Stochastic Point Processes

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1. Introduction

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

Useful to investigate biophysics and neural networks

**stochastic point process models**

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

Numeric simulation generates random point process realization
⇒ spike train

Useful to make statistical predictions for spike train analysis
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

\[ t_1, t_2, \ldots, t_n \]

discrete representation (list)

101000010001000000000010100101000000100010100000000001

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.
Inter-spike intervals

inter-spike intervals
continuous data
Spike count

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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 $X_i, i = 1, 2, \ldots$ 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 prominent 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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What is a good time resolution $\Delta t$ for simulating a series of action potentials?

APs have a duration of about 1-2 ms; thus as useful time resolution is: $\Delta t \leq 1$ ms
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The ratio $\lambda = p / \Delta t$ 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 $\lambda = 5/s$ (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 \(t\):

\[
P(N(t, t + \delta t) = 1 | H_t) = \lambda \delta t + O(\delta t^2)
\]
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 \(t\)

\[
P(N(t, t + \delta t) = 1|H_t) = 1
\]

**Definition**

The **Poisson process** of intensity \(\lambda\) 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 \(\Delta t \to 0\).
Poisson process | **count** distribution

\[ P\{N(A) = k\} = \frac{\mu^k}{k!} e^{-\mu} \]
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\[ A = (0, t]; \quad \mu = \lambda \cdot t \]

\[ P\{N(A) = k\} = \frac{(\lambda \cdot t)^k}{k!} e^{-\lambda t} \]
Example 1: radioactive decay of $^{239}$Pu (half-life: 4110 years).

- continuous time intervals
- discrete event count
Example 2: rain drops

- continuous space intervals
- discrete event count
Poisson process | from **count** to **interval** distribution

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

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

\[
Pr\{X_1 > t\} = P\{N(t) = 0\} = \frac{\lambda t^0}{0!} e^{-\lambda t} = e^{-\lambda t}
\]
Model classes

constant intensity $\lambda$

<table>
<thead>
<tr>
<th>Poisson</th>
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<tbody>
<tr>
<td>• exponential interval distribution</td>
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<tr>
<td>• Poisson count distribution</td>
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<tr>
<td>• events are uniformly distributed in time</td>
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<tr>
<td>• special case of gamma process</td>
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</tbody>
</table>
**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

\[ \uparrow = \text{replacement from a homogeneous population} \]
**Definition**

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

**Thus**

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- 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.
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 histogram from a total of 1530 ISIs. The mean interval length is $m = 58.7$ ms, i.e. the average rate can be approximated by $\lambda \approx \frac{1}{m} = 17.03/s$. The blue curve fits a gamma distribution, the red curve fits a log-normal distribution. Modified from: [1]

Prominent interval distributions used for renewal models of neural spiking
Model classes

constant intensity $\lambda$

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

**Renewal**
- iid interval distribution
  - $FF = CV^2$
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 $\lambda$ by the explicitly time-dependent intensity function $\lambda(t)$ and define the nonhomogenous Poisson process for all $t$ and for $\delta \to 0^+$

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

The instantaneous probability is still independent of the process history!
Non-homogenous Poisson process

Bernoulli approximation:

![Graphs showing the Bernoulli approximation for a non-homogenous Poisson process.](image-url)
Model classes

**constant intensity $\lambda$**

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

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

**dynamic intensity $\lambda(t)$**

- non-homogenous Poisson

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** $\lambda(t)$

\[
t' = \Lambda(t) = \int_0^t \lambda(s) \, ds
\]
**constant intensity $\lambda$**

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

**dynamic intensity $\lambda(t)$**

- non-homogenous Poisson
- rate-modulated Renewal

Model classes

- increasing importance of process history
4. Non-Renewal Point Processes

- modeling serial interval correlation
- modeling spike-frequency adaptation
- *In vivo* intracellular recordings, somatosensory cortex in the anesthetized rat

