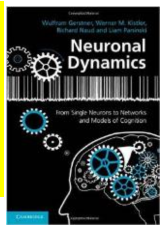
Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Week 11 – Variability and Noise: Autocorrelation

Wulfram Gerstner
EPFL, Lausanne, Switzerland

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



11.1 Variation of membrane potential
- white noise approximation

11.2 Autocorrelation of Poisson

11.3 Noisy integrate-and-fire
- superthreshold and subthreshold

11.4 Escape noise
- stochastic intensity

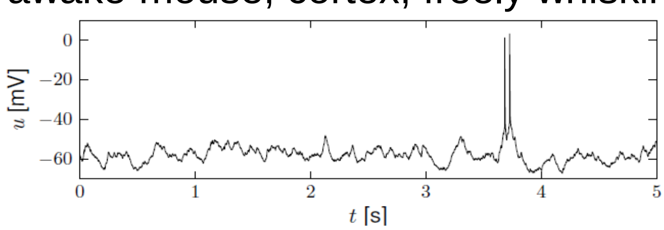
11.5 Renewal models

11.1 Review from week 10

Spontaneous activity *in vivo*

Variability
- of membrane potential?
- of spike timing?

awake mouse, cortex, freely whisking,



Crochet et al., 2011

11.1 Review from week 10

In vivo data
→ looks 'noisy'

In vitro data
→ fluctuations

Fluctuations
-of membrane potential
-of spike times

fluctuations=noise?

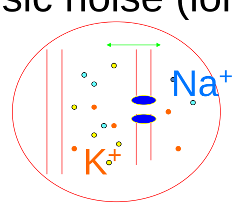
relevance for coding?

source of fluctuations?

model of fluctuations?

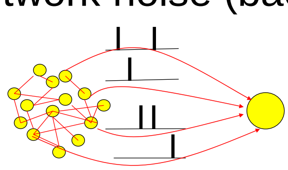
11.1. Review from week 10

- Intrinsic noise (ion channels)



-Finite number of channels
-Finite temperature

-Network noise (background activity)



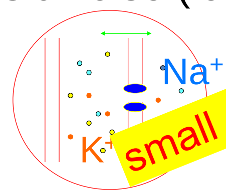
-Spike arrival from other neurons
-Beyond control of experimentalist

11.1. Review from week 10

In vivo data
→ looks 'noisy'

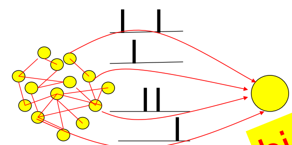
In vitro data
→small fluctuations
→nearly deterministic

- Intrinsic noise (ion channels)



small contribution!

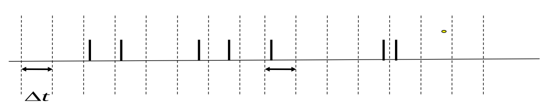
-Network noise



big contribution!

11.1 Review from week 10: Calculating the mean

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



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

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

mean: assume Poisson process

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

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

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

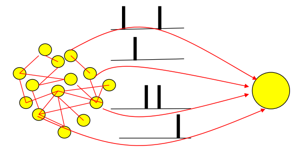
$$\langle x(t)\rangle = \int dt'\, f(t-t')\;\rho(t')$$

rate of inhomogeneous Poisson process

use for exercises
use for next slides

11.1. Fluctuation of potential

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

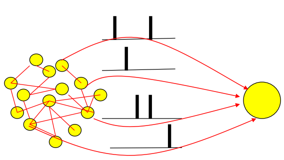


Passive membrane

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

Passive membrane
=Leaky integrate-and-fire
without threshold

11.1. Fluctuation of current/potential



Synaptic current pulses of shape α

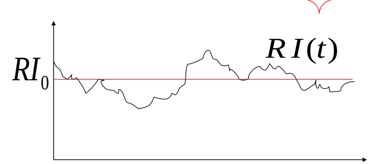
$$RI^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$

