Neuroinformatics and Theoretical Neuroscience
Institute of Biology – Neurobiology

Bernstein Center for
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Stochastic Point Processes

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Oct 13, 2011

1. Inroduction

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

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

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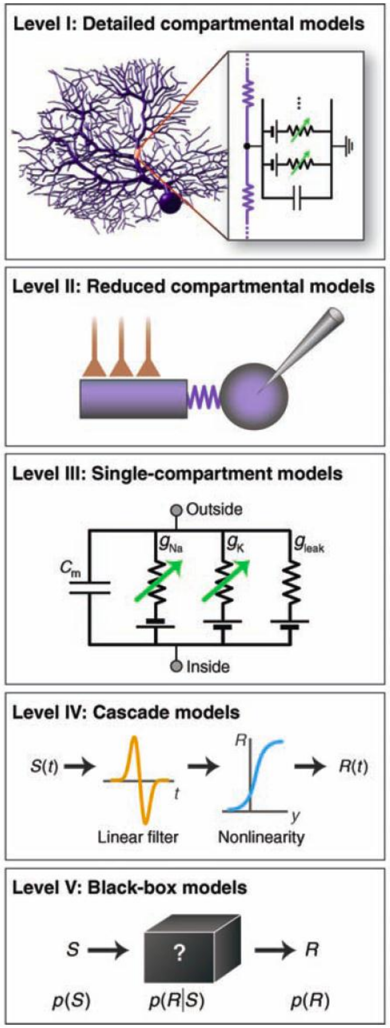


Herz A, Gollisch T, Machens CK, Jaeger D (2006)
Modeling Single-Neuron Dynamics and Computations: A Balance of Detail and Abstraction. Science 314, p. 80–84

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).

In computational neuroscience point processes are used *to simulate* single neuron activity and *to predict* the statistical measures of spiking activity.

Spike Train Representation

‘ spike train ‘

discrete time series of events

Spike Train Representation

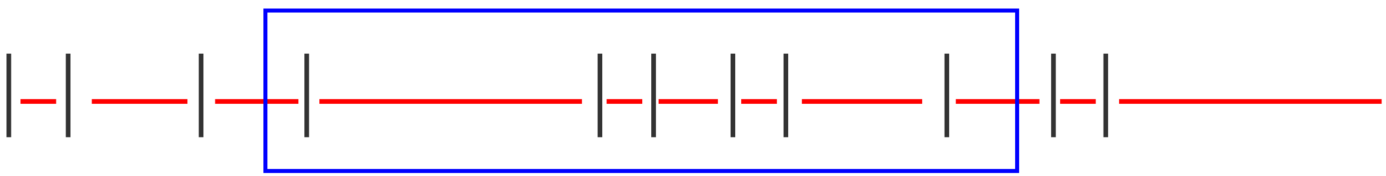
discrete representation (*list*)

1010000100010000000000101001010000010001010000000001

binary representation (*array*)

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.

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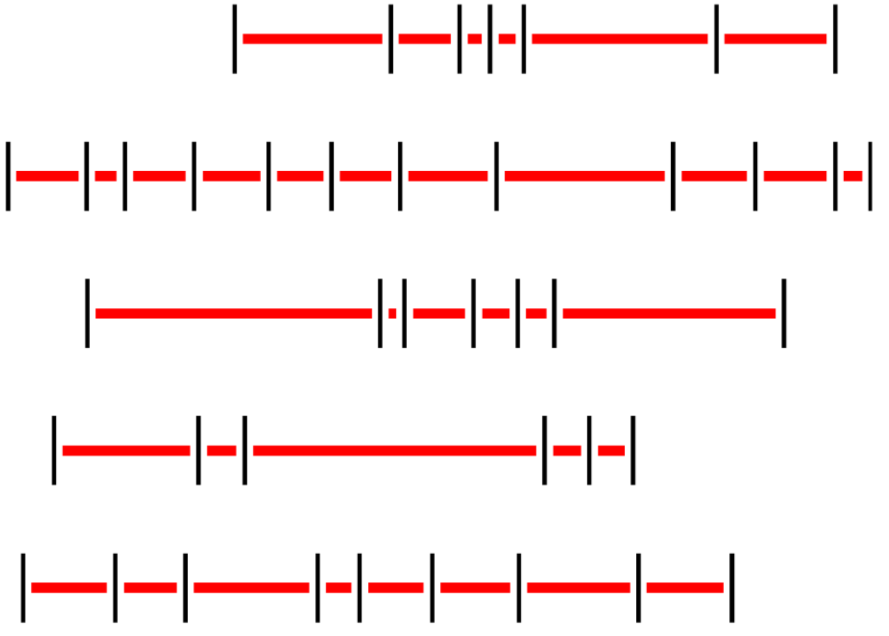
binary representation



inter-spike intervals
continuous data

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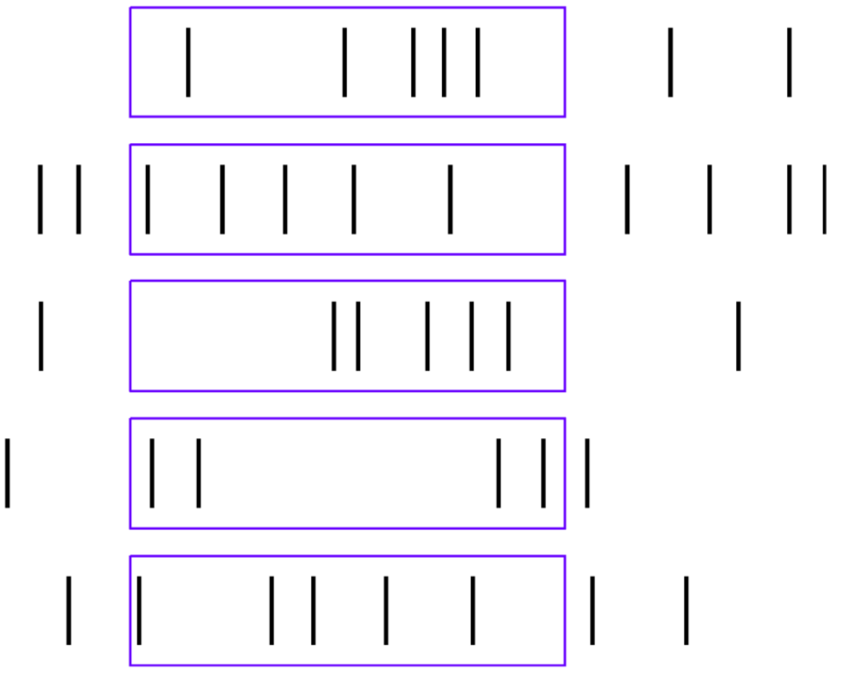

spike count

discrete data

2. Stationary Point Processes

- interval and count random variables
- Bernoulli process
- Poisson process
- renewal process

