Noise and the Neural Code

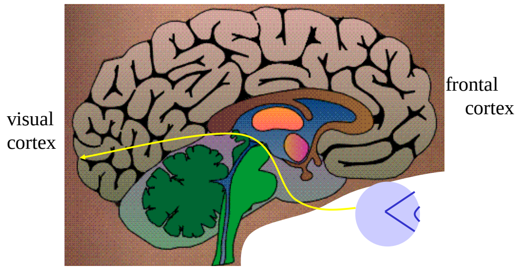
Lecture 8
of
Neural Networks and Biological Modeling

Wulfram Gerstner, EPFL

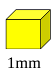
BOOK: Spiking Neuron Models,
W. Gerstner and W. Kistler
Cambridge University Press, 2002

Chapters 1.4-1.6 and 5.1-5.2

The Brain – macrosopic view

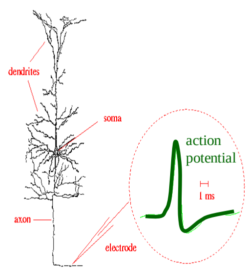


The Brain – microsopic view

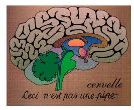


10 000 neurons
3 km wires

Signal:
action potential (spike)

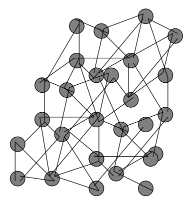


The Brain: a highly connected system



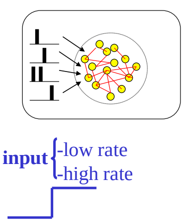
Brain

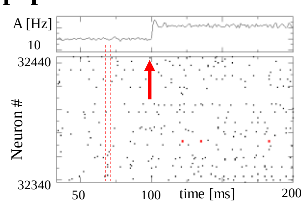
High connectivity:
systematic, organized in local populations
but **seemingly random**



Distributed architecture
10^{10} neurons
10^{4} connections/neurons

Random firing in a population of neurons





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

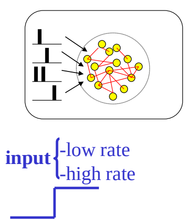
Brunel, J. Comput. Neurosc. 2000
Mayor and Gerstner, Phys. Rev E. 2005

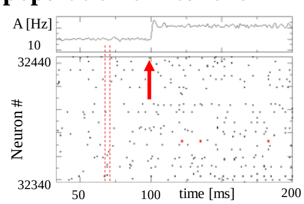
Population activity

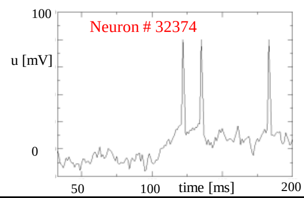
$$A(t) = \frac{n(t;t+\Delta t)}{N_{pop}\,\Delta t}$$

Average
(over a population of N_{pop} neurons)
of the number of spikes
per time bin (e.g. $\Delta t = 2$ms)

Random firing in a population of neurons



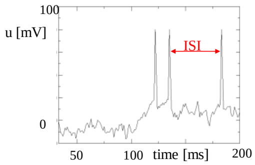


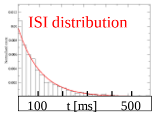


Population
- 50 000 neurons
- 20 percent inhibitory
- **randomly connected**

Variability of spike trains =noise?

- Variability of interspike intervals (ISI)



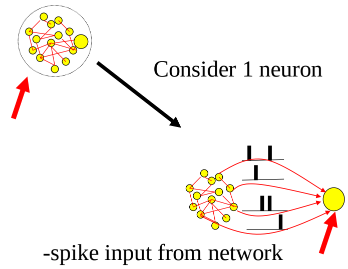


Variability of spike trains:
broad ISI distribution

Brunel,
J. Comput. Neurosc. 2000
Mayor and Gerstner,
Phys. Rev E. 2005
Vogels and Abbott,
J. Neuroscience, 2005

