Week 6 – part 1 : Escape noise

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Neuronal Dynamics:
Computational Neuroscience of Single Neurons

Week 6 – Noise models:
Escape noise

Wulfram Gerstner

EPFL, Lausanne, Switzerland

6.1 Escape noise
- stochastic intensity and point process

6.2 Interspike interval distribution
- Time-dependend renewal process
- Firing probability in discrete time

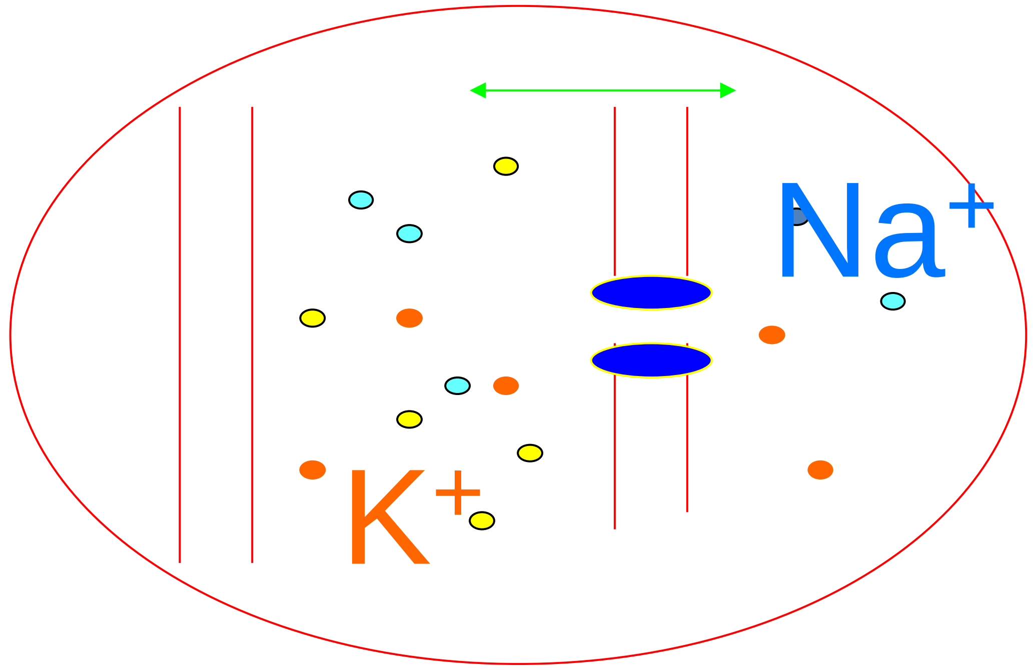
6.3 Likelihood of a spike train
- likelihood function

6.4 Comparison of noise models
- escape noise vs. diffusive noise

6.5. Rate code vs. Temporal Code
- timing codes
- stochastic resonance

Neuronal Dynamics – Review: Sources of Variability

- Intrinsic noise (ion channels)



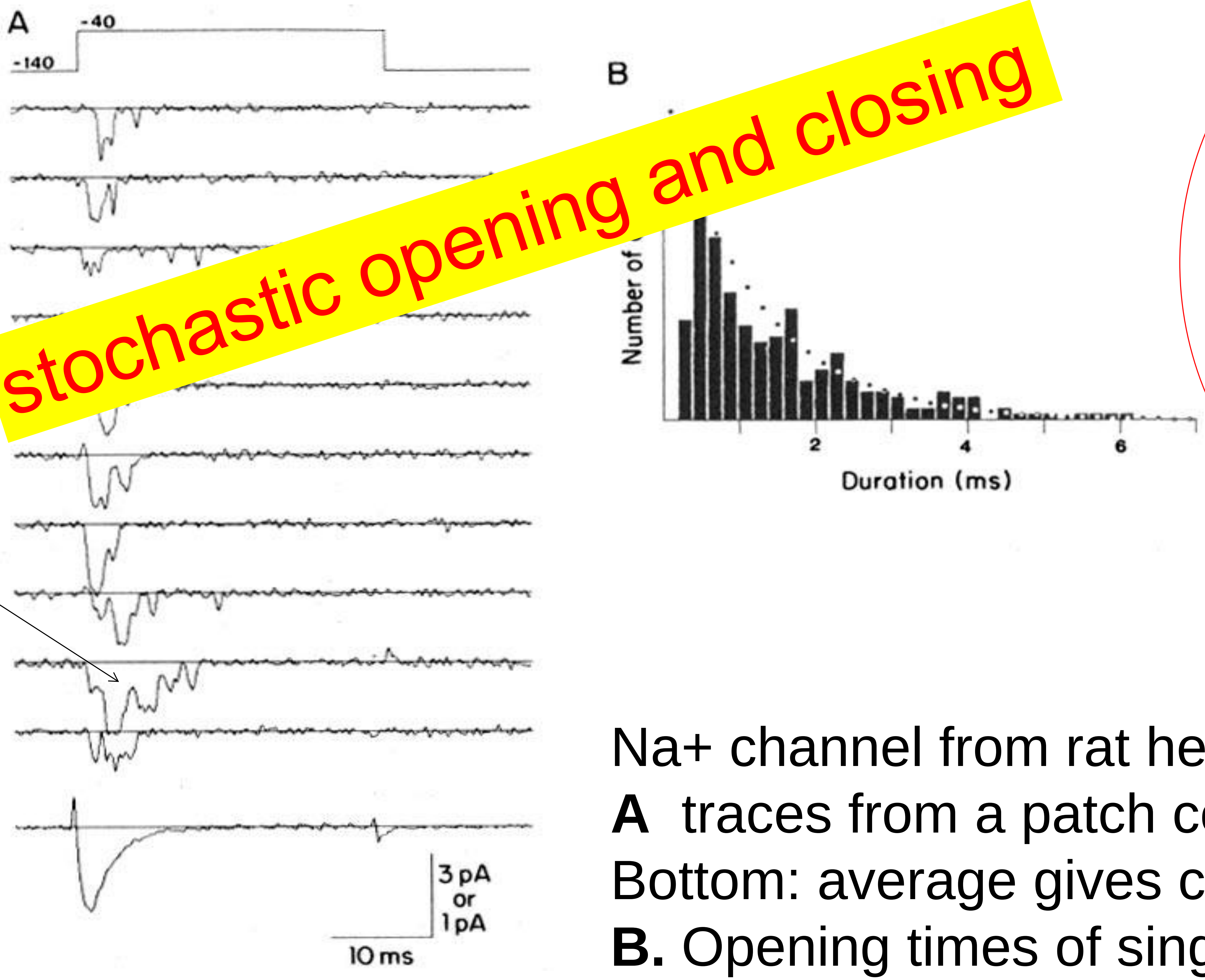
-Finite number of channels

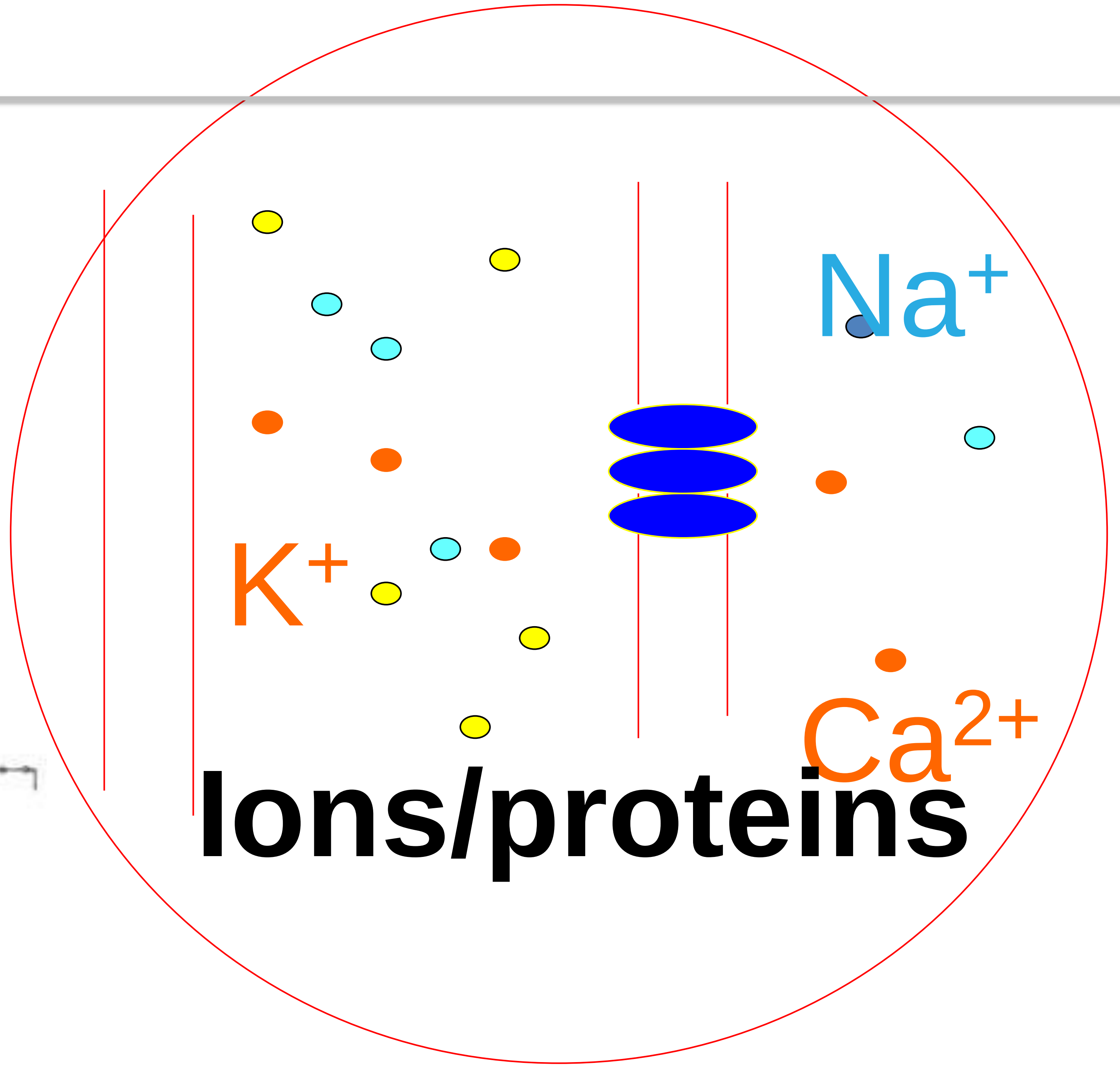
-Finite temperature

Review from 2.5 Ion channels

Steps:
Different number
of channels

stochastic opening and closing

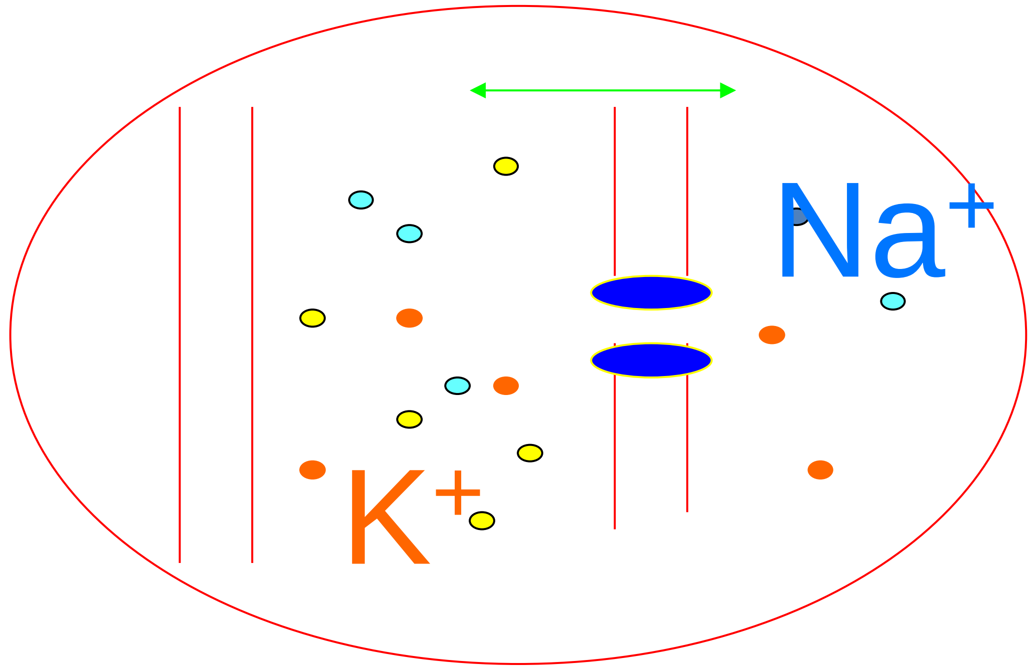




Na+ channel from rat heart *(Patlak and Ortiz 1985)*
A traces from a patch containing several channels.
Bottom: average gives current time course.
B. Opening times of single channel events

Neuronal Dynamics – Review: Sources of Variability

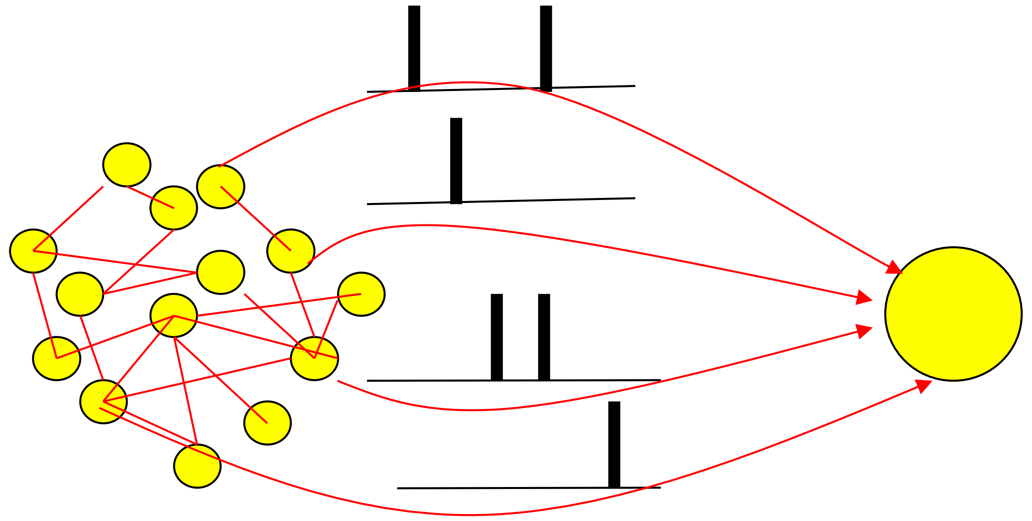
- Intrinsic noise (ion channels)



-Finite number of channels
-Finite temperature

small contribution!

-Network noise (background activity)



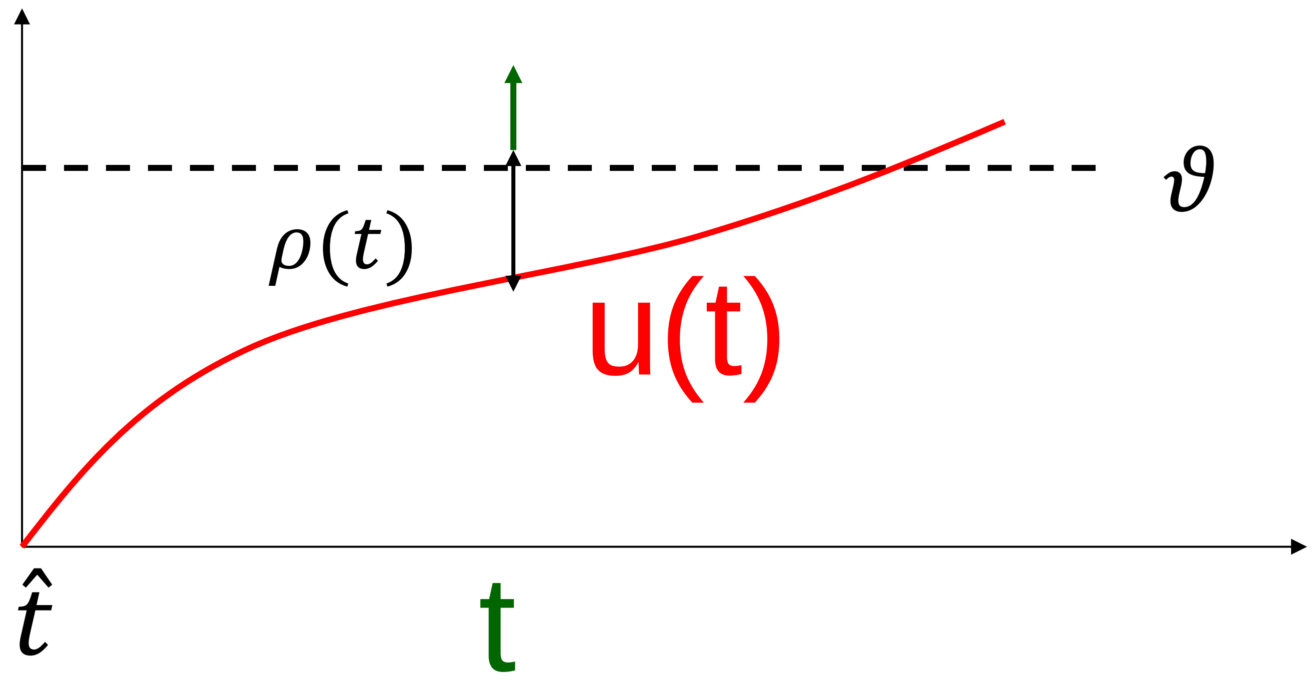
-Spike arrival from other neurons
-Beyond control of experimentalist

big contribution!

Noise models?

Noise models

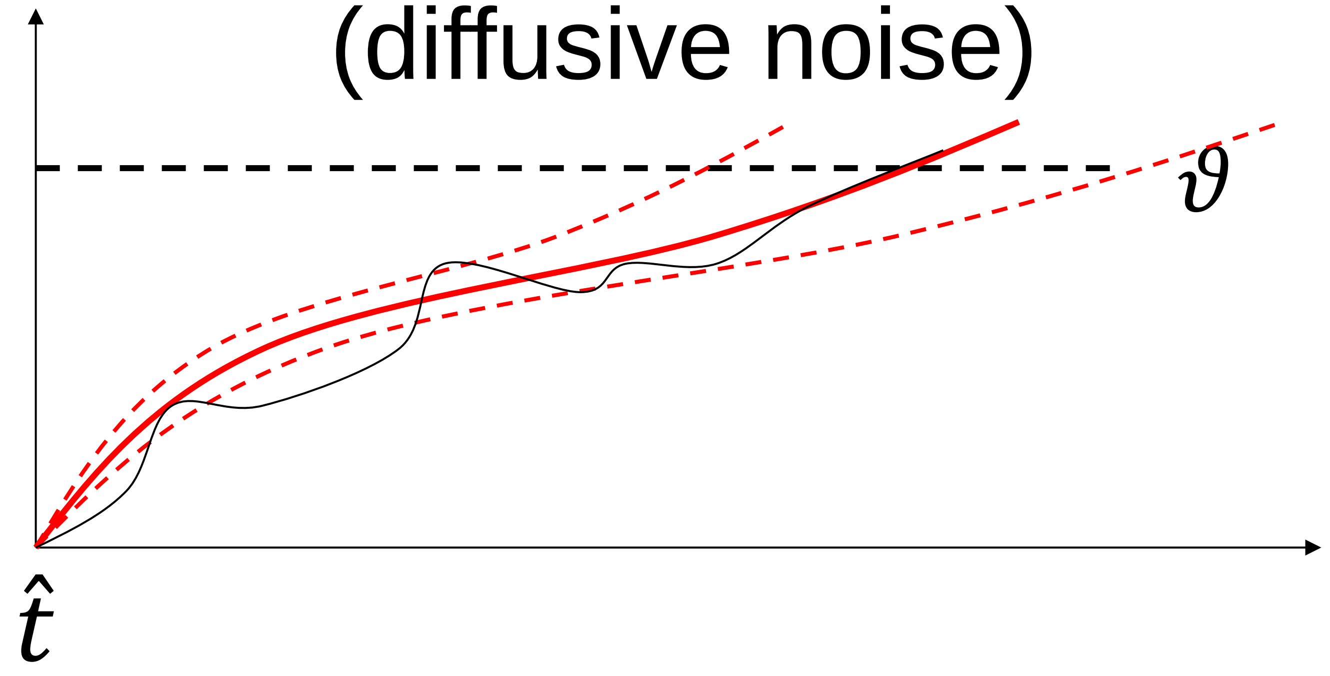
escape process,
stochastic intensity



escape rate

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

stochastic spike arrival
(diffusive noise)



noisy integration

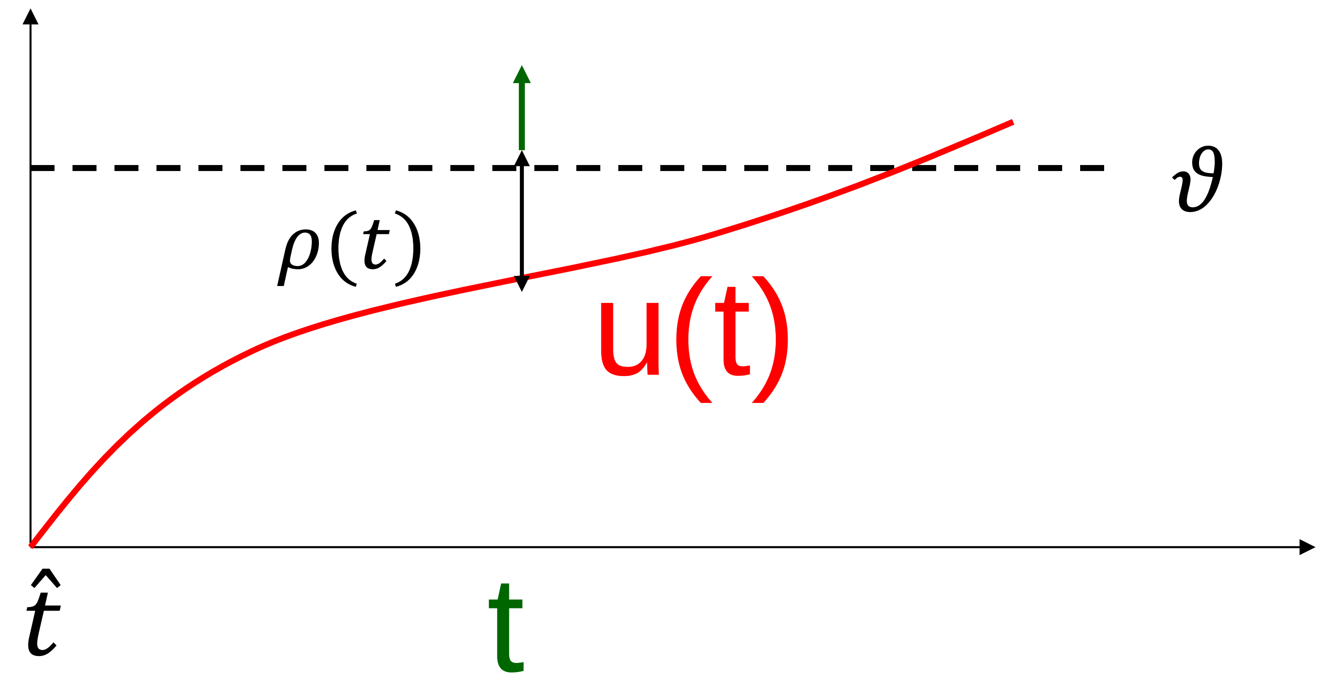
$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$

Now:
Escape noise!

