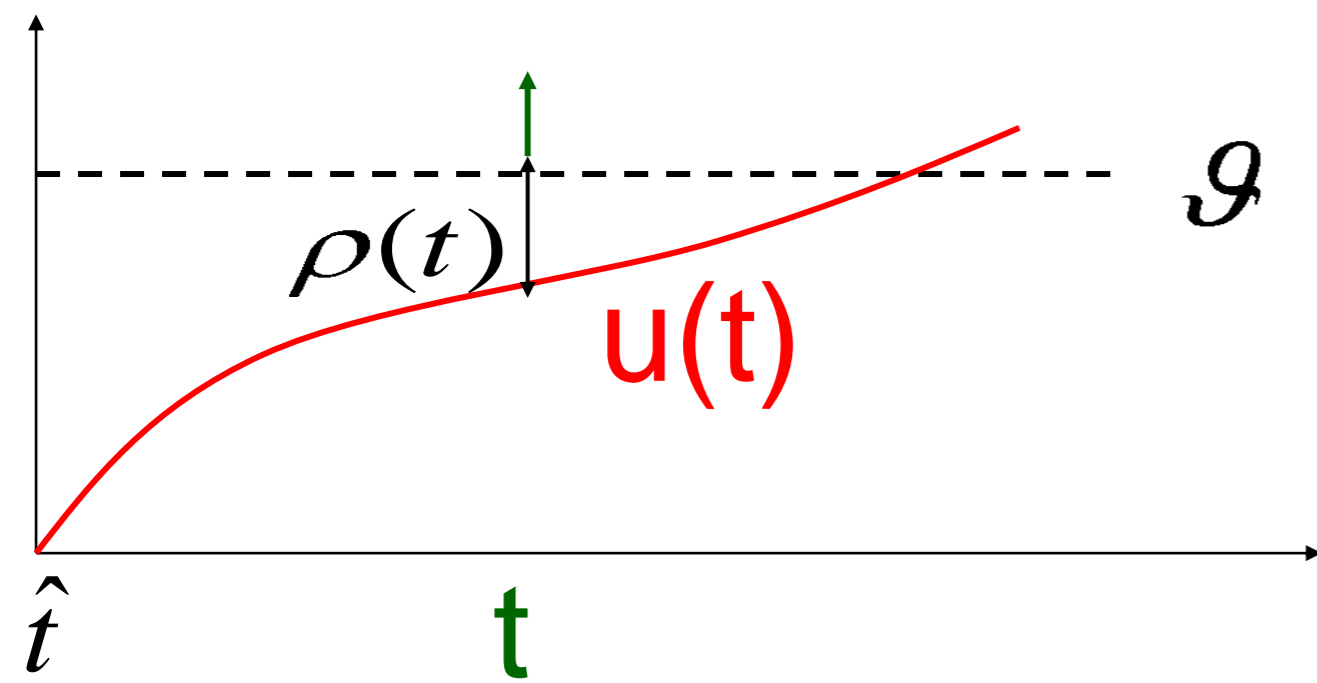
- Spike arrival from other neurons
- Beyond control of experimentalist

Noise models?

big contribution!

Noise models

escape process,
stochastic intensity

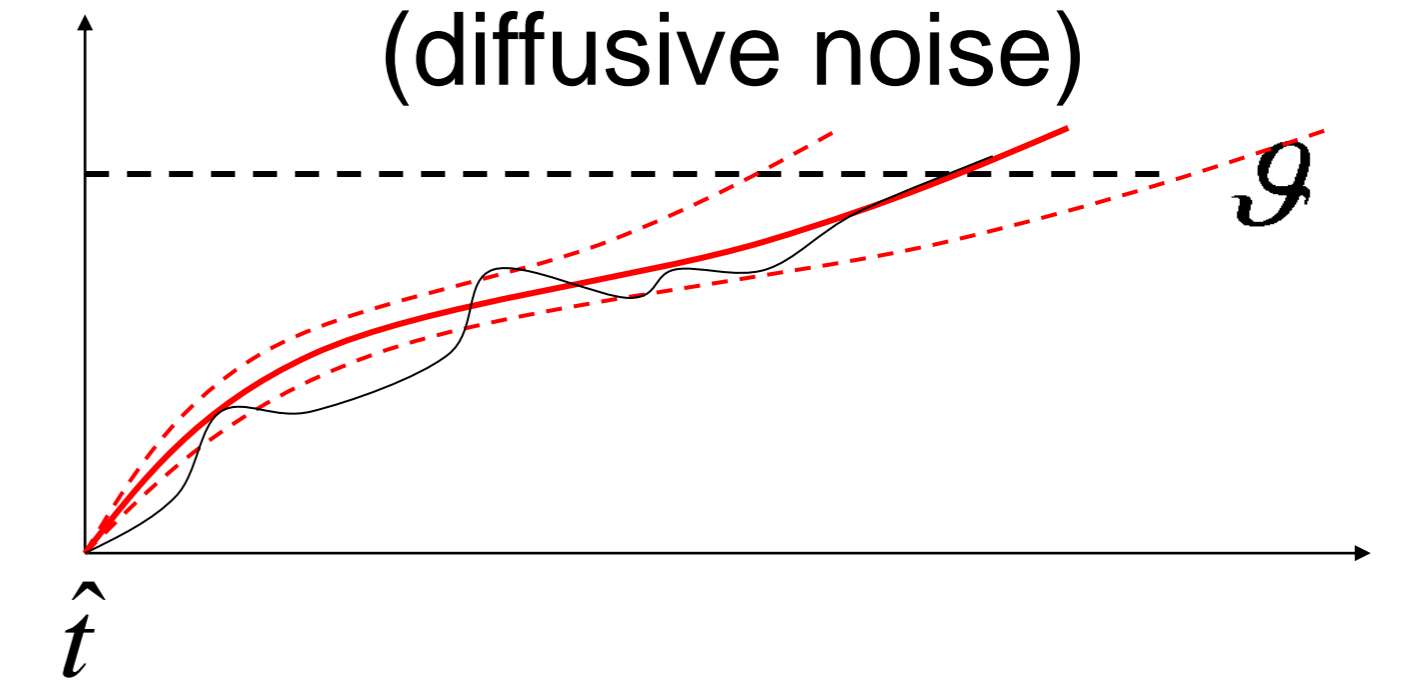


escape rate

$$\rho(t) = f(u(t) - \mathcal{G})$$

Now:
Escape noise!

stochastic spike arrival
(diffusive noise)



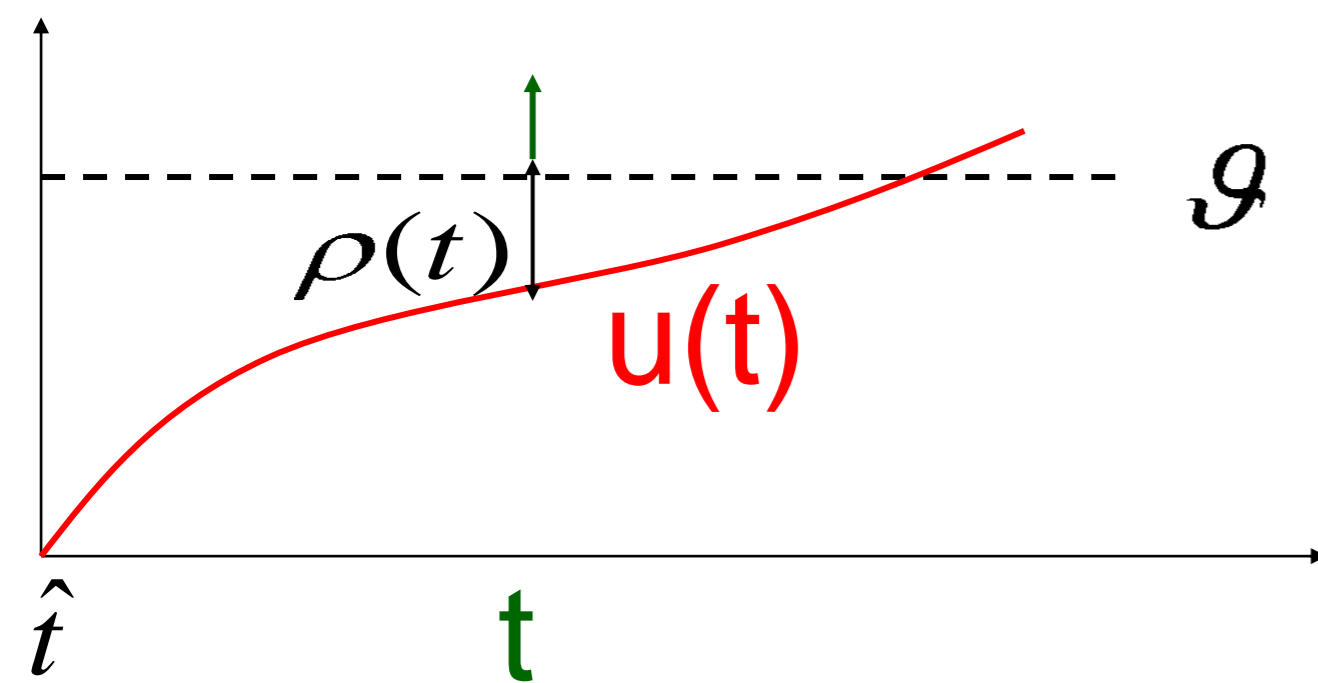
noisy integration

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

Relation between the two models:
later

Neuronal Dynamics – 8.4 Escape noise

escape process

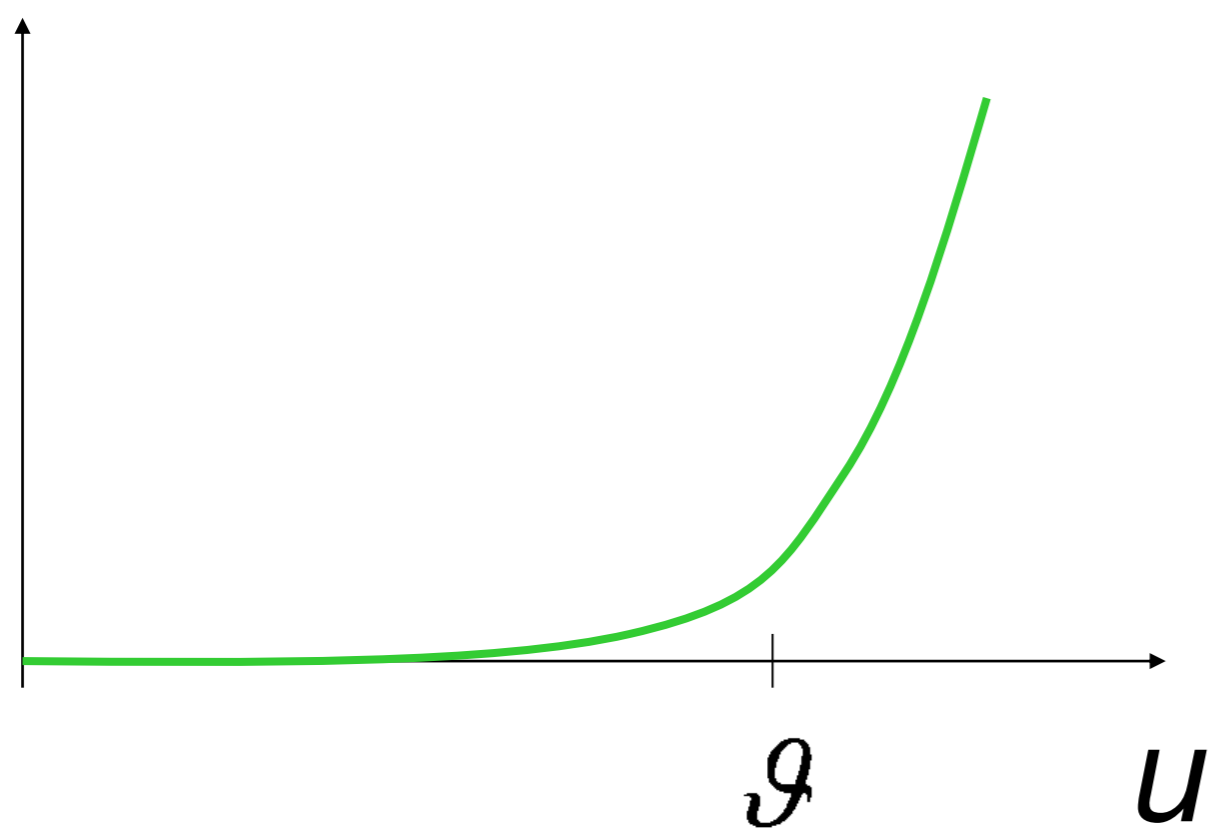


escape rate

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

escape rate

$$\rho(t) = f(u(t) - \mathcal{G})$$



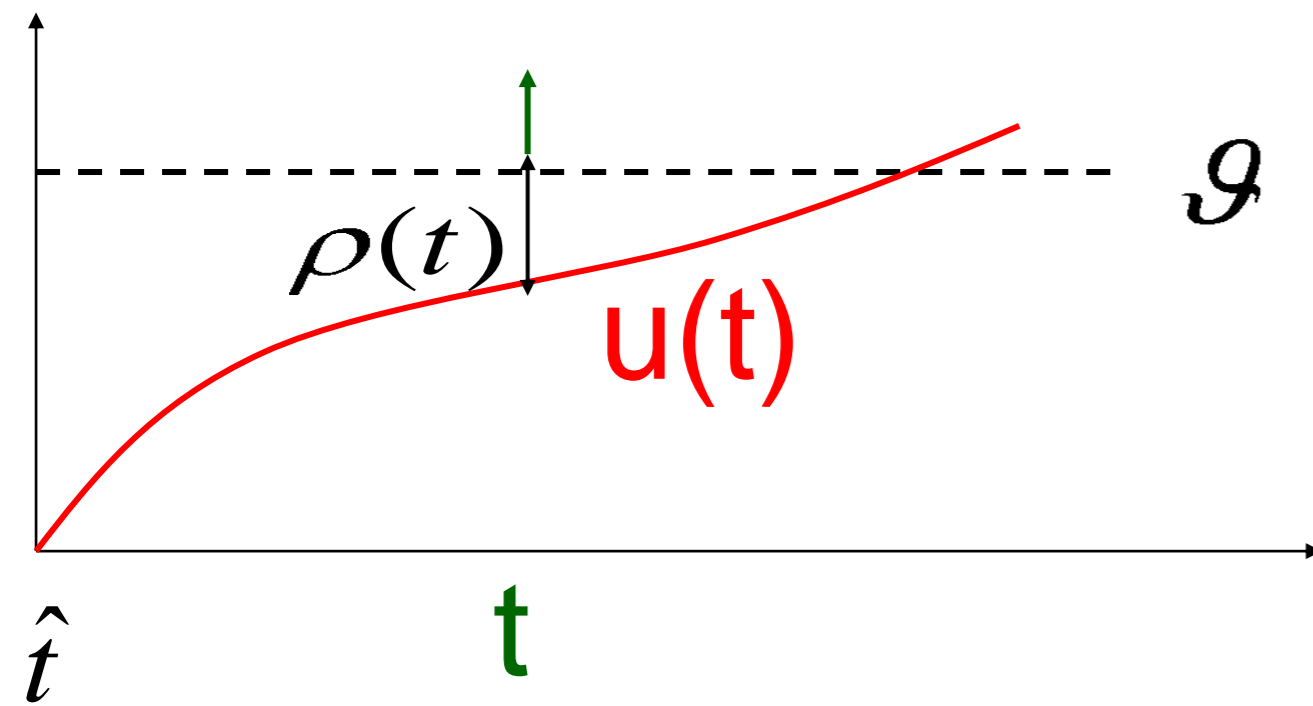
Example: leaky integrate-and-fire model

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

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

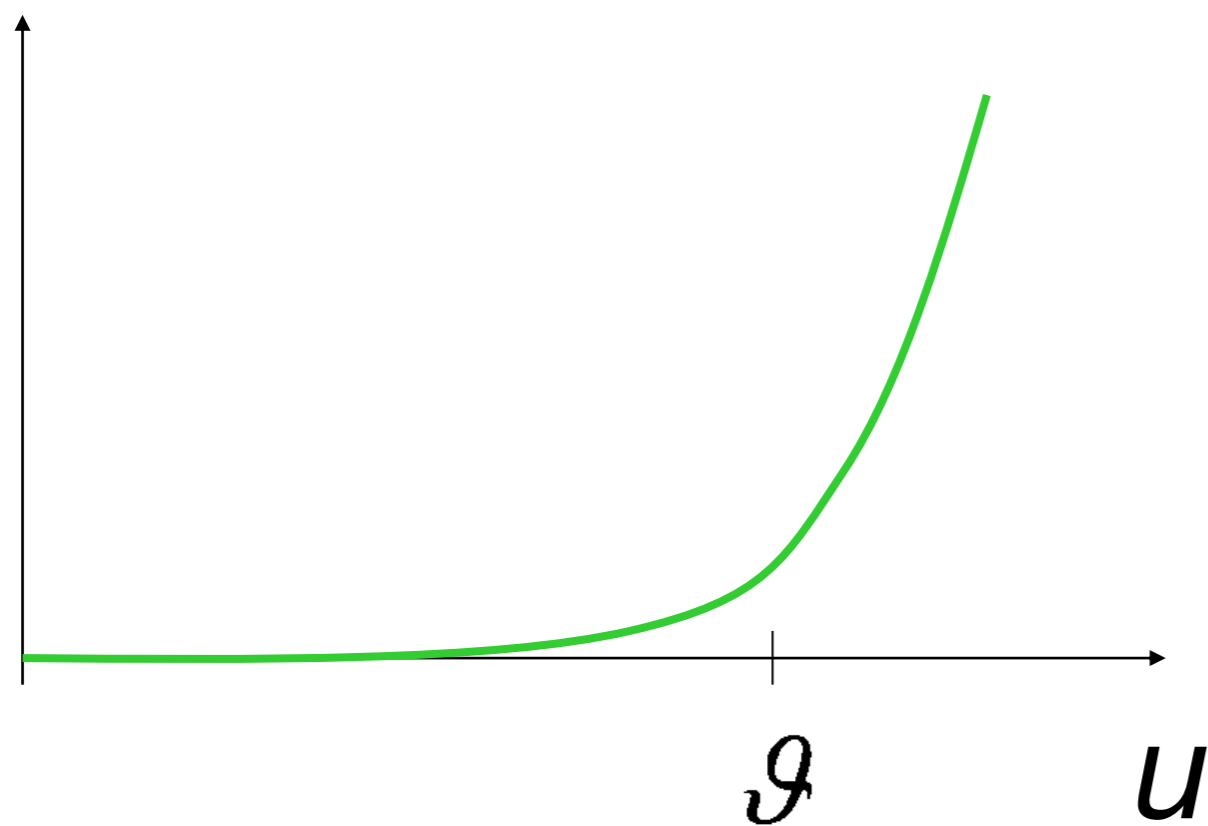
Neuronal Dynamics – 8.4 stochastic intensity