EPSC

Blackboard,
Math detour:
White noise

Passive membrane

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

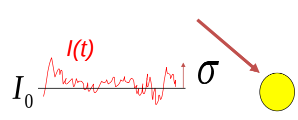


$$I^{syn}(t) = I_0 + I^{fluct}(t)$$

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

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

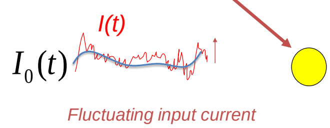
$$\langle \xi(t)\xi(t') \rangle = a^2 \tau\, \delta(t - t')$$



Fluctuating input current

11.1 Calculating autocorrelations

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



Autocorrelation

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

Blackboard, Math detour

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

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

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

Mean:

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

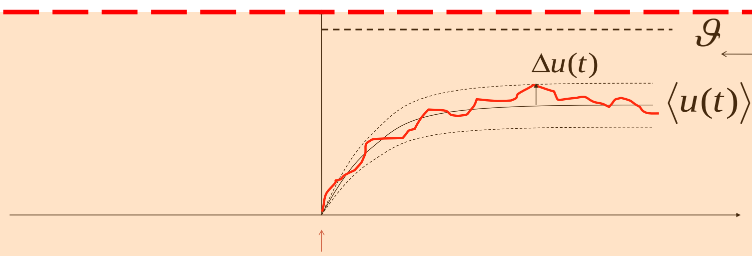
$$\langle x(t)\rangle = \int ds\, f(s)\, [I_0(t-s) + \langle \xi(t-s)\rangle]$$

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

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

- $\boxed{\langle \xi(t')\xi(t'')\rangle}$

White noise: Exercise 1.1-1.2 now



Assumption:
far away from theshold

Input starts here

Next lecture: 10:15

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

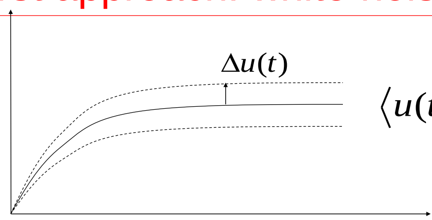
Variance of voltage at time *t*

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

Report variance as function of time!

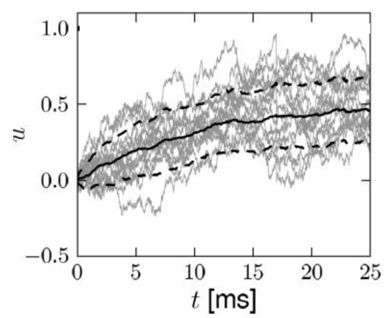
11.1 Calculating autocorrelations for stochastic spike arrival

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



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

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



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

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

Math argument

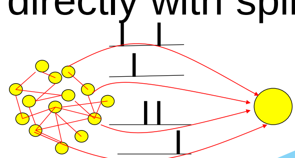
$$\langle [\Delta u(t)]^2\rangle = \sigma_u^2 [1 - \exp(-2t/\tau)]$$

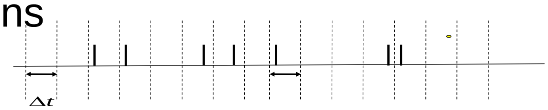
later $p(u,t) = \frac{1}{\sqrt{2\pi\,\langle \Delta u^2(t)\rangle}} \exp\left\{ -\frac{[u(t|\hat{t}) - u_0(t)]^2}{2\,\langle \Delta u^2(t)\rangle} \right\}$

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

11.1 Calculating autocorrelations: second approach

work directly with spike trains





Blackboard,
Math detour

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

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

Autocorrelation

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

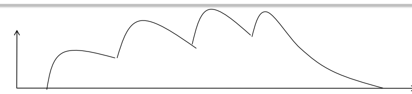
$$\langle x(t)x(\hat{t})\rangle = \int dt' \int dt'' f(t-t') f(\hat{t} - t'') \langle S(t')S(t'')\rangle$$