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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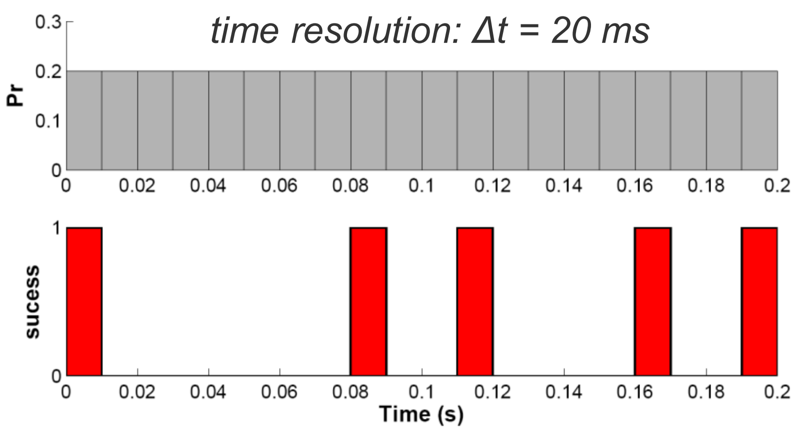

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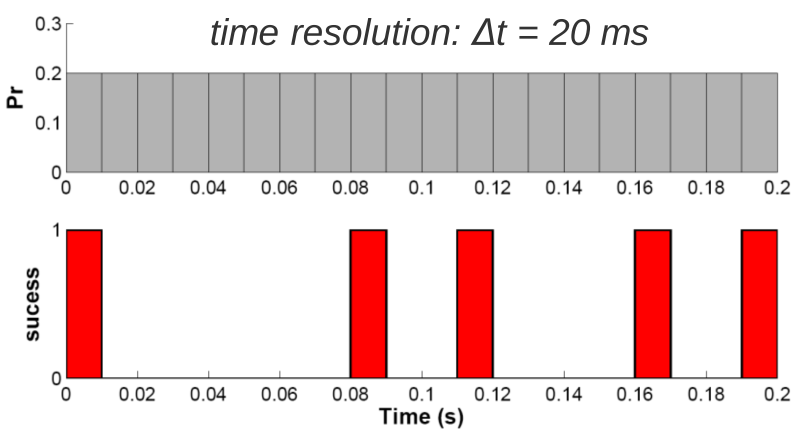
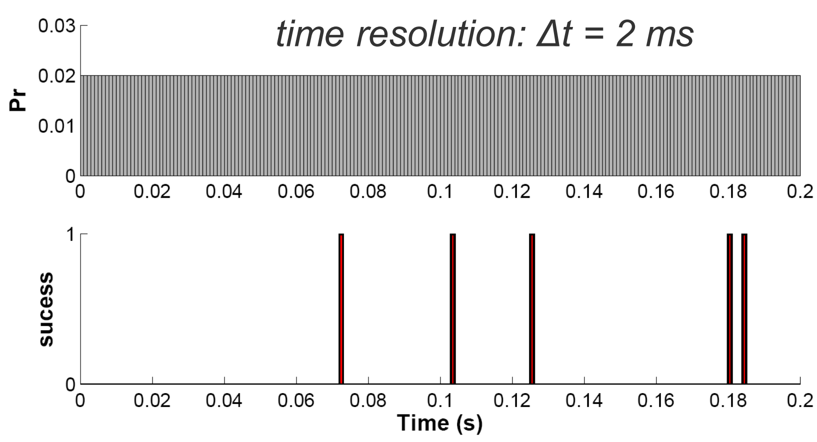
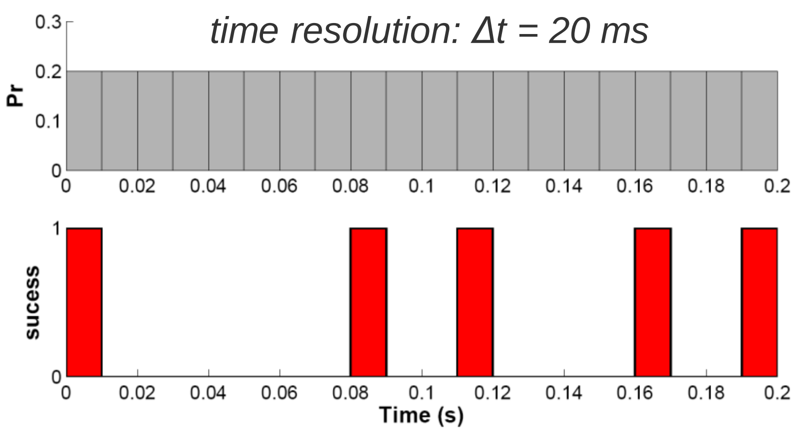
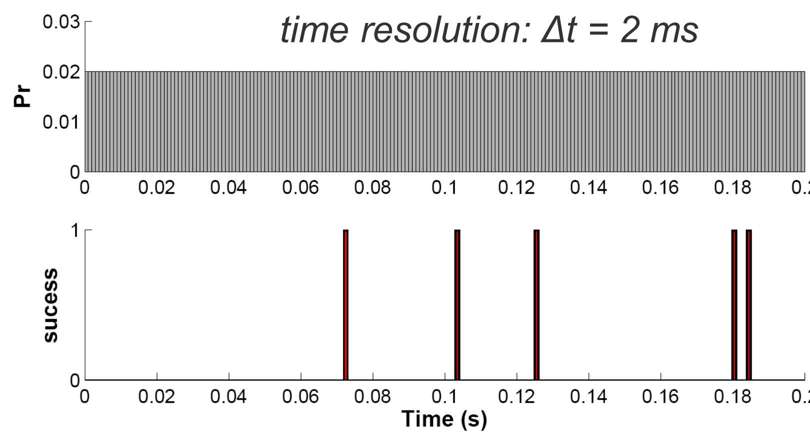




What is a good time resolution Δt for simulating a series of action potentials ?

