Freie Universität Berlin

Neuroinformatics and Theoretical Neuroscience
Institute of Biology – Neurobiology

bccn berlin

Bernstein Center for
Computational Neuroscience

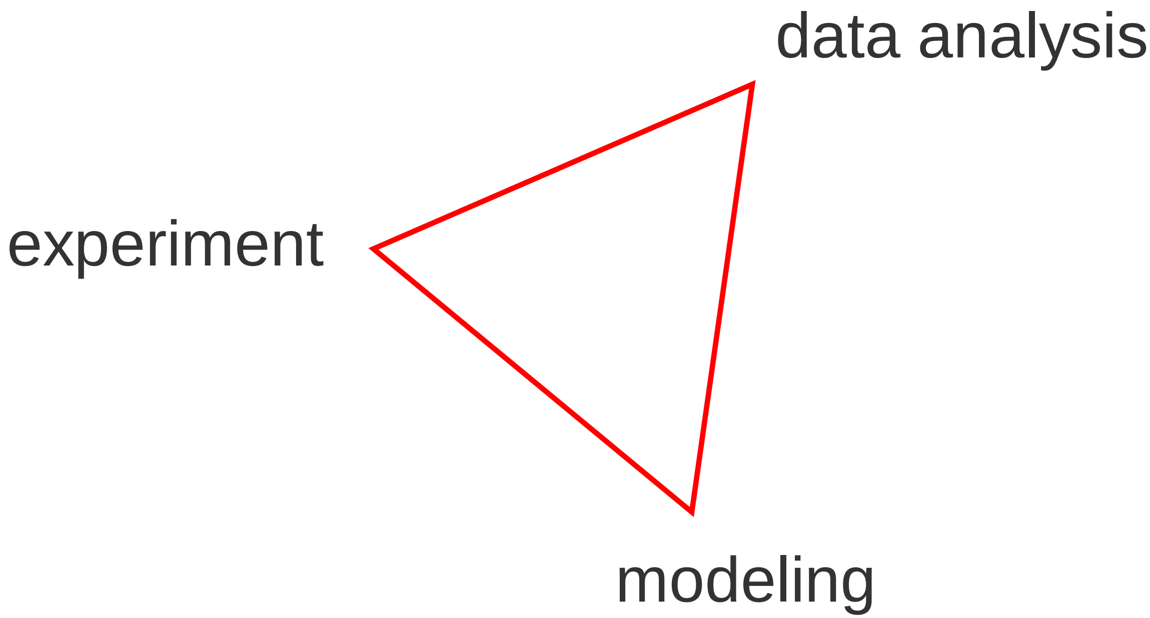
Introductory Lecture

Single Neuron Analysis

Stochastic Point Processes | Spike Train Statistics

Martin Nawrot

Graduate Course: SPP 1665, FZJ Jülich, Nov 26, 2014


data analysis
experiment
modeling

Part I : Stochastic Point Processes

1. Experimental Spike Trains

2. Stochastic Point Processes

Part I : Stochastic Point Processes

1. Experimental Spike Trains

2. Stochastic Point Processes

Part II : Spike Train Statistics

3. Firing Rate Estimation

4. Empirival Interval and Count Statistics
- Coefficient of Variation (CV) of the ISIs
- Fano Factor (FF) of the spike count

5. Combined Analysis FF vs. CV, real world data
- effect serial interval correlation
- across trial non-stationaritz of data

1. Experimental Spike Trains

- intracellular recording
- extracellular recording
- spike sorting
- spike train representation

Recording Techniques | electrophysiology vs. imaging

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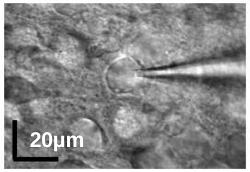
electrophysiology

- direct measurement of neuronal signals

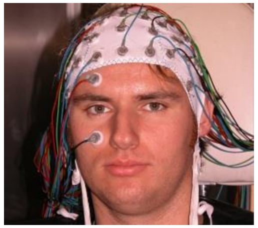


intracellular recording from
- single neurons / dendrites

extracellular recording of
- action potentials (SUA/MUA) *and*
- local field potential (LFP, indirect)

- measurement of electric mass signals

electrocorticography (ECoG)
- epicortical field potentials

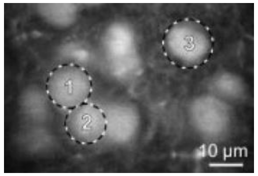


electroencephalography (EEG)

magnetoencephalography (MEG)

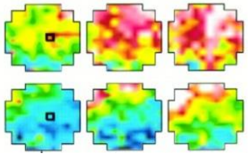
imaging

- visualization of single neuron activity

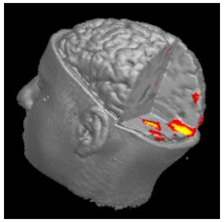


optical imaging of intracellular Ca activity
- *in vitro* / *in vivo*
- 2D / 3D

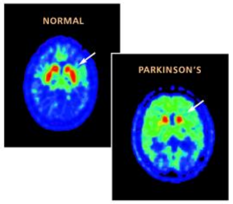
- visualization of average activity



optical imaging with voltage sensitive dyes



functional magnetic resonance imaging (fMRI)



positron emission tomography (PET)

© Clemens Boucsein

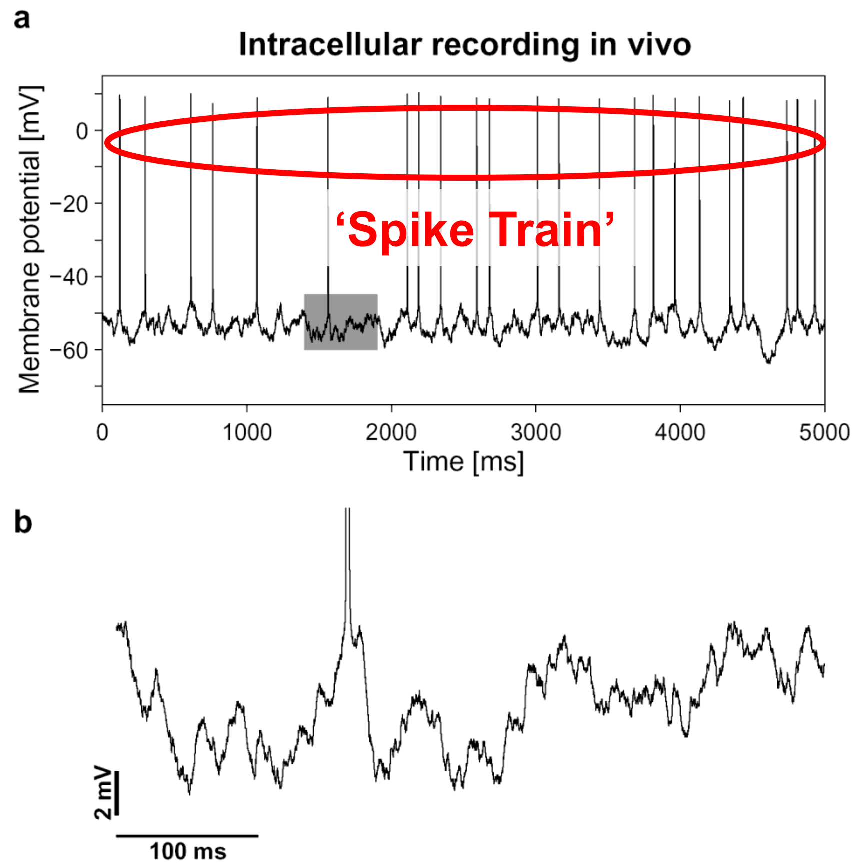
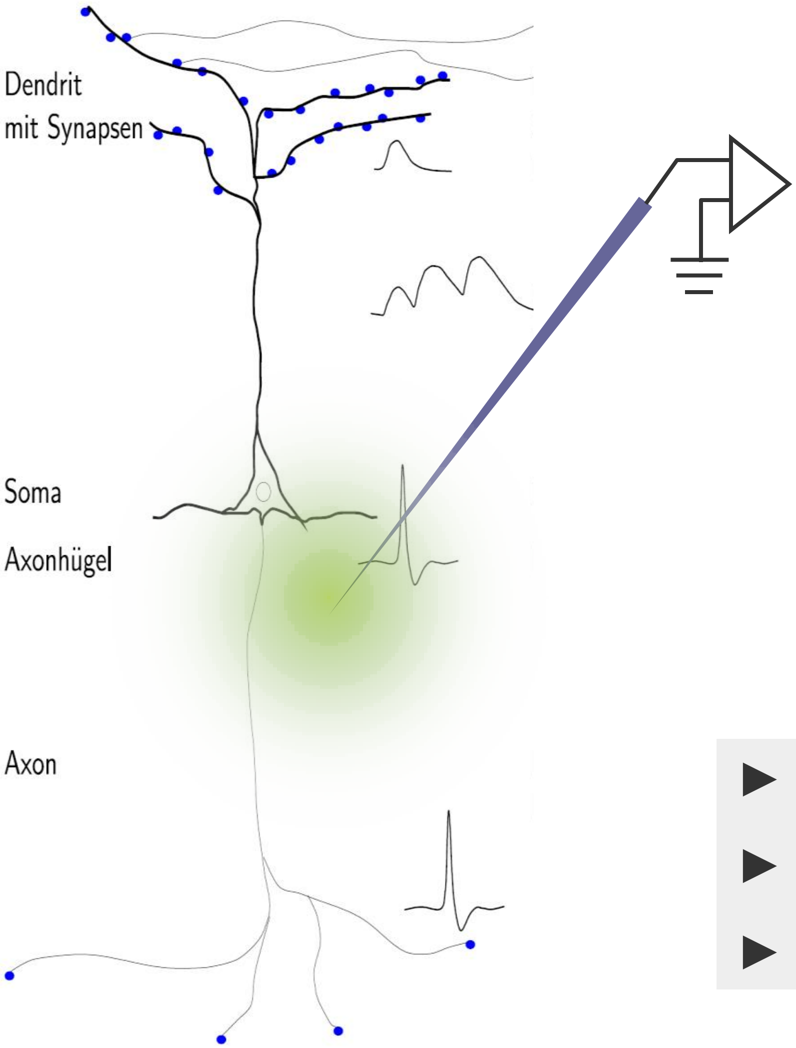
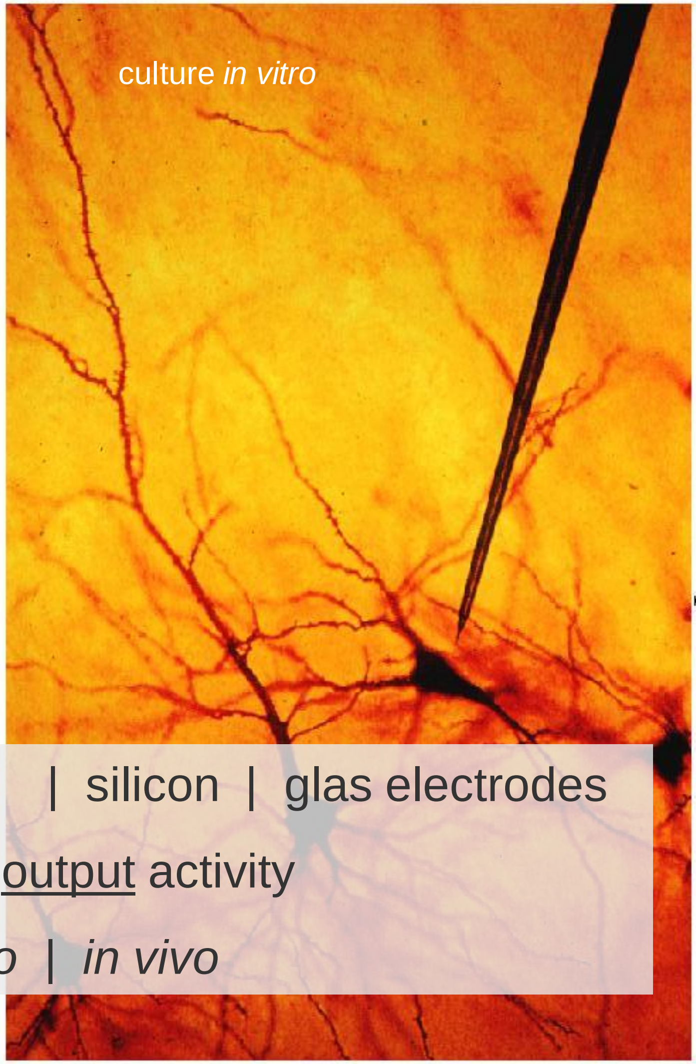


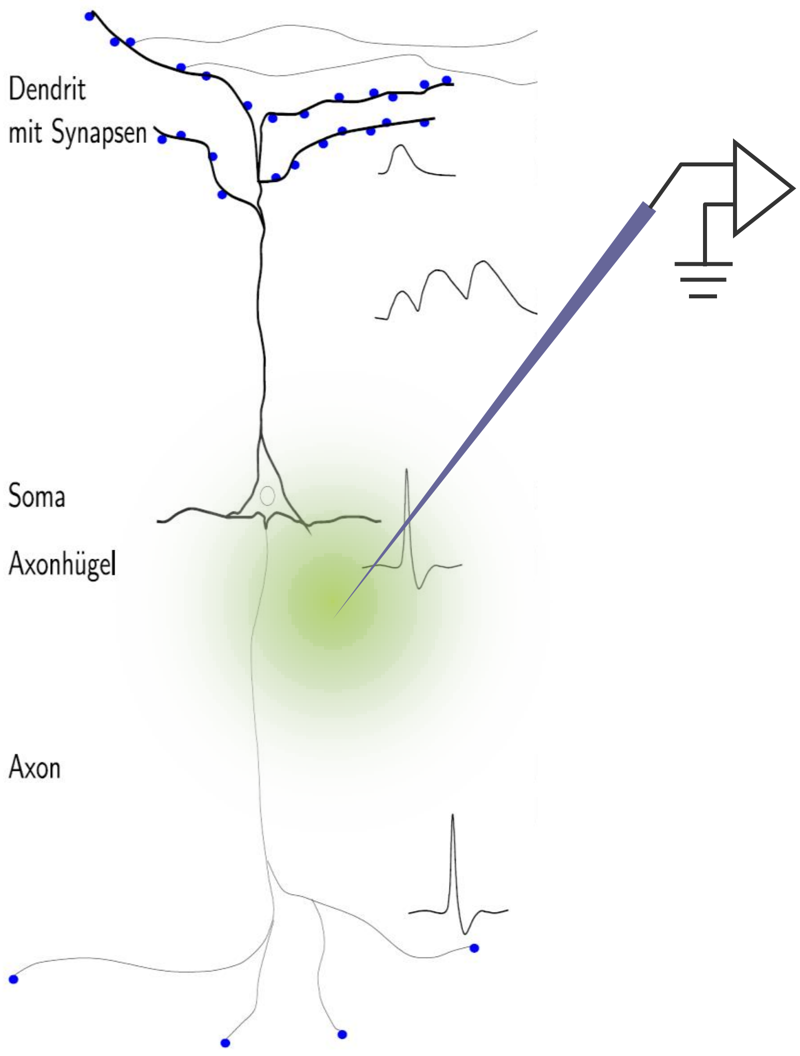
Figure 1. Permanent background input *in vivo* causes dynamic fluctuations of the membrane potential and drives the neuron to spontaneous spiking activity. (A) Membrane potential recorded intracellularly in the frontal cortex of the anesthetized rat. Presynaptic inputs from several hundreds or thousand of presynaptic neurons cause depolarization of the cell to a resting potential of about $-50\,\mathrm{mV}$ and salient fluctuations of the membrane potential. (B) The enlarged cut-out from A reveals the fine structure of the signal that results form the superposition of many single EPSPs and IPSPs and gives an impression of the time scale on which these fluctuations take place. Data by courtesy of Detlef Heck (Léger, Stern, Aertsen, & Heck, 2003).