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

11.1 Mean and autocorrelation of filtered spike signal



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

$$F(s)$$

Filter

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

Assumption: stochastic spiking

rate $\nu(t)$

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

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

Autocorrelation of output

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

$$\langle x(t)x(t') \rangle = \int F(s)F(s') \underbrace{\langle S(t-s)S(t'-s') \rangle}_{\text{Autocorrelation of input}} dsds'$$

Autocorrelation of input

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Week 11 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

11.1 Variation of membrane potential
- white noise approximation

11.2 Autocorrelation of Poisson

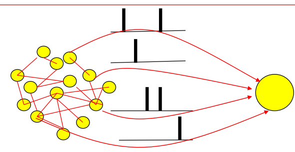
11.3 Noisy integrate-and-fire
- superthreshold and subthreshold

11.4 Escape noise
- stochastic intensity

11.5 Renewal models

11.2 Autocorrelation of Poisson (preparation)

Justify autocorrelation of spike input:
Poisson process in discrete time



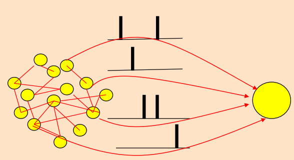
Stochastic spike arrival:

Blackboard

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

Firing independent between one time step and the next

Exercise 3 now: Poisson process in continuous time



Stochastic spike arrival:
excitation, total rate

Next lecture: 10:40

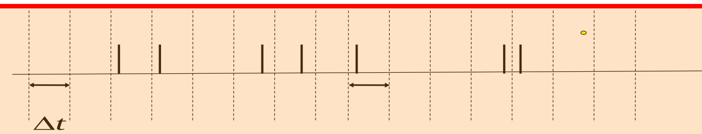
In each small time step Δt
Prob. Of firing $p = \nu \, \Delta t$

Firing independent between one time step and the next

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

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

Quiz – 1. Autocorrelation of Poisson



The Autocorrelation (continuous time)

spike train

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

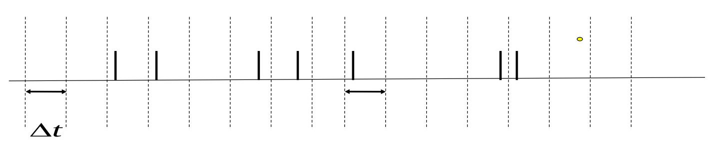
Has units

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

11.2. Autocorrelation of Poisson

math detour now!

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



spike train

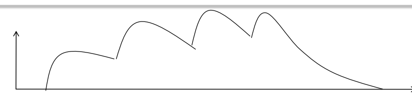
Probability of spike in time step:

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

Autocorrelation (continuous time)

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

11.2. Autocorrelation of Poisson: units



$$S(t) = \sum_f \delta(t - t^f) \qquad F(s) \qquad x(t) = \int F(s) S(t-s) ds$$

Assumption: stochastic spiking (Poisson)

rate $\nu(t)$

Autocorrelation of output

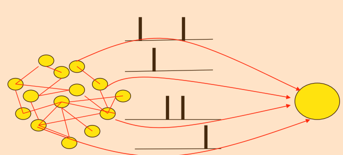
$$\langle x(t) x(t') \rangle = \left\langle \int F(s) S(t-s) ds \int F(s') S(t'-s') ds' \right\rangle$$

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

Autocorrelation of input (Poisson)

We integrate twice!