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

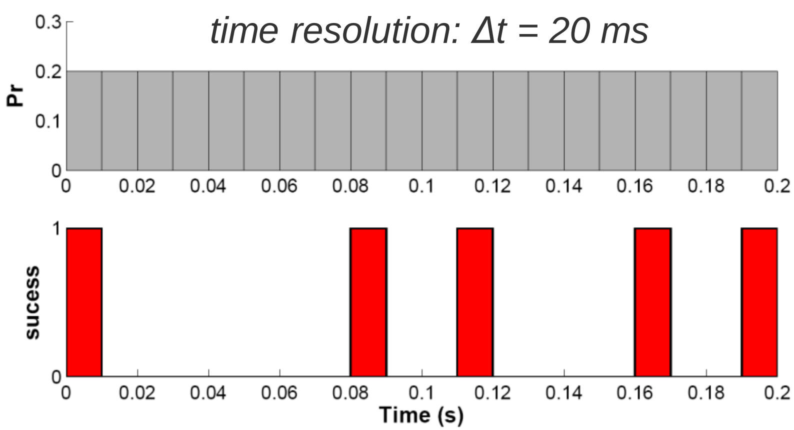


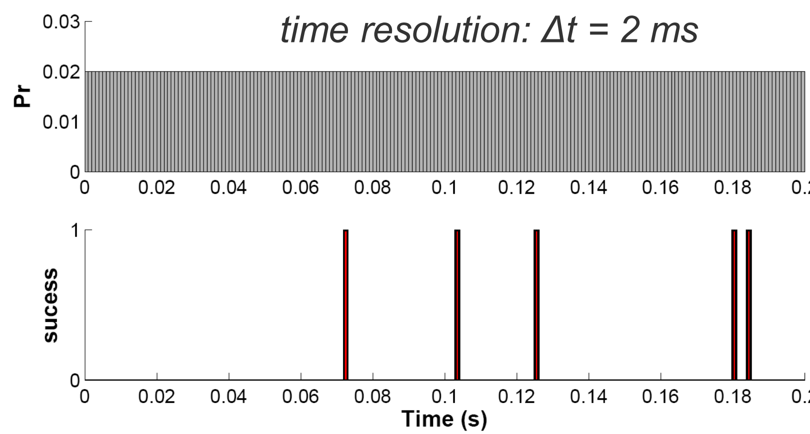


What is a good time resolution Δt for simulating a series of action potentials ?

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).





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

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

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

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

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

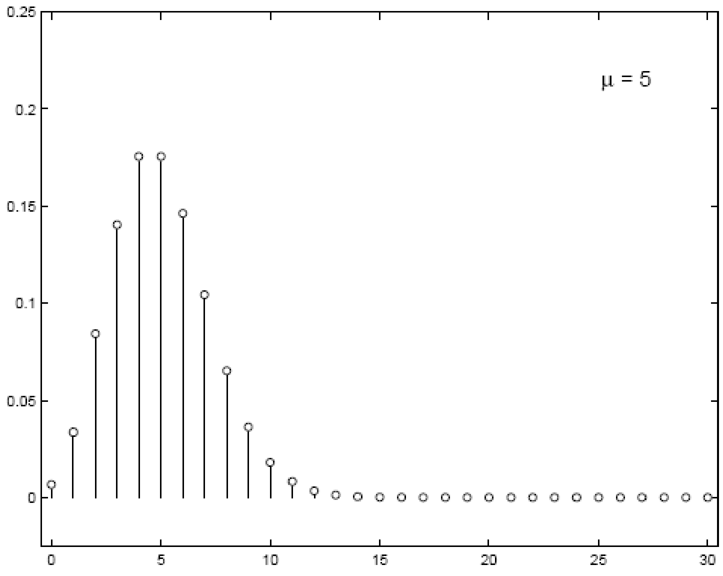
Definition

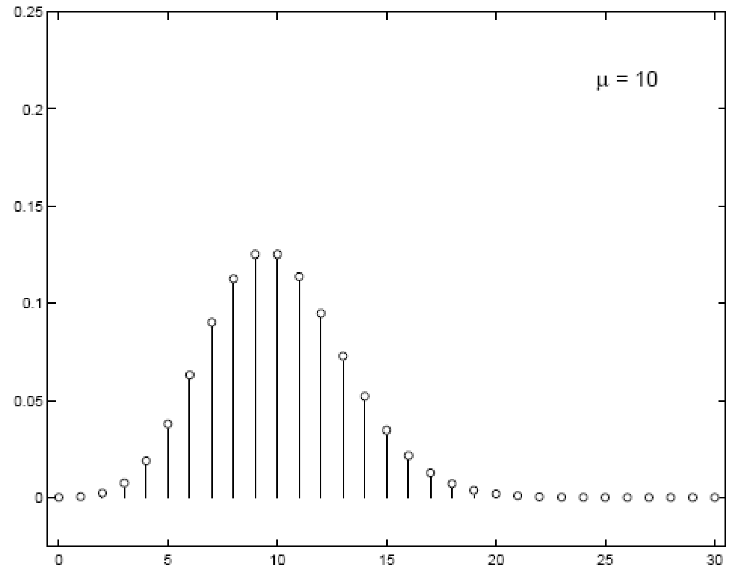
The **Poisson process** of intensity λ is defined by the requirements that for all t and for $\delta \to 0+$

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

- 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 $\Delta t \to 0$.

