Population Rate Models and Coding : Transients, PSTH, and reverse correlations

Lecture 11
Course: *Neural Networks and Biological Modeling*

Coding properties
single neuron vs population
forward correlation and PSTH

Book: Spiking Neuron Models, Chapter 7.4

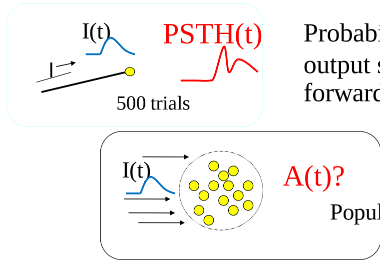
Reverse correlation
reverse correlation and optimal stimulus
reverse correlation and filter properties

Population dynamics
Transients and noise models

Wulfram Gerstner
EPFL

Book: Spiking Neuron Models, Chapter 6.3, 7.1, 7.2

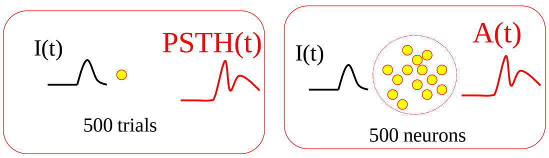
Coding Properties of Spiking Neuron Models



Probability of
output spike ?
forward correlation

Population activity?

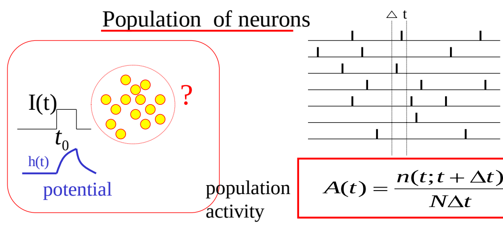
Theoretical Approach



- population dynamics
- response to single input spike (forward correlation)

Use population models to understand PSTH

Population of neurons



population activity

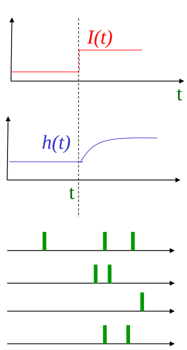
$$A(t) = \frac{n(t;t+\Delta t)}{N\Delta t}$$

N neurons,
- same type (e.g., excitatory)
---> population response ?

A - Poisson Neurons?

B - Integrate-and-fire neurons (e.g., SRM)?

Example: Poisson Neuron



Probability to fire spike in Δt

$$P(t;t+\Delta t) = \rho(t)\,\Delta t$$

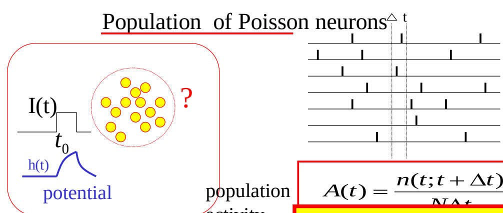
$$\tau \frac{d}{dt} h(t) = -h(t) + R\,I(t)$$

instantaneous rate

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

Blackboard

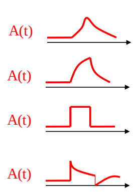
Population of Poisson neurons



population activity

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

Students – what is correct?



$$\tau \frac{d}{dt} A(t) = -A(t) + g(h(t))$$

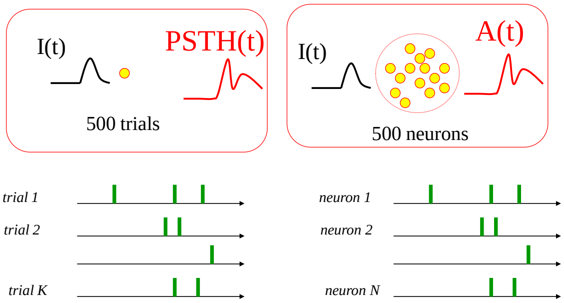
$$A(t) = g(h(t)) = g(\int \kappa(s) I(t-s) ds)$$

$$A(t) = g(I(t))$$

Poll!!!

$$A(t) = g(I(t), I'(t))$$

Example: Poisson Neuron

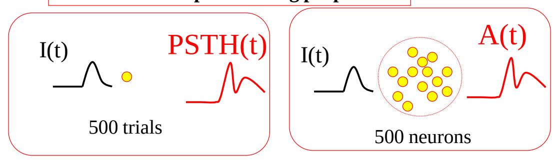


$\langle N_{sp}(t;t+\Delta t) \rangle = K \cdot \rho(t)\, \Delta t$

$PSTH(t) = \frac{N_{sp}}{K\, \Delta t} = \rho(t)$

$A(t) = \left\langle \frac{N_{sp}(t;t+\Delta t)}{N\, \Delta t} \right\rangle = \rho(t)$

