Week 8 – parts 4-6 Noisy Output: Escape Rate and Soft Threshold

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Biological Modeling of Neural Networks

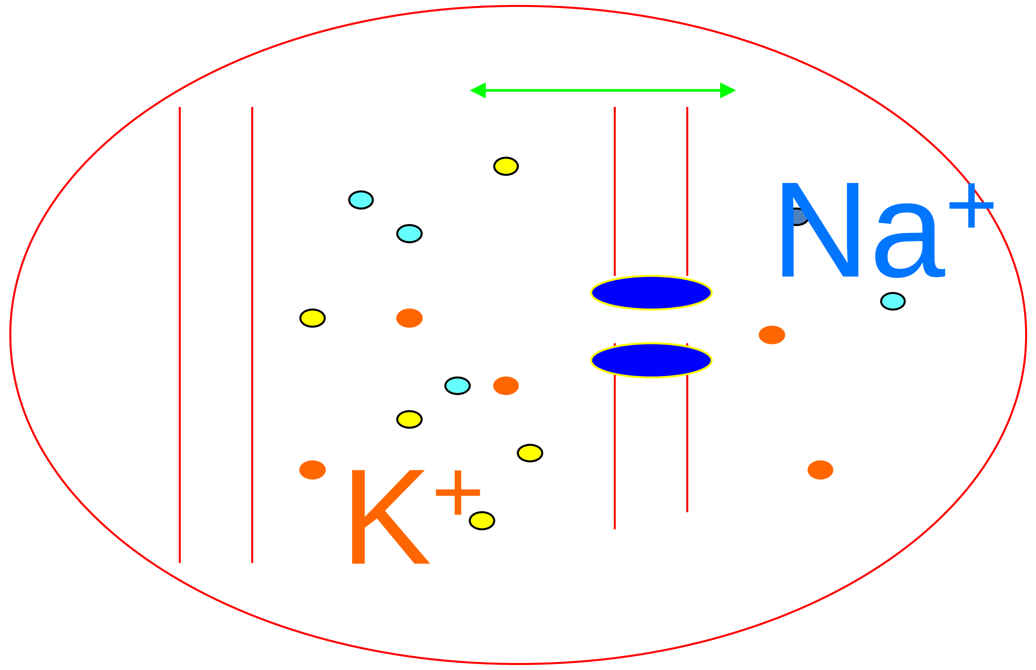
Week 8 – Noisy output models: Escape rate and soft threshold

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Neuronal Dynamics – Review: Sources of Variability

- Intrinsic noise (ion channels)

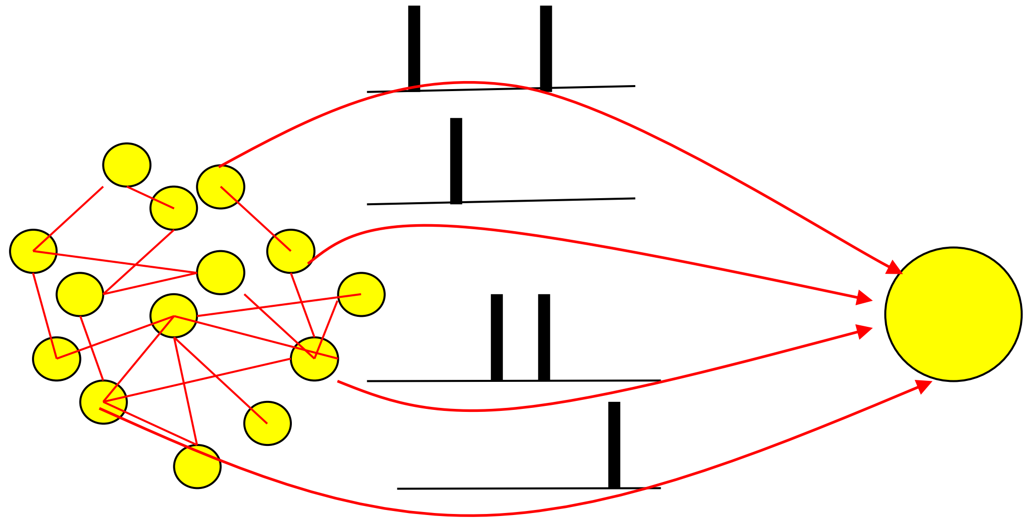


-Finite number of channels

-Finite temperature

small contribution!

-Network noise (background activity)



-Spike arrival from other neurons

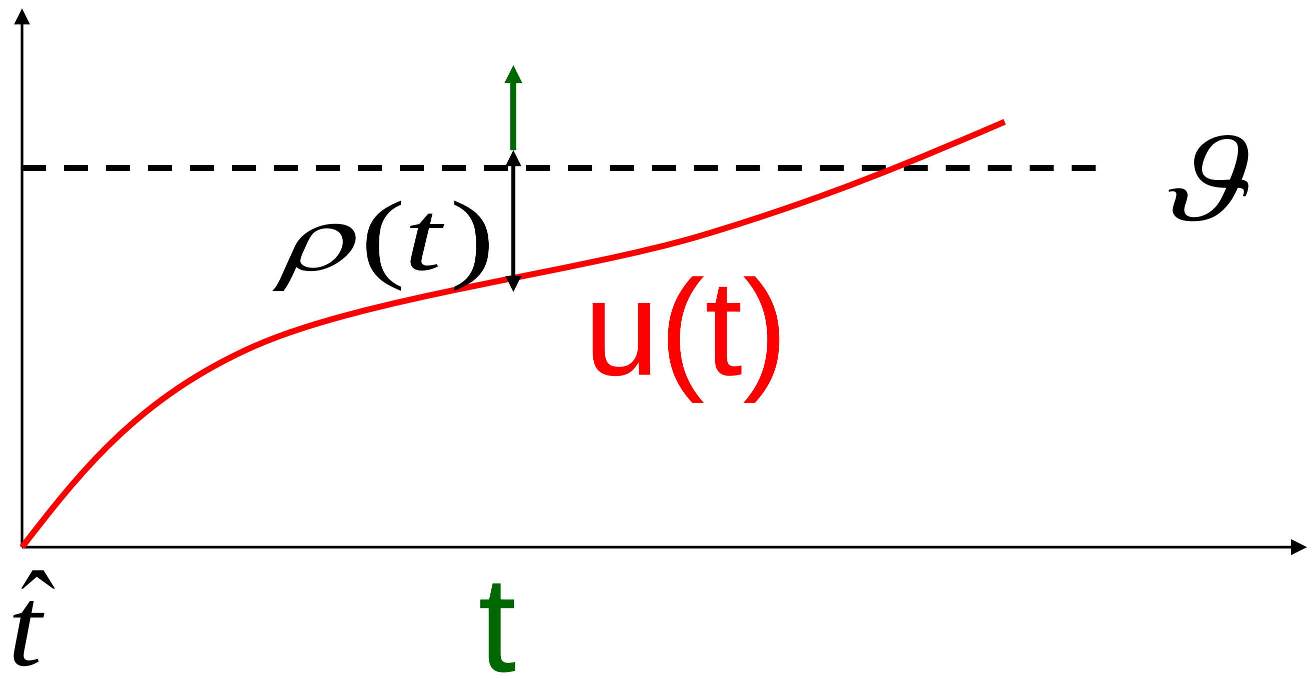
-Beyond control of experimentalist

big contribution!

Noise models?

Noise models

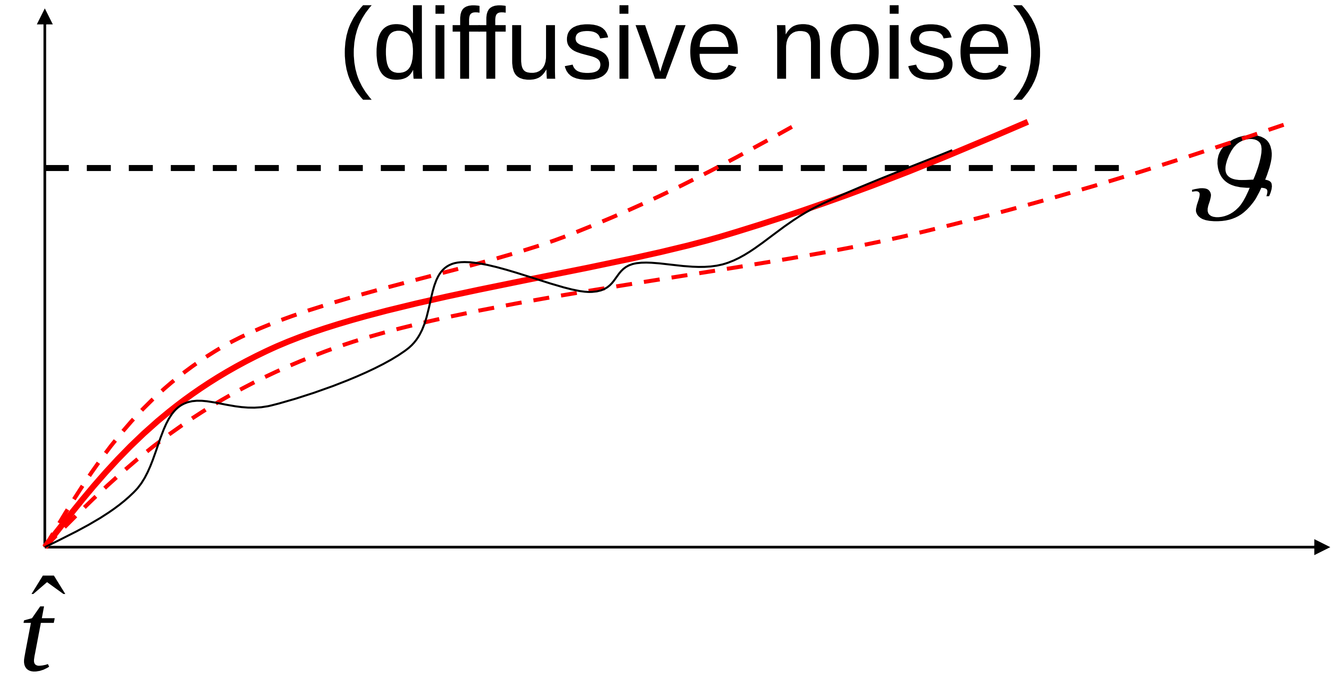
escape process,
stochastic intensity



escape rate

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

stochastic spike arrival
(diffusive noise)



noisy integration

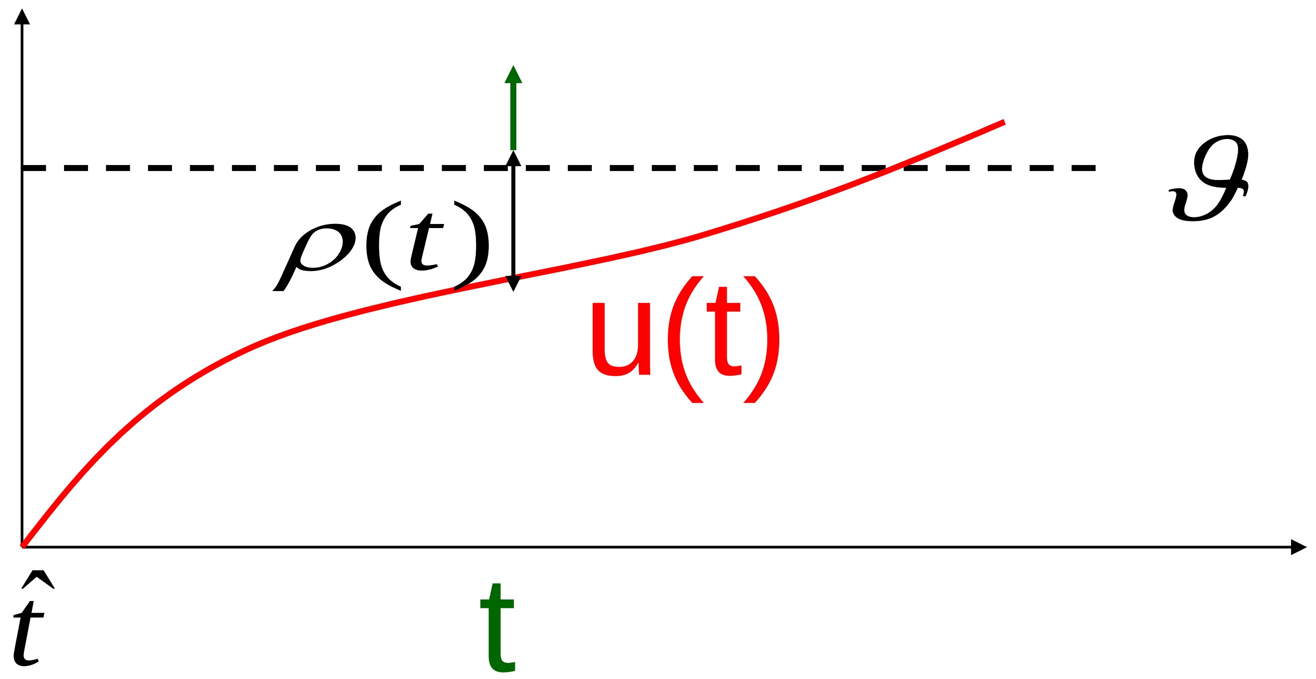
$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$

Now:
Escape noise!