Extracellular Recording

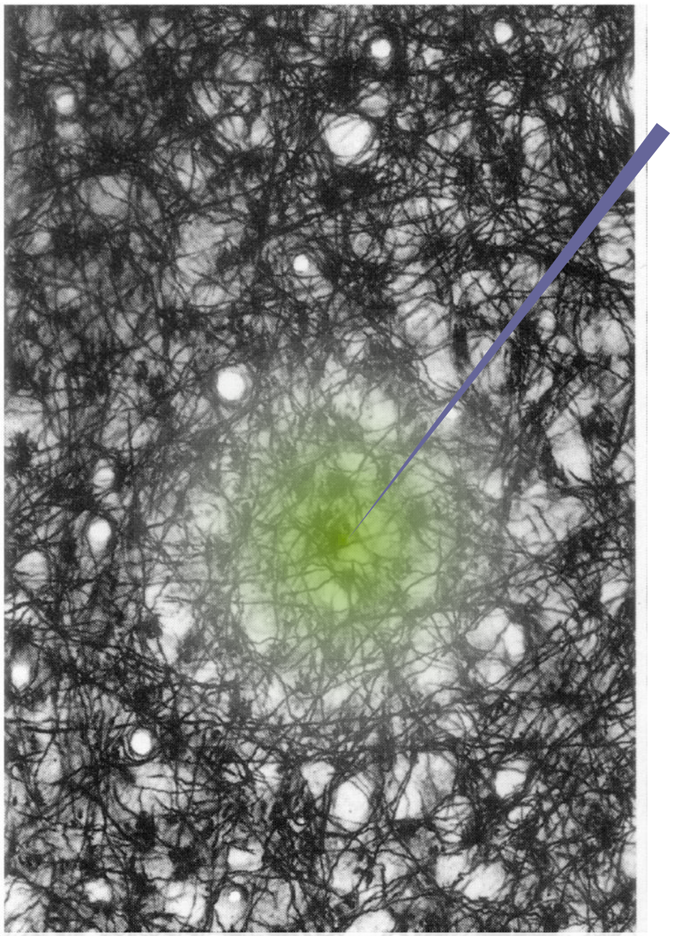




- ► metal | silicon | glas electrodes
- ► spike <u>output</u> activity
- ► *in vitro* | *in vivo*



Cortex

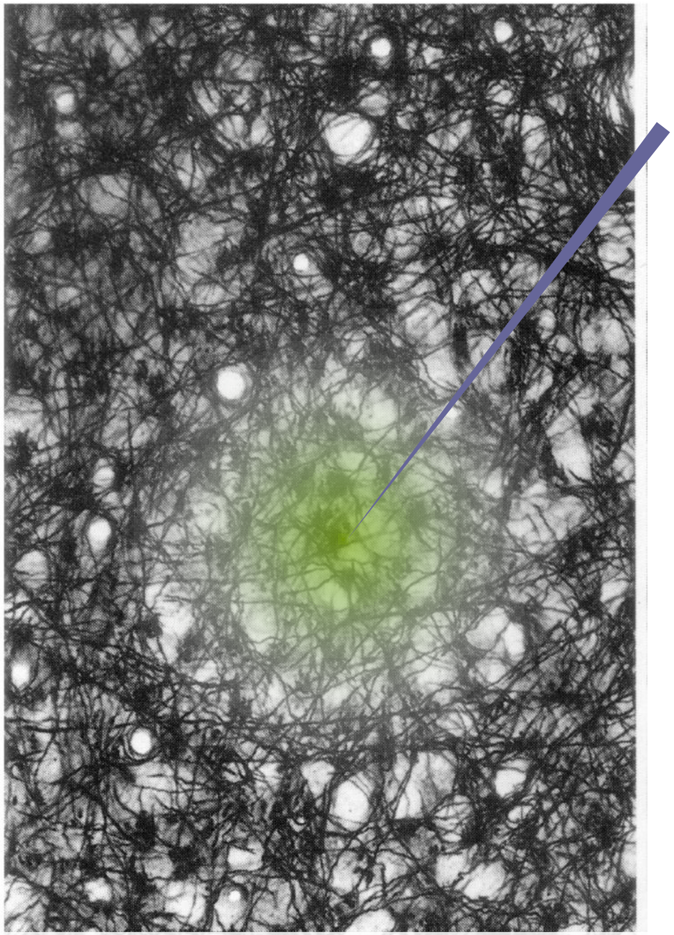


Valentino Braitenberg & Almut Schüz
Cortex: Statistics and Geometry of Neuronal Connectivity
Springer, Berlin, 1998 (Second Edition)

Extracellular Recording | recording sphere

Total volume	$2 \times 87\,\text{mm}^3$
Total number of neurons	16 000 000
Number of sensory input fibres	$<$ 1 000 000
Length of axonal tree	10–40 mm
Length of dendritic tree	4 mm
Range of axons	1/0.2 mm
Range of dendrites	0.2 mm
Density of neurons	90 000 $/\text{mm}^3$
Density of axons	4 km/mm^3
Density of dendrites	0.4 km/mm^3
Density of synapses	700 000 000 $/\text{mm}^3$
Synapses per neuron	8 000
Probability of synaptic contact	0.1
Relative density of axons	$10^{-5}/10^{-3}$
Relative density of dendrites	10^{-3}

Cortex



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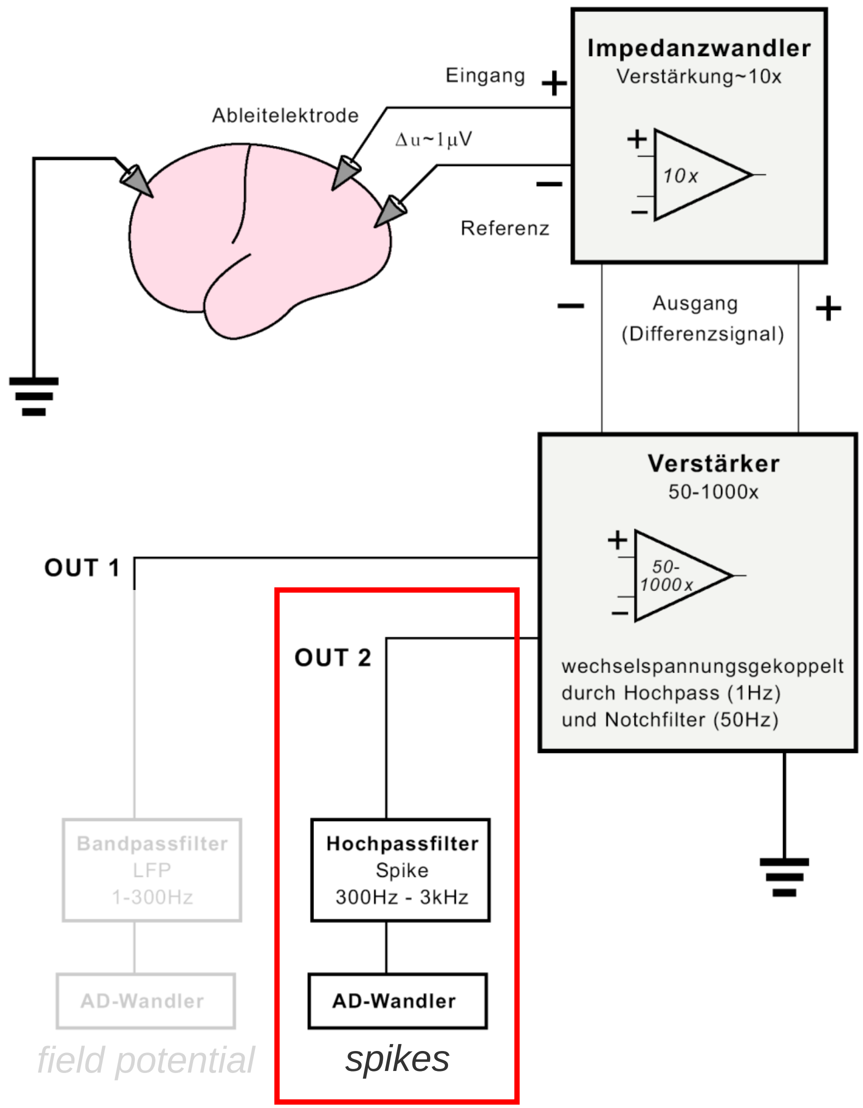
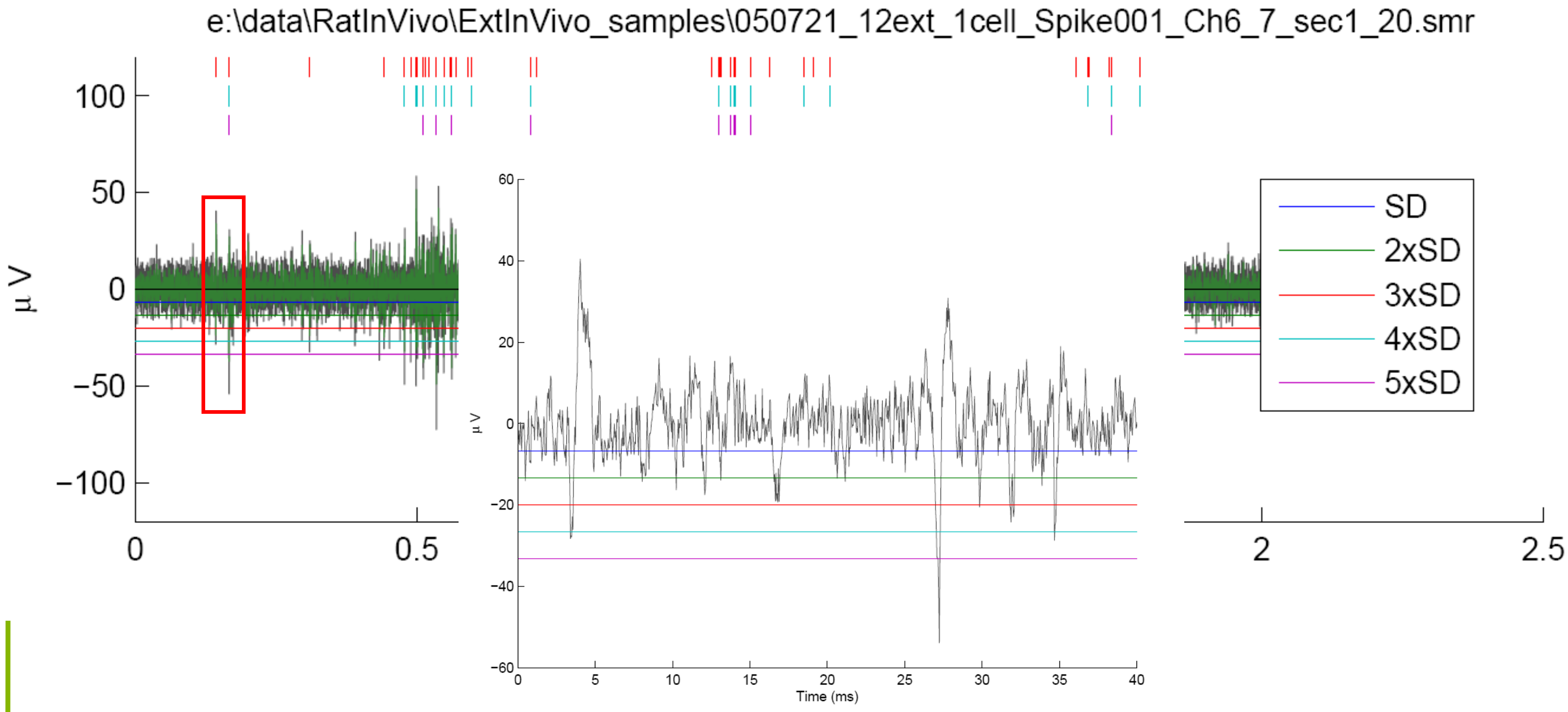
Springer, Berlin, 1998 (Second Edition)

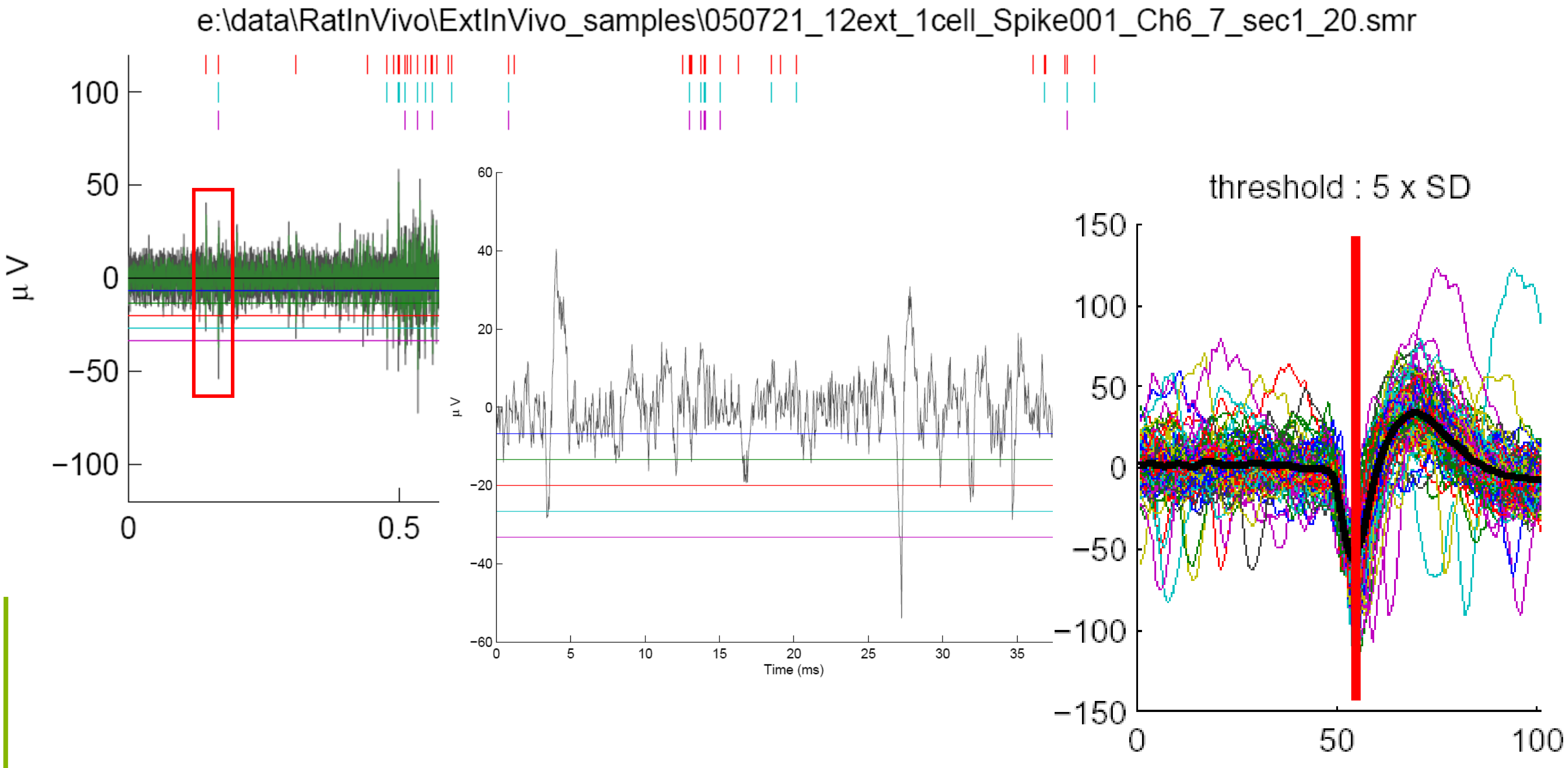
Extracellular Recording | electrophysiological setup



Extracellular Recording | raw signal and Multi Unit Activity [MUA]



Extrazelluläre Aufnahmen im somatosensorischen Kortex der Ratte. Spontanaktivität unter Anästhesie.
Data Curtsey: Clemens Boucsein und Dymphie Suchanek, Neurobiologie & Biophysik, Universität Freiburg, Germany



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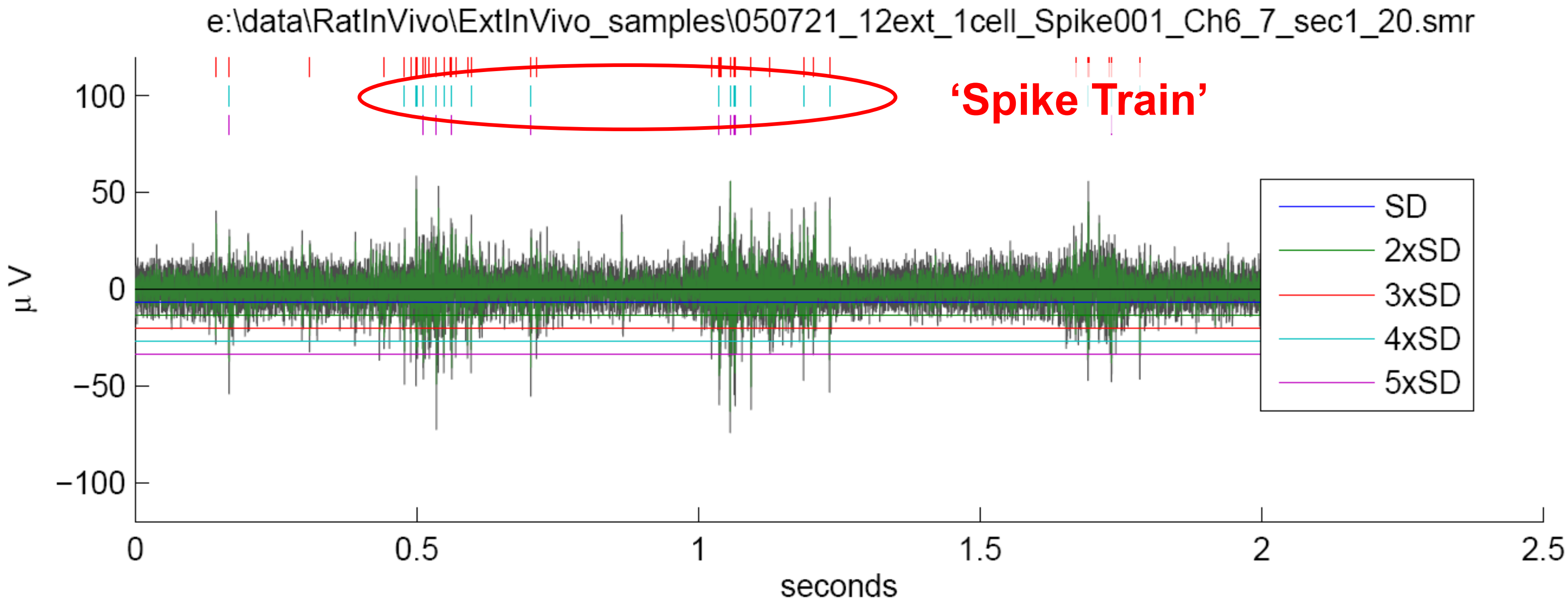