Measures of temporal coding properties:

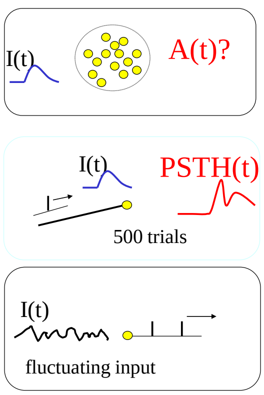


- **-Peri-Stimulus Time Histogram (PSTH)** (single neuron, several repetitions)
- **-Population activity *A(t)*** (population of neurons, single trial)
- **-Reverse correlation**

Identical for homogeneous population

(this statement holds for all neuron models, Not only Poisson neurons)

Coding Properties of Spiking Neuron Models



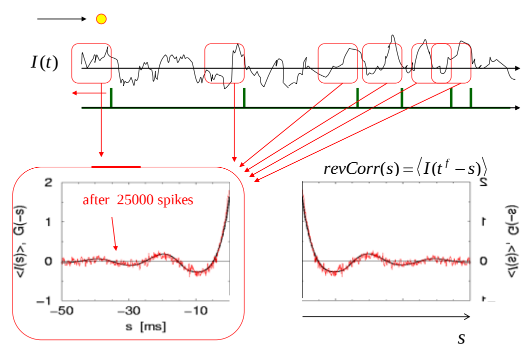
Probability of output spike (given *I(t)*)?

forward correlation

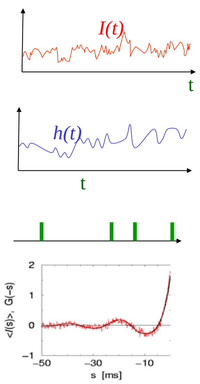
reverse correlation

Typical input (given *output spike*)?

Reverse-Correlation (schematic)



Example:reverse correlation for linear Poisson Neuron



Probability to fire spike in Δt

$P(t;t+\Delta t) = \rho(t)\, \Delta t$

instantaneous rate

$\rho(t) = h(t) = \int \kappa(s) I(t-s) ds$

Claim: spike triggered average of input

$revCorr(s) = \langle I(t^f - s) \rangle$

is the best stimulus to trigger a spike

Step 1: best stimulus is propto $I_1(t) = \kappa(-t)$ *now Exerc*

Step 2: revCorr $\langle I(t^f - s) \rangle = \kappa(s)$

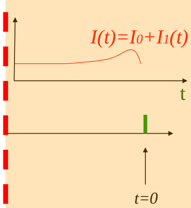
Exercise 1 NOW: Reverse correlation=optimal stimulus

Linear Poisson Neuron

Probability to fire spike in Δt

$P(t;t+\Delta t) = \rho(t)\, \Delta t$

instantaneous rate



$\rho(t) = h(t) = \int \kappa(s) I(t-s) ds$

$= \sum_n \kappa_n I(t - n\Delta t)$

Next lecture 10h15

Show that the optimal stimulus to generate a spike at t=0 under a constraint

$\int I_1^2(t) dt = const$

is

$I_1(t) \propto \kappa(-t)$

Population Rate Models and Coding : Transients, PSTH, and reverse correlations

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Coding properties
single neuron vs population
forward correlation and PSTH

Reverse correlation
reverse correlation and optimal stimulus
reverse correlation and filter properties

Population dynamics
Transients and noise models

Wulfram Gerstner
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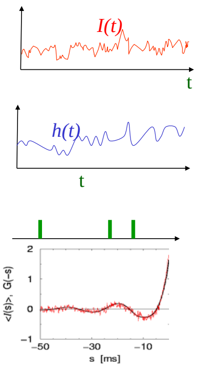
Example: reverse Correlation for linear Poisson Neuron



Probability to fire spike in Δt

$P(t;t+\Delta t)=\rho(t)\;\Delta t$

instantaneous rate

$\rho(t)=h(t)=\int \kappa(s) I(t-s) ds$

$=\sum_n \kappa_n I(t-n\Delta t)$

Blackboard

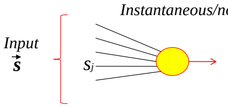
Step 2: Linear (or nonlinear)
Poisson model,
White noise input, mean zero,
Circular distribution