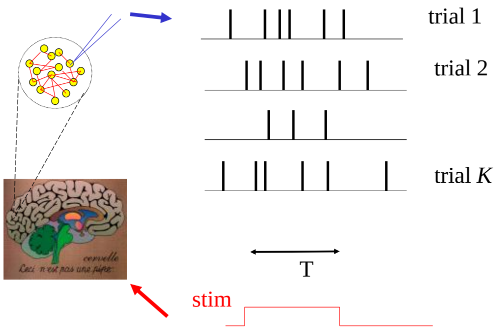
here in simulations, but
also in vivo

Input to a single neuron



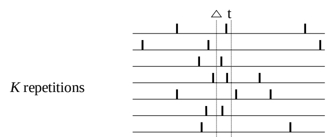
-spike input from network
-externally controlled experimental stimulus

Variability of spike trains across repetitions

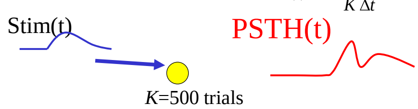


Variability of spike trains =noise?

- Variability across repetitions



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



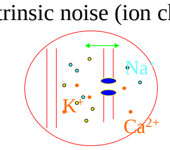
Lecture 8 – noise and the neural code

- Variability in the brain:
Variability=noise?

-Variability in the brain:
modeling the variability?

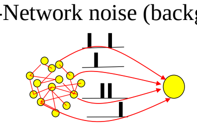
Variability of spike trains =noise?
sources of noise

- Intrinsic noise (ion channels)



-Finite number of channels
-Finite temperature

-Network noise (background activity)

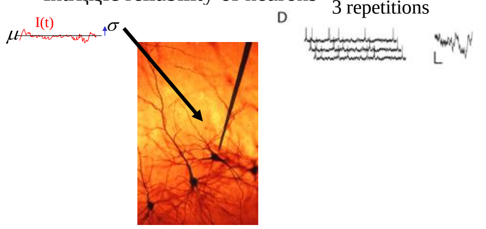


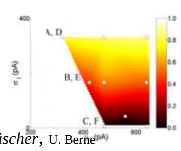
-Spike arrival from other neurons
-Beyond control of experimentalist

→ Check intrinisic noise by removing the network

Precise temporal coding of single neurons

Intrinsic reliability of neurons





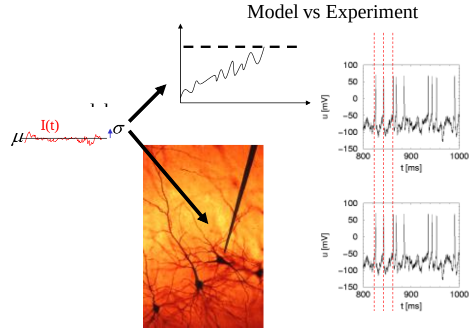
See also:
Mainen&Sejnowski, Science1995

Exp. Data:
A. Rauch, H.Lüscher, U. Berne

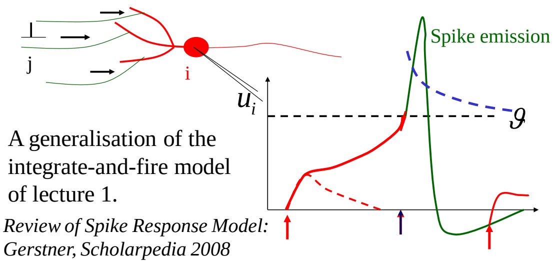
Precise temporal coding of single neurons

Intrinsic reliability of neurons

Model vs Experiment



Spike Response Model (SRM)



A generalisation of the integrate-and-fire model of lecture 1.

Review of Spike Response Model: Gerstner, Scholarpedia 2008

2 variables

potential

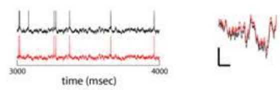
$$u(t) = \eta(t-\hat{t}) + \int_0^\infty \varepsilon(t-t',s) I(t-s)ds + \dots$$

$\vartheta(t)$ dynamic threshold

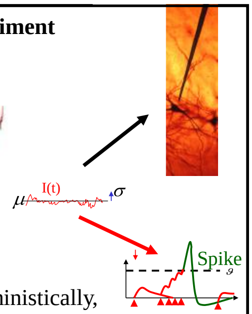
Compare SRM model with experiment

A

model vs exper.