Relation between the two models:
later

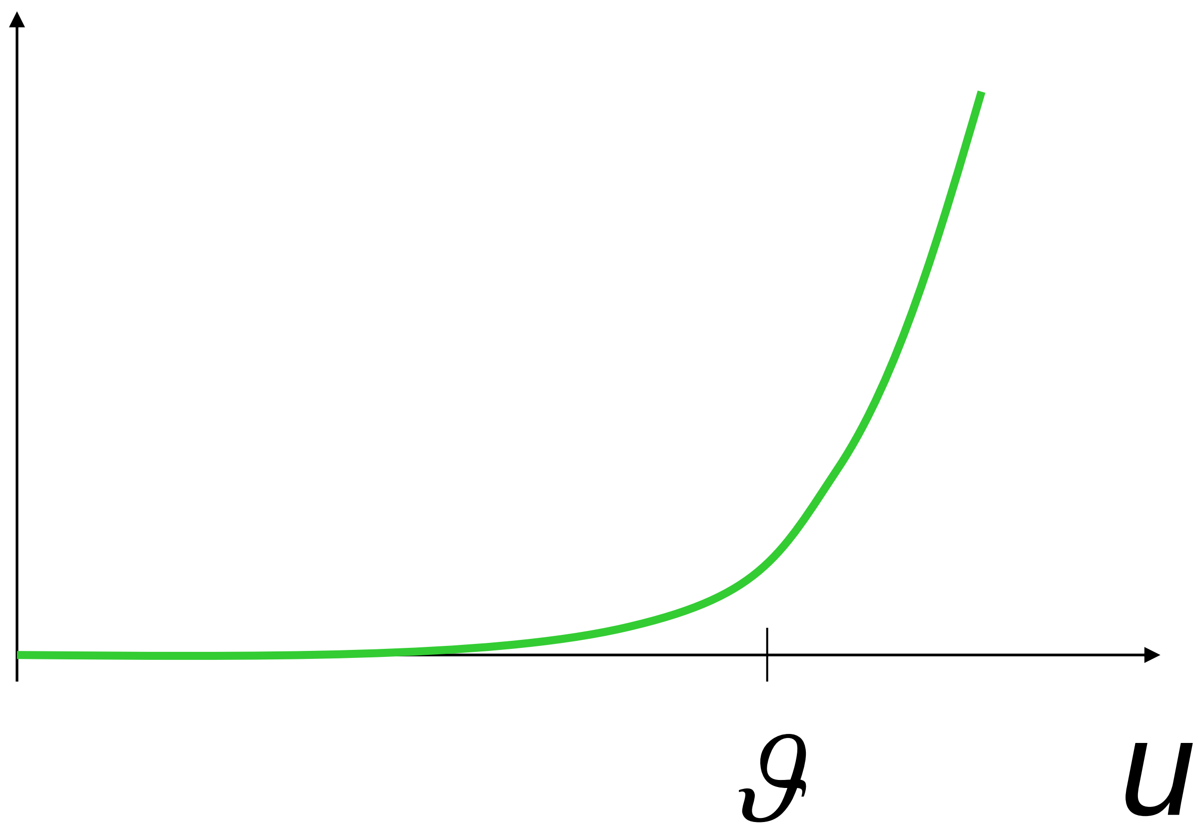
Neuronal Dynamics – 8.4 Escape noise

escape process



escape rate

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



escape rate

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

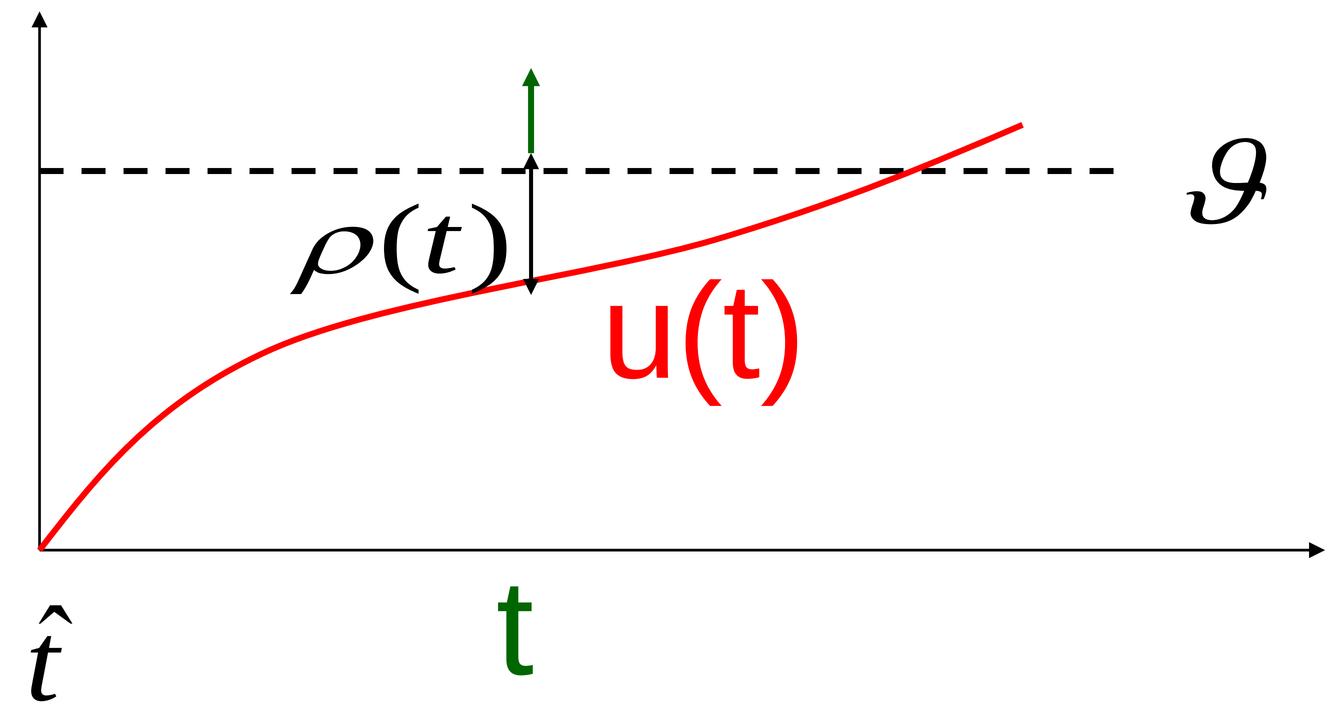
Example: leaky integrate-and-fire model

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

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

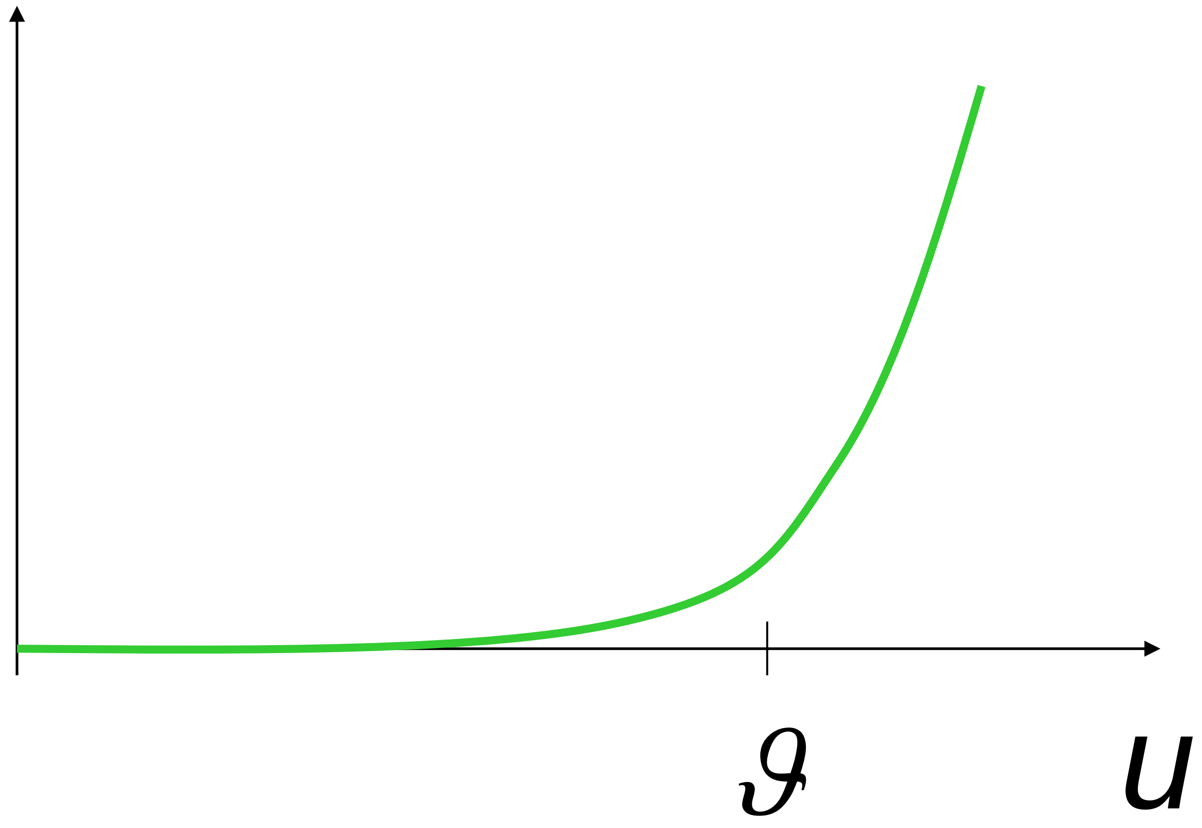
Neuronal Dynamics – 8.4 stochastic intensity

escape process



escape rate

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



Escape rate = stochastic intensity
of point process

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

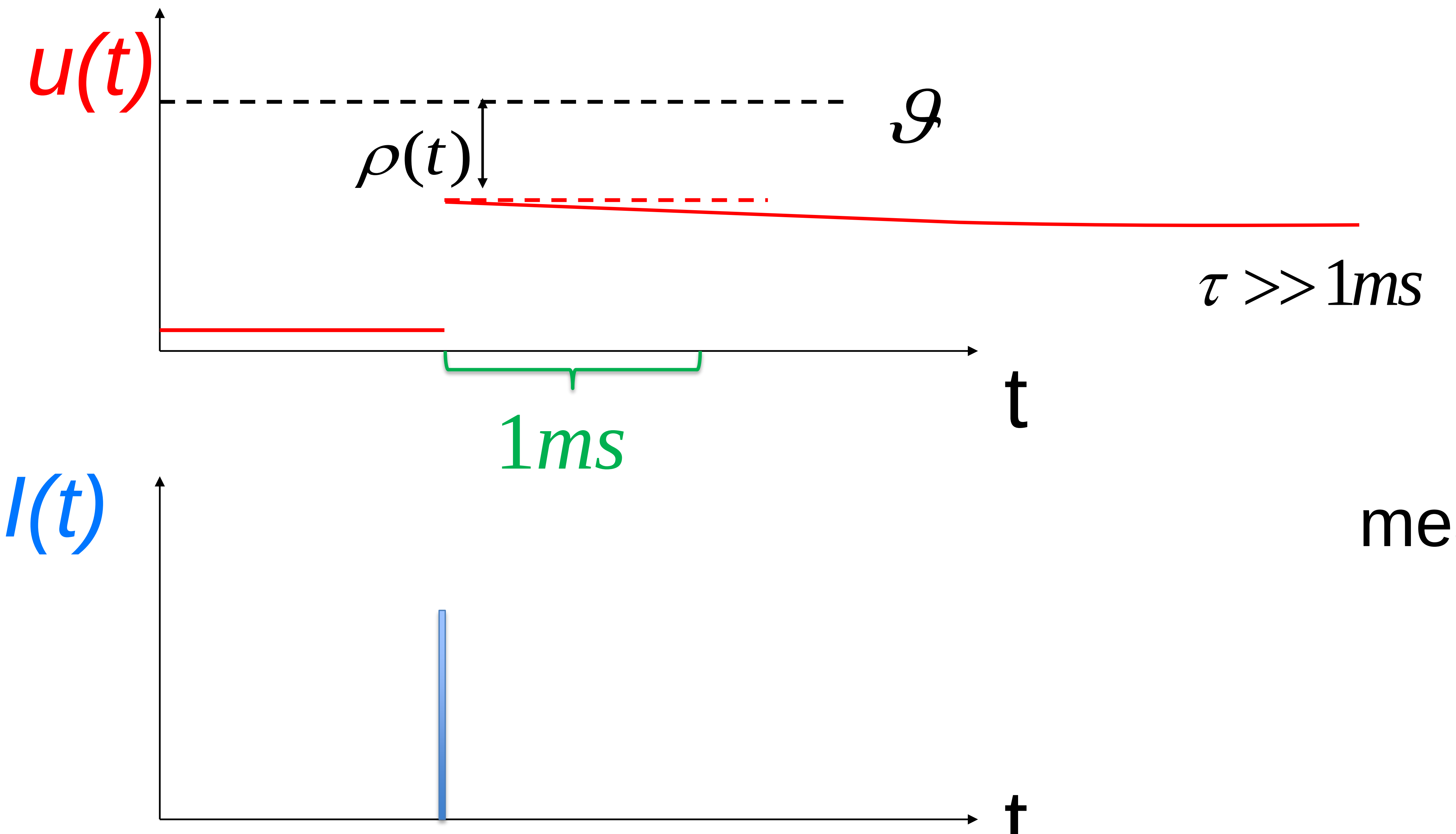
examples

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

$$\rho(t) =$$

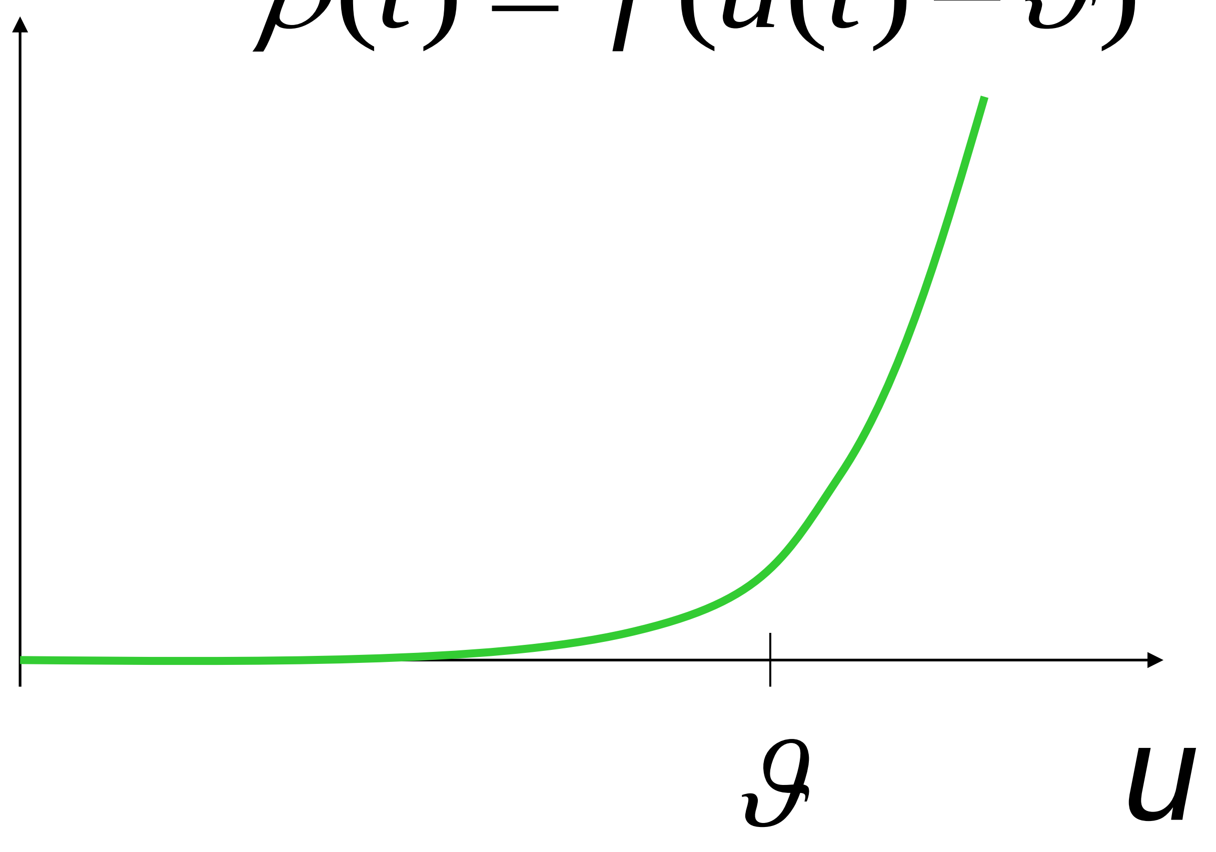
Neuronal Dynamics – 8.4 mean waiting time

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



escape rate

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

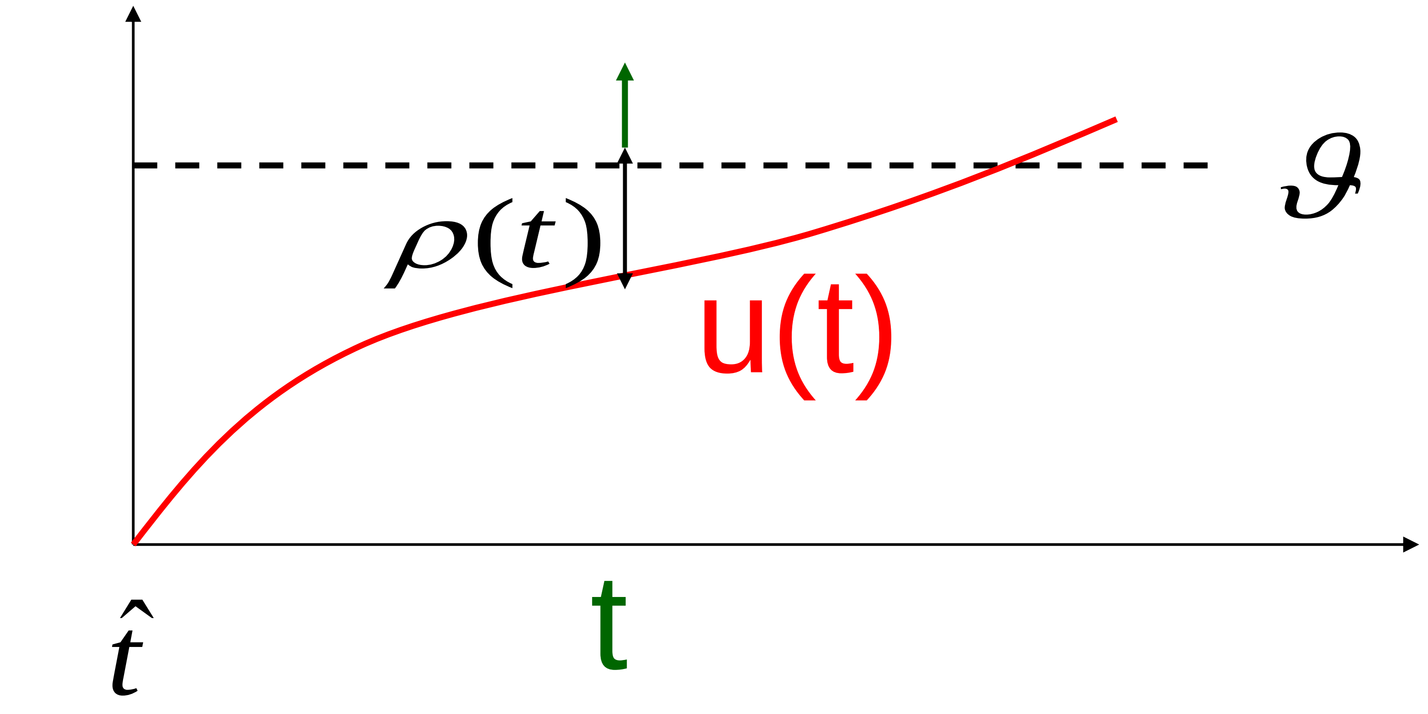


mean waiting time, after switch

Blackboard, Math detour

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

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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