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





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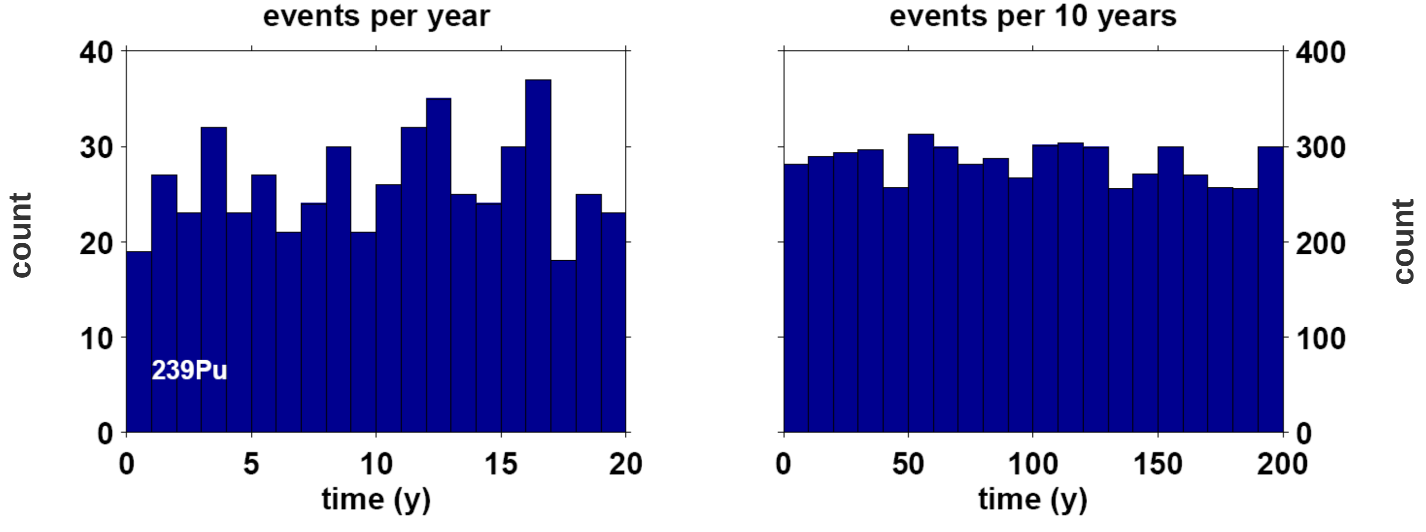
$$P\{N(A) = k\} = \frac{\mu^k}{k!}\, e^{-\mu}$$

$$A = (0, t]; \qquad \mu = \lambda \cdot t$$

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

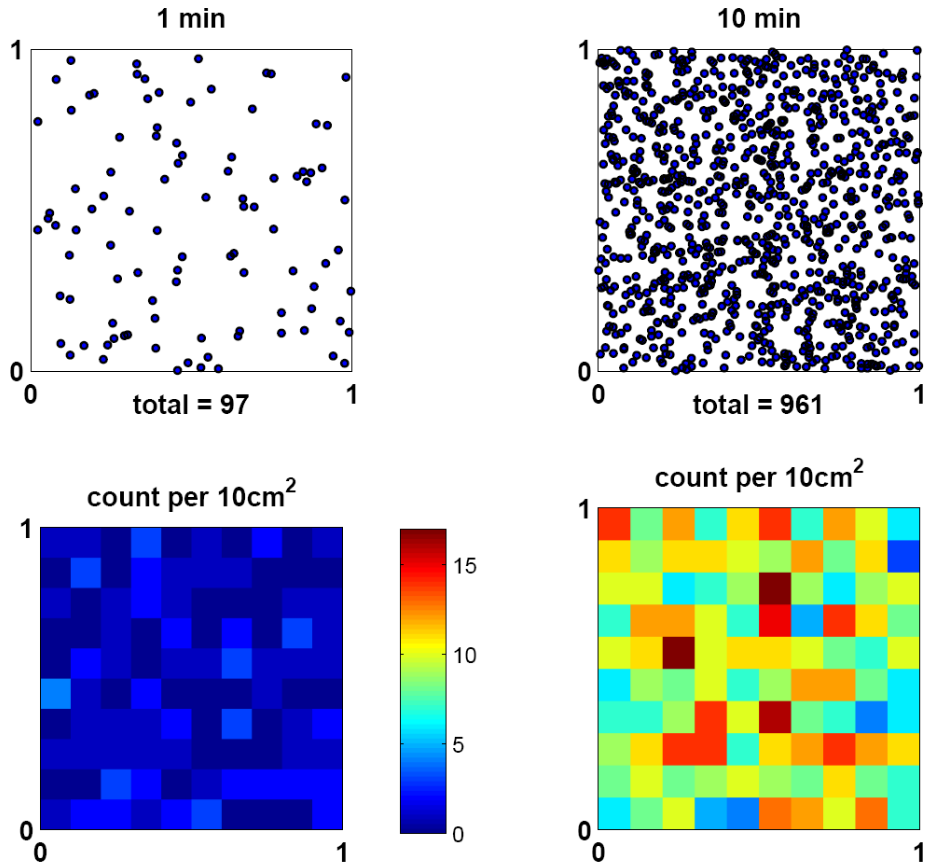
Example 1: radioactive decay of 239Pu (half-life : 4110 years).

- continuous time intervals
- discrete event count



Example 2: rain drops

- continuous space intervals
- discrete event count



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

$$P\{X_k > t\} = Pr\{N(t) < k\}$$

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

constant intensity λ

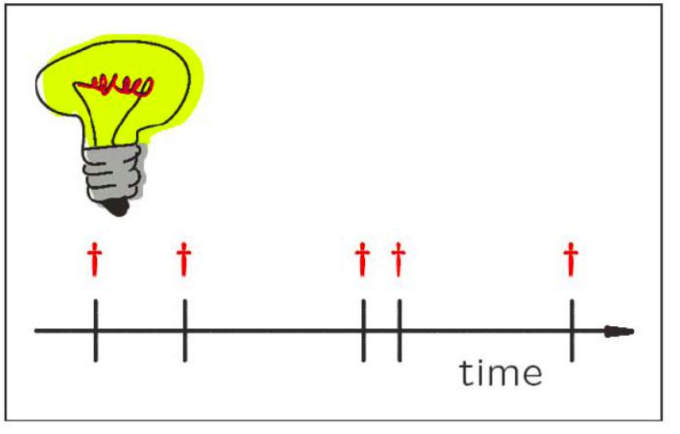
Poisson
• exponential interval distribution
• Poisson count distribution
• events are uniformly distributed in time
• special case of gamma process

Definition

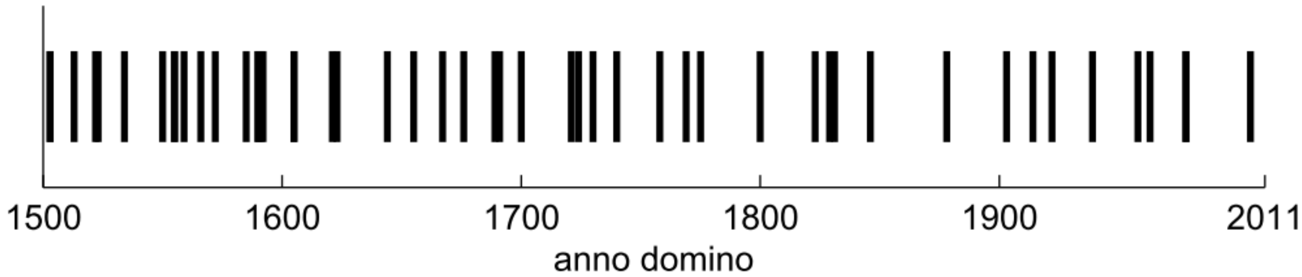
inter-event intervals are **independent** and **identically distributed** (iid)

