Computational Neuroscience: Neuronal Dynamic

EPFL

Week 11 – Variability and Noise: Autocorrelation

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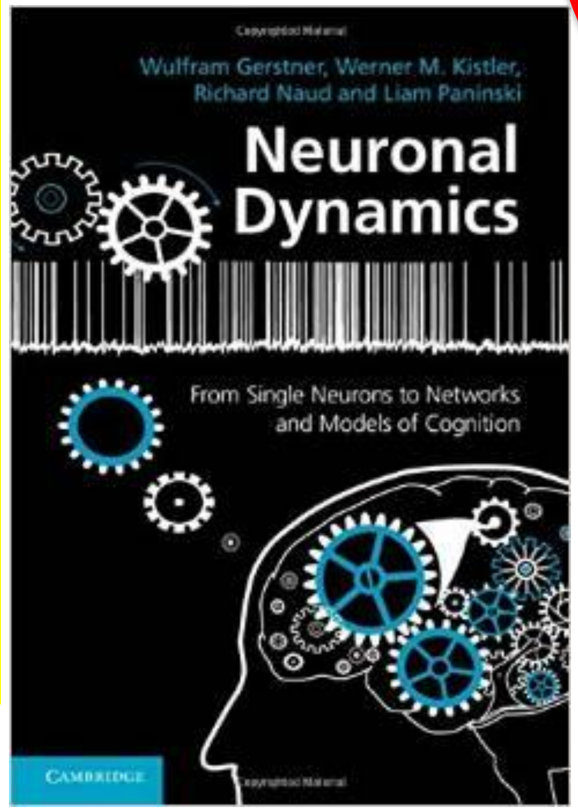
Reading for week 11:
NEURONAL DYNAMICS
Ch. 7.5.1, Ch. 8.1-8.3,
Ch. 9.1-9.4



Cambridge Univ. Press

Lecture 6 of video series
https://lcnwww.epfl.ch/gerstner/NeuronalDynamics-MOOCall.html

11.1 Escape noise
- stochastic intensity

11.2 Renewal models
- interspike interval distribution

11.3 Likelihood of a spike train

11.4 Comparison of noise models

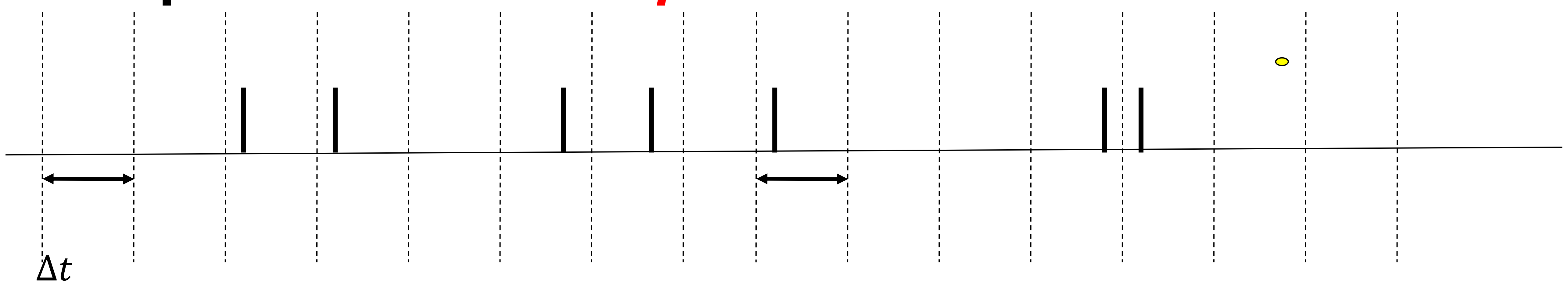
11.5 Rate code vs/ Temporal code

Neuronal Dynamics – Poisson process versus white noise

Probability of spike in time step:

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

spike train



Probability of spike
in step *n* **AND** step *k*
→ Autocorrelation in discrete time

See also Exercise last week!

Mean in continuous time:

$$\langle S(t)\rangle = \nu(t)$$

Autocorrelation in continuous time:

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

caused by mean

White noise: mean zero

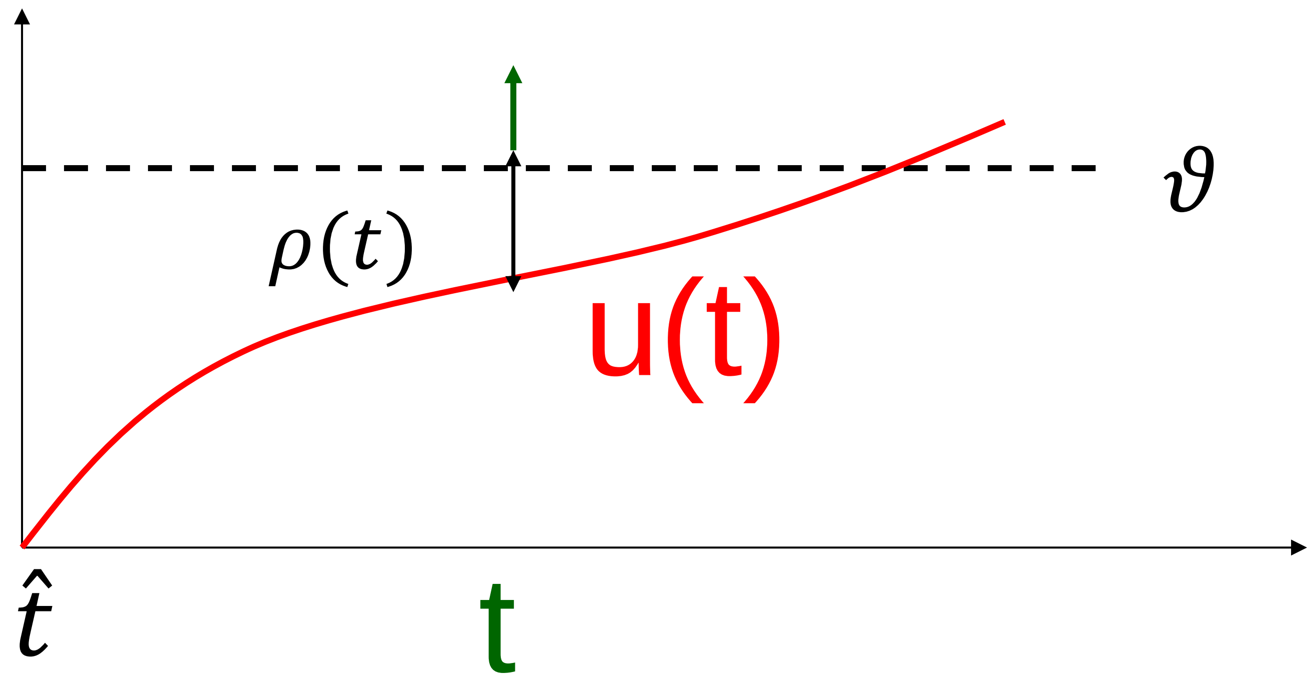
$$\langle \xi(t)\rangle = 0$$

White noise: autocorrlation

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

Noise models

escape process,
stochastic intensity

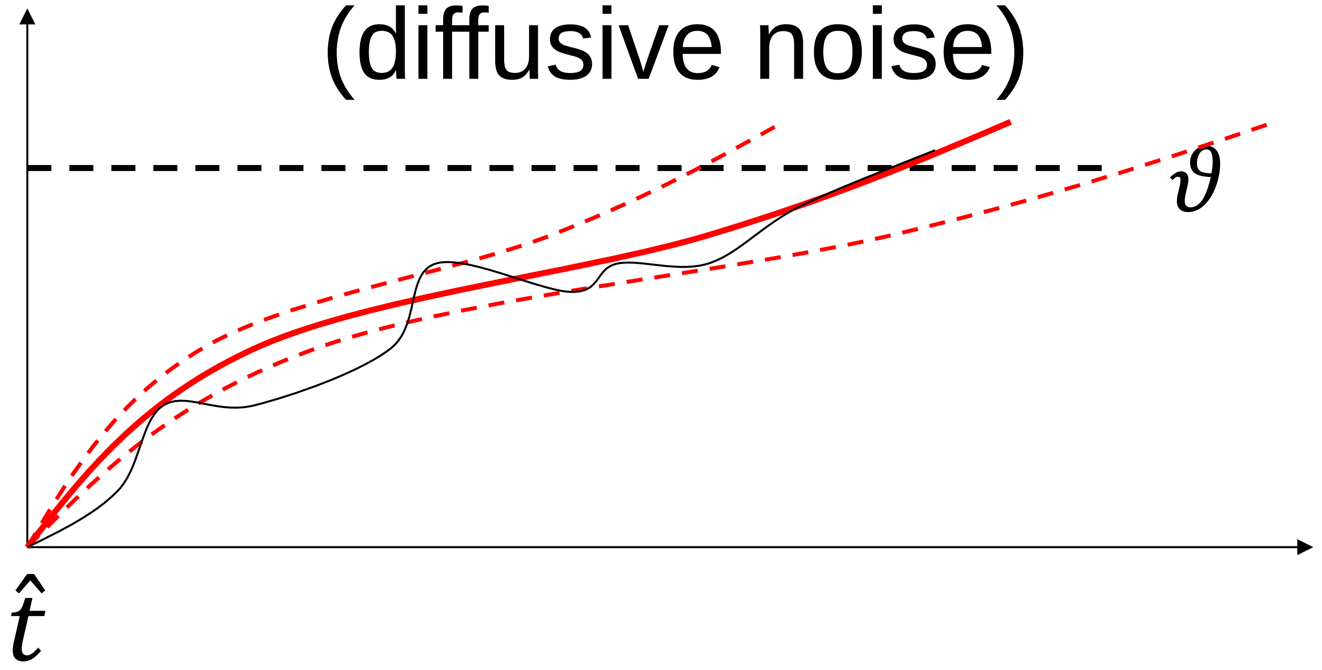


escape rate

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

Now:
Escape noise!

stochastic spike arrival
(diffusive noise)