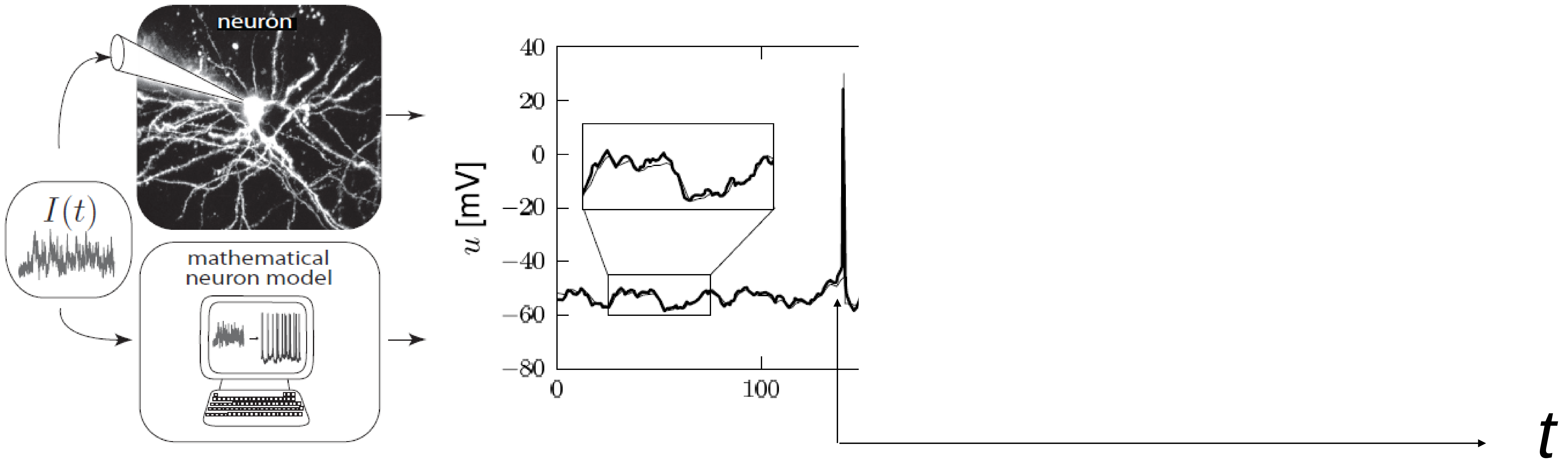
8.2 Autocorrelation of Poisson

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

→ *escape rate*

Example:
nonlinear integrate-and-fire model

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

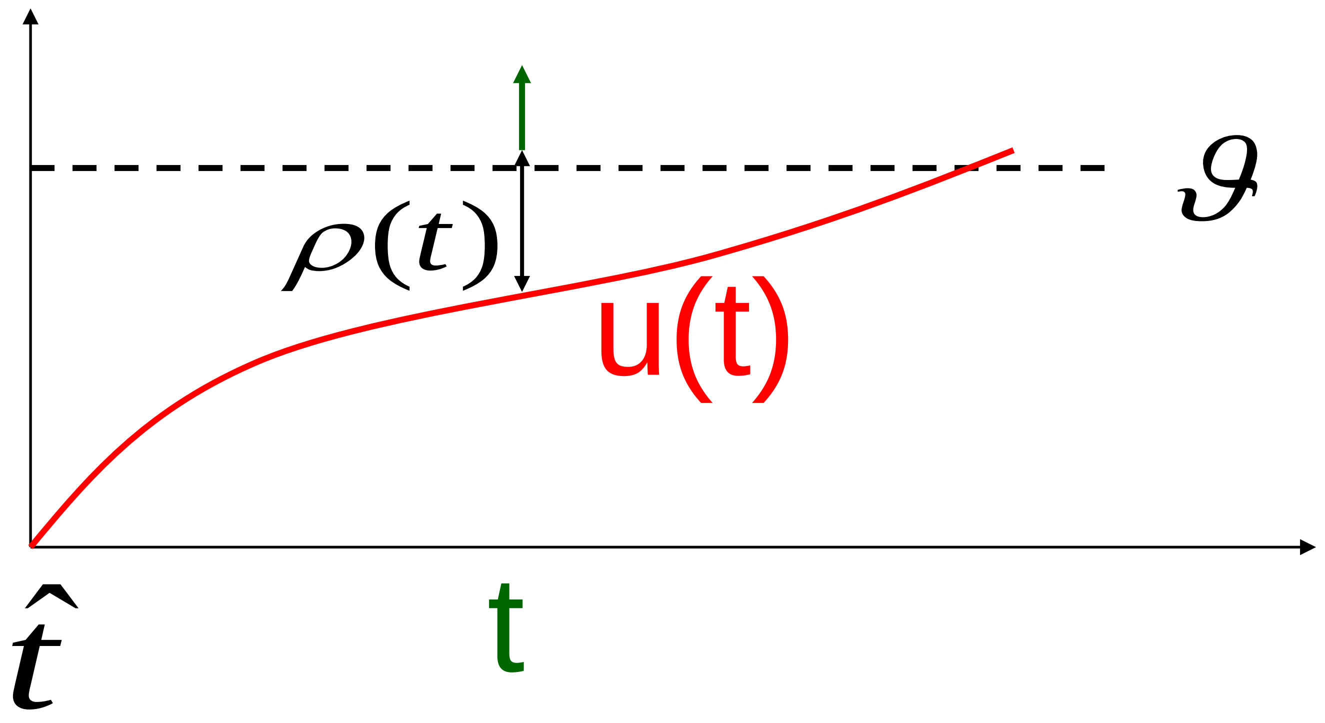
$$\textit{if spike at } t^f \Rightarrow u\left(t^f + \delta\right) = u_r$$

Example:
exponential stochastic intensity

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

Neuronal Dynamics – 8.5. Interspike Interval distribution

escape process



escape rate

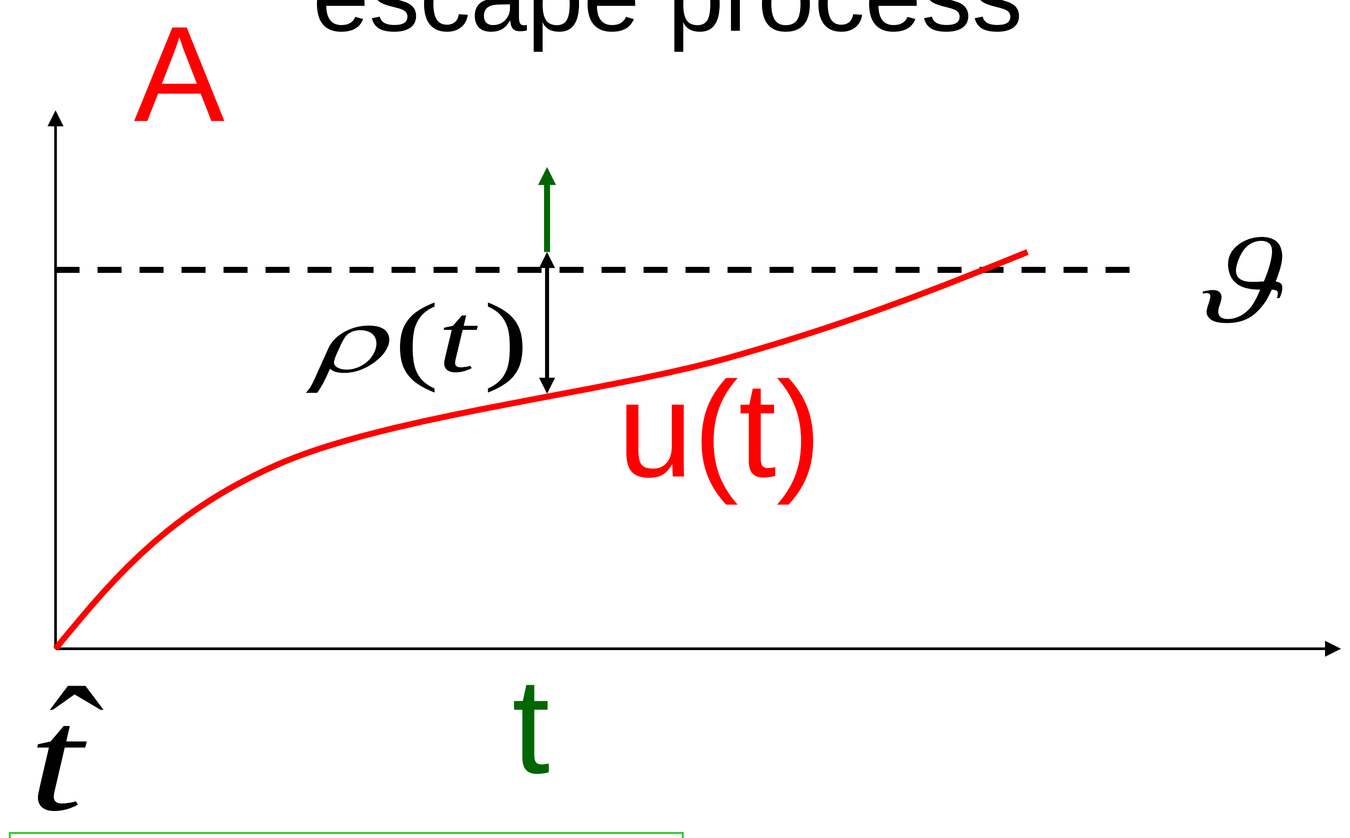
$$\rho(t) = f(u(t) - \vartheta)$$

Survivor function

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

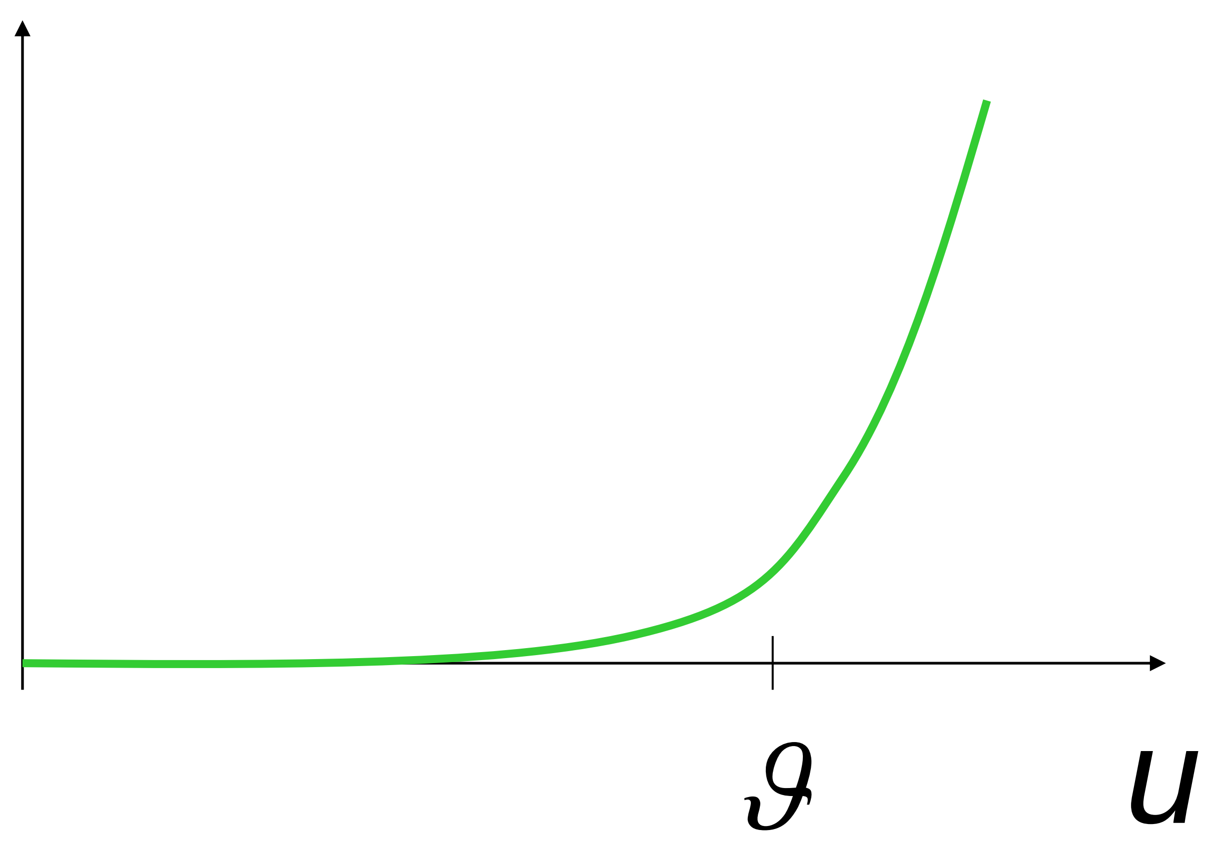
Neuronal Dynamics – 8.5. Interspike Intervals