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



† = replacement from a homogeneous population


1500
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Definition

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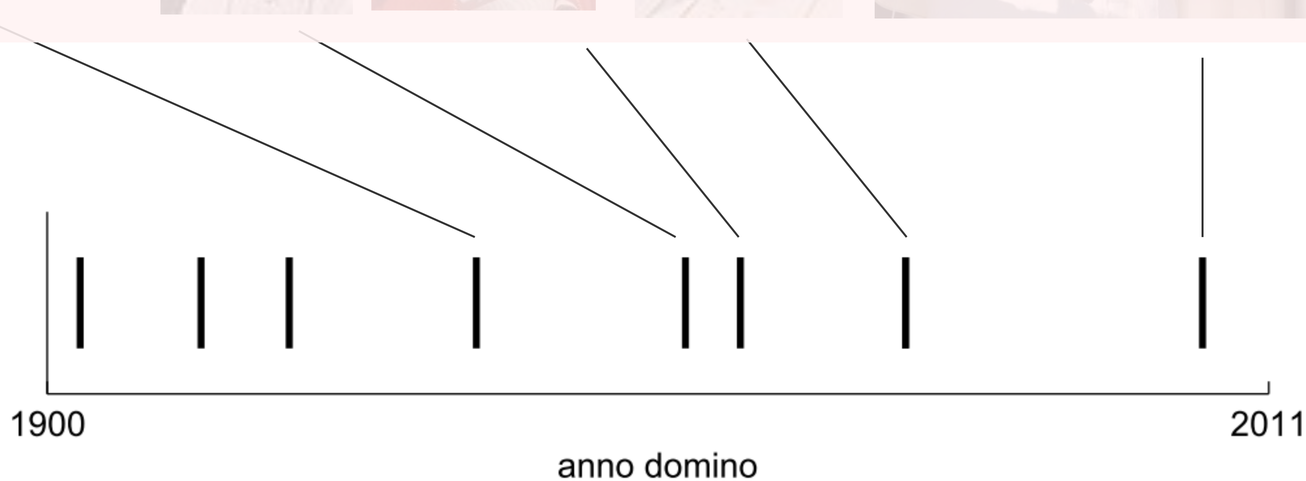
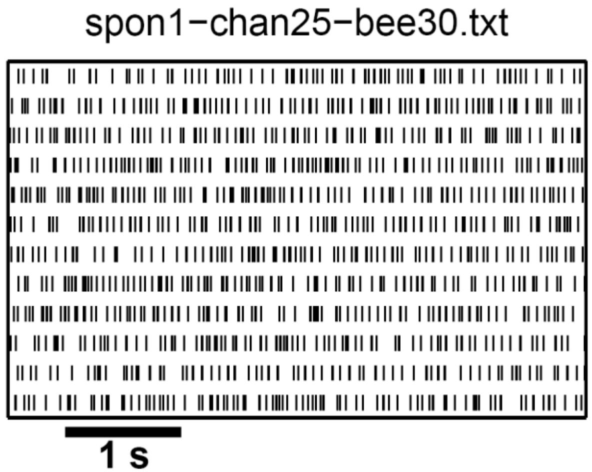
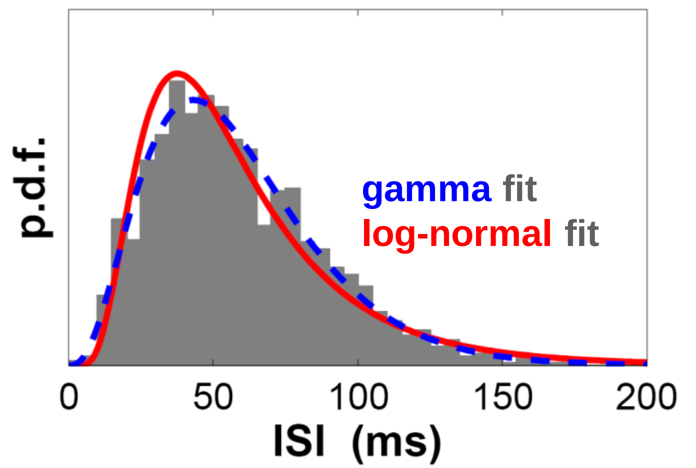