$\mathrm{RevCorr}(s)=\kappa(-s)$

Reverse correlations: space only

Blackboard

Instantaneous/no time



Prob(spike| $\vec{s}$ *) =p(*$\vec{s}$*)*

$p(\vec{s})=g(\sum_j k_j s_j)=g(\vec{k}^T\vec{s})$

Linear-Nonlinear-Poisson Model (LNP)

$revCorr(\vec{s})=\vec{k}$

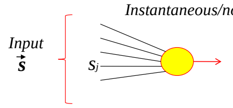
Schwartz&Simoncelli, 2001

Holds even for non-linear Poisson model

Reverse correlations: space only

Instantaneous/no time

Linear-Nonlinear-Poisson Model (LNP)



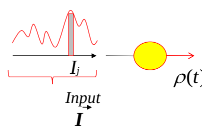
Prob(spike| $\vec{s}$ *) =p(*$\vec{s}$*)*

$p(\vec{s})=g(\sum_j k_j s_j)=g(\vec{k}^T\vec{s})$

Reverse correlations: time only

$revCorr(\vec{s})=\vec{k}$

$revCorr(\vec{I})=\vec{k}$



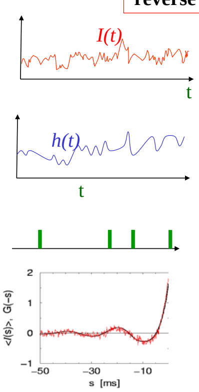
instantaneous rate

$\rho(t)=g(h(t))=g(\int \kappa(s) I(t-s) ds)$

$=g(\sum_j \kappa_j I_j(t-n\Delta t))$

$=g(\sum_j k_j I_j)=g(\vec{k}^T\vec{I})$

reverse correlation for linear Poisson Neuron



Probability to fire spike in Δt

$P(t;t+\Delta t)=\rho(t)\;\Delta t$

instantaneous rate

$\rho(t)=h(t)=\int \kappa(s) I(t-s) ds$

Claim: spike triggered average of input

$revCorr(s)=\langle I(t^f-s)\rangle$

is the best stimulus to trigger a spike

Step 1: best stimulus is propto $I_1(t)=\kappa(-t)$ ✓

Step 2: revCorr $\langle I(t^f-s)\rangle=\kappa(s)$ ✓

Exercise: Reverse correlation and PSTH and popul. response

Consider a spiking neuron with the following features:

An input spike evokes at time t_f *evokes a current*

$\tau_s \frac{d}{dt} i(t)=-i(t)+\delta(t-t_f)$

Synaptic current i(t) evokes a potential

$\tau \frac{d}{dt} h(t)=-h(t)+i(t)$

Probability to fire spike in Δt *is*

$P(t;t+\Delta t)=\rho(t)\;\Delta t$

With $\rho(t)=h(t)$

Next lecture 11h15

a) Calculate the PSTH in response to a single input spike at time t_0

b) Calculate the RevCorr under the assumption of random spike arrival

c) Calculate the response of a population of these neurons to a change in the spike arrival rate from r_0 *to* r_1

Population Rate Models and Coding :
Transients, PSTH, and reverse correlations

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Wulfram Gerstner
EPFL

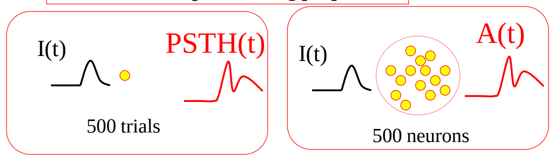
Coding properties
single neuron vs population
forward correlation and PSTH

Reverse correlation
reverse correlation and optimal stimulus
reverse correlation and filter properties

→ **Population dynamics**
Poisson vs. Integrate-and-fire/SRM
Transients and noise models
Population activity (integral equation approach)

Book:
W. Gerstner and W. Kistler,
Spiking Neuron Models,
Chapter 6.3, 7.1, 7.2

Measures of temporal coding properties:



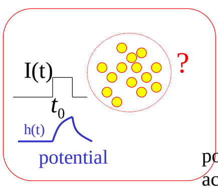
-**Peri-Stimulus Time Histogram (PSTH)**
(single neuron, several repetitions)
-**Population activity** ***A(t)***
(population of neurons, single trial)