Relation between the two models:
later this week (lecture 6.4)

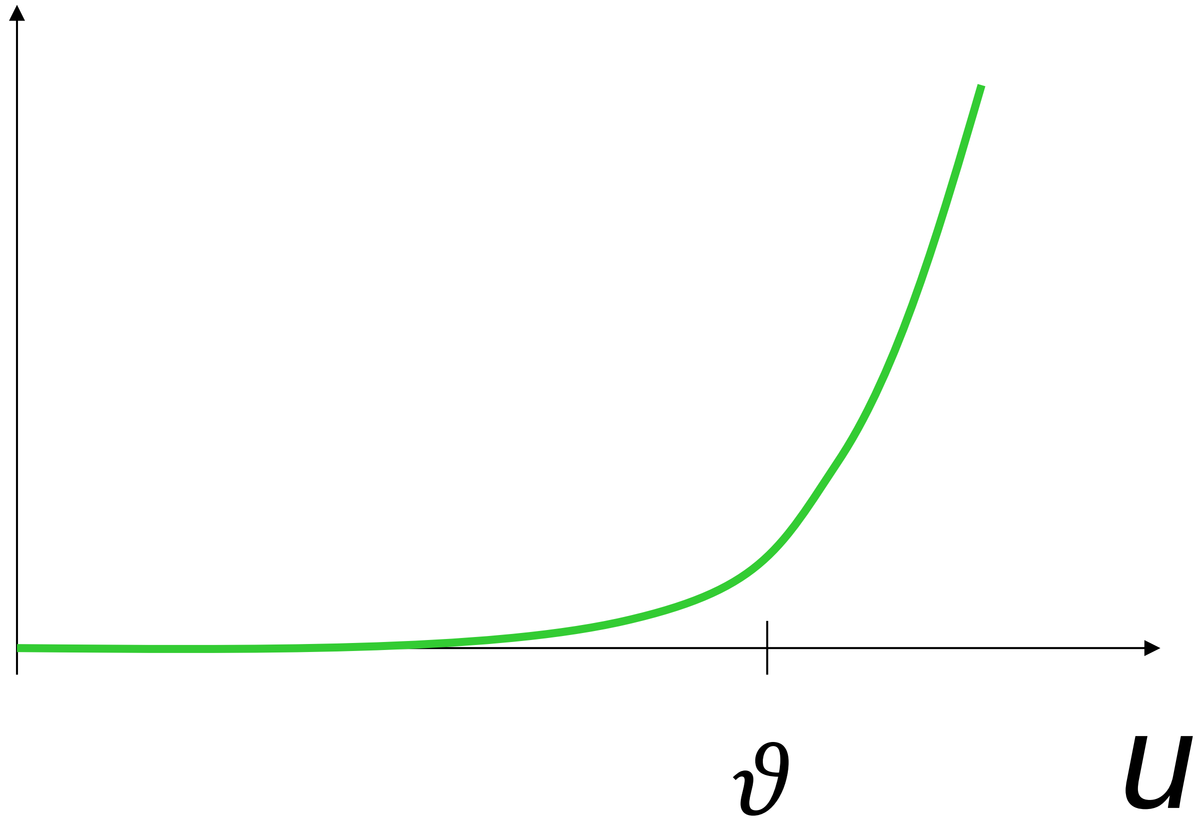
Neuronal Dynamics – 6.1 Escape noise

escape process



escape rate

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



escape rate

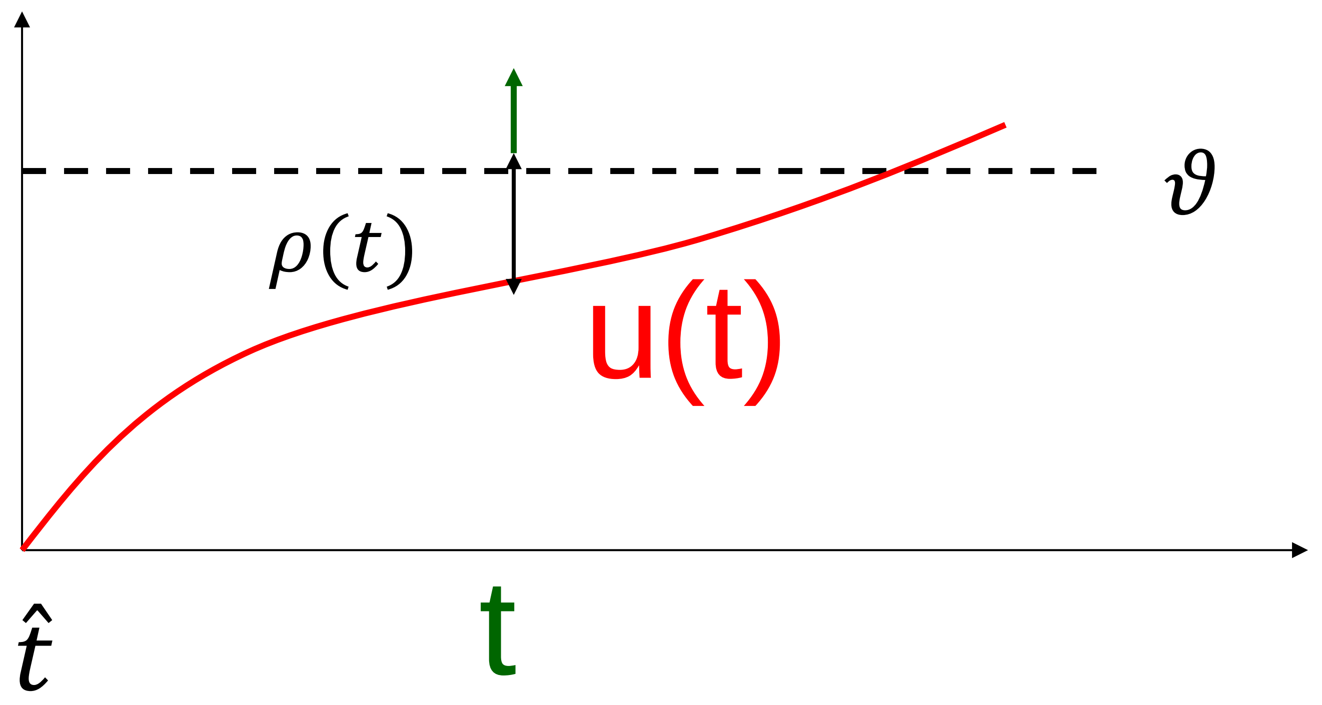
$$\rho(t) = \rho_\vartheta \exp\left(\frac{u(t) - \vartheta}{\Delta}\right)$$

Example: leaky integrate-and-fire model

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

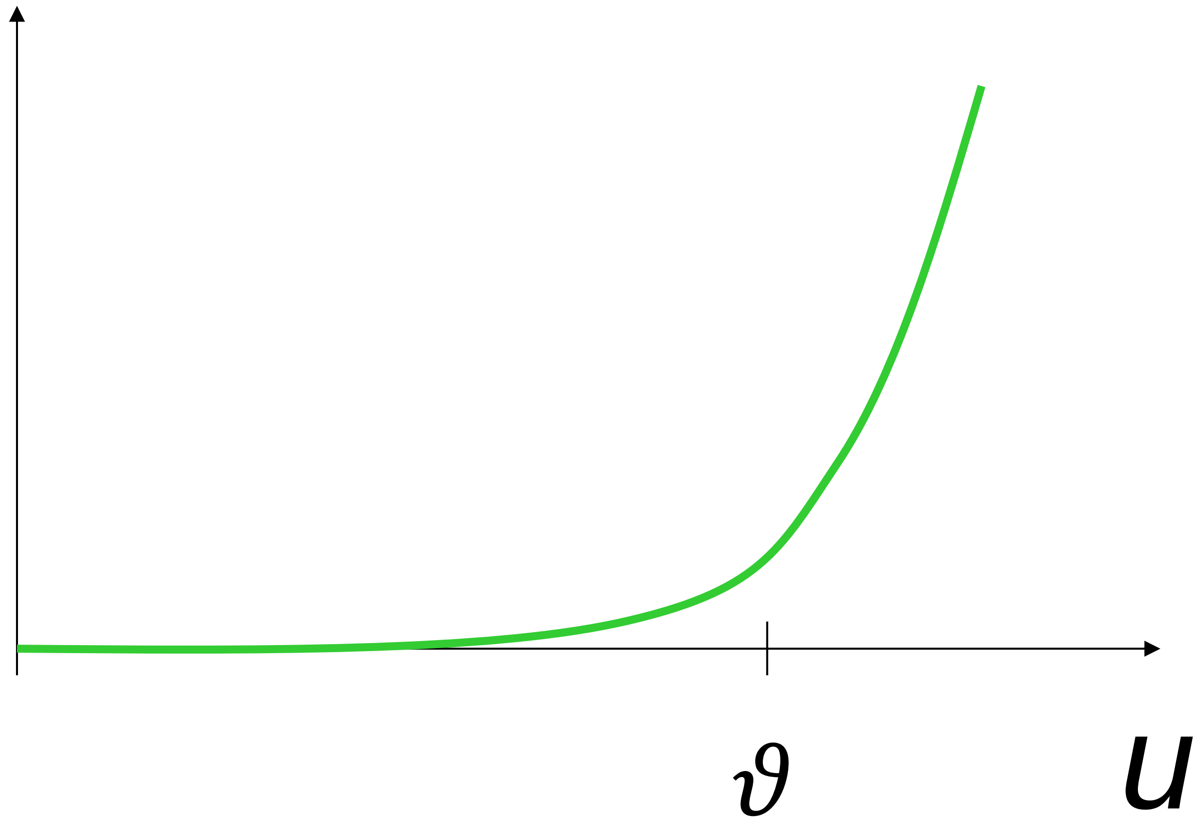
$$if\ spike\ at\ t^f \Rightarrow u(t^f + \delta) = u_r$$

escape process



escape rate

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



Escape rate = stochastic intensity of point process

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

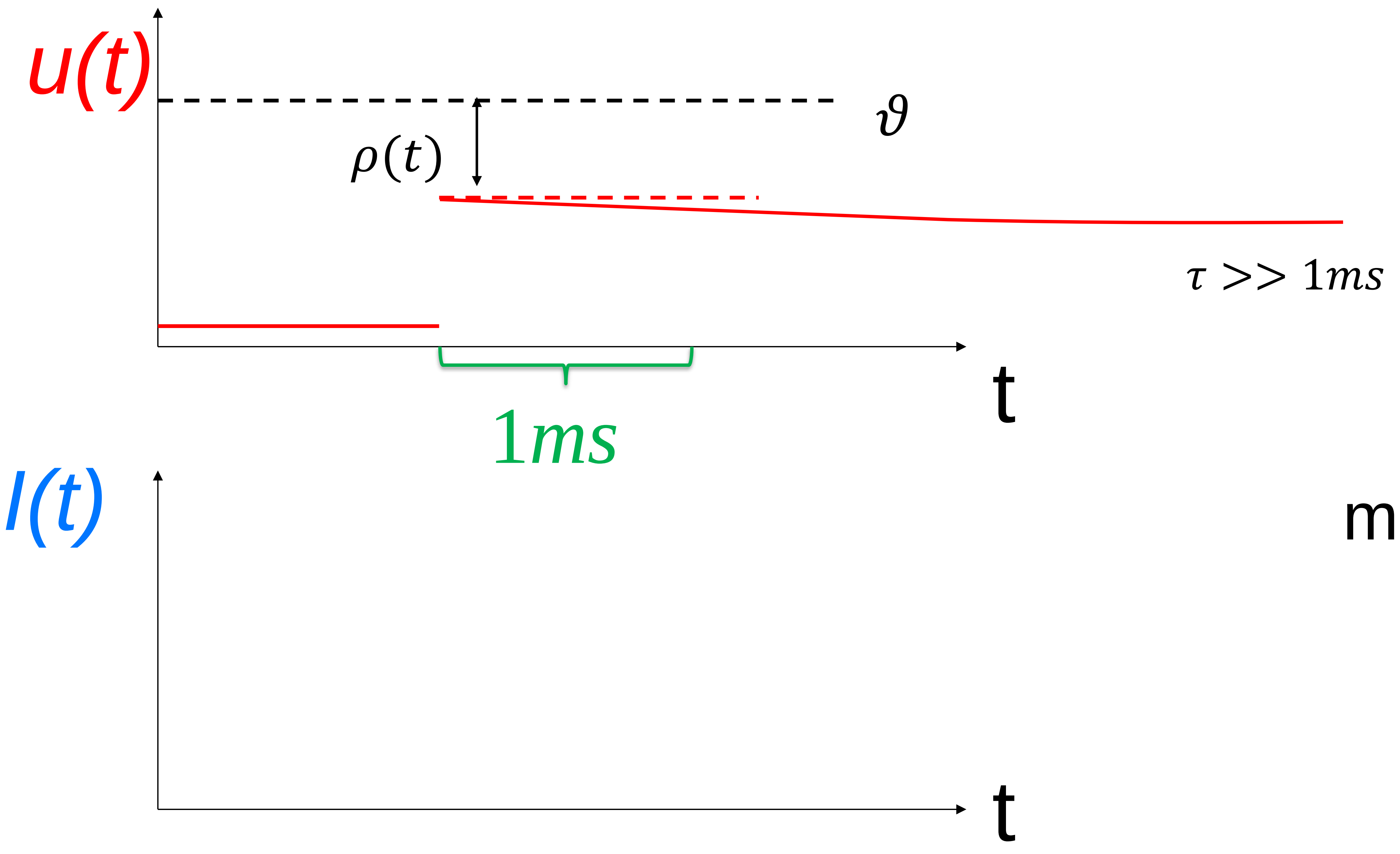
examples

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

$$\rho(t) =$$

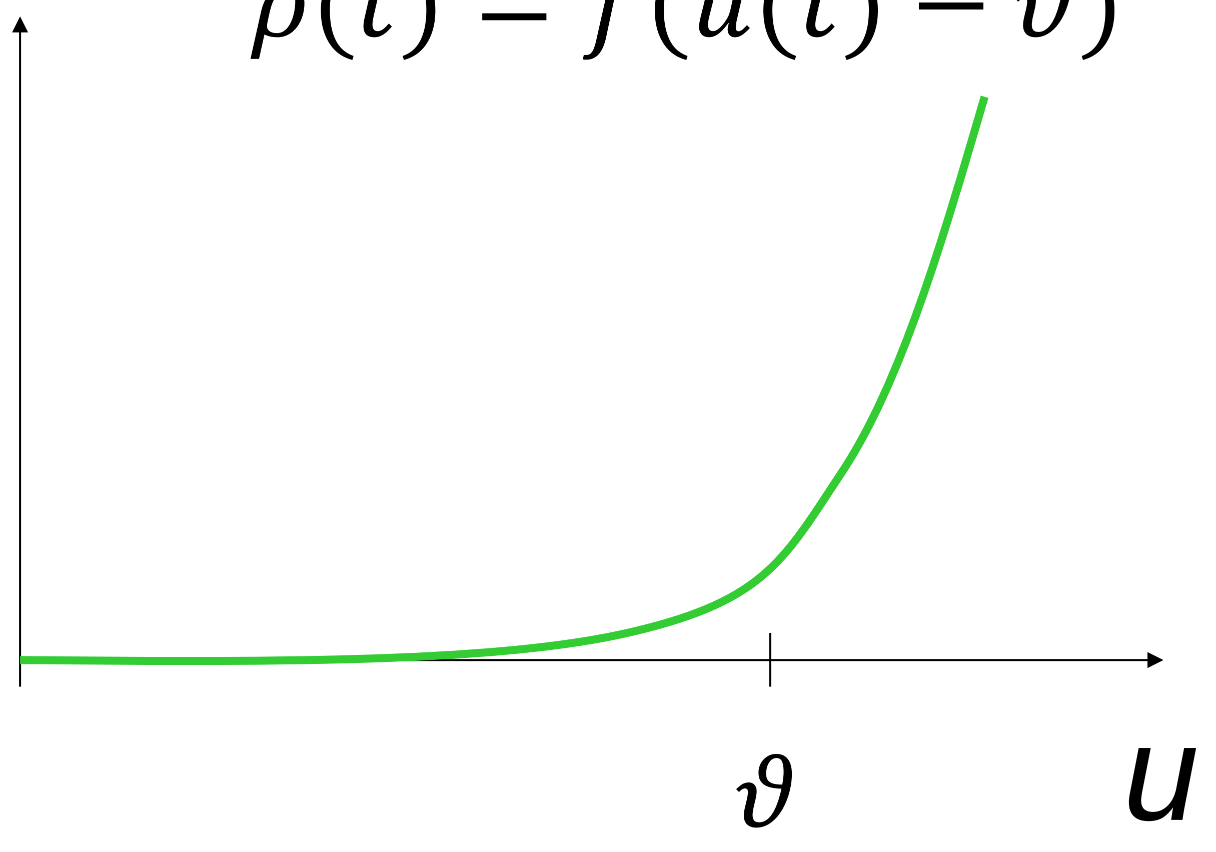
Neuronal Dynamics – 6.1 mean waiting time

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



escape rate

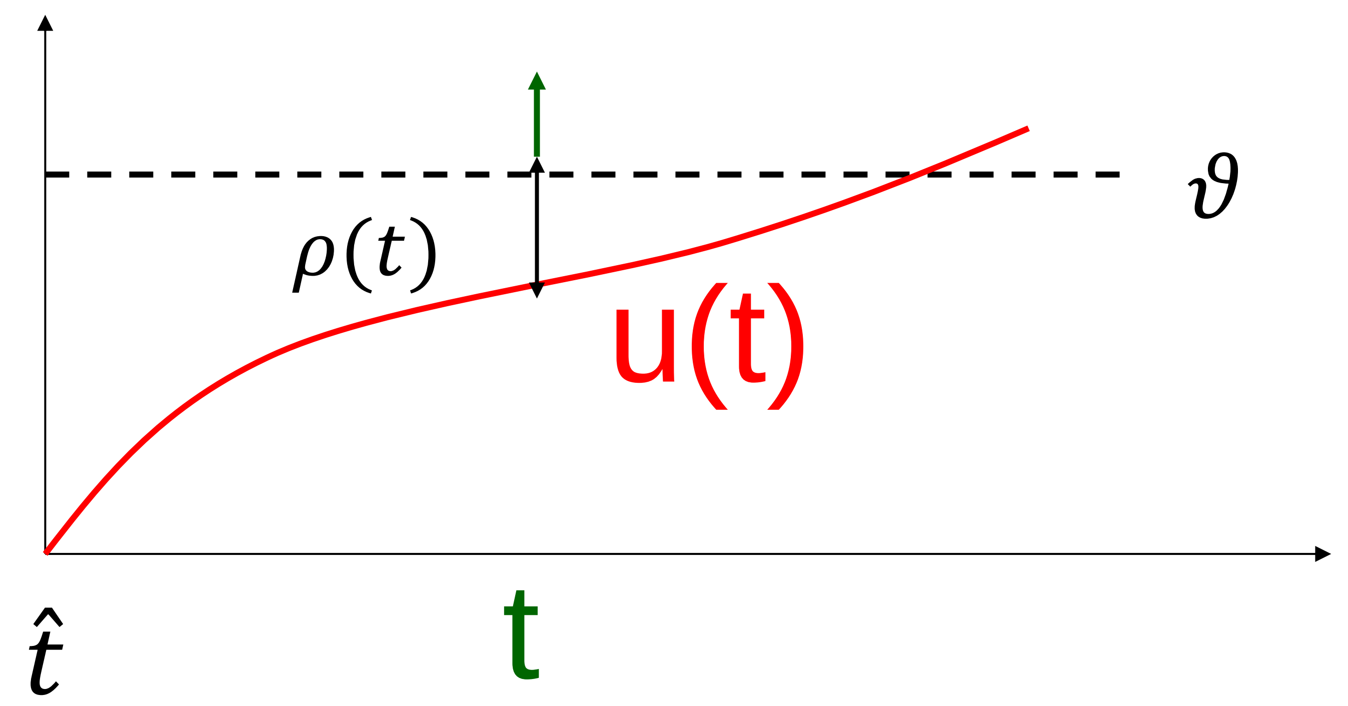
$$\rho(t) = f(u(t) - \vartheta)$$



mean waiting time, after switch

Escape rate = stochastic intensity
of point process

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



Neuronal Dynamics – Quiz 6.1.

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
[ ] 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 6 – part 2 : Interspike intervals and renewal processes

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Week 6 – Noise models: Escape noise

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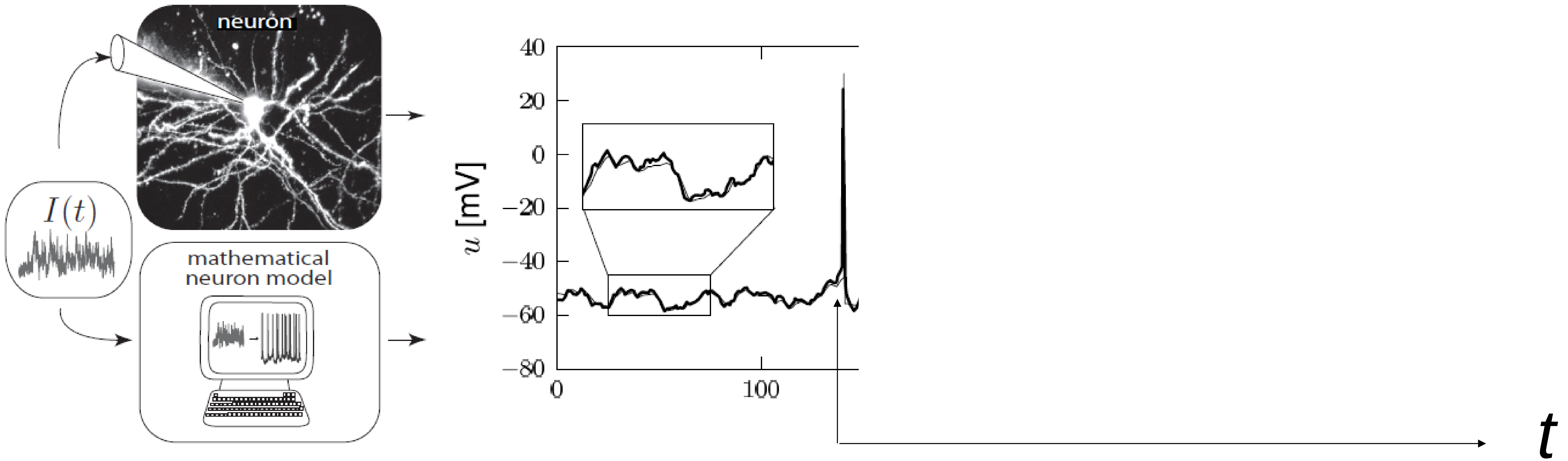
Neuronal Dynamics – 6.2. Interspike Intervals



deterministic part of input

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

noisy part of input/intrinsic noise

→ *escape rate*

Example:
nonlinear integrate-and-fire model

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

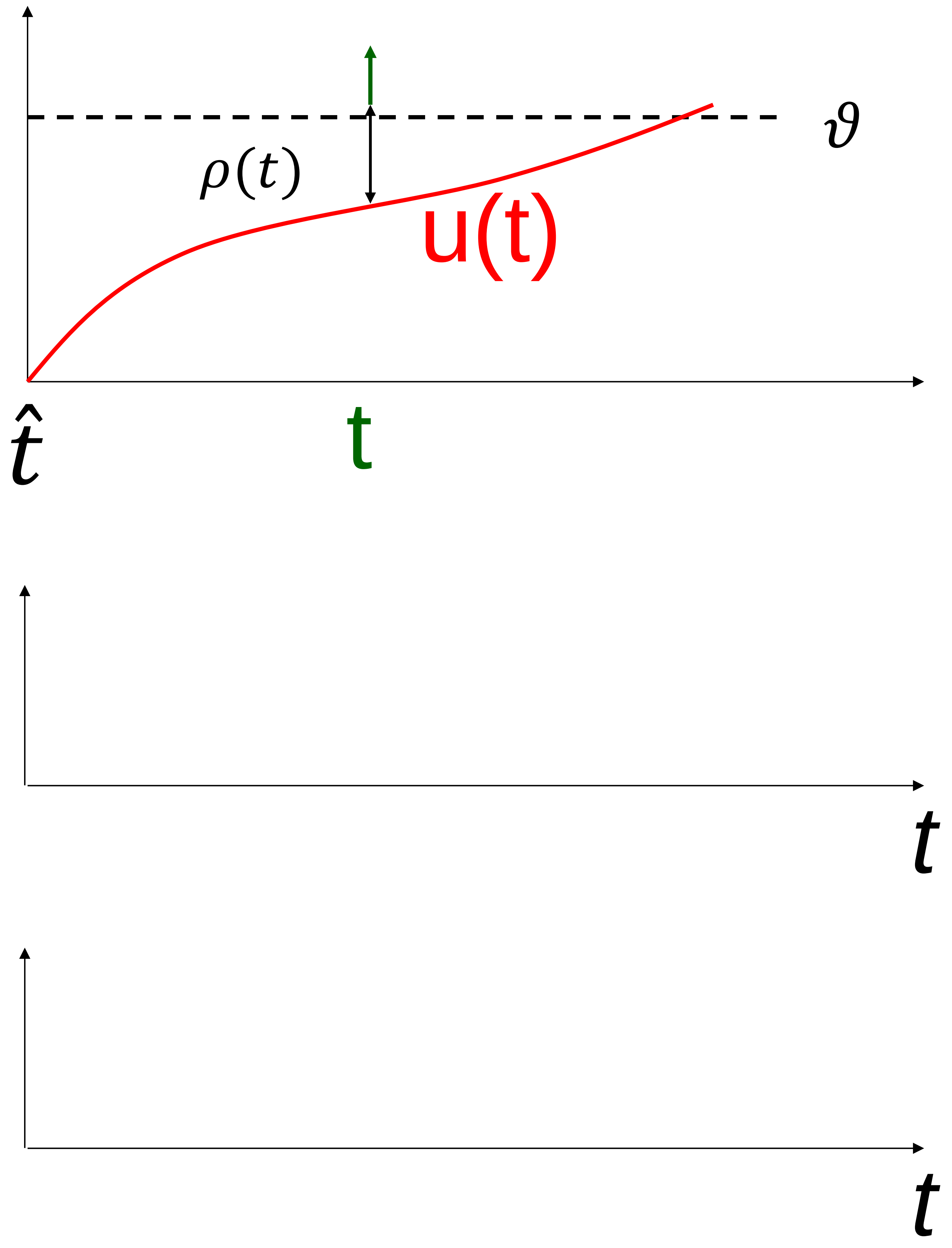
$$if spike at t^f \Rightarrow u(t^f + \delta) = u_r$$