escape process



escape rate

$$\rho(t) = f(u(t) - \mathcal{G})$$



Escape rate = stochastic intensity
of point process

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

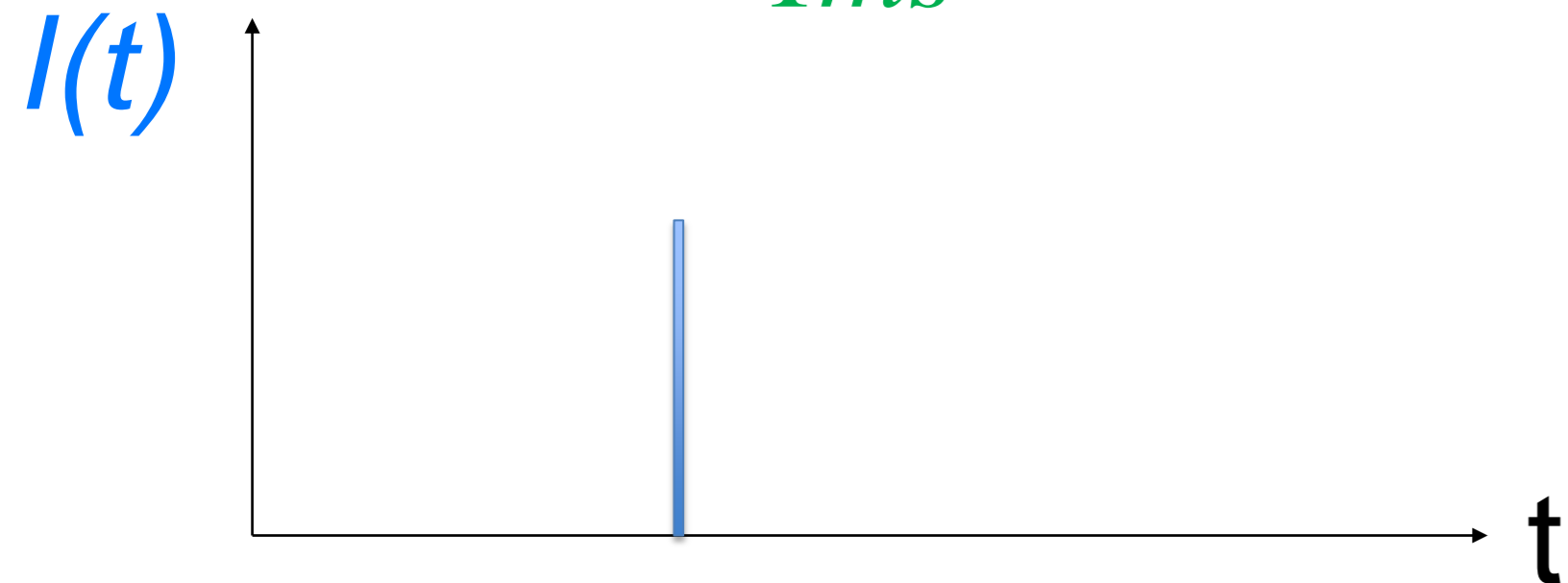
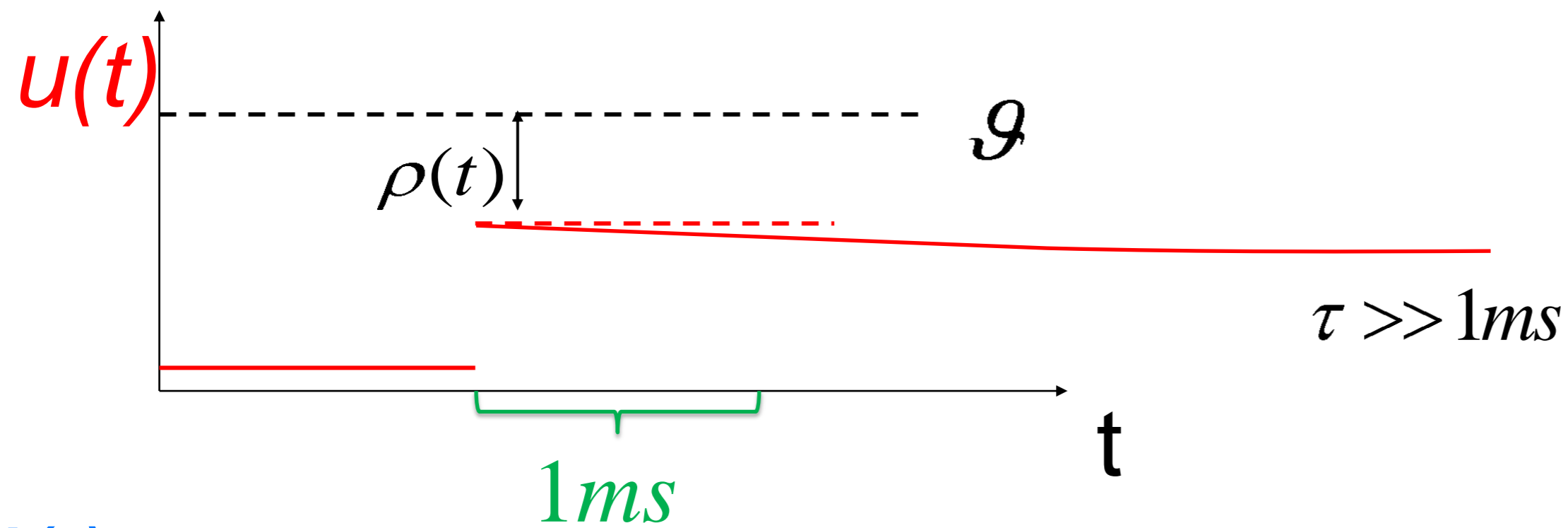
examples

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

$$\rho(t) =$$

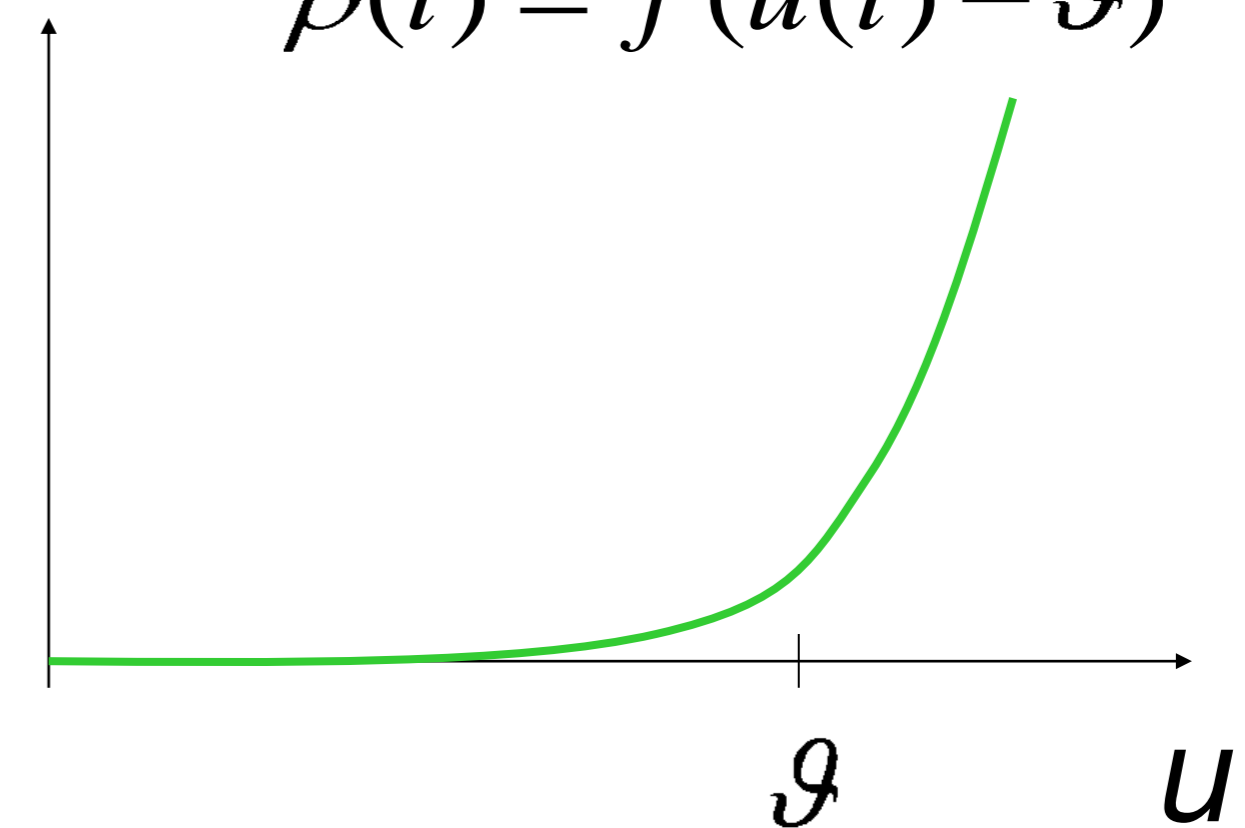
Neuronal Dynamics – 8.4 mean waiting time

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



escape rate

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



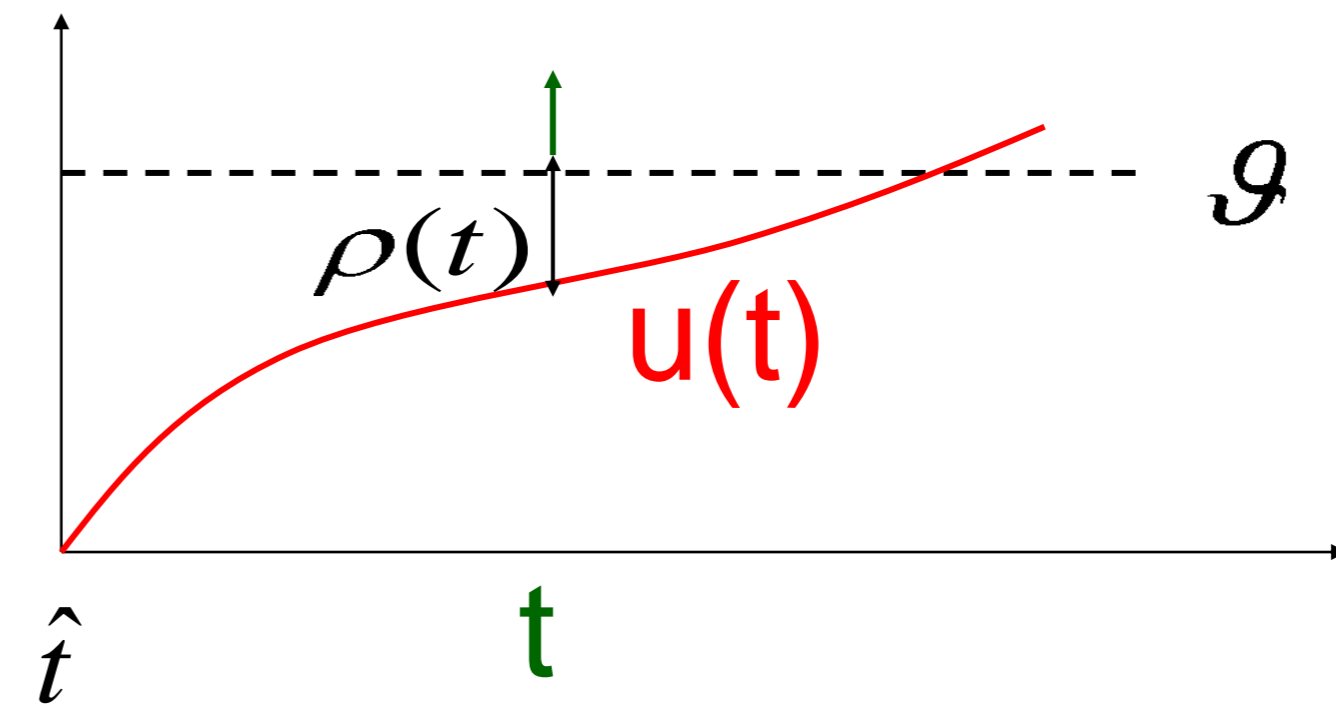
mean waiting time, after switch

Blackboard,
Math detour

Neuronal Dynamics – 8.4 escape noise/stochastic intensity

Escape rate = stochastic intensity
of point process

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



Neuronal Dynamics – Quiz 8.4

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

Week 8 – part 5 : Renewal model



Biological Modeling of Neural Networks

Week 8 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

8.1 Variation of membrane potential

- white noise approximation

8.2 Autocorrelation of Poisson

8.3 Noisy integrate-and-fire

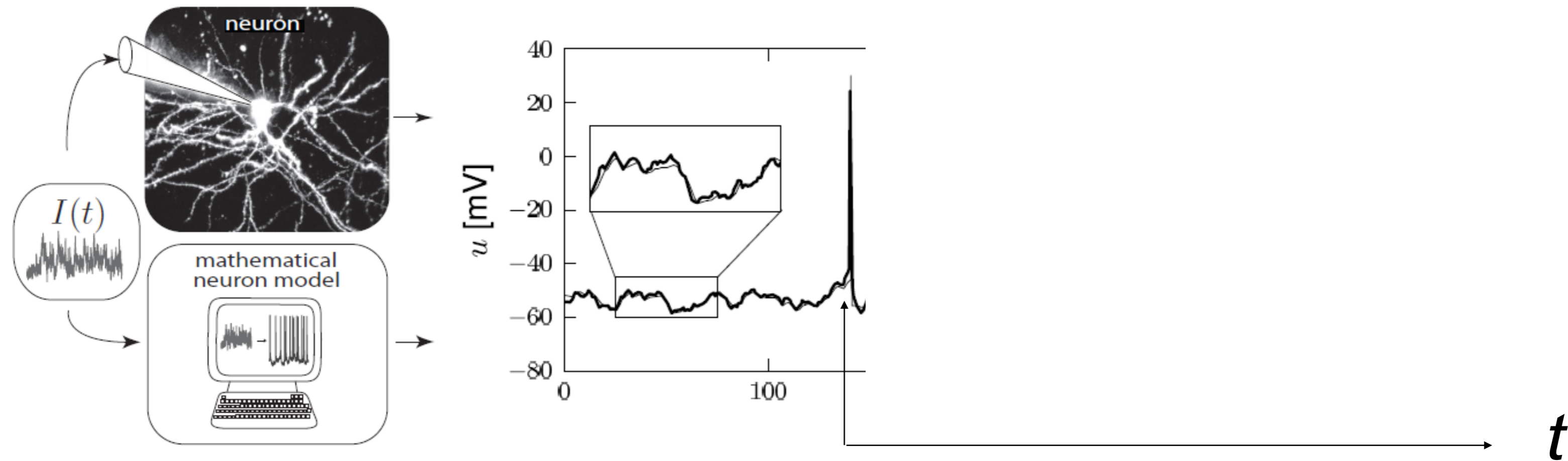
- superthreshold and subthreshold

8.4 Escape noise

- stochastic intensity

8.5 Renewal models

Neuronal Dynamics – 8.5. Interspike Intervals



deterministic part of input

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

noisy part of input/intrinsic noise

\rightarrow *escape rate*

Example:
nonlinear integrate-and-fire model

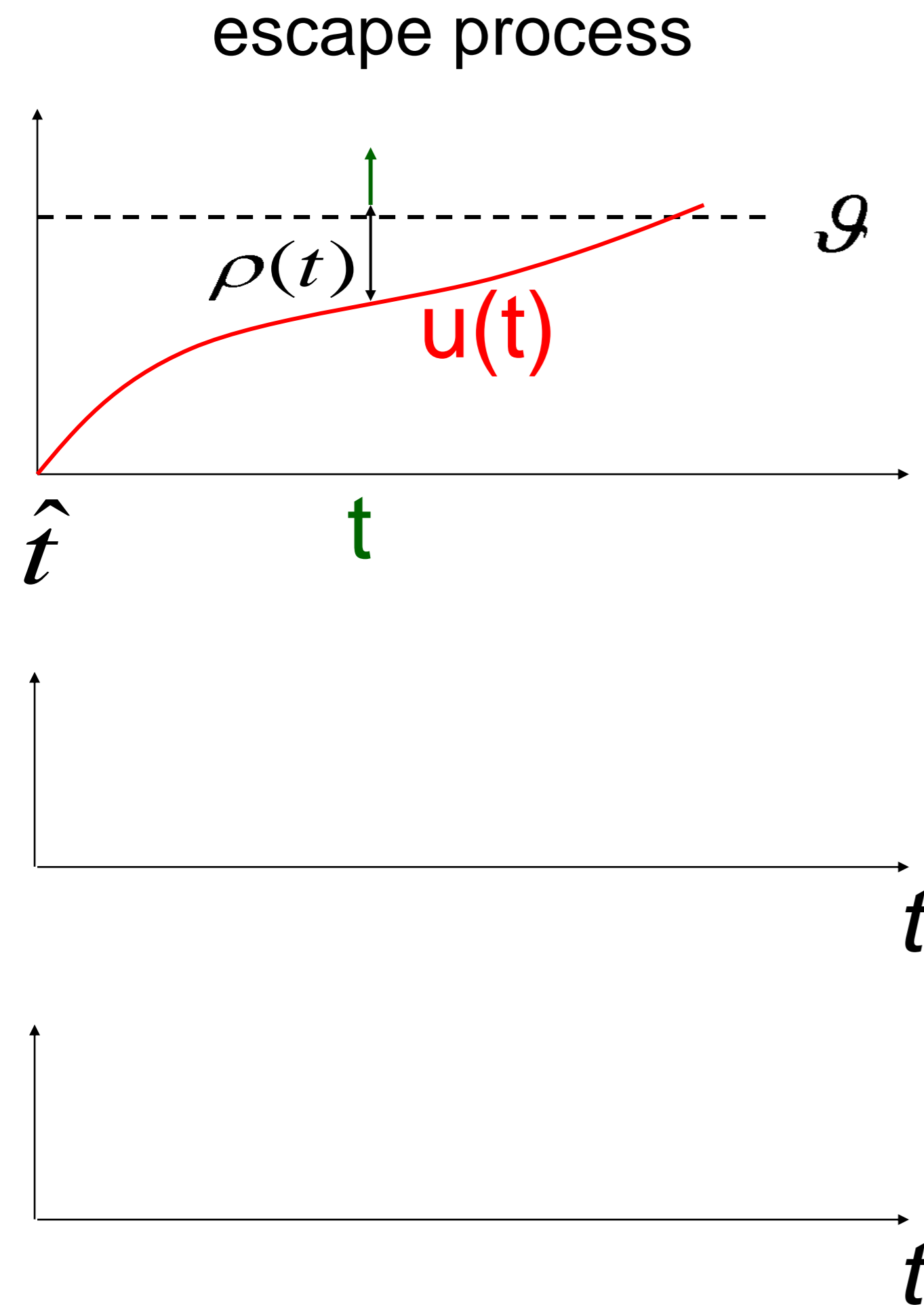
$$\tau \cdot \frac{d}{dt} u = F(u) + RI(t)$$