- spontaneous activity (no stimulation)
Non-renewal spike trains | experimental evidence

Experiments by Clemens Boucsein & Dymphie Suchanek
University of Freiburg, Germany

a

Neuron index

\[
\begin{align*}
-0.3 & \quad -0.2 & \quad -0.1 & \quad 0 & \quad 0.1 & \quad 1 & \quad 8 \\
\end{align*}
\]

\[
\begin{align*}
\text{SRC} & \quad \text{\textbullet} & \quad \text{\textbullet} & \quad \text{\textbullet} & \quad \text{\textbullet} \\
\end{align*}
\]

- 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
<table>
<thead>
<tr>
<th>Reference</th>
<th>Model System &amp; Neuron Type</th>
<th>SC</th>
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<tbody>
<tr>
<td>Ratnam and Nelson (2000)</td>
<td>Weak electric fish, isolated $P$-type Receptors afferent</td>
<td>-0.52</td>
</tr>
<tr>
<td>Chacron et al. (2000)</td>
<td>Weak electric fish, isolated $P$-type Receptors afferent</td>
<td>-0.35</td>
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<td>Neiman and Russell (2004)</td>
<td>Paddle fish, sensory Ganglion</td>
<td>$\sim$ -0.4</td>
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<td>Floyd et al. (1982)</td>
<td>Cat splanchnic and hypogastric nerves in vivo</td>
<td>-0.3</td>
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<tr>
<td>Levine (1996)</td>
<td>Goldfish retina, Ganglion cells in vivo</td>
<td>-0.13</td>
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<tr>
<td>Rodieck (1967)</td>
<td>Cat Retina, Ganglion cells in vivo</td>
<td>-0.06</td>
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<tr>
<td>Kuffler et al. (1957)</td>
<td>Cat Retina, Ganglion cells in vivo</td>
<td>-0.17</td>
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<tr>
<td>Tsuchitani and Johnson (1985)</td>
<td>Cat Lateral Superior Olive in vivo</td>
<td>-0.2</td>
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<tr>
<td>Nawrot et al. (2007)</td>
<td>Rat Somatosensory Cortex (S1) in vivo, regular spiking cells</td>
<td>-0.21</td>
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<tr>
<td>Nawrot et al. (2007)</td>
<td>Rat Somatosensory Cortex (S1) in vitro, pyramidal cells</td>
<td>-0.07</td>
</tr>
<tr>
<td>Engel et al. (2008)</td>
<td>Rat medial entorhinal cortex in vitro Layer II stellate and Layer III pyramidal neurons</td>
<td>[-0.1,-0.4]</td>
</tr>
<tr>
<td>Farkhooi et al. (2008)</td>
<td>Honeybee central brain in vivo Mushroom body extrinsic neurons</td>
<td>-0.15</td>
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Table 1: Negative 1st order serial interval correlation in different preparations and cell types.

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

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

where

- \( \varepsilon_s \) i.i.d. with specific mean and finite variance.
- \( \beta_i \) correlation coefficient for lag \( i \) and \( |\beta| < 1 \)

We propose the following process to model inter-event intervals

\[
\Delta_s = \exp(X_s) = \exp(\beta X_{s-1} + \varepsilon_s)
\]

When we choose \( \varepsilon_s \) normal distributed with mean \( \mu \) and variance \( \sigma^2 \) then \( \Delta_s \) is log-normal distributed.

Model classes

*constant intensity* $\lambda$

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

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

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

*dynamic intensity* $\lambda(t)$

- **non-homogenous Poisson**
- **rate modulated Renewal**

Increasing importance of process history
Measures of interval and count variability

Coefficient of variation (interval variability)

\[ CV^2 = \frac{\text{Var}(ISI)}{\text{mean}^2(ISI)} \]

Fano factor (count variability)

\[ FF = \frac{\text{Var}(\text{count})}{\text{mean}(\text{count})} \]

definition of relations for renewal process

\[ FF = CV^2 \]