Example:
exponential stochastic intensity

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

Neuronal Dynamics – 6.2. Interspike Interval distribution

escape process



escape rate

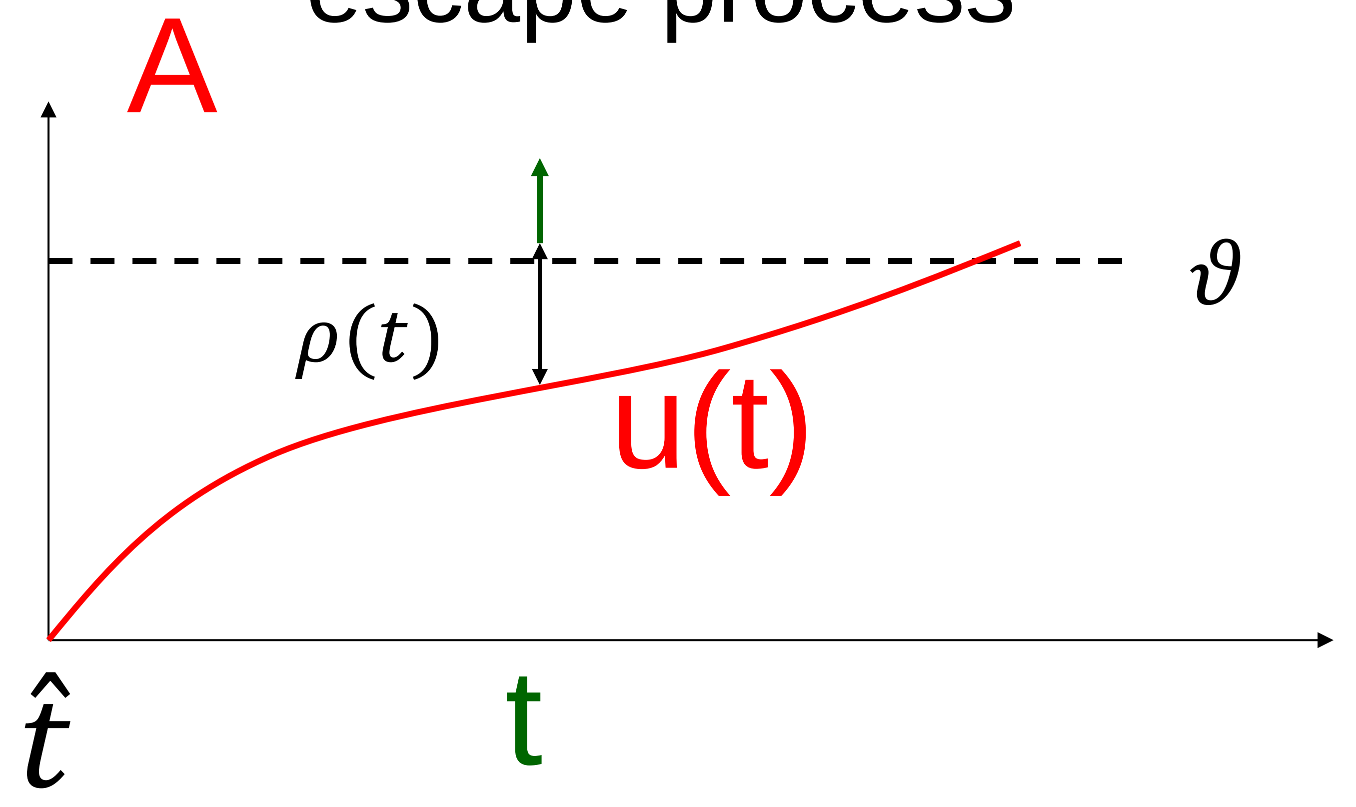
$$\rho(t) = f(u(t) - \vartheta)$$

Survivor function

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

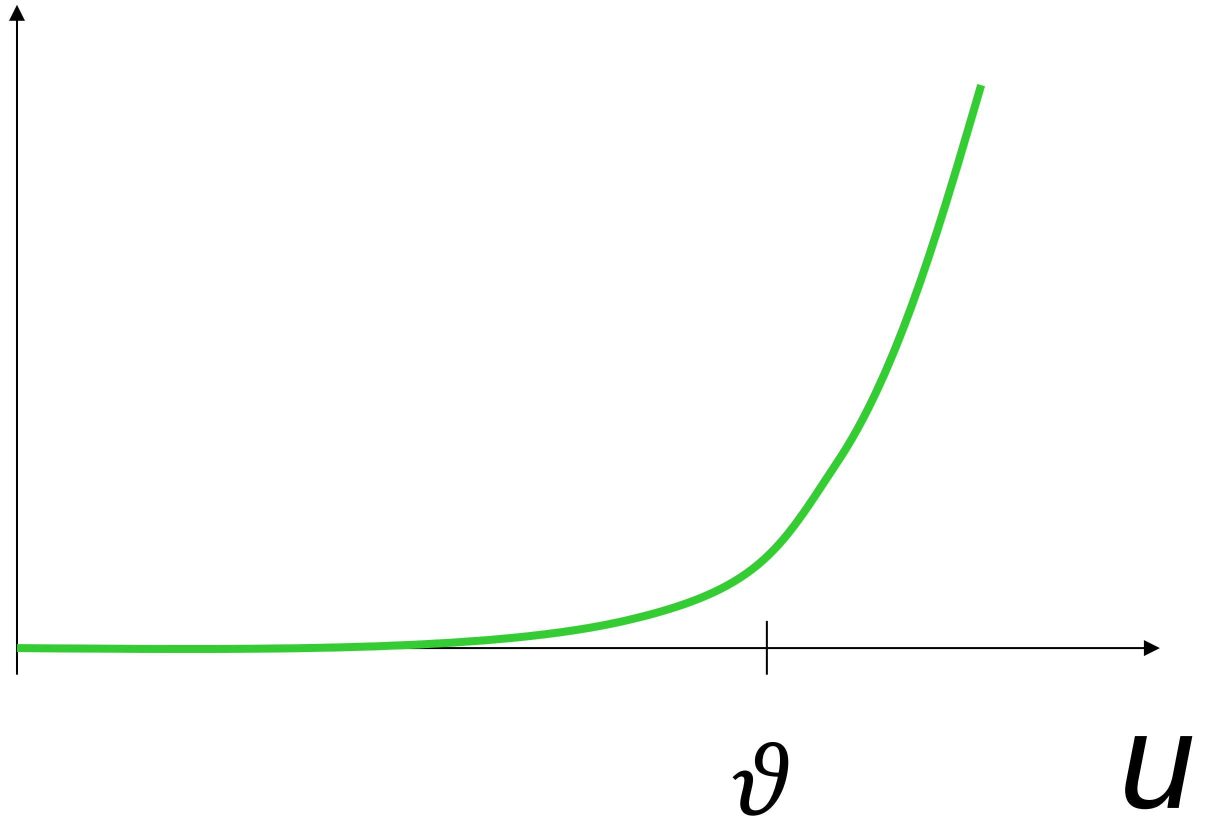
Neuronal Dynamics – 6.2. Interspike Intervals

escape process



escape rate

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



Survivor function

Examples now

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

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

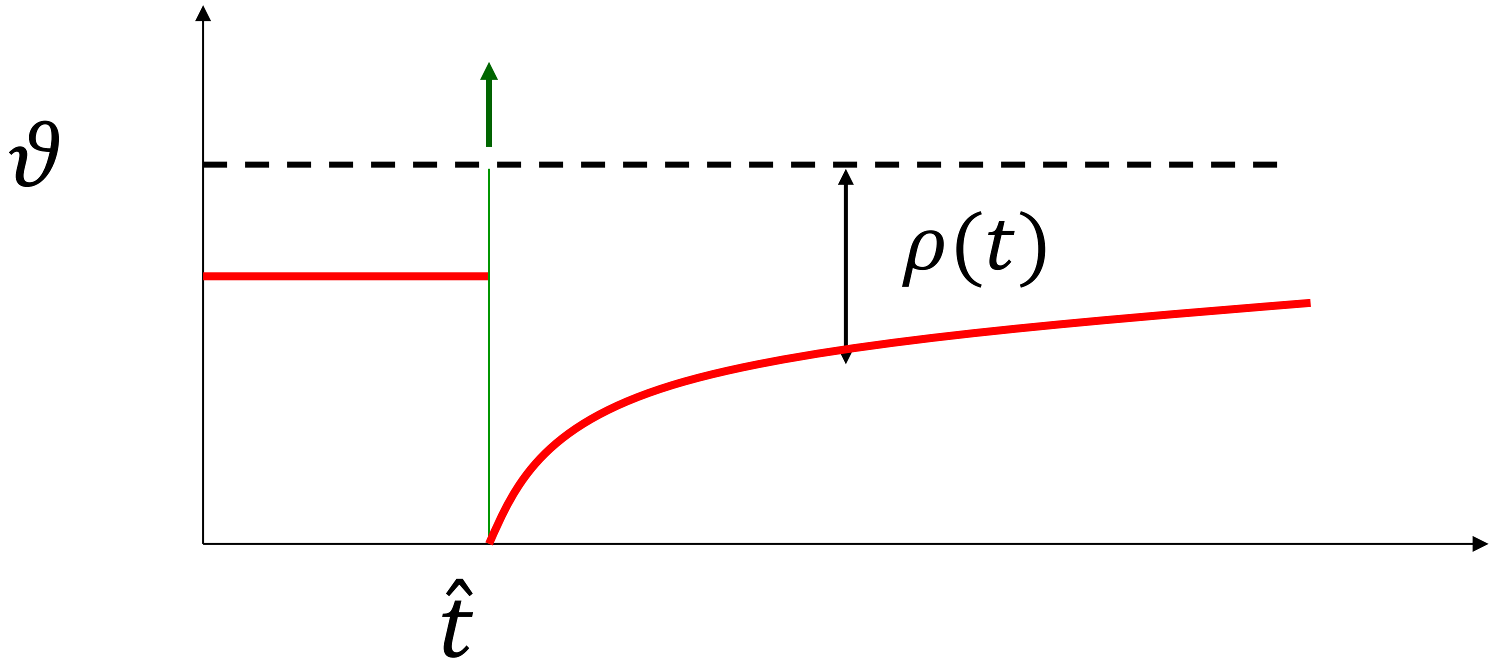
Interval distribution

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

escape rate

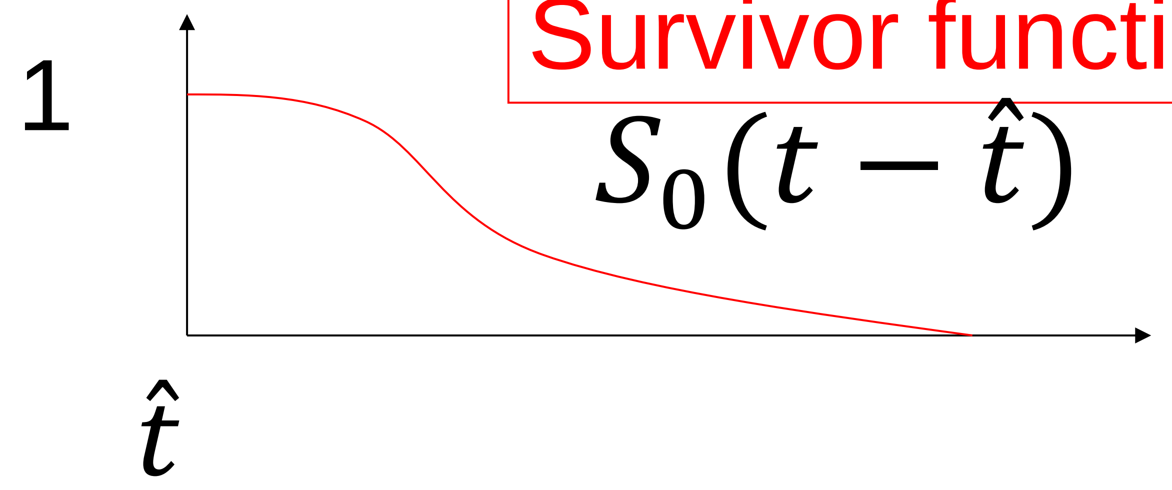
Survivor function

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



escape rate

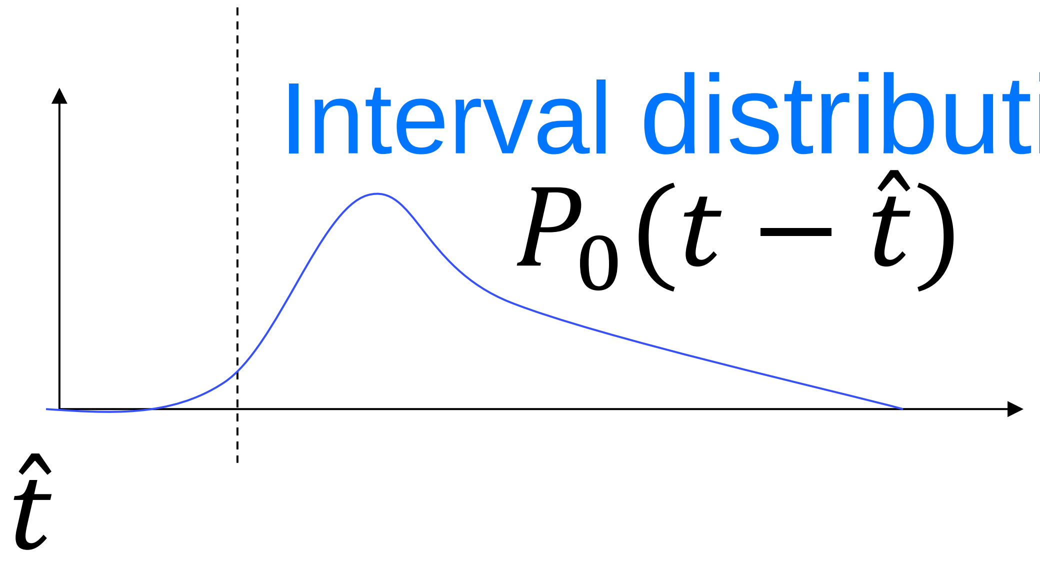
$$\rho(t|\hat{t}) = f(u(t|\hat{t})) = \rho_\vartheta \exp(u(t|\hat{t}) - \vartheta)$$



Survivor function

$S_0(t - \hat{t})$

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



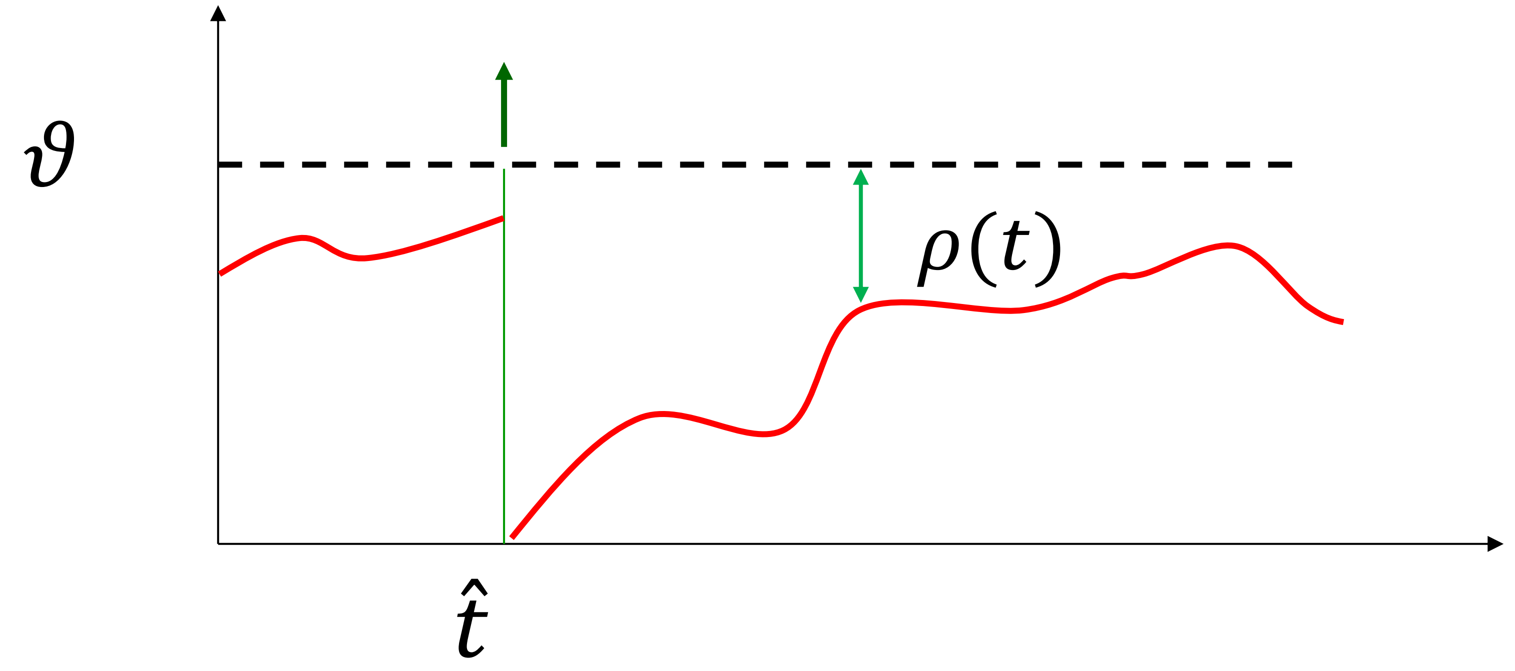
Interval distribution

$P_0(t - \hat{t})$

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

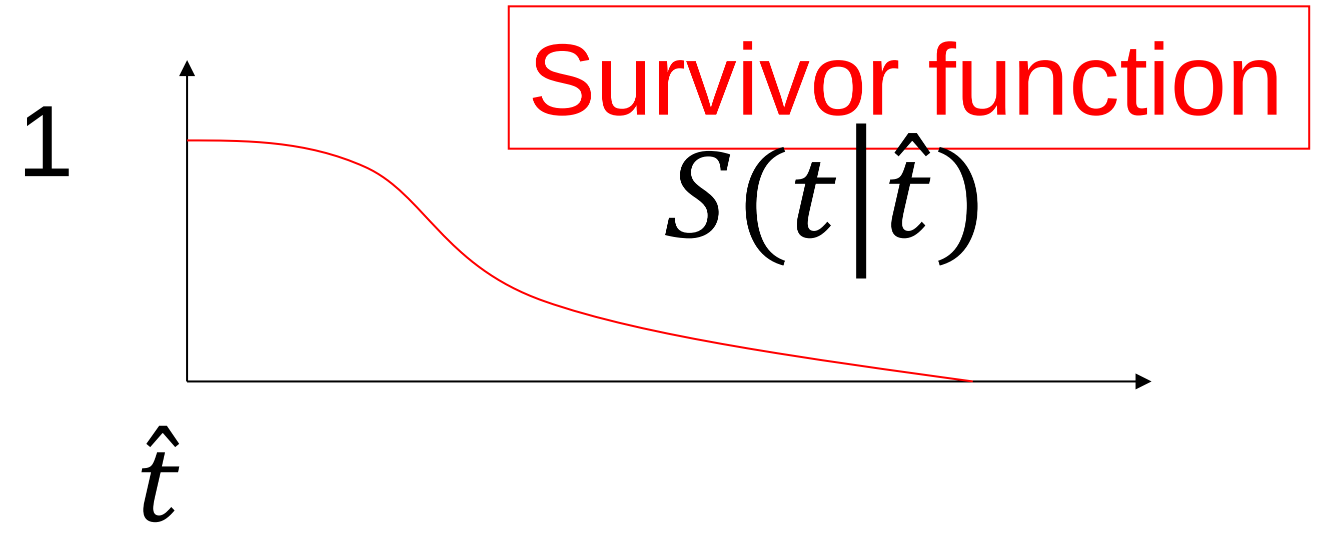
$$= -\frac{d}{dt} S(t|\hat{t})$$

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

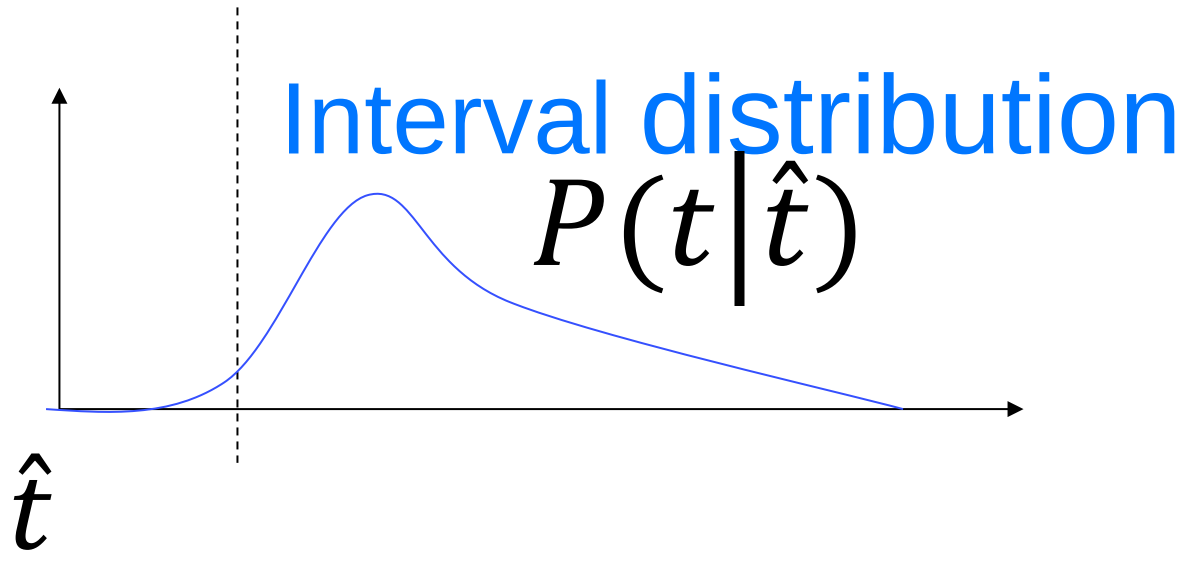


escape rate

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



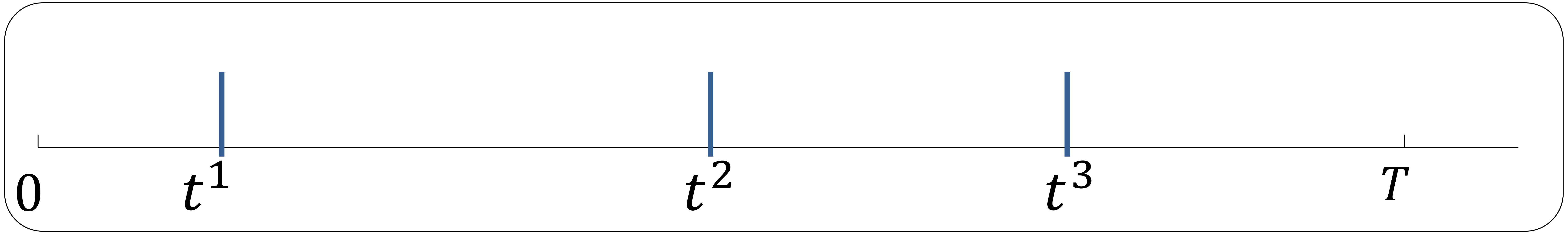
$$S(t|\hat{t}) = \exp(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})dt')$$



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

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

Neuronal Dynamics – 6.2. Firing probability in discrete time



Probability to survive 1 time step

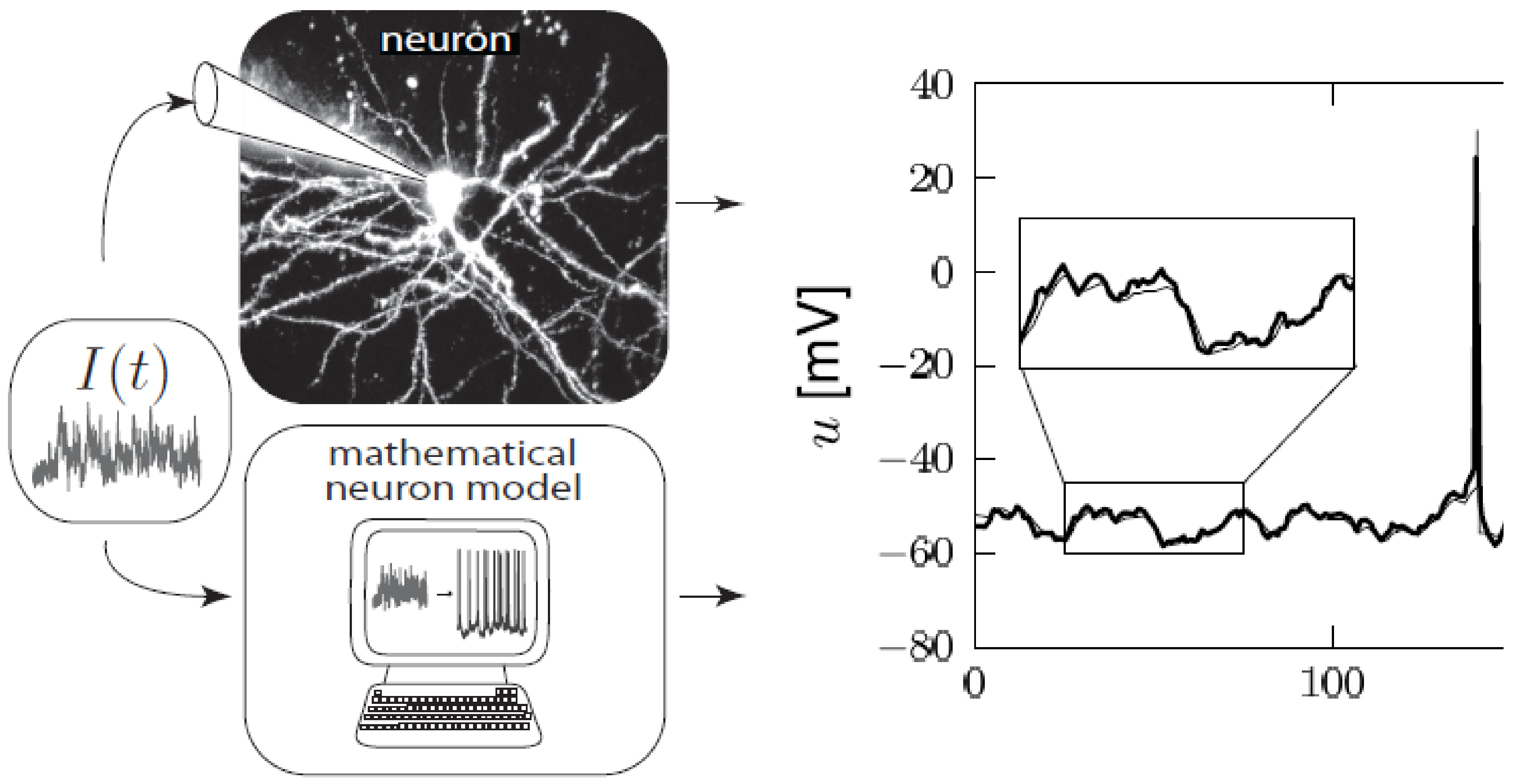
$$S(t_{k+1}|t_k) = \exp[-\int_{t_k}^{t_{k+1}} \rho(t')dt']$$

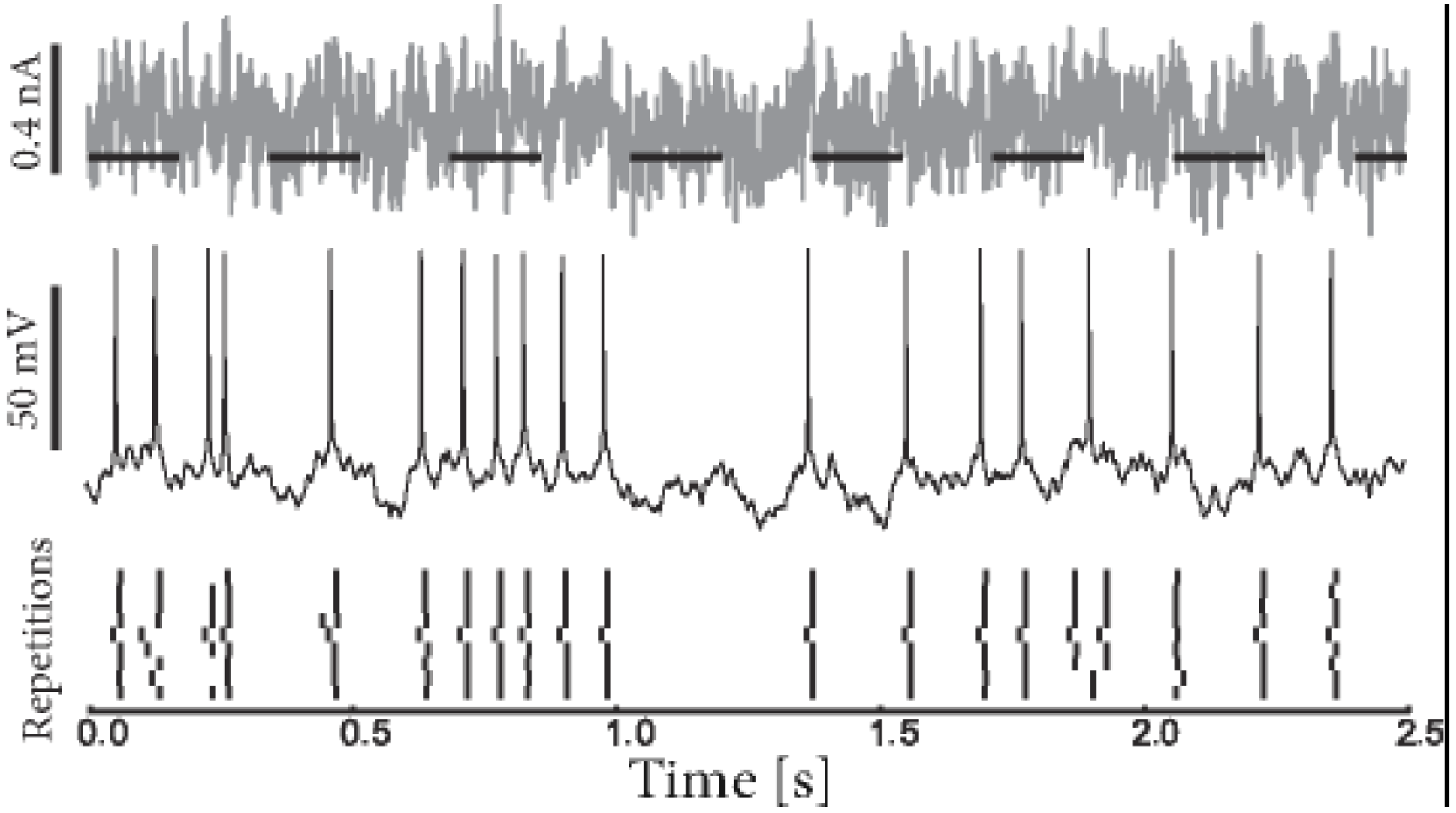
$$S(t_{k+1}|t_k) = \exp[-\rho(t_k)\Delta] = 1 - P_k^F$$