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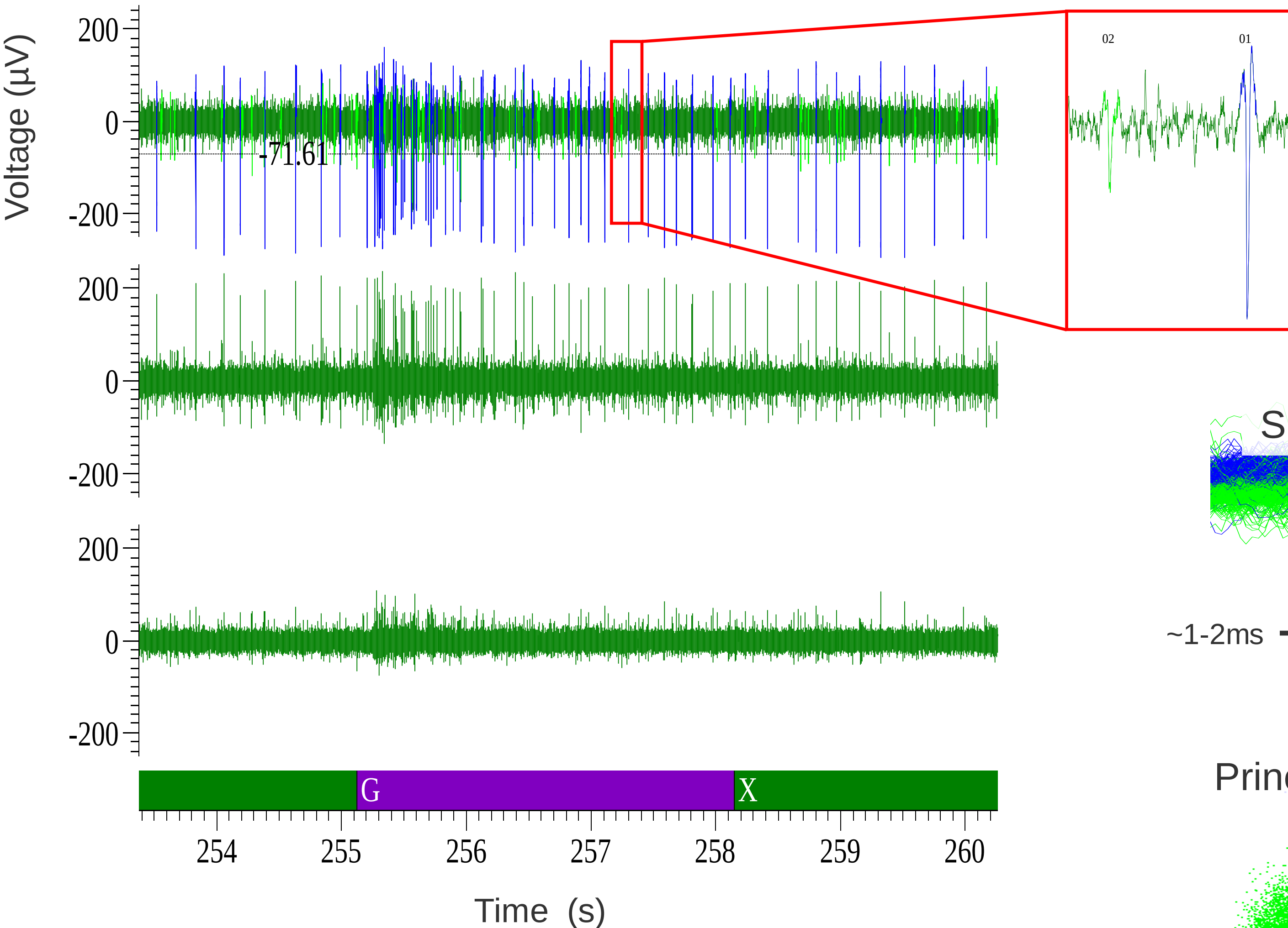
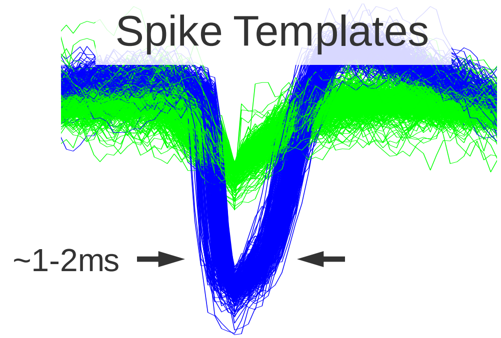
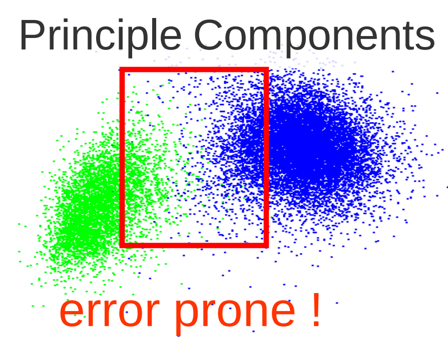
Extracellular Recording | spike sorting: Single Unit Activity [SUA]







Extracellular recording from α-extrinsic neurons of the honeybee mushroom body. Response to odor stimulus.

Data Curtsey: Dr. Martin Strube-Bloss, Neurobiologie, Freie Universität Berlin, Germany

Estimated number of spike sorting errors :

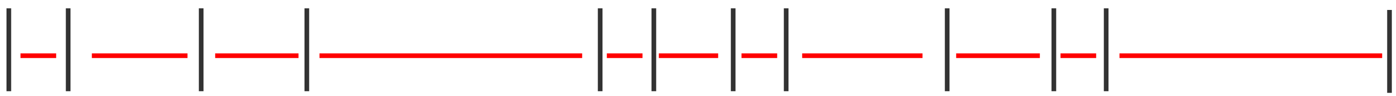
	[1]	[2]
false positive rate :	13%	~10%
false negative rate:	9%	~10%

single *unit* activity ≠ single *neuron* activity

Joshua, Elias, Levine, Bergman (2007) J Neurosci Meth doi: jneumeth.2007.03.012

Pouzat, Delescluse, Viot, Diebolt (2004) J Neurophysiol 91

Spike Train Representation



‘ spike train ‘

discrete time series of events

discrete representation
(*list*)

1010000100010000000000101001010000010001010000000001

binary representation
(*array*)

2. Stochastic Point Processes

- interval and count random variables
- Bernoulli process
- Poisson process
- renewal process
- nonhomogenous Poisson process
- non-renewal processes

A ***point*** is a discrete event that occurs in continuous time (or space). We regard action potentials as point events ignoring their amplitude and duration.

A ***point process*** is a mathematical description of a process that generates points in time (or space) according to defined stochastic rules (probability distribution).

Only a *finite number of events* are generated within a *finite time observation interval* (true for neural spike train).

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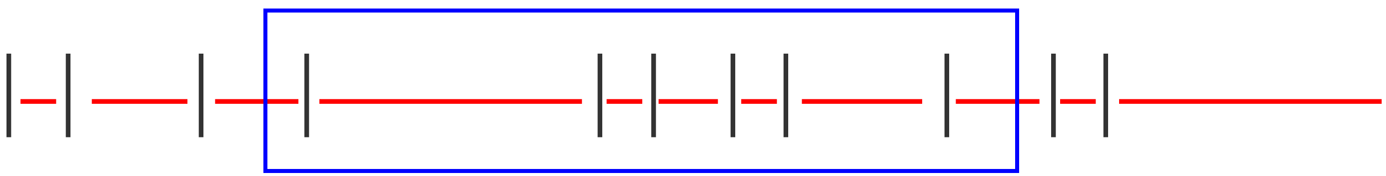
2 basic random variables :

- inter-event intervals *X* (continuous random variable)
- number of spikes *N* (discrete random variable) in interval of length T



Any point process definition uniquely determines its interval and count stochastic, and both random variables are related.

10100001000100000000001010010100000100010100000000001

binary representation

Bernoulli process: intuitive model

A Bernoulli process is *discrete* in time (space). It consists of a finite or infinite sequence of independent random variables $X_i, i = 1, 2, ...$ such that

$$\Pr\{X_i = 1\} = p \quad \text{and} \quad \Pr\{X_i = 0\} = (1 - p) \quad \forall i$$

A Bernoulli process is a sequence of *independent* trials and thus the Bernoulli process is *memoryless*. The prominant example is repeated coin flipping where $p = 0.5$. We call trials i where $X_i = 1$ a success. The number of successes m in n trials (equiv. to count distribution) follows the Binomial distribution.

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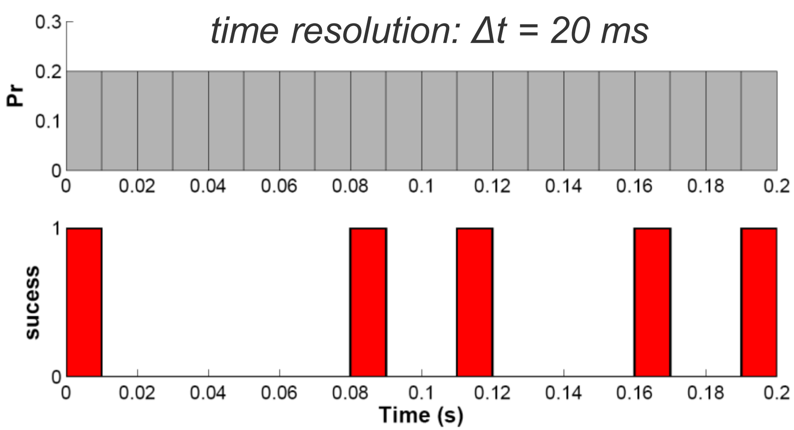

Bernoulli process

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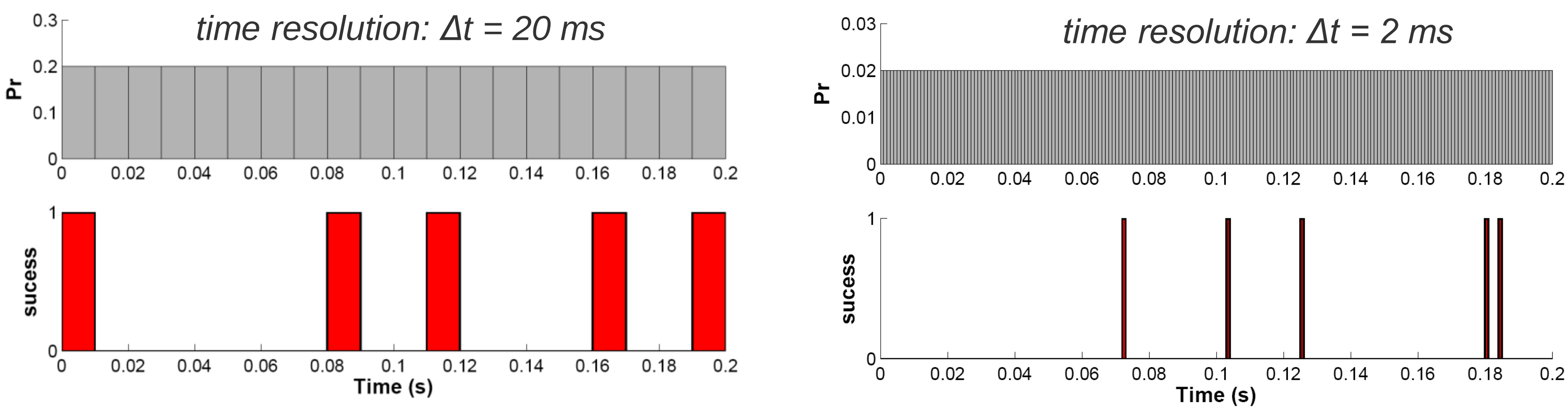
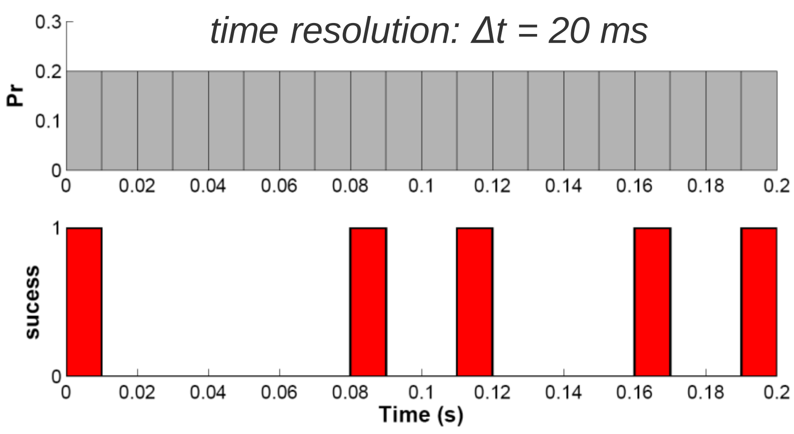
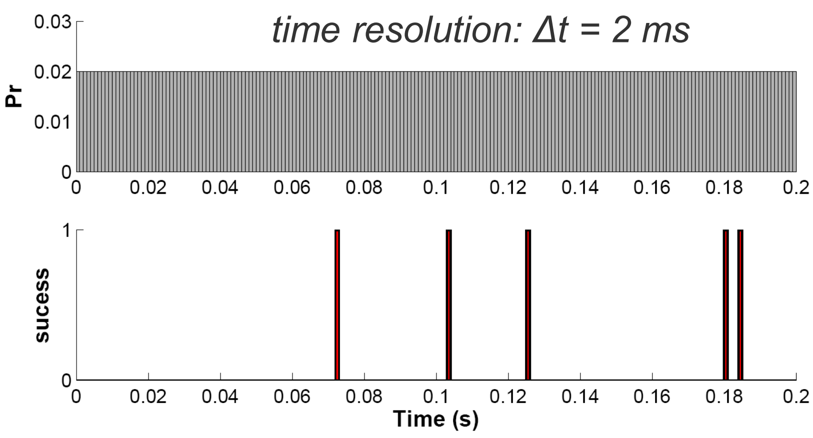


What is a good time resolution Δt for simulating a series of action potentials ?

APs have a duration of about 1-2ms; thus as useful time resolution is: Δt ≤1 ms

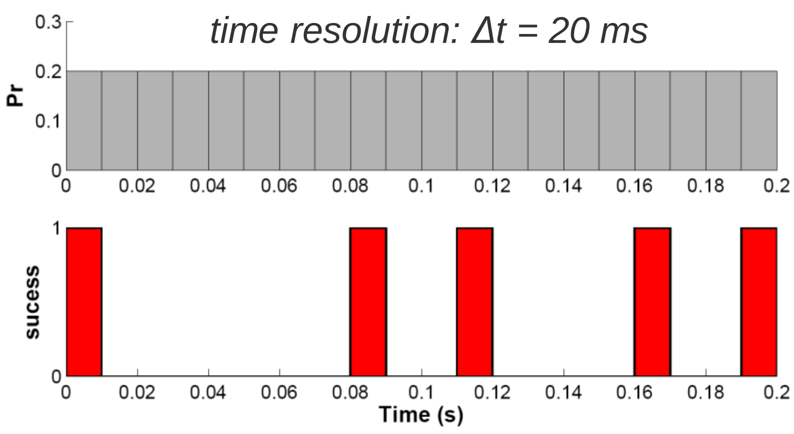


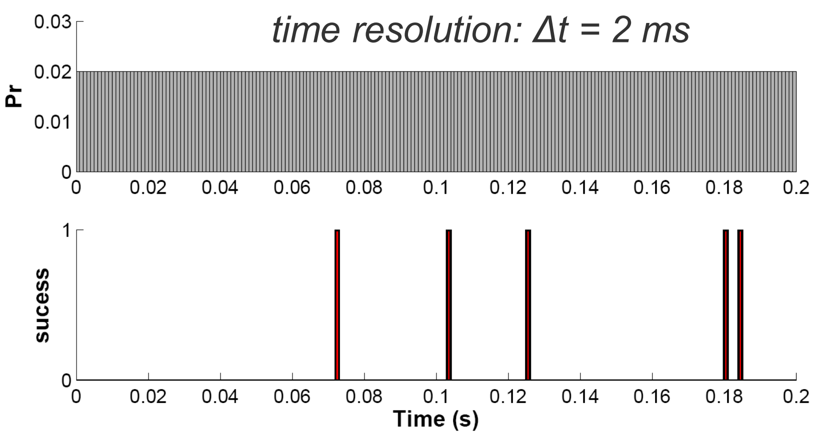


What is a good time resolution Δt for simulating a series of action potentials ?

APs have a duration of about 1-2ms; thus as useful time resolution is: Δt ≤1 ms

The ratio **λ = p / Δt** is called the **intensity** of the process and determines the rate of point occurrences, identified with the neuronal firing rate. In both examples below the rate is λ = 5/s (expectation: 5 events per second).





Model classes

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constant intensity λ

Poisson

- exponential interval distribution
- Poisson count distribution
- events are uniformly distributed in time
- special case of gamma process

increasing importance of process history

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One possibility to define a point process is the **complete intensity function**.

Consider a point process as defined on the complete time axis (−∞,+∞). Let H_t denote the **history of the process**, i.e. a specification of the position of all points in (−∞, t]. Then a general description of this process maybe formulated in terms of the probabilities of observing a single event at an arbitrary time t

$$P(N(t, t + \delta t) = 1|H_t\}$$

Definition

The **Poisson process** of intensity λ is defined by the requirements that for all t and for δ→0+

$$P\{N(t, t + \delta t) = 1|H_t\} = \lambda\delta + o(\delta)$$

- the only process for which all events are completely independent
- ‘simple process’, often used for the description of neural spiking
- the Bernoulli process approximates the Poisson process for Δt → 0.

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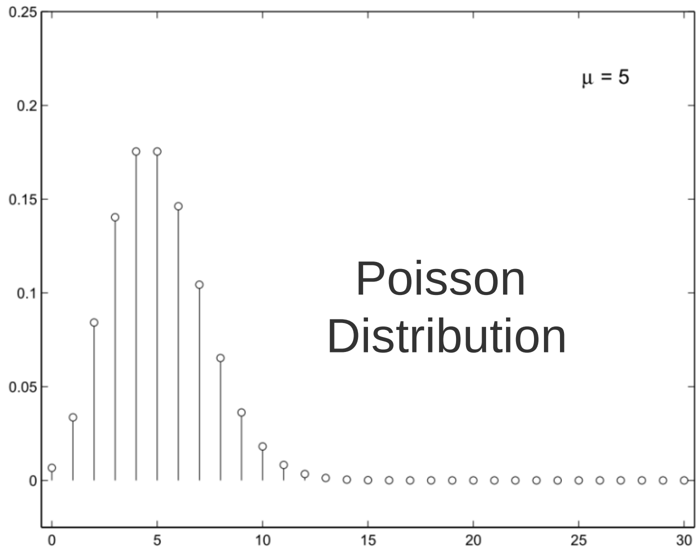
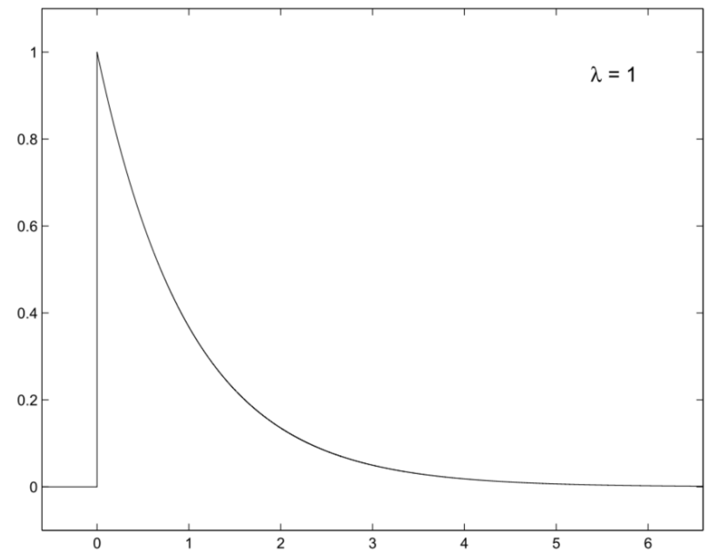
discrete event count

continuous inter-event intervals





$$P\{N(A)=k\} = \frac{(\lambda\, t)^k}{k!}\, e^{-\lambda\, t}$$

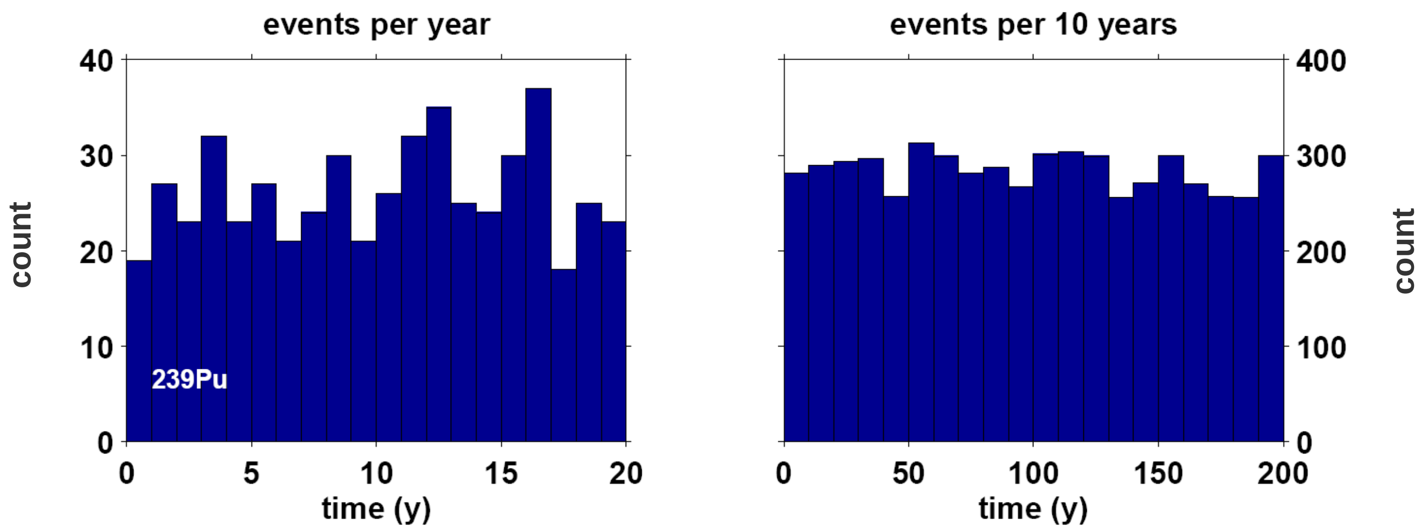
$$\Pr\{X_1 > t\} = P\{N(t)=0\} = \frac{\lambda\, t^0}{0!}\, e^{-\lambda\, t} = e^{-\lambda\, t}$$

FF = 1

CV^2 = 1

Example 1: radioactive decay of 239Pu (half-life : 4110 years).