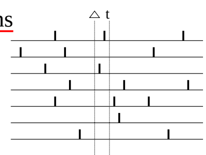
-**Reverse correlation**
for linear Poisson neuron,
all three measure the filter k

Identical for homogeneous population

(this statement holds for all neuron models, Not only Poisson neurons)

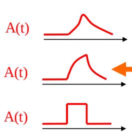
Population of neurons





population activity

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



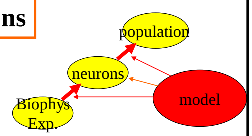
$$\tau \frac{d}{dt} A(t) = -A(t) + g(h(t))$$

$$A(t) = g(h(t)) = g(\int \kappa(s) I(t-s) ds)$$

$$A(t) = g(I(t))$$

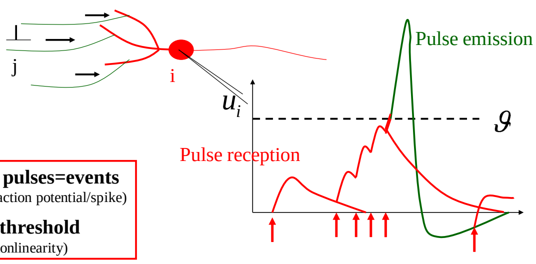
Poisson neuron model

Population dynamics of spiking model neurons

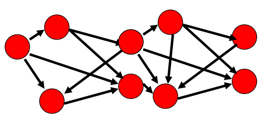


1. Neuron model
   → -Spike/threshold
2. Population dynamics
   -Population effects: rapid transient
   -Neuron models with escape noise
   -Population equations
3. Application to Coding
   -Rapid signaling
   -PSTH
   -Reverse correlation

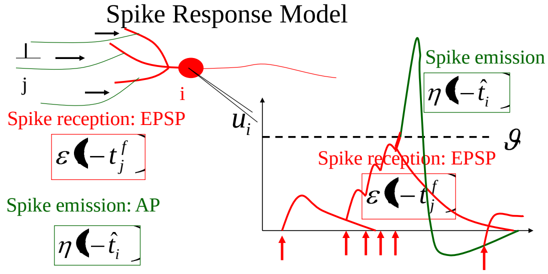
Simple neuron model



- **pulses=events**
  (action potential/spike)
- **threshold**
  (nonlinearity)



Spike Response Model

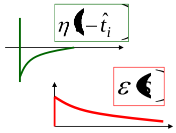


Last spike of i   All spikes, all neurons

$$u_i(t) = \eta(t-\hat{t}_i) + \sum_j \sum_f w_{ij}\, \varepsilon(t-t_j^f)$$ linear

$$u_i(t) = \vartheta \Rightarrow \text{Firing: } \hat{t}_i = t$$ threshold

Spike Response Model



Spike emission: AP

Response to current pulse

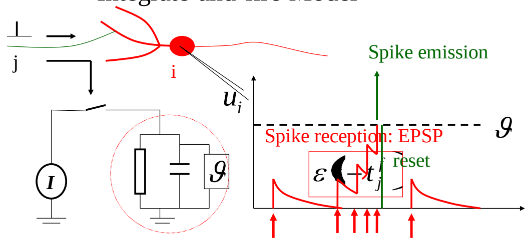
potential Last spike of i external input

$$u_i(t) = \underline{\eta(t-\hat{t}_i)} + \underbrace{\int \varepsilon(t-\hat{t}_i, s) I(t-s) ds}_{\text{input potential}}$$

potential

$$u(t|\hat{t}) = \underline{\eta(t-\hat{t})} + \underline{h(t)}$$

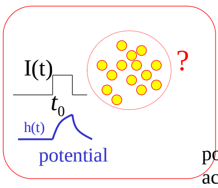
Integrate-and-fire Model

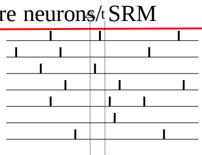


$$\tau \cdot \frac{d}{dt} u_i = -u_i + RI(t) \quad \text{linear}$$

$$u_i(t) = \vartheta \Rightarrow \text{Fire+reset} \quad \text{threshold}$$

Population of Integrate-and-Fire neurons/SRM

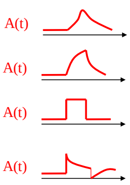




population activity

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

Students – what is correct?