Exercise 2 **Homework:** stochastic spike arrival



Stochastic spike arrival:
excitation, total rate $\langle S(t) \rangle = \nu$

Synaptic current pulses

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

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

1. Assume that for t>0 spikes arrive stochastically with rate ν
   - Calculate mean voltage
2. Assume autocorrelation $\langle S(t) S(t') \rangle = \nu\, \delta(t - t') + \nu^2$
   - Calculate $\langle u(t) u(t) \rangle = ?$

Biological Modeling of Neural Networks

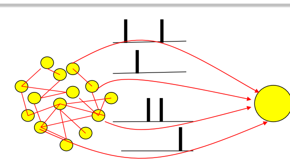
Week 11 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

11.3 Noisy Integrate-and-fire

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



Passive membrane

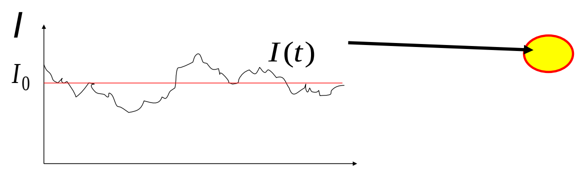
$$\tau \frac{d}{dt} u = -(u - u_{rest}) \quad + R I^{syn}(t)$$

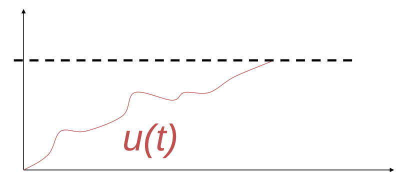
Passive membrane
=Leaky integrate-and-fire
without threshold

ADD THRESHOLD
→ Leaky Integrate-and-Fire

11.3 Noisy Integrate-and-fire

effective noise current





LIF

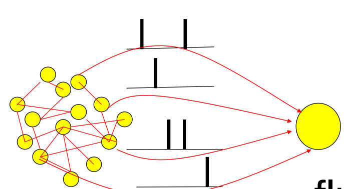
$$\tau \frac{d}{dt}u = -(u - u_{rest}) \quad + R\,I(t)$$

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

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

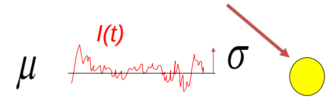
noisy input/
diffusive noise/
stochastic spike
arrival

11.3 Noisy Integrate-and-fire



Random spike arrival

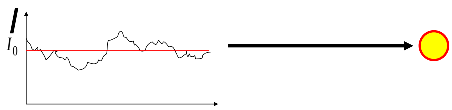
fluctuating input current



fluctuating potential

11.3 Noisy Integrate-and-fire (noisy input)

stochastic spike arrival in I&F – interspike intervals



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

white noise

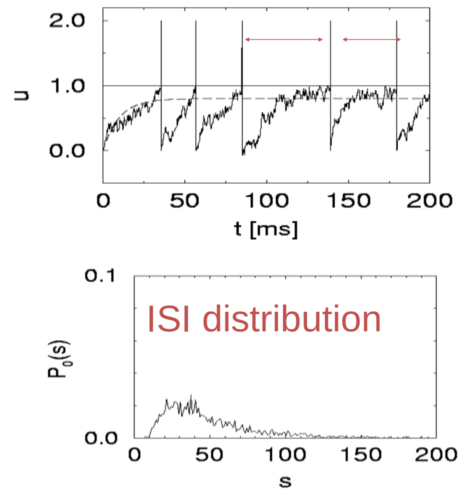


Image:
Gerstner et al. (2014),
Neuronal Dynamics,

11.3 Noisy Integrate-and-fire (noisy input)

Superthreshold vs. Subthreshold regime

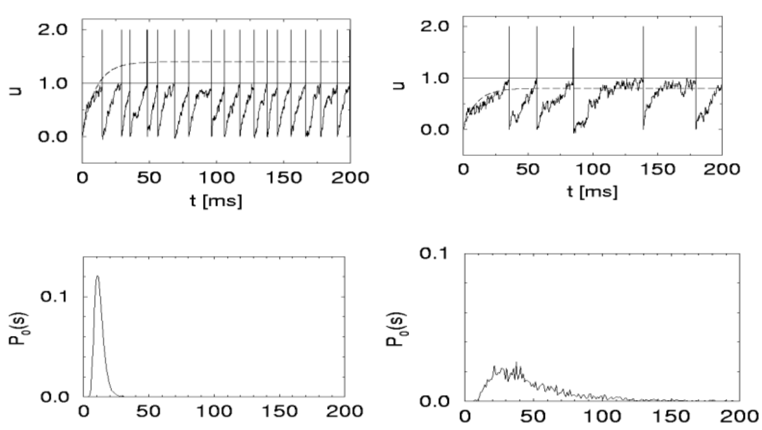


Image:
Gerstner et al. (2014),
Neuronal Dynamics,
Cambridge Univ. Press;
See: Konig et al. (1996)