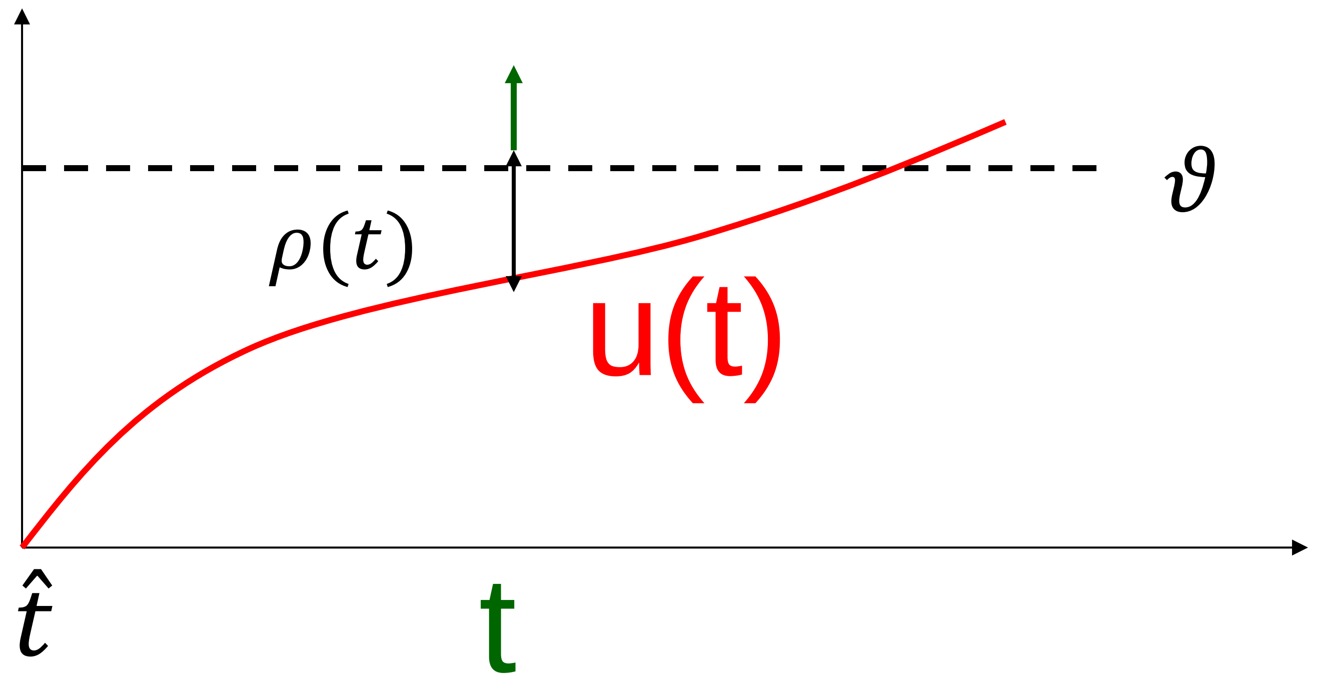
noisy integration

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

Relation between the two models:
Section 11.4

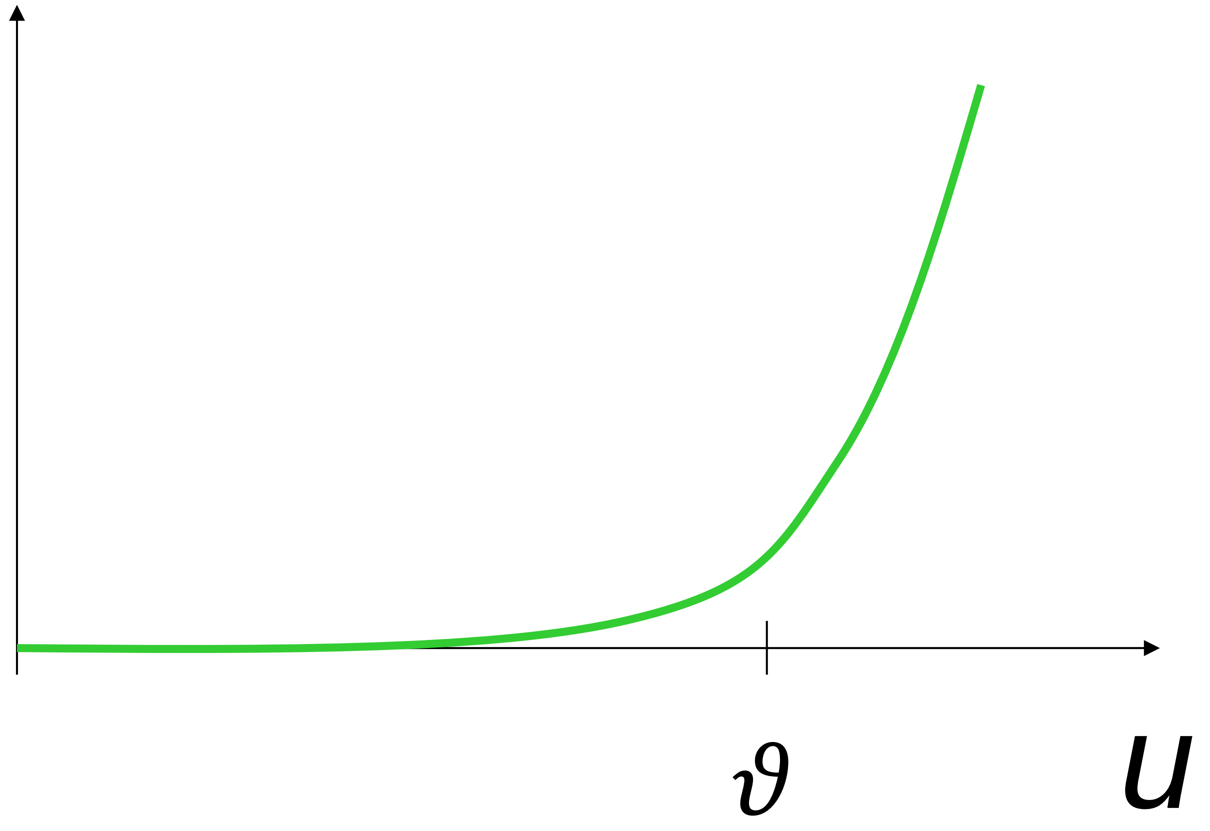
Neuronal Dynamics – 11.1 Escape noise

escape process



escape rate

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



escape rate

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

Example: leaky integrate-and-fire model

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

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

Neuronal Dynamics – Quiz 11.1.

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

[ ] The escape rate is bounded (e.g. a sigmoidal function) : 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

11.1 Summary: Escape noise

All noise models are ad hoc. White noise is an approximation of stochastic spike arrival – compared to the Poisson model the 'mean' is removed (and integrated in the deterministic part of driving current I). We can think of white noise and Poisson noise as 'noise in the input'.

In this section we focus 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 'firing probability' turns into the stochastic intensity of spike firing $\rho(t) = f[u(t) - \theta]$ which has units of a rate. We can think of escape noise as a noise in the output.

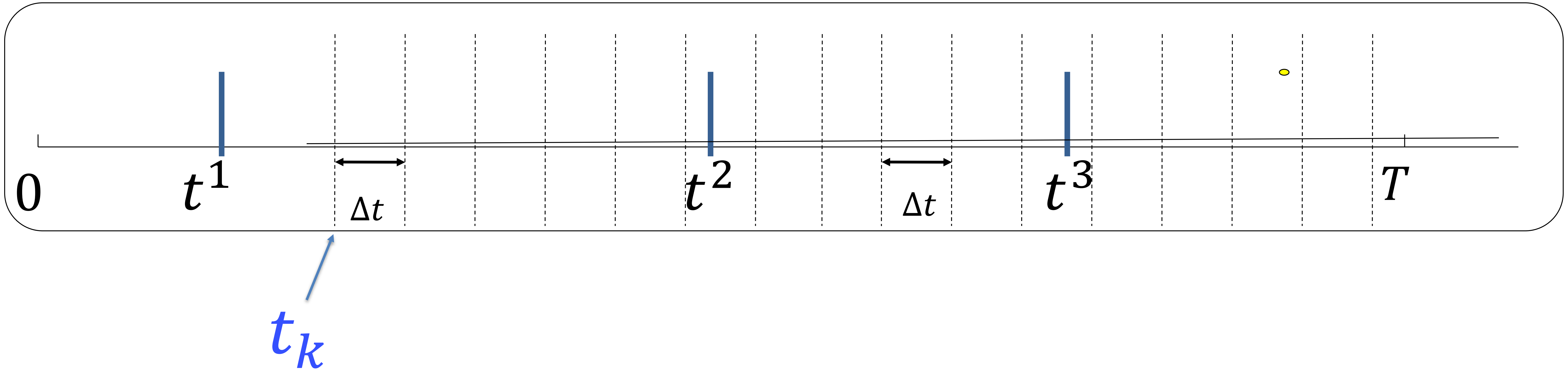
Escape noise can be combined with a leaky integrate-and-fire model: As soon as a spike is fired, the membrane potential is reset to a lower value so that a second spike becomes unlikely. In this case a good choice of the function f is an exponential.

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

; $\frac{c}{\Delta} = \rho_\vartheta$ 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.

11.2. Firing probability in discrete time



Probability to survive 1 time step

$\Delta t = \mathrm{t_{k+1}} - \mathrm{t_k}$

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

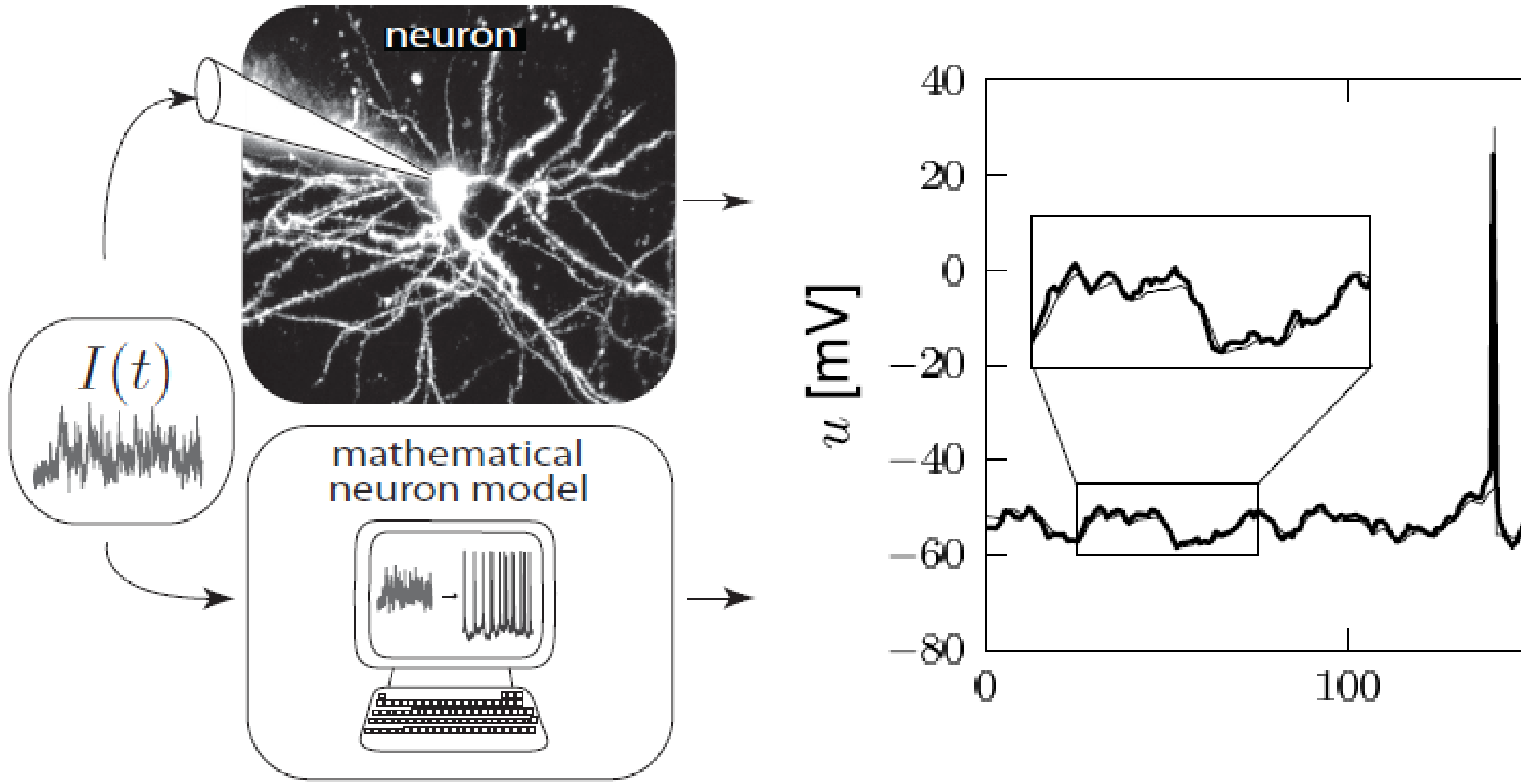
$$S(t_{k+1}|t_k) = \exp[-\rho(t_k)\Delta t] = 1 - P_k^F$$