- continuous time intervals
- discrete event count



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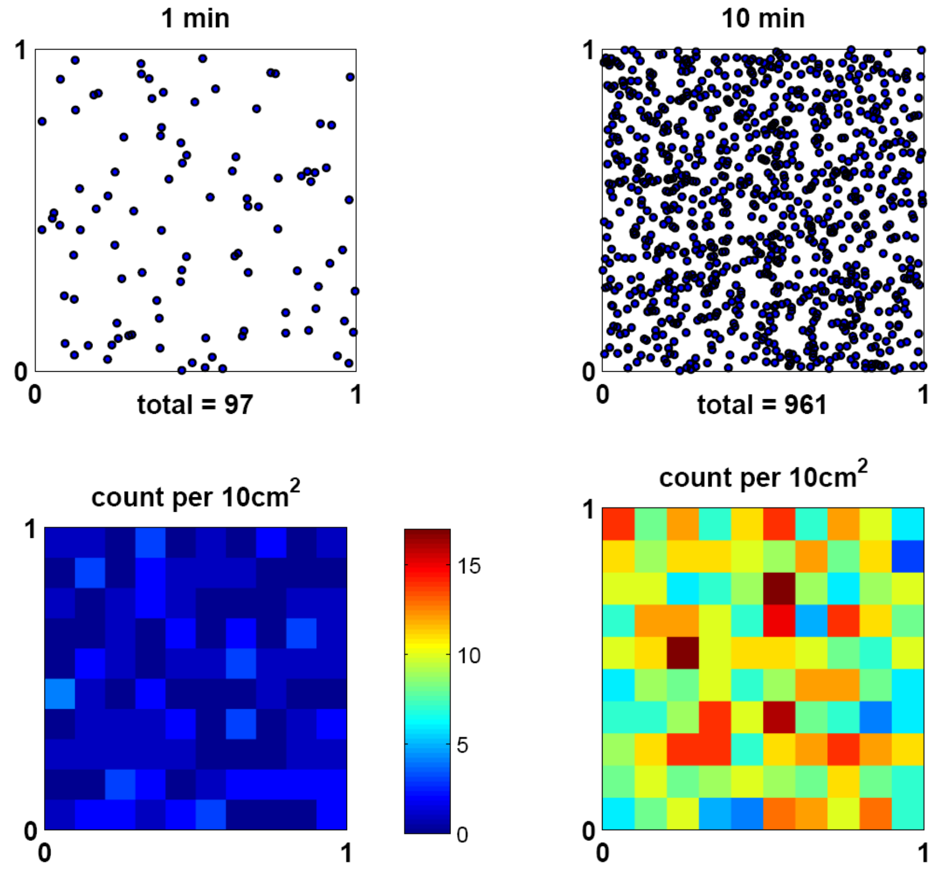
Example 2: rain drops

- continuous space intervals
- discrete event count



Model classes

constant intensity λ

Poisson

- exponential interval distribution
- Poisson count distribution
- events are uniformly distributed in time
- special case of gamma process

Renewal

- iid interval distribution
- FF = CV^2

increasing importance of process history

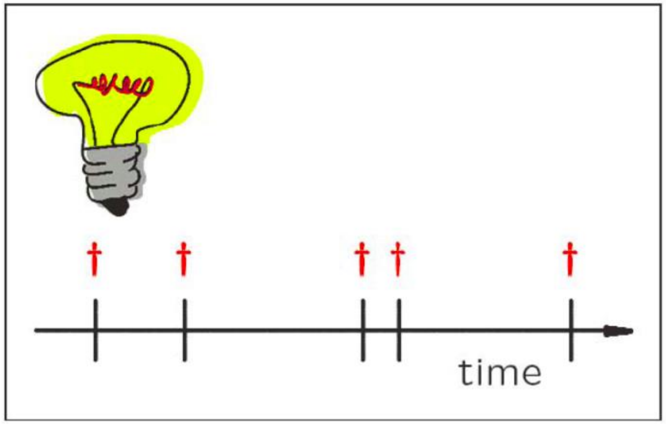
Definition

inter-event intervals are **independent** and **identically distributed** (iid)

Thus

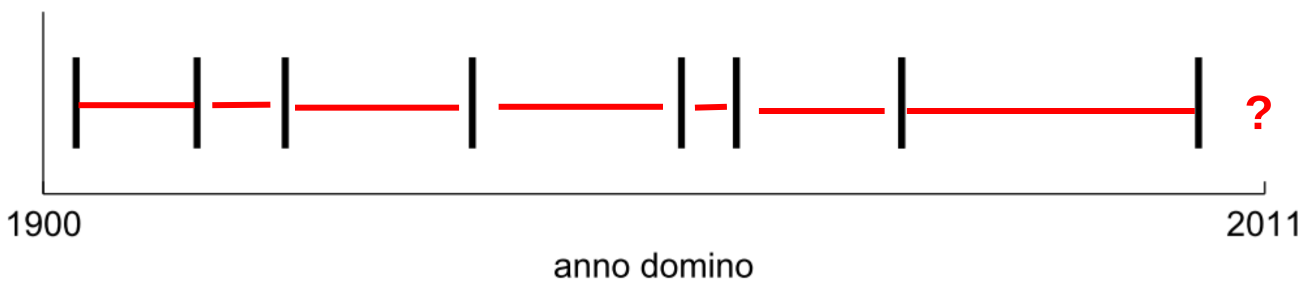
- individual intervals are serially independent
- process history is relevant only up to the previous event
- the intervals between successive points are mutually independent
- the Poisson process is a renewal process

Implies a constant intensity (rate)

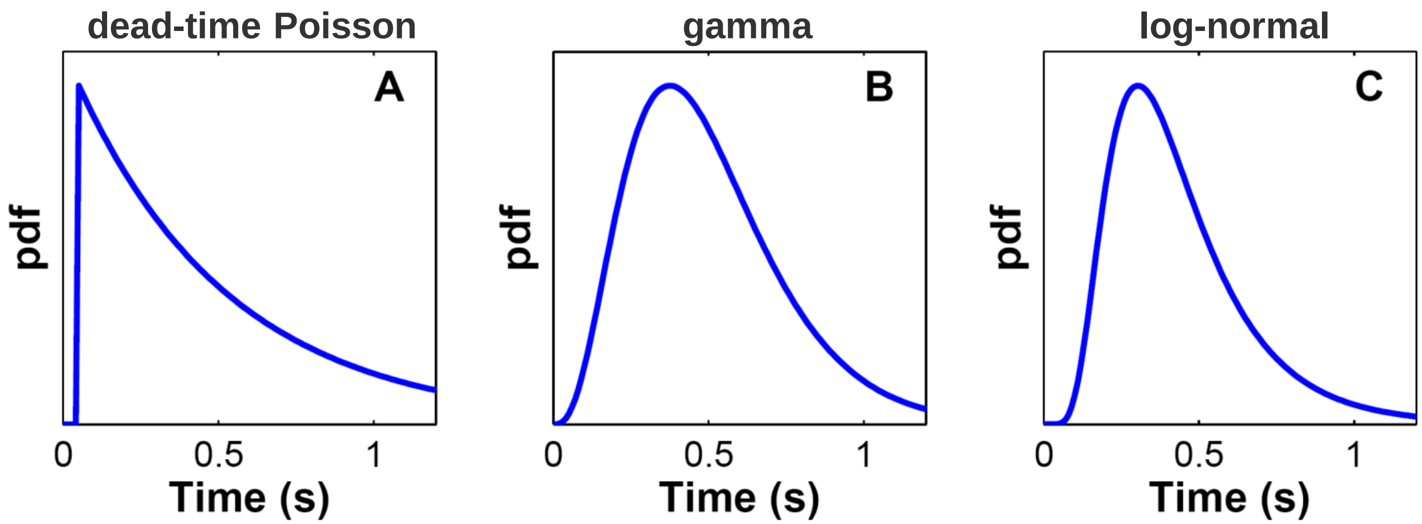


† = replacement from a homogeneous population

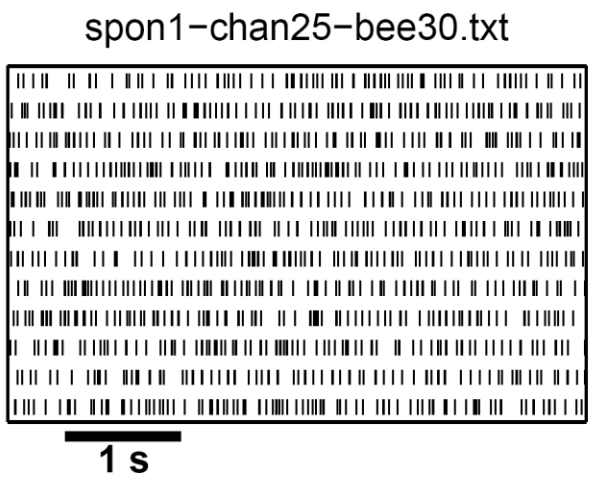
The Catholic Renewal Process

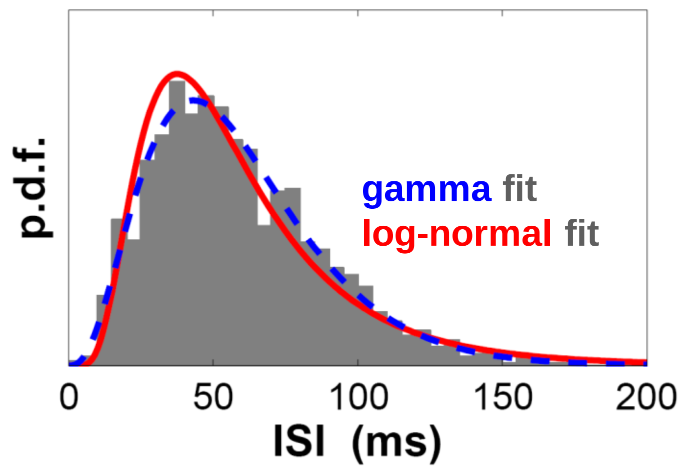


Prominent **interval** distributions used for renewal models of neural spiking



Poissonian Spiking is a myth !!





Extracellular single unit recording of spontaneous activity from a so-called extrinsic neuron of the honeybee mushroom body. The empirical interval distribution is estimated by the gray historgram from a total of 1530 ISIs. The mean interval length is $m = 58.7$ ms, i.e. the average rate can be approximated by $\lambda \approx 1/m = 17.03/$s. The blue curve fits a gamma distribution, the red curve fits a log-normal distribution. Modified from: [1]

[1] Farkhooi, Strube-Bloss, Nawrot (2009) Phys Rev E 79

Model classes

constant intensity λ | *dynamic intensity λ(t)*

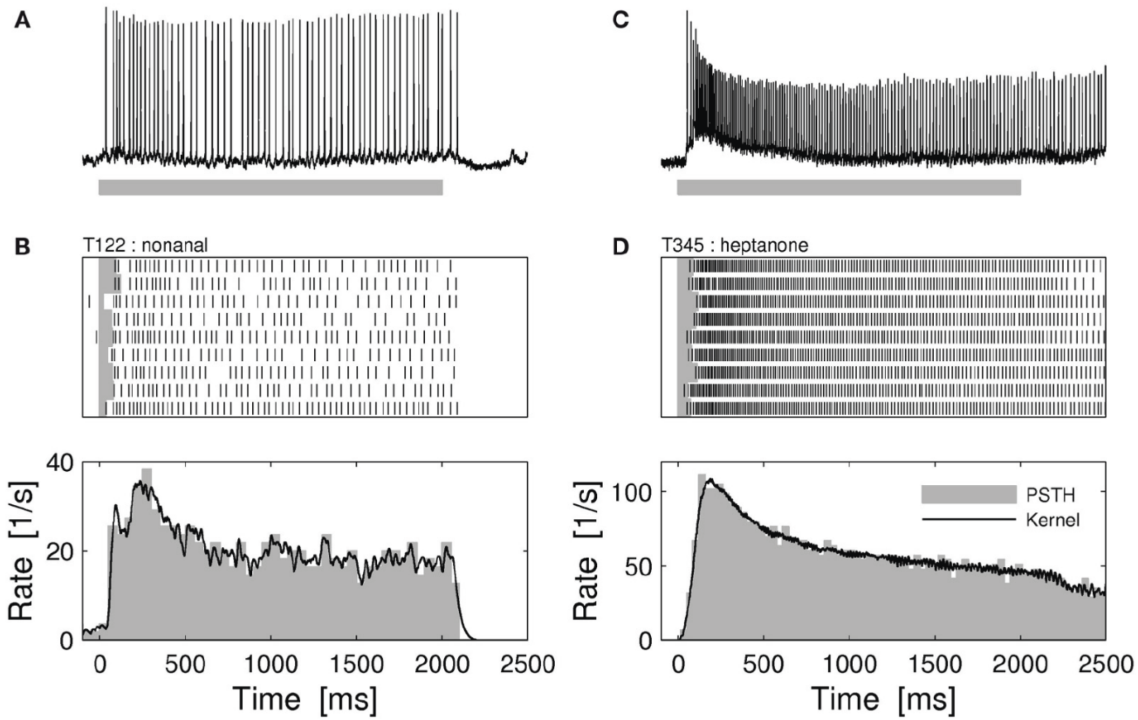
Poisson
- exponential interval distribution
- Poisson count distribution
- events are uniformly distributed in time
- special case of gamma process

non-homogenous Poisson

Renewal
- iid interval distribution
- FF = CV^2

increasing importance of process history

Motivation: The concept of a neuron's 'firing rate' is empirically motivated. Experimental repetitions allow to average spike count across trials. Individual neurons can **modulate their firing rate** with time.



Intracellular recordings from two individual projection neurons in the honeybee antennal lobe during odor stimulation. A,C: Single trial intracellular traces. B,D: Spike trains of repeated trials and firing rate estimates.