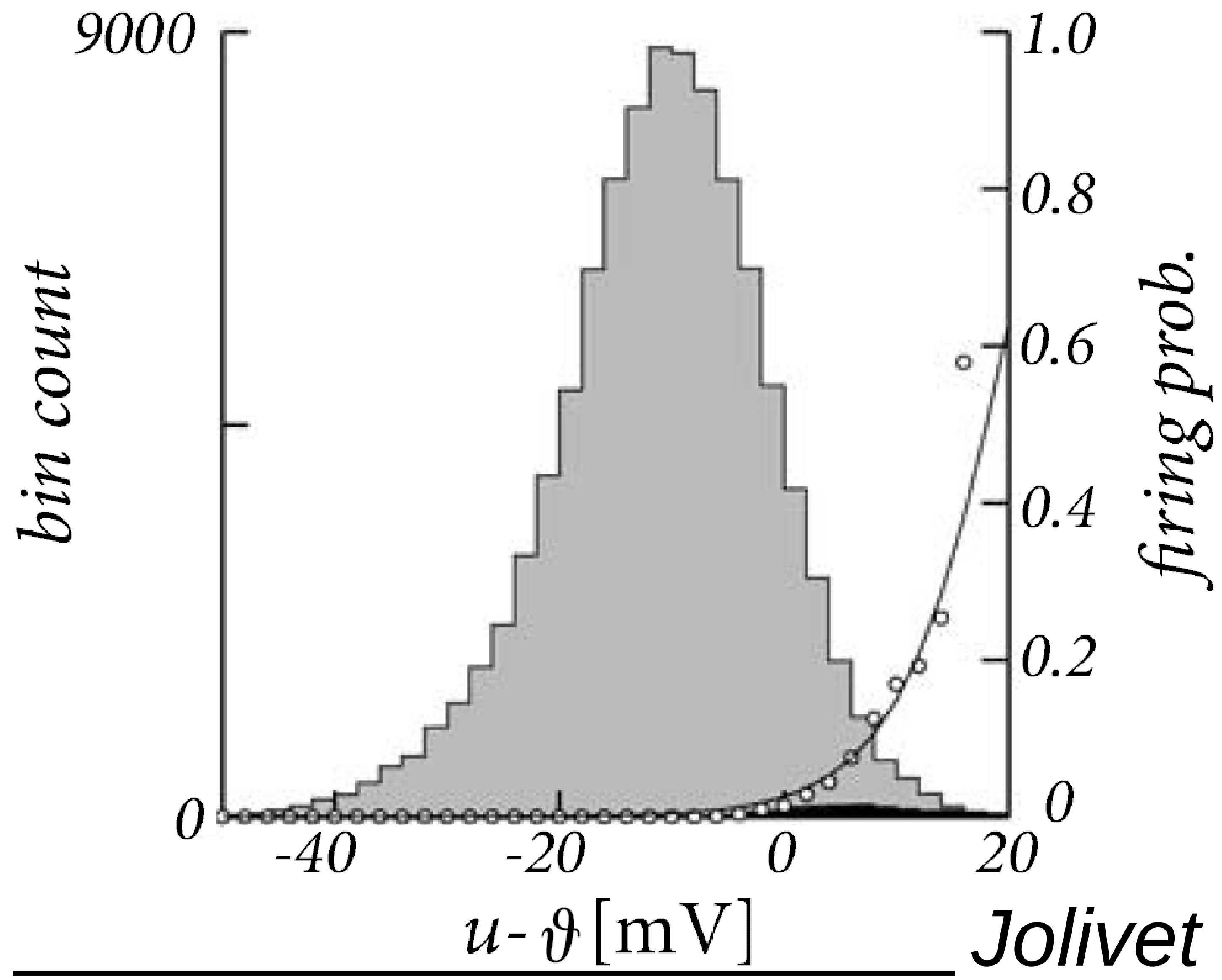
Probability to fire in 1 time step

$$P_k^F =$$

Neuronal Dynamics – 6.2. Escape noise - experiments







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

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

escape rate

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

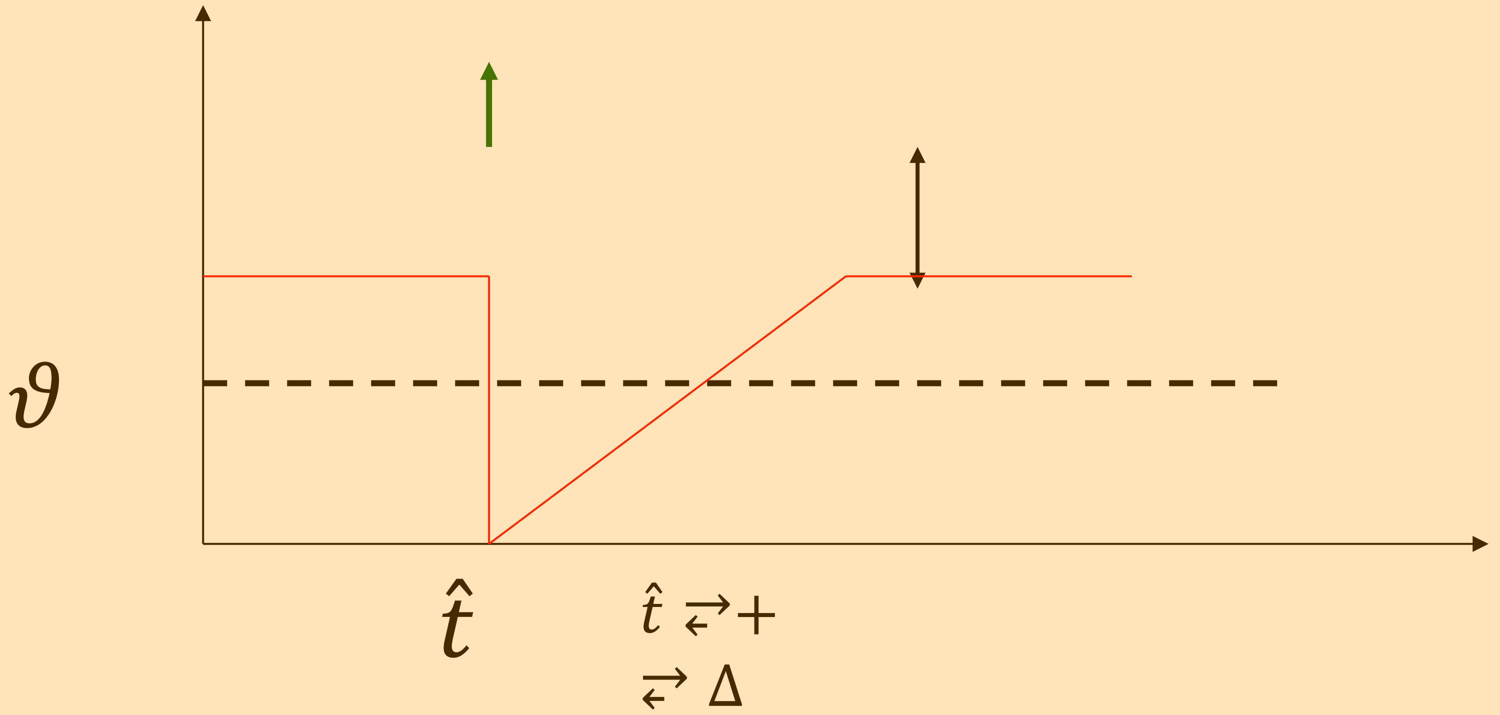
Escape noise = stochastic intensity

-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 7)

neuron with relative refractoriness, constant input

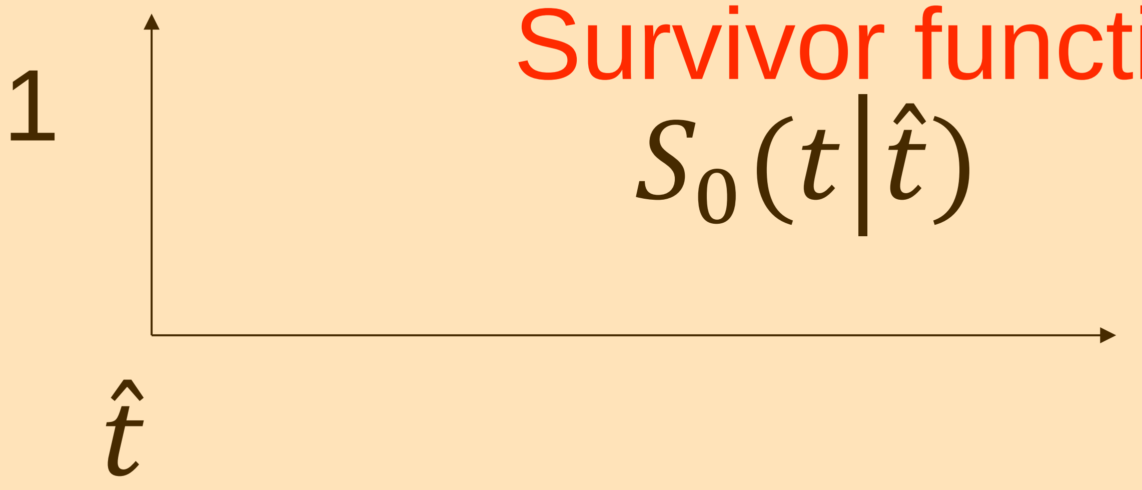


escape rate

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

Survivor function

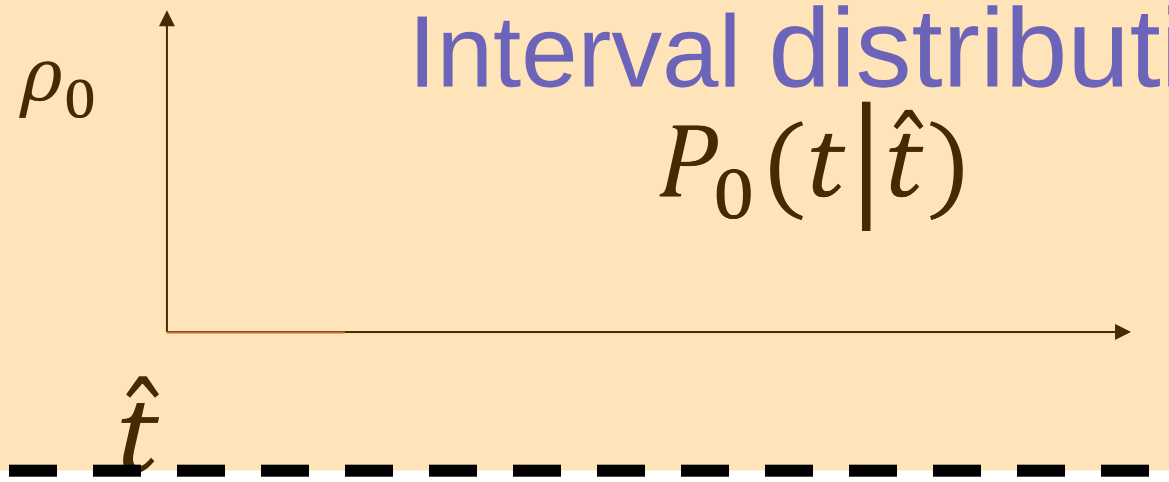
$S_0(t|\hat{t})$



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

Interval distribution

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



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

Week 6 – part 3 : Likelihood of a spike train

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Week 6 – Noise models:
Escape noise

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√ **6.1 Escape noise**
- stochastic intensity and point process

√ **6.2 Interspike interval distribution**
- Time-dependend renewal process
- Firing probability in discrete time

6.3 Likelihood of a spike train
- generative model

6.4 Comparison of noise models
- escape noise vs. diffusive noise

6.5. Rate code vs. Temporal Code
- timing codes
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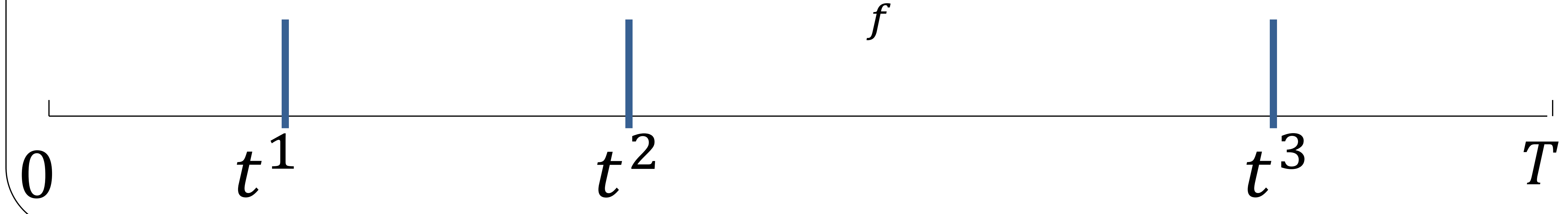
Neuronal Dynamics – 6.3. Likelihood of a spike train

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



Measured spike train with spike times $t^1, t^2, \ldots t^N$

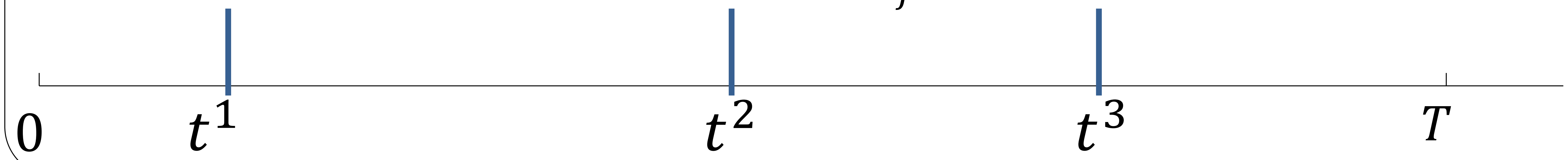
Explanation now:

Likelihood ***L*** that this spike train could have been generated by model?

$$L(t^1,\ldots,t^N) = \exp(-\int_0^{t^1} \rho(t')dt')\,\rho(t^1)\cdot\exp(-\int_{t^1}^{t^2} \rho(t')dt')\ldots$$

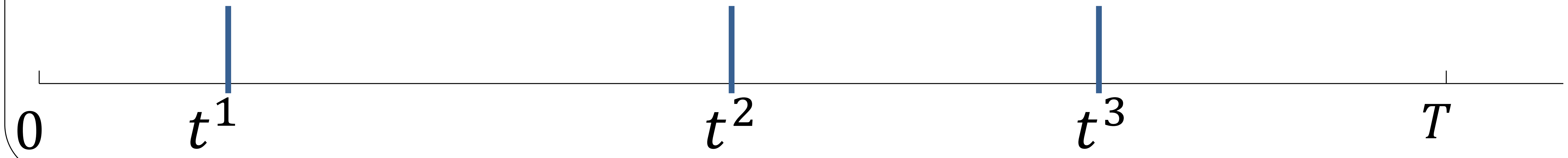
Neuronal Dynamics – 6.3. Likelihood of a spike train

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



Neuronal Dynamics – 6.3. Likelihood in discrete time

$n(t_k) = 1 \, if \, t_k < t^f \leq t_{k+1}$



Prob. to fire in $t_k < t \leq t_{k+1}$

$P_{t_k}^{\Delta}$

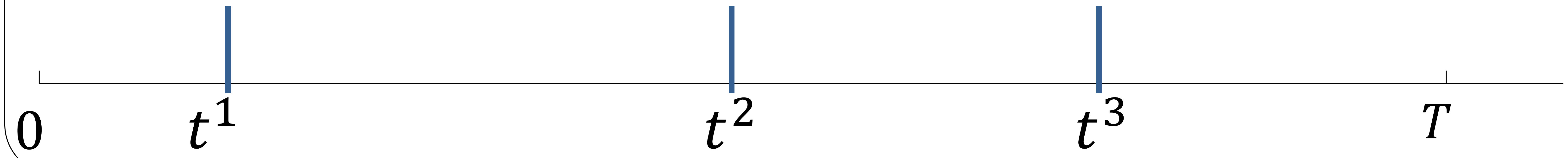
Prob. to be silent in $t_k < t \leq t_{k+1}$

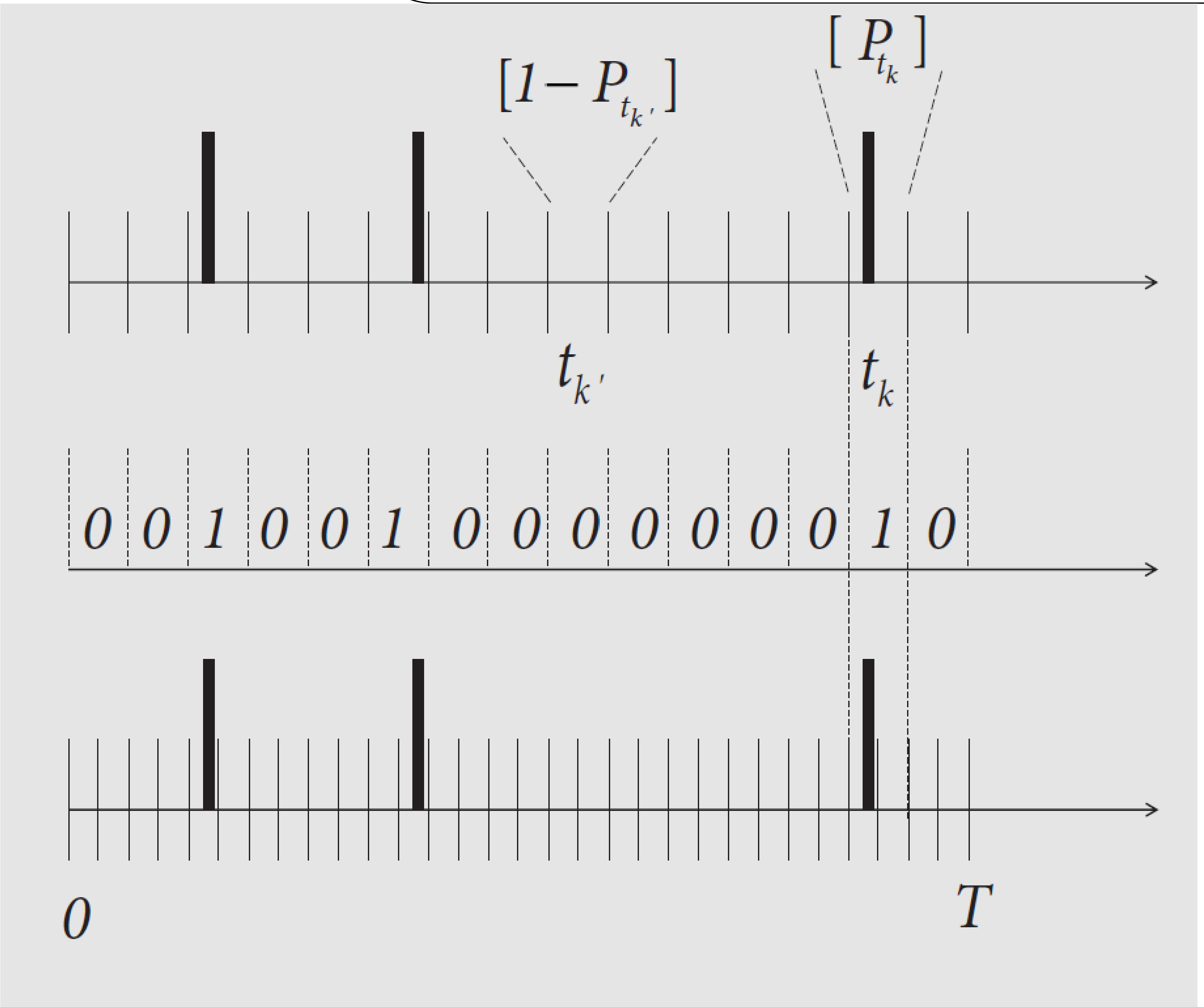
S^{Δ}

how about $\Delta \to 0$??

Neuronal Dynamics – 6.3. Likelihood in discrete time

$n(t_k) = 1 \, if \, t_k < t^f \le t_{k+1}$





$P_{t_k}^{\Delta}$

$\Delta \to 0$

Neuronal Dynamics – 6.3. Likelihood of a spike train

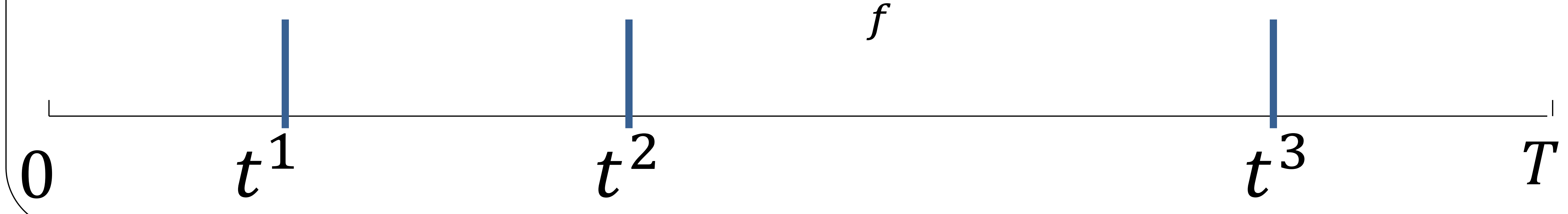
$$S(t) = \sum_f \delta(t - t^f)$$

$$L(t^1, \ldots, t^N) = \exp\left(-\int_0^{t^1} \rho(t')dt'\right) \rho(t^1) \cdot \exp\left(-\int_{t^1}^{t^2} \rho(t')dt'\right) \rho(t^2) \ldots \cdot \exp\left(-\int_{t^N}^{T} \rho(t')dt'\right)$$

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

Neuronal Dynamics – 6.3. Log-likelihood of a spike train

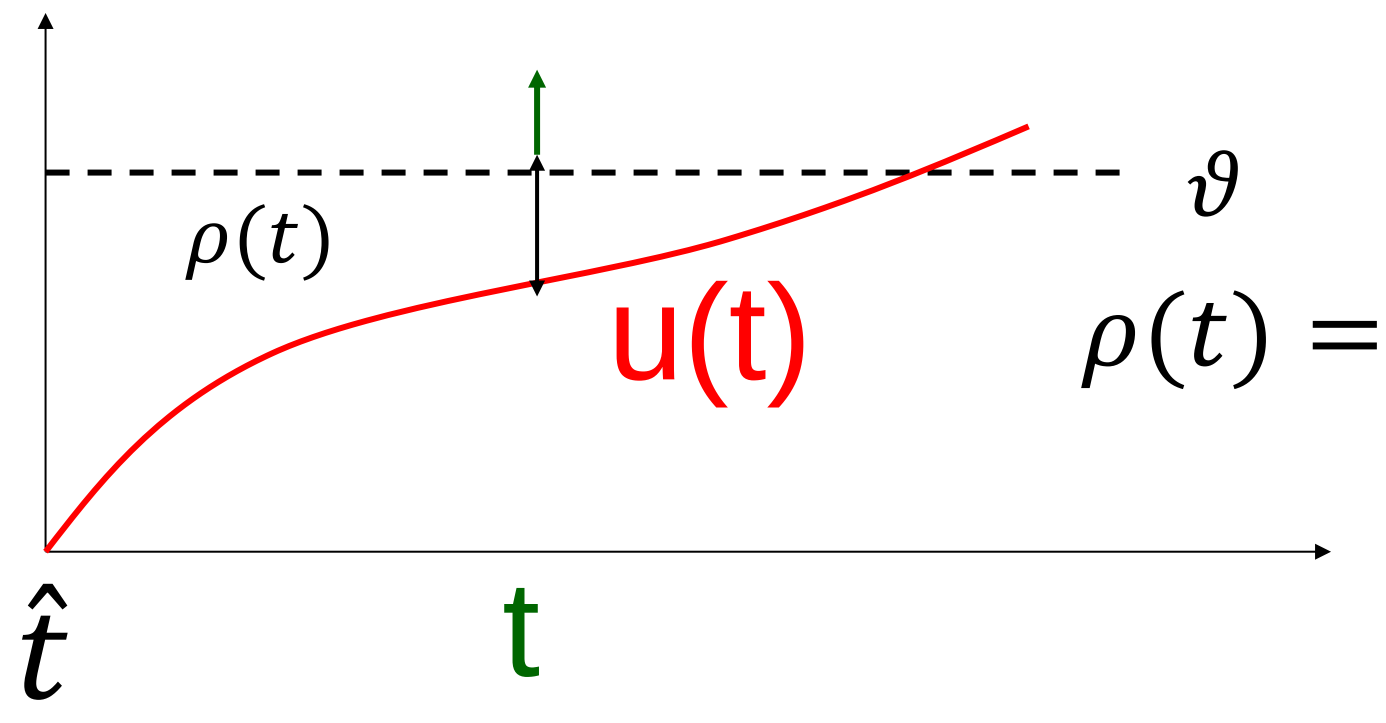
$$S(t) = \sum_f \delta(t - t^f)$$



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

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

Neuronal Dynamics – 6.3. generative model of a spike train



escape rate

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

generative model of spike train

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

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

Neuronal Dynamics – Quiz 6.2. Tick all correct answers

[ ] A leaky integrate-and-fire model with escape noise can be interpreted as a generative model of a spike train

[ ] For a leaky integrate-and-fire model with escape noise we can (numerically) calculate the likelihood that observed experimental data could have been generated by the model

[ ] Suppose we inject a time-dependent current into a real neuron and observe the resulting spike train. We the inject the same time-dependent current into a nonlinear integrate-and-fire model with exponential escape noise with parameter theta. For each choice of theta we can then calculate the likelihood that the model could have generated the observed spike train.