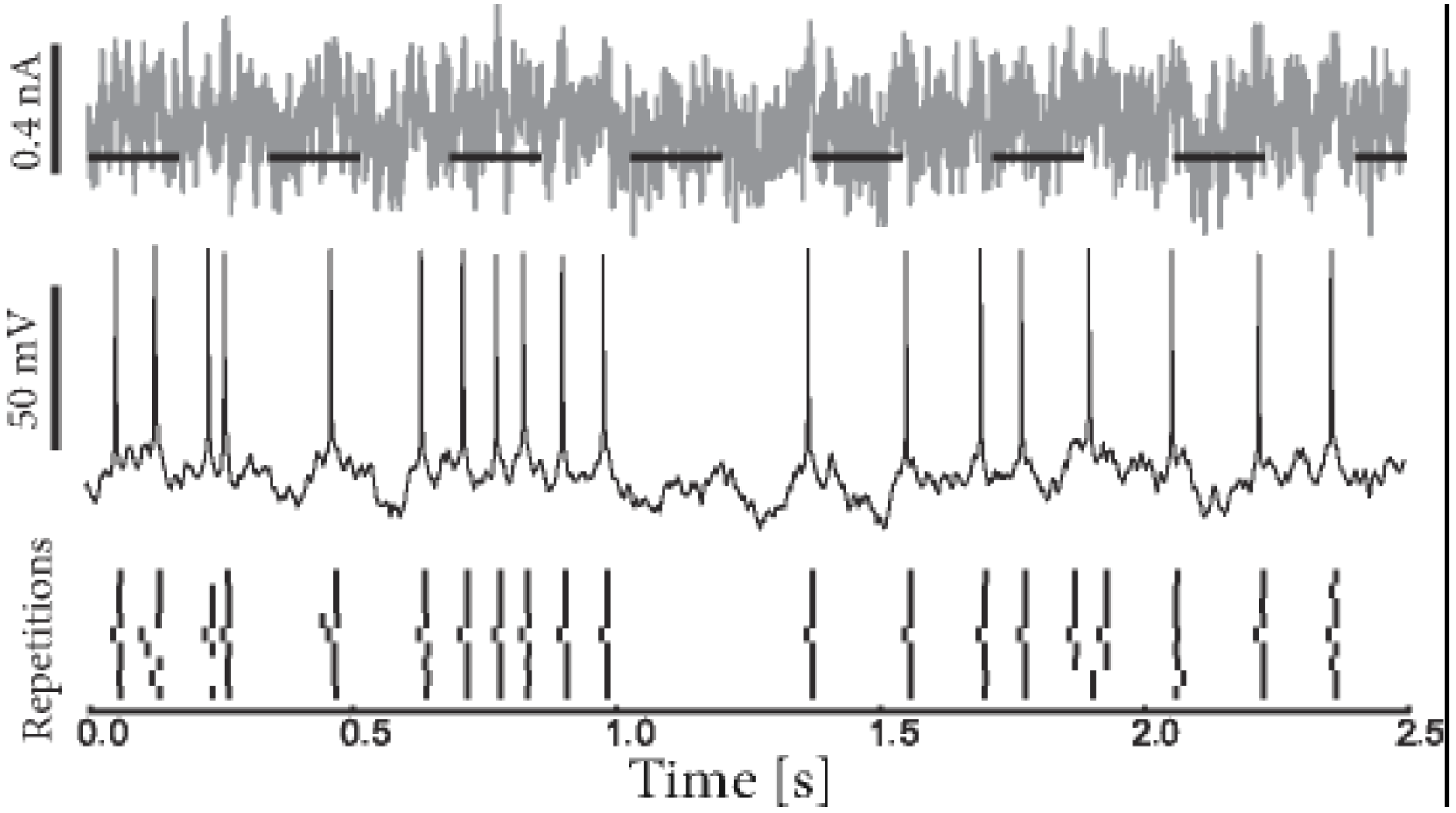
Probability to fire in 1 time step

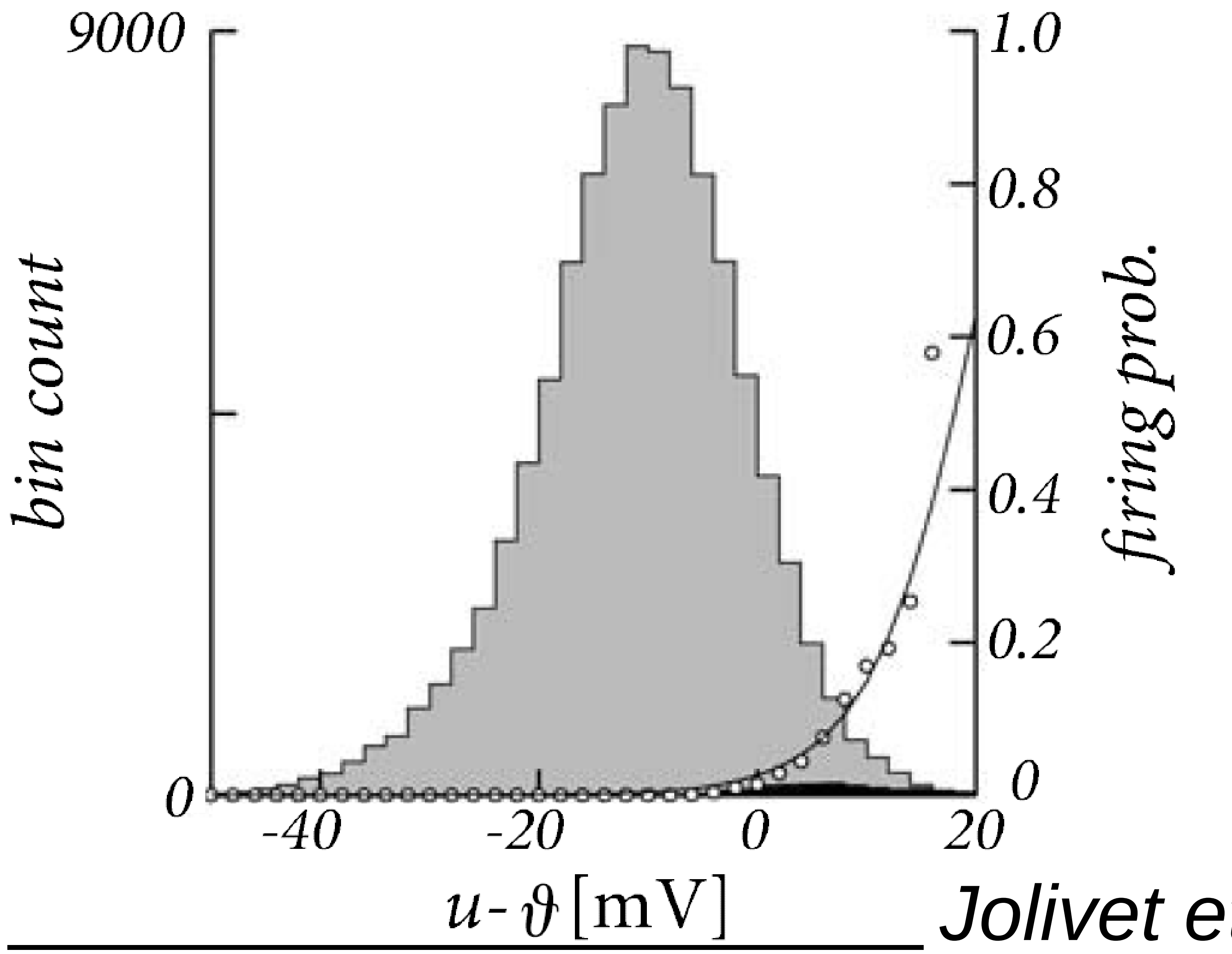
$$P^F(\Delta \mathrm{t}) = 1 - S(t + \Delta \mathrm{t}\,|\mathrm{t})$$

The probability $P^F(\Delta \mathrm{t})$ in discrete time is bounded even if the escape rate $\rho(t) = f(u - \vartheta)$ is not.

11.2. Escape noise - experiments







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

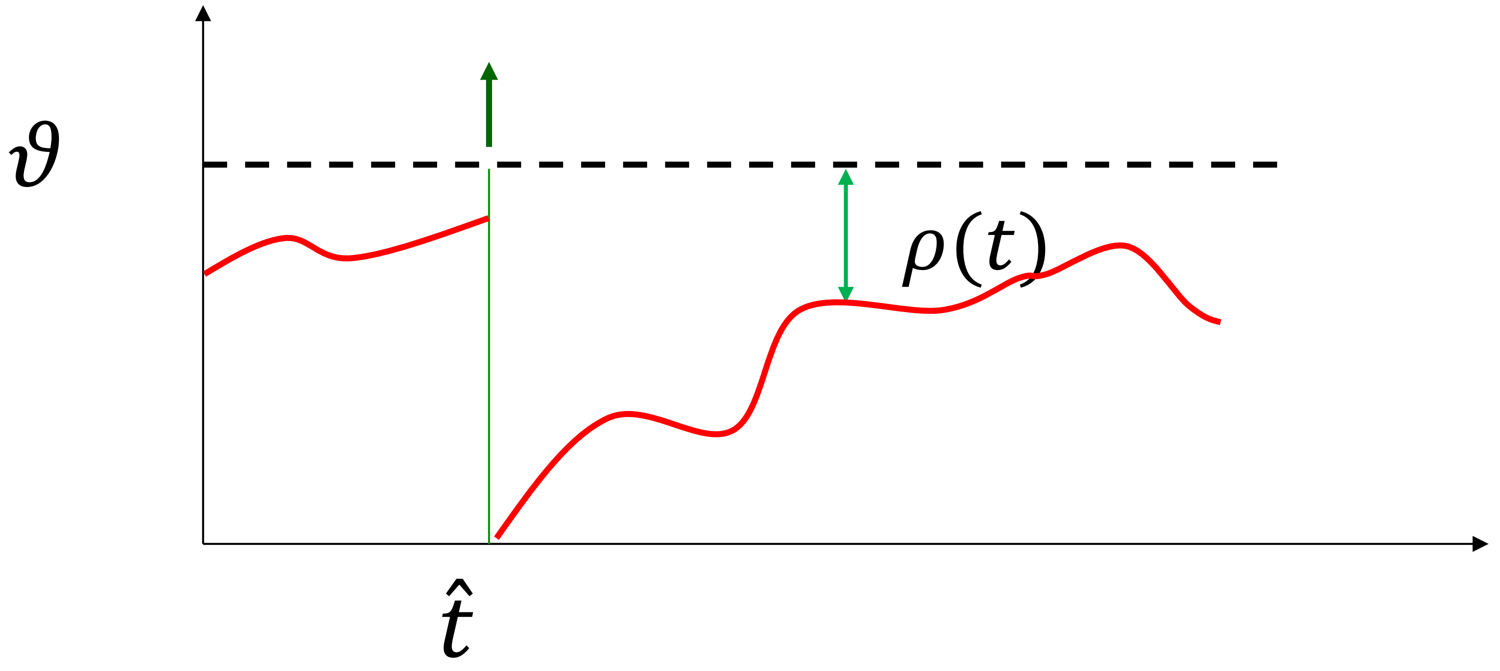
$$P_k^F = 1 - \exp[-\rho(t_k)\Delta]$$

escape rate

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

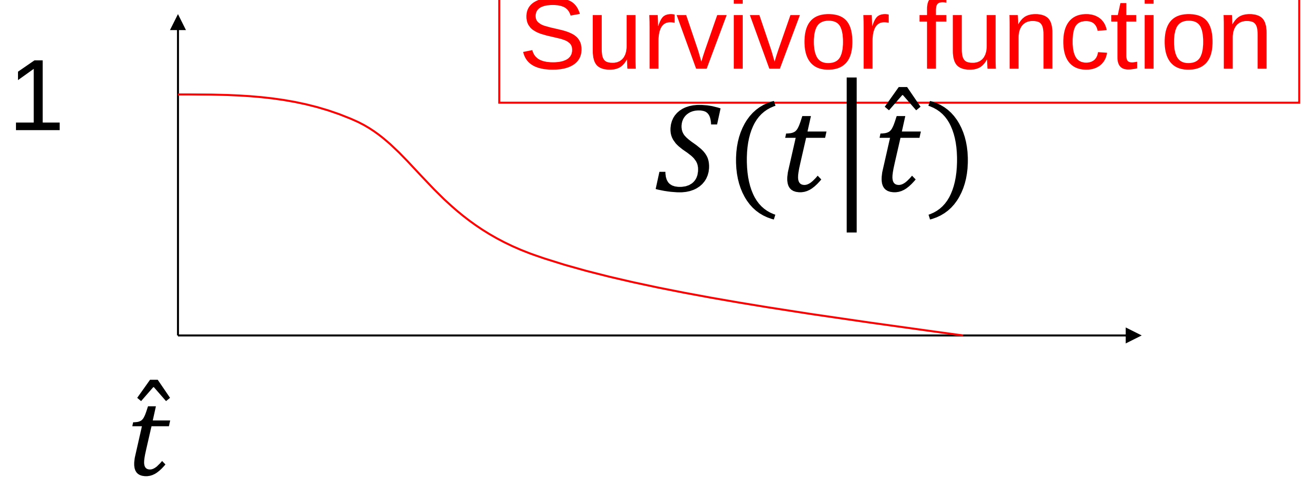
11.2. Time-dependent Renewal theory

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

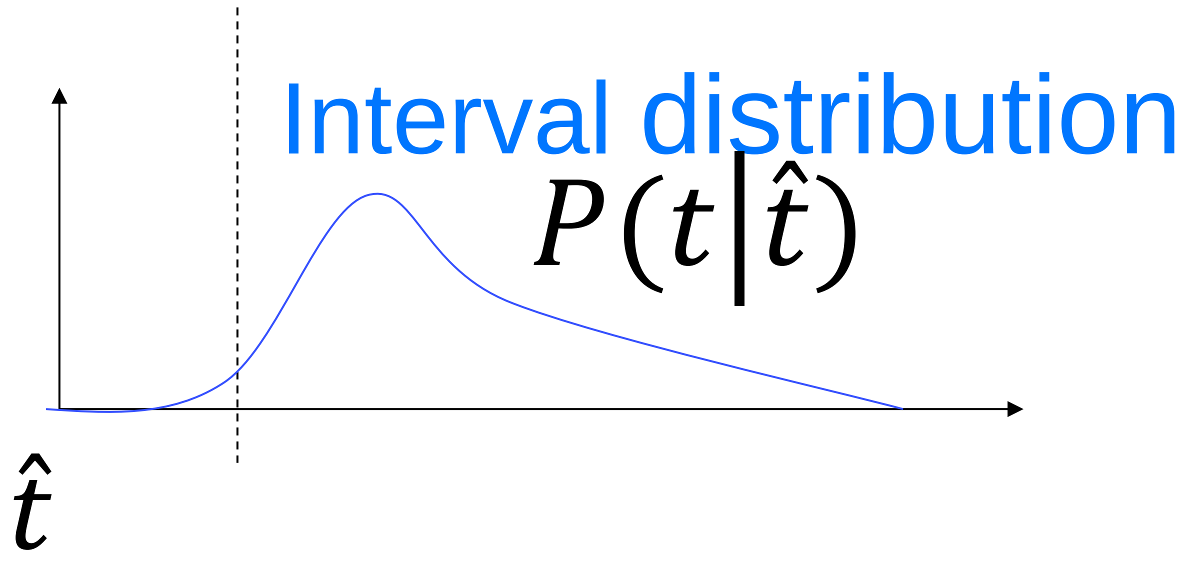


escape rate

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



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



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

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

Neuronal Dynamics – Quiz 11.2.