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

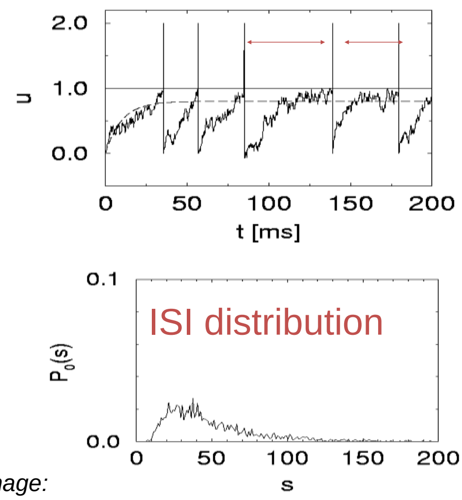
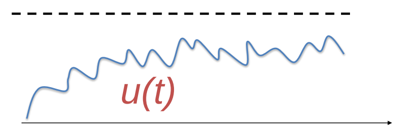


Image:
Gerstner et al. (2014),
Neuronal Dynamics,

noisy input/ diffusive noise/
stochastic spike arrival



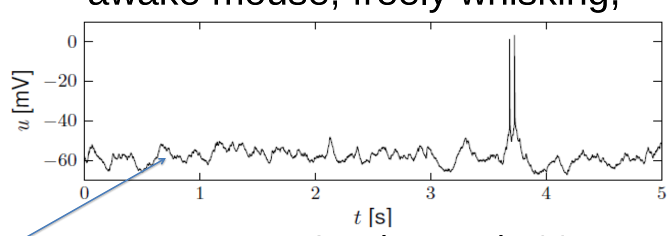
subthreshold regime:
- firing driven by fluctuations
- **broad ISI distribution**
- *in vivo* like

review- Variability in vivo

Spontaneous activity *in vivo*

Variability
of membrane potential?

awake mouse, freely whisking,



Crochet et al., 2011

Subthreshold regime

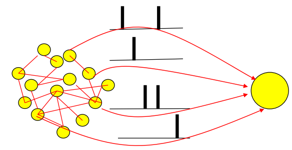
Image:
Gerstner et al. (2014),
Neuronal Dynamics,
Cambridge Univ. Press;
Courtesy of: Crochet et al. (2011)

11.3 Noisy Integrate-and-fire (noisy input)

Stochastic spike arrival:

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

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



Passive membrane

$$u(t) = \sum_k w_k \sum_f \varepsilon(t' - t_k^f)$$

$$= \sum_k w_k \int dt' \varepsilon(t - t') S_k(t')$$

fluctuating potential

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

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EPFL, Lausanne, Switzerland

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- white noise approximation

√ **11.2 Autocorrelation of Poisson**

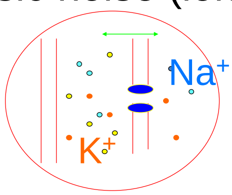
√ **11.3 Noisy integrate-and-fire**
- superthreshold and subthreshold

11.4 Escape noise
- stochastic intensity

11.5 Renewal models

Review: Sources of Variability

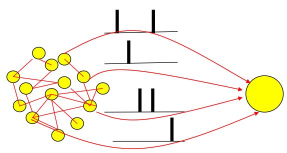
- Intrinsic noise (ion channels)



-Finite number of channels
-Finite temperature

small contribution!