Week 6 – part 4 : Comparison of noise models

Neuronal Dynamics:
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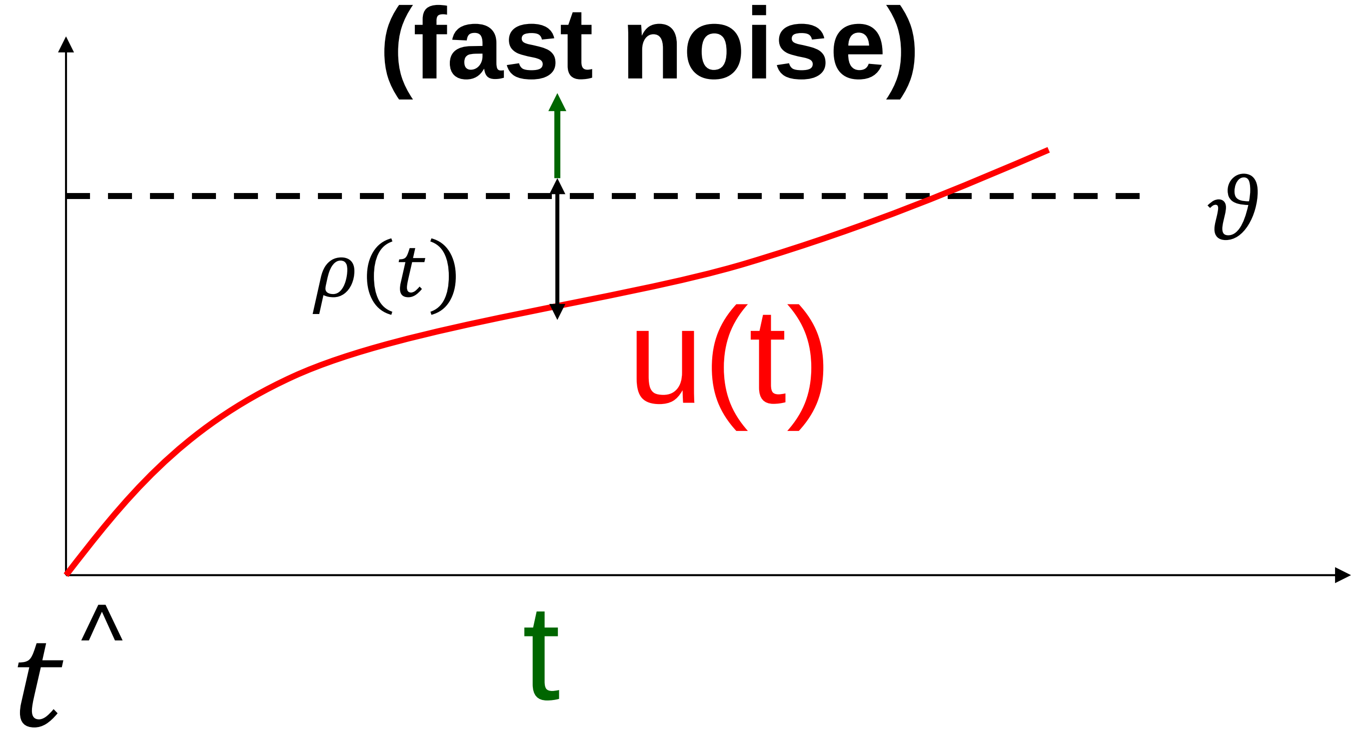
Week 6 – Noise models:
Escape noise

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Neuronal Dynamics – 6.4. Comparison of Noise Models

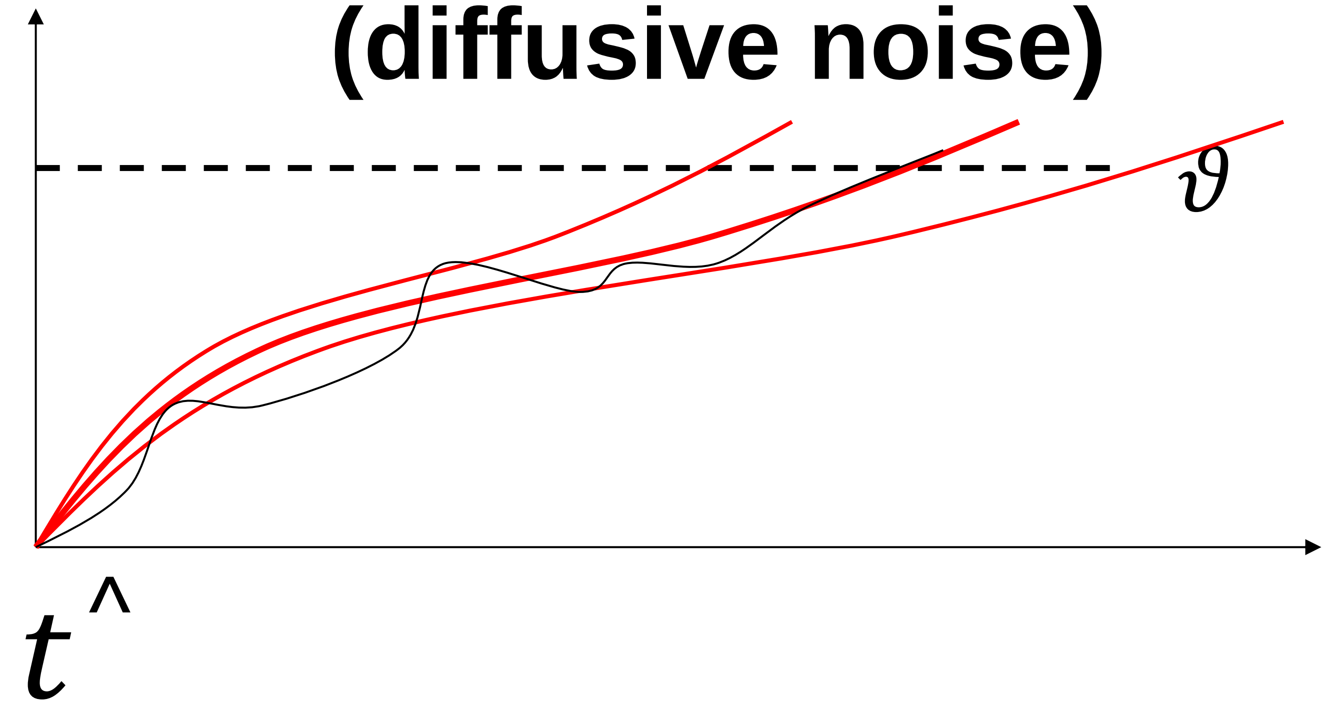
escape process
(fast noise)



escape rate

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

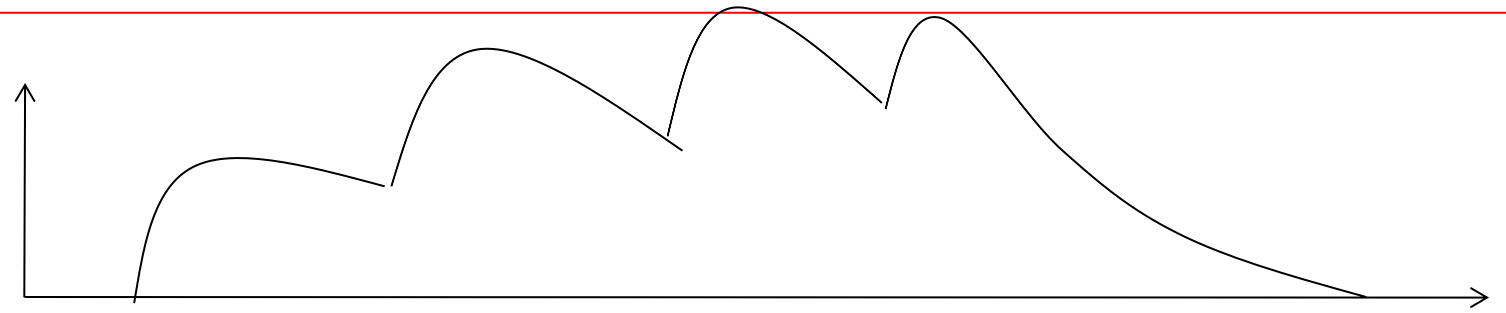
stochastic spike arrival
(diffusive noise)



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

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

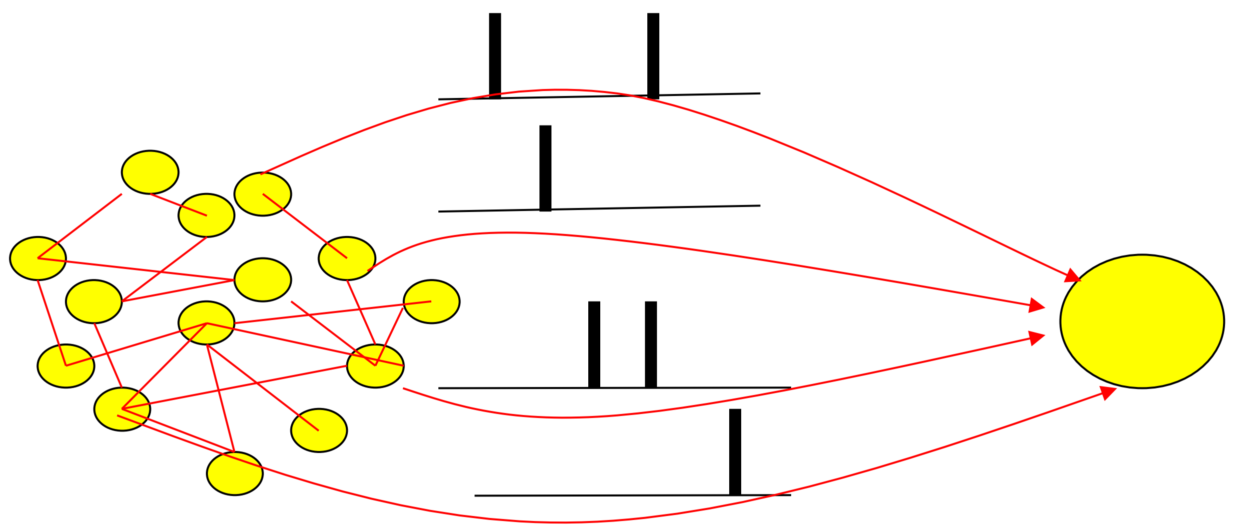
Autocorrelation of output

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

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

Autocorrelation of input

Diffusive noise (stochastic spike arrival)



Stochastic spike arrival:
excitation, total rate R_e
inhibition, total rate R_i
Synaptic current pulses

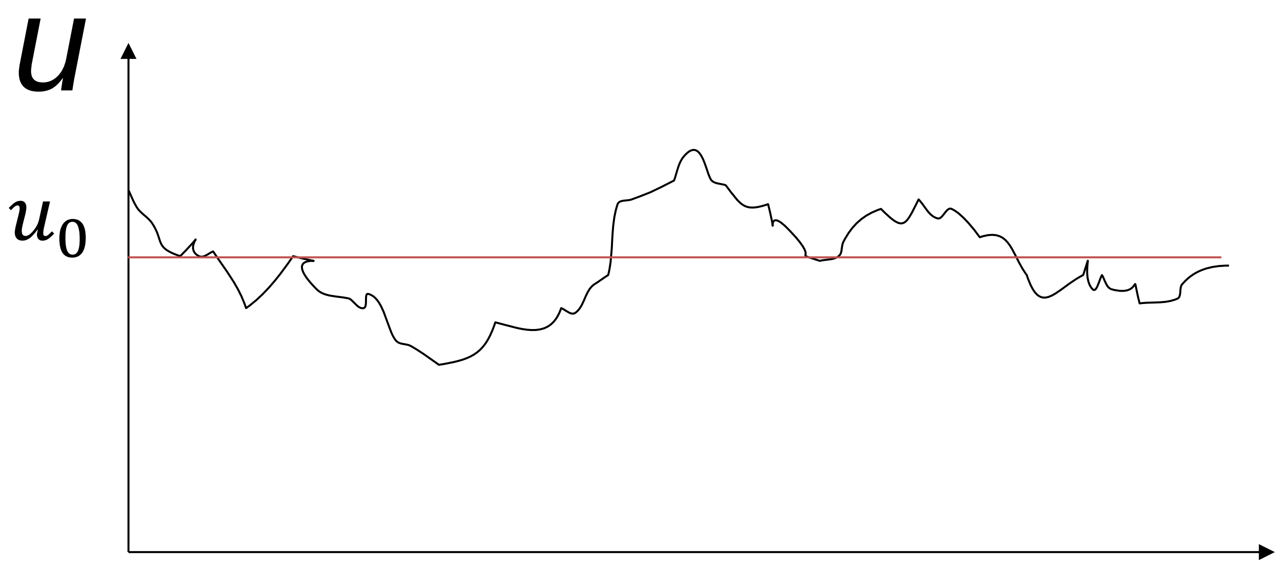
$$\tau \frac{d}{dt}u = -(u - u_{rest}) + \sum_{k,f} \frac{q_e}{C}\delta(t - t_k^f) - \sum_{k',f'} \frac{q_i}{C}\delta(t - t_{k'}^{f'})$$

EPSC

IPSC

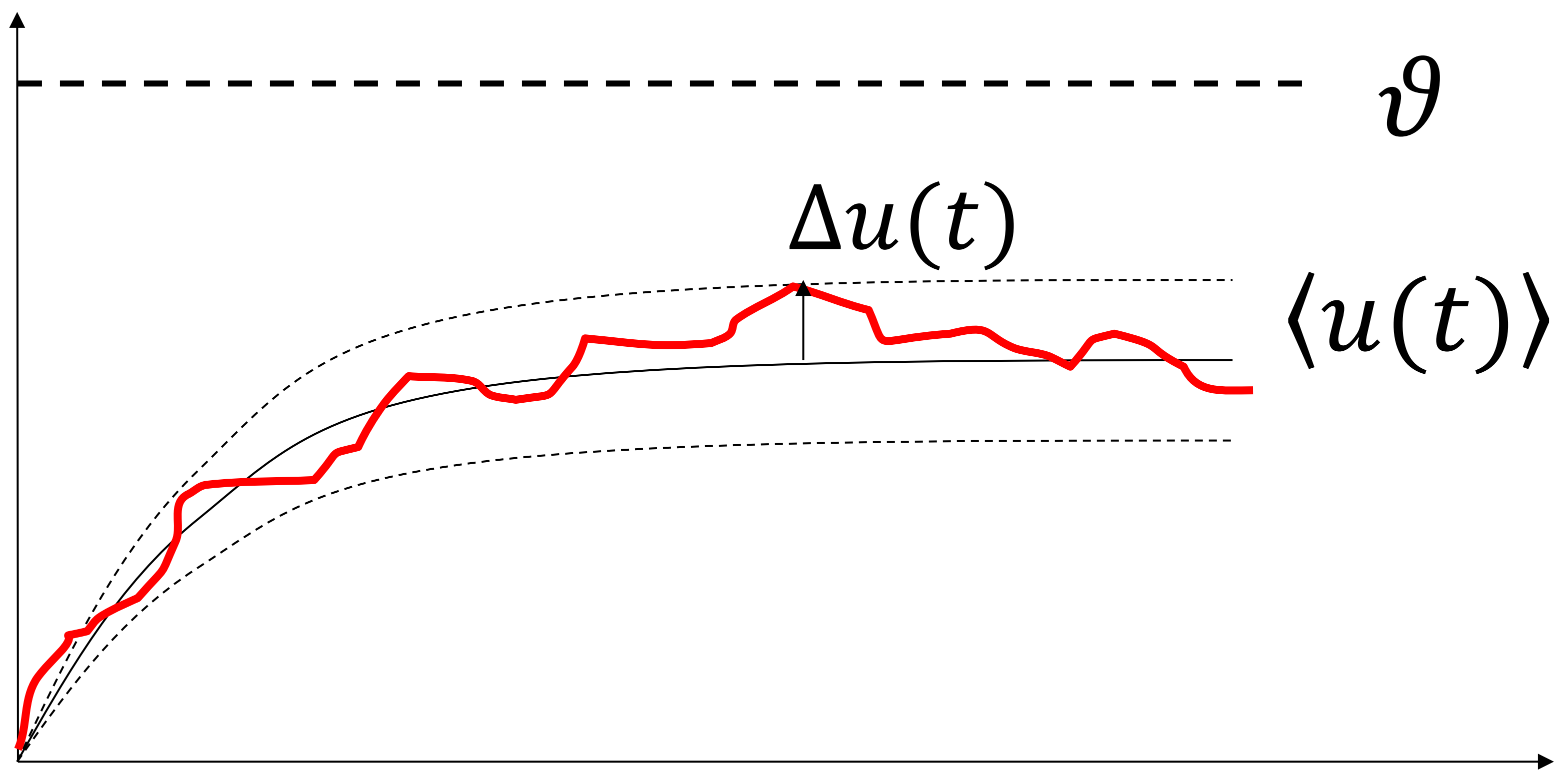
$$\tau \frac{d}{dt}u = -(u - u_{rest}) + RI(t) + \xi(t)$$

Blackboard

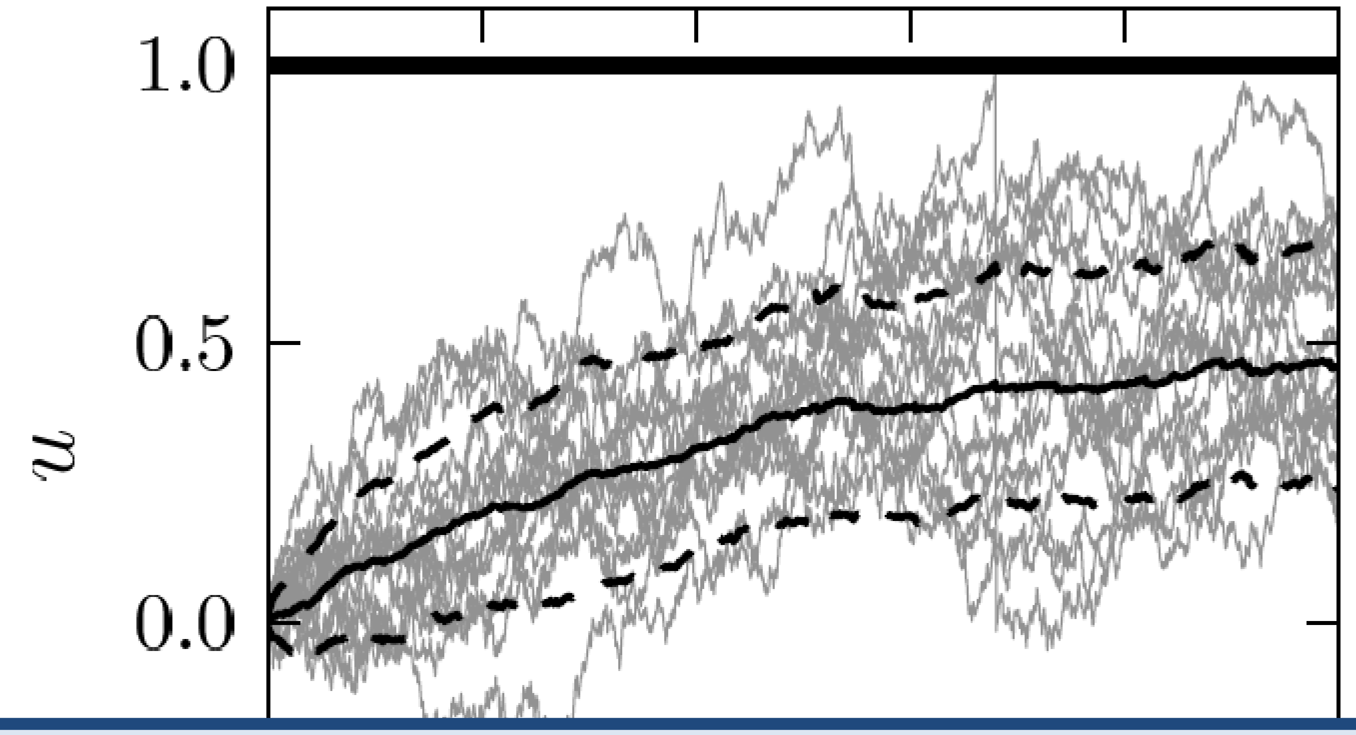


Langevin equation,
Ornstein Uhlenbeck process

Diffusive noise (stochastic spike arrival)



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

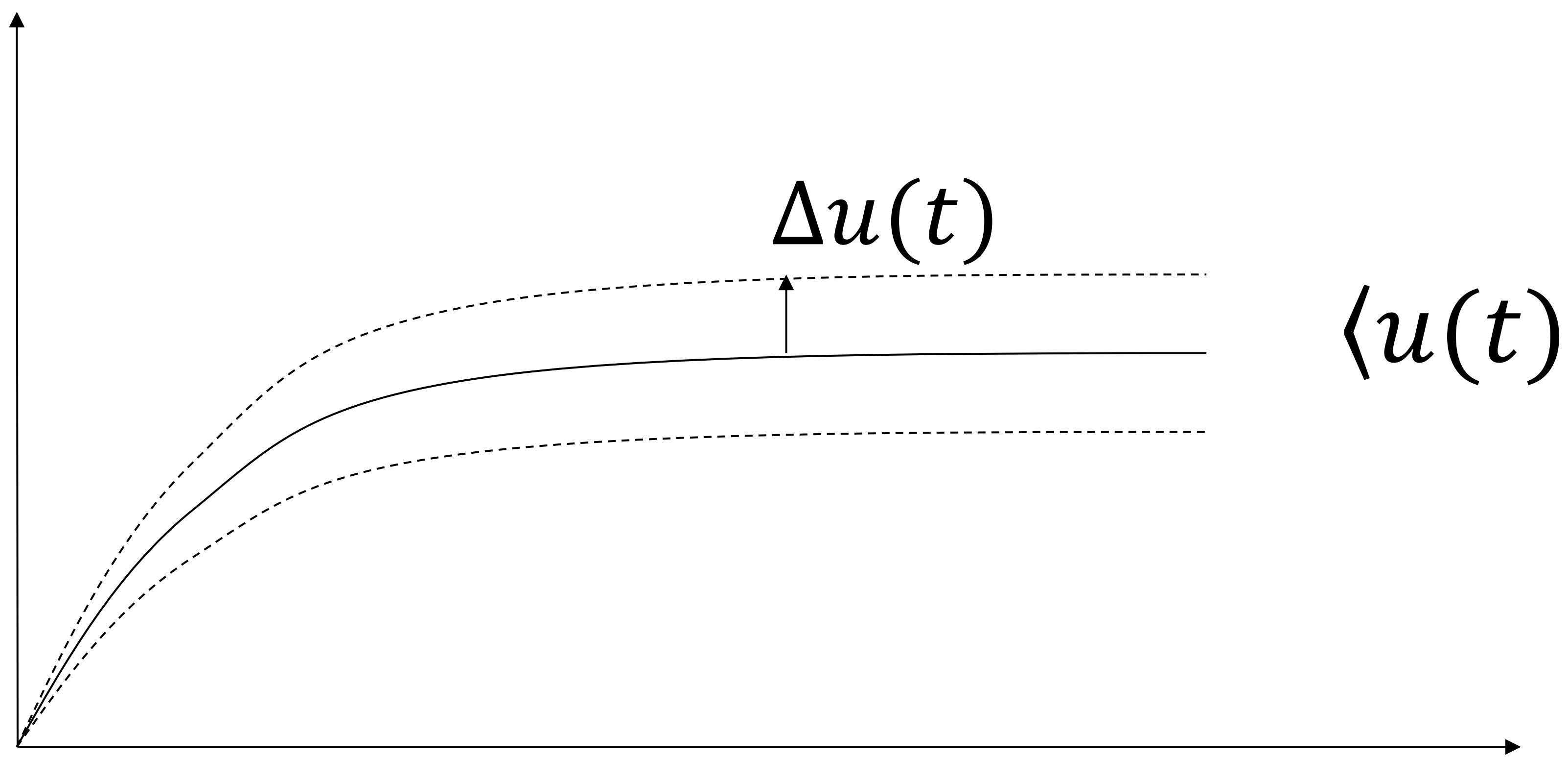


$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

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

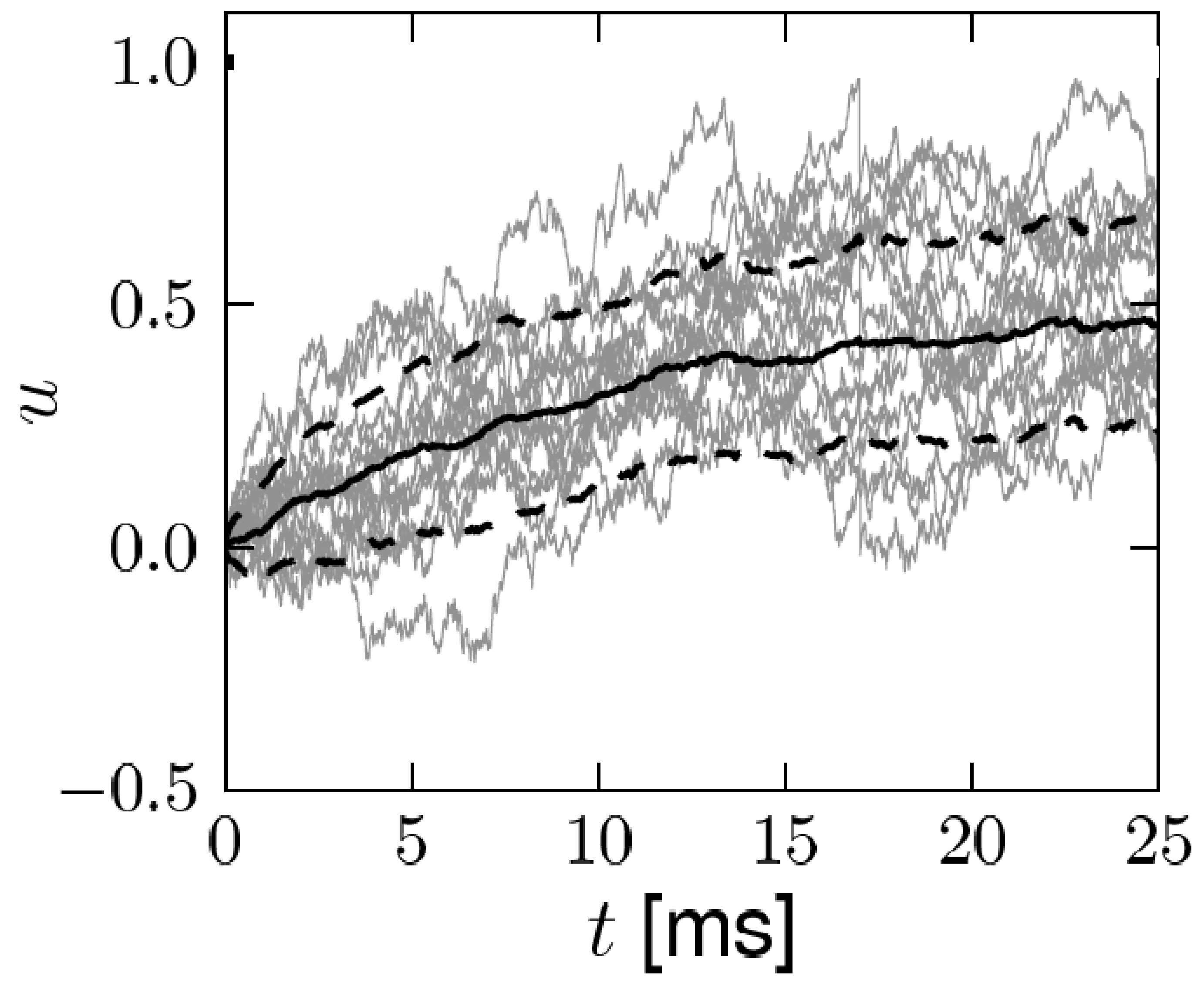
Math argument:
- *no threshold*
- *trajectory starts at known value*