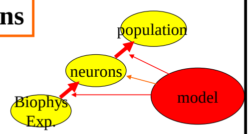
$$\tau \frac{d}{dt} A(t) = -A(t) + g(h(t))$$

$$A(t) = g(\underline{h(t)}) = g\left(\int \kappa(s) I(t-s) ds\right)$$

$$A(t) = g(\underline{I(t)})$$

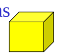
$$A(t) = g(I(t), I'(t))$$

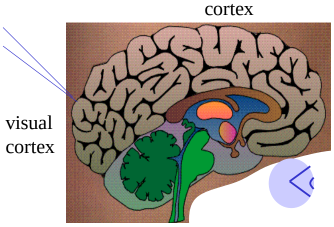
Population dynamics of spiking model neurons



1. Neuron model
   - -Spike/threshold
2. Population dynamics
   - -Population effects: rapid transients
   - -Neuron models with escape noise
   - -Population equations
3. Application to Coding
   - -Rapid signaling
   - -PSTH
   - -Reverse correlation

~10 000 neurons
~3 km wires
populations/columns
~1000 local inputs
~15% connectivity
excitatory/inhibitory





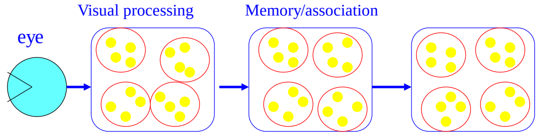
How fast is neuronal signal processing?

animal -- no animal

Simon Thorpe *Nature*, 1996

psychophysical experiment
30 images in 30 seconds

Show video



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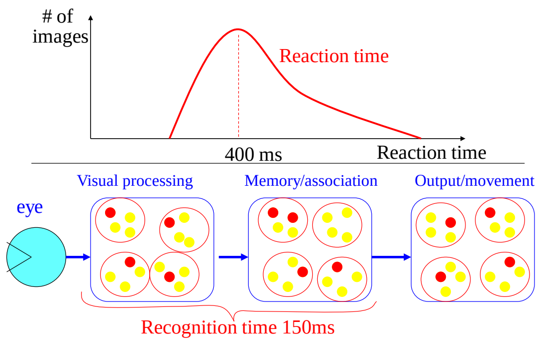
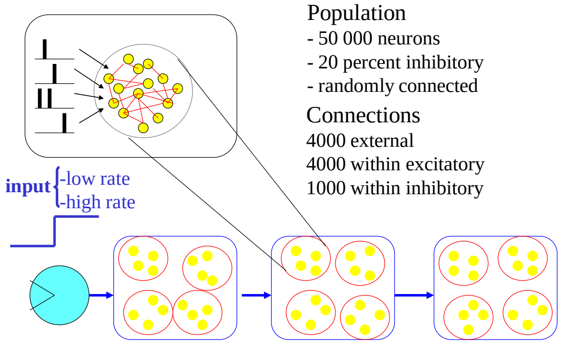


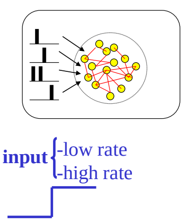
Signal transmission in populations of neurons

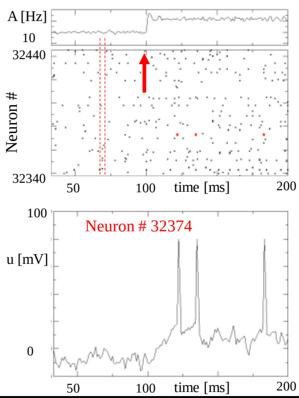


Population
- 50 000 neurons
- 20 percent inhibitory
- randomly connected

Connections
4000 external
4000 within excitatory
1000 within inhibitory

Signal transmission in populations of neurons





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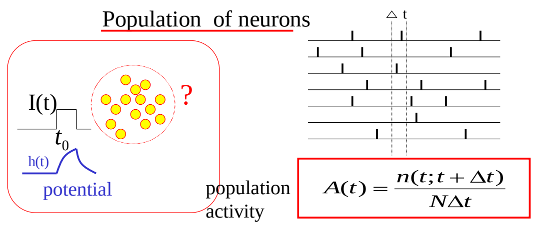