-Network noise (background activity)



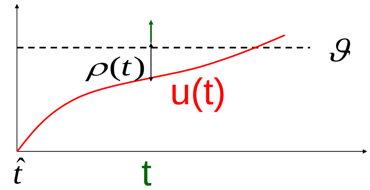
-Spike arrival from other neurons
-Beyond control of experimentalist

Noise models?

big contribution!

11.4 Noise models: Escape noise vs. input noise

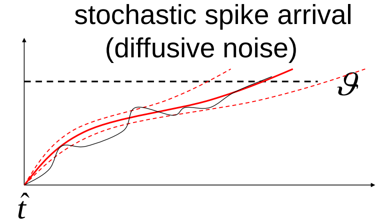
escape process,
stochastic intensity



escape rate

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

stochastic spike arrival
(diffusive noise)



noisy integration

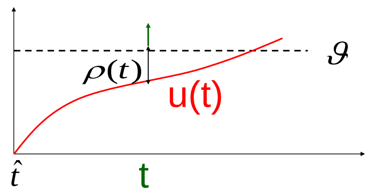
$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$

Now:
Escape noise!

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

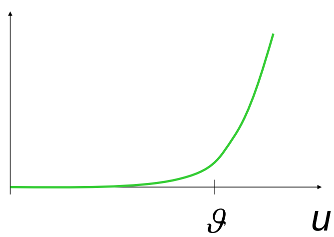
11.4 Escape noise

escape process



escape rate

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



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

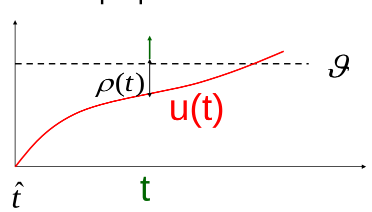
Example: leaky integrate-and-fire model

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

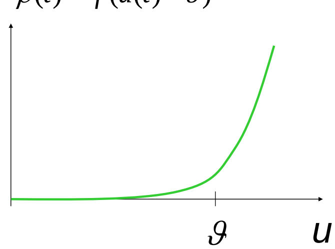
$$if\ spike\ at\ t^f \Rightarrow u\left(t^f + \delta\right) = u_r$$