Diffusive noise (stochastic spike arrival)



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

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



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

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

Math argument

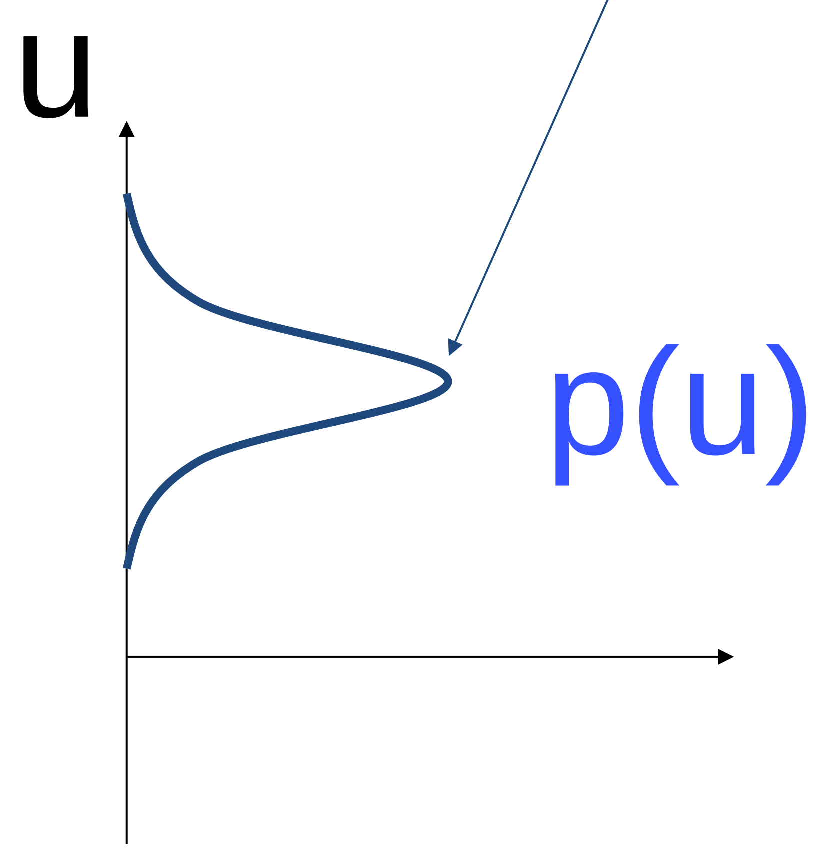
$$p(u,t) = \frac{1}{\sqrt{2\pi\,\langle \Delta u^2(t)\rangle}} \exp\left\{-\frac{[u(t|\hat{t}) - u_0(t)]^2}{2\,\langle \Delta u^2(t)\rangle}\right\}$$

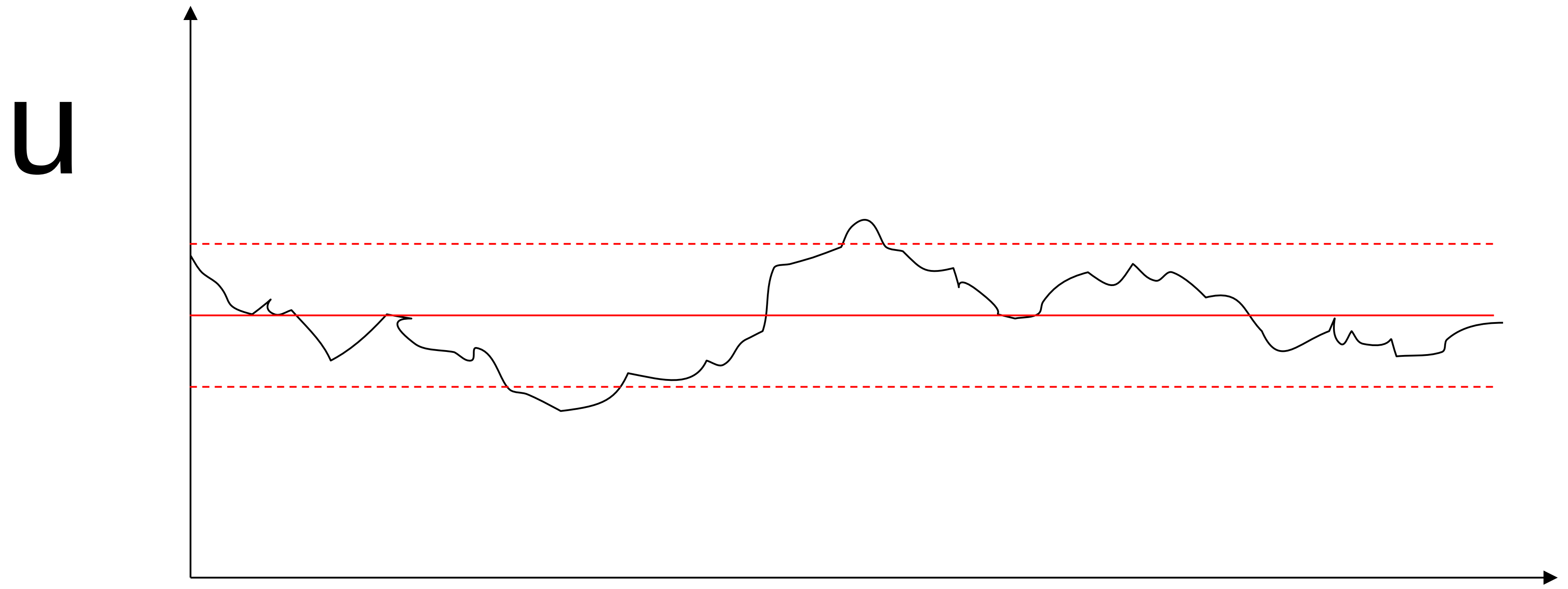
$$\langle [\Delta u(t)]^2\rangle = \sigma_u^2[1 - \exp(-2t/\tau)]$$

Neuronal Dynamics – 6.4. Diffusive noise/stoch. arrival

A) No threshold, stationary input

Membrane potential density: Gaussian





constant input rates
no threshold

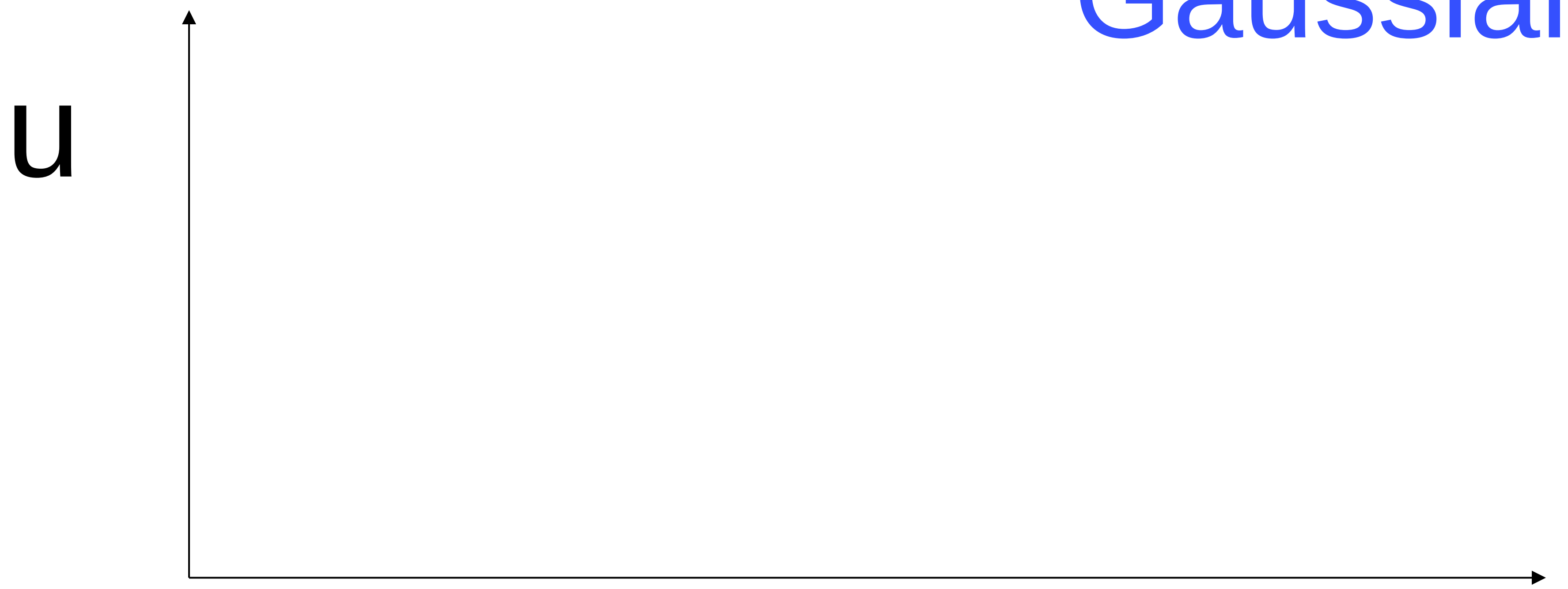
noisy integration

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

Neuronal Dynamics – 6.4. Diffusive noise/stoch. arrival

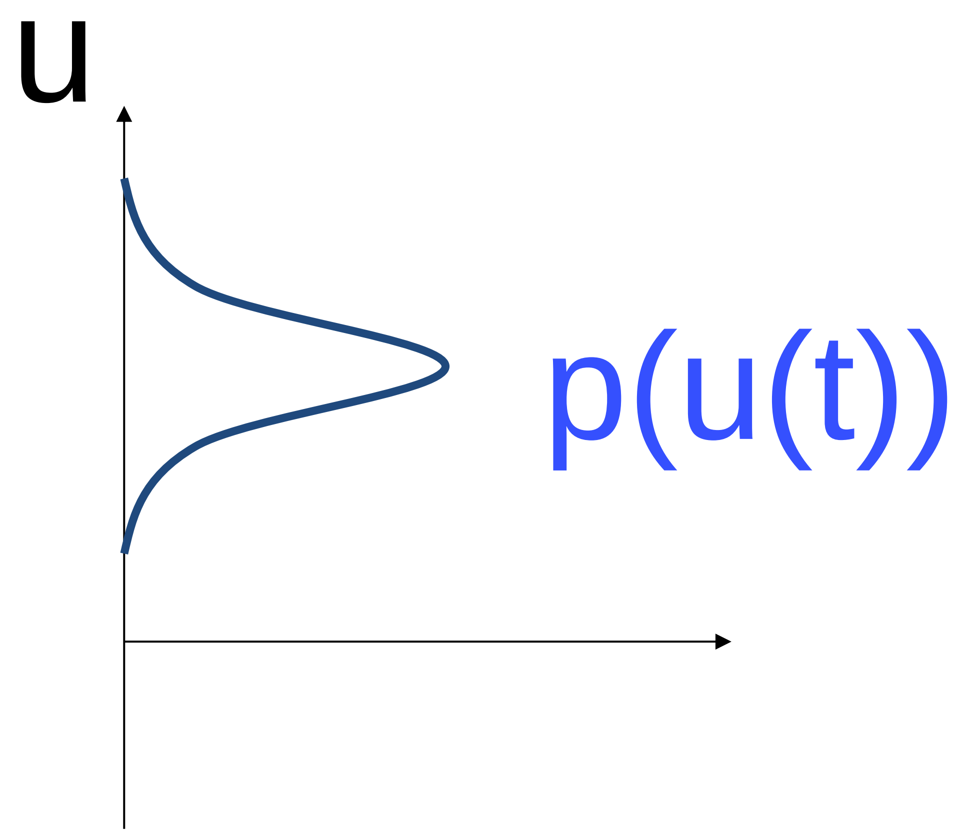
B) No threshold, oscillatory input

Membrane potential density:
Gaussian at time t



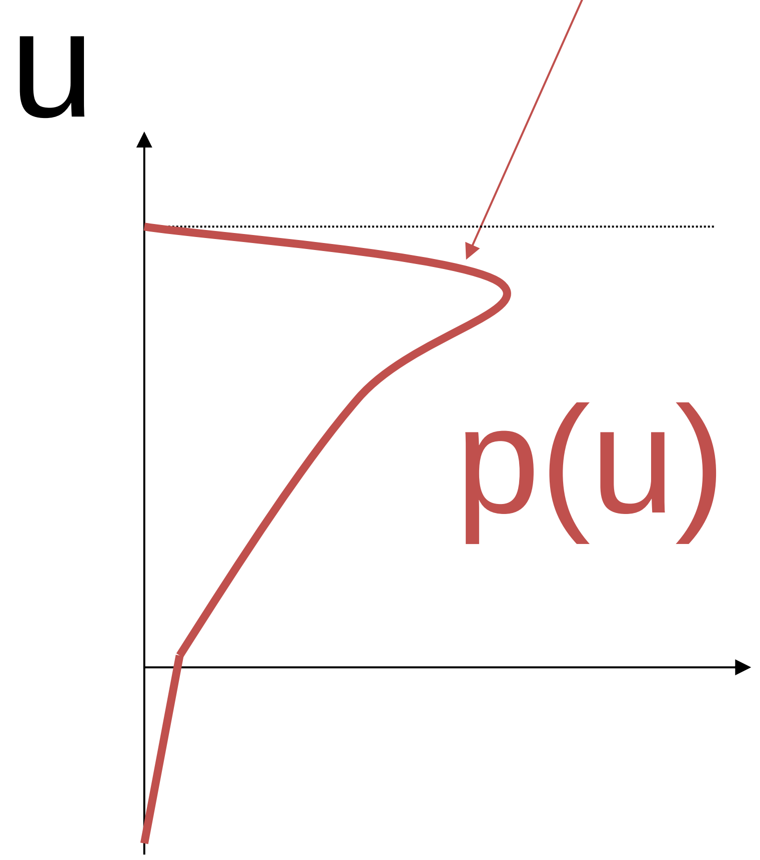
noisy integration

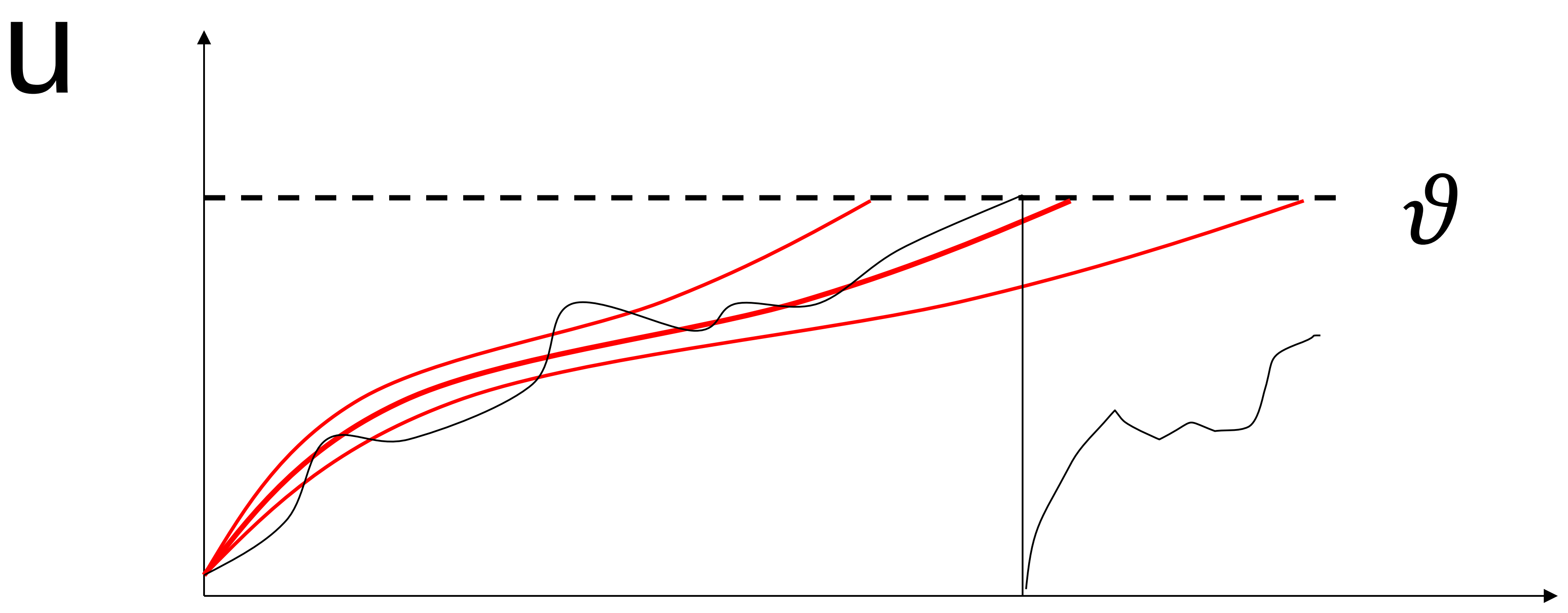
$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$



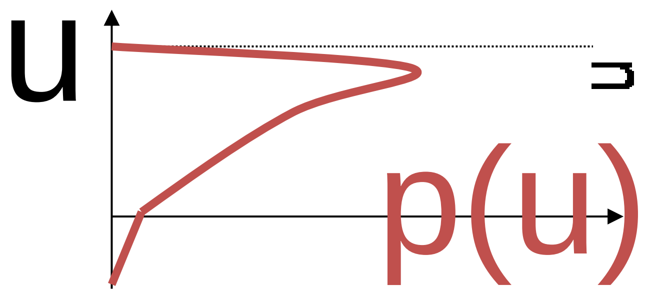
C) With threshold, reset/ stationary input