escape process



escape rate

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



Survivor function

Examples now

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

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

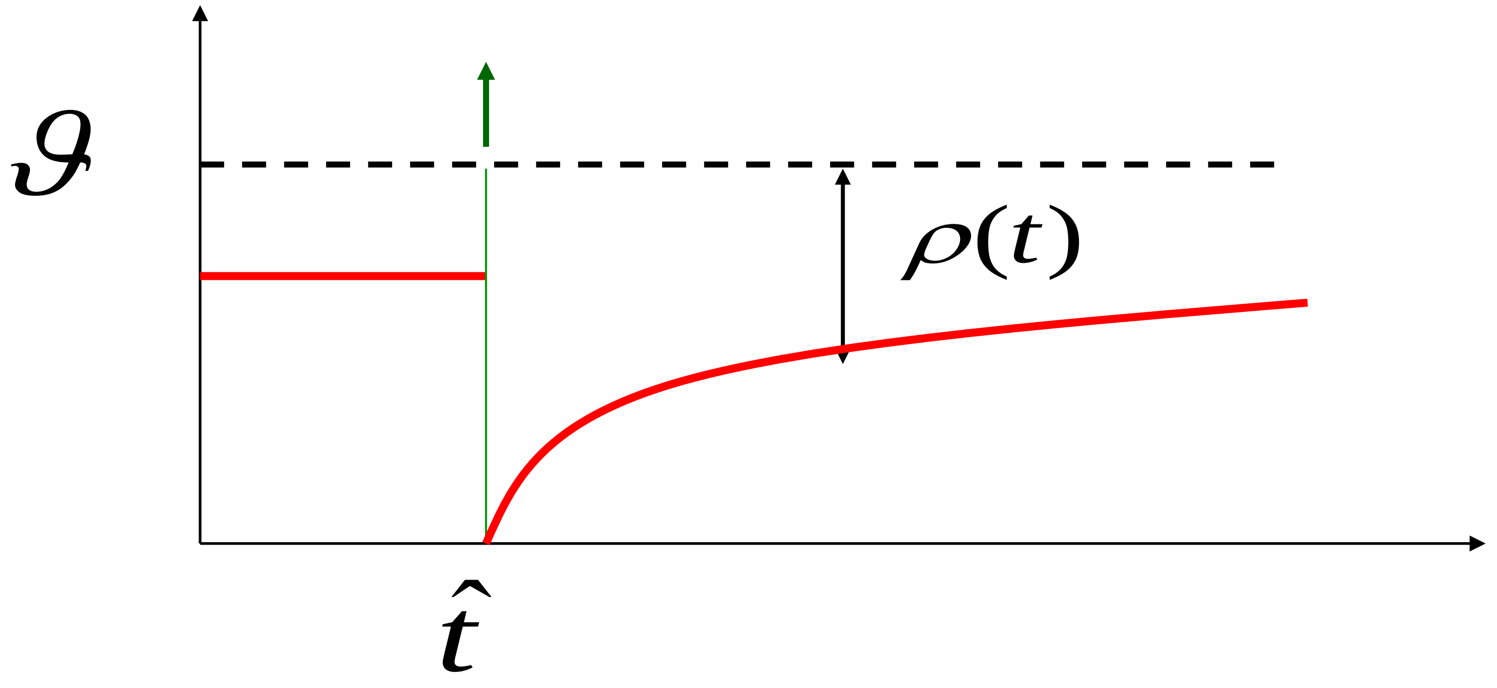
Interval distribution

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

escape rate

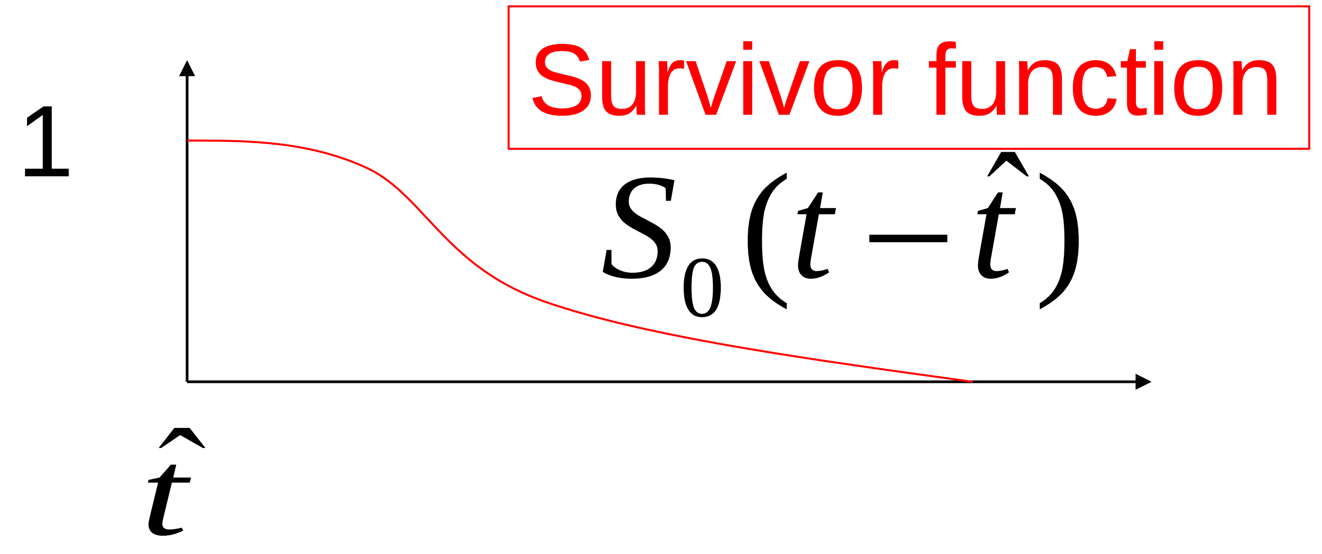
Survivor function

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

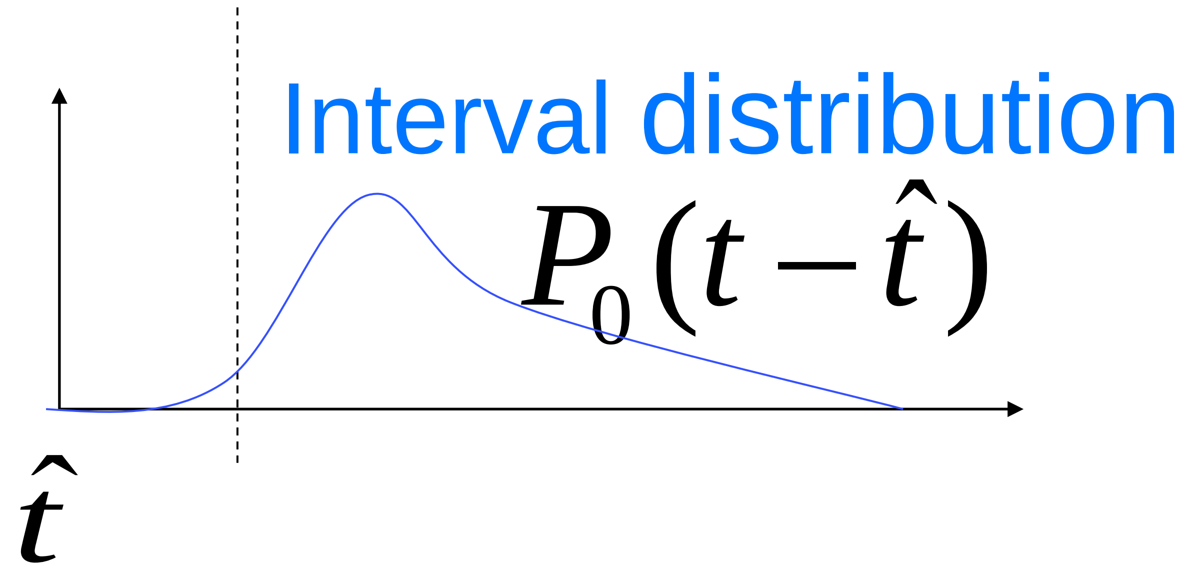


escape rate

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



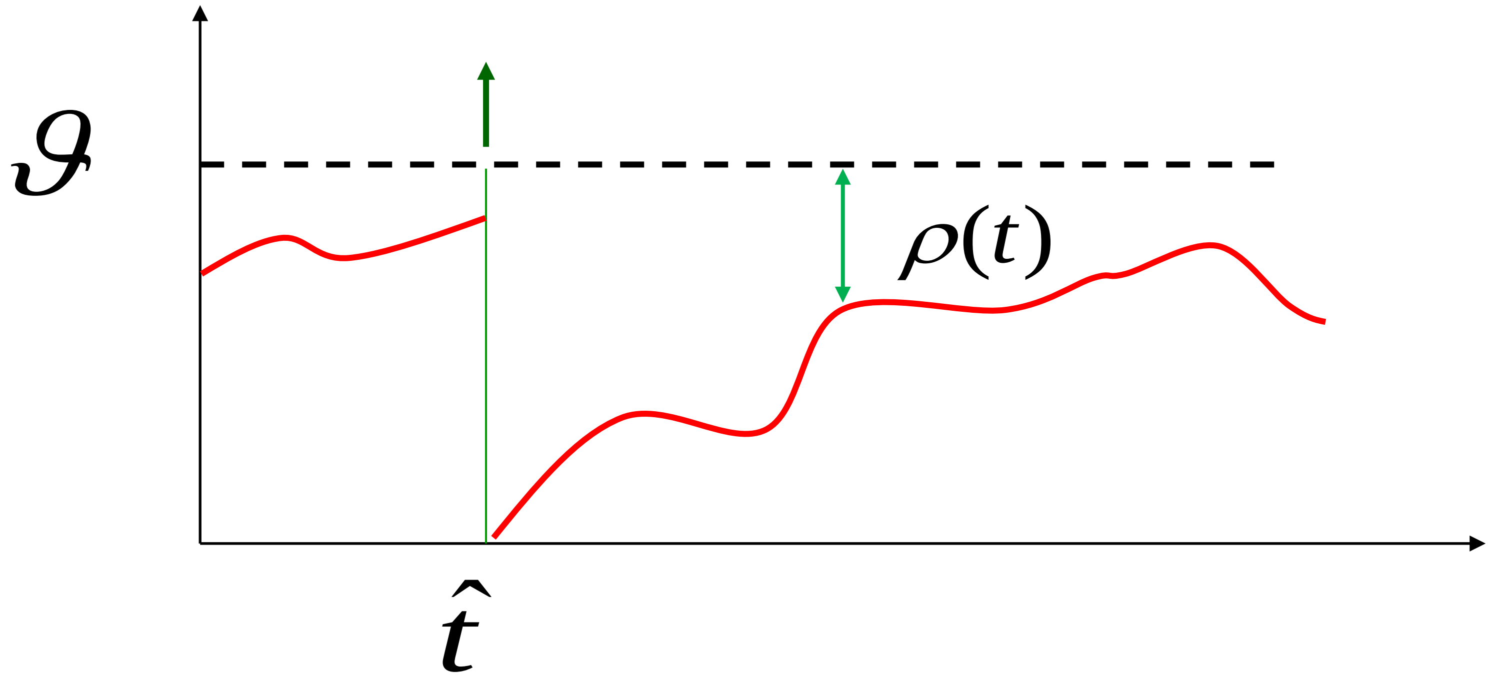
$$S(t|\hat{t}) = \exp\left(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})\,dt'\right)$$



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

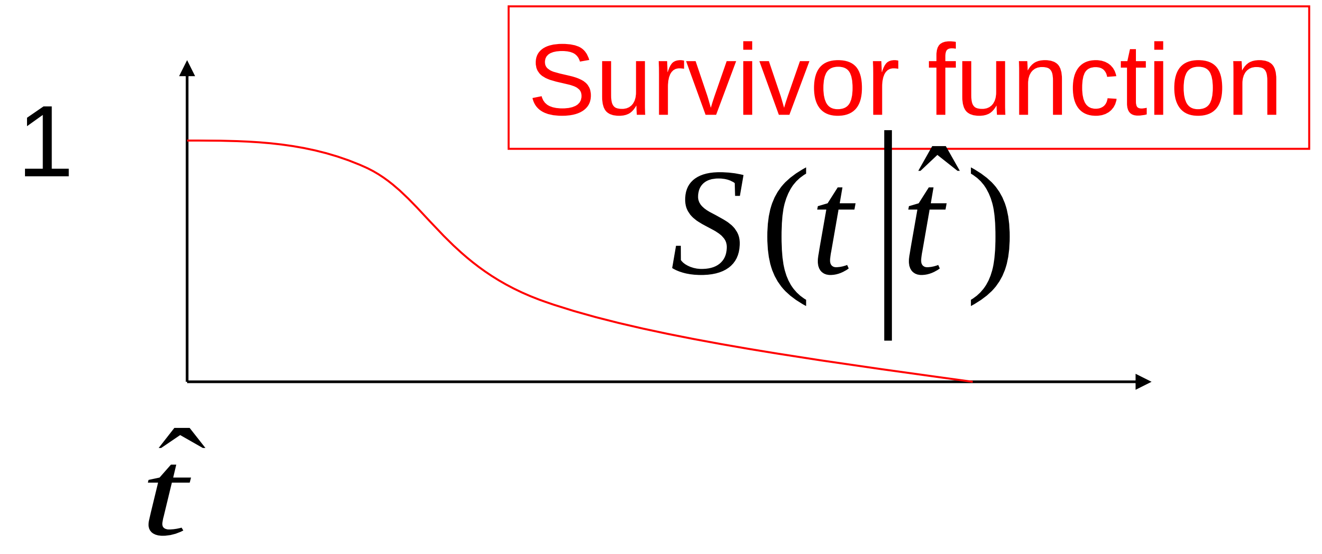
$$= -\tfrac{d}{dt} S(t|\hat{t})$$

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

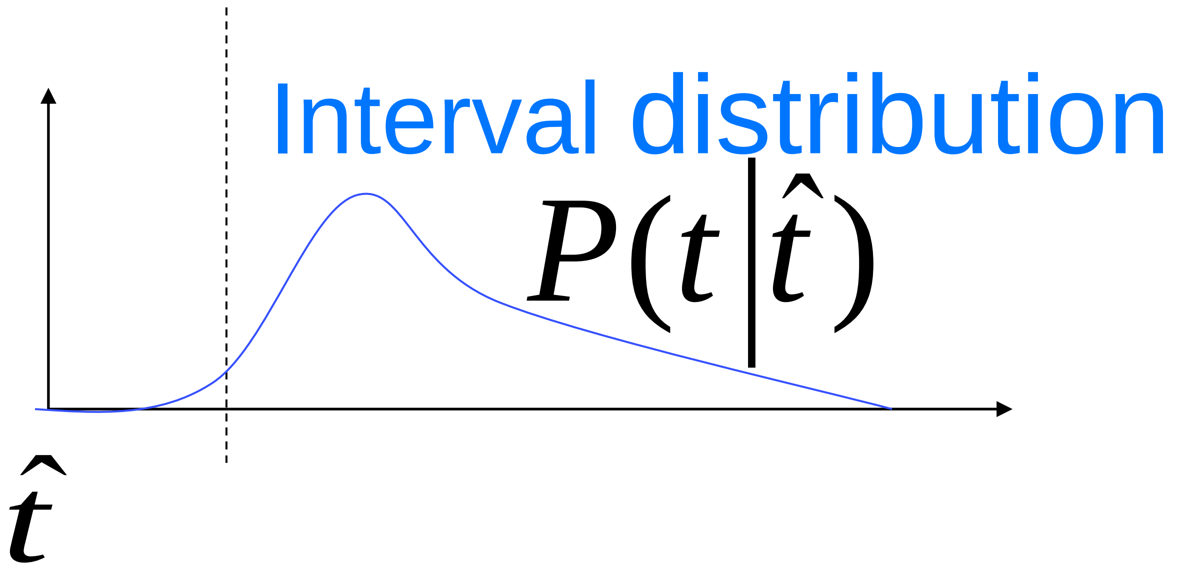


escape rate

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



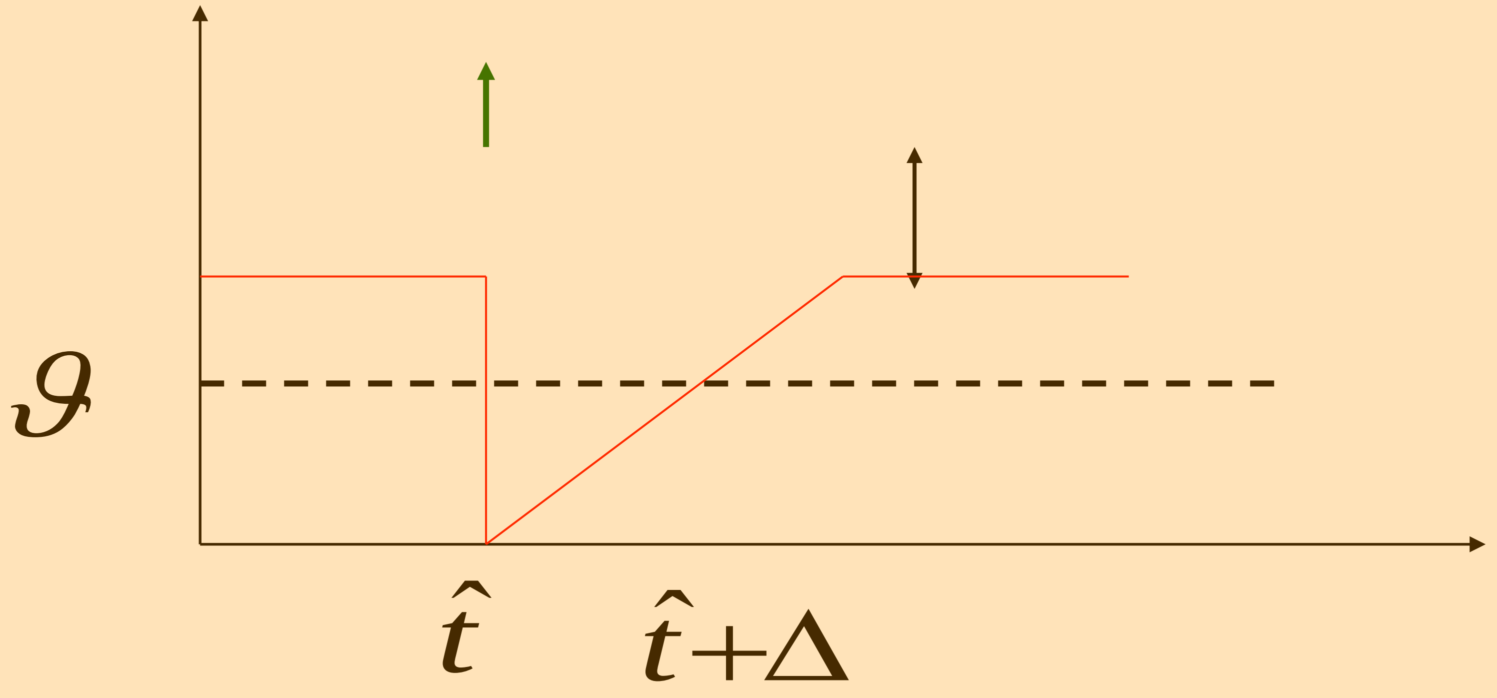
$$S(t|\hat{t}) = \exp(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})dt')$$



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

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

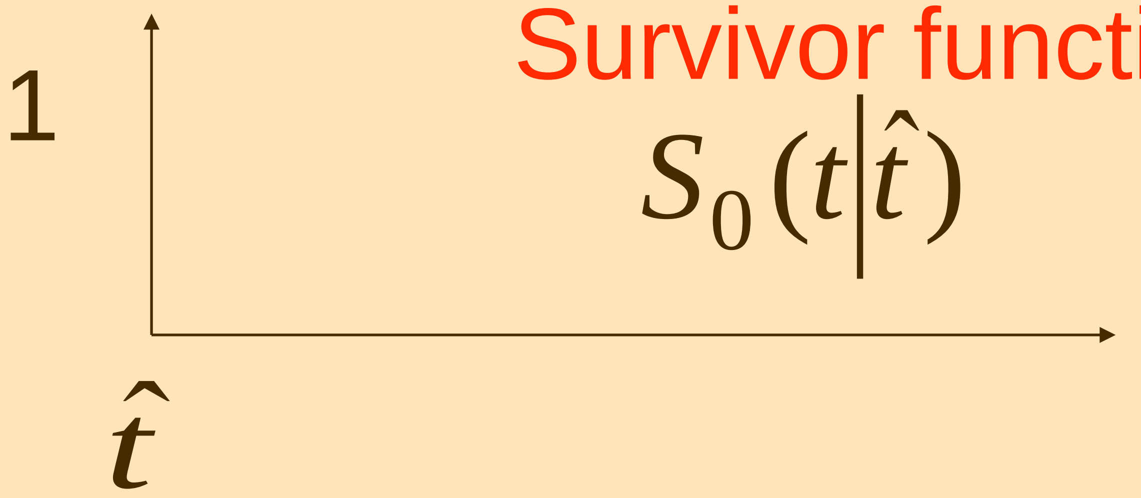
neuron with relative refractoriness, constant input



escape rate

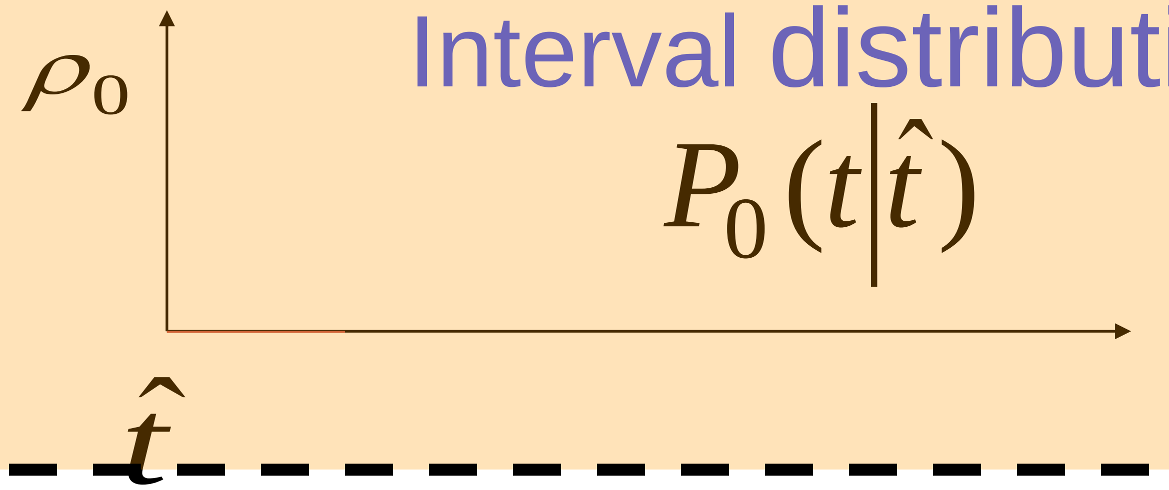
$$\rho(t) = \rho_0 \frac{u}{\vartheta} \quad for \;\; u > \vartheta$$