[1] Krofczik, Menzel, Nawrot (2008) Frontiers Comp Neurosci 1:3

Definition

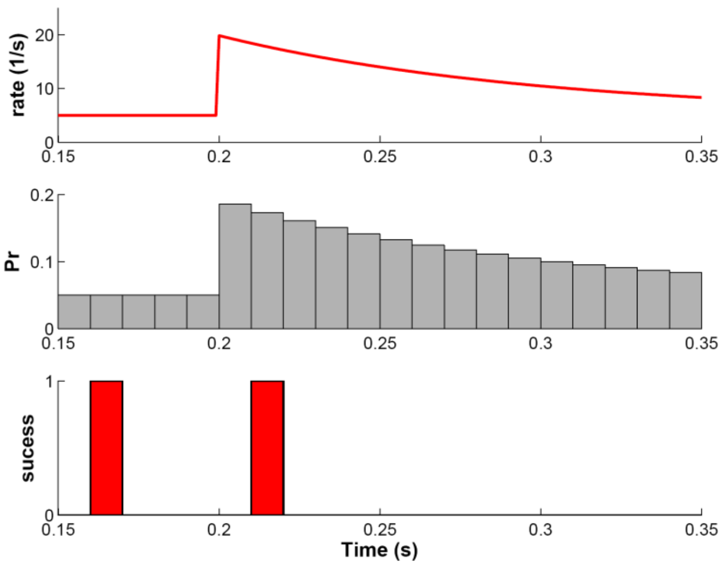
We substitute the constant intensity λ by the explicitly time-dependent intensity funtion λ(t) and define the **nonhomogenous Poisson** process for all t and for $\delta \to 0+$

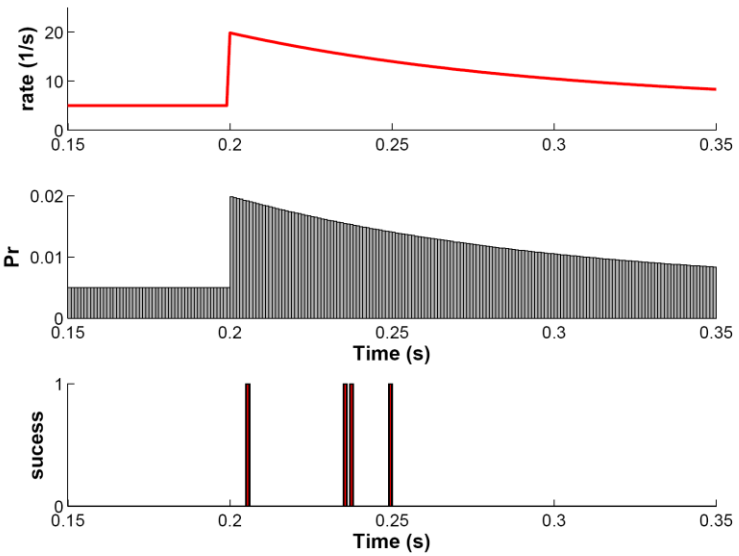
$$\text{Pr}\{N(t, t+\delta t) = 1 | H_t\} = \lambda(t)\,\delta.$$

The instantaneous probability is still independent of the process history!

note: firing rate is a concept

Bernoulli approximation:





Model classes

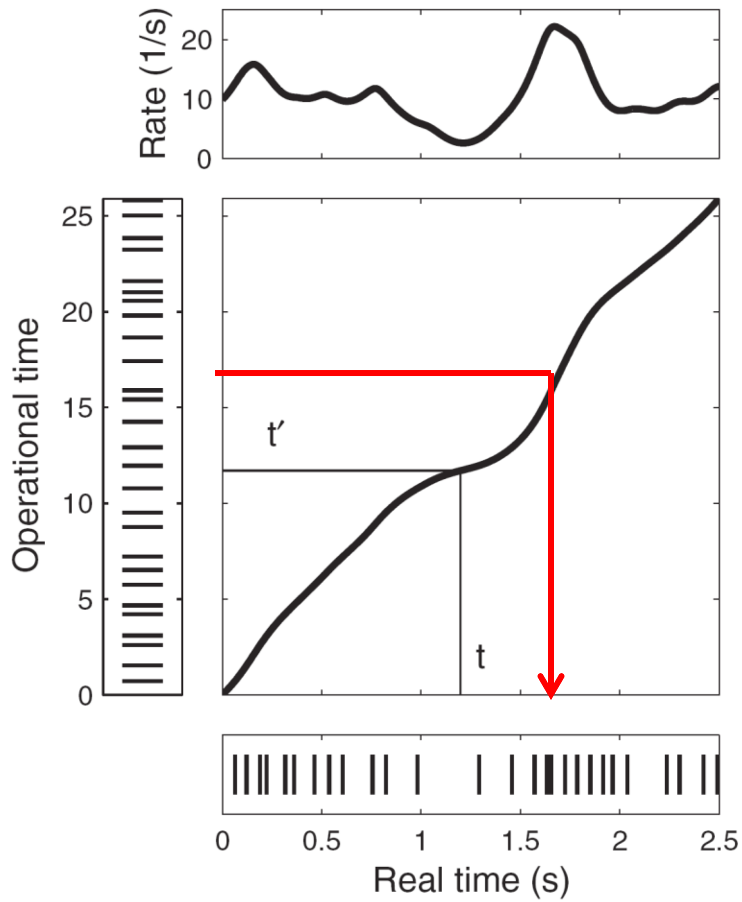
constant intensity λ	*dynamic intensity λ(t)*
Poisson • exponential interval distribution • Poisson count distribution • events are uniformly distributed in time • special case of gamma process	**non-homogenous Poisson**
Renewal • iid interval distribution • FF = CV^2	**Rate modulated Renewal**

increasing importance of process history

Time rescaling:

- simulate renewal process in ‘operational time’
- transform to ‘real time’

$$t' = \Lambda(t) = \int_0^t \lambda(s)\,\mathrm{d}s$$



Model classes

constant intensity λ	*dynamic intensity λ(t)*
Poisson • exponential interval distribution • Poisson count distribution • events are uniformly distributed in time • special case of gamma process	**non-homogenous Poisson**
Renewal • iid interval distribution • FF = CV^2	**Rate modulated Renewal**
stationary non-Renewal • constant intensity parameter • non-trivial history dependence • serial interval correlations	

increasing importance of process history

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An **autoregressive process** in its general linear form up to **lag *p*** reads

$$\boxed{X_s = \beta_1 X_{s-1}} + \beta_2 X_{s-2} + \ldots + \beta_p X_{s-p} + \varepsilon_s$$

where

ε_s i.i.d. with specific mean and finite variance.

β_i correlation coefficient for lag i and $|\beta| < 1$

We propose the following process to model inter-event intervals

$$\Delta_s = \exp(X_s) = \exp(\beta X_{s-1} + \varepsilon_s) \qquad (|\ \beta\ |< 1)$$

When we choose ***ε_s normal distributed*** with mean μ and variance σ^2 then ***Δ_s is log-normal*** distributed.

Farkhooi, Strube-Bloss, Nawrot (2009) Phys Rev E 79

Non-renewal point process model

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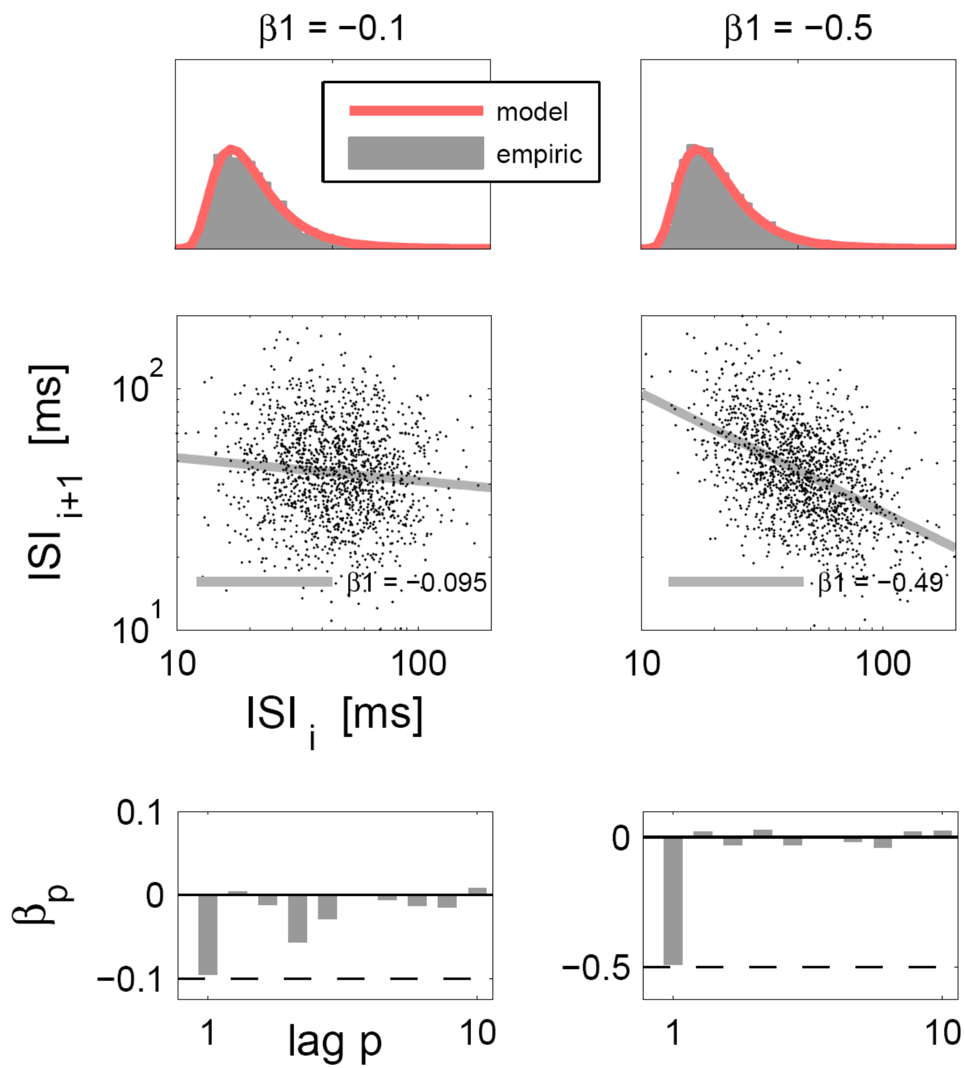
Numeric Simulation

log-normal

CV = 0.5



Farkhooi, Strube-Bloss & Nawrot (2009) Phys Rev E

Model classes

constant intensity λ	*dynamic intensity λ(t)*
Poisson • exponential interval distribution • Poisson count distribution • events are uniformly distributed in time • special case of gamma process	**non-homogenous Poisson**
Renewal • iid interval distribution • FF = CV^2	**Rate modulated Renewal**
stationary non-Renewal • constant intensity parameter • non-trivial history dependence • serial interval correlations	

increasing importance of process history

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Part I : Stochastic Point Processes

1. Experimental Spike Trains

2. Stochastic Point Processes

Part II : Spike Train Statistics

3. Firing Rate Estimation

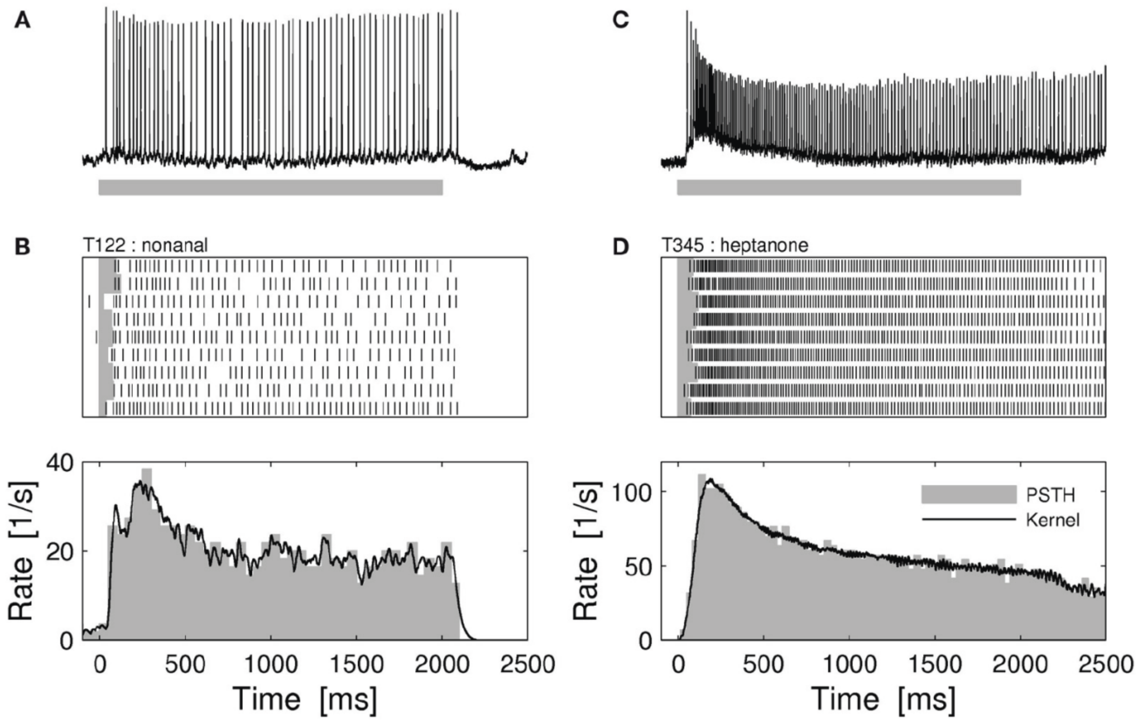
4. Empirival Interval and Count Statistics
   - Coefficient of Variation (CV) of the ISIs
   - Fano Factor (FF) of the spike count

5. Combined Analysis FF vs. CV^2 (real world data)
   - effect serial interval correlation
   - across trial non-stationaritz of data

3. Firing rate estimation

- Peri-Stimulus Time Histogram (PSTH)
- Kernel convolution

Motivation: The concept of a neuron's 'firing rate' is empirically motivated. Experimental repetitions allow to average the spike count across trials. Individual neurons can **modulate their firing rate** with time.



Intracellular recordings from two individual projection neurons in the honeybee antennal lobe during odor stimulation. A,C: Single trial intracellular traces. B,D: Spike trains of repeated trials and firing rate estimates.

Krofczik, Menzel, Nawrot (2008) Frontiers Comp Neurosci 1:3

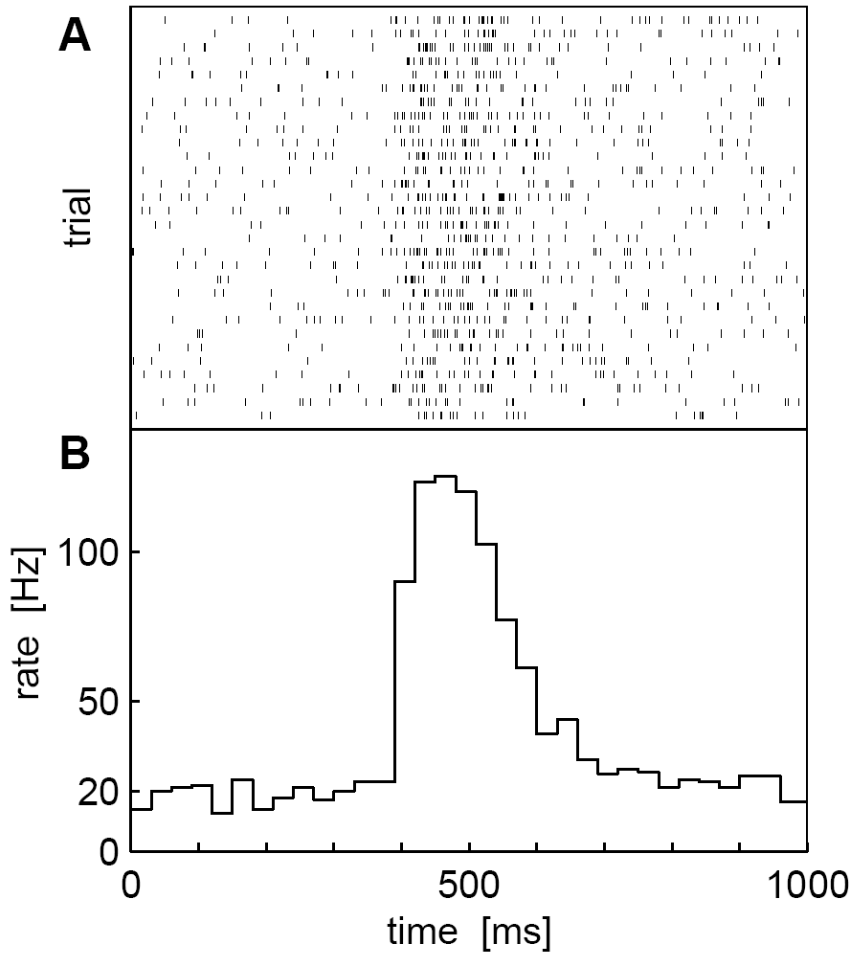
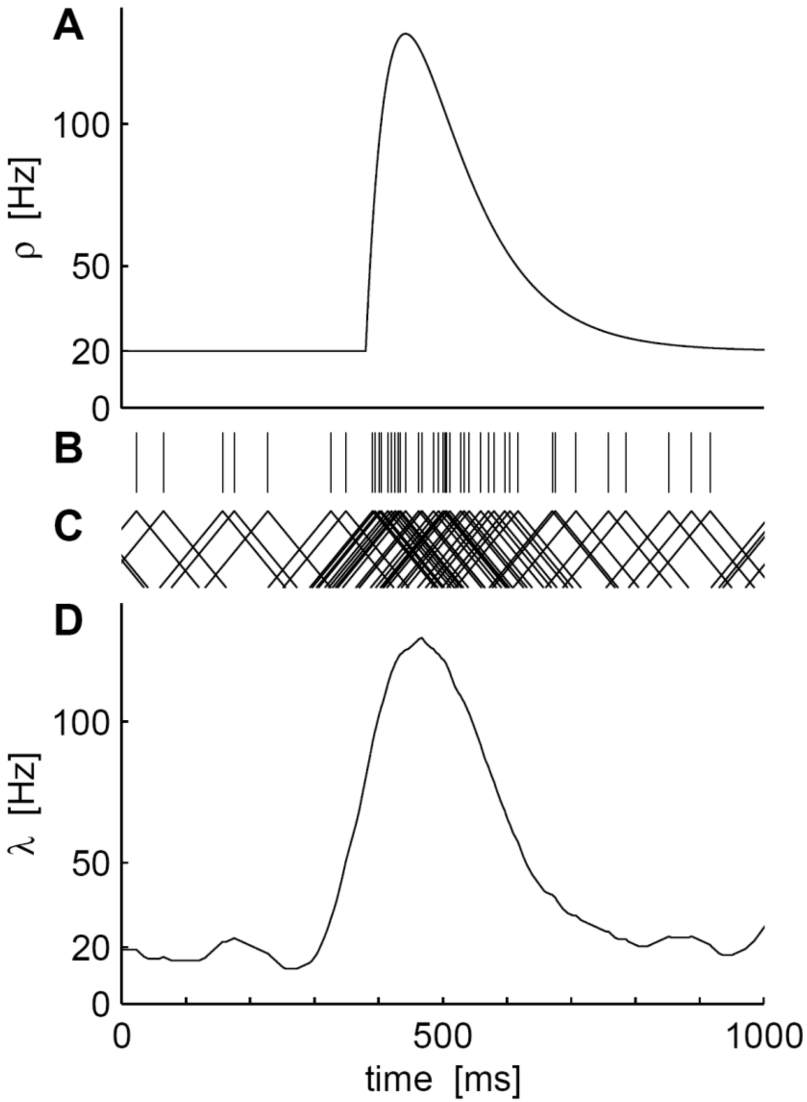


Fig. 1. Rate estimation by means of trial-averaging: the peri-stimulus time histogram (PSTH). (A) Raster display of spike events for 30 trial repetitions. (B) PSTH of average spike response, constructed from all 30 trials using a bin size of 30 ms.

Which are the parameters of this method that you have to choose ?

Nawrot, Aertsen, Rotter (1999) J Neurosci Meth 94



Which are the parameters of this method that you have to choose ?