population activity

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

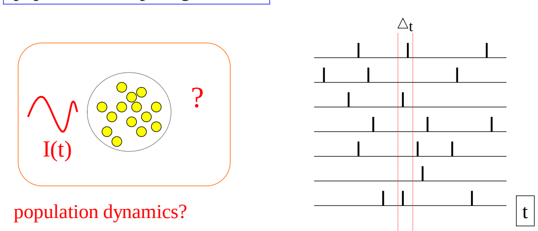
$$\tau \frac{d}{dt} A(t) = -A(t) + g(h(t))$$

$$A(t) = g(h(t)) = g\left(\int \kappa(s) I(t-s) ds\right)$$

$$A(t) = g(I(t))$$

$$A(t) = g(I(t), I'(t))$$

populations of spiking neurons



population dynamics?

population activity

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

Population dynamics of spiking model neurons

1. Neuron model
   - -Spike/threshold
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3. Application to Coding
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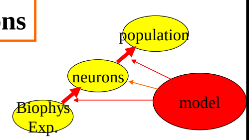
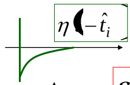
   - -Reverse correlation

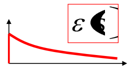


Analysis: Homogenous population (no coupling)

Spike emission: AP



Response to current pulse



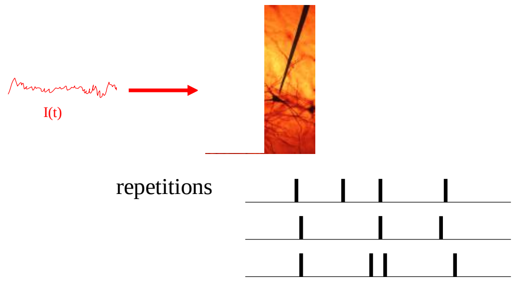
potential Last spike of i external input

$$u_i(t) = \underbrace{\eta(t-\hat{t}_i) + \int \varepsilon(s) I(t-s)\,ds}_{\text{input potential}}$$

potential

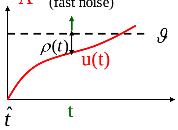
$$u(t|\hat{t}) = \eta(t-\hat{t}) + h(t)$$

Noise and unreliability



Noise models

A escape process (fast noise)



escape rate

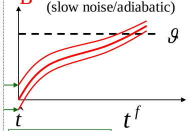
$$\rho(t) = f(u(t)-\vartheta)$$

Interval distribution

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

escape rate

B parameter changes (slow noise/adiabatic)



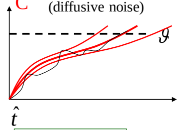
stochastic reset

Interval distribution

$$P_I(t|\hat{t}) = G_\sigma(t-t^f)$$

Gaussian about t^f

C stochastic spike arrival (diffusive noise)



noisy integration

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

noise

white (fast noise)

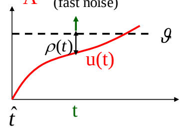
synapse (slow noise)

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

(Plesser&Gerstner 2000)
(Brunel et al., 2001)

Noise models

A escape process (fast noise)



escape rate

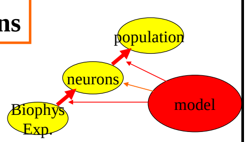
$$\rho(t) = f(u(t)-\vartheta)$$

Interval distribution

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

escape rate

Population dynamics of spiking model neurons



1. Neuron model
   - -Spike/threshold
2. Population dynamics
   - -Population effects: rapid transients
   - -Neuron models with escape noise
   - → -Population equations
3. Application to Coding
   - -Rapid signaling

Population Dynamics

$$\boxed{A(t) = \int_{-\infty}^{t} P_I(t|\hat{t})\,A(\hat{t})\,d\hat{t}}$$

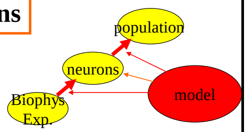
Time Dependent Interval Distribution

Blackboard

Normalization condition, with survivor function

$$\boxed{1 = \int_{-\infty}^{t} S_I(t|\hat{t})\,A(\hat{t})\,d\hat{t}}$$

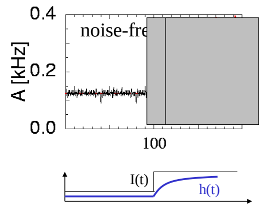
Population dynamics of spiking model neurons