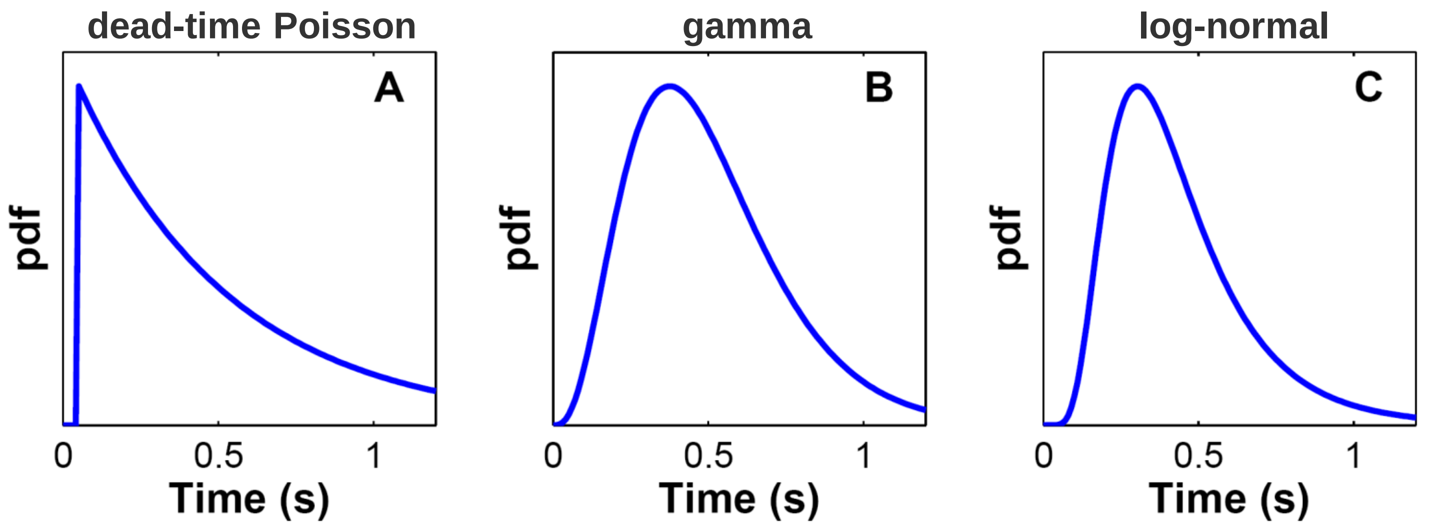




Extracellular single unit recording of spontaneous activity from a so-called extrinsic neuron of the honeybee mushroom body. The empirical interval distribution is estimated by the gray historgram from a total of 1530 ISIs. The mean interval length is $m = 58.7$ ms, i.e. the average rate can be approximated by $\lambda \approx 1/m = 17.03/\text{s}$. 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

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



constant intensity λ

Poisson

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

Renewal

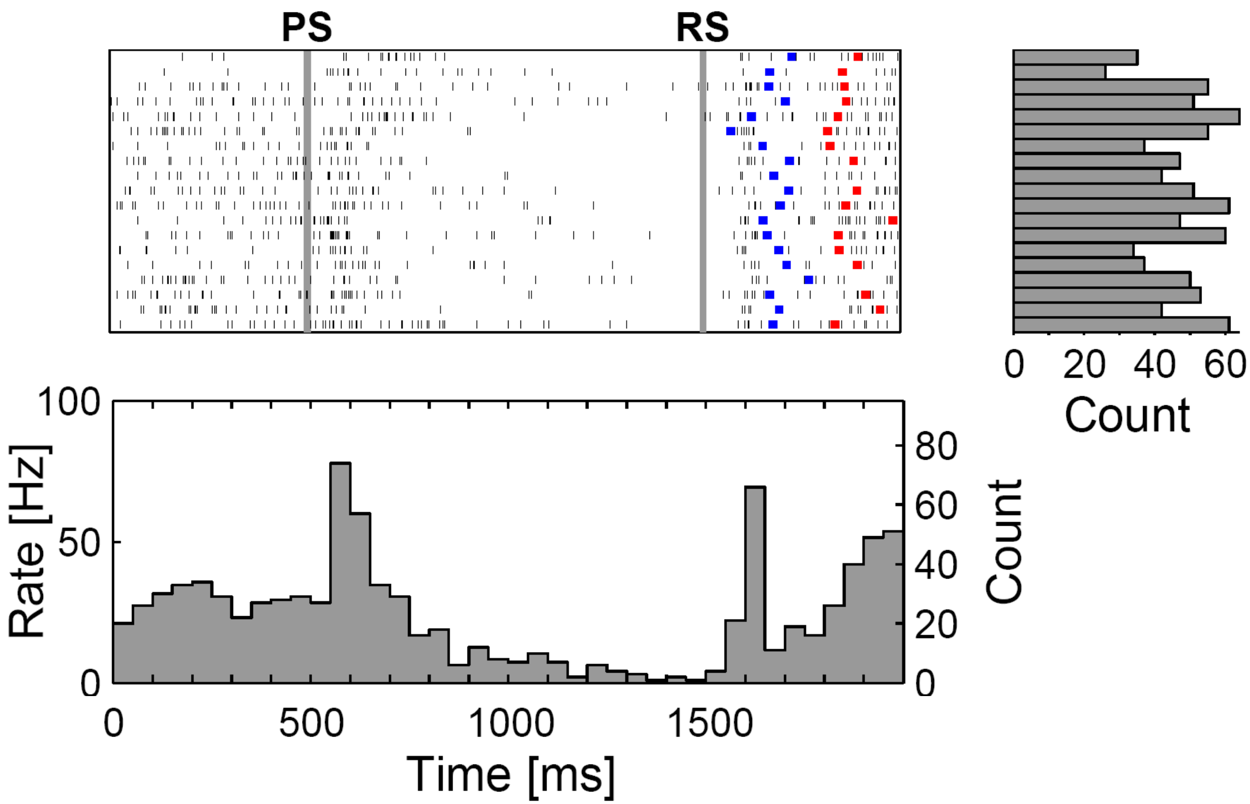
- iid interval distribution
- FF = CV^2

increasing importance of process history

3. Non- Stationary Point Processes

- nonhomogenous Poisson process
- non-renewal processes

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.



Single unit activity from primary motor cortex of the monkey during repeated reaching movement
Data Curtsey: Alexa Riehle, CNRS, Marseille