Consider a leaky integrate-and-fire model with escape noise

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

[ ] For large voltages, the firing probability in discrete time always saturates at 1

[ ] The firing probability in discrete time can be calculated from the Survivor function

[ ] For constant input, the distribution of intervals can be calculated.

[ ] The distribution of intervals has small or negligible values for very short intervals

[ ] An integrate-and-fire model with escape noise yields a time-dependent renewal model: If we know the ‘age’ of the neuron (time since last spike) and the time-dependent input I(t’) for t’<t we can predict the probability that it fires in a small interval around time t.

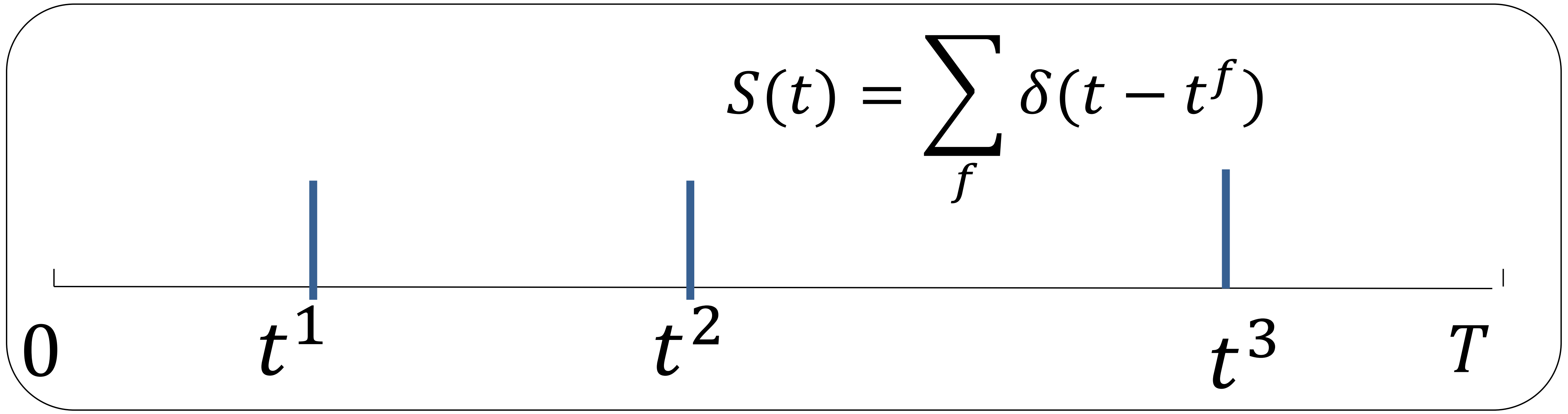
11.2 Summary: Renewal models

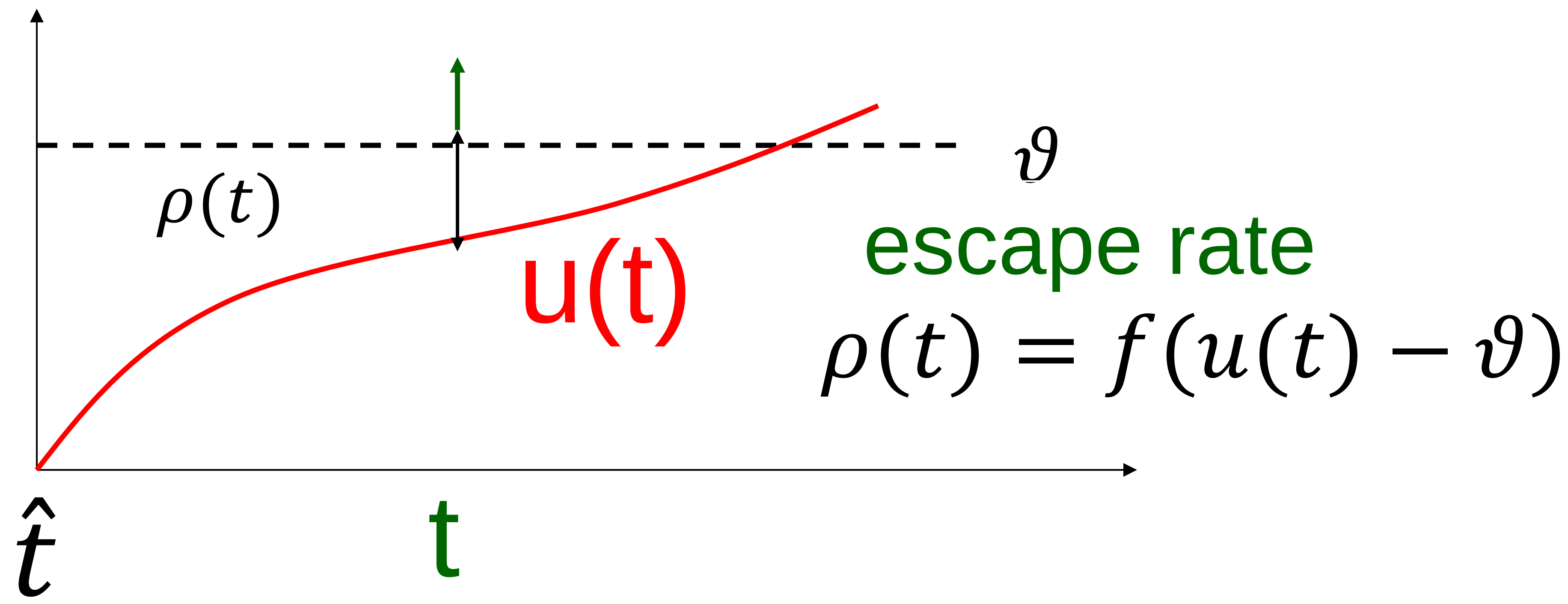
Even though the interspike-interval-distribution is most often used for STATIONARY data, (or constant input), we can also define an interspike-interval distribution for time-dependent input: Given an observed spike at time $\hat{t}$, and given that we know the time-dependent input up to time t, we ask: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

In the same way we can ask: Given an observed spike at time $\hat{t}$, 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$(t|\hat{t})$.
Similarly, given an observed spike at time $\hat{t}$, 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 $\rho(t|\hat{t})$, 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 $t - \hat{t}$. If the stochastic intensity (e.g., of a neuron model) only depends on the time difference $t - \hat{t}$ it is called a (stationary) renewal model. If it depends on $t - \hat{t}$ 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.

11.3. likelihood of a spike train





$$L^N(t^1, \ldots, t^N) = \exp\left(-\int_0^T \rho(t')dt'\right) \prod_f \rho(t^f)$$

$$\log L(t^1, \ldots, t^N) = -\int_0^T \rho(t')dt' + \sum_f \log \rho(t^f)$$

generative model of spike train

- generates spikes stochastically
- calculated likelihood that an **observed** experimental spike train **could have been generated**

Neuronal Dynamics – Quiz 11.3.

Consider a leaky integrate-and-fire model with escape noise

[ ] The term $\exp(-\int_{t_0}^{t_1} \rho(t')dt')$ represents the probability that the neuron fires in the interval $[t_0, t_1]$

[ ] The term $\exp(-\int_{t_0}^{t_1} \rho(t')dt')$ represents the probability that the neuron does not fire in the interval $[t_0, t_1]$

[ ] The term $(\int_{t_0}^{t_1} \rho(t')dt')$ represents the probability that the neuron fires in the interval $[t_0, t_1]$

[ ] The term $(\int_{t_0}^{t_1} \rho(t')dt')$ represents the expected number of spikes observed in the in the interval $[t_0, t_1]$

11.3 Summary: Likelihood of a spike train

Suppose an experimentalist has observed a spike train with spikes a times $\{t^1, ..., t^N\}$.
We ask how likely it is that this specific spike train could have been generated by 'my' neuron model.

As a neuron model we use a formal spiking neuron such as the leaky integrate-and-fire model with escape noise

$$\rho(t) = f(u(t) - \vartheta) \quad (1)$$

Given the observed spike times $t^1, ..., t^n$ < t up to time t, and the external input $I(t')$; $t' < t$ we calculate the membrane potential u(t). Given the membrane potential, equation (1) gives us the stochastic intensity. The likelihood that the observed spike train is then

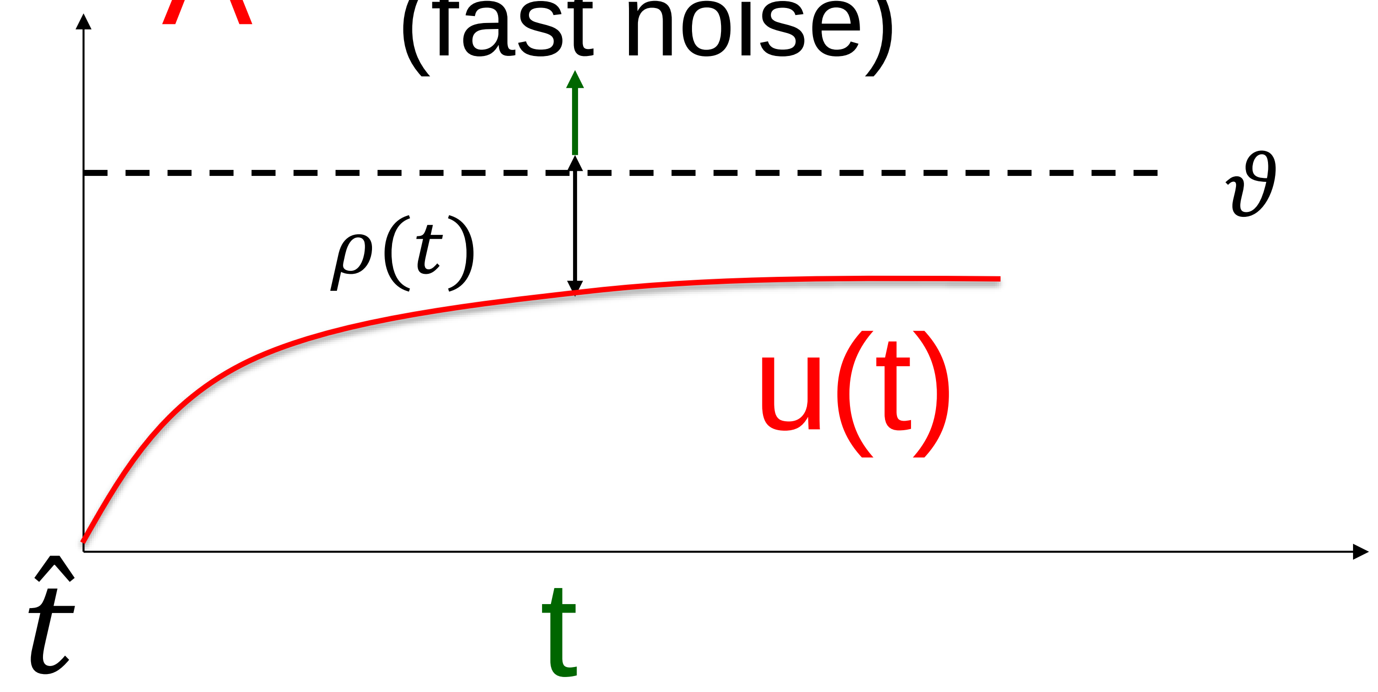
$$L^N(t^1, ..., t^N) = \exp(-\int_0^T \rho(t')dt') \prod_f \rho(t^f)$$