Nawrot, Aertsen, Rotter (1999) J Neurosci Meth 94
Shimazaki et al. (2009) J Comp Neurosci

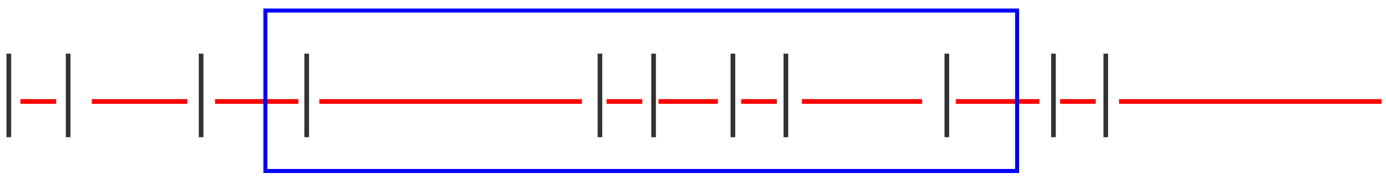
4. Empiric Interval and Count Statistics

- Coefficient of Variation (CV)
- Bias of estimation
- Fano factor FF

Experimentally we observe **variables** (observables)

2 basic random variables :

- inter-event intervals *X* (continuous random variable)
- number of spikes *N* (discrete random variable) in interval of length T



Any point process definition uniquely determines its interval and count stochastic, and both random variables are related.

1010000100010000000000101001010000010001010000000000 1

binary representation

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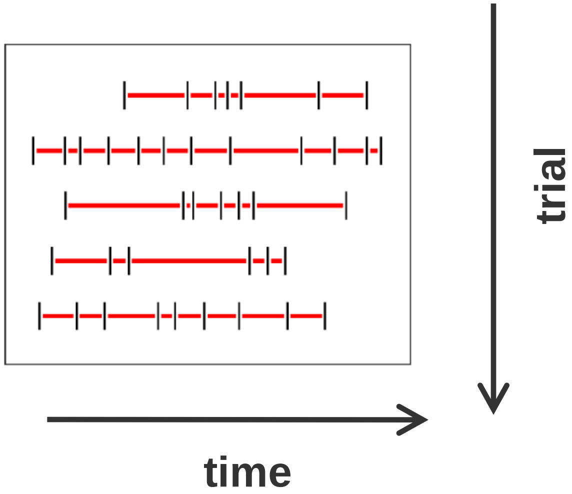
Coefficient of variation (interval variability)

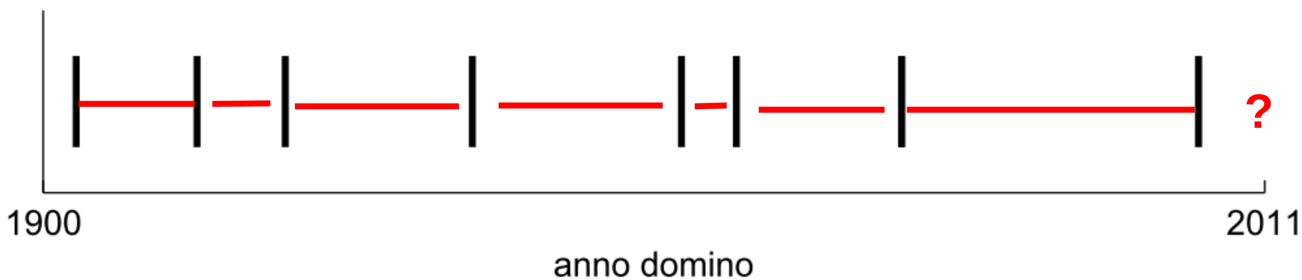
$$CV^2 = \frac{Var(ISI)}{mean^2(ISI)}$$



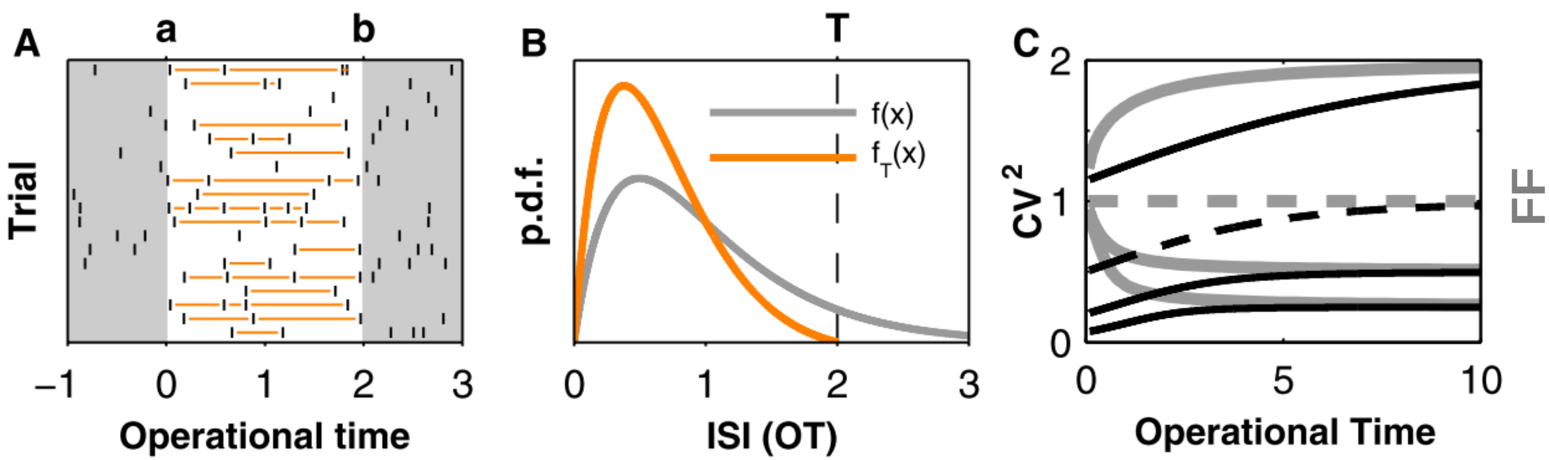
How could we estimate CV or CV^2 in an experimental setting without trials ?

$N_{>1500} = 49$

$CV\ (\Delta_{POPE}) = 0.79$



- Bias of empiric CV (a function of operational time)
- Practical consequence: use large windows ≥ 5 ISIs



$$\hat{f}(x) = \begin{cases} \eta^{-1}(T-x)f(x) & \text{for } x \in [0,T], \\ 0 & \text{otherwise,} \end{cases} \qquad \eta = \int_0^T (T-s)f(s)\,ds$$

Nawrot et al. (2008) J Neurosci Meth 169

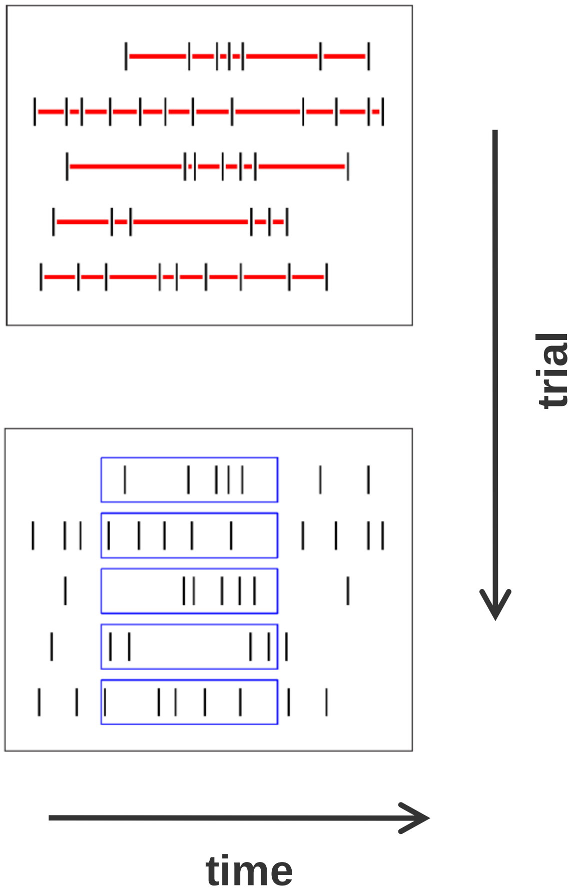
Nawrot (2010) In: Grün, Rotter (eds.), Springer Series Comp Neurosci 7

Coefficient of variation (interval variability)

$$CV^2 = \frac{Var(ISI)}{mean^2(ISI)}$$

Fano factor (count variability)

$$FF = \frac{Var(count)}{mean(count)}$$



How could we estimate FF in an experimental setting without trials ?

Coefficient of variation (interval variability)

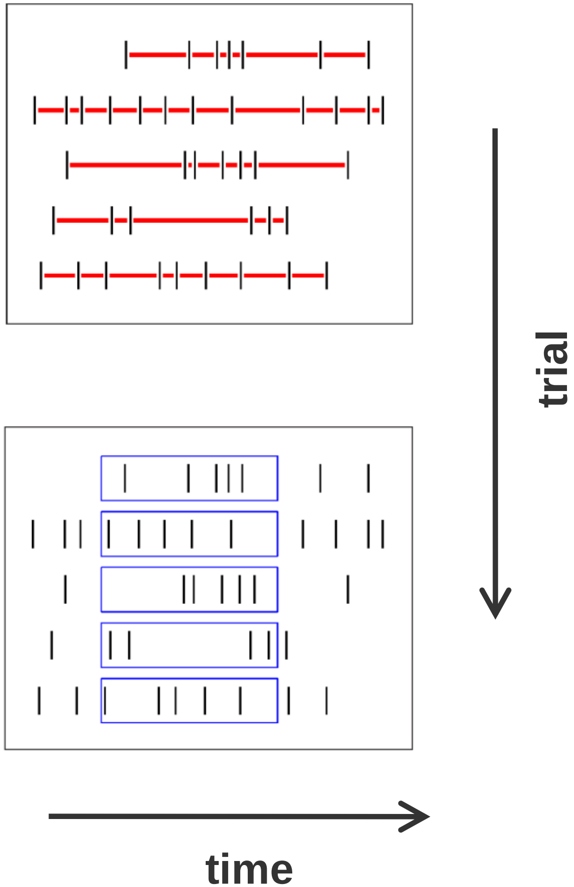
$$CV^2 = \frac{Var(ISI)}{mean^2(ISI)}$$

Fano factor (count variability)

$$FF = \frac{Var(count)}{mean(count)}$$

theoretic relation for **renewal process**

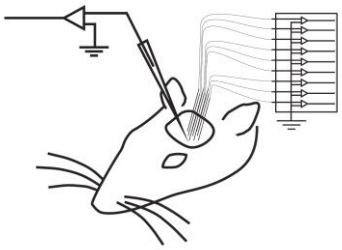
$$\boxed{FF = CV^2}$$

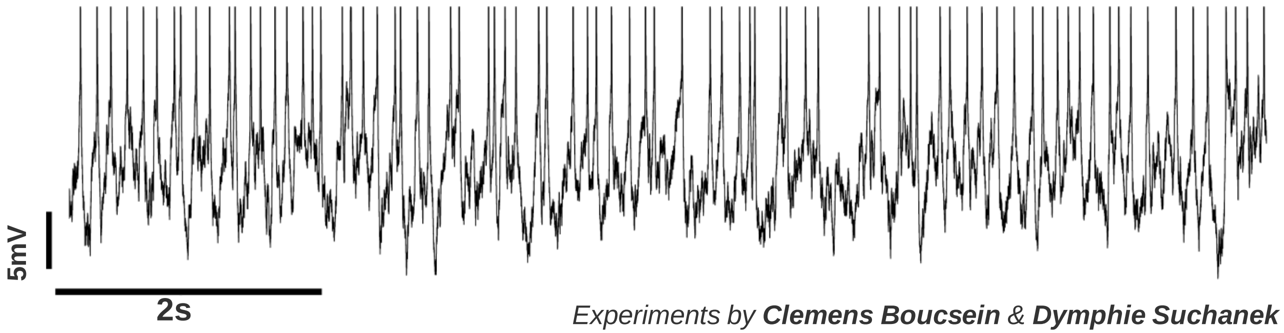


5. Combined Analysis FF vs. CV^2

- Serial correlation in experimental spike trains
- Non-stationarity across trials in experimental spike trains

Non-renewal spike trains | experimental evidence



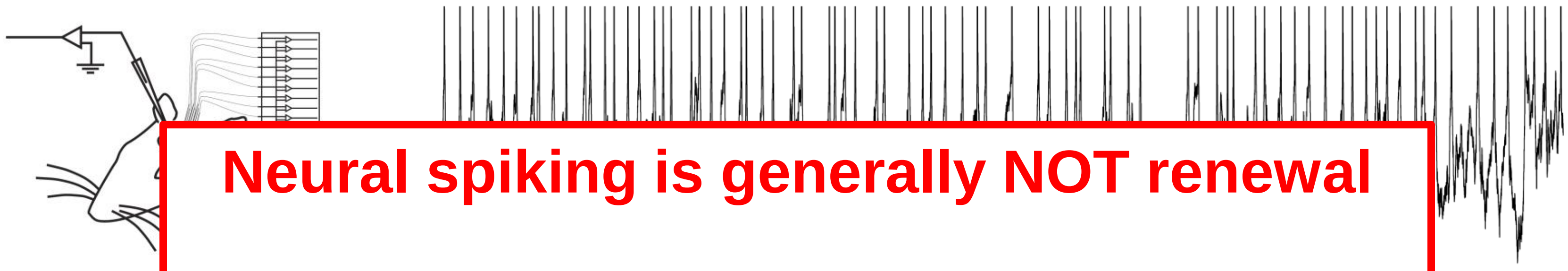


*Experiments by **Clemens Boucsein** & **Dymphie Suchanek***

University of Freiburg, Germany

- *In vivo* **intracellular** recordings, somatosensory cortex in the anesthetized rat

- **spontaneous activity** (no stimulation)

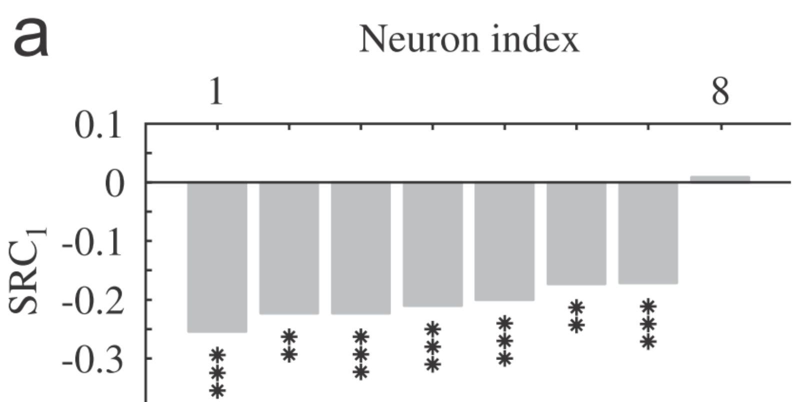


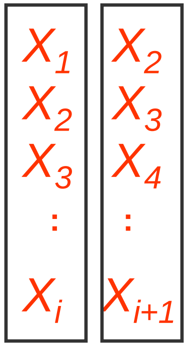
Neural spiking is generally NOT renewal

what could cause non-renewalty ?

...e Suchanek

...rg, Germany





- significant negative serial correlation of intervals in 7 of 8 cortical cells
- spiking process is *not* renewal

Nawrot et al. (2007) Neurocomputing 70: 1717-1722

Coefficient of variation
(of inter-spike intervals *X*)

$$CV^2 = \frac{Var(ISI)}{mean^2(ISI)}$$

Fano factor
(of spike count N)

$$FF = \frac{Var(count)}{mean(count)}$$

$$\boxed{\lim_{T\to\infty} \mathrm{FF} = \mathrm{CV}^2_{\infty}(1+2\,\xi) \quad \text{with } \xi = \sum_{i=1}^{\infty} \xi_i}$$

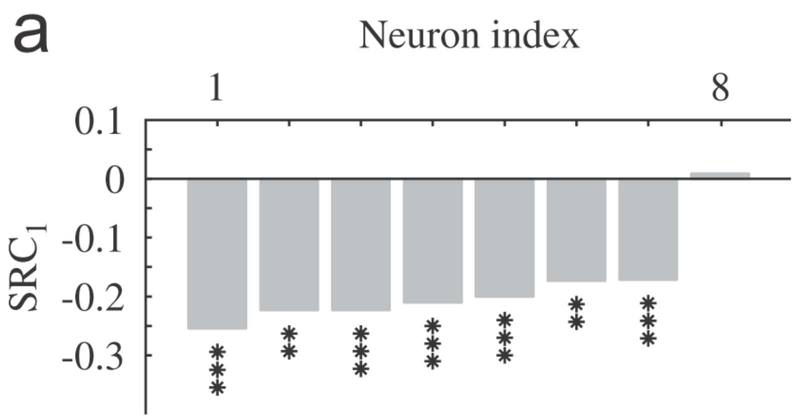
where ξi denote coefficients of serial interval correlation.