Survivor function



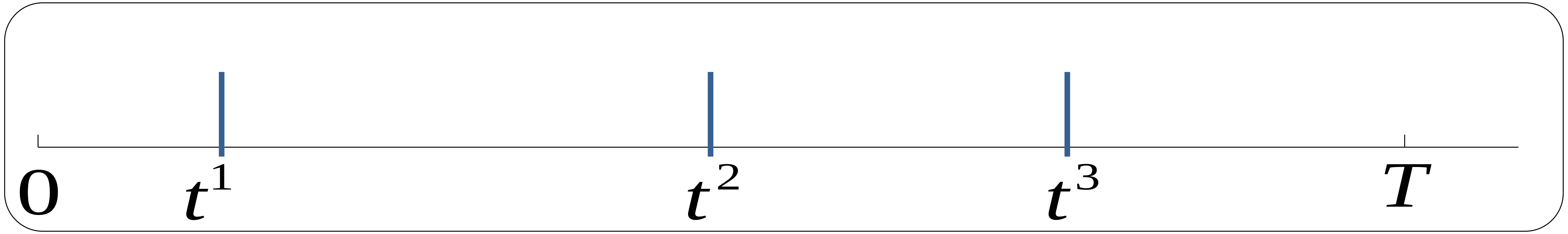
$$S_0(t|\hat{t}) = \Big\{$$

Interval distribution



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

Neuronal Dynamics – 8.5. Firing probability in discrete time



Probability to survive 1 time step

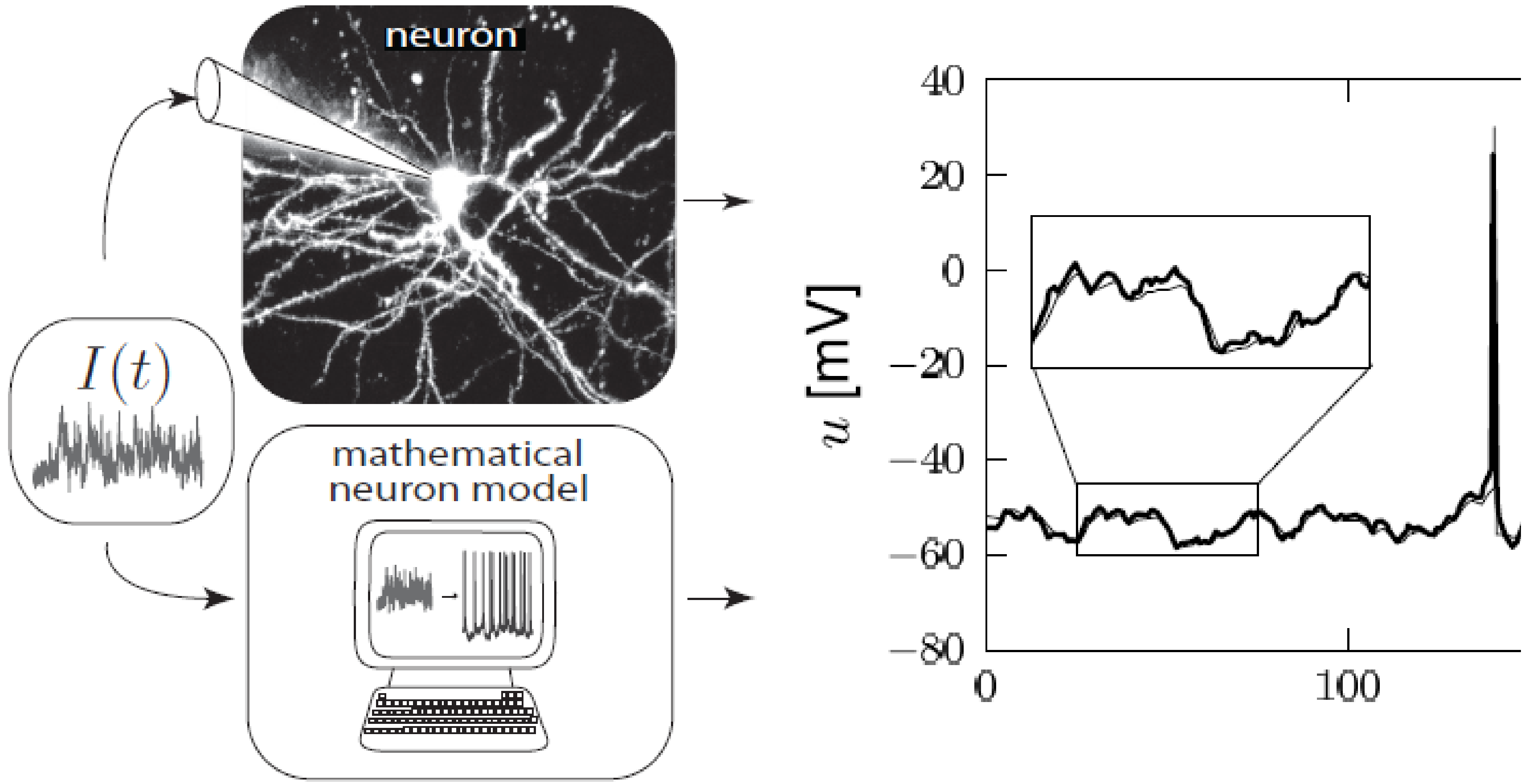
$$S(t_{k+1}|t_k) = \exp[-\int_{t_k}^{t_{k+1}} \rho(t')dt']$$

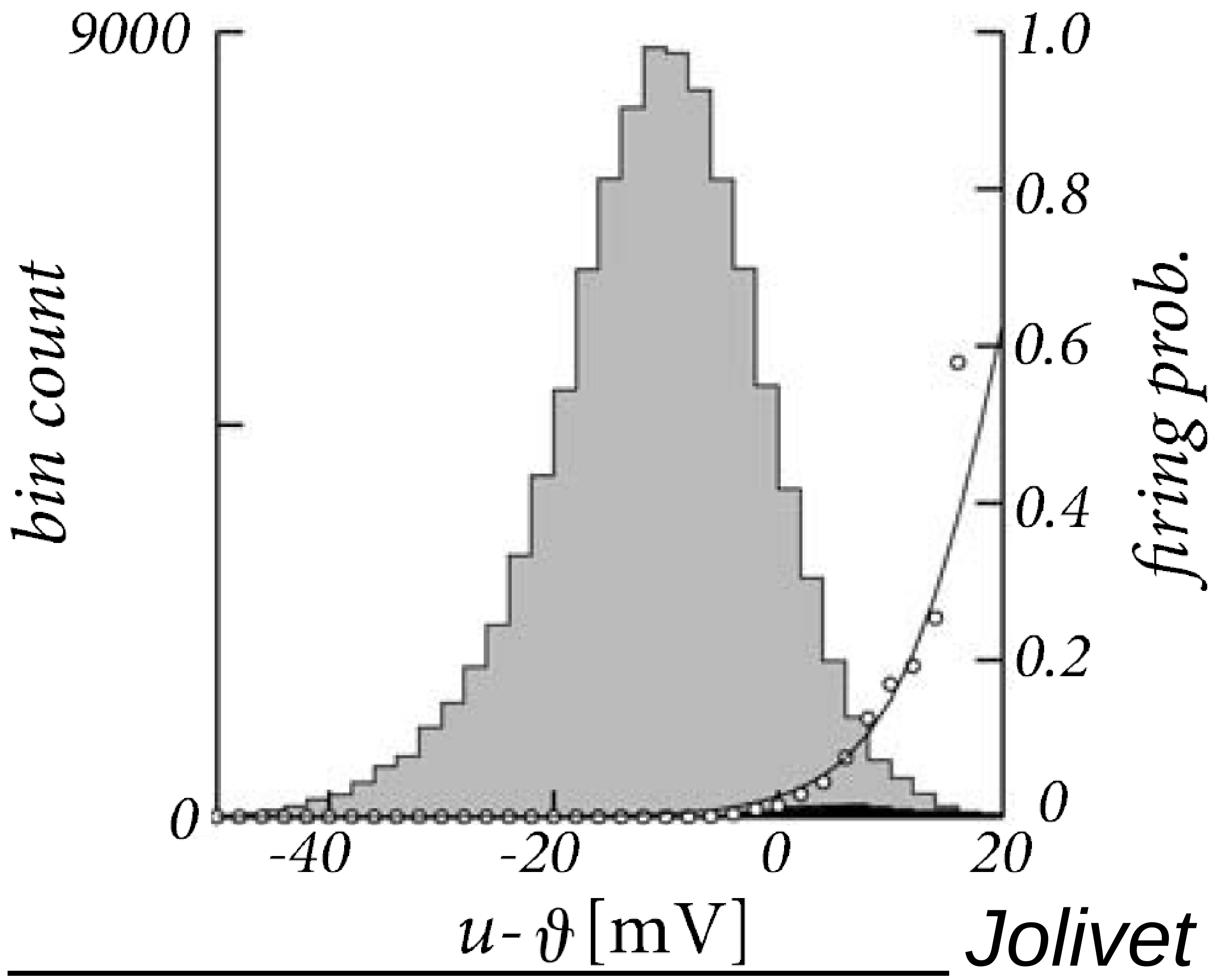
$$S(t_{k+1}|t_k) = \exp[-\rho(t_k)\Delta] = 1 - P_k^F$$

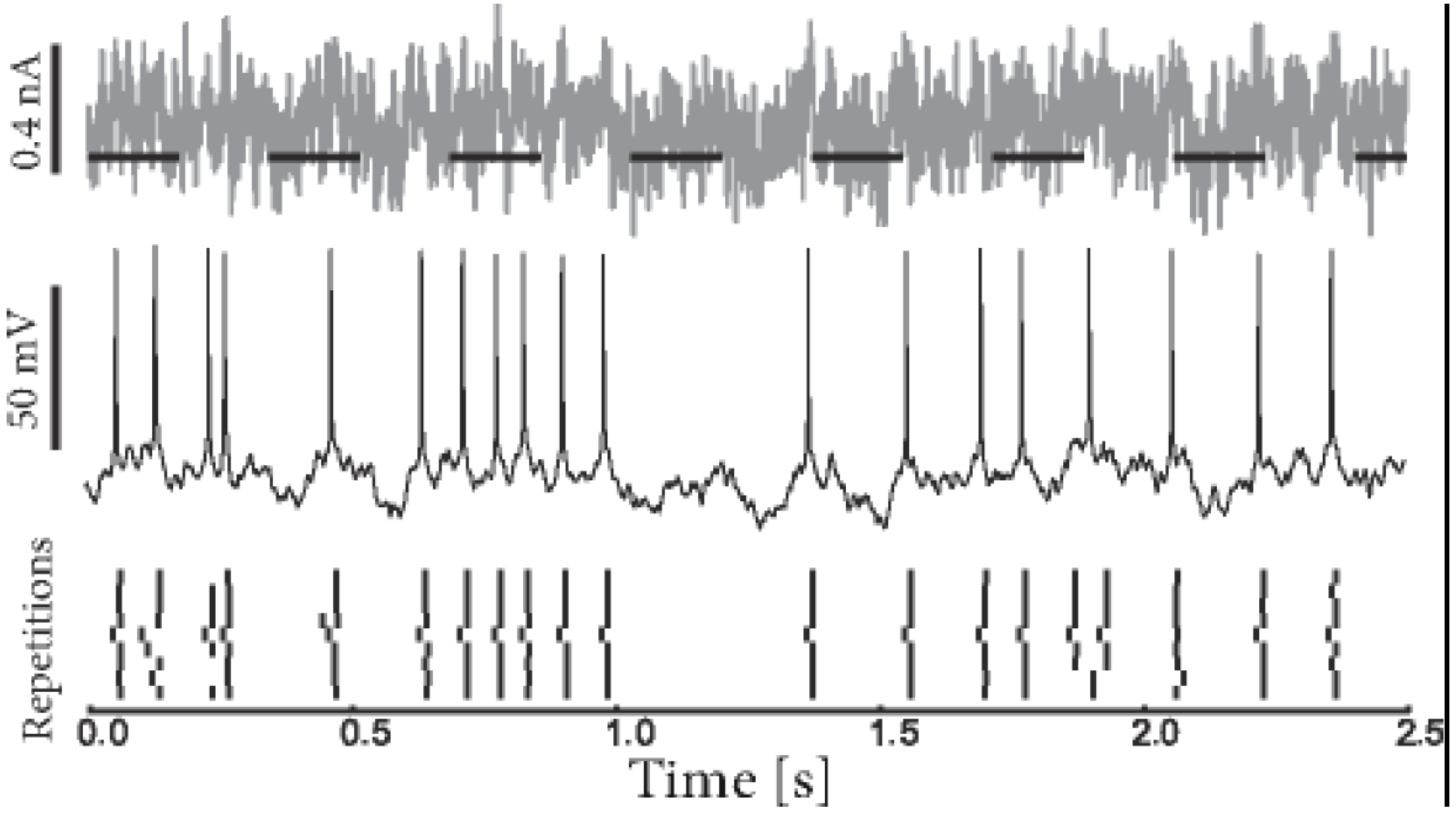
Probability to fire in 1 time step

$$P_k^F =$$

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

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

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

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Biological Modeling of Neural Networks

Week 8 – Noisy input models:

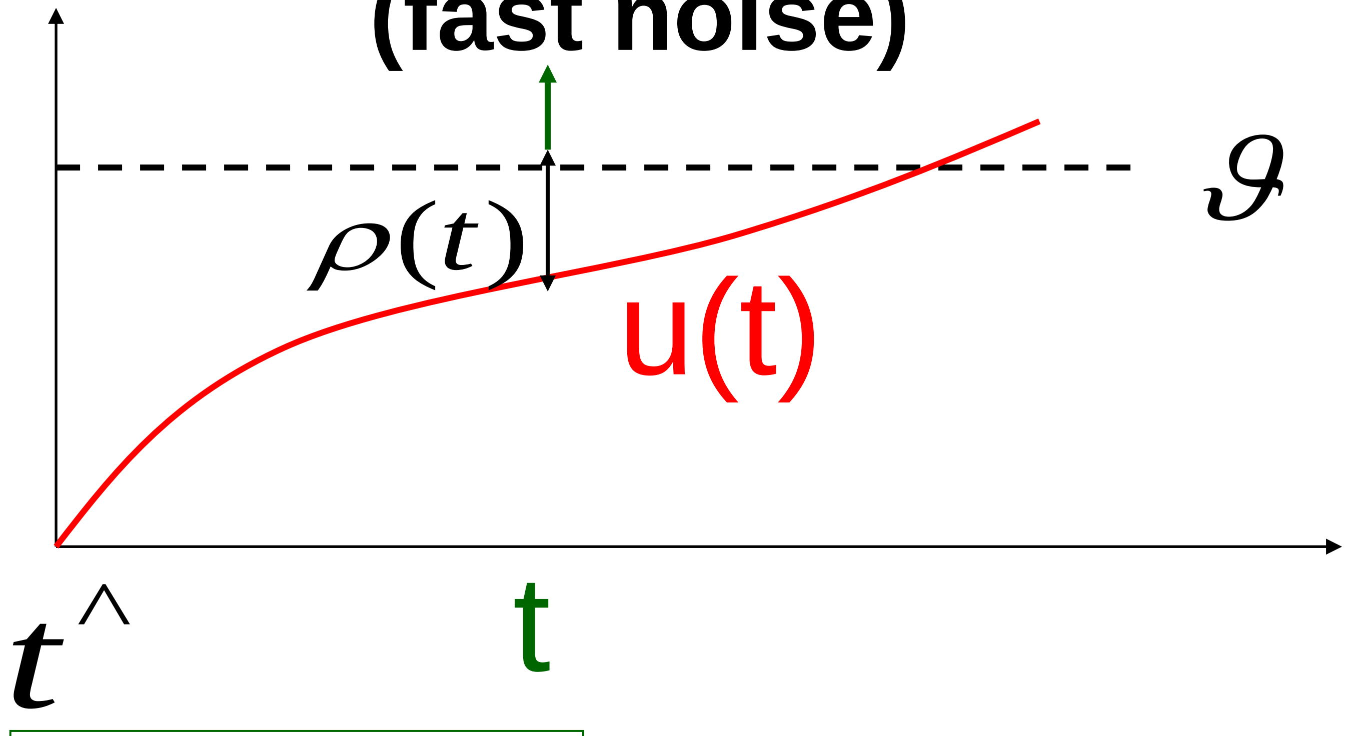
Barrage of spike arrivals

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Neuronal Dynamics – 8.6. Comparison of Noise Models