Jolivet et al.,
J. Comput. Neurosci. (2006)

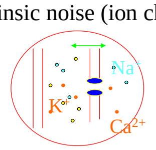


With time-dependent input currents,
- the neuron behaves nearly deterministically,
- can be predicted by simple neuron models,
- low intrinsic noise
- spikes can be predicted by SRM

Variability of spike trains =noise? sources of noise

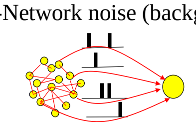
- Intrinsic noise (ion channels)

small effect



-Finite number of channels
-Finite temperature

-Network noise (background activity)



-Spike arrival from other neurons
-Beyond control of experimentalist

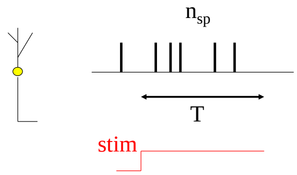
Presence of noise → limited neural coding power

Lecture 8 – noise and the neural code

- Variability in the brain: Variability=noise?

-Variability in the brain: modeling the variability?

Variability and Rate Coding



For constant stimulus, Interspike intervals vary

Rate $\quad \nu = \frac{n_{sp}(t;t+T)}{T}$

Rate defined as temporal average across stochastic spikes

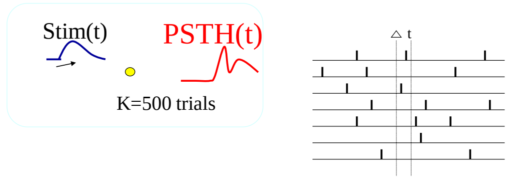
Only the mean number of spikes matters, timing irrelevant

Pure rate code = stochastic spiking → Poisson model

Variability across repetitions

Rate defined as average over stimulus repetitions

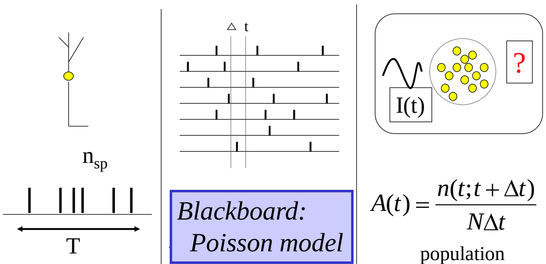
Peri-Stimulus Time Histogram



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

Pure rate code = stochastic spiking → Poisson model

The Problem of Neuronal Coding: Rate codes



Blackboard: Poisson model

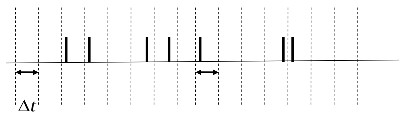
$$A(t) = \frac{n(t;t+\Delta t)}{N\Delta t}$$

population activity

Pure rate code = stochastic spiking → Poisson model

Homogeneous Poisson model: constant rate

Blackboard: Poisson model

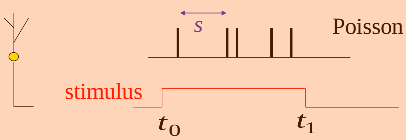


Probability of finding a spike $\quad P_F = \rho_0\,\Delta t$

Pure rate code = stochastic spiking → Poisson model

Exercise 1: Poisson neuron

Next lecture at 10:15

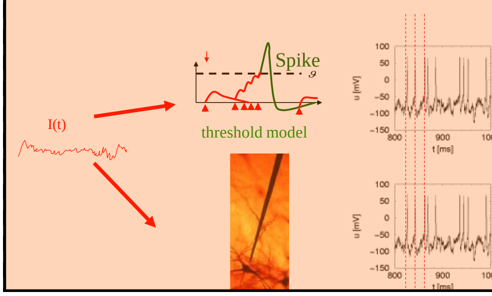


- Probability of NOT firing during time t?
- Interval distribution *p(s)?*
- How can we detect if rate switches from $\rho_0 \rightarrow \rho_1$

-2 neurons fire stochastically (Poisson) at 20Hz.
Percentage of spikes that coincide within +/-2 ms?