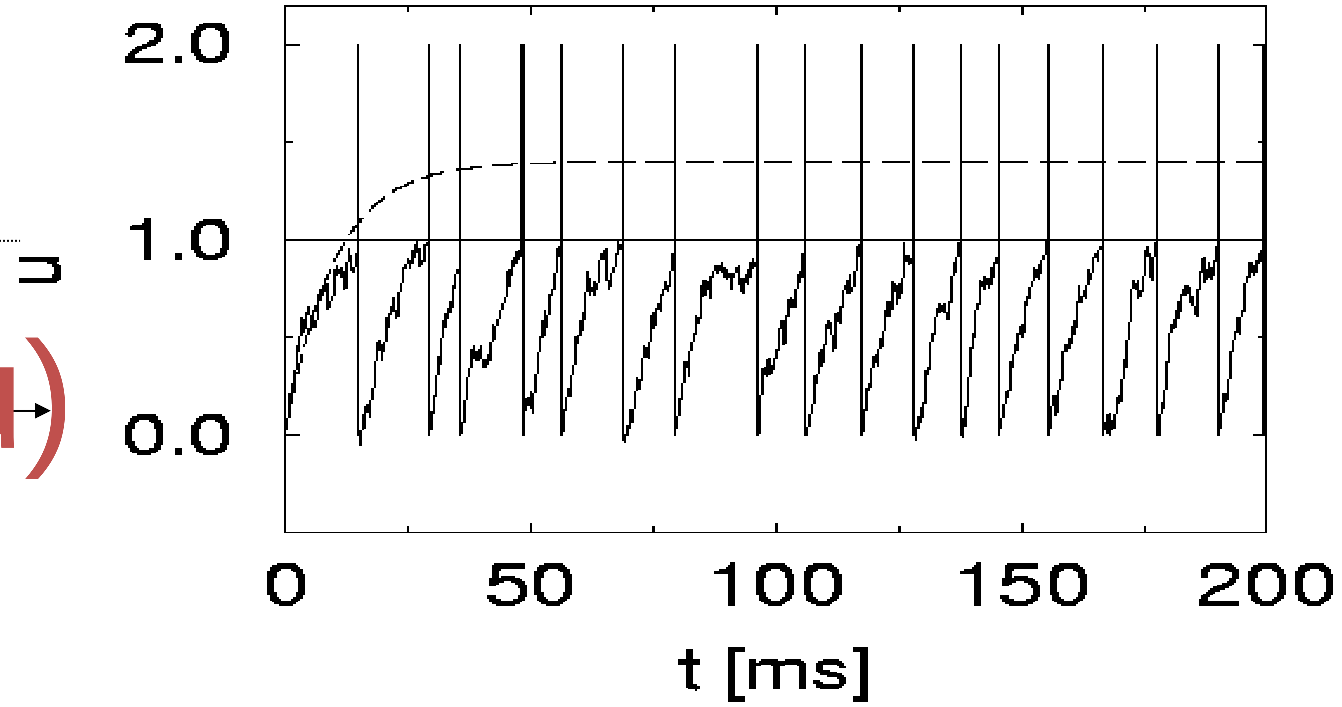
Membrane potential density

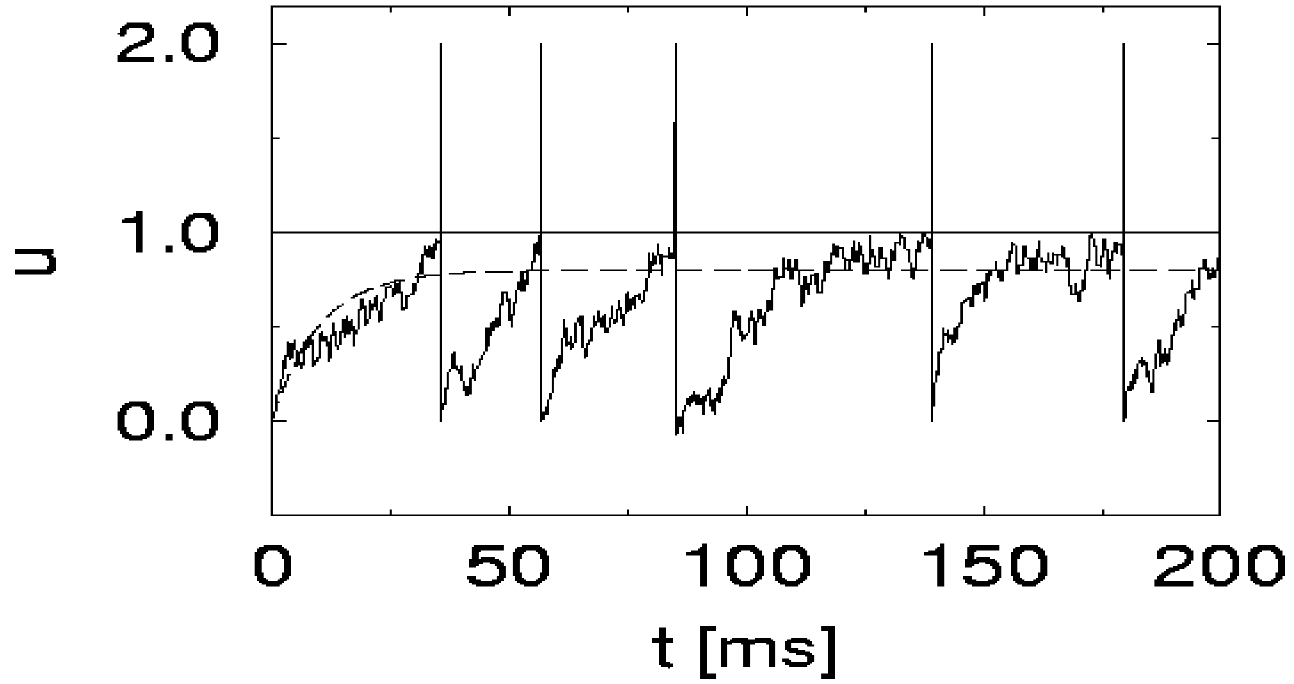




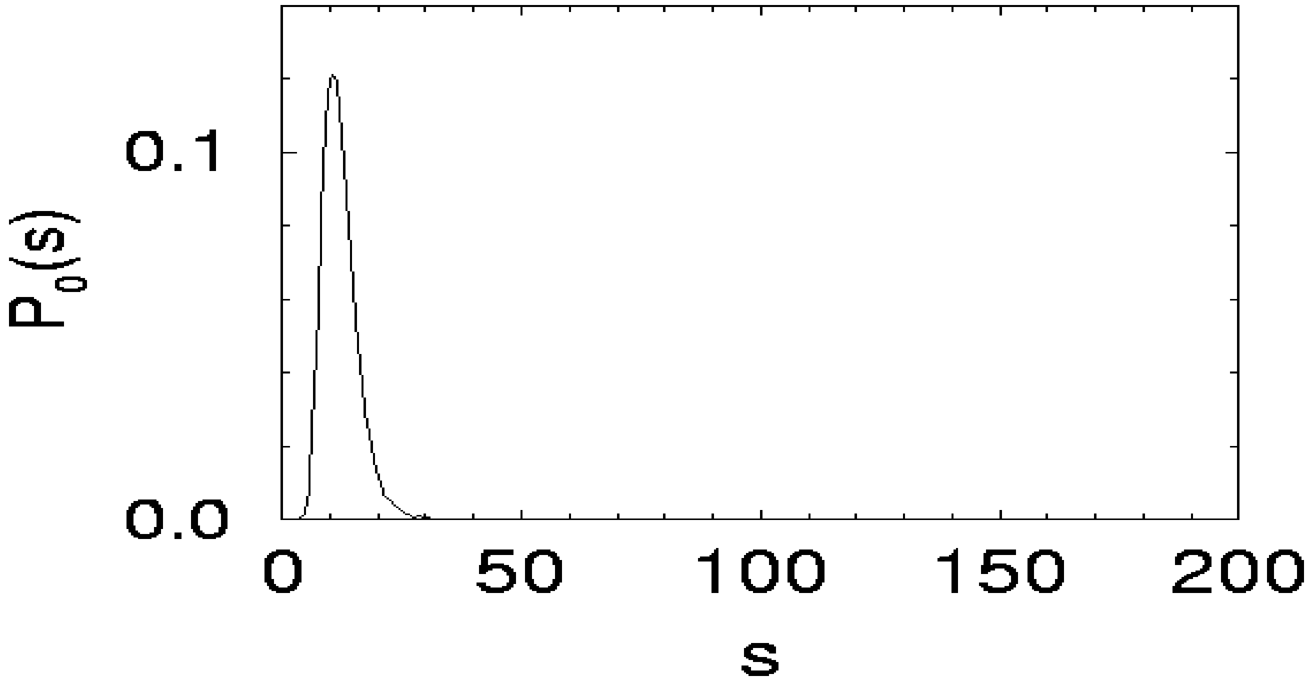
Superthreshold vs. Subthreshold regime

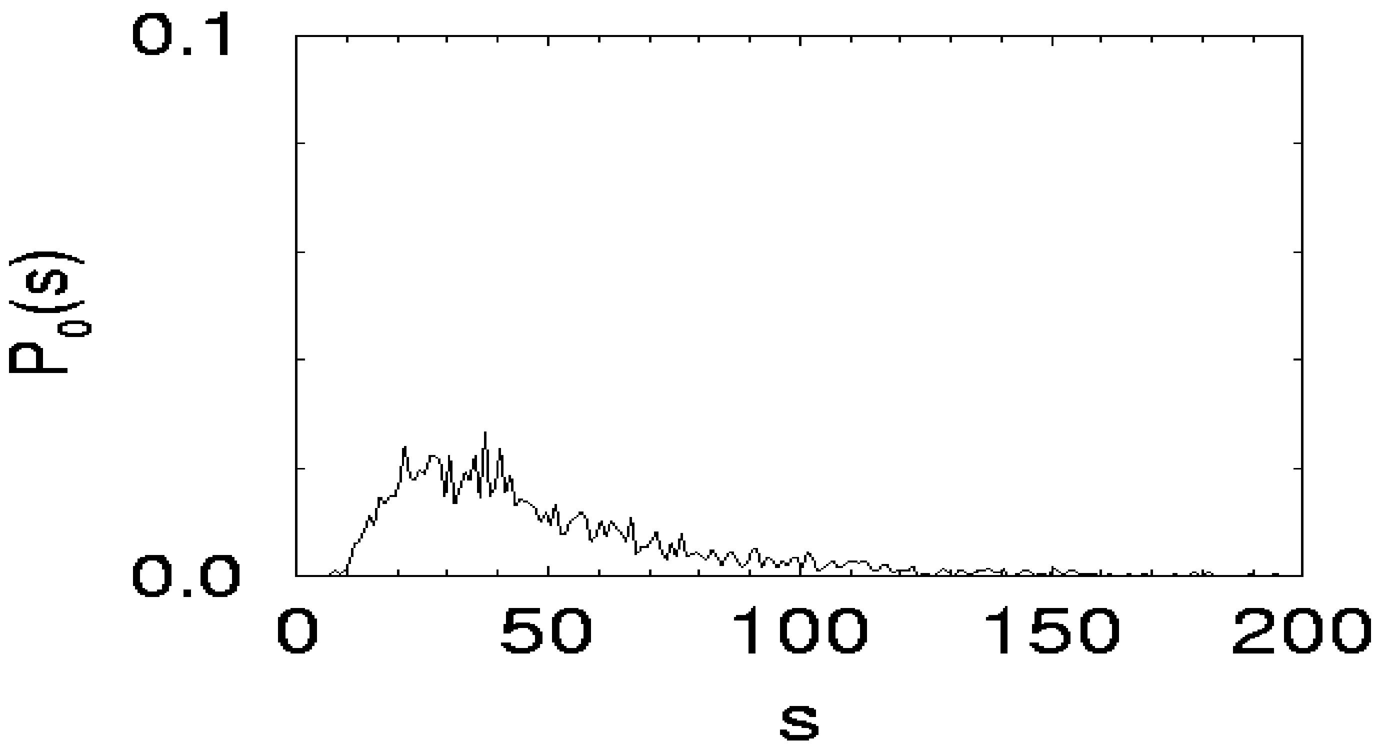






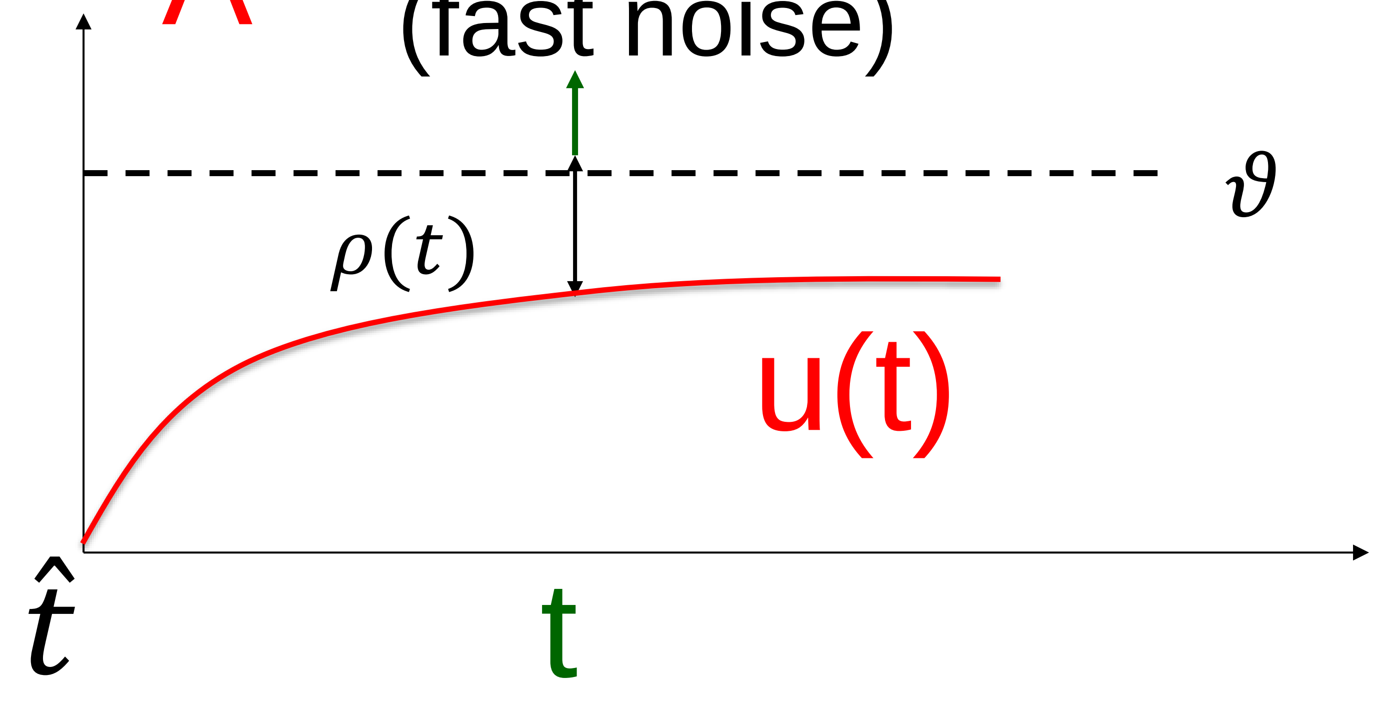
Nearly Gaussian subthreshold distr.





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:

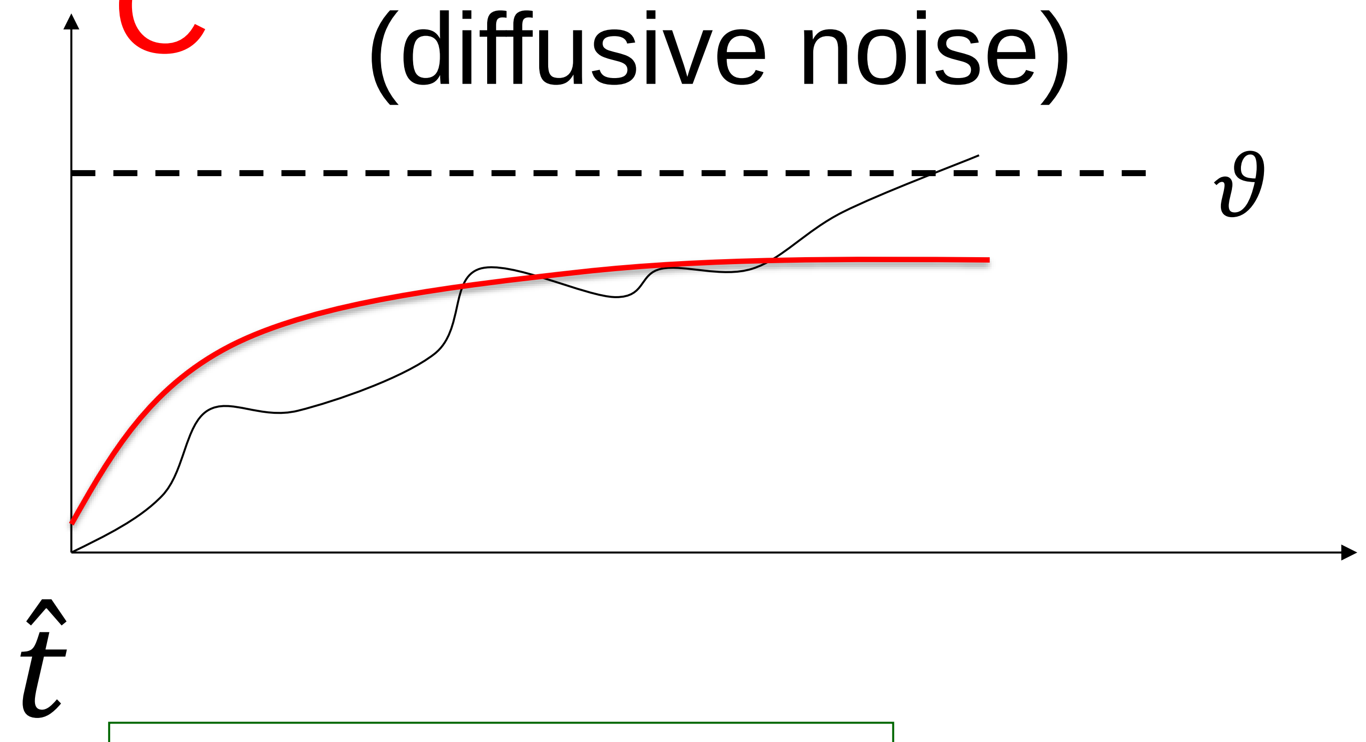
-Mean ISI

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

-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

white
(fast noise)

synapse
(slow noise)

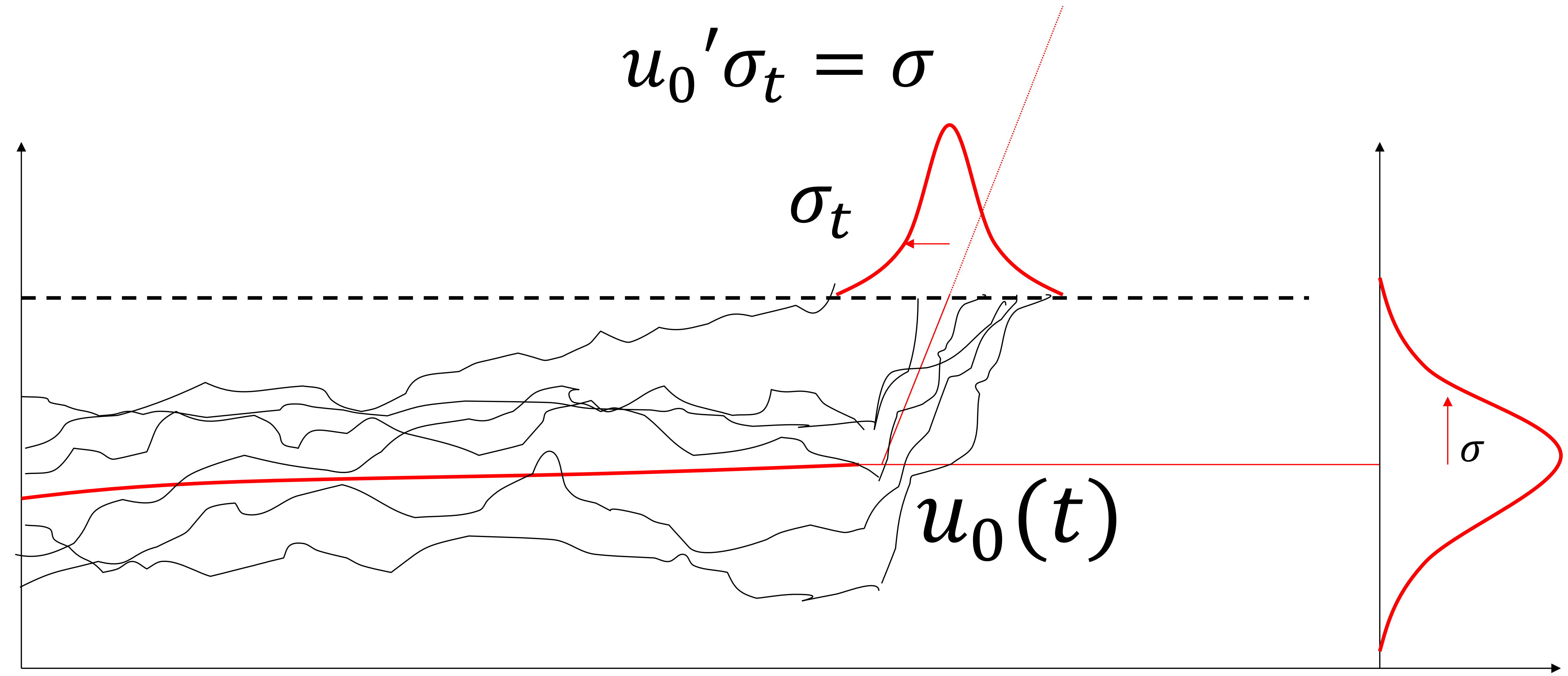
(Brunel et al., 2001)

Noise models: from diffusive noise to escape rates

noisy integration

ϑ

stochastic spike arrival
(diffusive noise)



escape rate

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

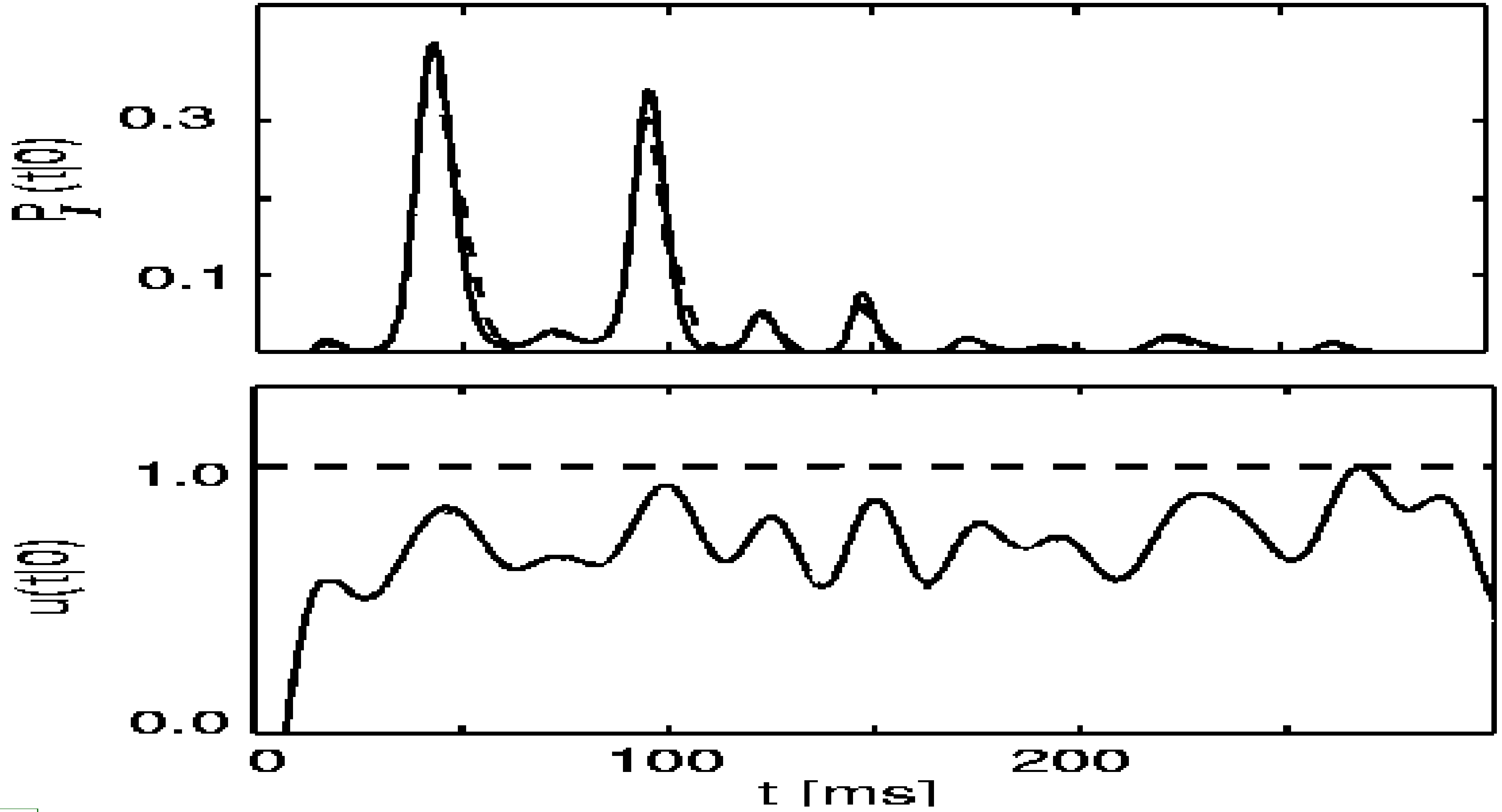
Comparison: diffusive noise vs. escape rates

Probability of first spike

diffusive

escape

subthreshold potential



escape rate

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

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

Week 6 – part 5 : Rate Codes versus Temporal Codes

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

Neuronal Dynamics:
Computational Neuroscience of Single Neurons

Week 6 – Noise models:
Escape noise

Wulfram Gerstner

EPFL, Lausanne, Switzerland

√ **6.1 Escape noise**
- stochastic intensity and point process

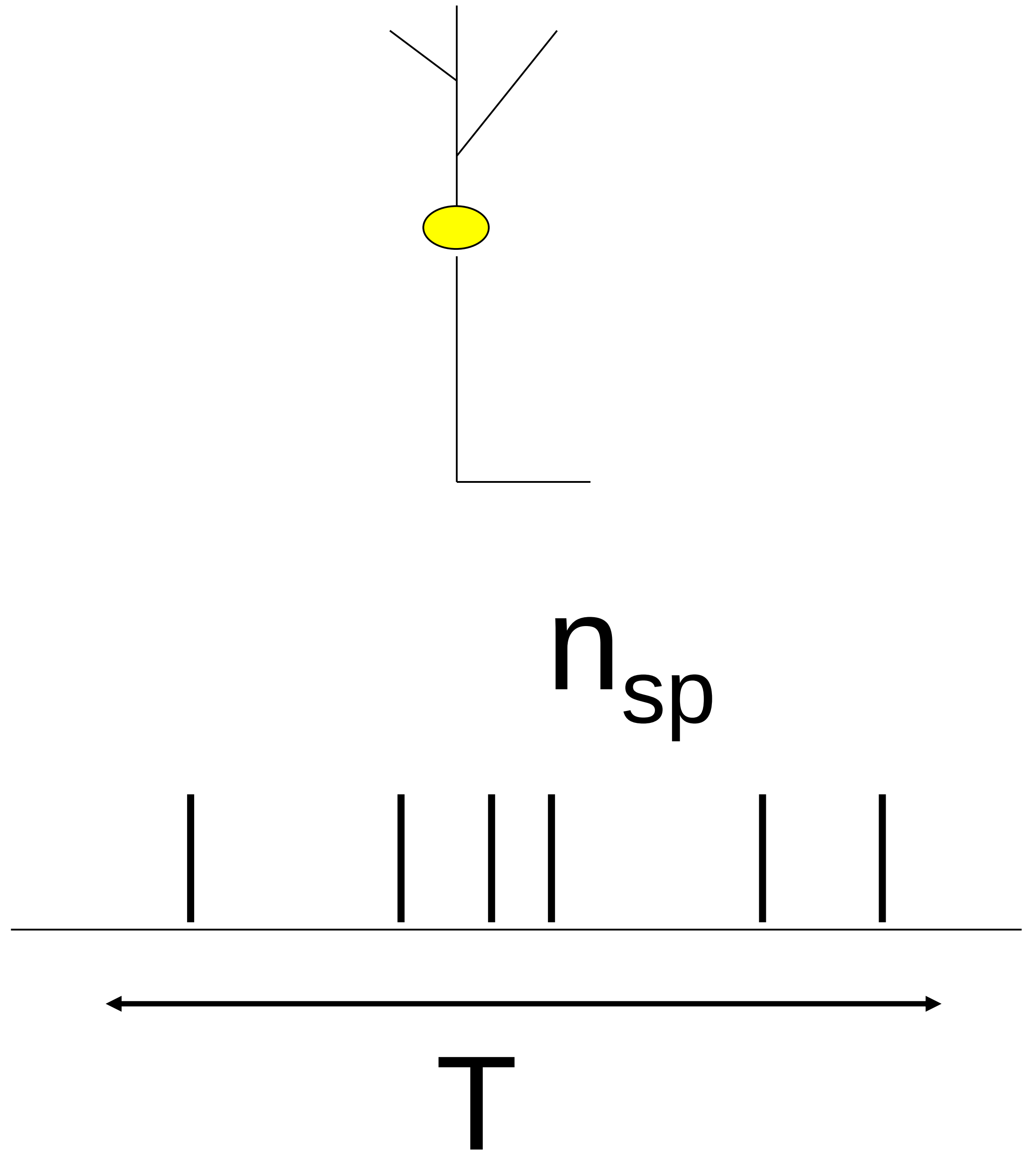
√ **6.2 Interspike interval distribution**
- Time-dependend renewal process
- Firing probability in discrete time

√ **6.3 Likelihood of a spike train**
- generative model

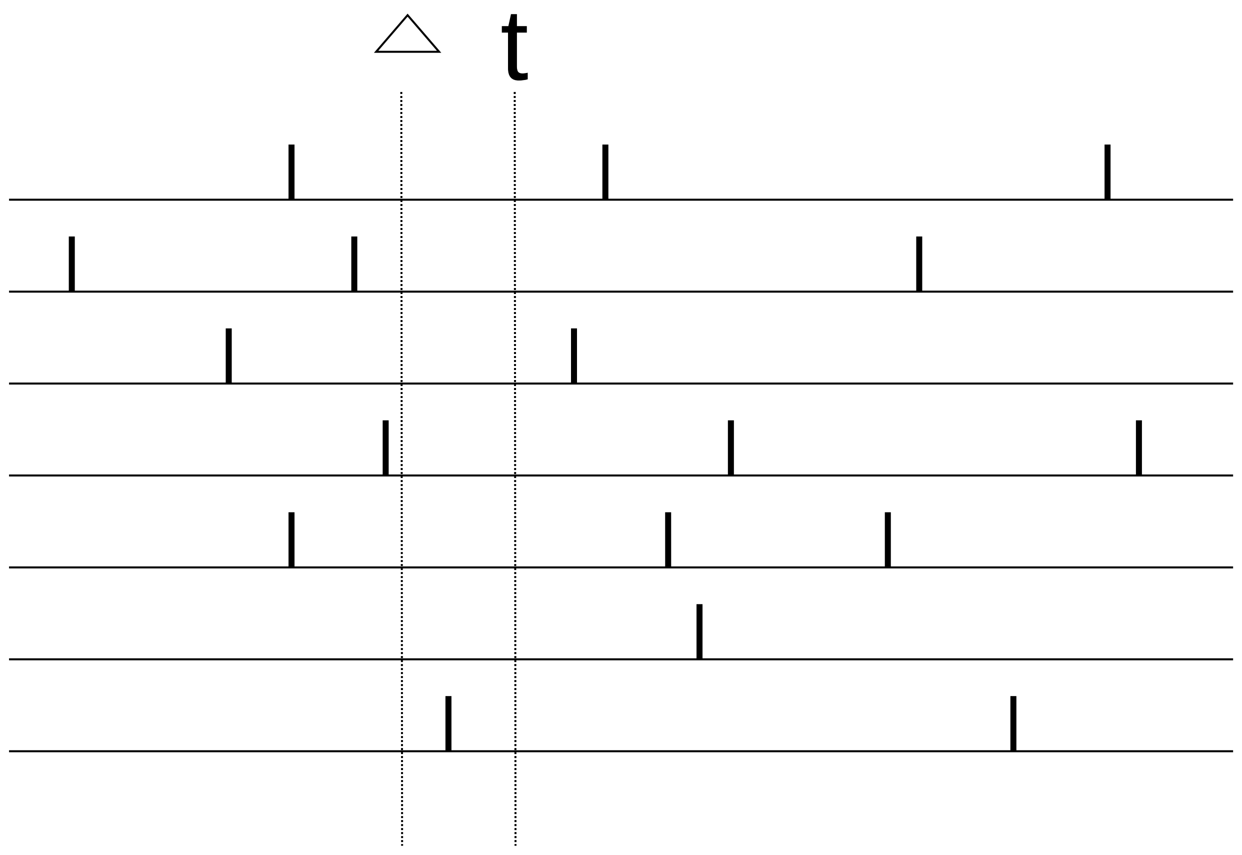
√ **6.4 Comparison of noise models**
- escape noise vs. diffusive noise