if spike at $t^f \Rightarrow u(t^f + \delta) = u_r$

Example:
exponential stochastic intensity

$$\rho(t) = f(u(t)) = \rho_g \exp(u(t) - \mathcal{G})$$

Neuronal Dynamics – 8.5. Interspike Interval distribution



escape rate

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

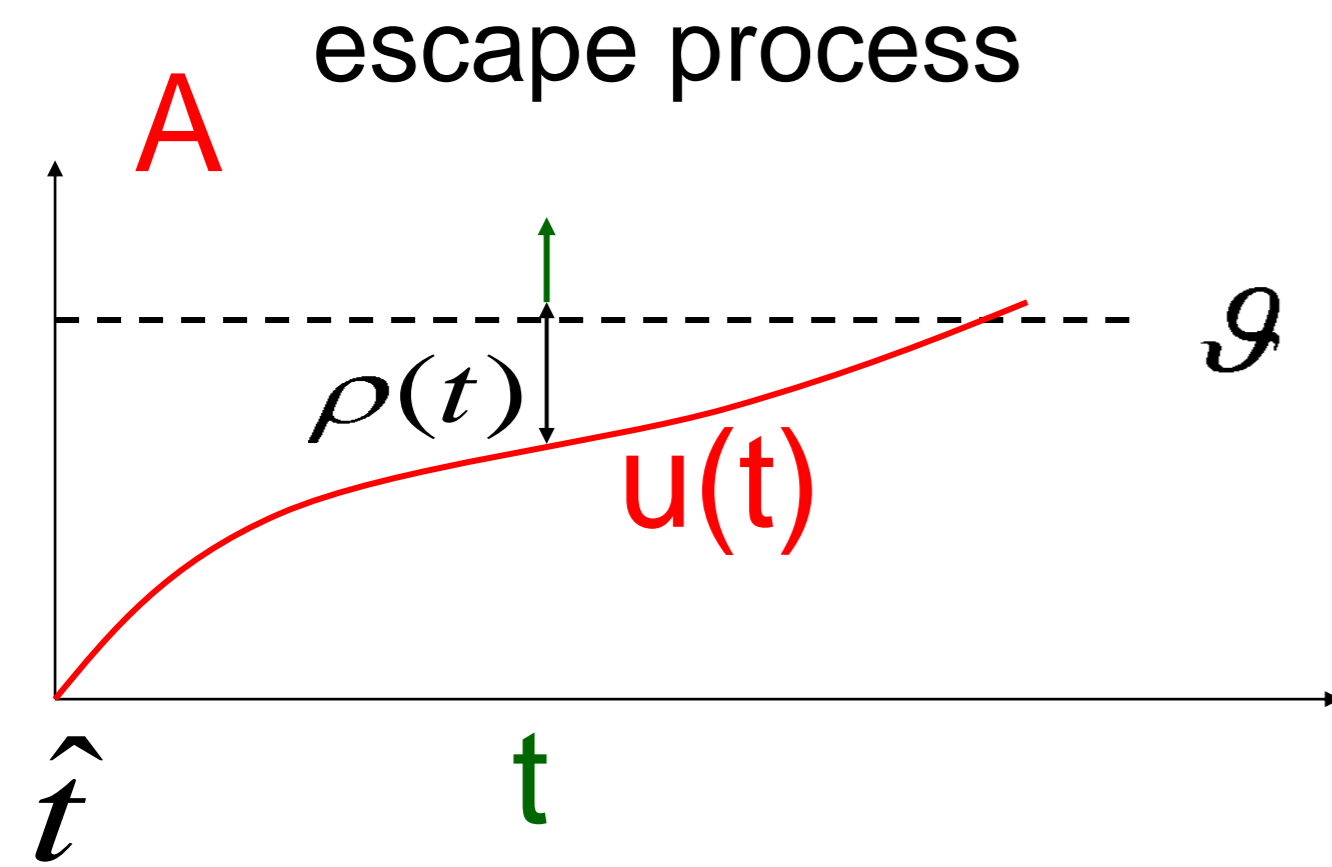
Survivor function

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

Neuronal Dynamics – 8.5. Interspike Intervals

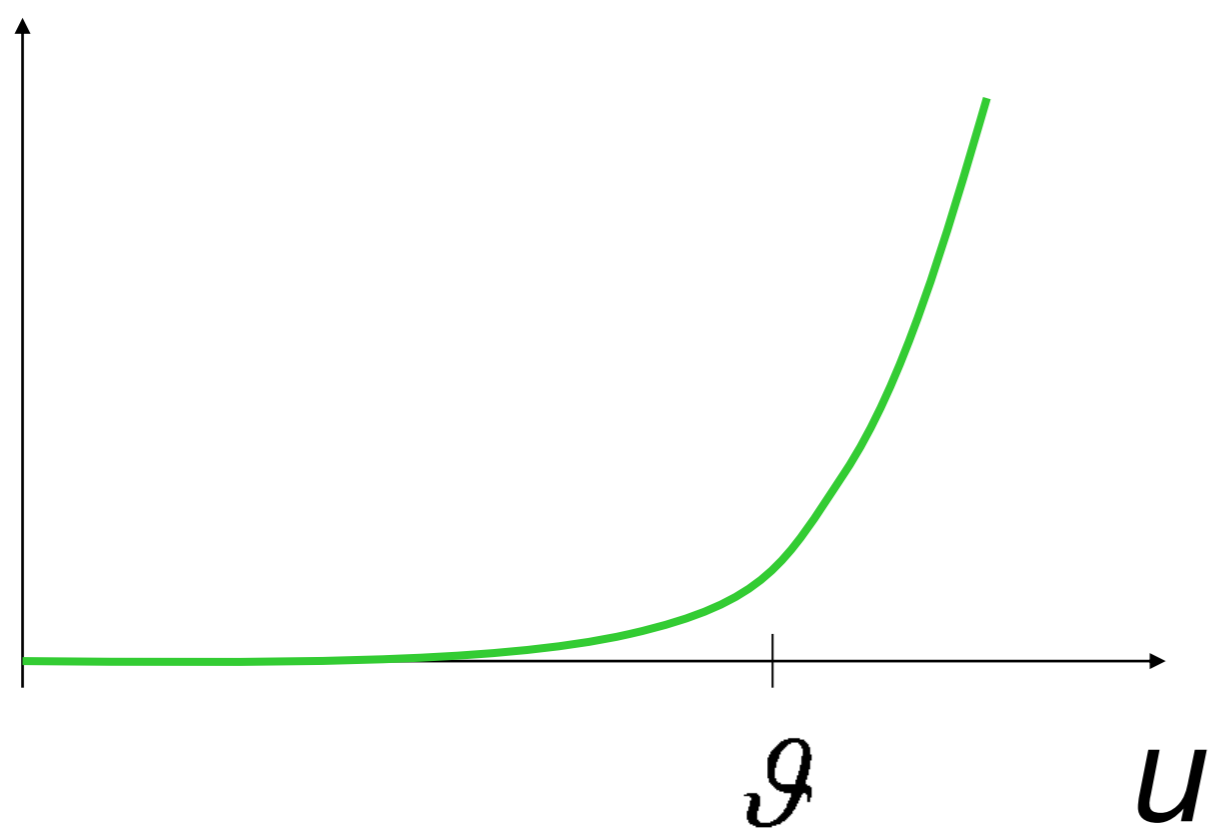
Survivor function

Examples now



escape rate

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



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

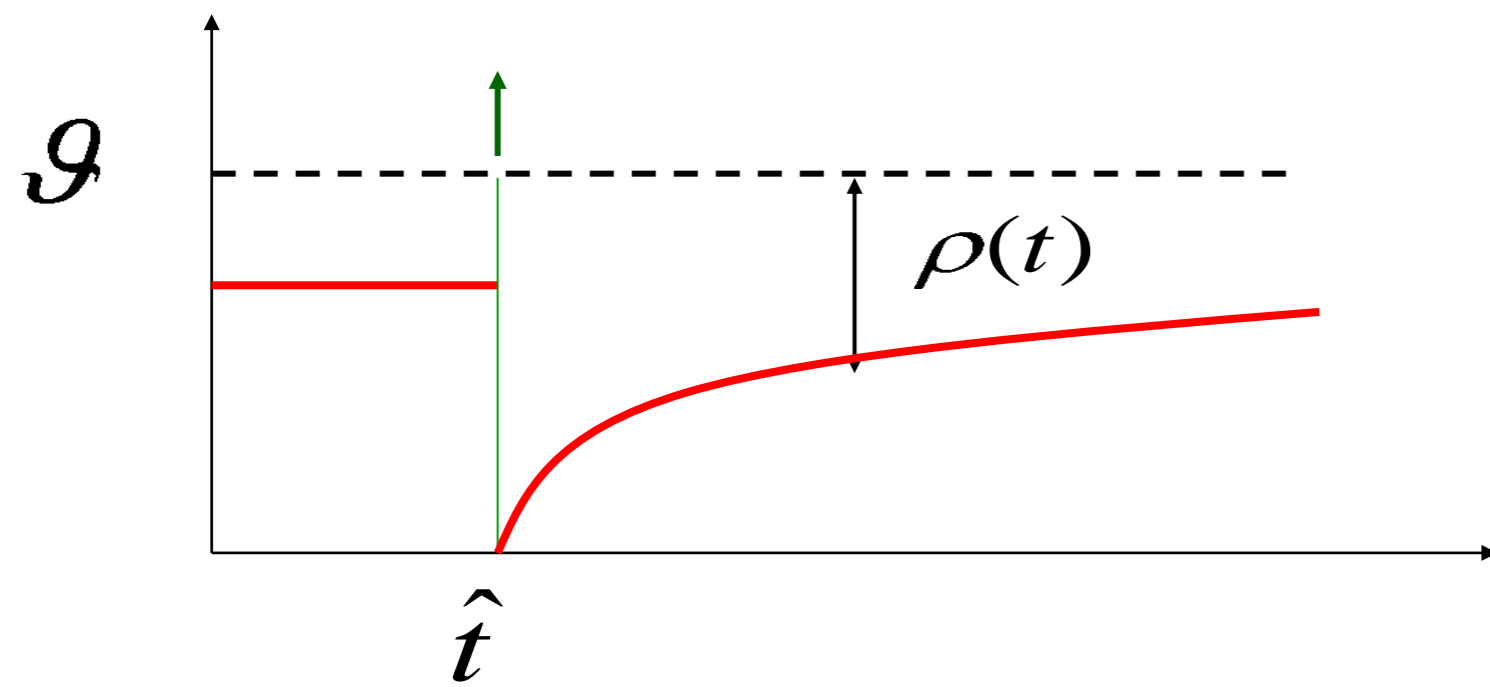
$$S_I(t|\hat{t}) = \exp\left(-\int_{\hat{t}}^t \rho(t') dt'\right)$$

Interval distribution

$$P_I(t|\hat{t}) = \underbrace{\rho(t)}_{\text{escape rate}} \cdot \underbrace{\exp\left(-\int_{\hat{t}}^t \rho(t') dt'\right)}_{\text{Survivor function}}$$

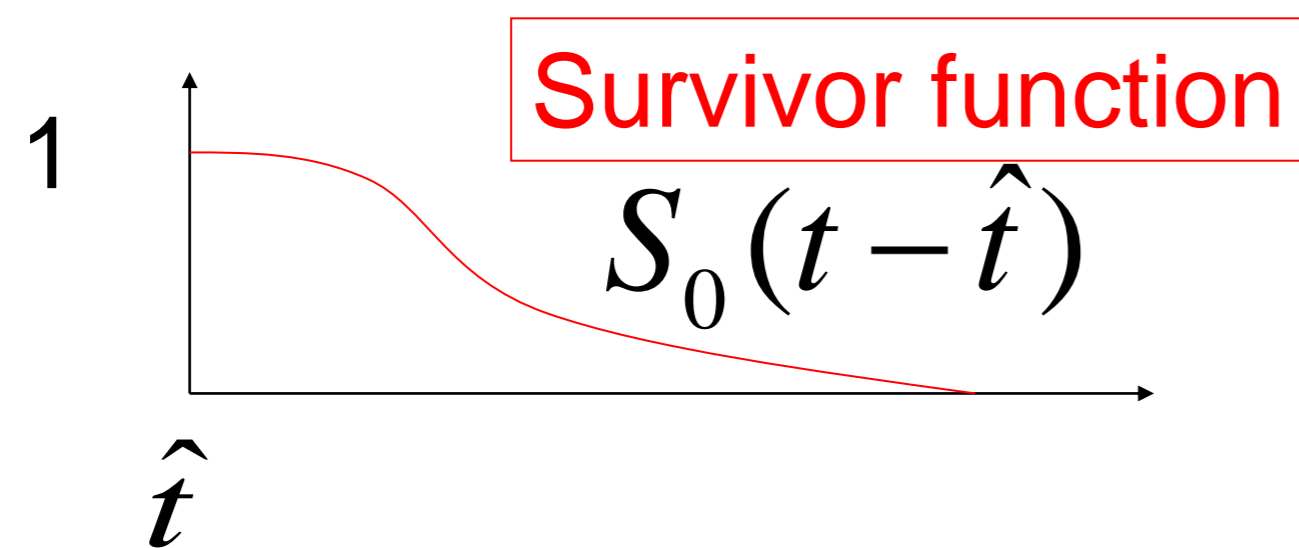
Neuronal Dynamics – 8.5. Renewal theory

Example: I&F with reset, constant input

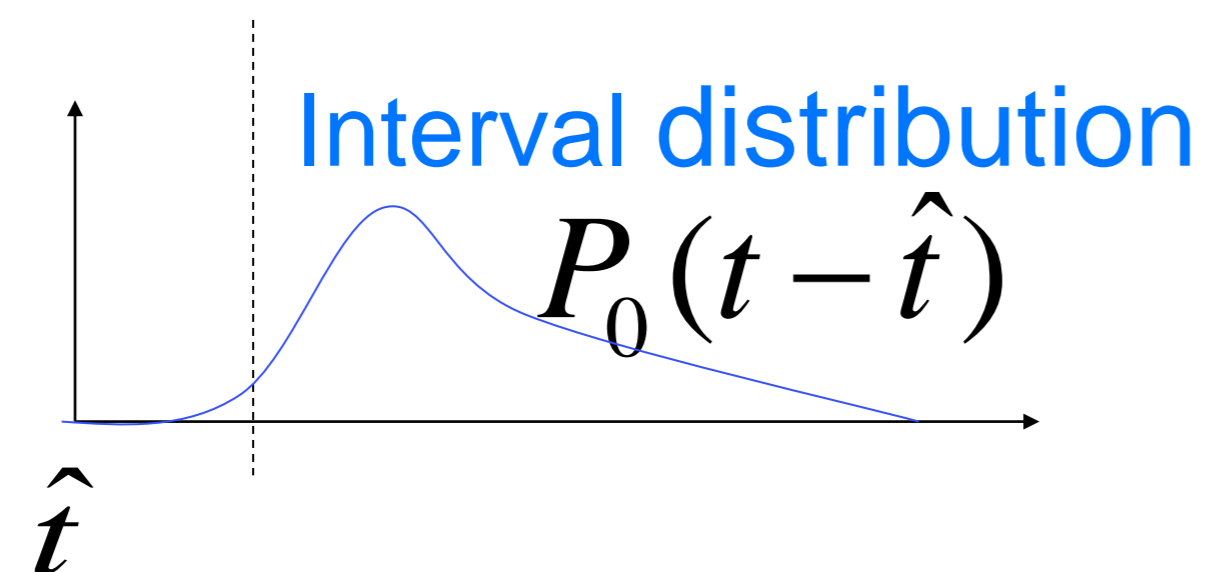


escape rate

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



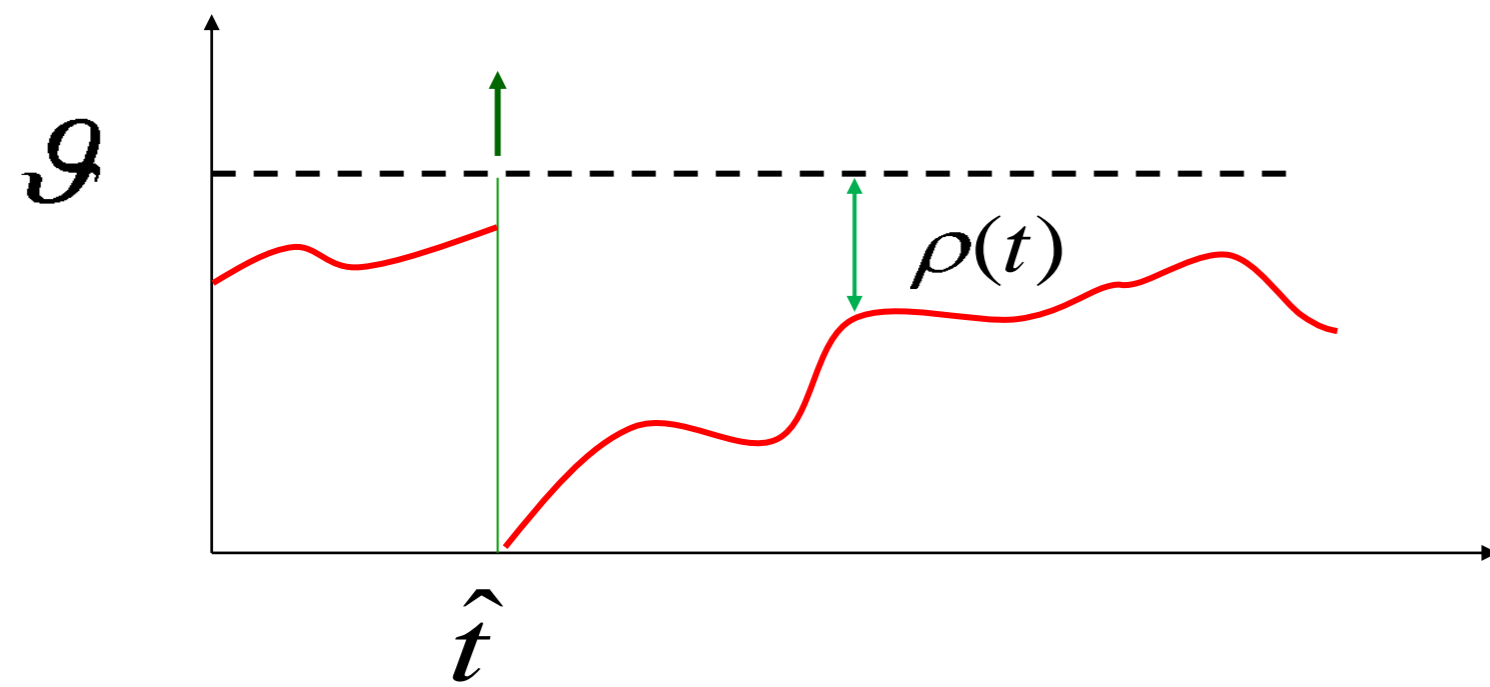
$$S(t|\hat{t}) = \exp\left(-\int_{\hat{t}}^t \rho(t'|\hat{t}) dt'\right)$$