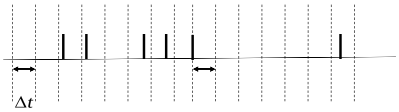
Exercise now:

2 neurons fire stochastically (Poisson) at 20Hz.
Percentage of spikes that coincide within +/-2 ms?



Homogeneous Poisson model: constant rate

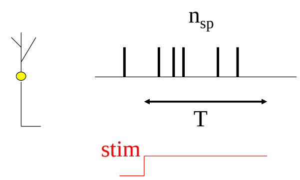
Blackboard: Solution of exercise Poisson model



Probability of finding a spike $P_F = \rho_0 \, \Delta t$

Pure rate code = stochastic spiking → Poisson model

The Problem of Neuronal Coding



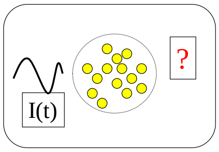
Rate $\nu = \frac{n_{sp}(t; t+T)}{T}$

Rate defined as temporal average of stochastic neuron

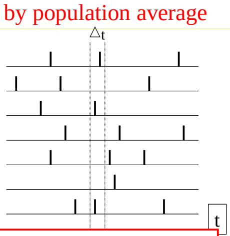
In order to decode/estimate the rate, several spikes are needed

CANNOT be the code: Reaction time!

The problem of neural coding:
population activity - rate defined by population average



population dynamics?

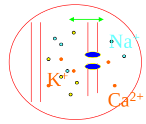


population activity $A(t) = \frac{n(t; t+\Delta t)}{N \Delta t}$

Pure rate code = stochastic spiking → Poisson model

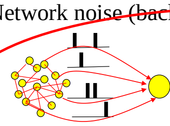
Variability of spike trains =noise?
sources of noise

- Intrinsic noise (ion channels)



-Finite number of channels
-Finite temperature

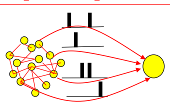
-Network noise (background activity)

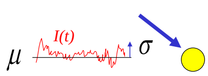


-Spike arrival from other neurons
-Beyond control of experimentalist

Analyze the effect

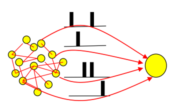
Compare: Input from the network





Fluctuating input current

Input from the network



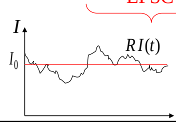
Assumption of Stochastic spike arrival:
network of exc. neurons,
total spike arrival rate ν_k

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

Synaptic current pulses of shape α

$$R I^{syn}(t) = \sum_k w_k \underbrace{\sum_f \alpha(t - t_k^f)}_{\text{EPSC}}$$

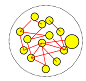
Blackboard: sum of EPSCs



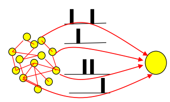
$$I^{syn}(t) = I_0 + I^{fluct}(t)$$

-Noise in the brain
-Variability=noise?
-Noise in a passive membrane
-Noise in Integrate-and-fire

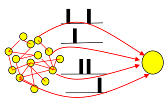
Input to a single neuron: stochastic spike arrival



Consider 1 neuron



Input from the network

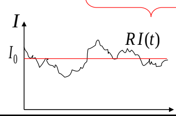


Assumption of Stochastic spike arrival:
network of exc. neurons,
total spike arrival rate ν_k

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

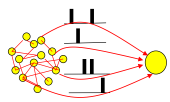
Synaptic current pulses of shape α

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



Blackboard: mean current

Homogeneous network (I&F)



Assumption of Stochastic spike arrival:
network of exc. neurons,
spike arrival rate ν_k

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

Synaptic current pulses of shape α

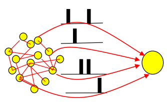
$$RI^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$

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

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

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

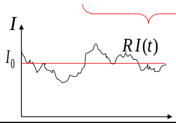
Input to a single neuron



Assumption of Stochastic spike arrival:
in network of exc. neurons,
total spike arrival rate *A(t)*