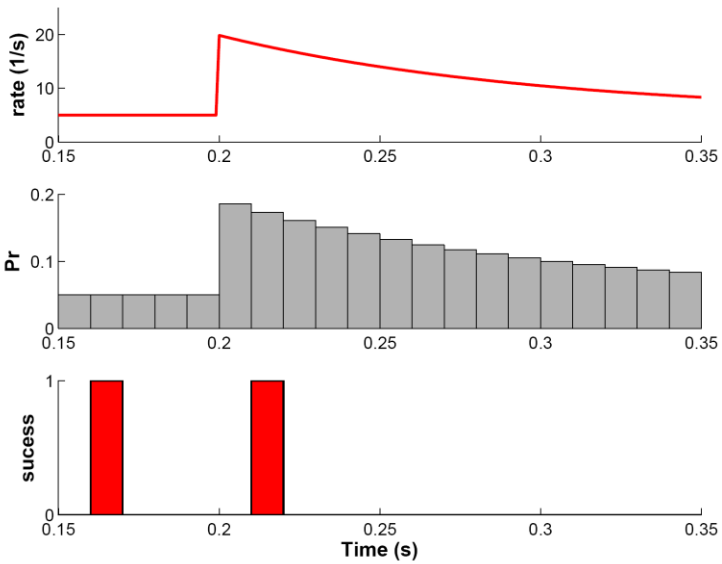
Definition

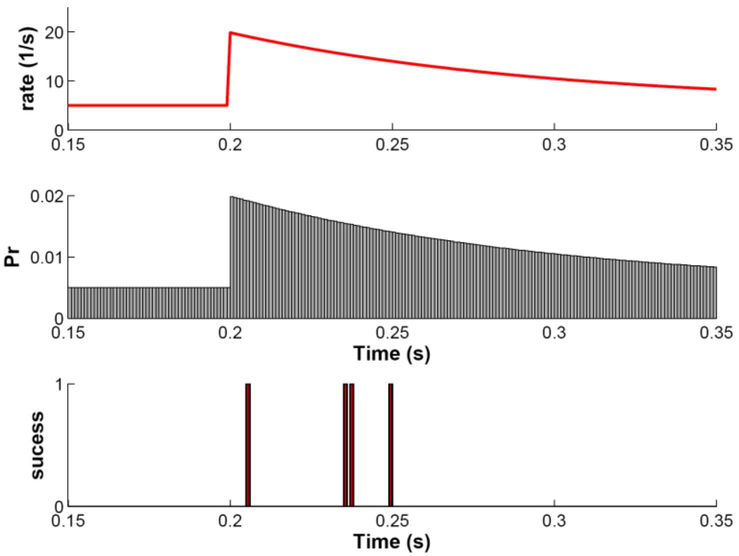
We substitute the constant intensity λ by the explicitly time-dependent intensity funtion λ(t) and define the **nonhomogenous Poisson** process for all t and for $\delta \rightarrow 0+$

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

The instantaneous probability is still independent of the process history!

Bernoulli approximation:





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

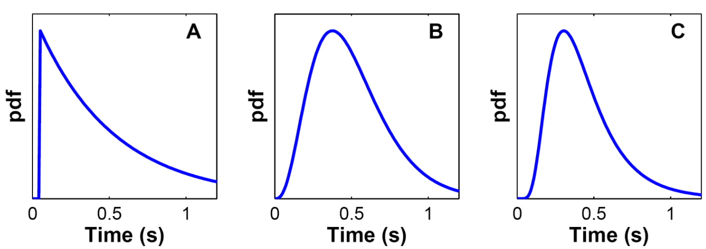
- iid interval distribution
- FF = CV^2

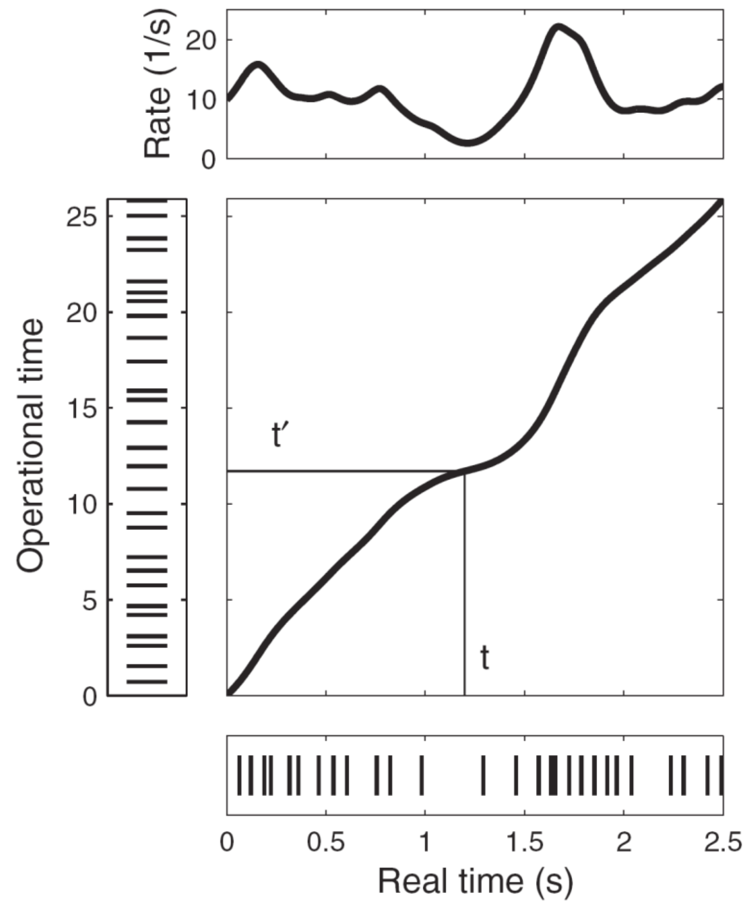
increasing importance of process history

Simulation with **time rescaling**:

- simulate renewal process in ‘**operational time**’ (with unit rate)
- transform to ‘real time’ using your **intensity function λ(t)**

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



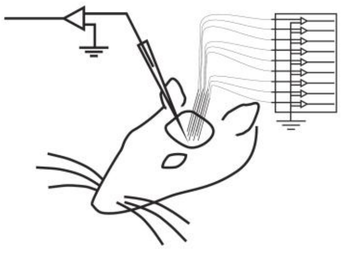


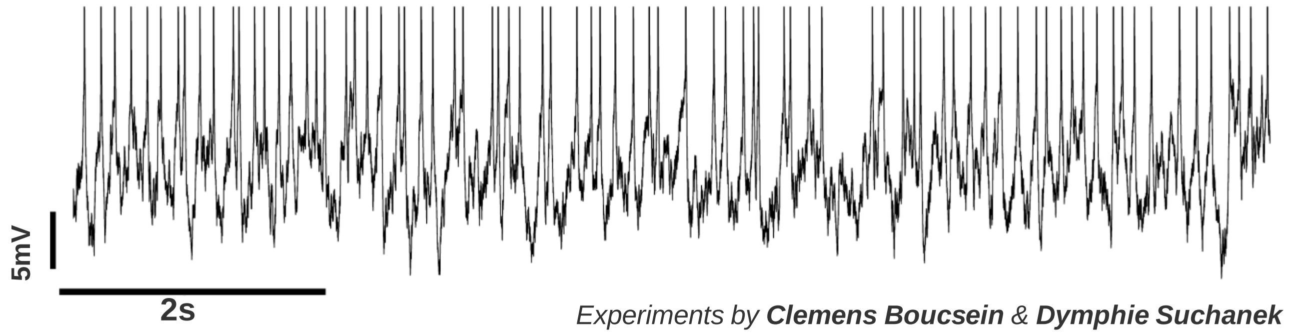
constant intensity λ	*dynamic intensity λ(t)*
Poisson • exponential interval distribution • Poisson count distribution • events are uniformly distributed in time • special case of gamma process	**non-homogenous Poisson**
Renewal • iid interval distribution • FF = CV^2	**rate-modulated Renewal**