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

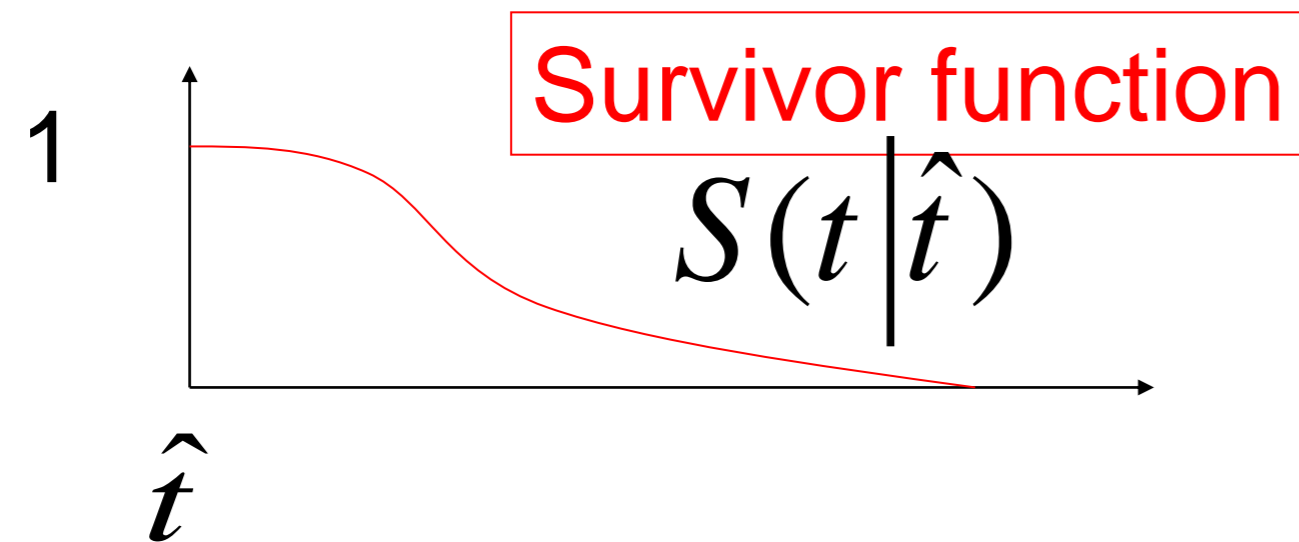
Neuronal Dynamics – 8.5. Time-dependent Renewal theory

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



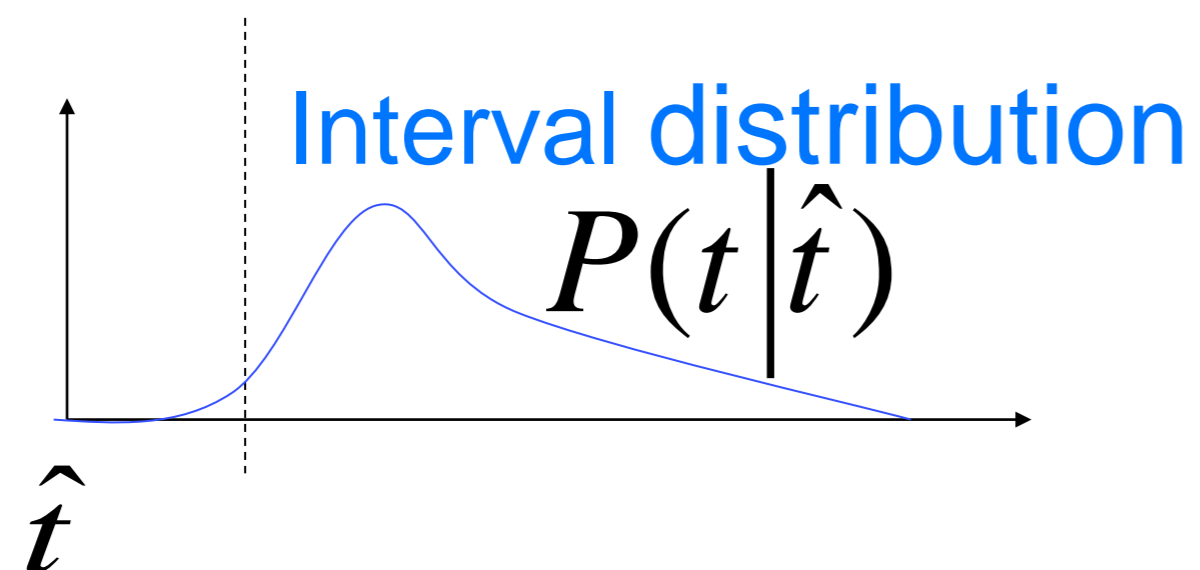
escape rate

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



Survivor function

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

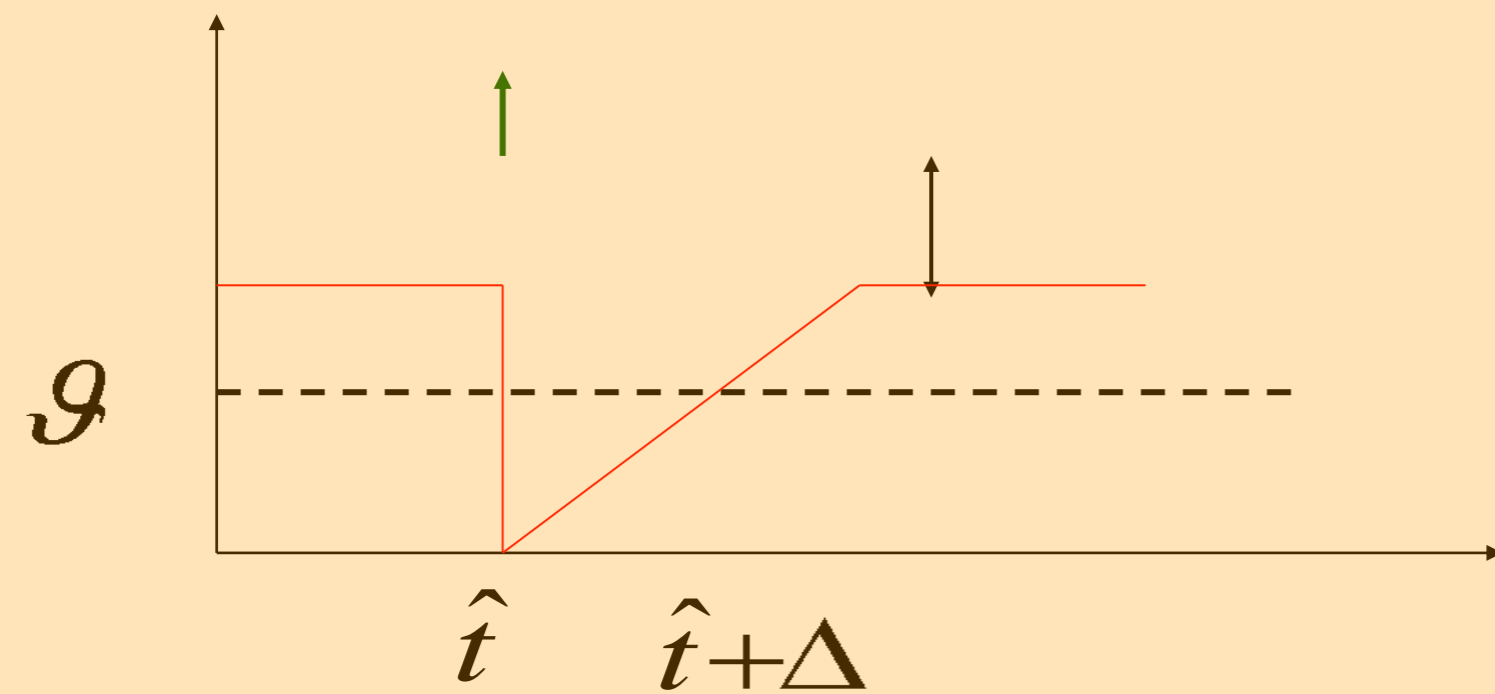


Interval distribution

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

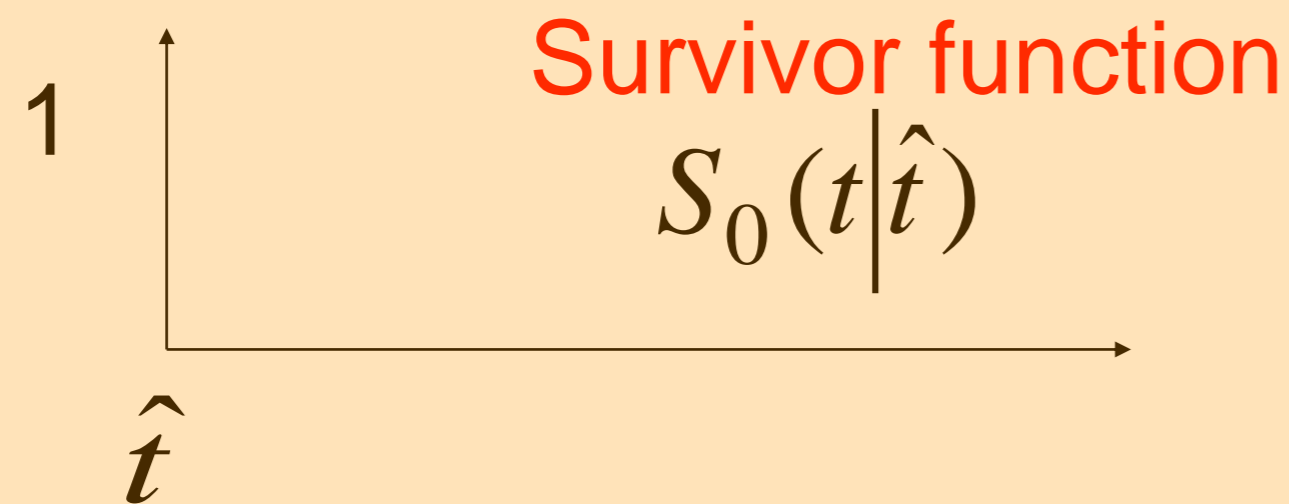
Neuronal Dynamics – Homework assignment

neuron with relative refractoriness, constant input

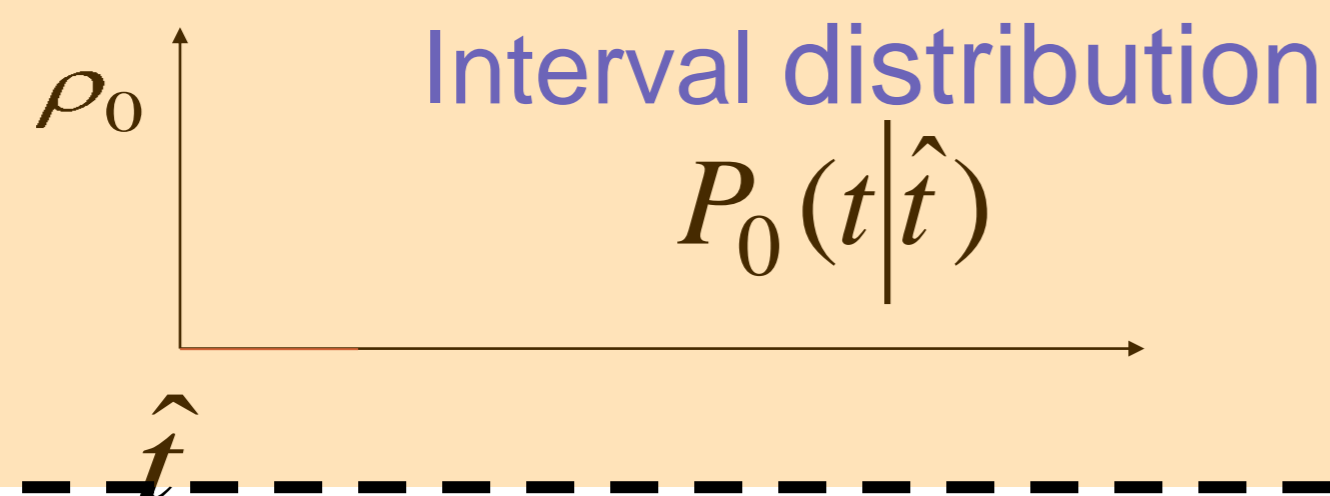


escape rate

$$\rho(t) = \rho_0 \frac{u}{\mathcal{G}} \text{ for } u > \mathcal{G}$$

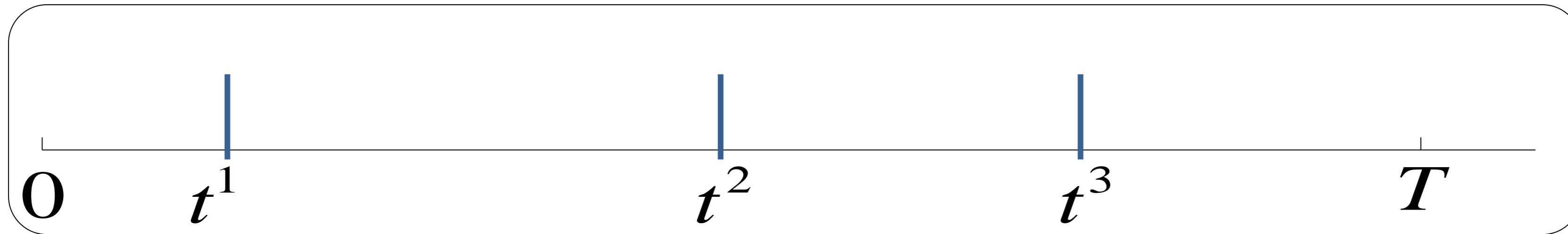


$$S_0(t | \hat{t}) = \left\{ \begin{array}{l} 1 \\ 0 \end{array} \right.$$



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

Neuronal Dynamics – 8.5. Firing probability in discrete time



Probability to survive 1 time step

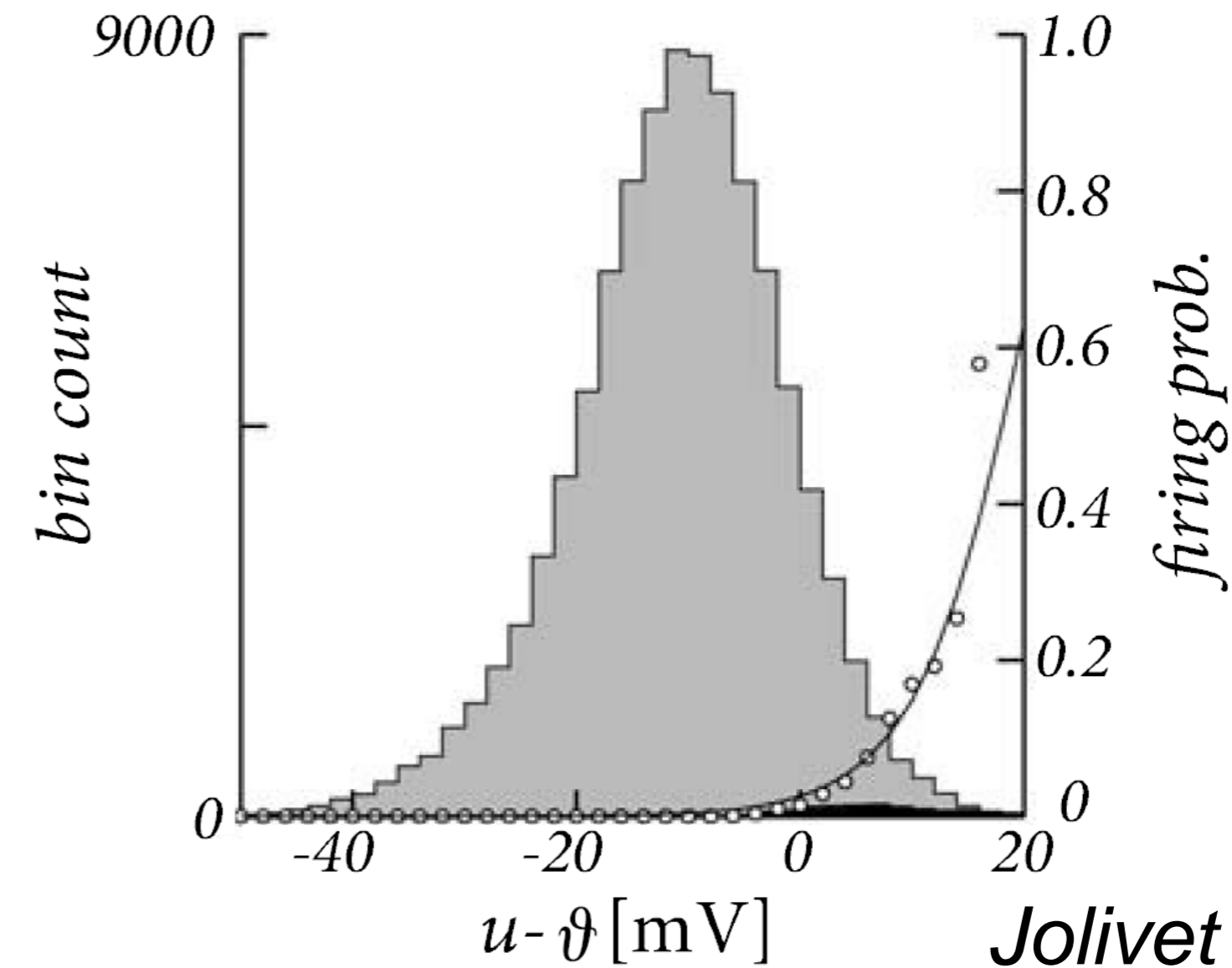
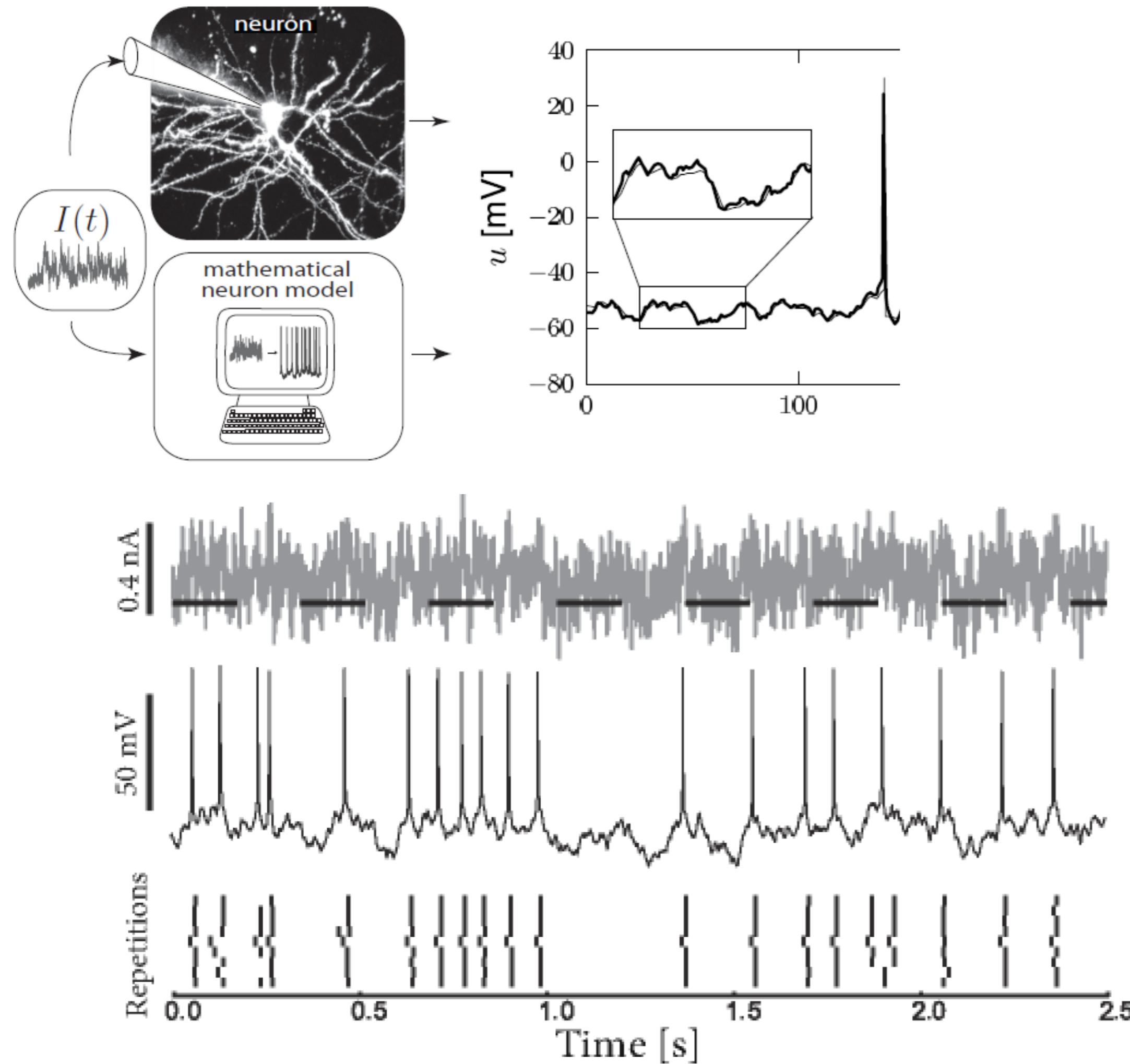
$$S(t_{k+1} | t_k) = \exp\left[-\int_{t_k}^{t_{k+1}} \rho(t') dt'\right]$$