6.5. Rate code vs. Temporal Code
- timing codes
- stochastic resonance

3 rate codes

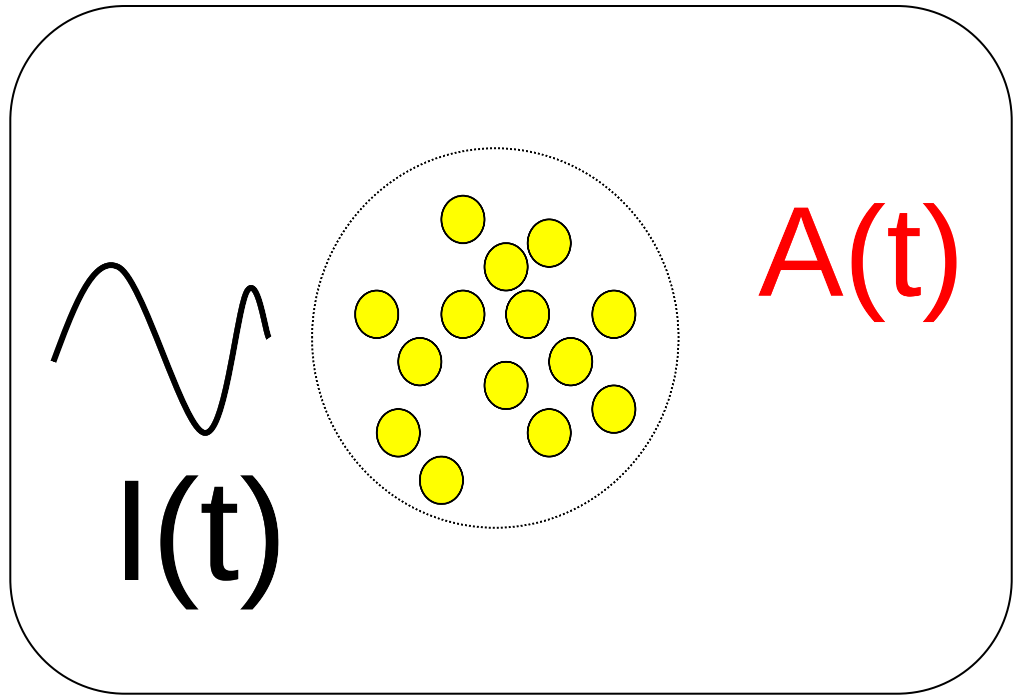


Temporal averaging



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

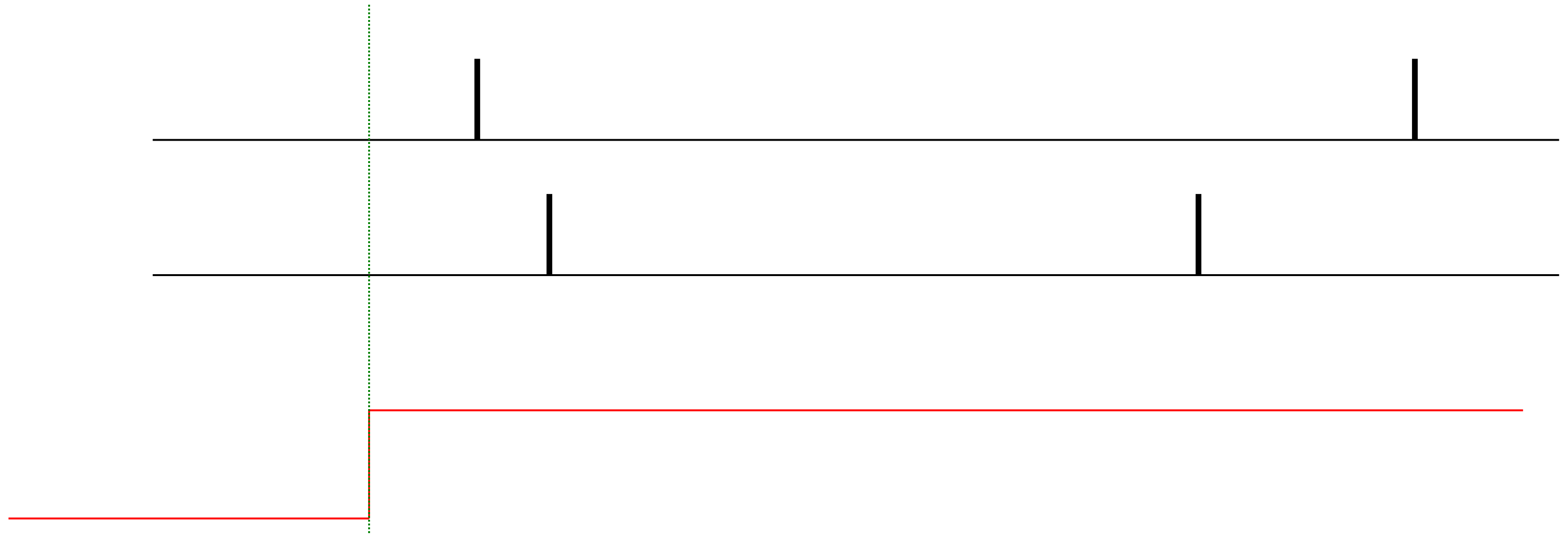
Trial averaging



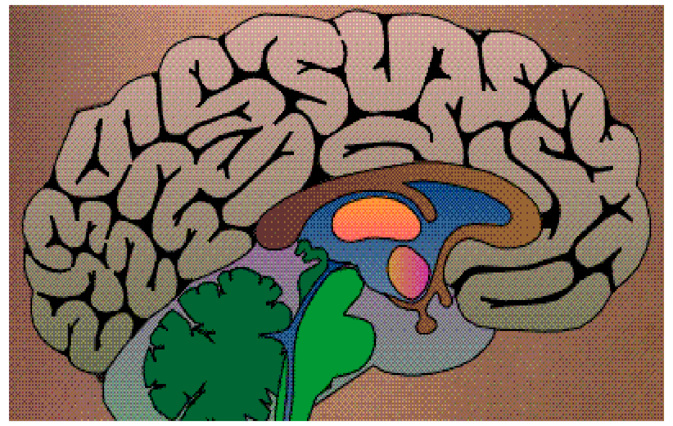
$$A(t) = \frac{n(t; t + \Delta t)}{N \Delta t}$$

population averaging

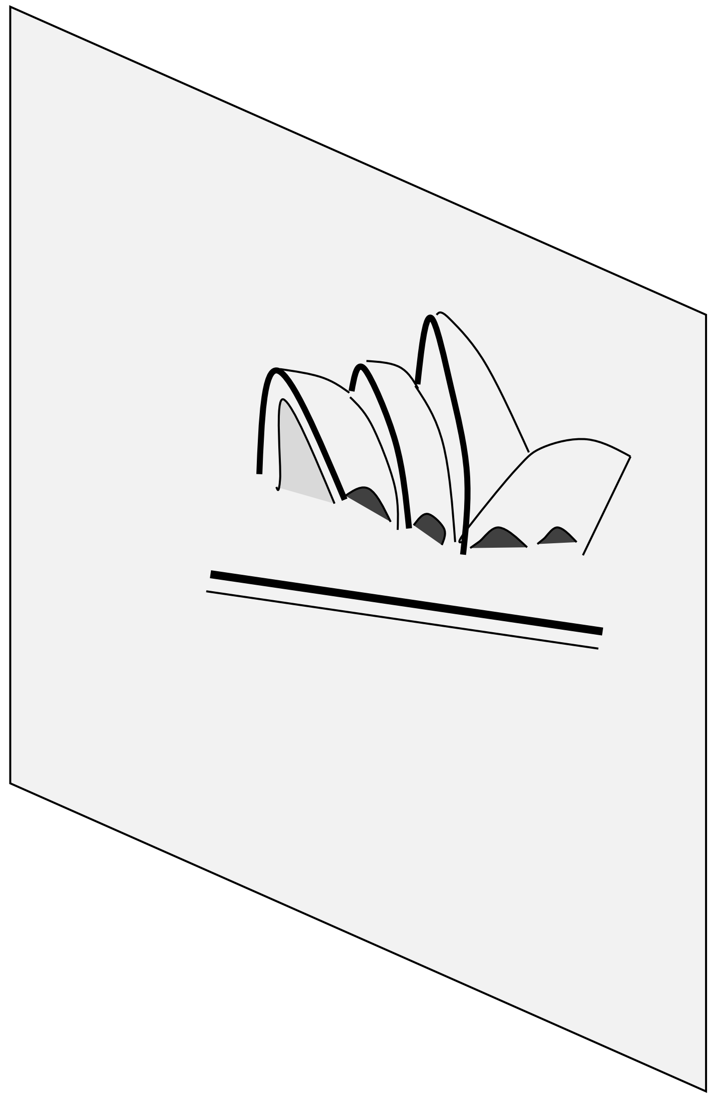
The problem of neural coding: temporal codes



Time to first spike after input

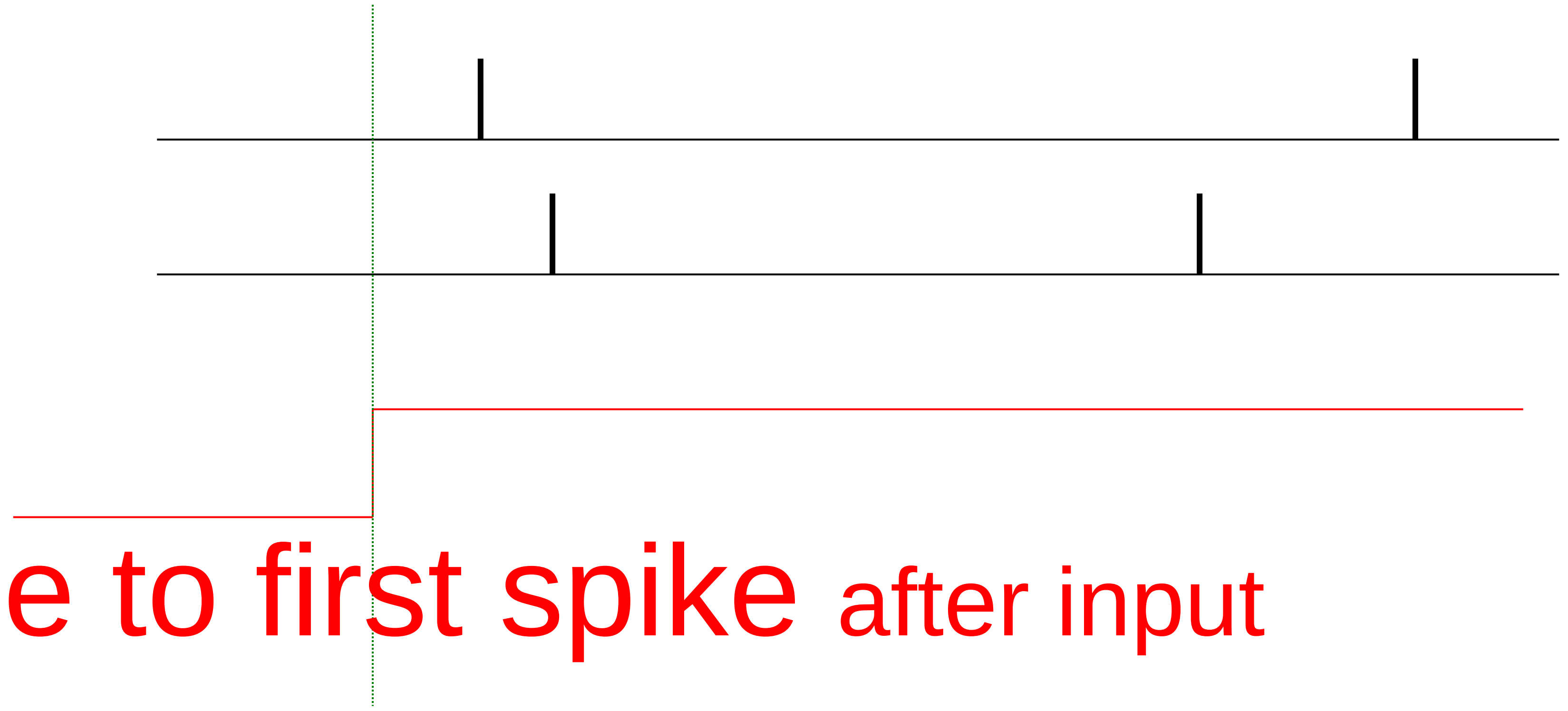


Brain

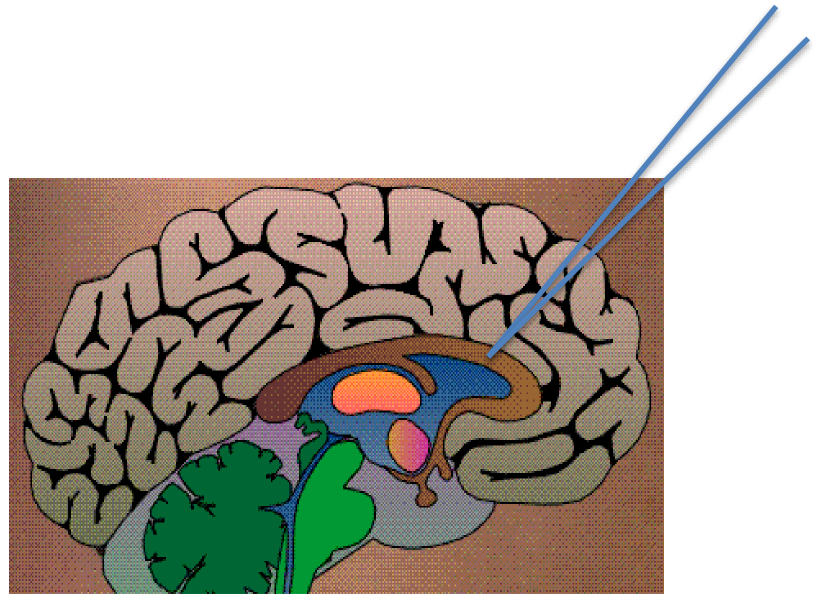


Neuronal Dynamics – 6.5. Temporal codes

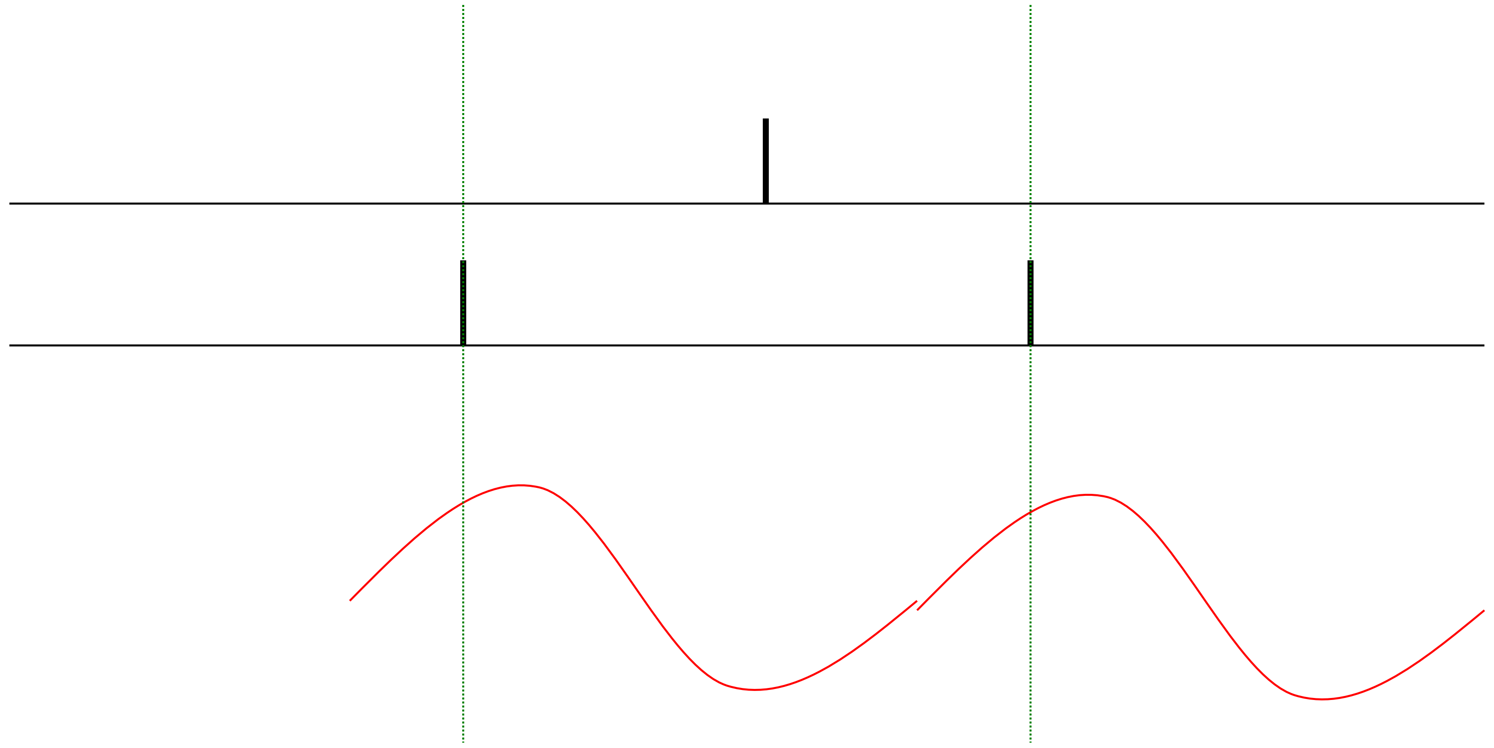
Spike timing codes:
-time-to-first spike
-phase code



Time to first spike after input



Brain

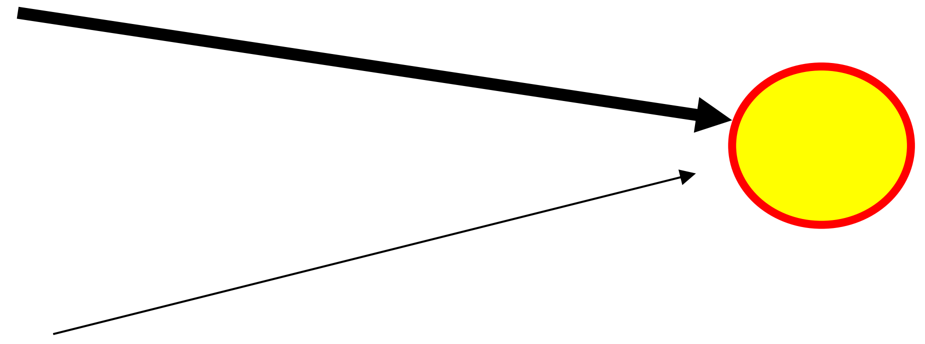


Phase with respect to oscillation

Neuronal Dynamics – 6.5. Stochastic Resonance

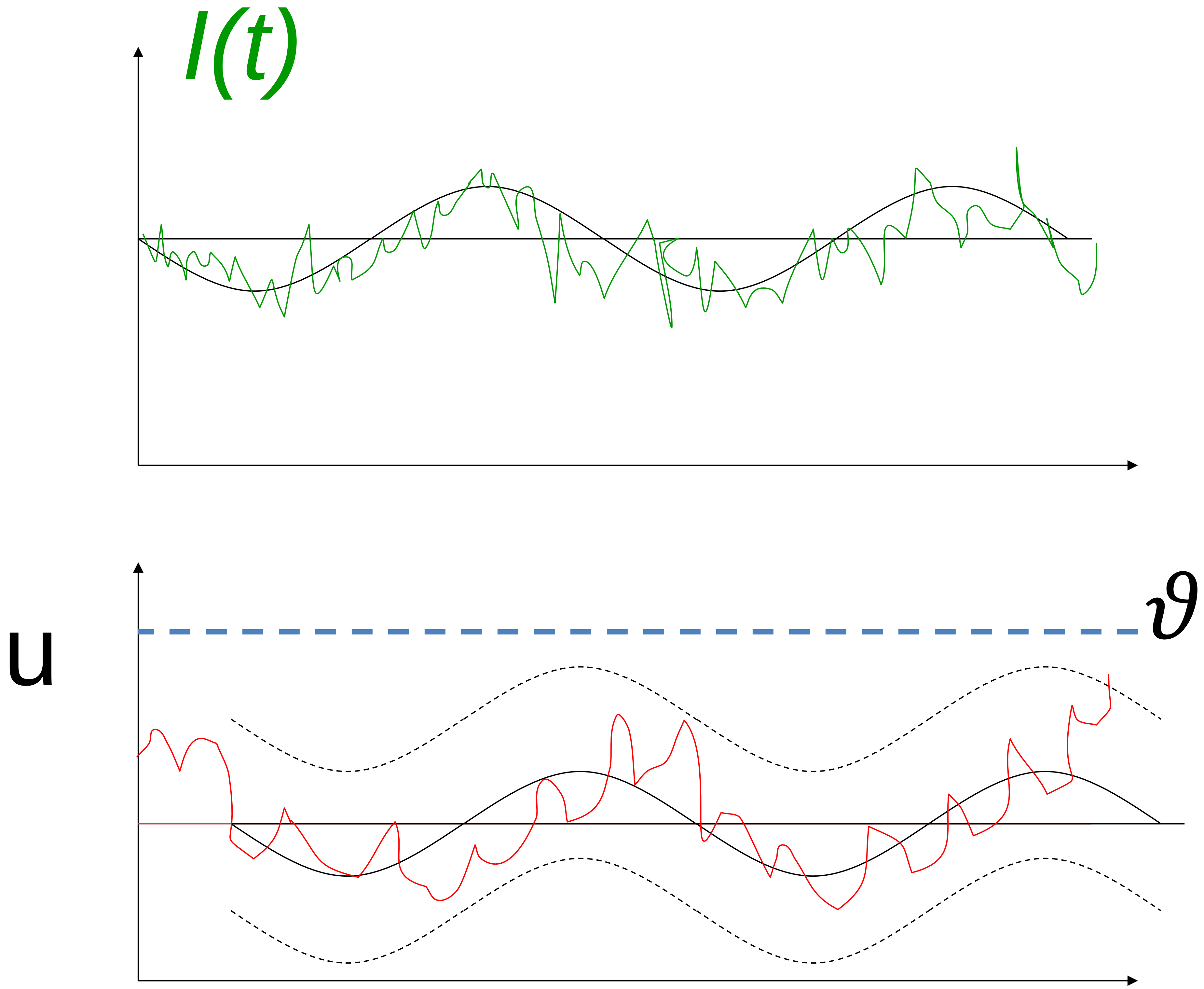
Stochastic Resonance: changing the noise level

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

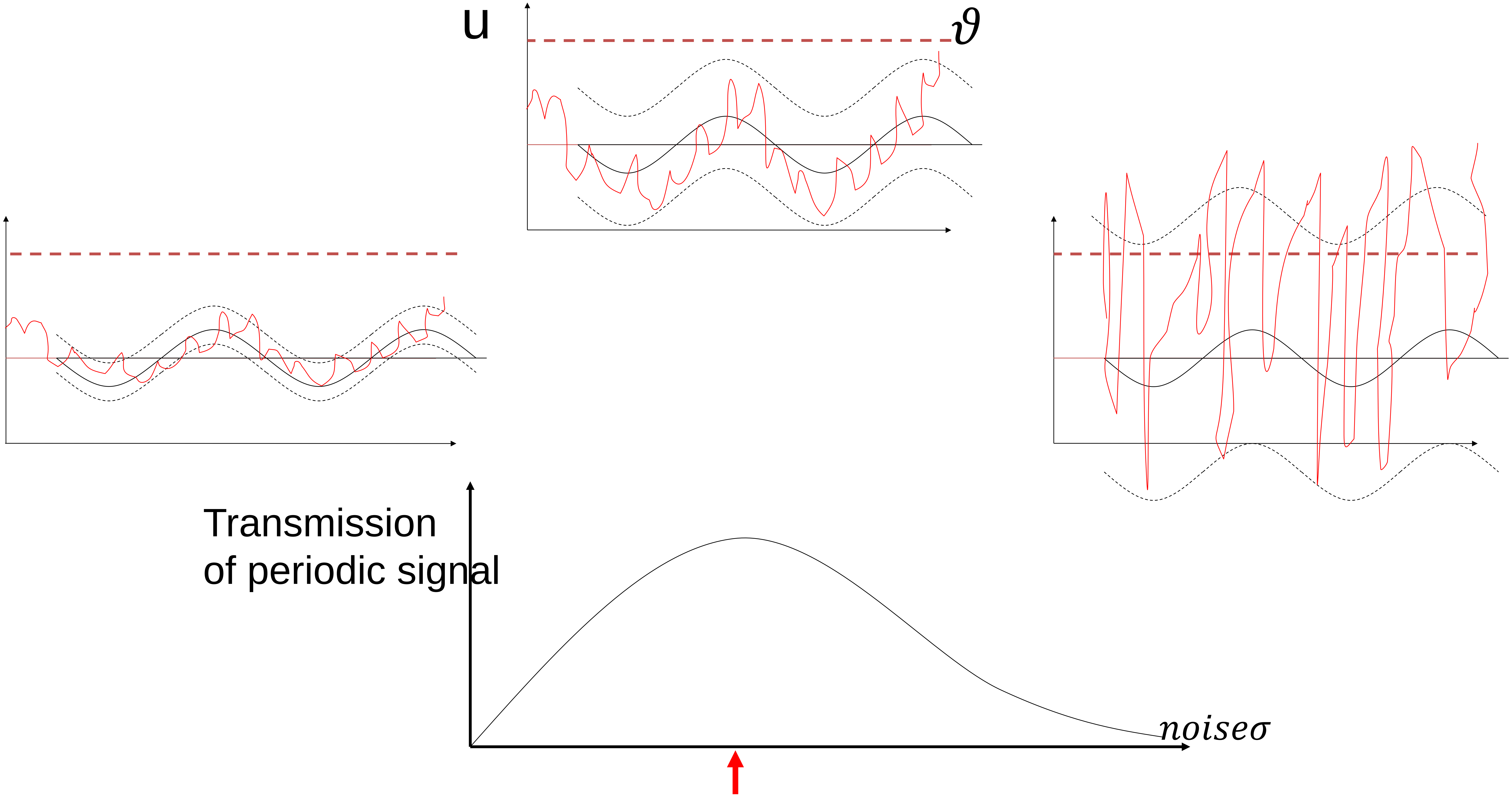


$$I^{noise}(t) = \sigma \xi(t)$$

Sinusoidal input
+ noise
+ threshold



Neuronal Dynamics – 6.5. Stochastic Resonance



Neuronal Dynamics – 6.5 Rate codes versus temporal codes

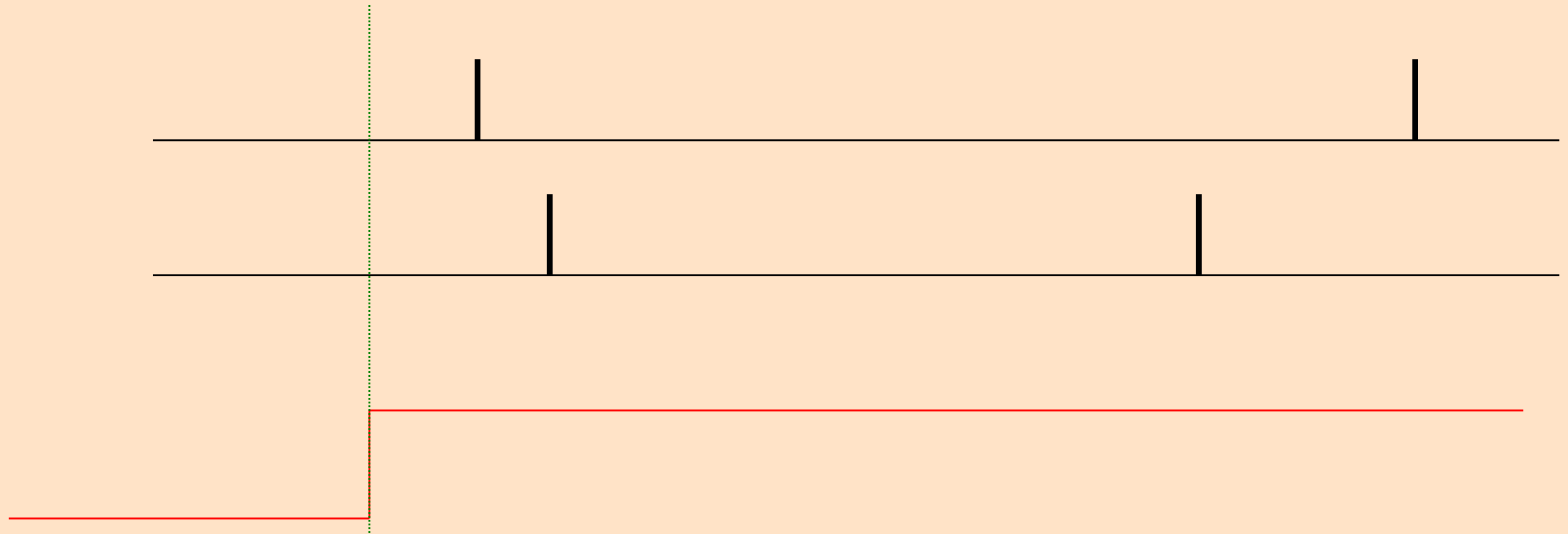
-Rate codes

- population rate

-Temporal Codes

- time-to-first spike
- phase of spike
- stochastic resonance

Neuronal Dynamics – Homework assignment



Time to first spike after input

With deterministic model
With Poisson model
With noisy IF (escape noise)