Neural noise and neural signals - spontaneous activity and signal transmission in models of single nerve cells

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Biweekly **tutorial** on wednesdays 9:15-10:45
given by Sergej Voronenko:
6.5., 20.5., 3.6., 17.6., 1.7., 15.7.

problems are handed out one or two weeks before the
tutorial; required **for passing**: 70% of the points

**Oral examination** before the new semester starts

**URL** of the lecture:
http://people.physik.hu-berlin.de/~neurophys/neusig/
General references

• Stochastic Processes in general ...
  - Gardiner *Handbook of Stochastic Methods* Springer (1985)
  - Cox & Isham *Point Processes* Chapman and Hall (1980)

• ... and in neuroscience:
  - Tuckwell *Stochastic Processes in the Neuroscience* SIAM (1987)
Motivation
Sensory signals are represented by sequences of electrical discharges - neural spike trains.
**Aim of the course**

**Analytical calculation** of the statistics of single-neuron activity, modeled by **dynamical systems** in a **stochastic framework**

### Spontaneous activity

- **neuron**
- **Noise**
- **Spike train**
- **Statistics:** Rate, Cv, ISI density & correlations; spike train spectrum & Fano factor

### Evoked activity

- **Stimulus**
- **neuron**
- **Noise**
- **Spike train**
- **Statistics:** Rate modulation, phase lag; signal-to-noise ratio, coherence, mutual information rate
Relations between different spike train statistics

How is the variability of the ISI related to the variability of the spike count?
Neural noise sources

noise sources (channel noise, synaptic noise, random presynaptic input) & their approximate description by a diffusion approximation
Interspike interval statistics as a first-passage problem
Interspike interval statistics as a first-passage problem

![Graphs showing probability density and firing rate](image)

Noise intensity

$D=0.02$
Rate coding of time-dependent stimuli

Leaky integrate-and-fire neuron with periodic stimulus

\[ \tau \frac{dv}{dt} = -v + \mu + \varepsilon \cos(2\pi F_{signal} t) + \xi(t) \]

Periodic modulation of firing rate

Information theory of neural spiking

How much info does the spike train carry about the sensory signal?

Relation to rate modulation and spontaneous activity?
Aim of the course

Analytical calculation of the statistics of single-neuron activity, modeled by dynamical systems in a stochastic framework

Spontaneous activity

Evoked activity

Statistics:
- Rate, Cv, ISI density & correlations; spike train spectrum & Fano factor
- Rate modulation, phase lag; signal-to-noise ratio, coherence, mutual information rate
Schedule

15.4. Motivation; spike-train statistics
22.4. Point processes: Poisson and other renewal processes
29.4. How much information does a spike train contain?
  6.5. Mutual information - direct estimates and lower bound
13.5. Beyond statistical models: Sources of neural noise and their incorporation into dynamical neuron models
20.5. Effective time-constant approximation & IF models: Fokker-Planck analysis (intro)
27.5. IF models: Fokker-Planck analysis of spontaneous activity
  3.6. IF models: Fokker-Planck analysis of driven activity
10.6. Stochastic resonance in driven IF models
17.6. Multi-dimensional IF models: colored noise, spike-frequency adaptation, subthreshold oscillations
24.6. Neural noise beyond the diffusion approximation
  1.7. Properties of spontaneous firing & signal transmission
  8.7. Signal transmission in neural populations of uncoupled neurons
15.7. Outlook: single neuron properties and the dynamics of recurrent networks
Spike train statistics
From the membrane dynamics to the point process

Spike train: \( x(t) = \sum \delta(t - t_i) \)
A stationary process - time-independent firing rate

Spike trains

Estimate for the firing probability in $dt$

\[ p(t, t + dt) = \frac{\text{# of neurons that fire in } (t, t + dt)}{\text{total # neurons}} \]

firing rate per unit time

\[ r(t) = \frac{p(t, t + dt)}{dt} \]

\[ r(t) = \left\langle \sum \delta(t - t_i) \right\rangle = \langle x(t) \rangle \]
A non-stationary process - time-dependent firing rate

Spike trains

Estimate for the firing probability in $dt$

$$p(t, t + dt) = \frac{\# \text{ of neurons that fire in } (t, t + dt)}{\text{total } \# \text{ neurons}}$$

Firing rate per unit time

$$r(t) = \frac{p(t, t + dt)}{dt}$$

$$r(t) = \left< \sum \delta(t - t_i) \right> = \left< x(t) \right>$$

Simple example: Poissonian spike train (homogeneous)

\[ x(t) = \sum \delta(t - t_i) \]

Defining property: all \( t_i \) are independent!
Only one parameter: the firing rate \( \rho \)

Three ways to simulate a Poisson process

1. draw \( N \) points from a uniform density along the \( t \)-axis

\[ \text{If } \frac{T_{\text{small}}}{T_{\text{large}}} \ll 1 \]

Poisson in \( T_{\text{small}} \)
with rate \( r = N/T_{\text{large}} \)
Simple example: Poissonian spike train (homogeneous)

\[ x(t) = \sum \delta(t - t_i) \]

Defining property: all \( t_i \) are independent!
Only one parameter: the firing rate \( \gamma \)

**Three ways to simulate a Poisson process**

2. discretize \( t \)-axis; draw independent random number for each bin

\[ \xi_8 < r\Delta t \Rightarrow \text{Spike in 8th bin} \]

\[ \xi_{13} > r\Delta t \Rightarrow \text{no Spike in 13th bin} \]
Simple example: Poissonian spike train (homogeneous)

\[ x(t) = \sum \delta(t - t_i) \]

Defining property: all \( t_i \) are independent!