$$S(t_{k+1} | t_k) = \exp[-\rho(t_k)\Delta] = 1 - P_k^F$$

Probability to fire in 1 time step

$$P_k^F =$$

Neuronal Dynamics – 8.5. Escape noise - experiments



*Jolivet et al. ,
J. Comput. Neurosc.
2006*

$$P_k^F = 1 - \exp[-\rho(t_k)\Delta]$$

escape rate

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

Neuronal Dynamics – 8.5. Renewal process, firing probability

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

Week 8 – part 6 : Comparison of noise models



Biological Modeling of Neural Networks

Week 8 – Noisy input models: Barrage of spike arrivals

Wulfram Gerstner

EPFL, Lausanne, Switzerland

8.1 Variation of membrane potential

- white noise approximation

8.2 Autocorrelation of Poisson

8.3 Noisy integrate-and-fire

- superthreshold and subthreshold

8.4 Escape noise

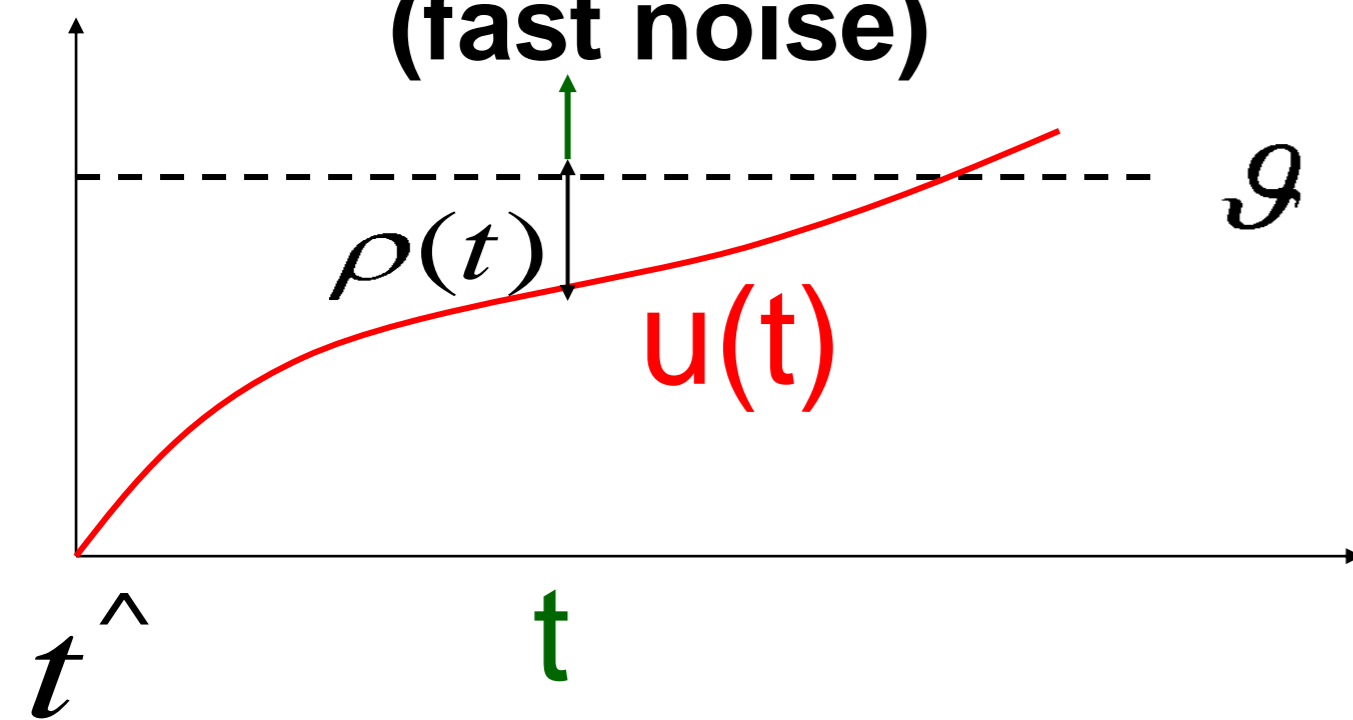
- stochastic intensity

8.5 Renewal models

8.6 Comparison of noise models

Neuronal Dynamics – 8.6. Comparison of Noise Models

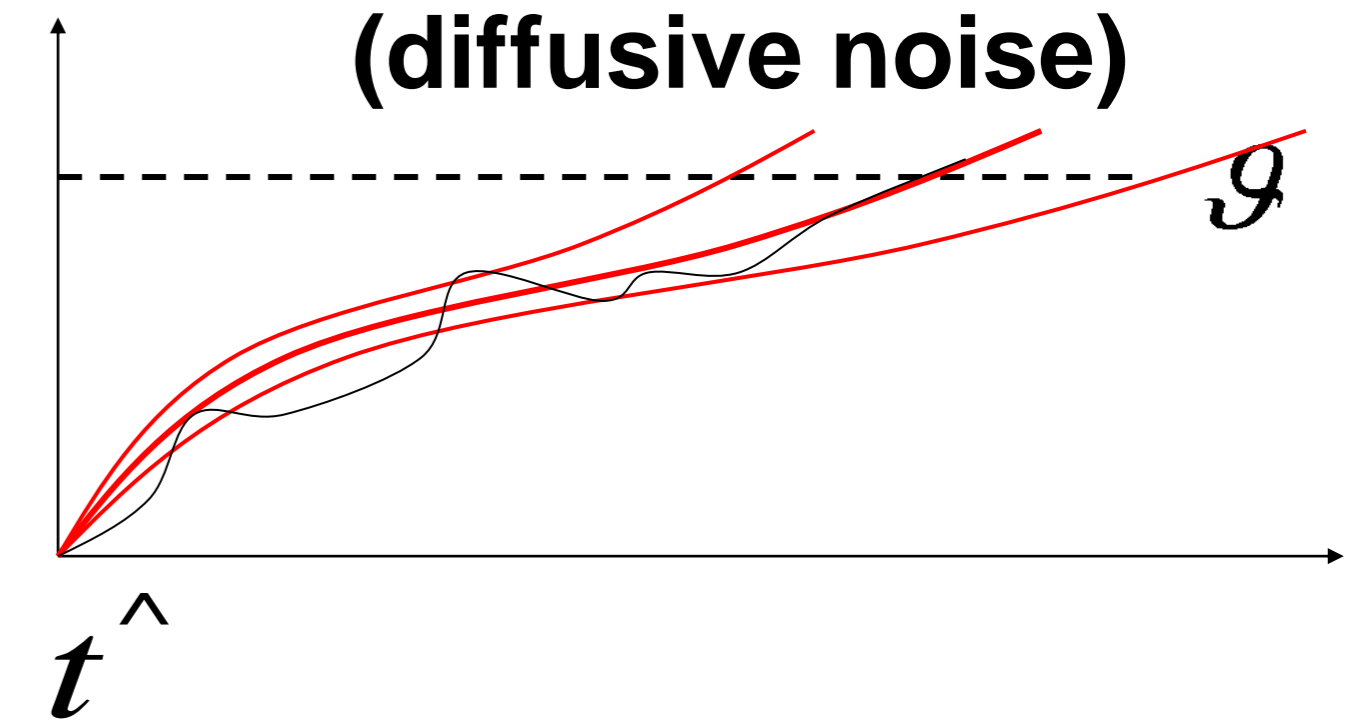
escape process
(fast noise)



escape rate

$$\rho(t) = f(u(t) - \mathcal{G})$$

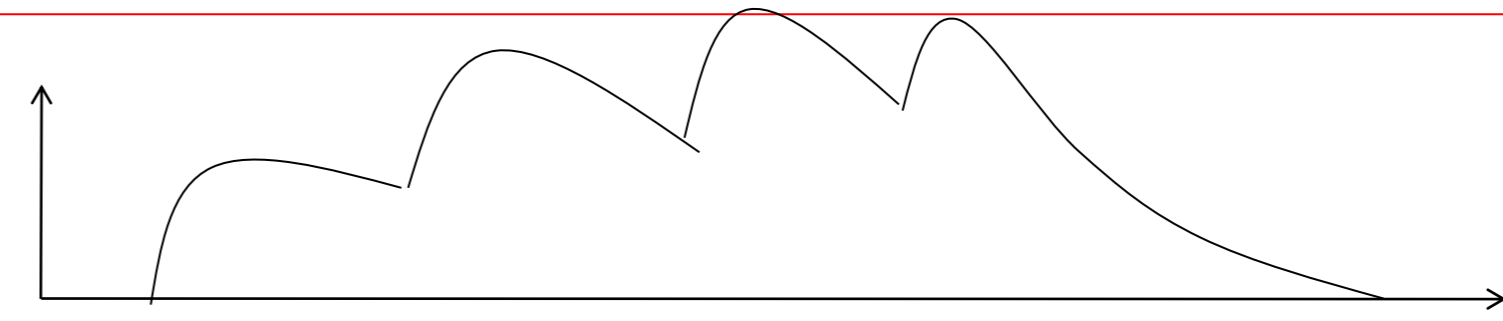
stochastic spike arrival
(diffusive noise)



noisy integration

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

Poisson spike arrival: Mean and autocorrelation of filtered signal



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

$$F(s)$$

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

Filter

Assumption:
stochastic spiking
rate $\nu(t)$

mean

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

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

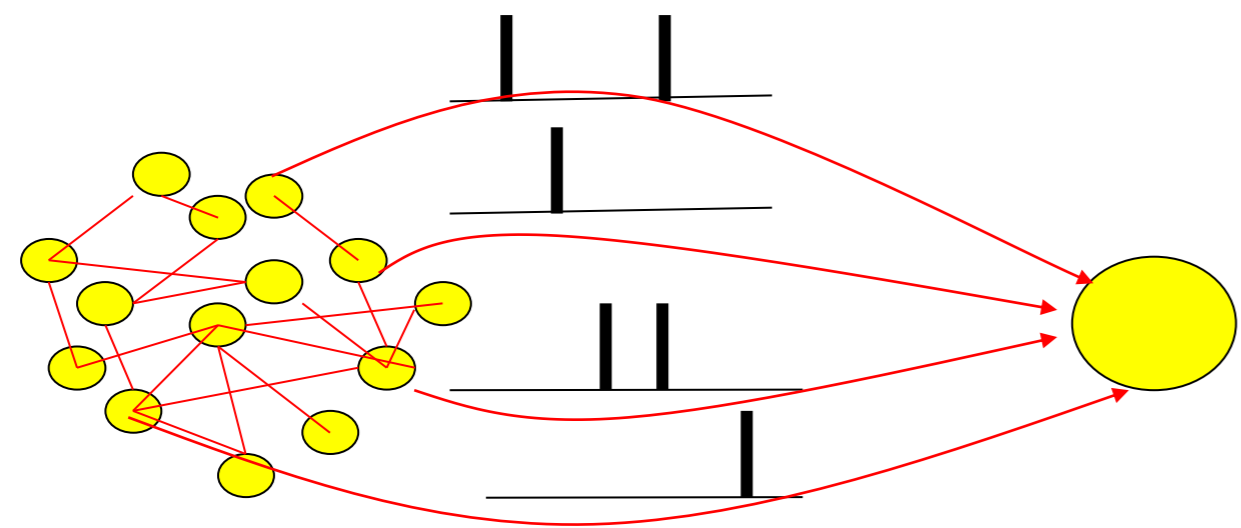
Autocorrelation of output

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

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

Autocorrelation of input

Diffusive noise (stochastic spike arrival)



Stochastic spike arrival:
 excitation, total rate R_e
 inhibition, total rate R_i

Synaptic current pulses

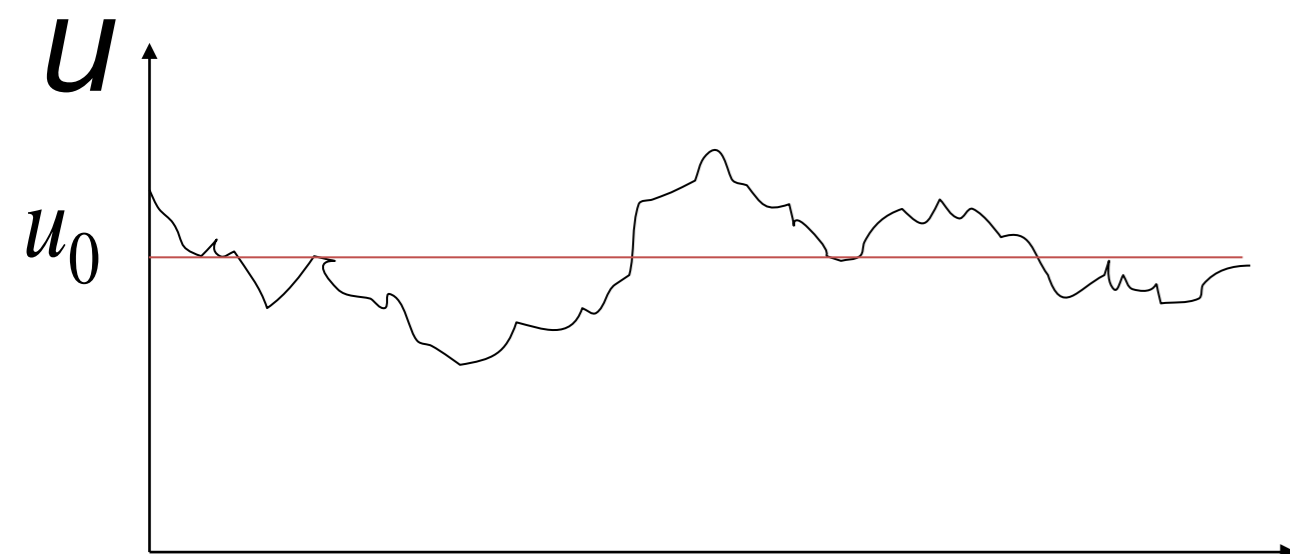
$$\tau \frac{d}{dt} u = -(u - u_{rest}) + \underbrace{\sum_{k,f} \frac{q_e}{C} \delta(t - t_k^f)}_{\text{EPSC}} - \underbrace{\sum_{k',f'} \frac{q_i}{C} \delta(t - t_{k'}^{f'})}_{\text{IPSC}}$$

EPSC

IPSC

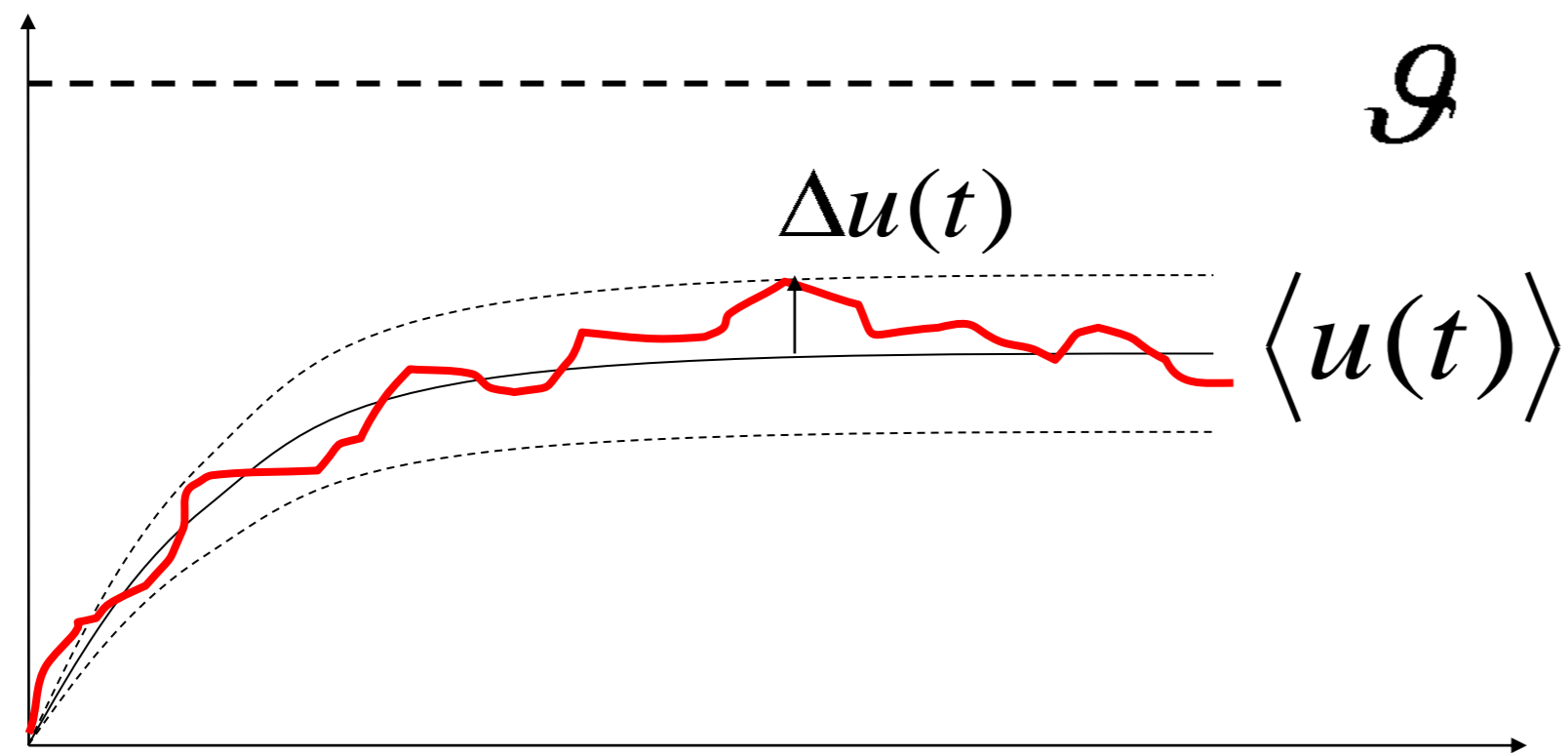
$$\tau \frac{d}{dt} u = -(u - u_{rest}) + RI(t) + \xi(t)$$