increasing importance of process history

4. Non - Renewal Point Processes

- modeling serial interval correlation
- modeling spike-frequency adaptation



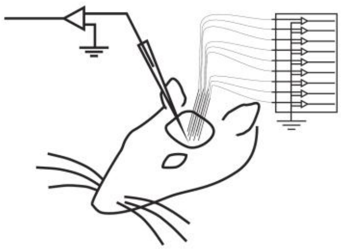


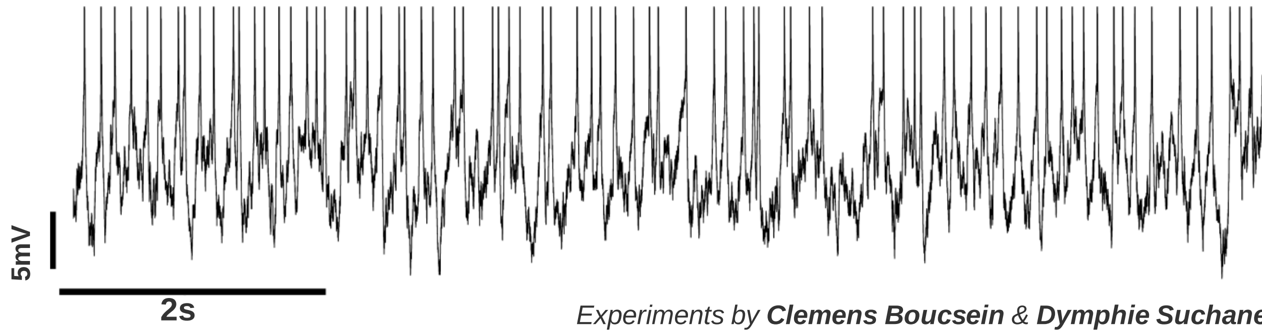
*Experiments by **Clemens Boucsein** & **Dymphie Suchanek***

University of Freiburg, Germany

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

- **spontaneous activity** (no stimulation)





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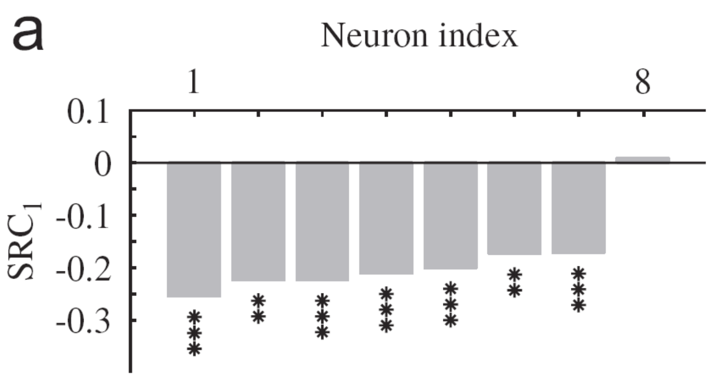

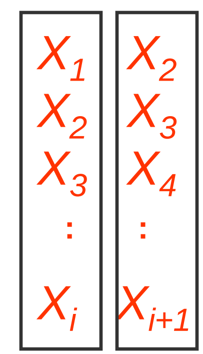

- significant negative serial correlation of intervals in 7 of 8 cortical cells
- spiking process is *not* renewal

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

Reference	Model System & Neuron Type	SC
Ratnam and Nelson (2000)	Weak electric fish, isolated P-type Receptors afferent	-0.52
Chacron et al. (2000)	Weak electric fish, isolated P-type Receptors afferent	-0.35
Neiman and Russell (2004)	Paddle fish, sensory Ganglion	$\sim$ -0.4
Floyd et al. (1982)	Cat splanchnic and hypogastric nerves *in vivo*	-0.3
Levine (1996)	Goldfish retina, Ganglion cells *in vivo*	-0.13
Rodieck (1967)	Cat Retina, Ganglion cells *in vivo*	-0.06
Kuffler et al. (1957)	Cat Retina, Ganglion cells *in vivo*	-0.17
Tsuchitani and Johnson (1985)	Cat Lateral Superior Olive *in vivo*	-0.2
Nawrot et al. (2007)	Rat Somatosensory Cortex (S1) *in vivo*, regular spiking cells	-0.21
Nawrot et al. (2007)	Rat Somatosensory Cortex (S1) *in vitro*, pyramidal cells	-0.07
Engel et al. (2008)	Rat medial entorhinal cortex *in vitro* Layer II stellate and Layer III pyramidal neurons	[-0.1,-0.4]
Farkhooi et al. (2008)	Honeybee central brain *in vivo* Mushroom body extrinsic neurons	-0.15

Table 1: Negative 1st order serial interval correlation in different preparations and cell types.

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

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

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constant intensity λ

dynamic intensity λ(t)

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non-homogenous Poisson

Renewal
- iid interval distribution
- $FF = CV^2$

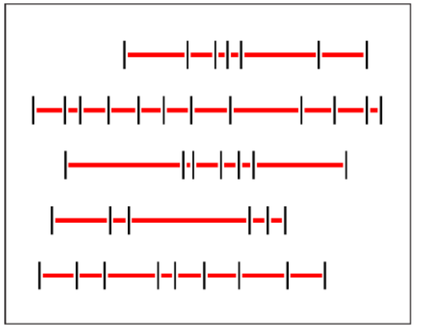
rate modulated Renewal

stationary non-Renewal
- constant intensity parameter
- non-trivial history dependence
- serial interval correlations

increasing importance of process history

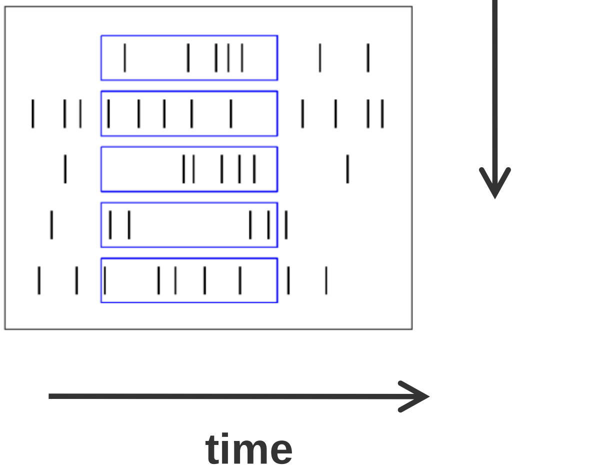
Coefficient of variation (interval variability)

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



Fano factor (count variability)

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



theoretic relation for **renewal process**

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