Only one parameter: the firing rate \( \lambda \)

Three ways to simulate a Poisson process

3. draw time interval to the next spike (Gillespie method)

\[ T_1 \quad T_2 \quad T_3 \]

Prob. density

\[ 0 \quad 0.2 \quad 0.4 \quad 0.6 \quad 0.8 \quad 1 \]

\[ 0 \quad 2 \quad 4 \quad 6 \quad 8 \quad 10 \]
Spike train power spectra are not flat in general

Spike train \( \rightarrow \) spike count \( \rightarrow \) diffusion process with drift

\[ \langle N(t) \rangle = \int_0^t dt' \langle x(t') \rangle = \int_0^t dt' r(t') \]

For a stationary process
\[ \langle N(t) \rangle = r_0 T \]
Fano factor does not always saturate ...

\[ F(t) = \frac{\langle \Delta N^2(t) \rangle}{\langle N(t) \rangle} \]
Interval statistics

Probability density $p(I)$ of the interspike interval (ISI)

Mean ISI $\langle I \rangle$

Variance of the ISI $\langle \Delta I^2 \rangle$

Coefficient of variation $C_V = \frac{\sqrt{\langle \Delta I^2 \rangle}}{\langle I \rangle}$

For a Poisson process $C_V = 1$
Examples for ISI densities

The moments do not determine the probability density

Example: \[ P(T) = \frac{1}{T \sqrt{2\pi}} \exp[-\log^2(x)/2] (1 + \varepsilon \sin(2\pi \log(x))) \]
N-th order intervals

interspike intervals (ISI)

with density $\rho(I)$

and

n-th order intervals

with densities $p_n(T_n)$
Interval correlations (in nonrenewal spike trains)

\[
\rho_k = \frac{\langle I_{i+k}I_i \rangle - \langle I_{i+k} \rangle \langle I_i \rangle}{\langle I_i^2 \rangle - \langle I_i \rangle^2}
\]

\[\rho_1 > 0 \quad \Rightarrow \quad \text{short short} \quad \text{long long long short}\]

\[\rho_1 < 0 \quad \Rightarrow \quad \text{short short} \quad \text{long long long short}\]
Interval correlations (in nonrenewal spike trains)

long-range positive correlations for auditory neurons


P-units in weakly electric fish


Electroreceptors in paddle fish


ISI correlations reviewed in
Akerberg & Chacron 2011
Renewal spike trains

All intervals are mutually independent!

Example: Poisson process

Consequence for the Fourier transforms of the n-th order interval density

\[ \tilde{p}_n(\omega) = \tilde{p}^n(\omega) \]
Relation between different spike train statistics

Time-averaged firing rate = inverse mean ISI
(stationary processes)

\[ r = \lim_{N \to \infty} \frac{N}{T_{\text{window}}} = \lim_{N \to \infty} \left( \frac{T_0}{N} + \frac{1}{N} \sum_{i=1}^{N} I_i + \frac{T_{N+1}}{N} \right)^{-1} = \frac{1}{\langle I \rangle} \]
Relation between different spike train statistics

Power spectrum - Fourier transforms of n-th order interval densities

\[ S(\omega) = \int_{-\infty}^{\infty} d\tau C(\tau) e^{i\omega \tau} = r_0 \int_{-\infty}^{\infty} d\tau [\delta(\tau) + m(\tau) - r_0] e^{i\omega \tau} \]

\[ = r_0 - r_0^2 \delta(\omega) + r_0 \int_{-\infty}^{\infty} d\tau \ m(\tau) e^{i\omega \tau} \]

With \( m(-\tau) = m(\tau) \) and \( m(\tau) = \sum_{n=1}^{\infty} p_n(\tau) \) one obtains for \( \omega > 0 \)

\[ S(\omega) = r_0 + r_0 \int_{0}^{\infty} d\tau \ m(\tau)(e^{i\omega \tau} + e^{-i\omega \tau}) = r_0 \left[ 1 + \sum_{n=1}^{\infty} \tilde{p}_n(\omega) + \tilde{p}_n^*(\omega) \right] \]

For a renewal spike train \( (\tilde{p}_n(\omega) = \tilde{p}^n(\omega)) \)

\[ S(\omega) = r_0 \left[ 1 + \frac{\tilde{p}}{1 - \tilde{p}} + \frac{\tilde{p}^*}{1 - \tilde{p}^*} \right] \]

\[ S(\omega) = r_0 \frac{1 - |\tilde{p}|^2}{|1 - \tilde{p}|^2} \]
Relation between different spike train statistics