The exponential decay term is the 'survival' probability without firing between two observed spikes; the product term is the likelihood that the model would fire at the actually observed times.
We have to integrate N times over t to get a unit-free quantity with constraint:

$$\int_0^T dt_1 \int_{t_1}^T dt_2 \int_{t_2}^T dt_3 \dots \int_{t_{N-1}}^T dt_N \, L^N(t^1, ..., t^N) \le 1$$

11.4. Comparison of Noise Models

A escape process
(fast noise)



escape rate

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

Interval distribution

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

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

escape rate

Survivor function

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

$t - \hat{t}$

Stationary input:

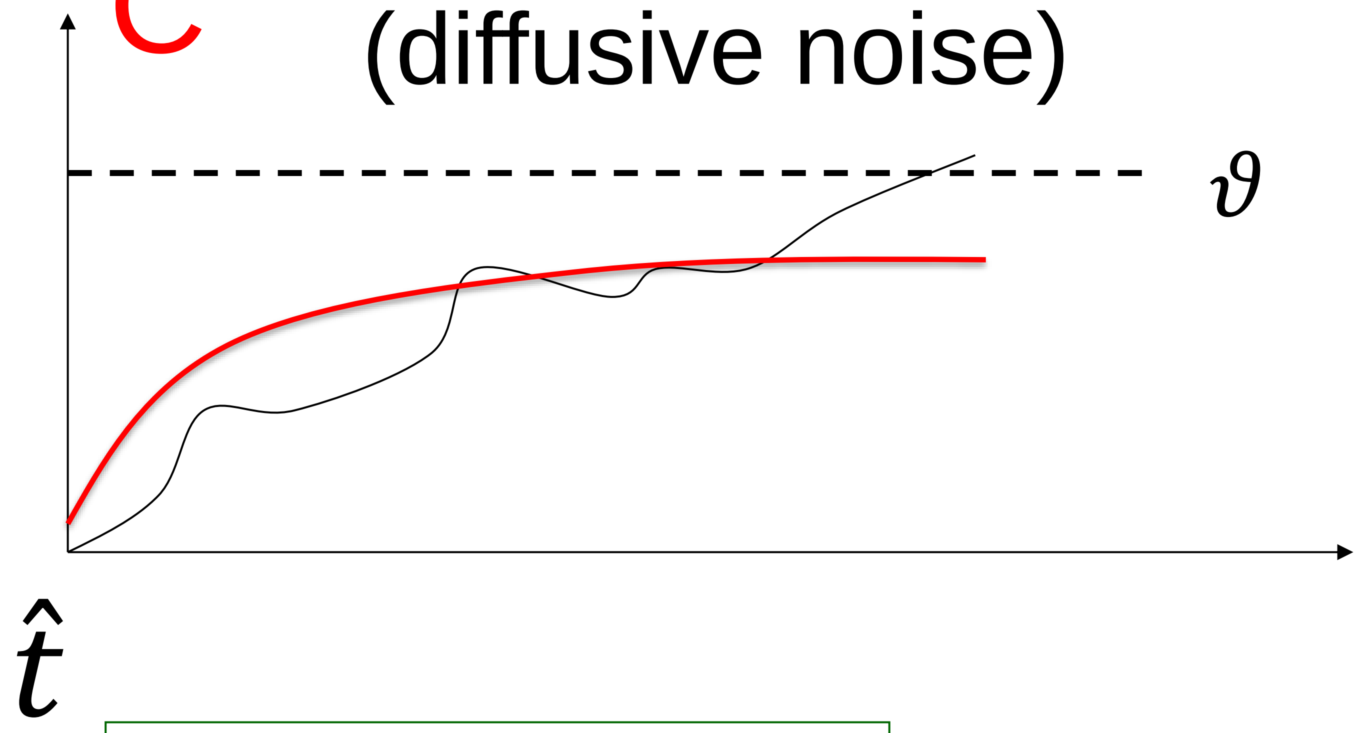
-Mean ISI

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

-Mean firing rate

$$f = \frac{1}{\langle s \rangle}$$

C stochastic spike arrival
(diffusive noise)



noisy integration

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

noise

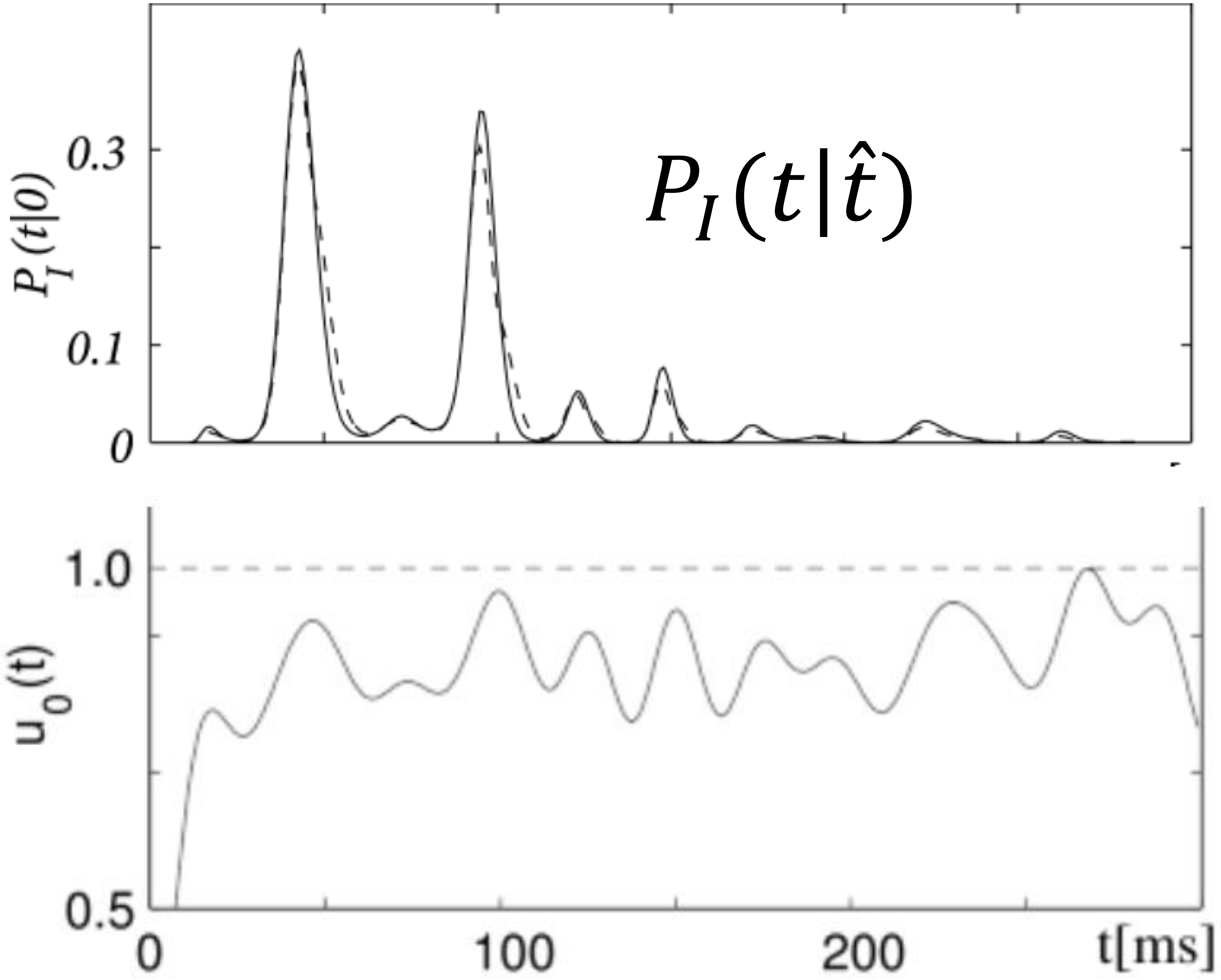
11.4. Comparison of Noise Models

Is there a choice for escape noise $\rho(t)$ that makes the two noise models 'similar'?

Probability of first spike

diffusive (solid line)
escape (dashed line)