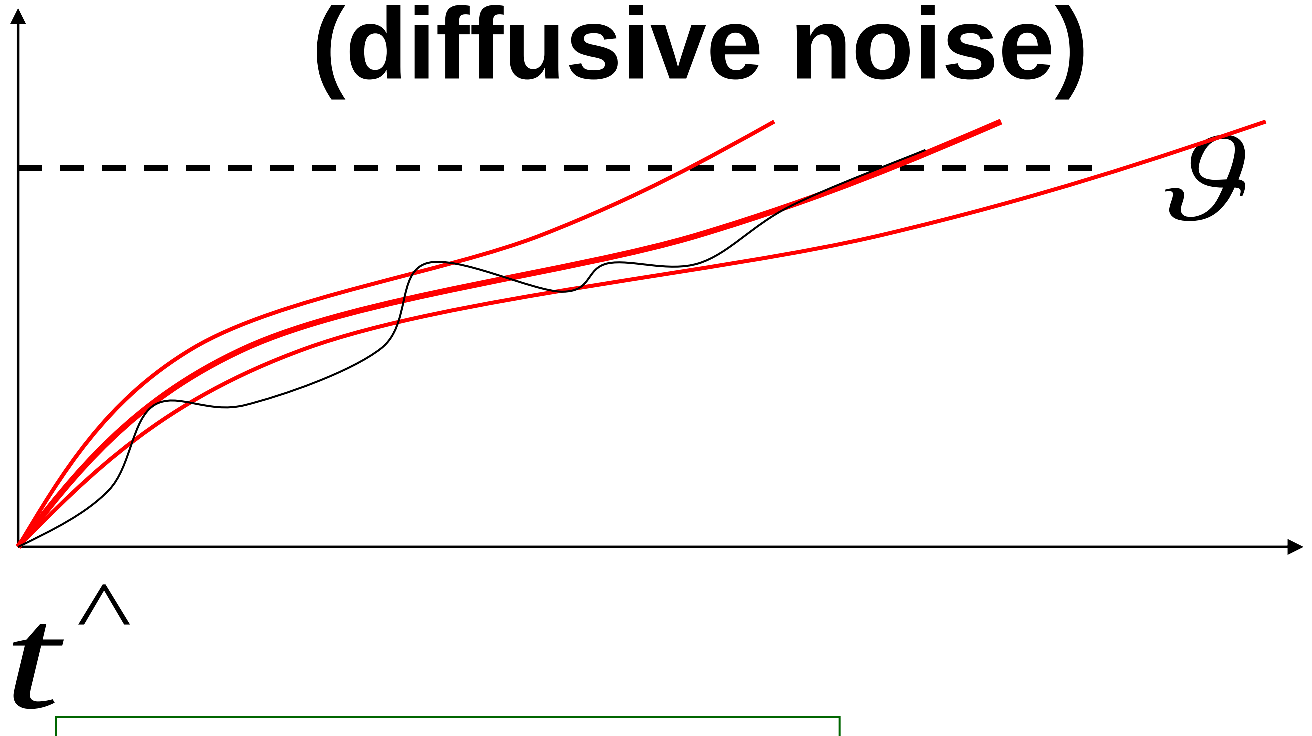
escape process
(fast noise)



escape rate

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

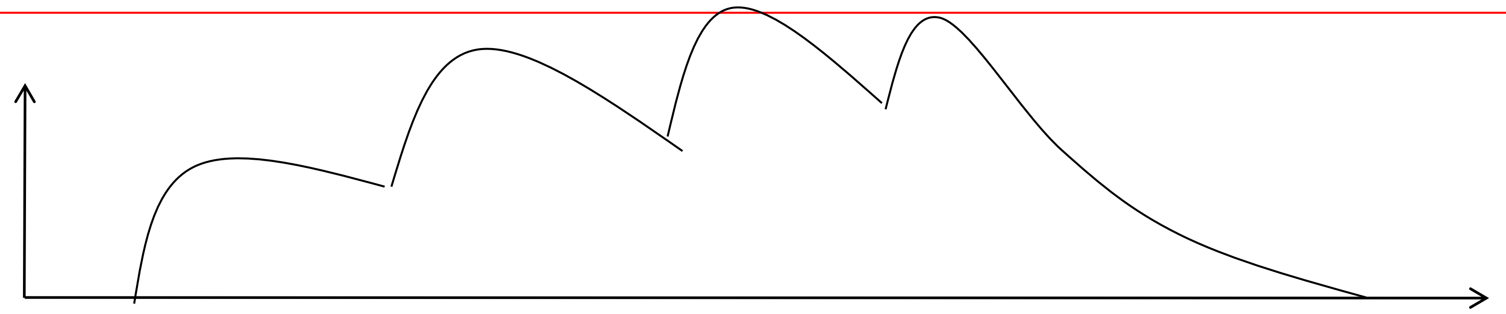
stochastic spike arrival
(diffusive noise)



noisy integration

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

Poisson spike arrival: **Mean and autocorrelation of filtered 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 $$\langle x(t) \rangle = \int F(s) \langle \nu(t-s) \rangle ds$$

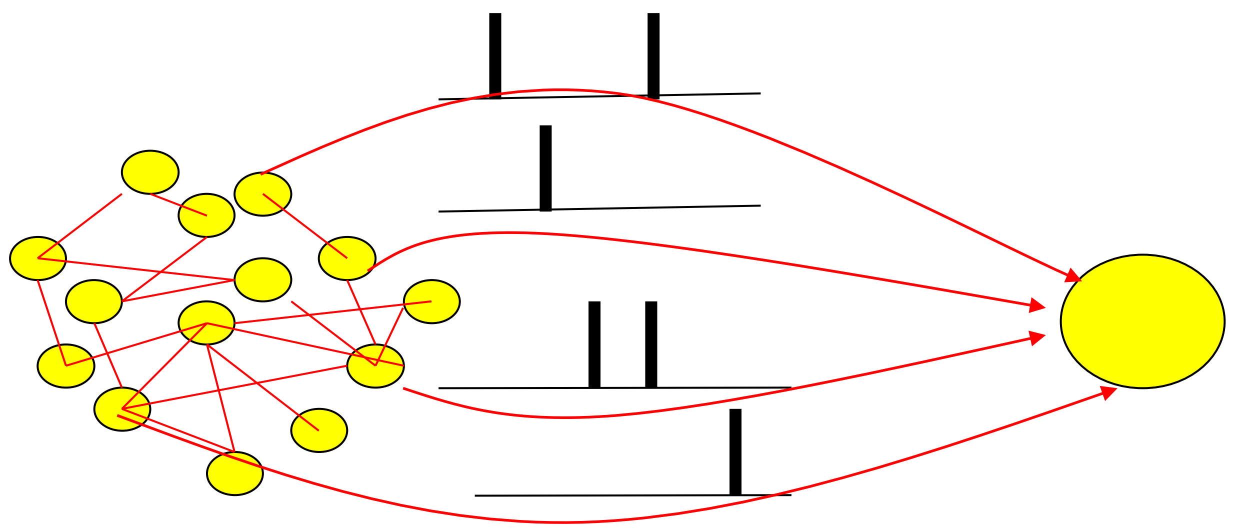
Autocorrelation of output

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

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

Autocorrelation of input

Diffusive noise (stochastic spike arrival)



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

Synaptic current pulses

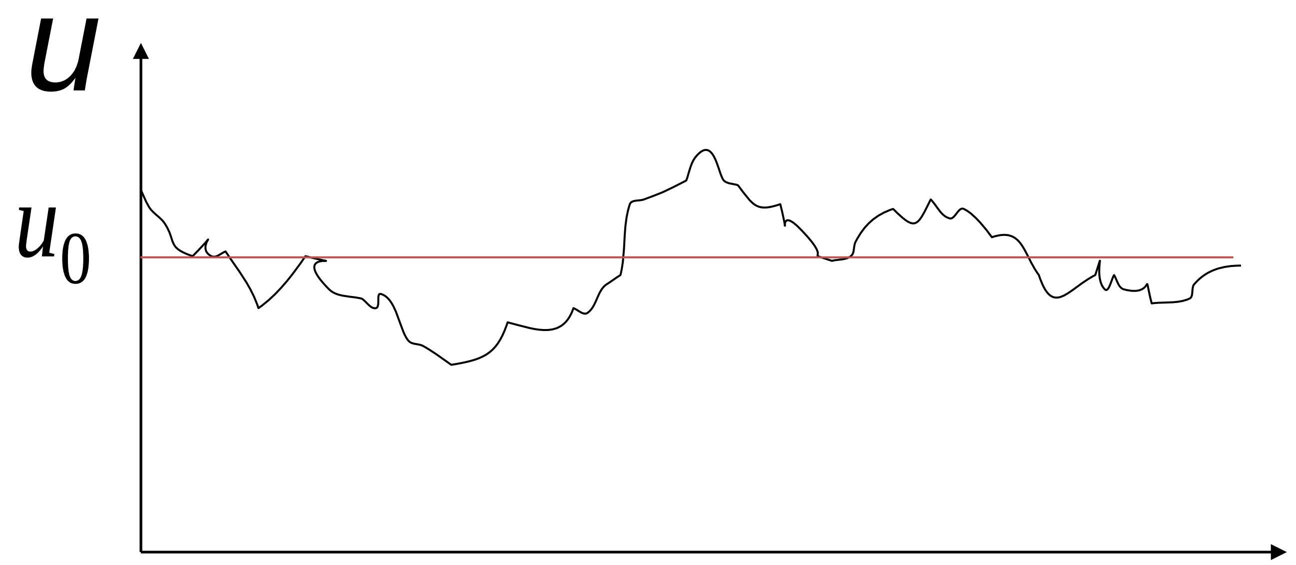
$$\tau \frac{d}{dt}u = -(u - u_{rest}) + \sum_{k,f} \frac{q_e}{C}\delta(t - t_k^f) - \sum_{k',f'} \frac{q_i}{C}\delta(t - t_{k'}^{f'})$$

EPSC

IPSC

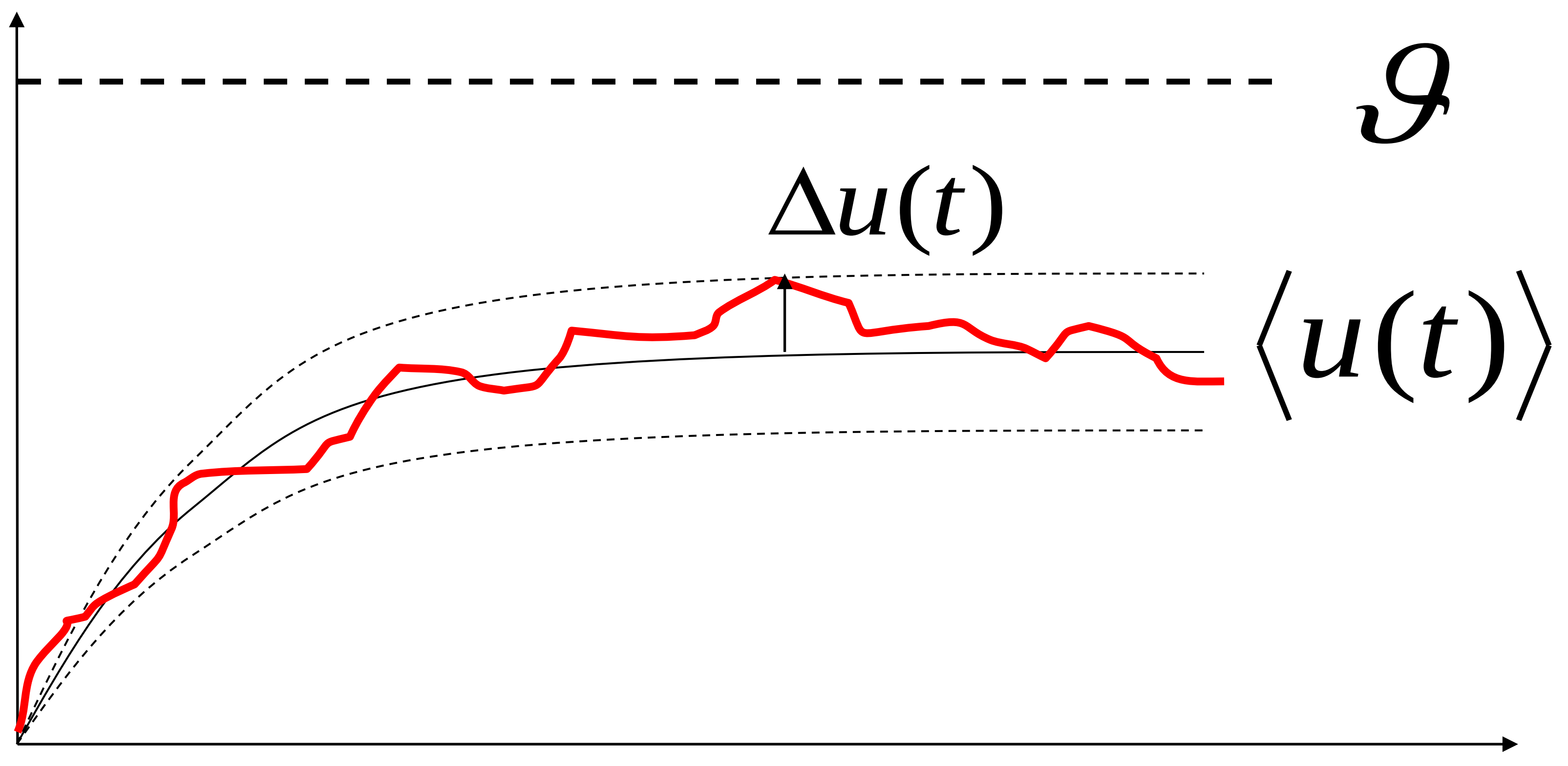
$$\tau \frac{d}{dt}u = -(u - u_{rest}) + R\,I(t) + \xi(t)$$

Blackboard

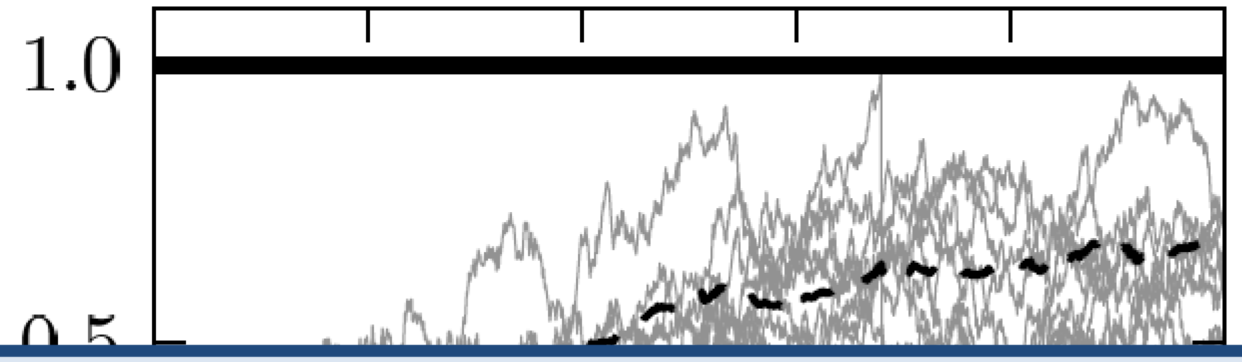


Langevin equation,
Ornstein Uhlenbeck process

Diffusive noise (stochastic spike arrival)