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

$$RI(t) = R\,[I_o + I_{noise}]$$

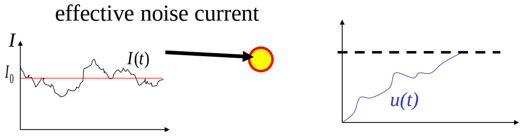


noise in neuron models

-Noise in the brain
-Variability=noise?
-Noise in a passive membrane
-Noise in Integrate-and-fire

stochastic spike arrival in I&F

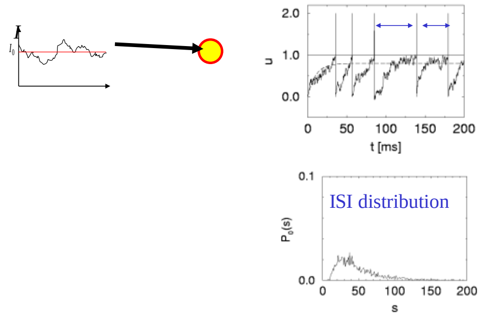
effective noise current



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

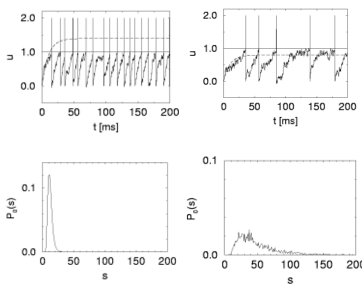
$$I(t) = I_o + I_{noise}$$

stochastic spike arrival in I&F – interspike intervals

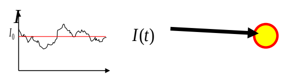


Diffusive noise (stochastic spike arrival)

Superthreshold vs. Subthreshold regime



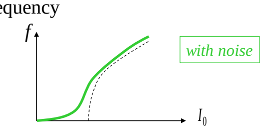
effective noise current



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

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

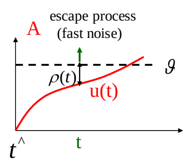
frequency



noise in neuron models

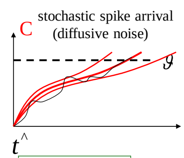
-Noise in the brain
-Variability=noise?
-Noise in a passive membrane
-Noise in Integrate-and-fire
- mathematical noise models

Noise models



escape rate

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

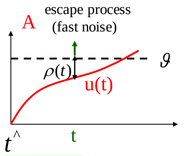


noisy integration

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

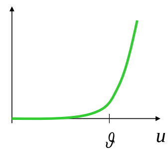
Blackboard:

Escape noise model



escape rate

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



Survivor function

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

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

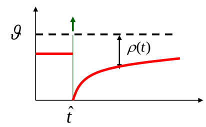
Interval distribution

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

Blackboard:

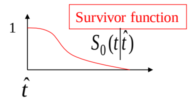
Escape Noise (noisy threshold)

Example 2): I&F with reset, constant input, exponential escape rate

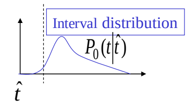


escape rate

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



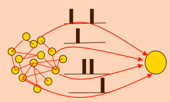
$$S(t|\hat{t}) = \exp\left(-\int_{\hat{t}}^{t} \rho(t'|\hat{t})dt'\right)$$



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

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

Exercise: calculate mean voltage u_0

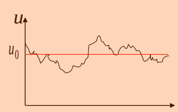


Assumption of Stochastic spike arrival:
network of exc. neurons,
total spike arrival rate ν_k

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

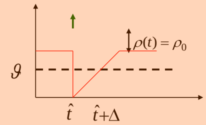
$$R I^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$

In-class exercise now
11:45-12:45



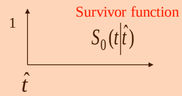
Escape Noise - exercise 3 now

Example 1): neuron with relative refractoriness, constant input

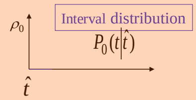


escape rate

$$\rho(t) = f(u(t) - \vartheta) = \begin{cases} \rho_0\,(u(t) - \vartheta) & for\, u(t) > \vartheta \\ 0 & for\, u(t) < \vartheta \end{cases}$$



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



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

In-class exercise and
Discussion of miniproj

The end