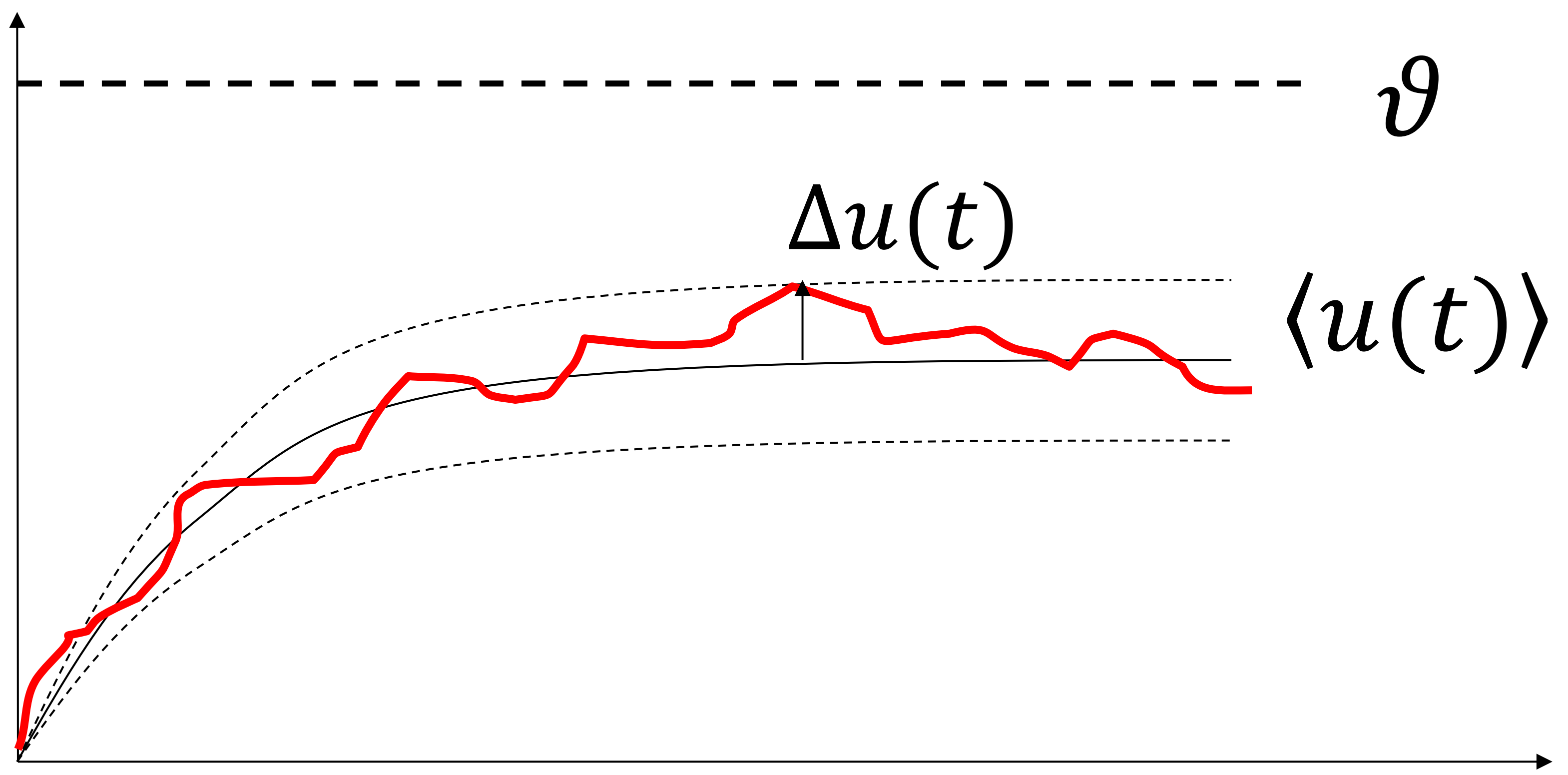
subthreshold potential



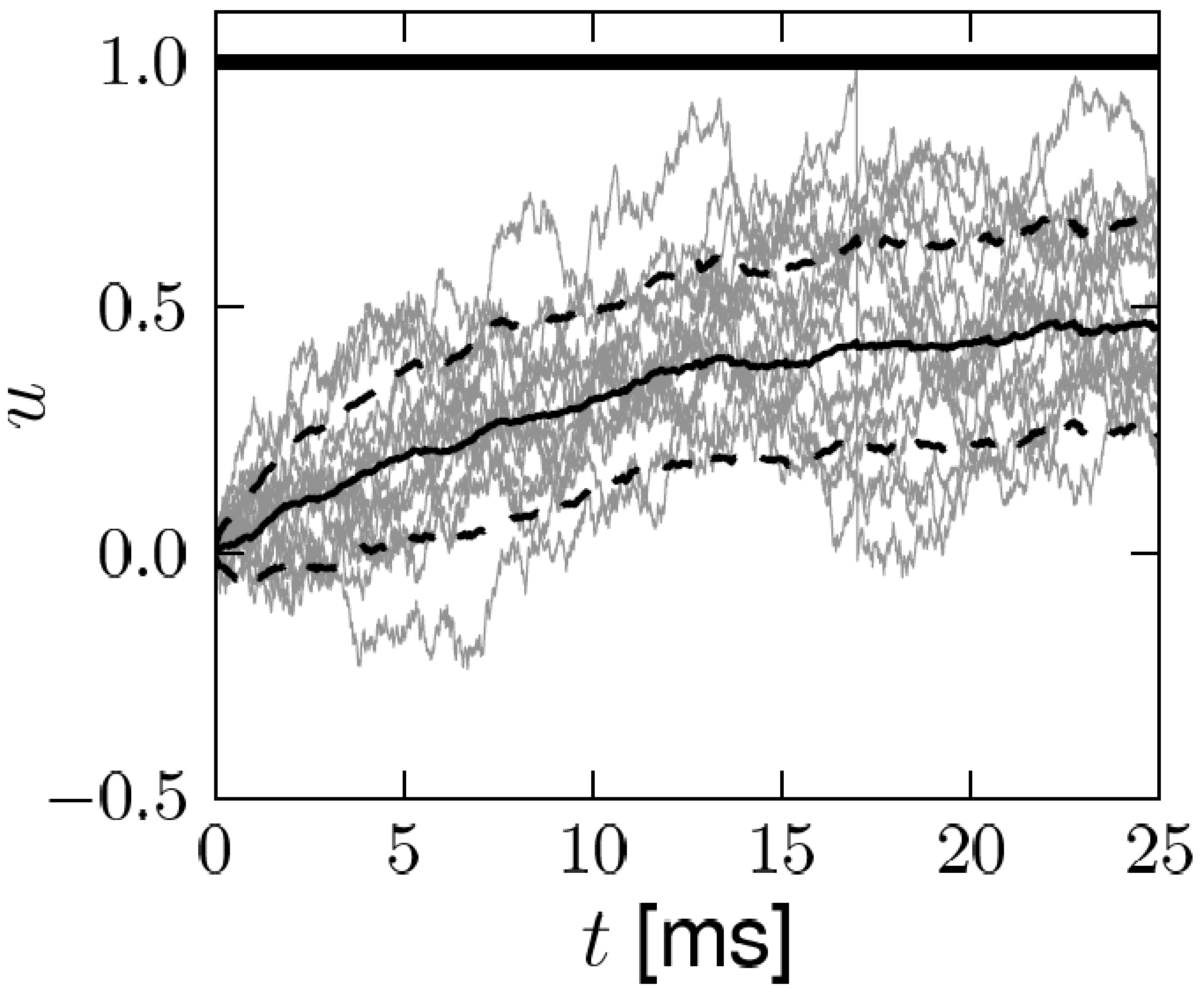
escape rate (Arrhenius&Currtent model)

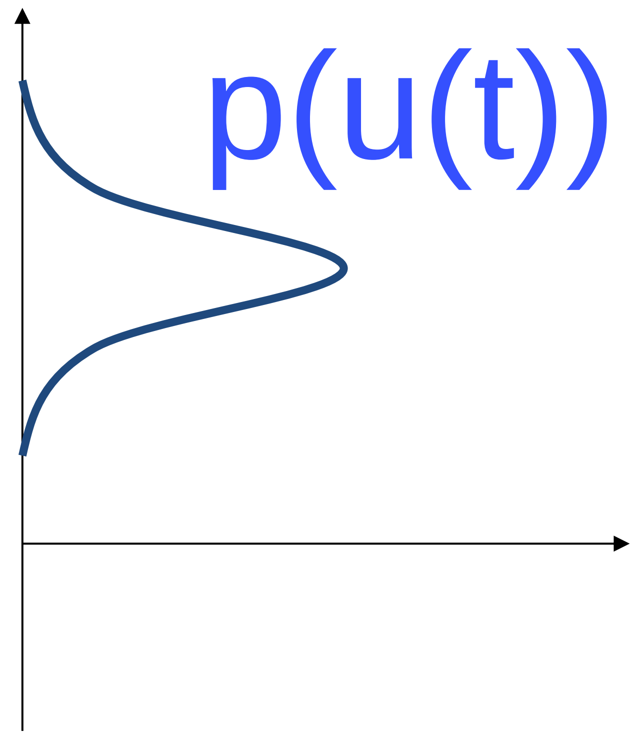
$$\rho(t) = f(u_0(t), u'_0(t)) \propto \exp\left(-\frac{(u_0(t)-\vartheta)^2}{\sigma^2}\right) \left[\frac{c_1}{\tau} + \frac{c_2[u'_0(t)]_+}{\sigma}\right]$$

11.4 Diffusive noise (stochastic spike arrival), far below threshold



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





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

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

Math argument:

- no threshold

- trajectory starts at known value

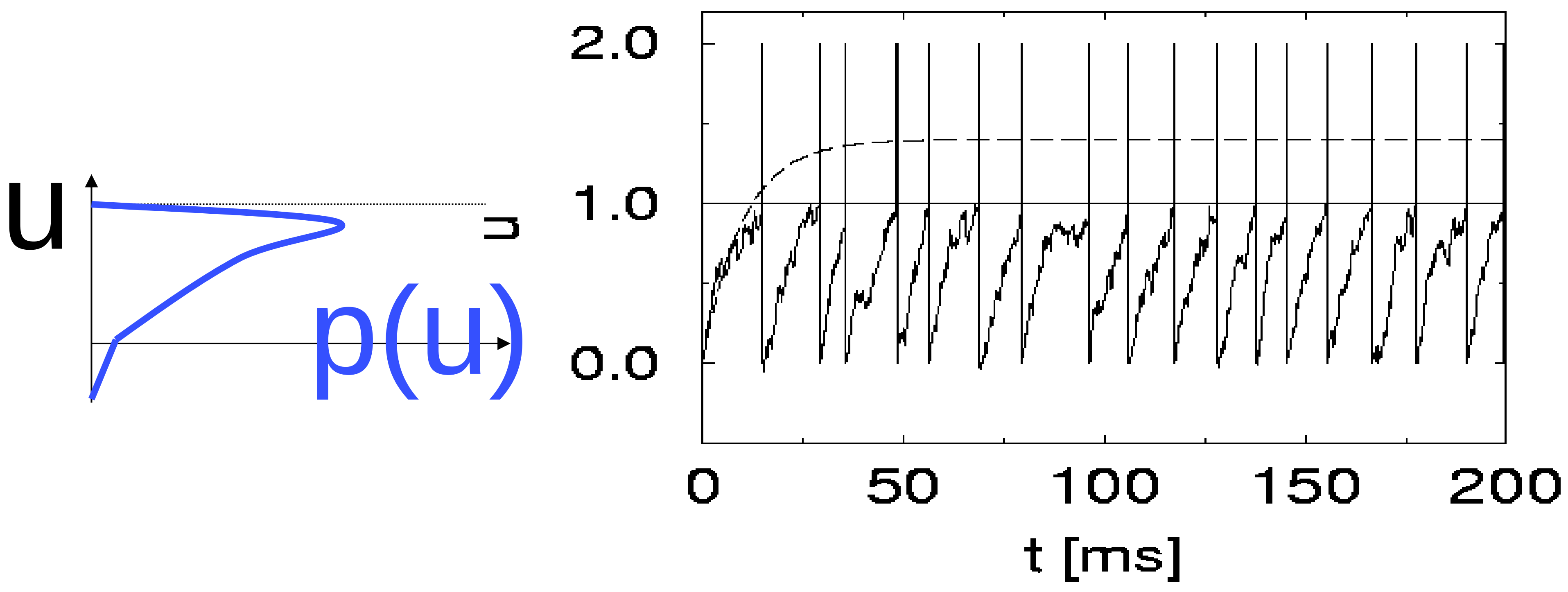
→ Gaussian distribution around

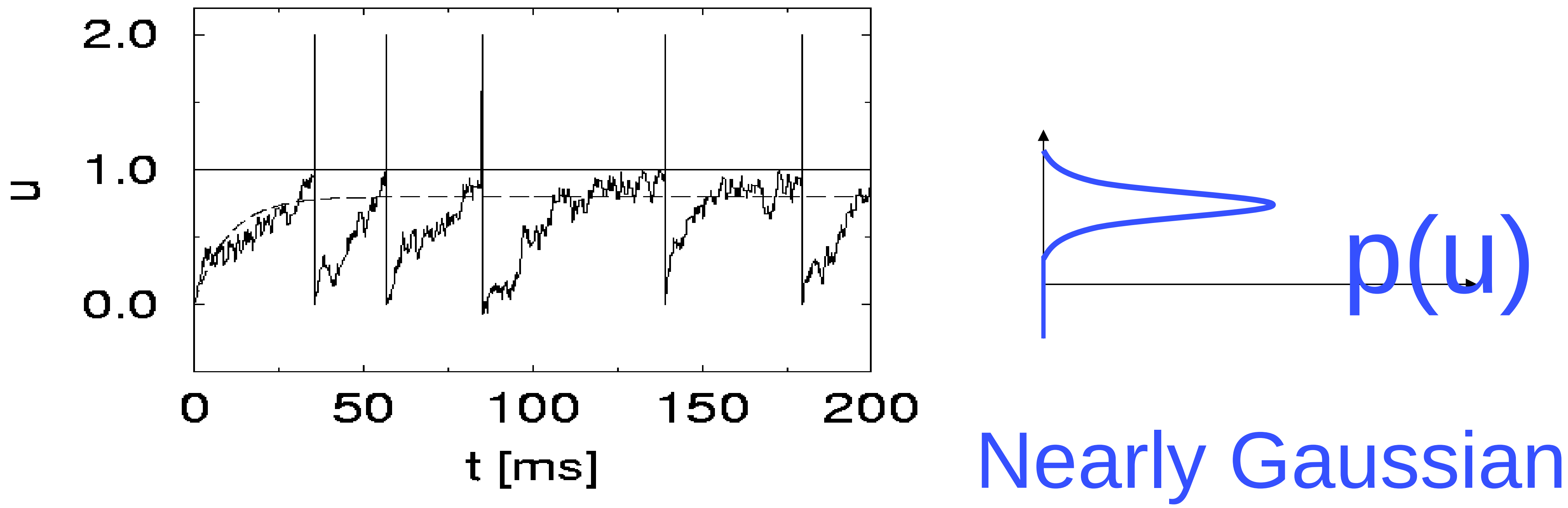
→ Mean='deterministic trajectory'