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

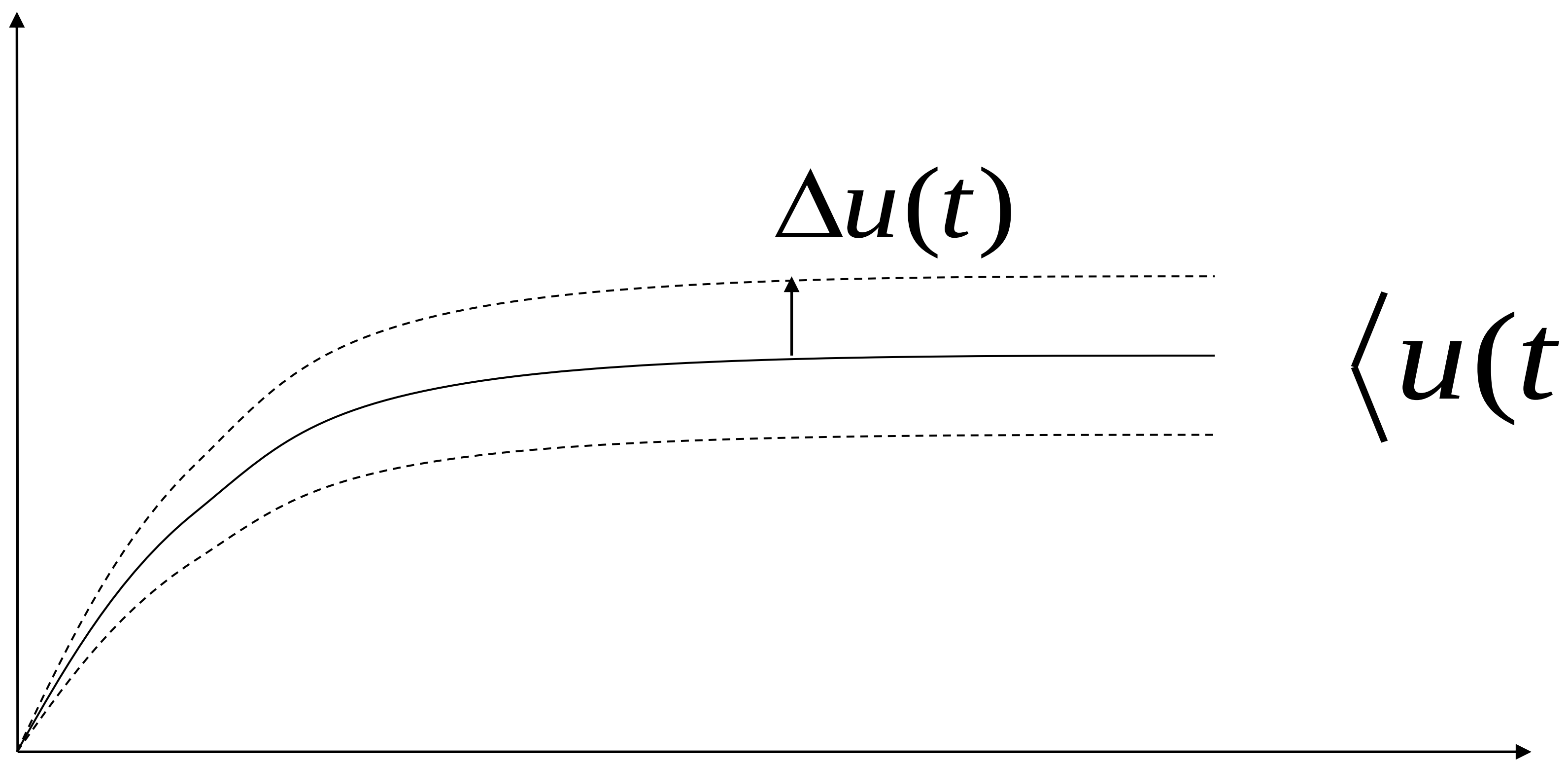


$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

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

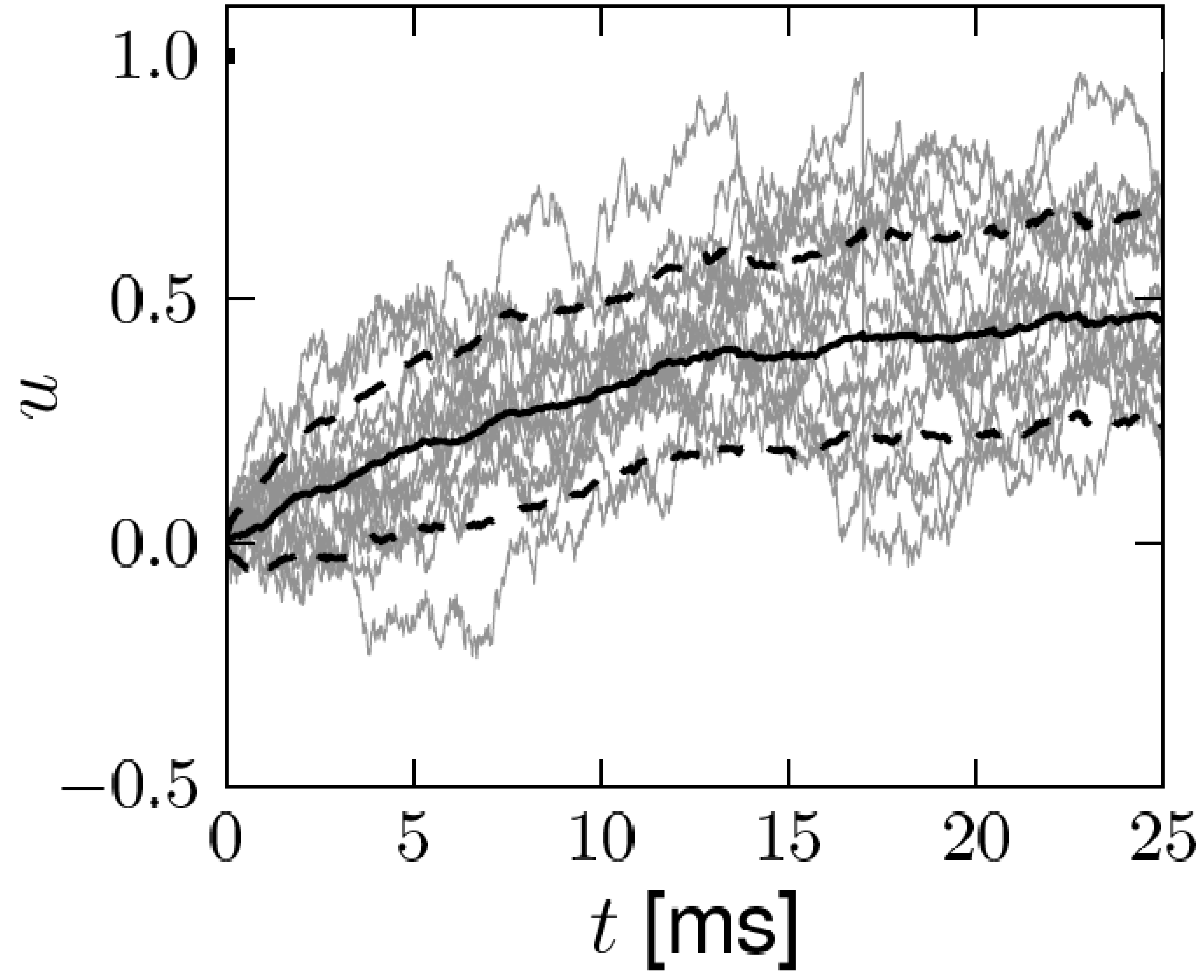
Math argument:
- *no threshold*
- *trajectory starts at known value*

Diffusive noise (stochastic spike arrival)



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

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



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

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

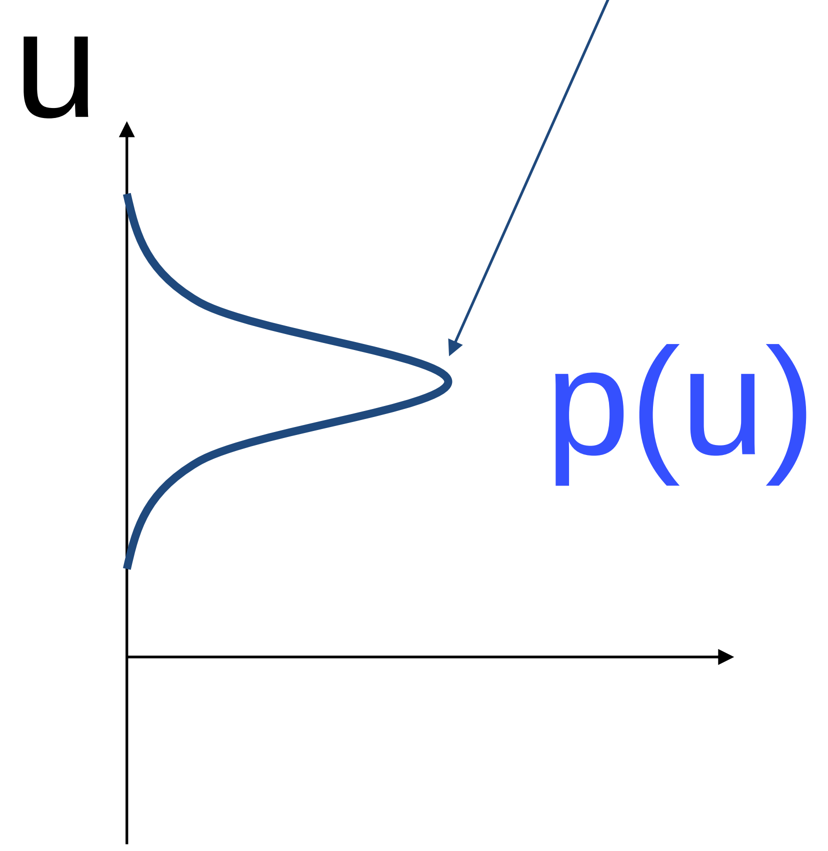
Math argument

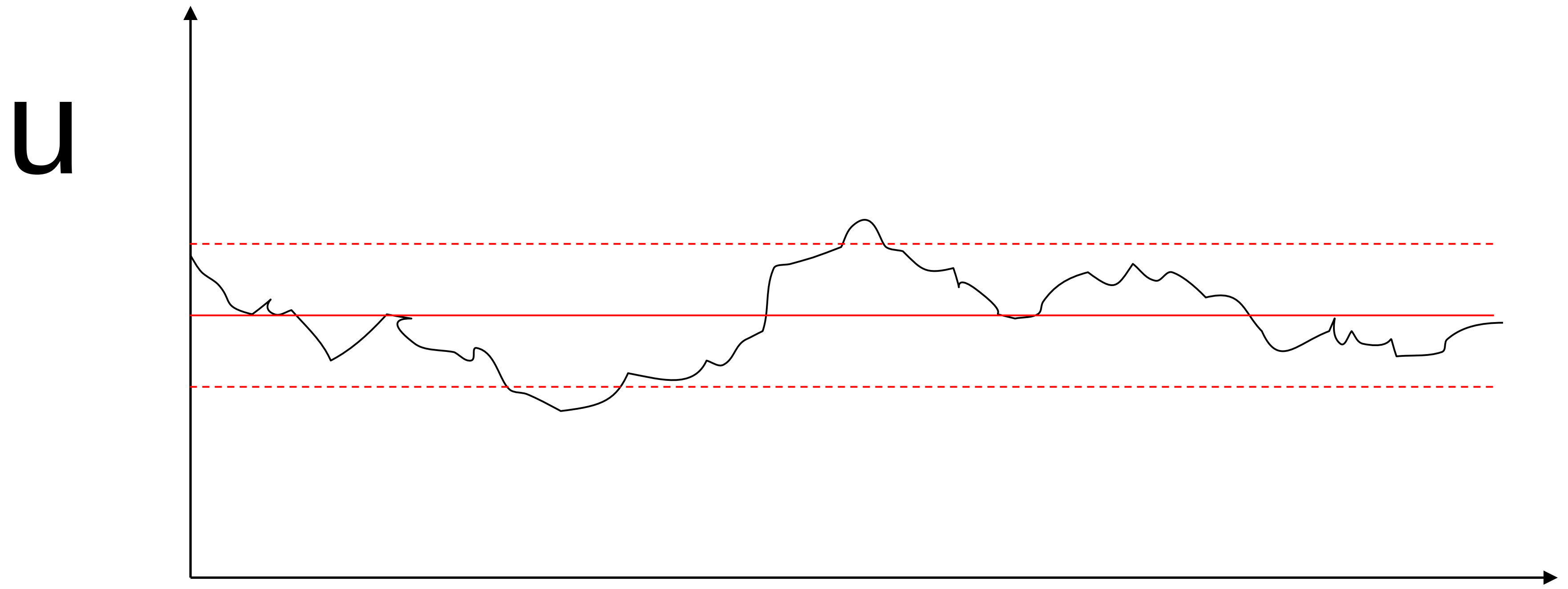
$$p(u,t) = \frac{1}{\sqrt{2\pi \langle \Delta u^2(t) \rangle}} \exp\left\{ -\frac{[u(t|\hat{t}) - u_0(t)]^2}{2 \langle \Delta u^2(t) \rangle} \right\}$$

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

A) No threshold, stationary input

Membrane potential density: Gaussian





constant input rates
no threshold

noisy integration

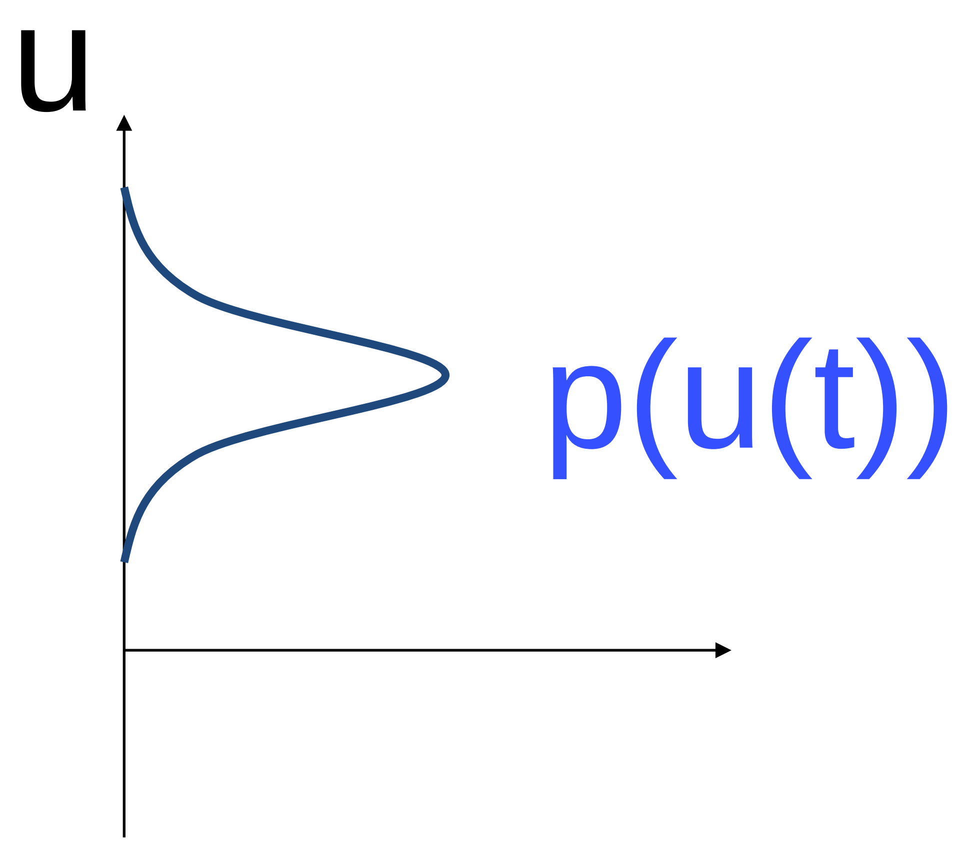
$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$

B) No threshold, oscillatory input

Membrane potential density:
Gaussian at time t

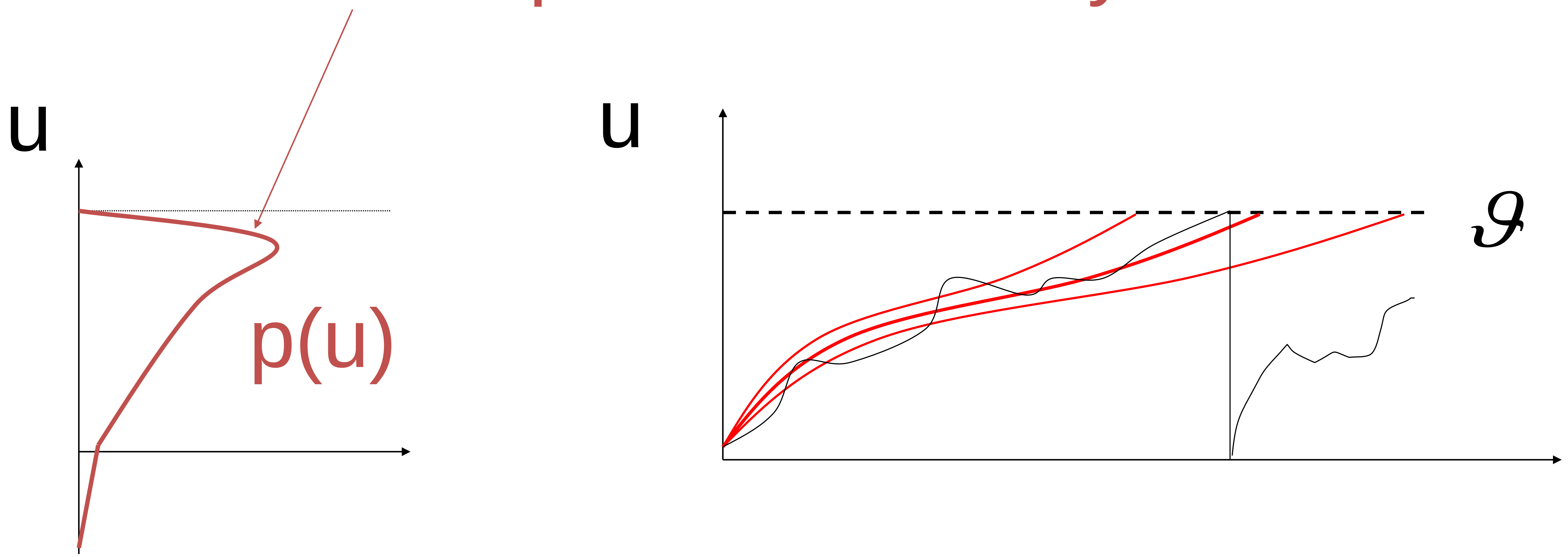
noisy integration

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



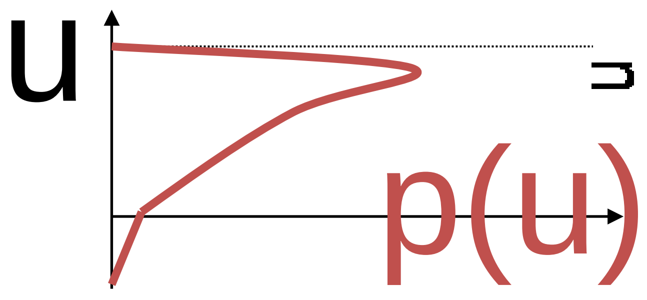
C) With threshold, reset/ stationary input