Thus, for equilibrium **renewal processes** we expect:

$$\boxed{\mathbf{FF \approx CV^2}}$$

Cox and Lewis (1966); Farkhooi, Müller, Nawrot (2011) Phys Rev E 83

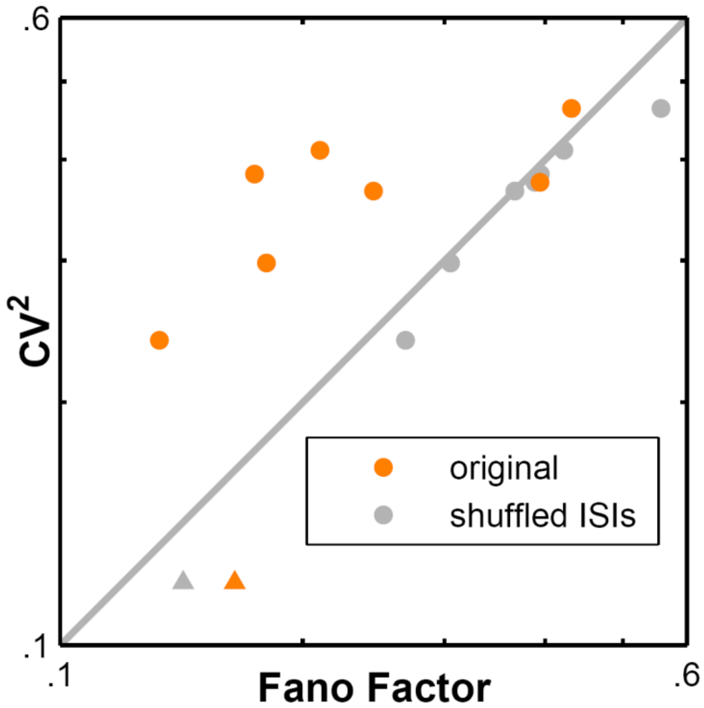
- Cortical neurons *in vivo* show small FF ≈ 0.25
- Non-renewal behavior FF < CV² (a *sink* of variability)



$$\lim_{T \to \infty} FF = CV^2 \left(1 + 2 \sum_{i=1}^{\infty} SRC_i \right)$$

Nawrot et al. (2007) Neurocomputing 70: 1717-1722

- Cortical neurons *in vivo* show small FF ≈ 0.25
- Non-renewal behavior FF < CV^2 (a *sink* of variability)

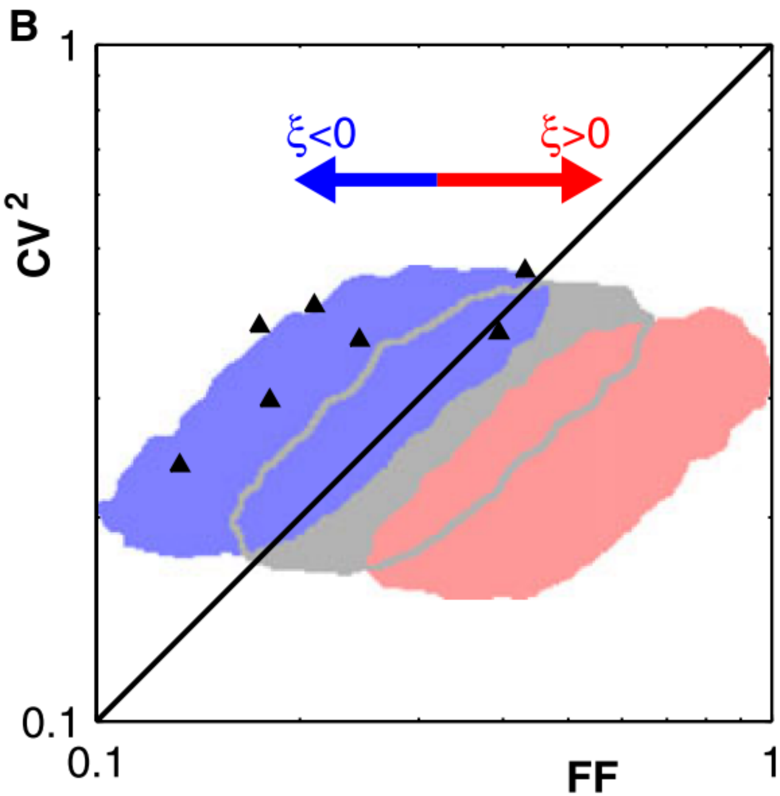


$$\boxed{FF < CV^2 \leq 0.5}$$

$$\lim_{T \to \infty} FF = CV^2 \left(1 + 2 \sum_{i=1}^{\infty} SRC_i \right)$$

Nawrot et al. (2007) Neurocomputing 70: 1717-1722

Non-renewal autoregressive point process



$$\lim_{T\to\infty} FF = CV^2\left(1 + 2\sum_{i=1}^{\infty} SRC_i\right)$$

Nawrot (2010) In: Grün, Rotter (eds.), Springer Series Comp Neurosci 7

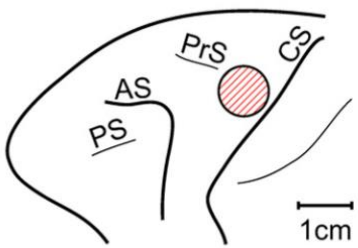
Non-renewal spike trains | experimental evidence

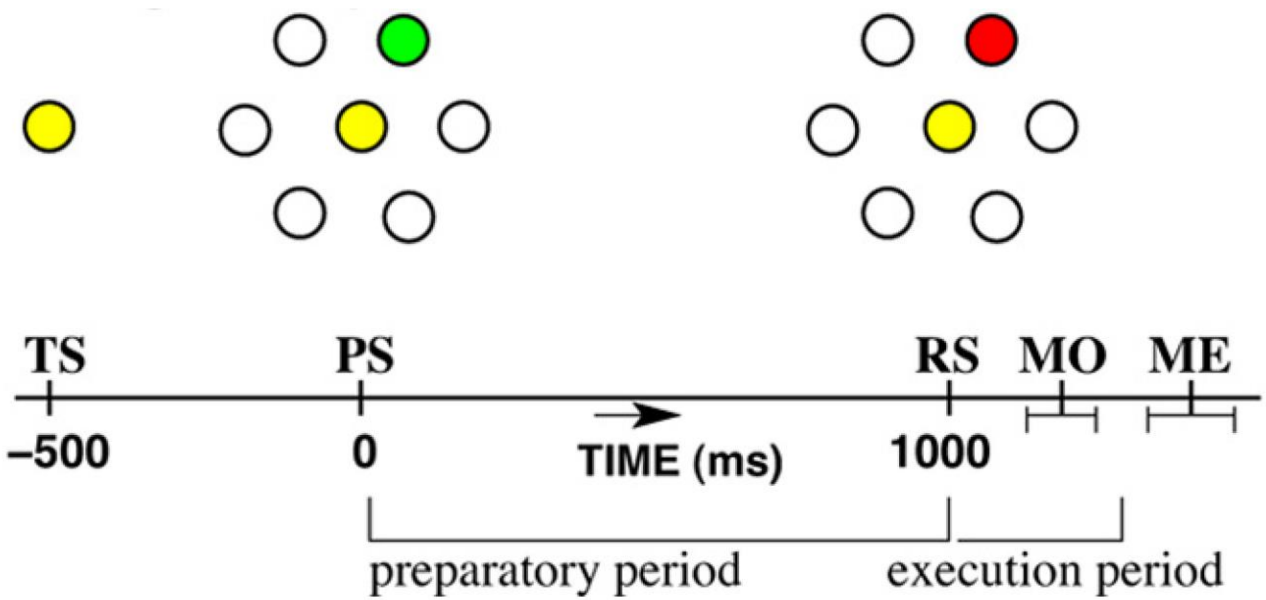
TABLE I. Reports on negative first-order serial interval correlation in different preparations and cell types.

Ref.	Model system and neuron type	SC[a]
[16]	Weakly electric fish, isolated *P*-type receptors afferent	−0.52
[17]	Weakly electric fish, isolated *P*-type receptors afferent	−0.35
[26]	Weakly electric fish, electrosensory line lobe, pyramidal cells *in vivo*	−0.29
[18]	Paddle fish, sensory ganglion	∼−0.4
[27]	Cat splanchnic, and hypogastric nerves *in vivo*	−0.3
[19]	Goldfish retina, ganglion cells *in vivo*	−0.13
[21]	Cat retina, ganglion cells *in vivo*	−0.06
[20]	Cat retina, ganglion cells *in vivo*	−0.17
[22]	Cat lateral superior olive *in vivo*	−0.2
[24]	Rat somatosensory cortex ($S1$) *in vivo*, regular spiking cells	−0.21
[24]	Rat somatosensory cortex ($S1$) *in vitro*, pyramidal cells	−0.07
[25]	Rat medial entorhinal cortex *in vitro* layer II stellate and layer III pyramidal neurons	[−0.1, −0.4][b]
III[c]	Honeybee central brain *in vivo* mushroom body extrinsic neurons	−0.15

[a]SC: serial correlation coefficient; for the estimation method, refer to the respective reference.
[b]This study reported a rate dependent serial correlation.
[c]Refer to Sec. III.

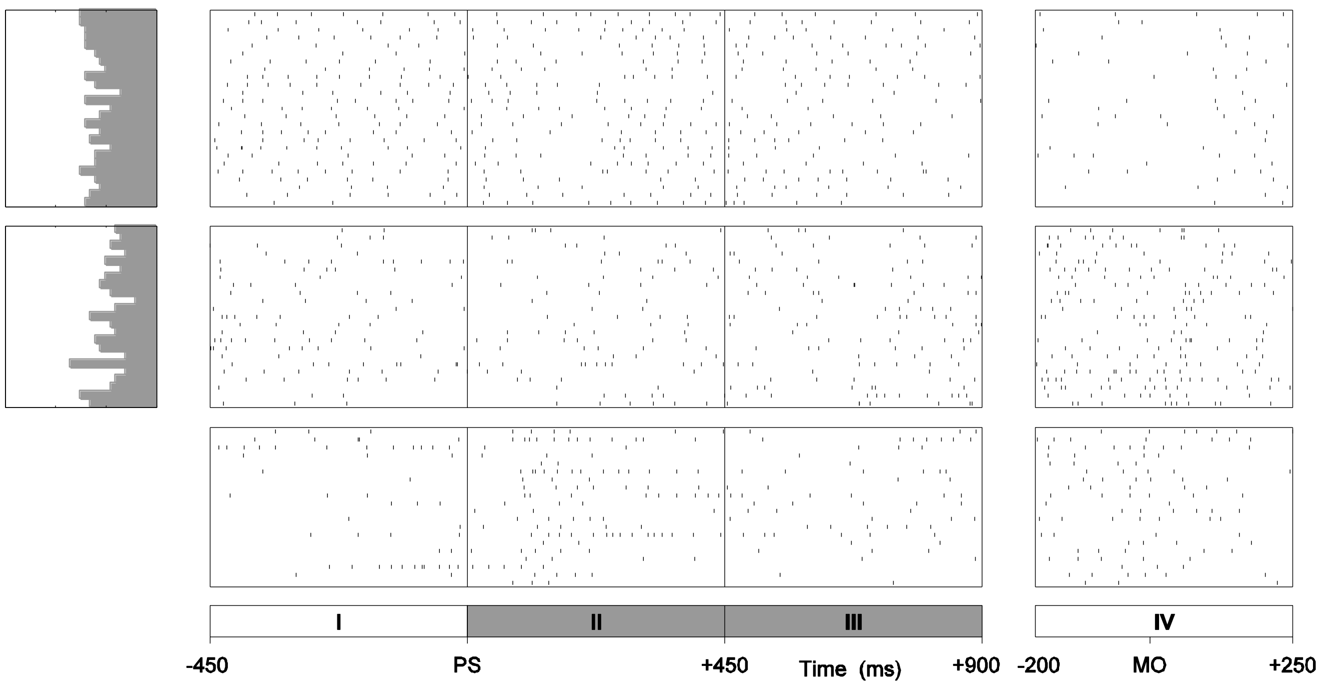
Farkhooi, Strube-Bloss, Nawrot (2009) Phys Rev E 79



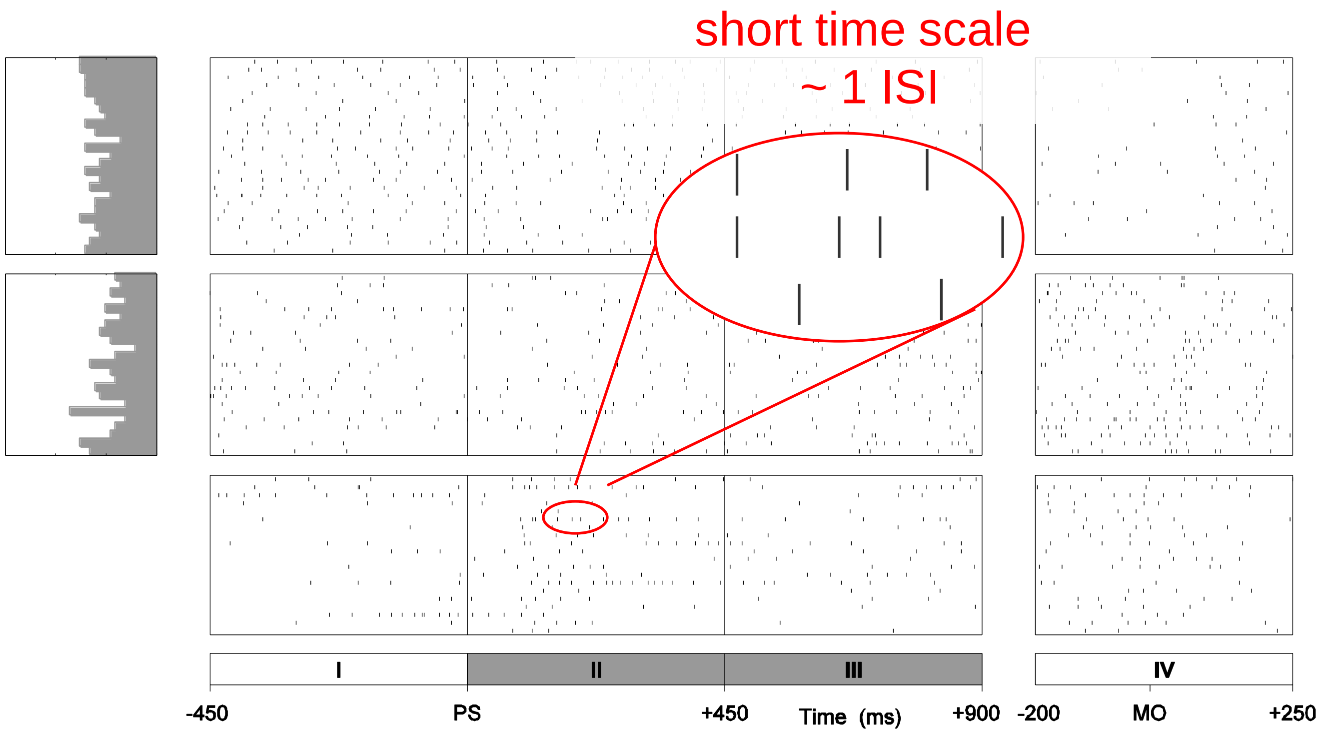


Experiments by ***Alexa Riehle,*** *CNRS & Université Marseille*

Variability in the Motor Cortex



- Interval variability: CV2



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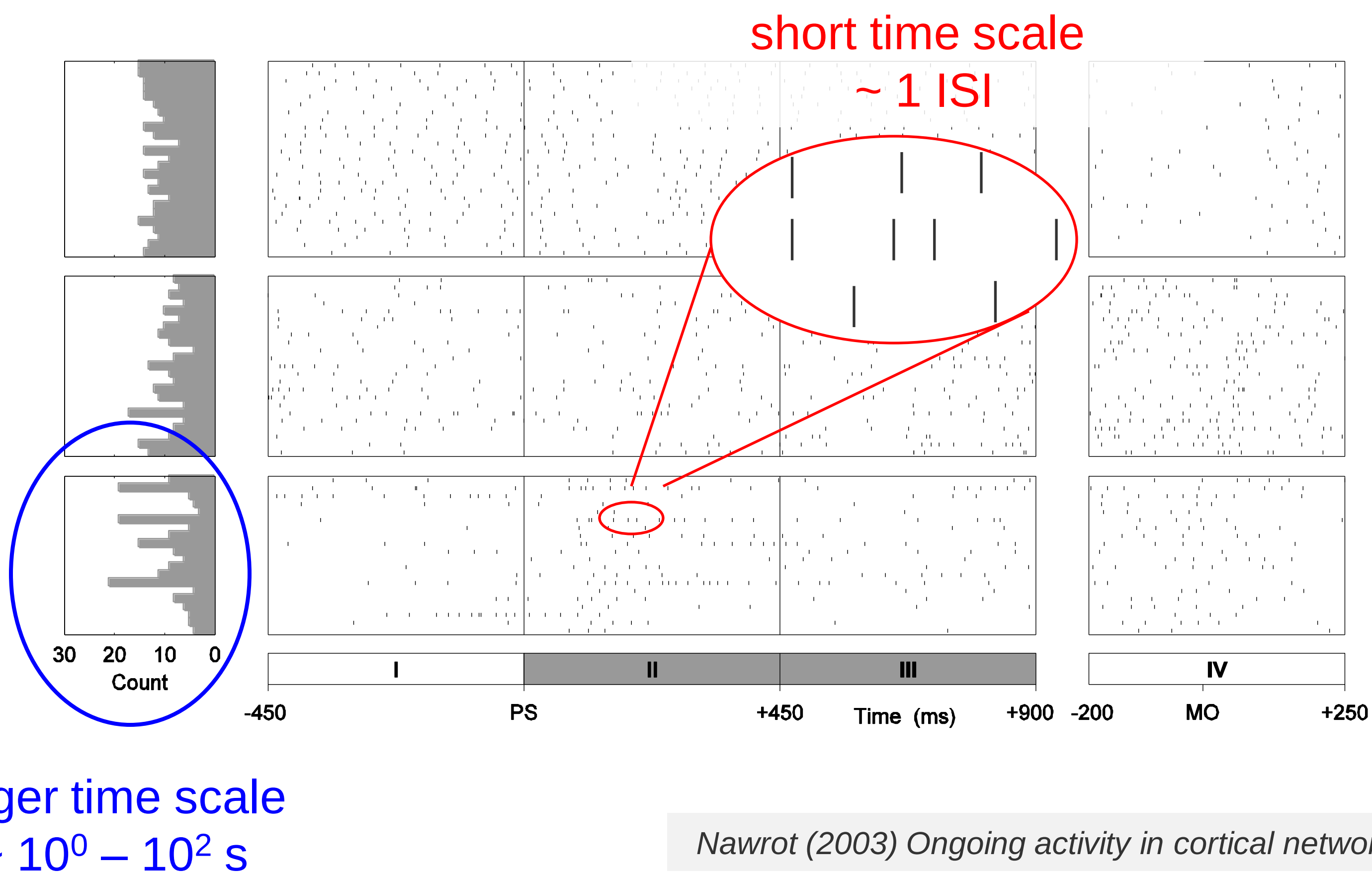
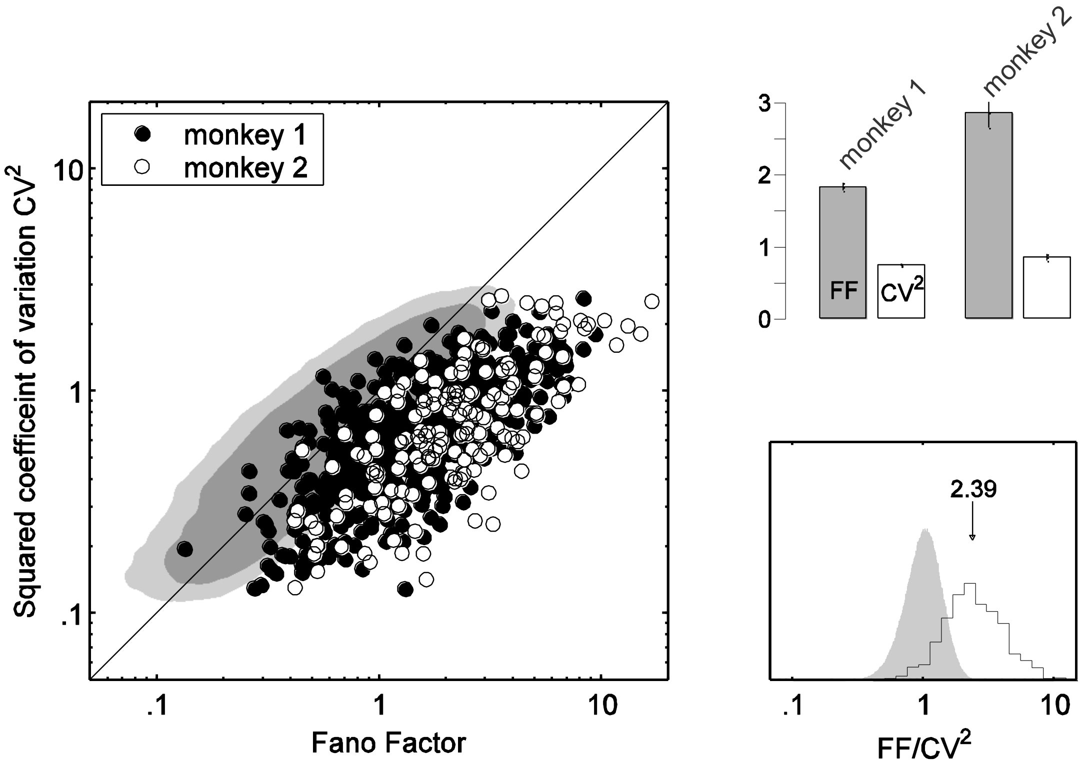
- Interval variability: CV2
- Spike count variability: FF