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

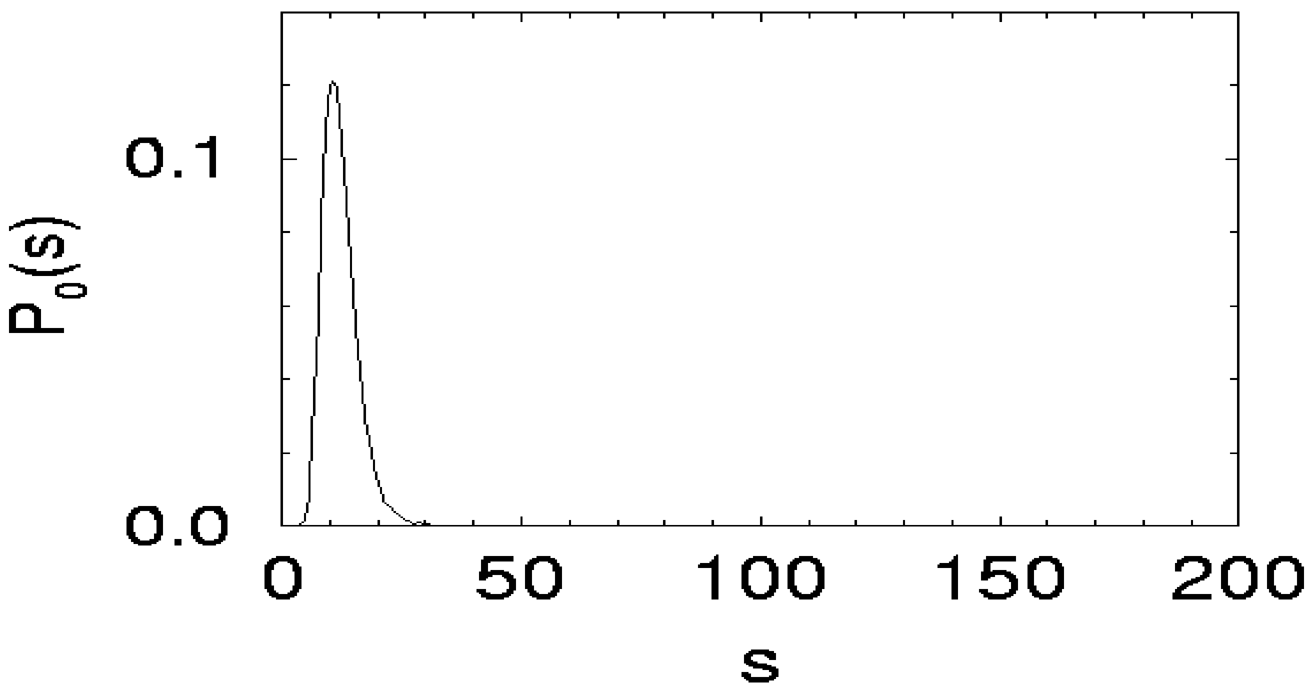
11.4. Diffusive noise/stochastic arrival: Two regimes

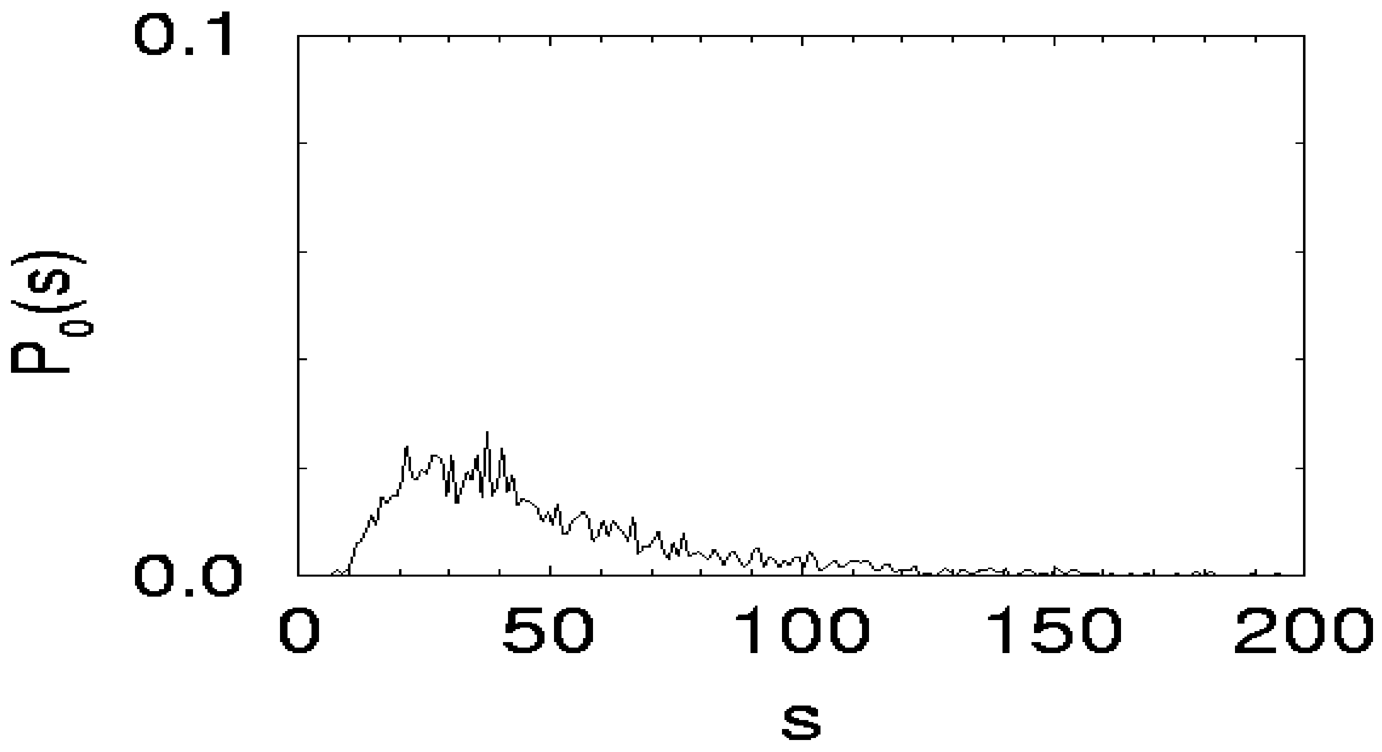
Superthreshold vs. Subthreshold regime





Nearly Gaussian subthreshold distr.

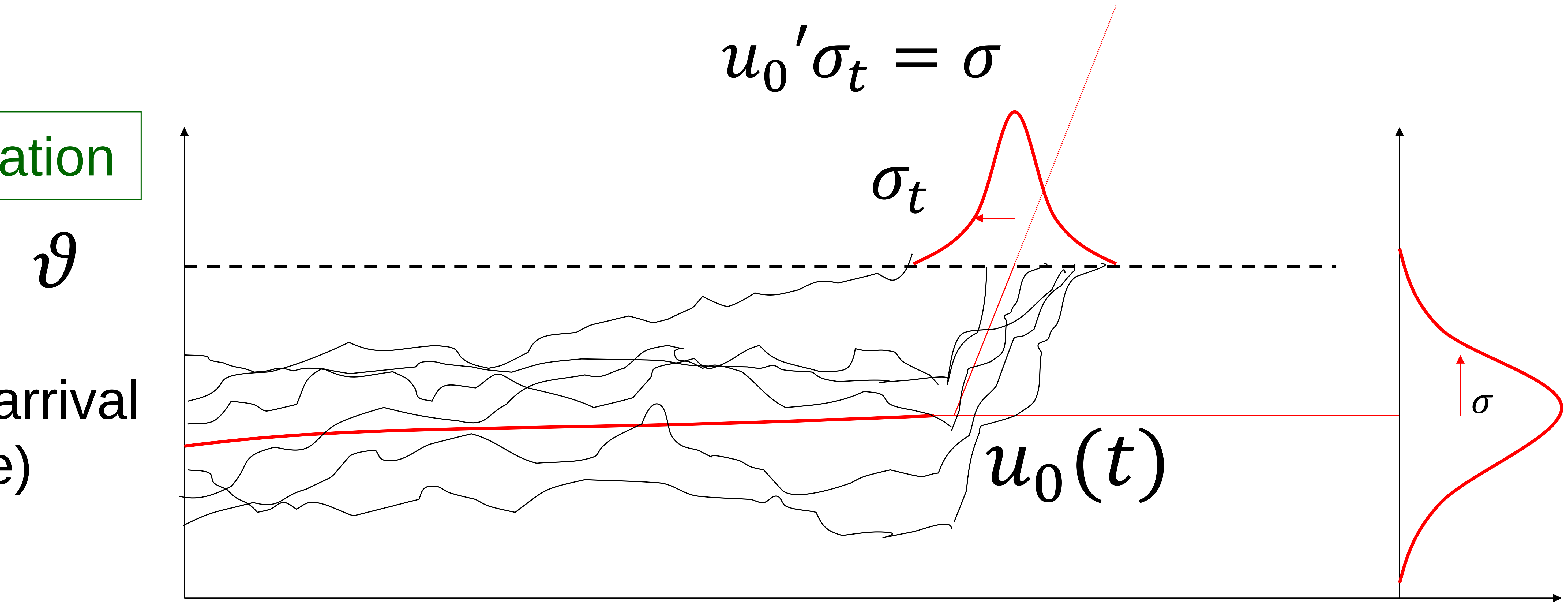




11.4 Superthreshold regime: role of slope u'

noisy integration

stochastic spike arrival
(diffusive noise)



escape rate

$$\rho(t) = f(u_0(t), u'_0(t)) \propto \quad u'_0(t)$$

Neuronal Dynamics – Quiz 11.4.

Compare a leaky integrate-and-fire model with escape noise
And a leaky integrate-and-fire model with stochastic spike arrival

[ ] Both models are equivalent.
[ ] There is no exact equivalence, but there is a reasonable approximation.
[ ] In an escape noise model, the escape rate may also depend on the slope of the trajectory

11.4 Summary: Comparison of noise models

We have seen two noise models:

1) Stochastic spike arrival can be considered as noise in the input, described either as a Poisson process or as a white noise. In a computer implementation of white noise, you have to call in each time step a random number generator. Since the random number is applied as an addition input current, the membrane potential shows fluctuations that are not white but have a finite autocorrelation time.
2) Escape noise can be considered as noise in the output, described by a stochastic intensity, also called escape rate that depends on the difference between threshold and voltage. In a computer implementation of escape noise, you call in each time step a random number generator. The random number decides whether the neuron fires or not. The membrane potential has no noise.

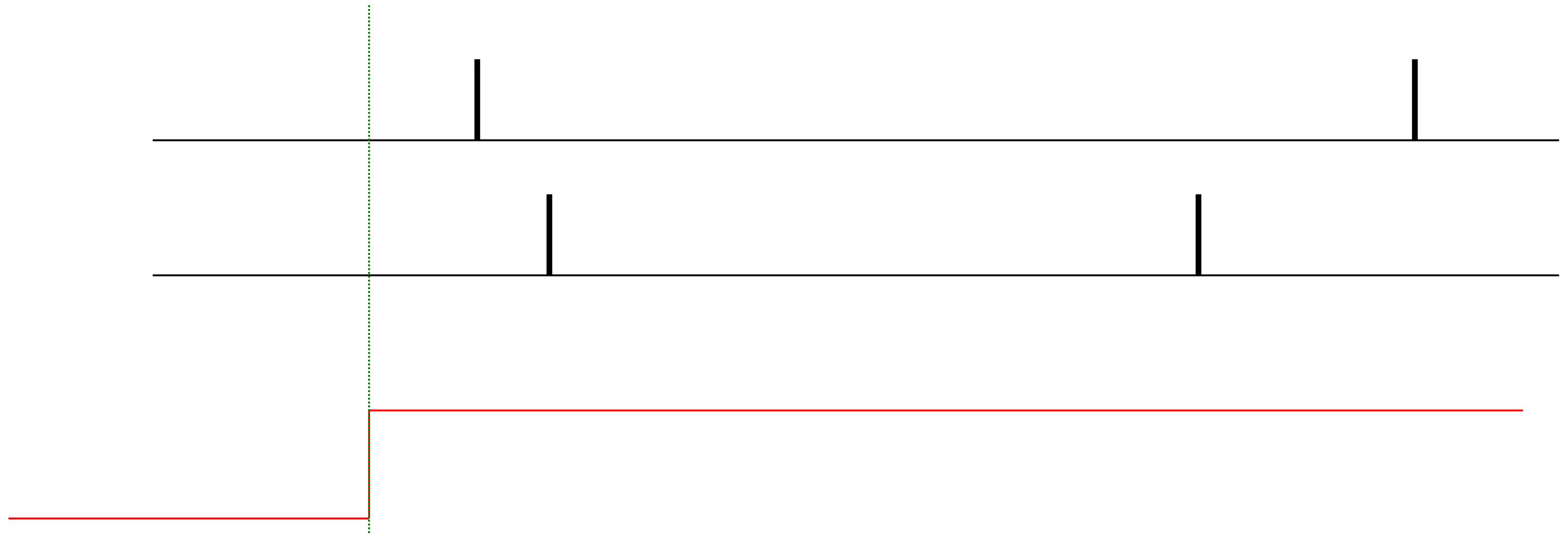
The two models are conceptually different and there is no exact mapping from one to the other. Nevertheless, we can observe that

(i) In the subthreshold regime, the diffusive noise model leads to a Gaussian distribution around the deterministic distribution. Hence it is rare that one of the fluctuations hits the threshold. Heuristically, the stochastic intensity (escape rate) of the escape model should hence depend on the membrane potential density at threshold.