Blackboard

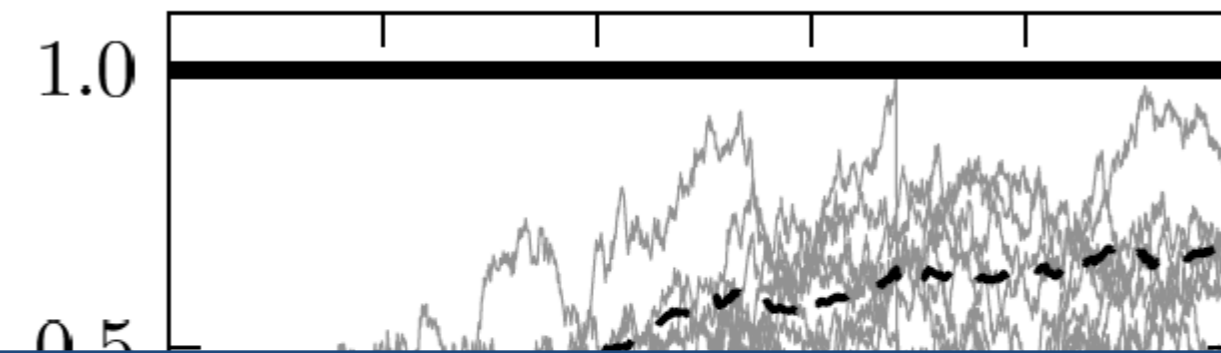


Langevin equation,
 Ornstein Uhlenbeck process

Diffusive noise (stochastic spike arrival)



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



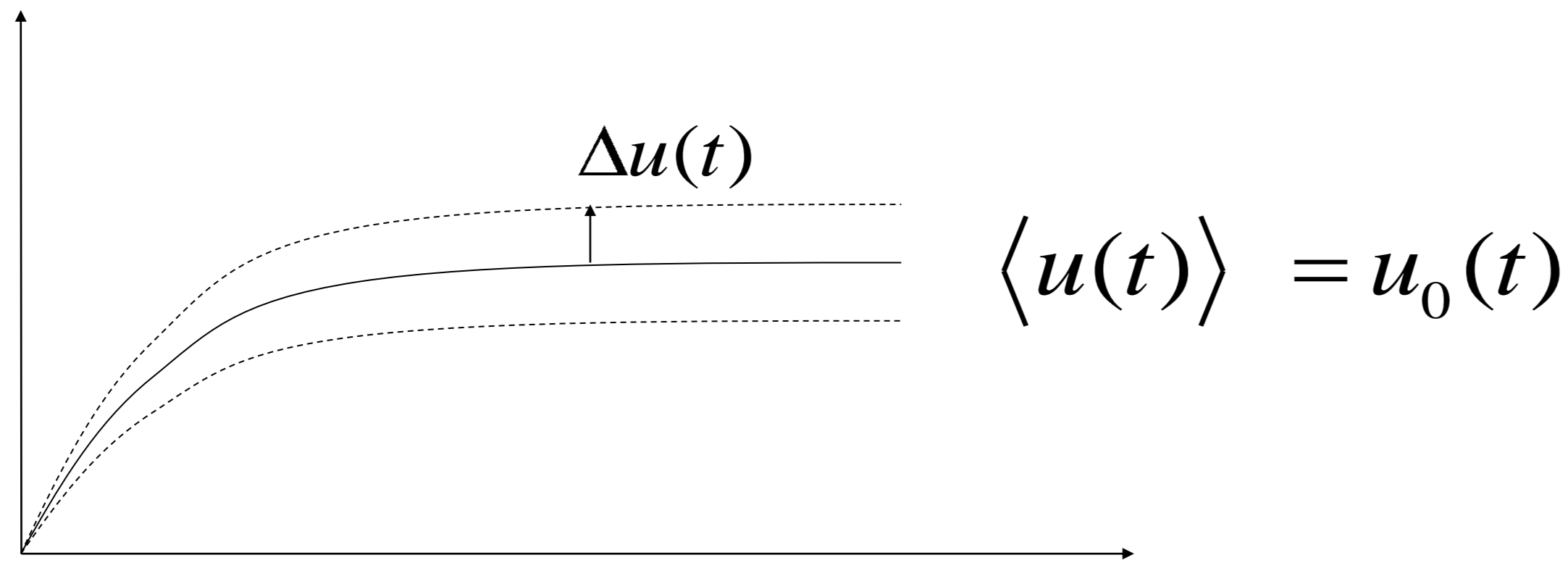
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t)u(t) \rangle - \langle u(t) \rangle^2 =$$

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

Math argument:

- *no threshold*
- *trajectory starts at known value*

Diffusive noise (stochastic spike arrival)



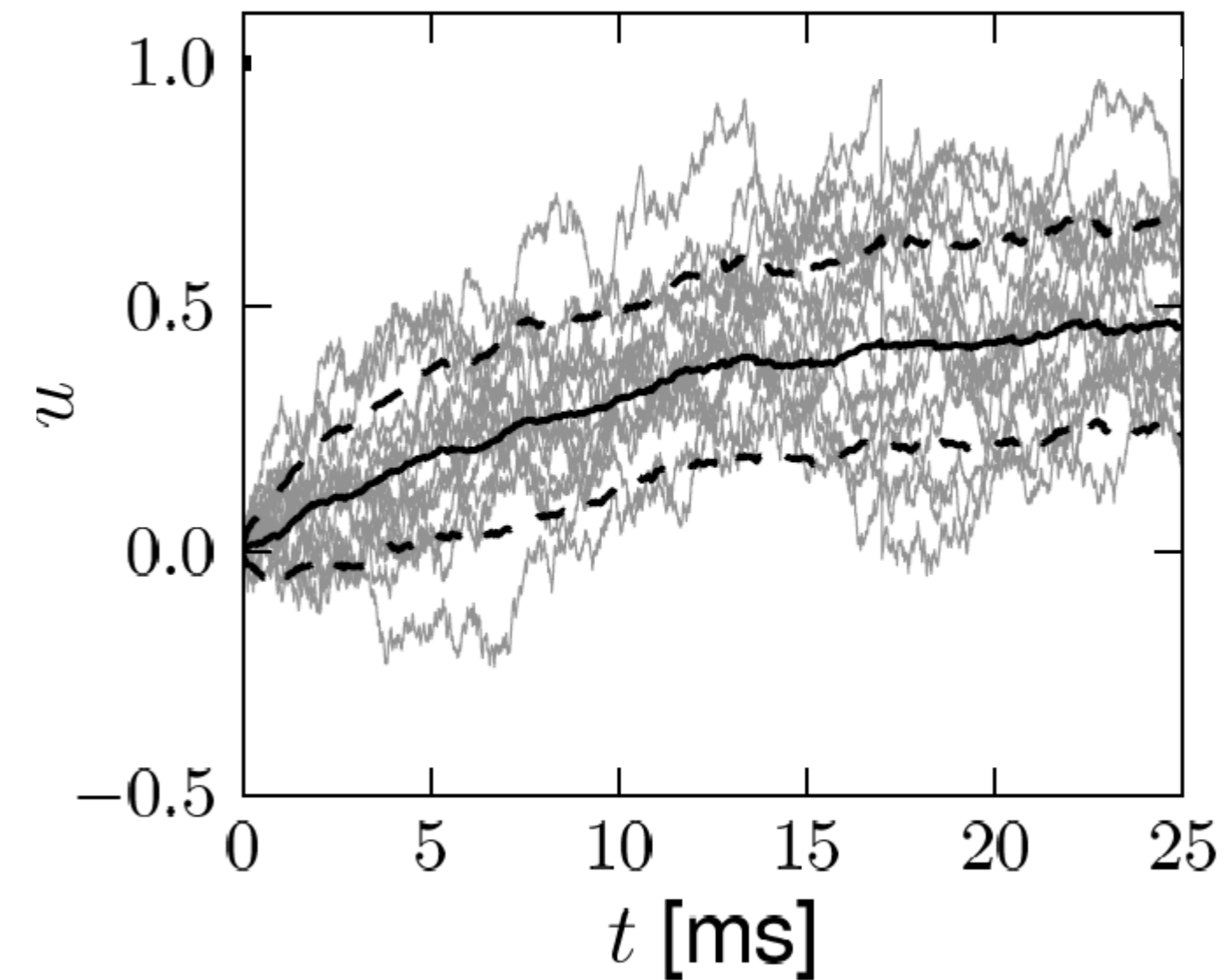
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t)u(t) \rangle - \langle u(t) \rangle^2 =$$

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

Math argument

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

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

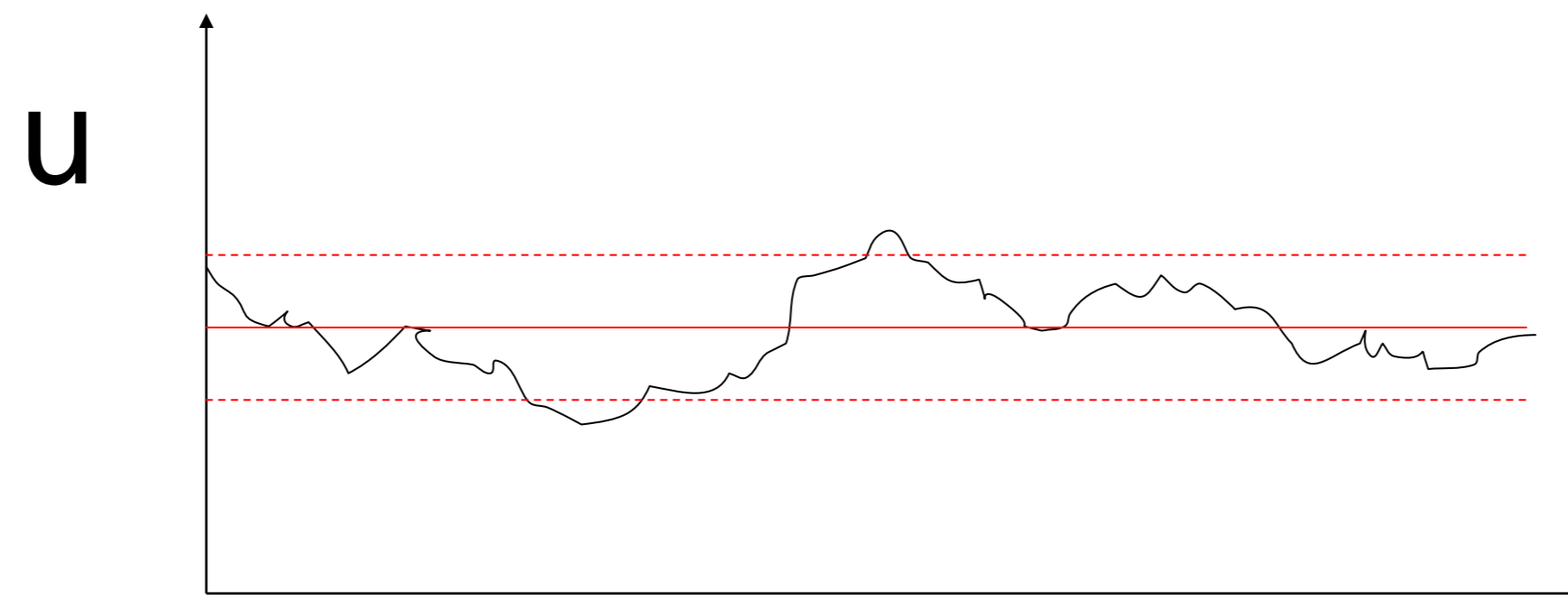
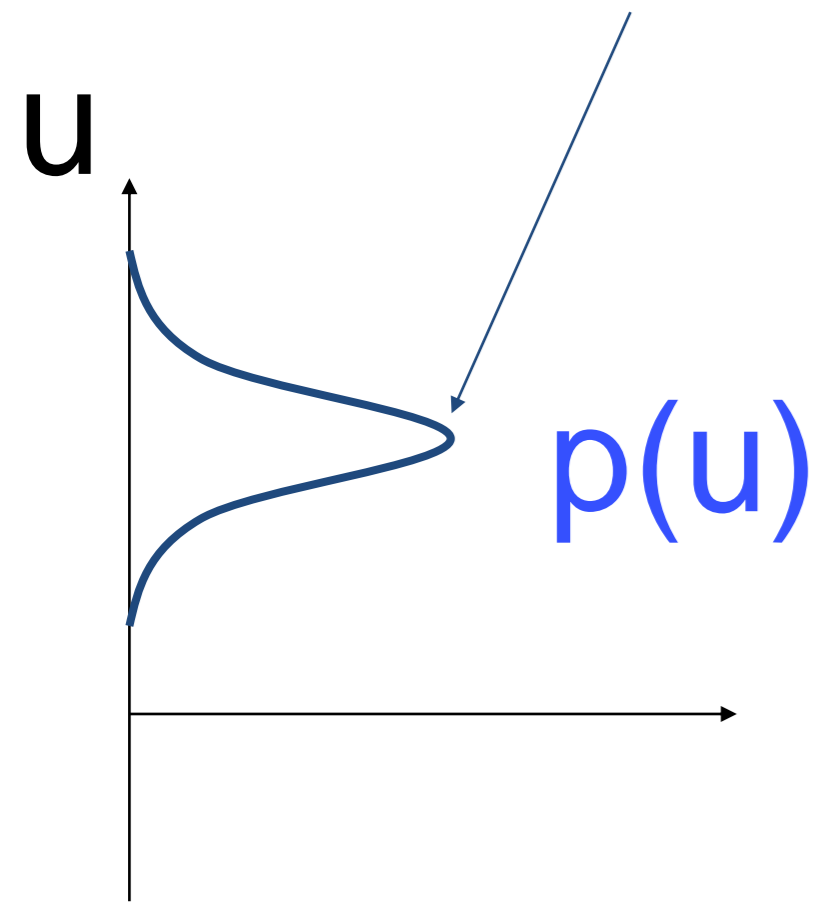