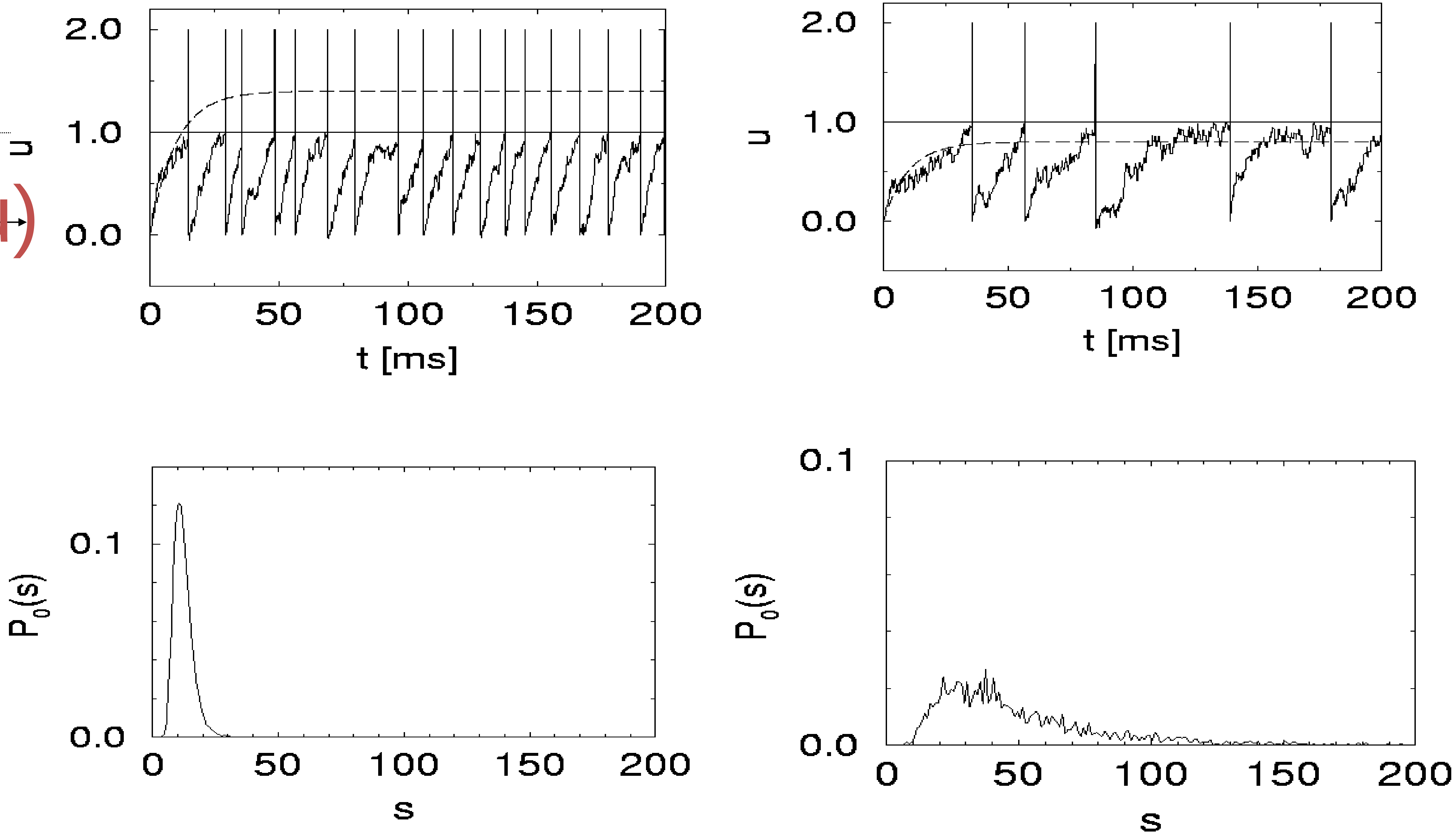
Membrane potential density



Neuronal Dynamics – 8.6. Diffusive noise/stoch. arrival

Superthreshold vs. Subthreshold regime

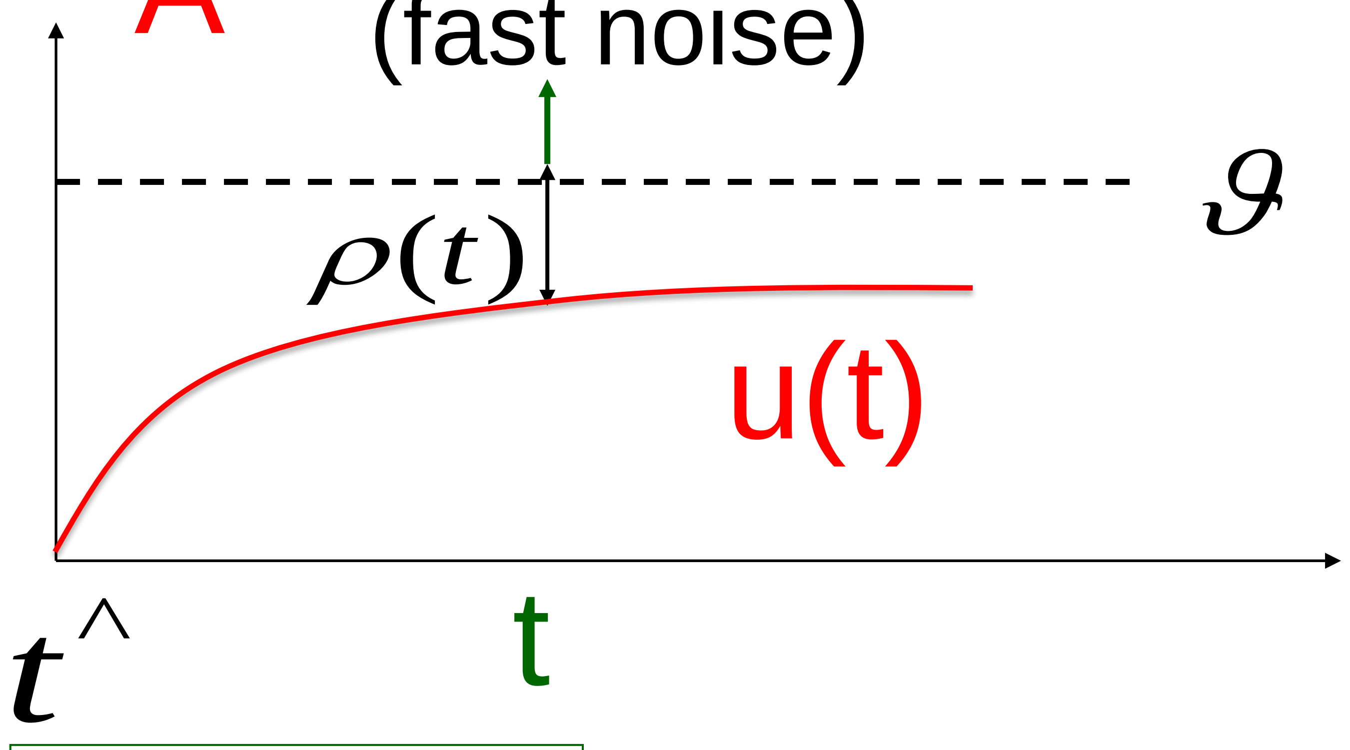




Nearly Gaussian subthreshold distr.

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

Neuronal Dynamics – 8.6. Comparison of Noise Models



escape rate

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

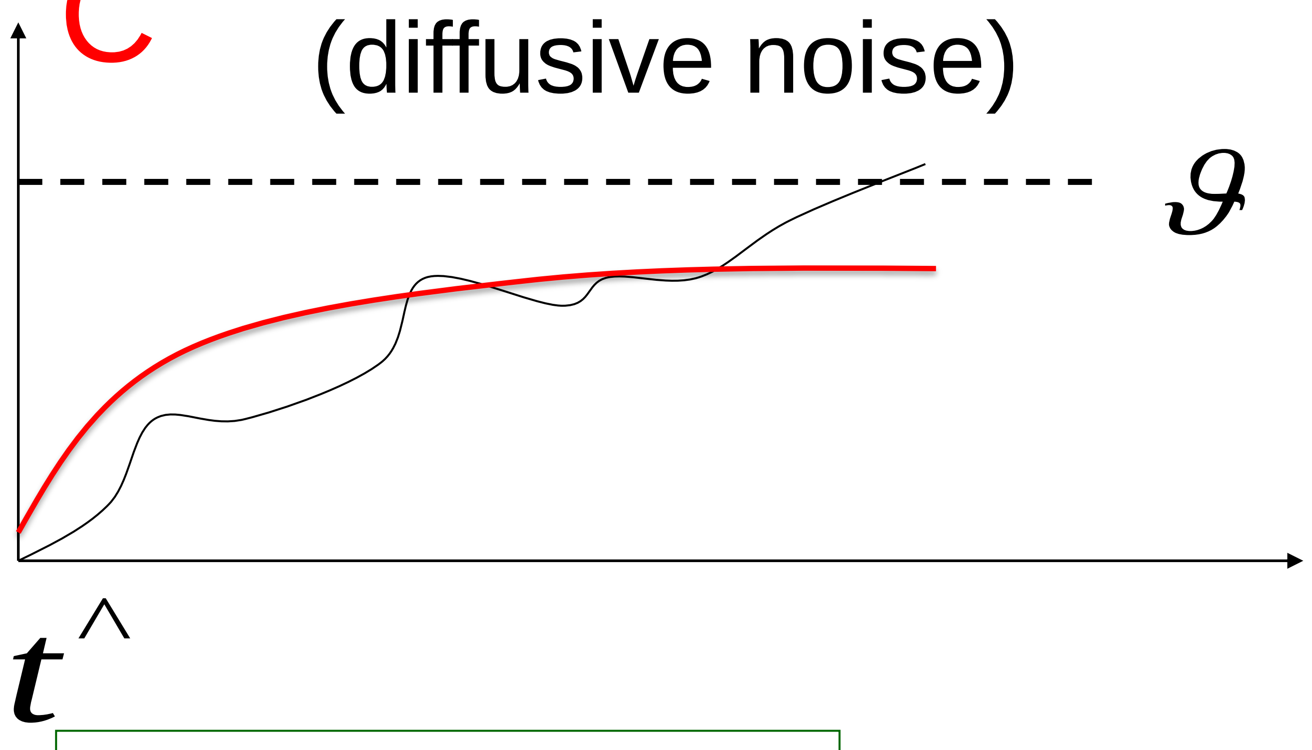
Interval distribution

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

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

escape rate

Survivor function



noisy integration

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

noise

white
(fast noise)

synapse
(slow noise)

$P_I(t|\hat{t})$: first passage time problem

(Brunel et al., 2001)

Stationary input:

-Mean ISI

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

Siegert 1951

-Mean firing rate

Diffusive noise

- distribution of potential
- mean interspike interval

FOR CONSTANT INPUT

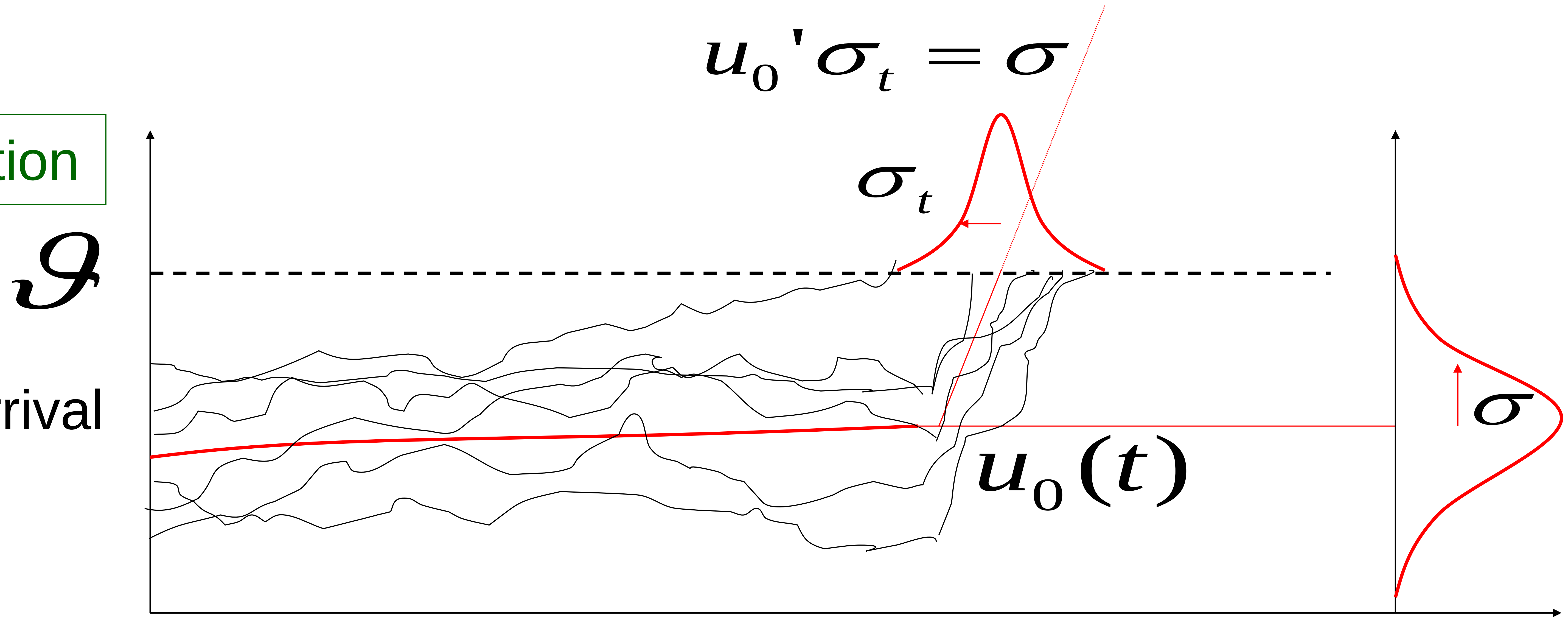
- time dependent-case difficult

Escape noise

- time-dependent interval distribution

Noise models: from diffusive noise to escape rates

noisy integration



stochastic spike arrival
(diffusive noise)

escape rate

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

Comparison: diffusive noise vs. escape rates

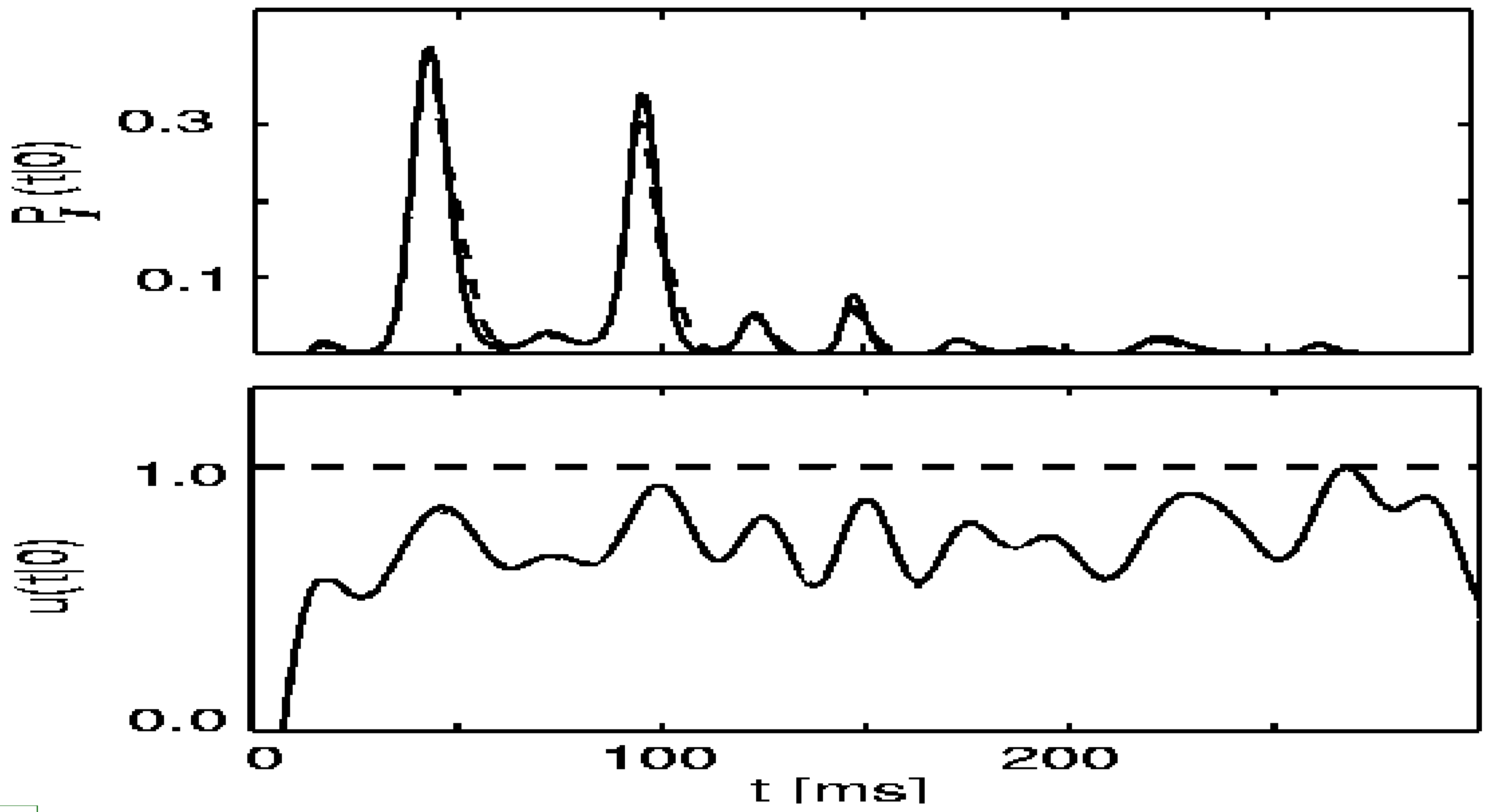
Plesser and Gerstner (2000)

Probability of first spike

diffusive

escape

subthreshold potential



escape rate

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

Diffusive noise

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

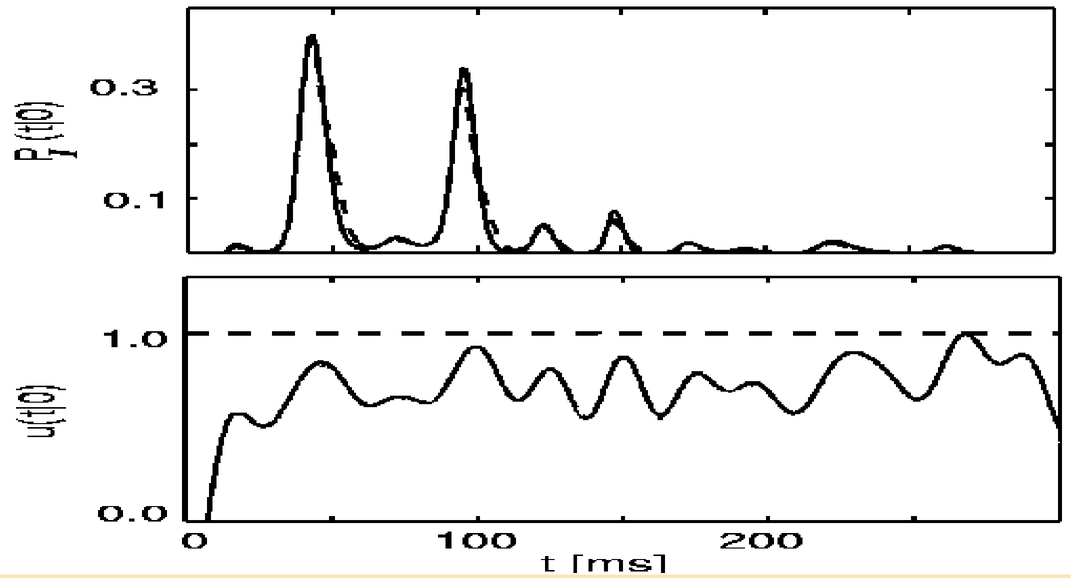
Escape noise

- 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 determinstic reference trajectory is **closest** to the threshold.
[ ] The interspike interval vanishes for very long intervals if the determinstic 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.