Nawrot (2003) Ongoing activity in cortical networks. PhD Thesis

► cortical neurons *in vivo* disagree with renewal prediction



$FF >> CV^2$

Nawrot (2010) In: Grün, Rotter (eds.), Springer Series Comp Neurosci 7

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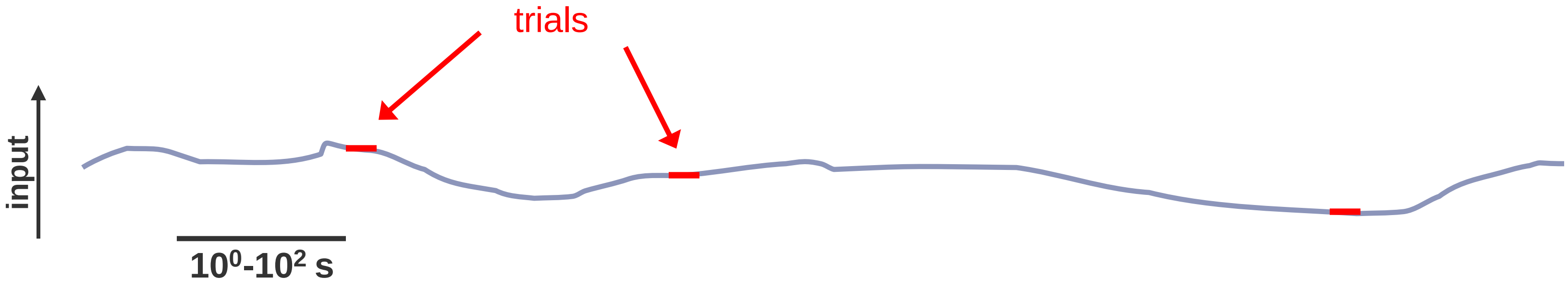
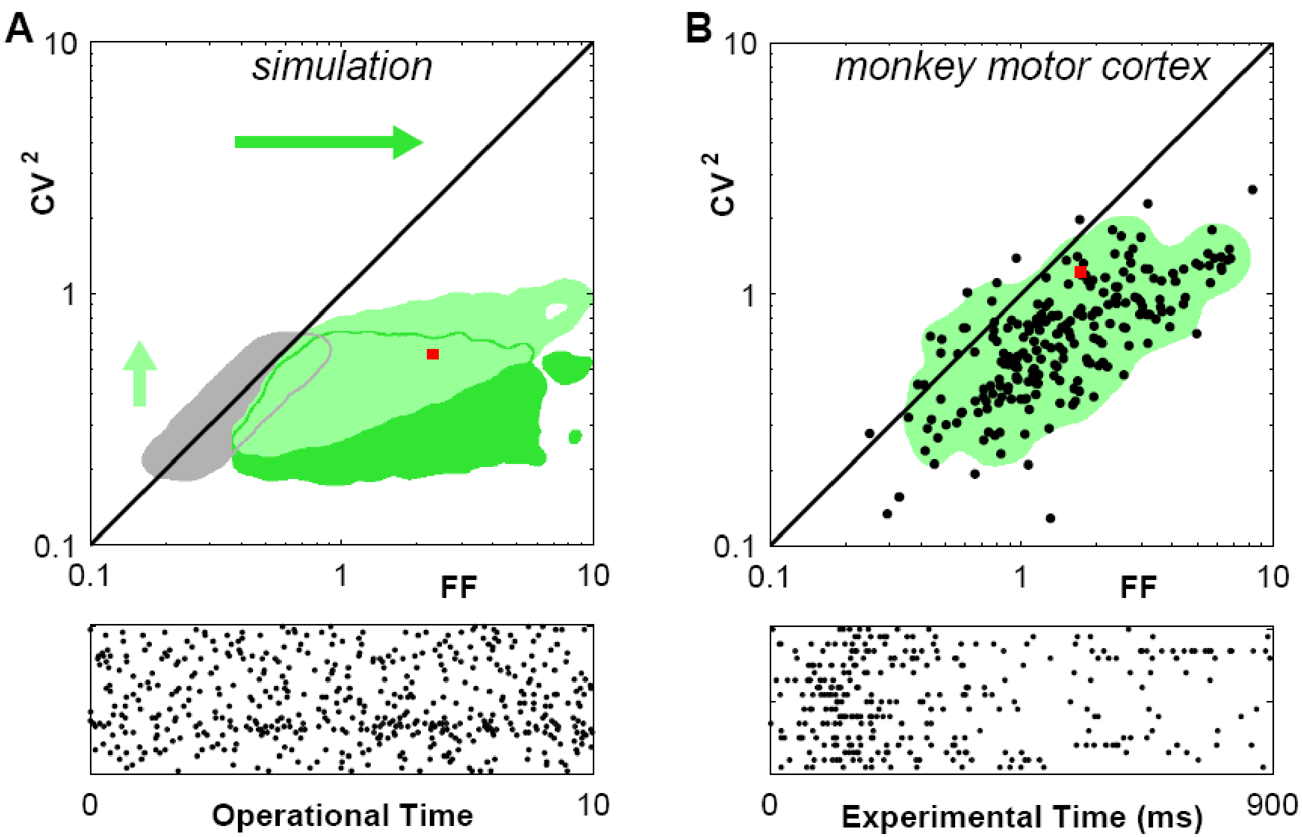
Slow modulation of the network state (background)

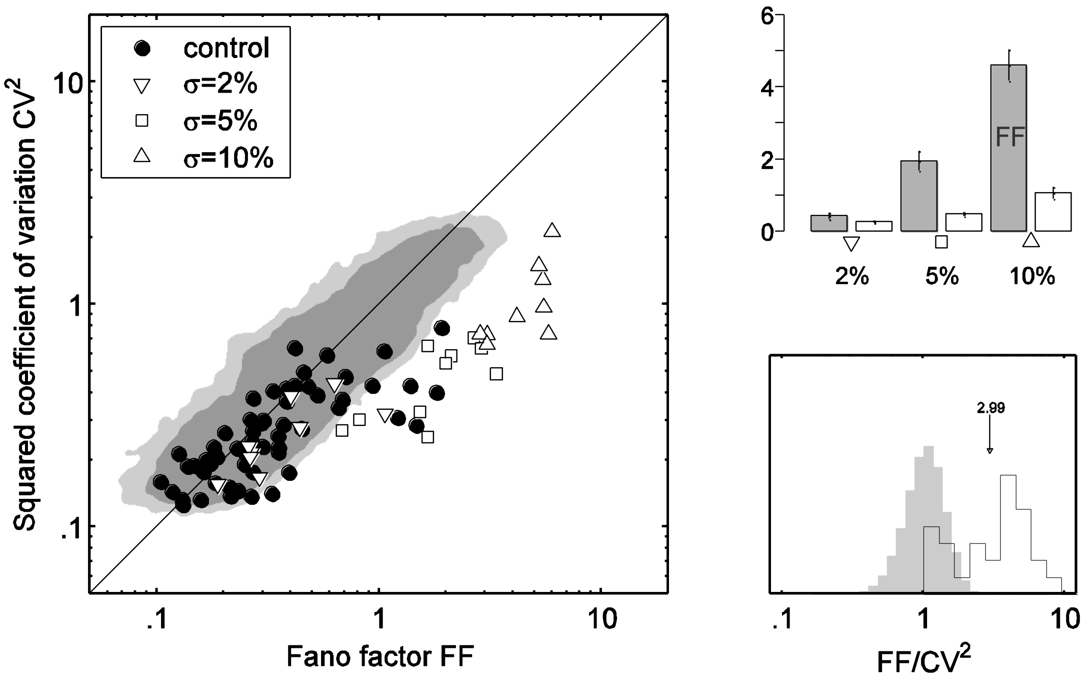



A
simulation
CV 2
FF
10
1
0.1
0.1
1
10
Operational Time
0
10
B
monkey motor cortex
CV 2
FF
10
1
0.1
0.1
1
10
Experimental Time (ms)
0
900

in vitro test of the model

5–10% input variability boosts output variability (~ by factor 2-10)

$$FF > CV^2$$

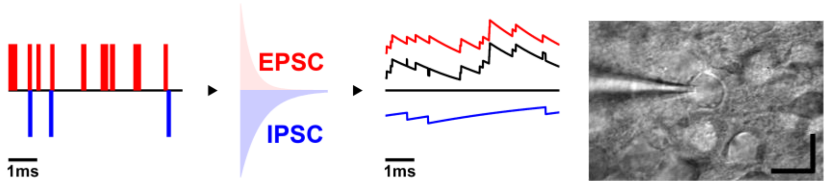


FF > 1.5

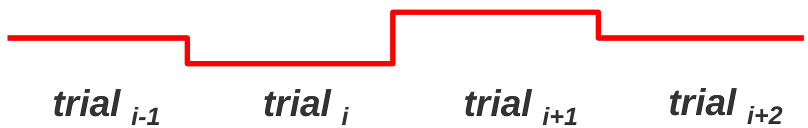
Rotter, Riehle, Rodriguez, Aertsen, Nawrot (2005) Soc. Neurosci. Abstr. 276.7

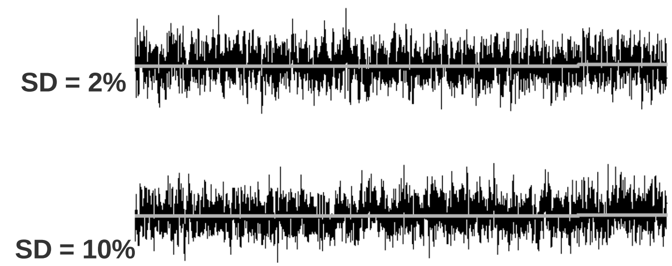
A Model of slow network state dynamics

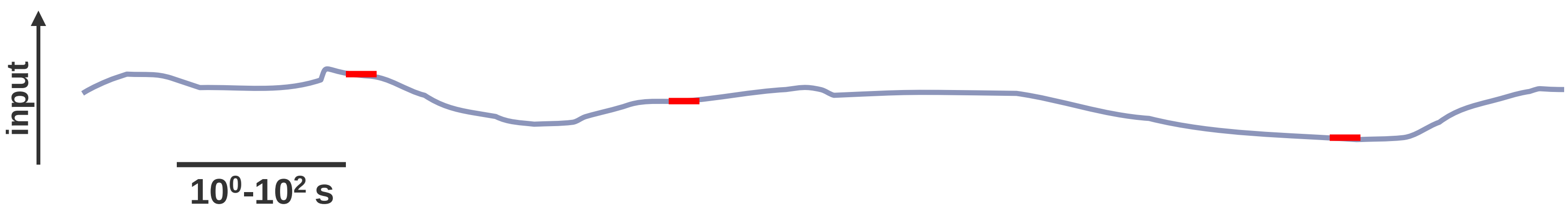
in vitro test of the model



$$
\begin{aligned}
I_i &= I_\phi + I_{\theta,i} \\
&= [I_\phi + E(I_\theta)] + \Delta I_{\theta,i} \\
&= I_{\text{net}} + \Delta I_{\theta,i}.
\end{aligned}
$$



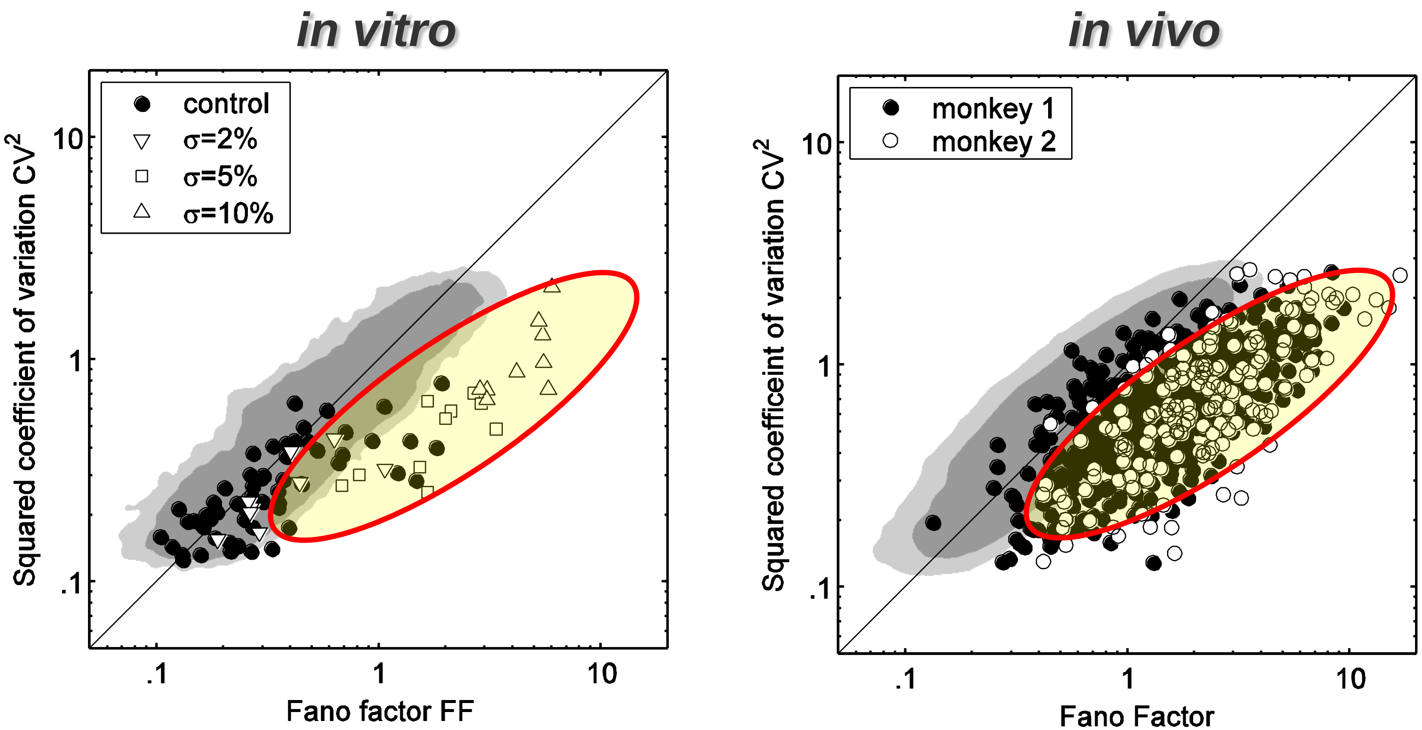




in vitro test of the model

5–10% input variability boosts output variability (~ by factor 2-10)

model of slow activity modulation can explain excess variability



Rotter, Riehle, Rodriguez, Aertsen, Nawrot (2005) Soc. Neurosci. Abstr. 276.7

THANKS (a.u.)

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Thomas Rost
Berlin, Germany

Eilif Müller
Lausanne, Switzerland

Ad Aertsen
Freiburg, Germany

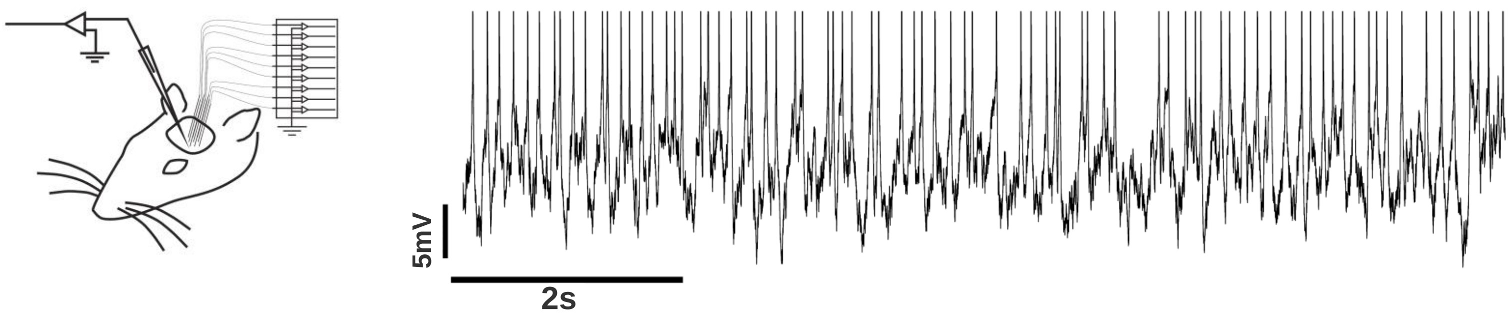
Stefan Rotter
Freiburg, Germany

Sonja Grün
Jülich, Germany

Additional Material

Experiments *by Clemens Boucsein and Yamina Seamari, Uni Freiburg*

- *In vivo* **intracellular** recordings from *cortical neurons* in anesthetized rat
- **spontaneous activity** (no stimulation)



A1_data_set_040528_boucsein

Nawrot et al. (2007) Neurocomputing 70: 1717-1722

Computational *versus* Stochastic Models

computational models

- abstract or biophysical models
- deterministic input/output relation

- Type I / Type II models
- Integrate & Fire
- McCulloch Pitts
- ...

Computer simulations translate synaptic inputs into spike output
$\Rightarrow$ spike train

Useful to investigate biophysics and neural networks

stochastic point process models

- abstract mathematical definition
- probabilistic theory (‘randomnes’)
- no input/output conversion

Numeric simulation generates random point process realization
=> spike train

Useful to make statistical predictions for spike train analysis