11.4 stochastic intensity

escape process



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



Escape rate = stochastic intensity of point process

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

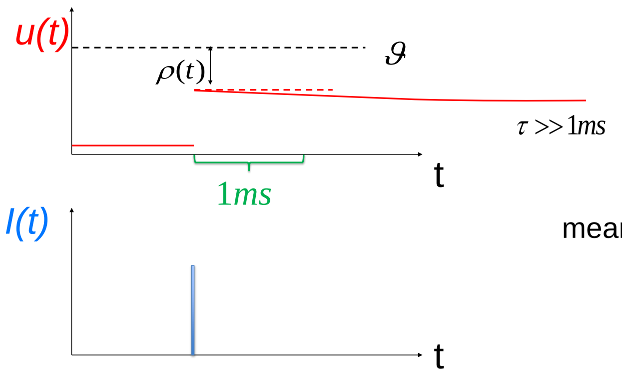
examples

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

$$\rho(t) =$$

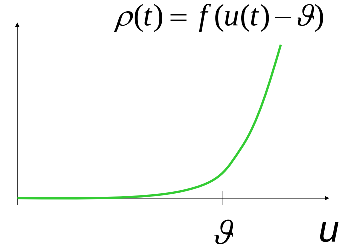
11.4 mean waiting time

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



escape rate

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



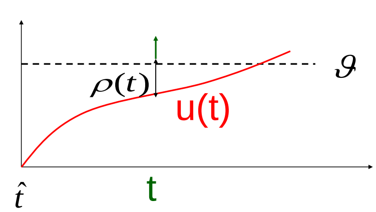
mean waiting time, after switch

Blackboard,
Math detour

11.4 escape noise/stochastic intensity

Escape rate = stochastic intensity
of point process

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



Quiz 4

Escape rate/stochastic intensity in neuron models

[ ] The escape rate of a neuron model has units one over time
[ ] The stochastic intensity of a point process has units one over time
[ ] For large voltages, the escape rate of a neuron model always saturates at some finite value
[ ] After a step in the membrane potential, the mean waiting time until a spike is fired is proportional to the escape rate
[ ] After a step in the membrane potential, the mean waiting time until a spike is fired is equal to the inverse of the escape rate
[ ] The stochastic intensity of a leaky integrate-and-fire model with reset only depends on the external input current but not on the time of the last reset
[ ] The stochastic intensity of a leaky integrate-and-fire model with reset depends on the external input current AND on the time of the last reset

Biological Modeling of Neural Networks

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

Week 11 – Variability and Noise: Autocorrelation

Wulfram Gerstner

EPFL, Lausanne, Switzerland

11.1 Variation of membrane potential
- white noise approximation

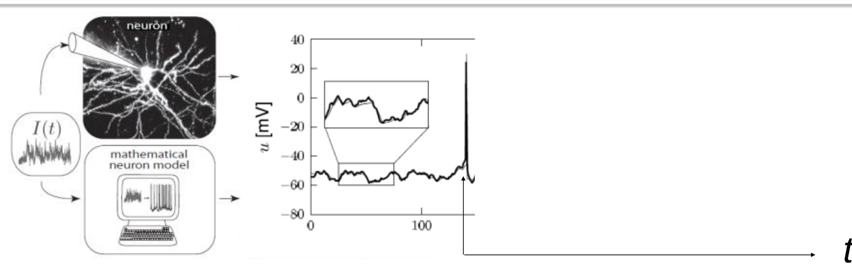
11.2 Autocorrelation of Poisson

11.3 Noisy integrate-and-fire
- superthreshold and subthreshold

11.4 Escape noise
- stochastic intensity

11.5 Renewal models

11.5. Interspike Intervals for time-dependent input



deterministic part of input

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

Example:
nonlinear integrate-and-fire model

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

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

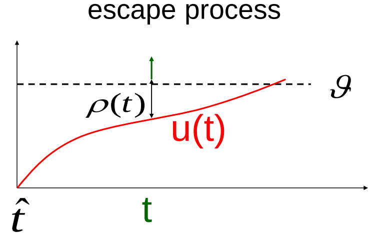
noisy part of input/intrinsic noise
→ *escape rate*

Example:
exponential stochastic intensity

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

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

escape process



escape rate

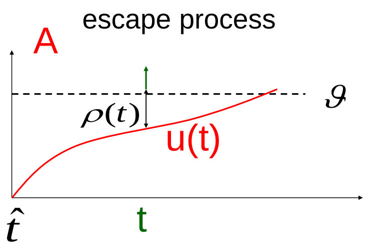
$$\rho(t) = f(u(t) - \vartheta)$$

Blackboard

Survivor function

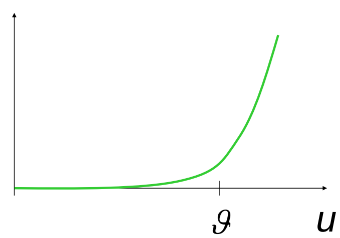
$$\tfrac{d}{dt} S_I(t|\hat{t}) = -\rho(t)\, S_I(t|\hat{t})$$

11.5. Interspike Intervals



escape rate

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



Survivor function

Examples now

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

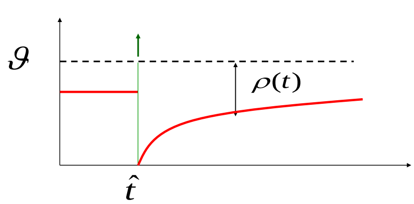
$$S_I(t|\hat{t}) = \underbrace{\exp(-\int_{\hat{t}}^{t} \rho(t')dt')}$$