$$\langle [\Delta u(t)]^2 \rangle = \sigma_u^2 [1 - \exp(-2t / \tau)]$$

Neuronal Dynamics – 8.6. Diffusive noise/stoch. arrival

A) No threshold, stationary input

Membrane potential density: Gaussian



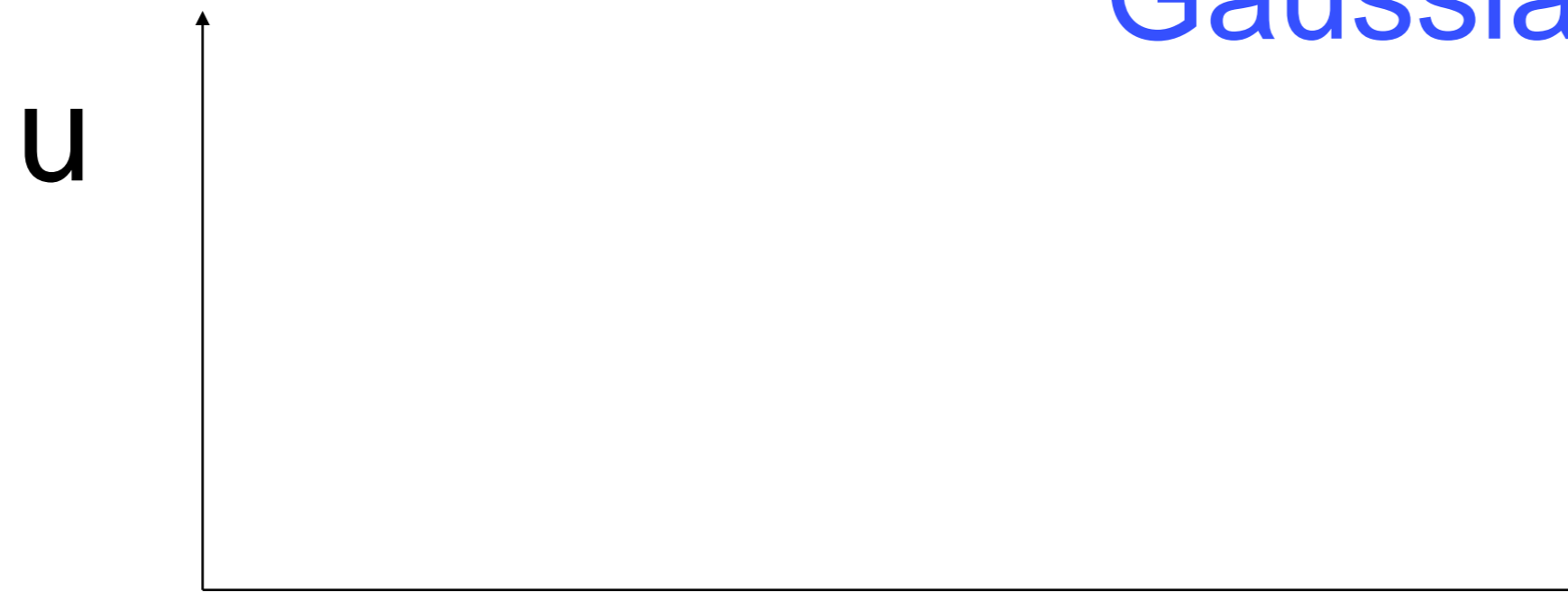
constant input rates
no threshold

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

Neuronal Dynamics – 8.6 Diffusive noise/stoch. arrival

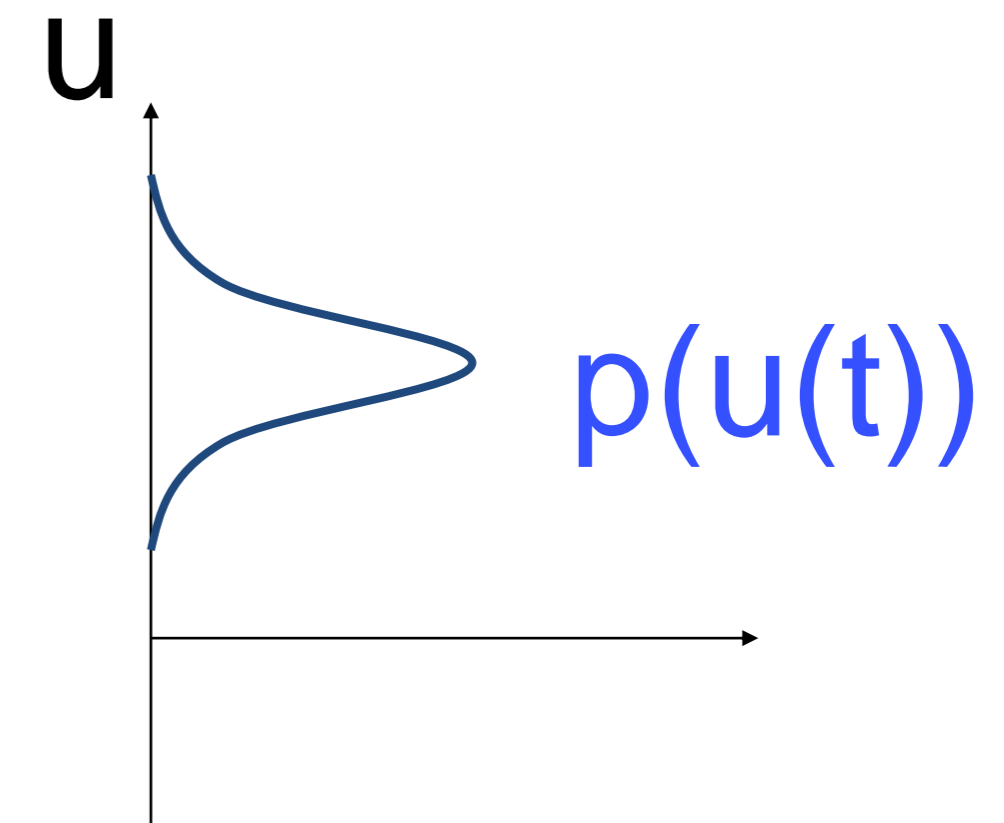
B) No threshold, oscillatory input

Membrane potential density:
Gaussian at time t



noisy integration

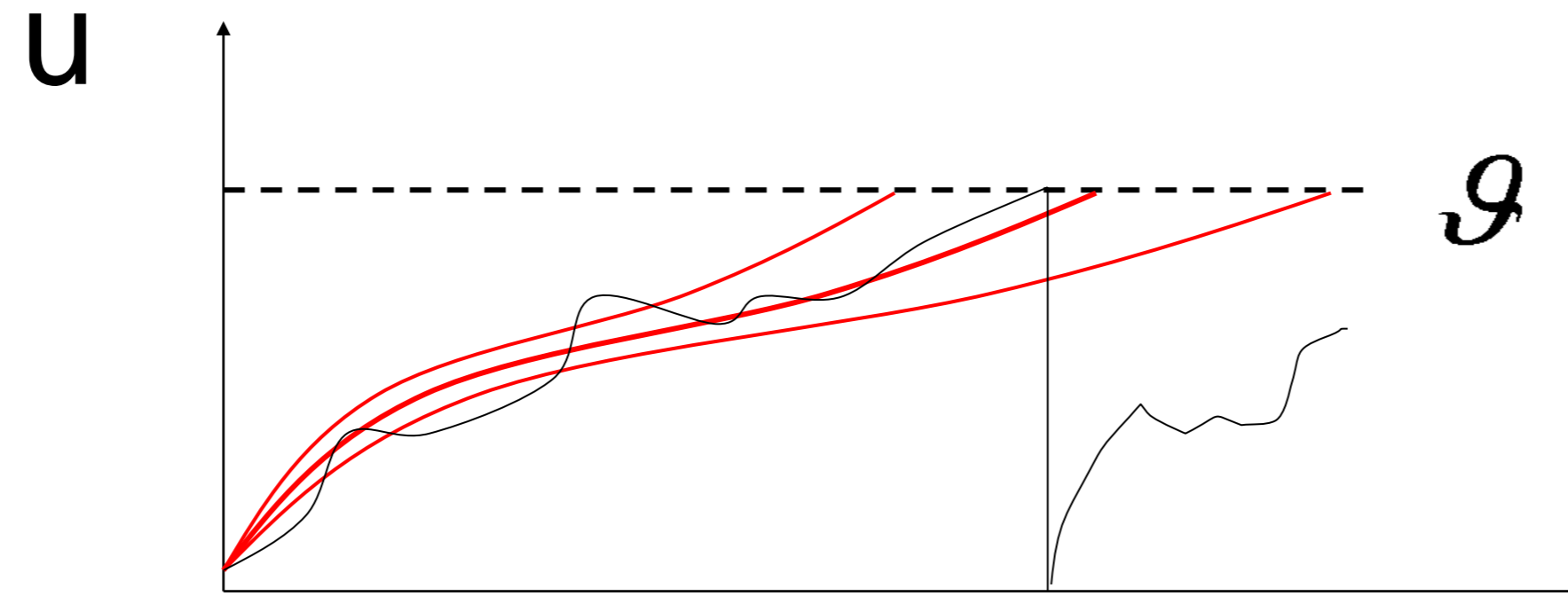
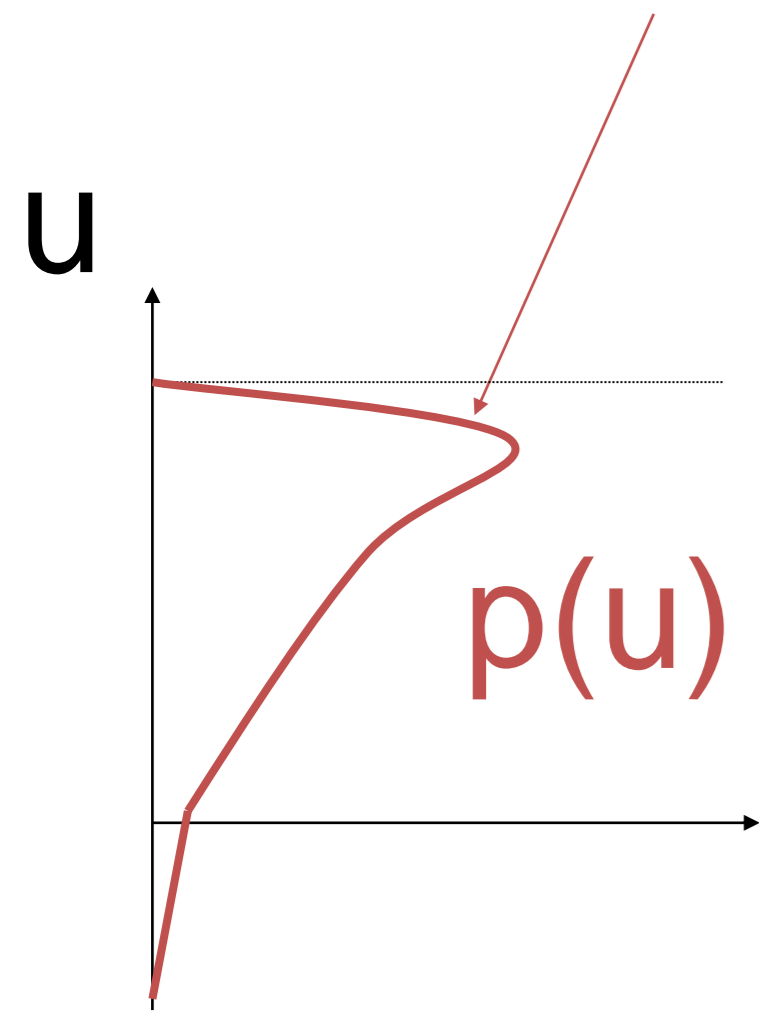
$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$



Neuronal Dynamics – 6.4. Diffusive noise/stoch. arrival

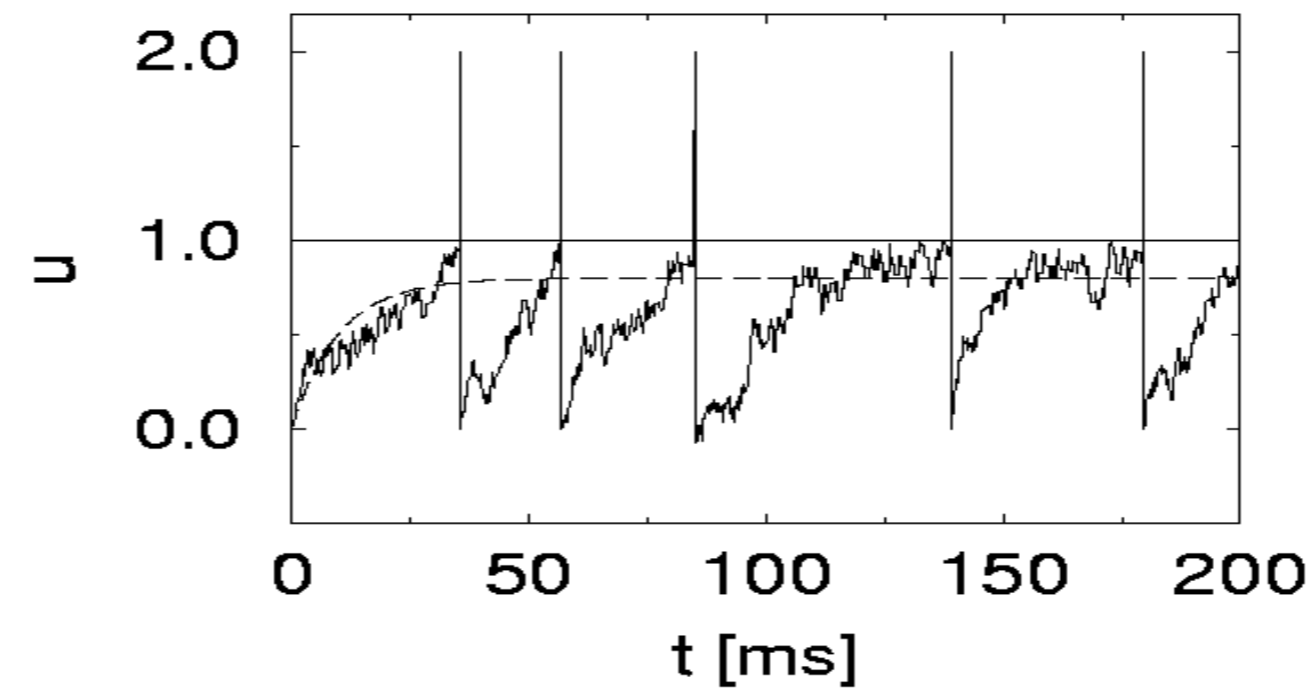
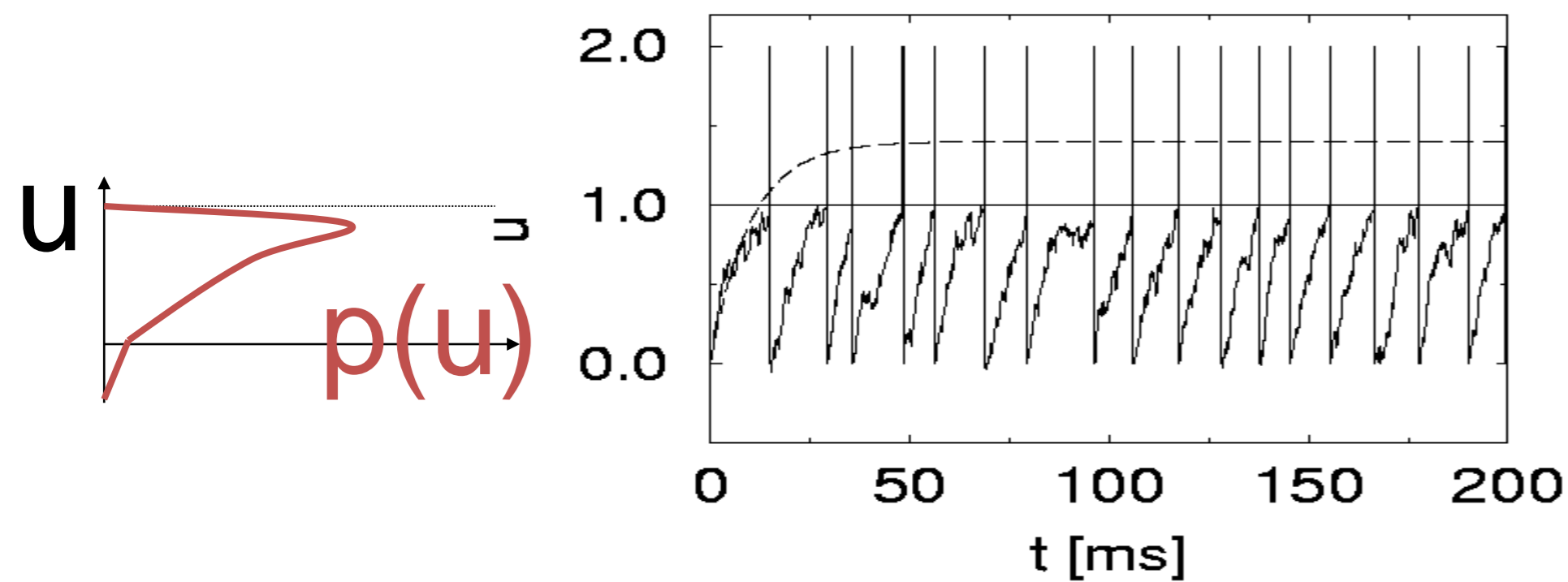
C) With threshold, reset/ stationary input

Membrane potential density



Neuronal Dynamics – 8.6. Diffusive noise/stoch. arrival

Superthreshold vs. Subthreshold regime



Nearly Gaussian
subthreshold distr.

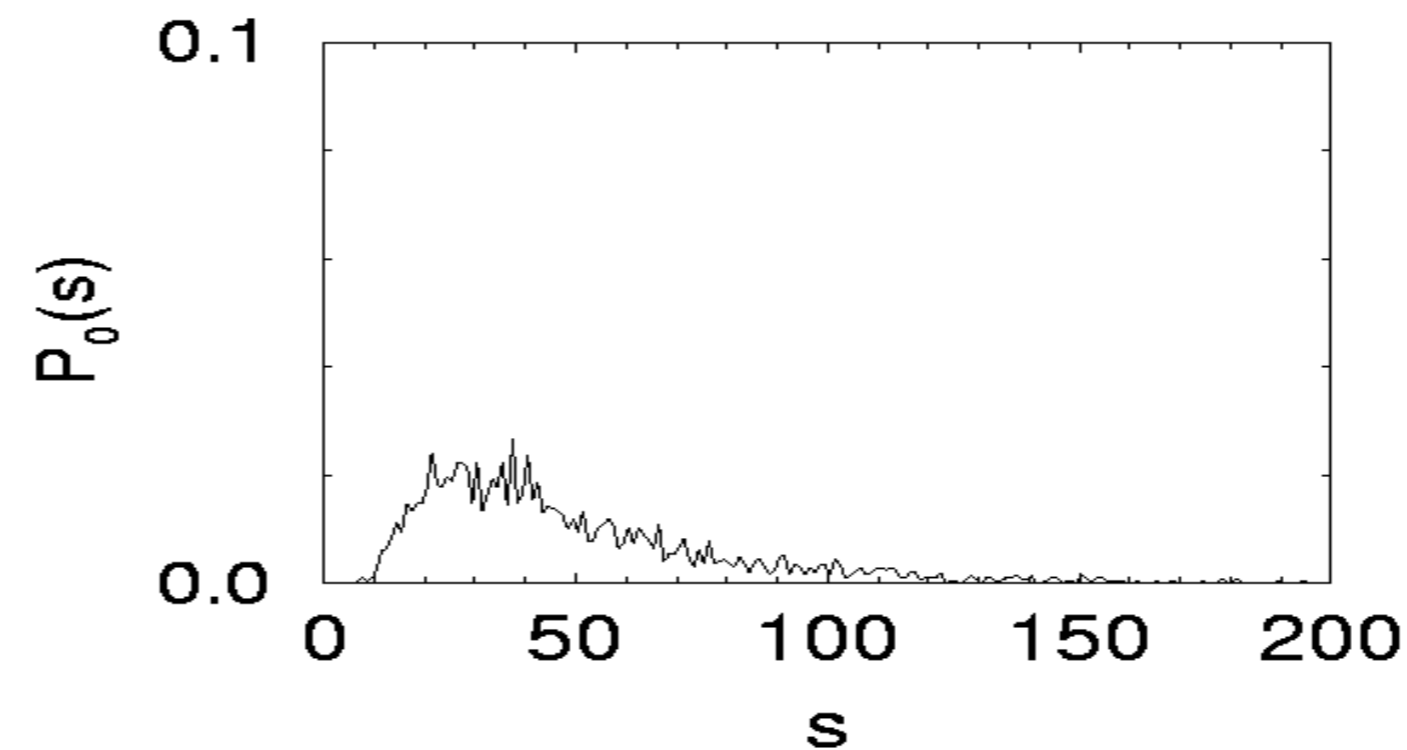
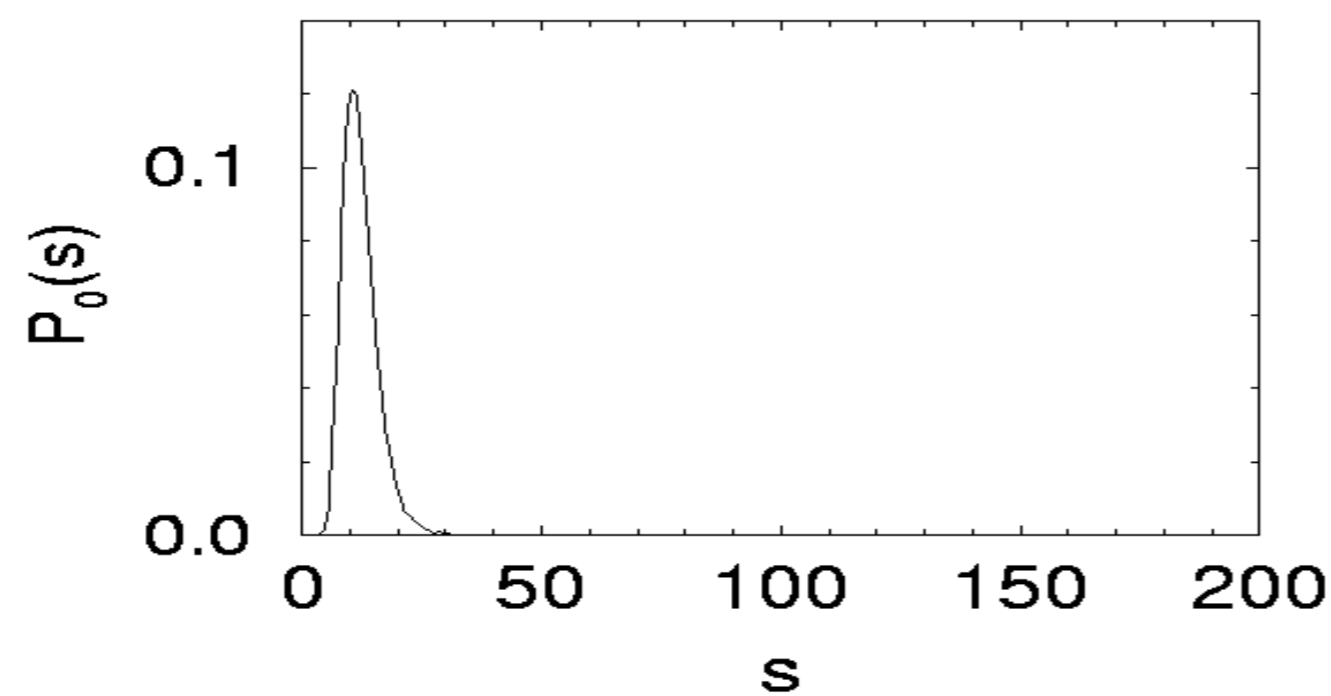
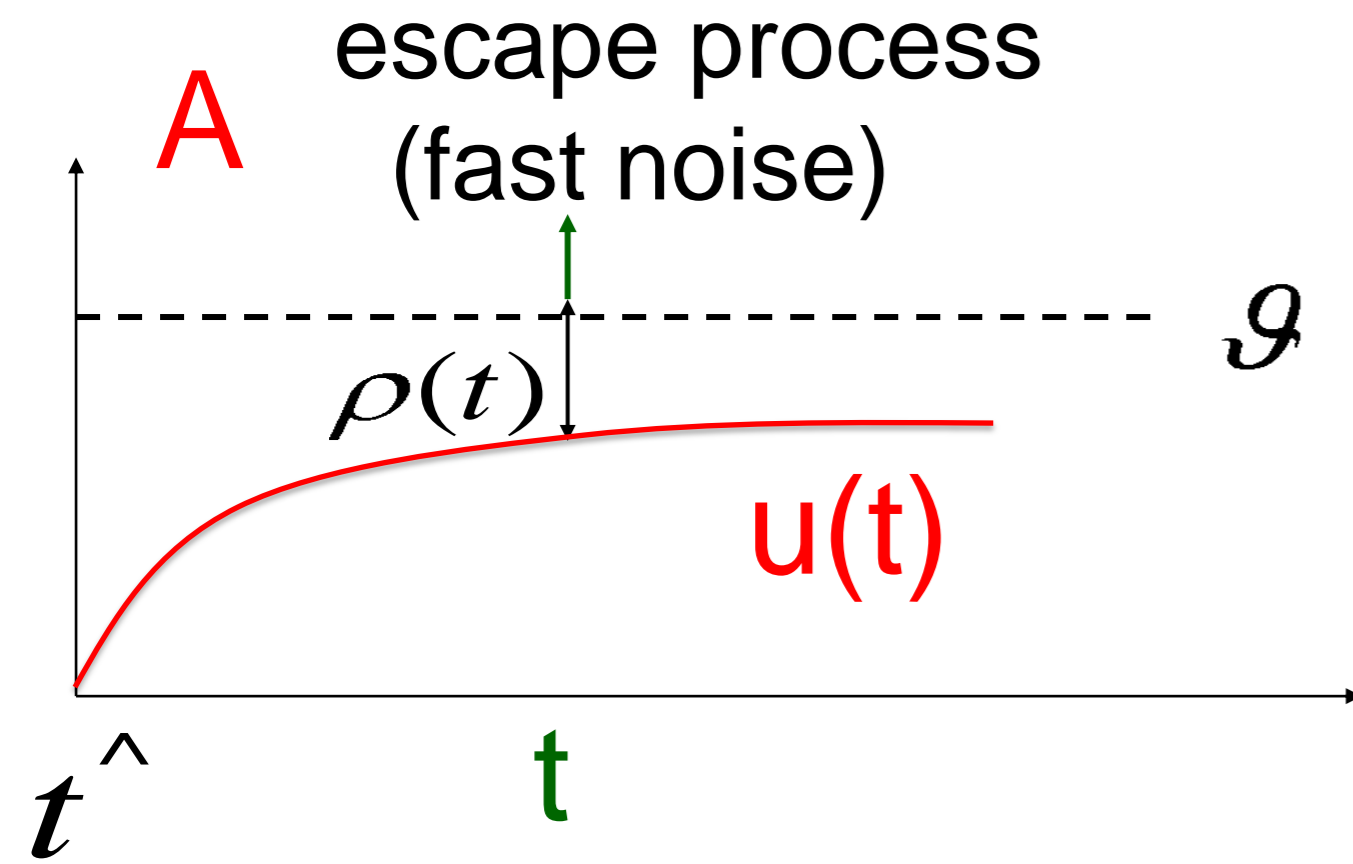