1. Neuron model
   -Spike/threshold
2. Population dynamics
   -Population effects: rapid transients
   -Neuron models with escape noise
   -Population equations
3. Application to Coding
   -Rapid signaling

Rapid transients

no noise



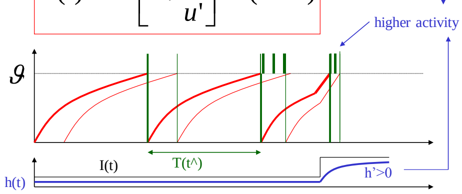
Population Dynamics

$$A(t) = \int_{-\infty}^{t} P_I(t|\hat{t})\, A(\hat{t})\, d\hat{t}$$

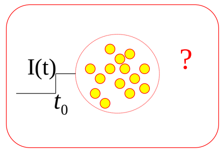
Example: noise-free $P_I(t|\hat{t}) = \delta(t-\hat{t}-T(\hat{t}))$

Blackboard *(and exerc. 3)*

$$A(t) = \left[1+\frac{h'}{u'}\right]\cdot A(t-T)$$



Theory of transients



noise-free

$$A(t) = \left[1+\frac{h'}{u'}\right]\cdot A(t-T)$$

potential

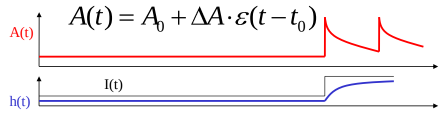
$$u(t|\hat{t}) = \eta(t-\hat{t}) + \underbrace{\int \varepsilon(s)\, I(t-s)\, ds}_{\text{input potential}}$$

External input, step current
No lateral coupling

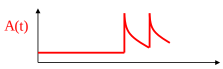
Blackboard

input potential $h(t) \longrightarrow h'(t) = \varepsilon(t-t_0)$

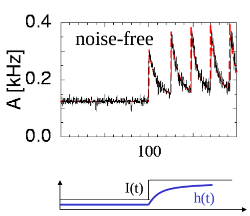
$$A(t) = A_0 + \Delta A \cdot \varepsilon(t-t_0)$$



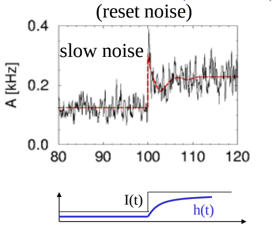
Theory of transients



no noise

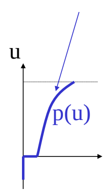


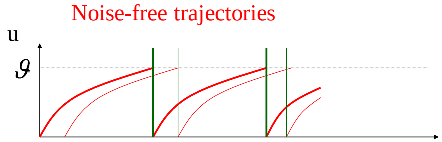
slow noise (adiabatic)
(reset noise)



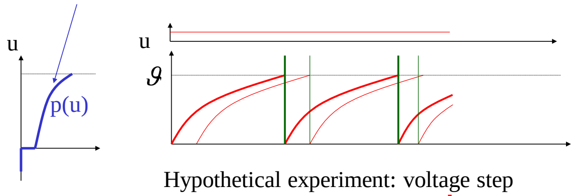
Membrane potential density

Noise-free trajectories

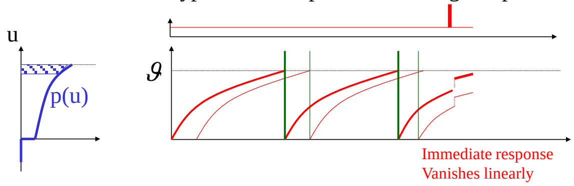




Membrane potential density



Hypothetical experiment: voltage step



Exercise 3 NOW!: population of noise-free SRM

Show: Population of noise-free SRM with threshold condition

$$SRM: \quad u(t) = \eta(t-\hat{t}) + h(t) = \vartheta$$

Population Dynamics

$$A(t) = \int_{-\infty}^{t} P_I(t|\hat{t}) A(\hat{t})\, d\hat{t}$$

ex 2,3 + miniproject 12h00

oise-free $P_I(t|\hat{t}) = \delta(t-\hat{t}-T(\hat{t}))$

Leads to

$$A(t) = \left[1 + \frac{h'}{u'}\right] \cdot A(t-T)$$

Hint:

$$\int f(x)\delta(x-x_0)dx = f(x_0)$$

$$\int f(x)\delta(g(x))dx = \int f(x(y))\delta(y)\frac{dx}{dy}dy$$