Interval distribution

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

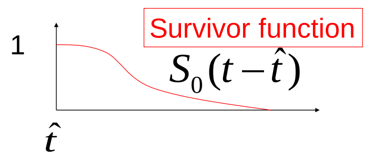
11.5. Renewal theory

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

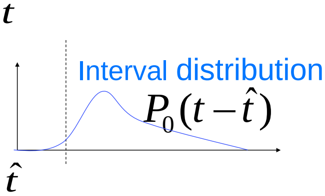


escape rate

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



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

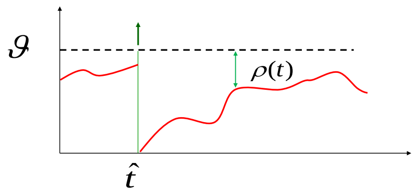


$$P(t|\hat{t}) = \rho(t|\hat{t}) \exp(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})dt')$$

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

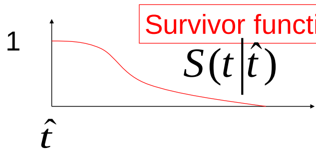
11.5. Time-dependent Renewal theory

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

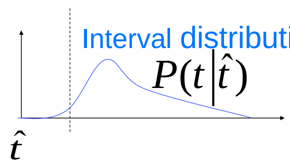


escape rate

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



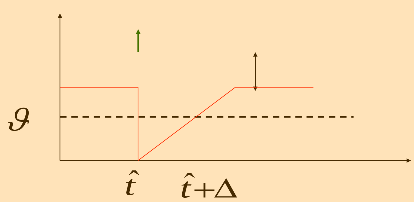
$$S(t|\hat{t}) = \exp(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})dt')$$



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

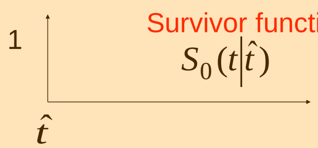
Homework assignement: Exercise 4

neuron with relative refractoriness, constant input

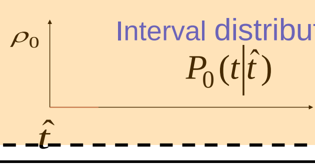


escape rate

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



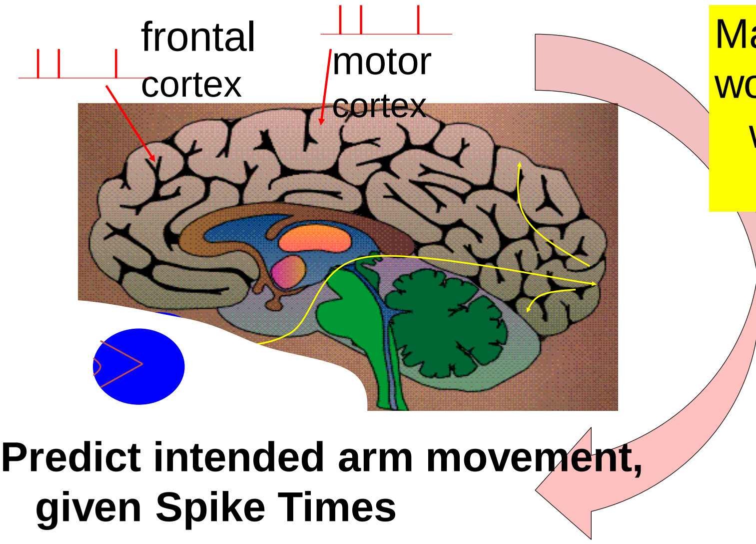
$$S_0(t|\hat{t}) = \{$$



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

Outlook: Helping Humans

Application: Neuroprosthetics



Many groups world wide work on this problem!

Model of 'Decoding'

Predict intended arm movement, given Spike Times

11.5. Renewal process, firing probability

THE END

Escape noise = stochastic intensity

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

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

→ basis for modern methods of neuron model fitting