Image:
Gerstner et al. (2013)
Cambridge Univ. Press;
See: Konig et al. (1996)

Neuronal Dynamics – 8.6. Comparison of Noise Models



escape rate

$$\rho(t) = f(u(t) - \mathcal{G})$$

Interval distribution

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

escape rate

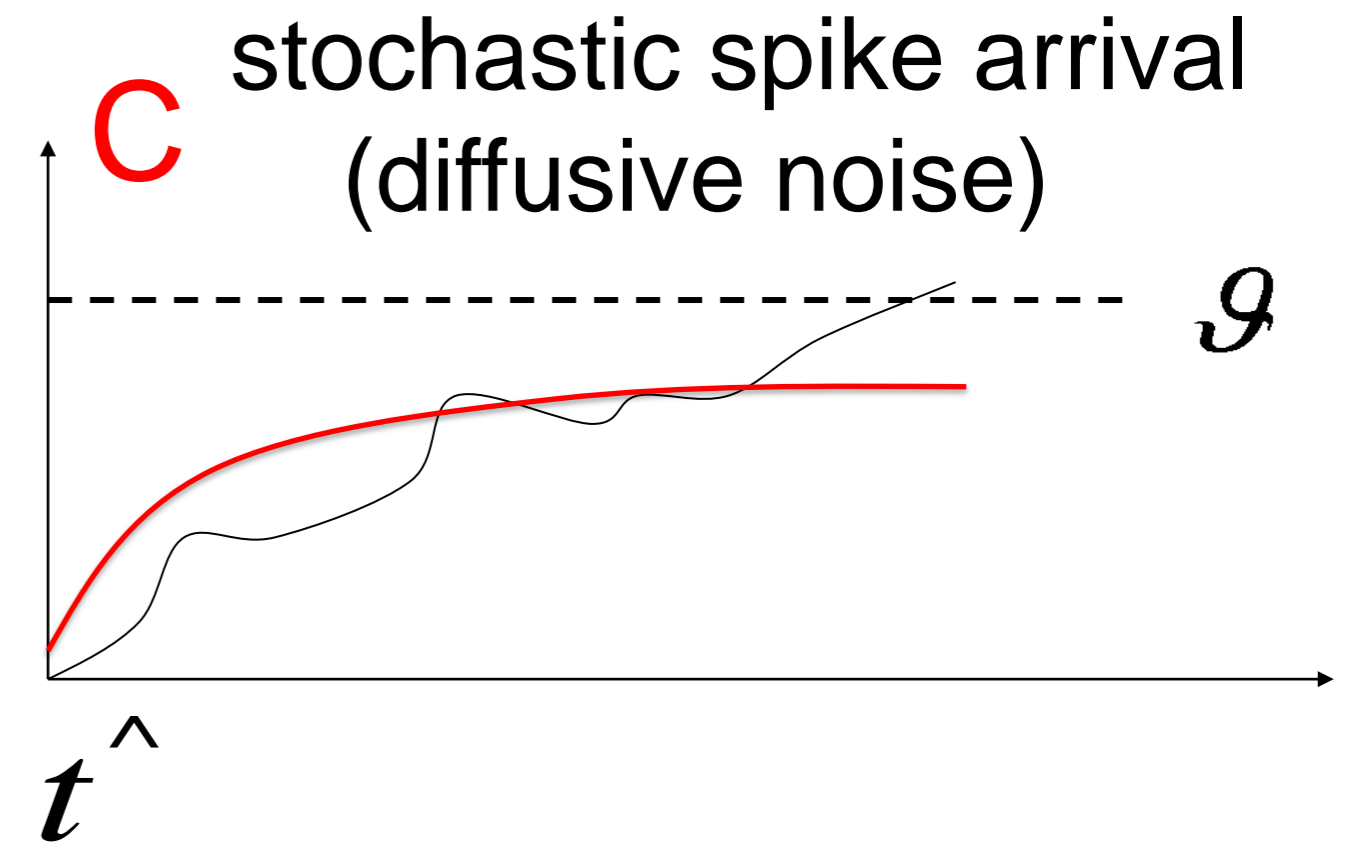
Survivor function

Stationary input:
-Mean ISI

$$\langle s \rangle = \tau_m \sqrt{\pi} \int_{\frac{u_r - h_0}{\sigma}}^{\frac{\vartheta - h_0}{\sigma}} du \exp(u^2) [1 + \operatorname{erf}(u)]$$

Siegert 1951

-Mean firing rate



noisy integration

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

noise

white (fast noise) : first passage time problem (Brunel et al., 2001)
synapse (slow noise)

Neuronal Dynamics – 8.6 Comparison of Noise Models

Diffusive noise

- distribution of potential
- mean interspike interval

FOR CONSTANT INPUT

- time dependent-case difficult

Escape noise

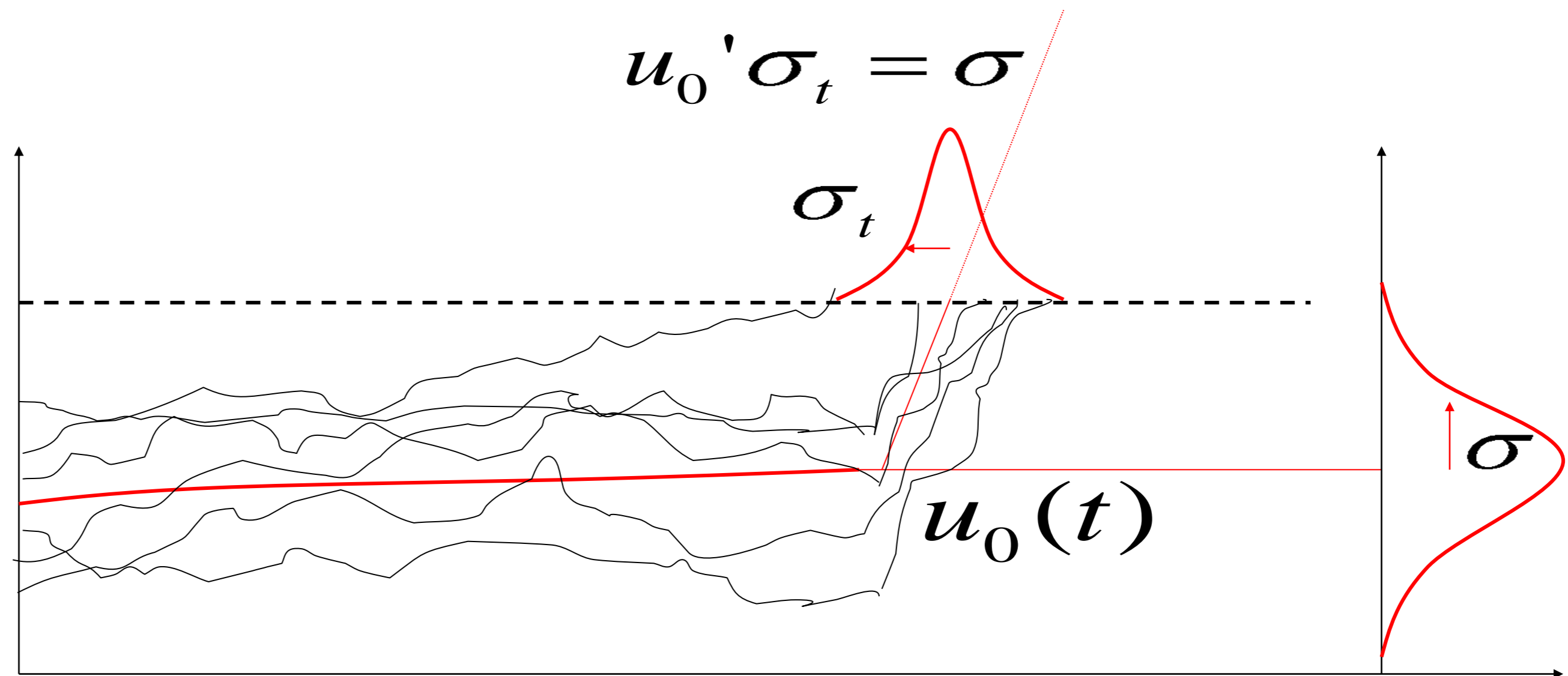
- time-dependent interval distribution

Noise models: from diffusive noise to escape rates

noisy integration

\mathcal{G}

stochastic spike arrival
(diffusive noise)

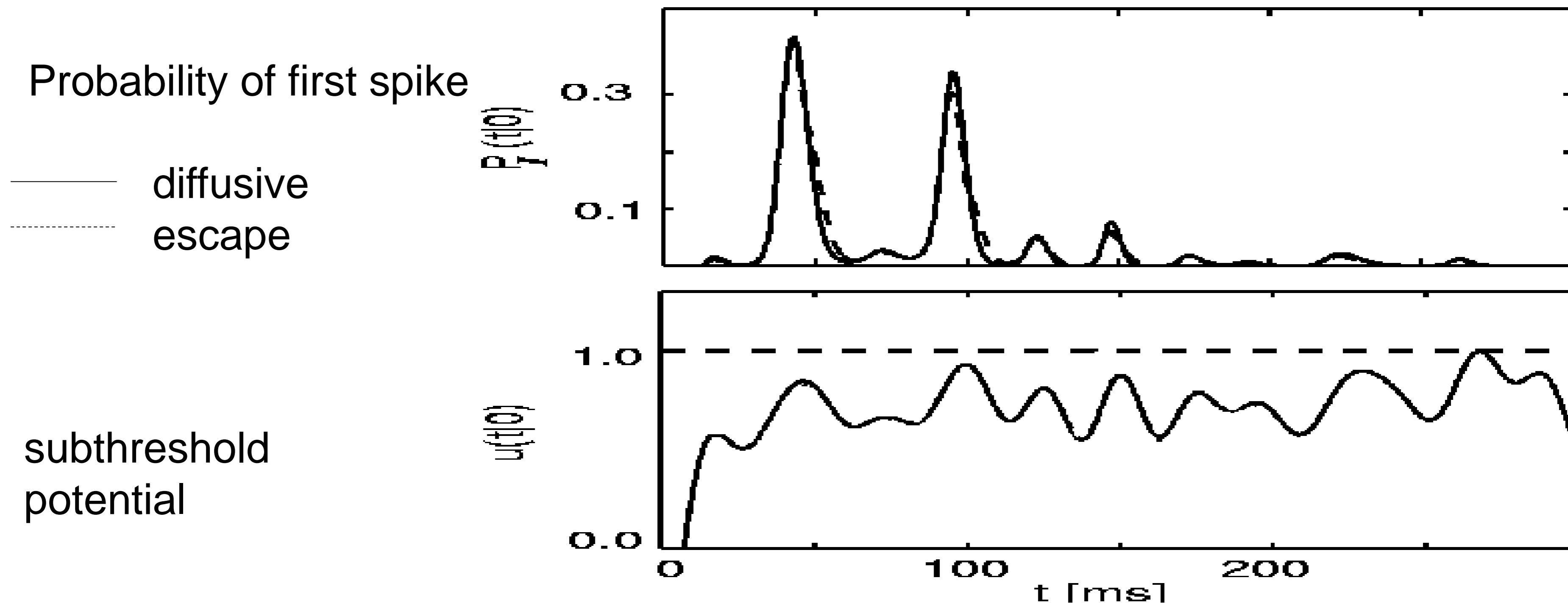


escape rate

$$\rho(t) = f(u_0(t), u_0'(t)) \propto \frac{\exp\left(-\frac{(u_0(t) - \mathcal{G})^2}{2\sigma^2}\right)}{\text{erf}\left((u_0(t) - \mathcal{G}) / \sigma\right)} [1 + u_0'(t)]$$

Comparison: diffusive noise vs. escape rates

Plesser and Gerstner (2000)



escape rate

$$\rho(t) = f(u_0(t), u'_0(t)) \propto \exp\left(-\frac{(u_0(t) - \mathcal{G})^2}{2\sigma^2}\right) [1 + u'_0(t)]$$

Neuronal Dynamics – 8.6 Comparison of Noise Models

Diffusive noise

- represents stochastic spike arrival
- easy to simulate
- hard to calculate

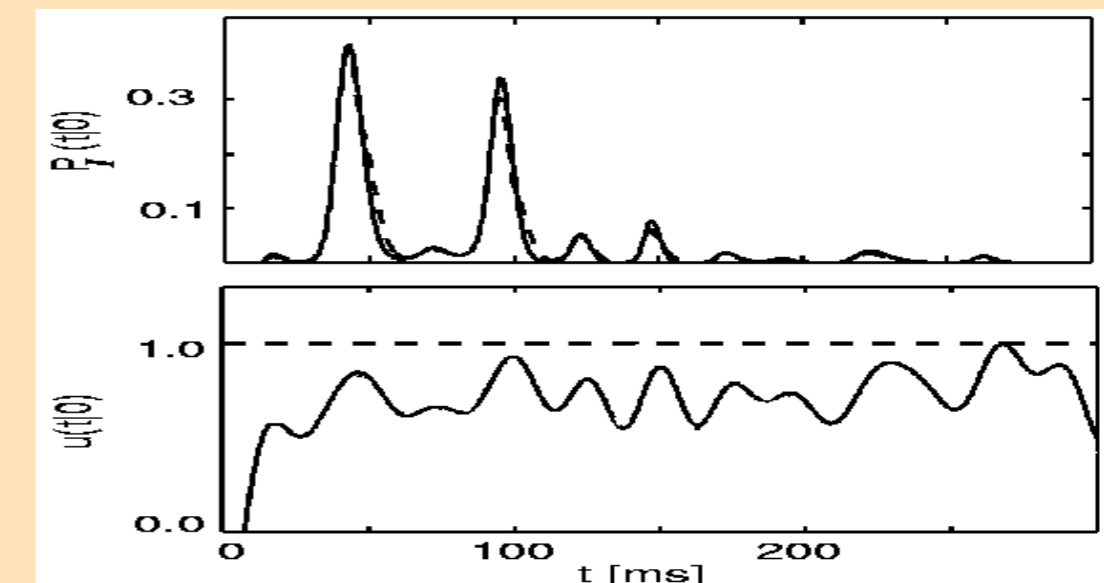
Escape noise

- represents internal noise
- easy to simulate
- easy to calculate
- approximates diffusive noise
- basis of modern model fitting methods

Neuronal Dynamics – Quiz 8.4.

A. Consider a leaky integrate-and-fire model with diffusive noise:

- The membrane potential distribution is always Gaussian.
- The membrane potential distribution is Gaussian for any time-dependent input.
- The membrane potential distribution is approximately Gaussian for any time-dependent input, as long as the mean trajectory stays 'far' away from the firing threshold.
- The membrane potential distribution is Gaussian for stationary input in the absence of a threshold.
- The membrane potential distribution is always Gaussian for constant input and fixed noise level.



B. Consider a leaky integrate-and-fire model with diffusive noise for time-dependent input. The above figure (taken from an earlier slide) shows that

- The interspike interval distribution is maximal where the deterministic reference trajectory is **closest** to the threshold.
- The interspike interval vanishes for very long intervals if the deterministic reference trajectory has stayed close to the threshold before - even if for long intervals it is very close to the threshold.
- If there are several peaks in the interspike interval distribution, peak n is always of smaller amplitude than peak $n-1$.
- I would have ticked the same boxes (in the list of three options above) for a leaky integrate-and-fire model with escape noise.