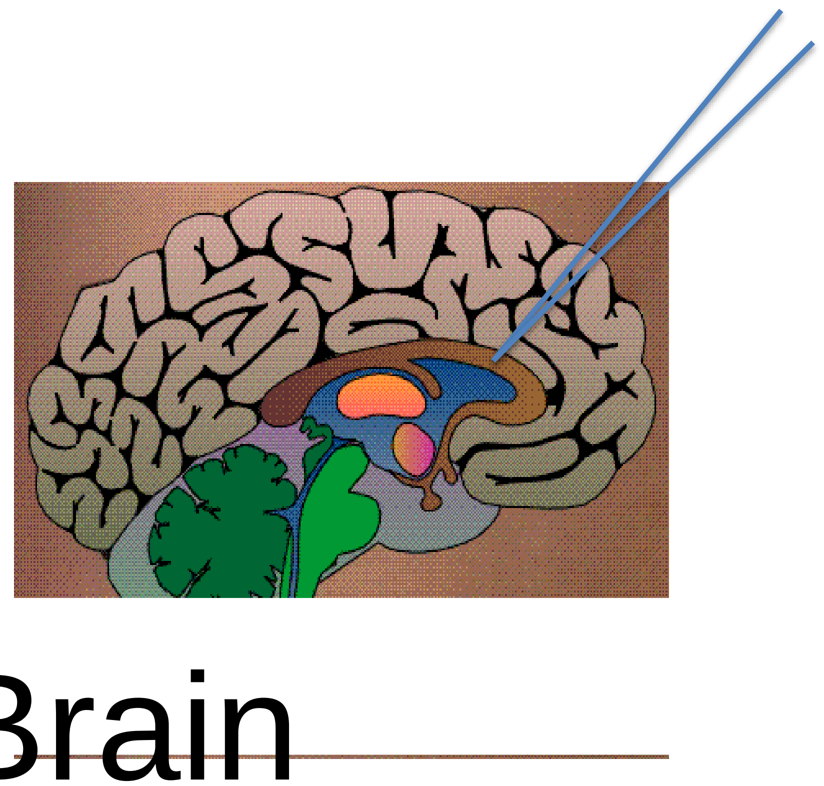
(ii) In the superthreshold regime, the deterministic trajectory is actively pushed across the threshold and traverses the threshold with finite slope u'. This leads to a second term in the escape rate that needs to added to the term from (i). The two terms together provide a reasonable mapping.

11.5. Temporal codes

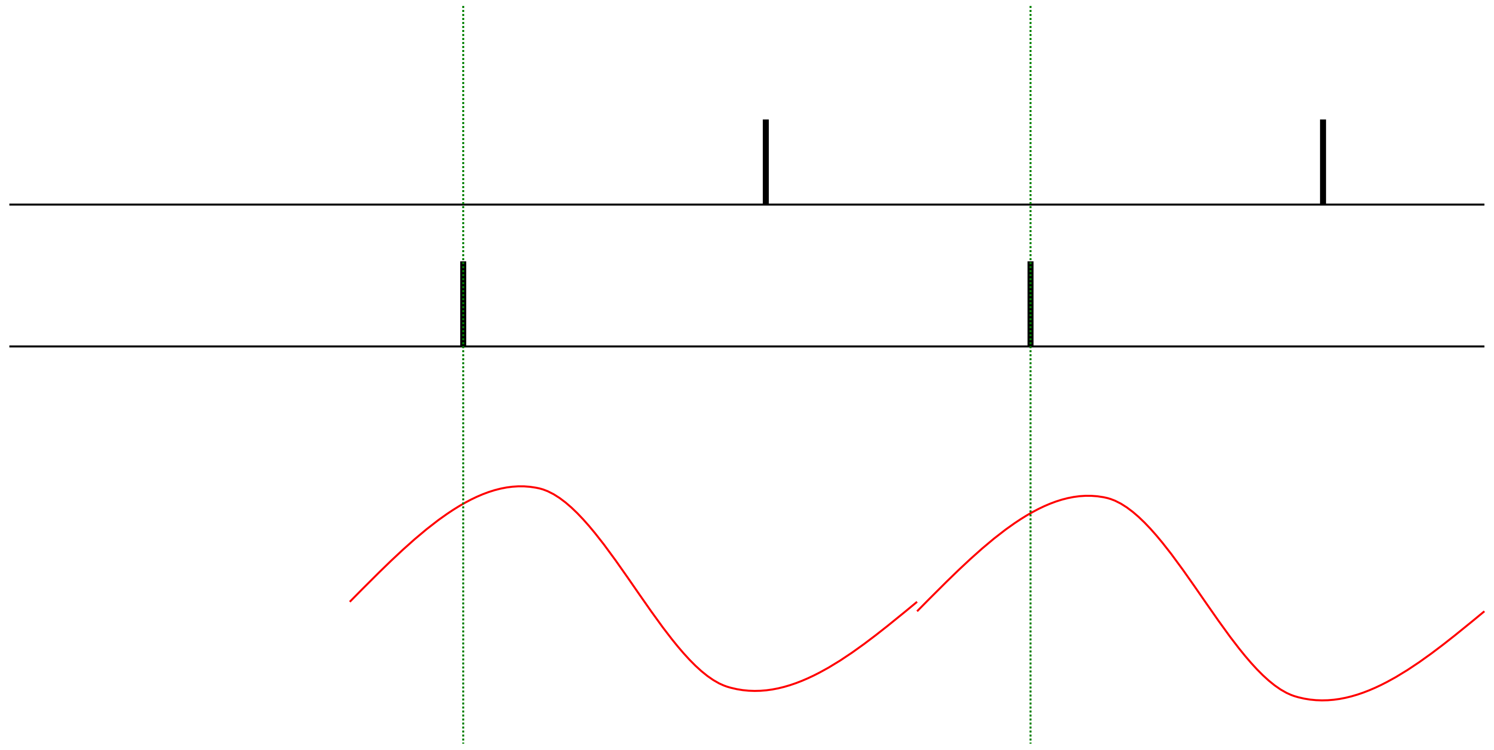
Spike timing codes:
-time-to-first spike
-phase code



Time to first spike after input



Brain



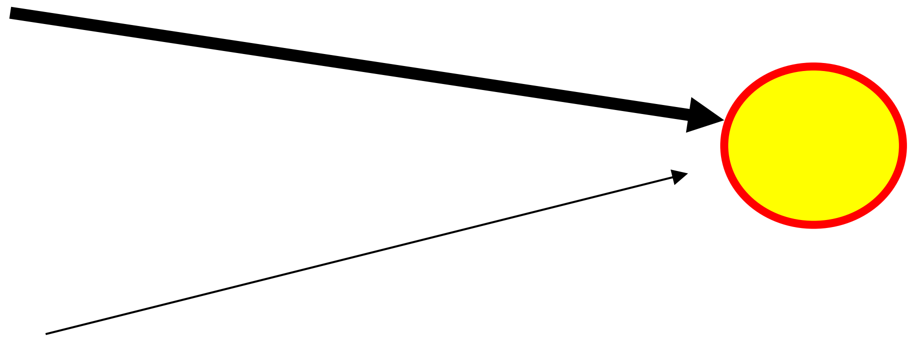
Phase with respect to oscillation

11.5. Stochastic Resonance

Stochastic Resonance: changing the noise level in subthreshold regime

$$I(t) = I_0 \cos(\omega t)$$

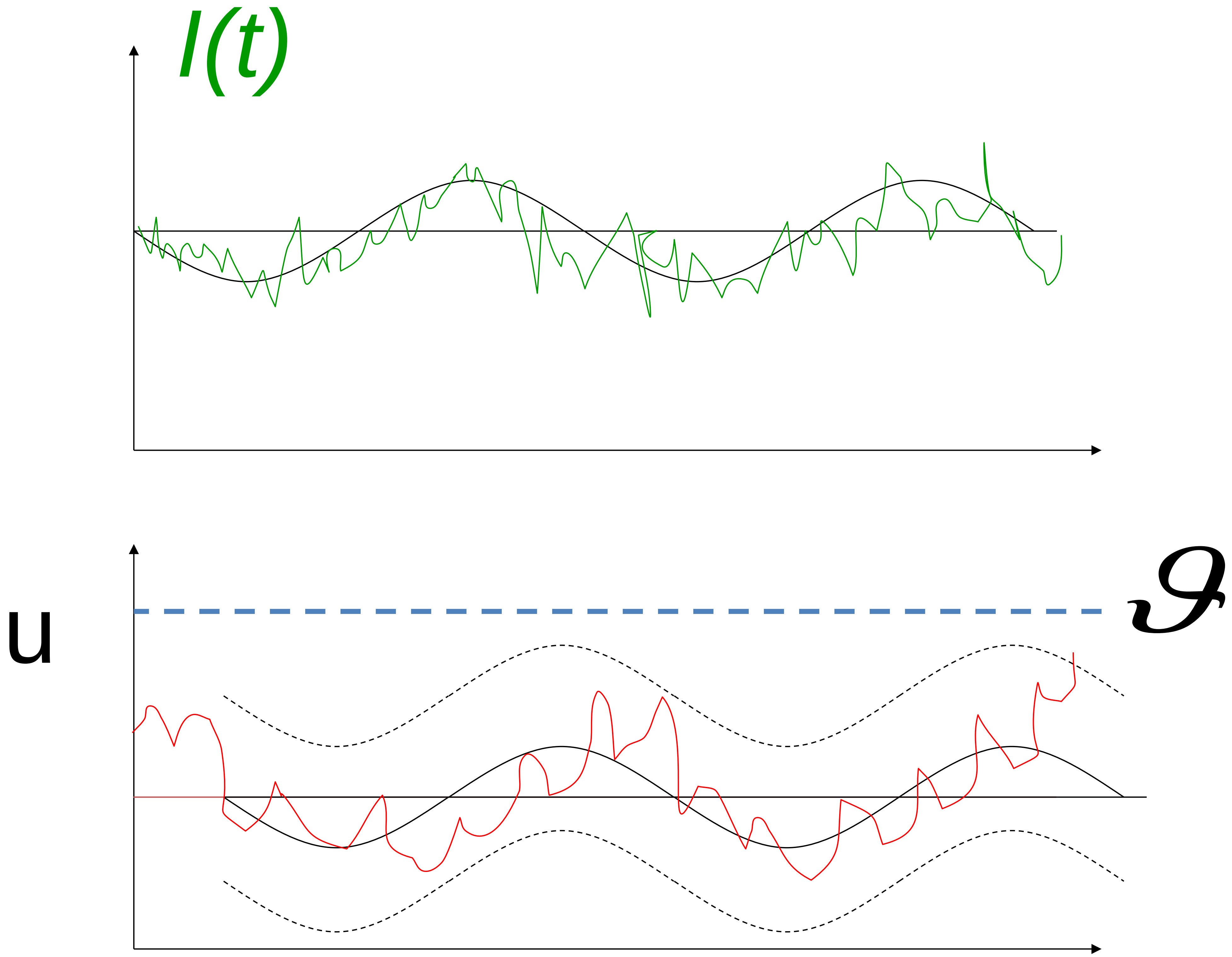
$$I^{noise}(t) = \sigma \, \xi(t)$$



Sinusoidal input

+ noise

+ threshold



11.5. Summary Renewal process, firing probability

Famous temporal codes are

(i) TTFS coding: Time-to-First-Spike. The coding scheme assumes that a novel input is switched on abruptly. Different neurons respond at different times after the onset of the input. This coding scheme is probably relevant in the retina and in the ear.

(ii) Phase coding: The coding scheme assumes that there is an ongoing slow oscillation that is running in the background. Different neurons respond at different phases with respect to the background oscillation. This coding scheme is probably relevant in the hippocampus.