Zero frequency limit of the power spectrum - interval variability and correlations

\[ S(0) = r_0 C_V^2 \left[ 1 + 2 \sum_{k=1}^{\infty} \rho_k \right] \]

Zero frequency limit of the power spectrum - long-term count variability

\[ S(0) = \lim_{t \to \infty} r_0 F(t) \]
Relation between different spike train statistics

Given the $n$-th order interval densities $\rightarrow$ calculation of variances $\langle \Delta T^2_n \rangle$. Variances and SCC obey (Cox and Lewis, 1966)

$$\langle \Delta T^2_n \rangle / \langle \Delta T^2_1 \rangle = n + 2 \sum_{k=1}^{n-1} (n-k) \rho_k$$

For a renewal spike train
$$\rho_k = 0, \quad k > 0$$

$$\langle \Delta T^2_n \rangle = n \langle \Delta T^2_1 \rangle$$

For a nonrenewal spike train
$$\langle \Delta T^2_n \rangle \neq n \langle \Delta T^2_1 \rangle$$
Relation between different spike train statistics

Given the $n$-th order interval densities → calculation of variances $\langle \Delta T_n^2 \rangle$. Variances and SCC obey (Cox and Lewis, 1966)

$$\frac{\langle \Delta T_n^2 \rangle}{\langle \Delta T_1^2 \rangle} = n + 2 \sum_{k=1}^{n-1} (n-k) \rho_k$$

from which we find

$$\rho_k = \frac{\langle \Delta T_{k+1}^2 \rangle + \langle \Delta T_{k-1}^2 \rangle}{2\langle \Delta T_1^2 \rangle} - \frac{\langle \Delta T_k^2 \rangle}{\langle \Delta T_1^2 \rangle}$$

Last time ...

Spike train statistics

Spike count

\[ N(t) = \int_{0}^{t} dt' x(t') \]

its mean, variance, Fano factor

Last time ...

Spike train statistics

Interspike intervals

\[ I_i = t_{i+1} - t_i \]

its probability density function (pdf), mean, variance, coefficient of variation (CV), serial correlation coefficient (SCC)
Last time ...

Spike train statistics

N-th order intervals

\[ T_{k,i} = t_{i+k} - t_i \]

its probability density function (pdf),

\[ p_n(T) \]
**Last time ...**  For a stationary process:

1. Firing rate \( r_0 = 1 / \langle I \rangle \)

2. n-th order interval variance
   \[
   \langle \Delta T_n^2 \rangle = n \langle \Delta I^2 \rangle \left[ 1 + 2 \sum_{k=1}^{n-1} \left( 1 - \frac{k}{n} \right) \rho_k \right]
   \]

3. Interval correlation coefficient \( \rho_k = \frac{\langle \Delta T_{k+1}^2 \rangle + \langle \Delta T_{k-1}^2 \rangle - 2 \langle \Delta T_k^2 \rangle}{2 \langle \Delta I^2 \rangle} \)

4. Power spectrum \( S(f) = r_0 \left( 1 + \sum_{n=1}^{\infty} \tilde{p}_n(f) + \tilde{p}_n^*(f) \right) \)
   \[
   \longrightarrow \text{renewal process: } S(f) = r_0 \frac{1 - |\tilde{p}(f)|^2}{|1 - \tilde{p}(f)|^2}
   \]

5. Fano factor \( S(0) = r_0 \lim_{t \to \infty} F(t) \)
   \[
   \text{nonrenewal: } S(0) = r_0 C_v^2 \left[ 1 + 2 \sum_{k=1}^{\infty} \rho_k \right]
   \]
   \[
   \text{renewal: } S_{\text{renewal}}(0) = r_0 C_v^2 \lim_{t \to \infty} F(t) = C_v^2
   \]
Negative ISI correlations cause a drop in spectral power at low frequency

electroreceptor (P-units) in the weakly electric fish

Chacron et al. _Proc. SPIE_ 2005
Negative ISI correlations cause a drop in spectral power at low frequency

electroreceptor (P-units) in the weakly electric fish

\[ r_0 C_v^2 \left( 1 + 2 \sum_{k=1}^{\infty} \rho_k \right) \]

Chacron et al. *Proc. SPIE* 2005
Gamma process - ISI density and spike train power spectrum

\[ r_0 C_v^2 = 1 \]
\[ r_0 C_v^2 = 1/2 \]
\[ r_0 C_v^2 = 1/25 \]
Summary: spike-train statistics

- Point processes can be characterized
  • by spike train (rate) and count statistics (Fano factor)
  • by interval statistics (ISI and nth-order intervals, interval correlations)

- ISI densities often unimodal; spectra non-flat --- not well described by Poisson statistics!

- Spike train and interval statistics are related in a nontrivial manner

References

- Cox & Isham *Point Processes* Chapman and Hall (1980)