Signal & Data Analysis in Neuroscience 2016

Part 4: Single Spike Train

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Single Spike Train

- The last session focused on generating a statistical model of spike train generation. Specifically, the Poissonian neuron.
- This lesson will focus on statistical descriptors of spike trains and their relation to the underlying model of the spiking.

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Overview

- Single ISI measures
- Multiple ISI measures

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TIH/ISI

- ISI = Inter spike interval
  - Time difference between adjacent spikes
- TIH = Time interval histogram
  - The histogram of the time difference between adjacent spikes.

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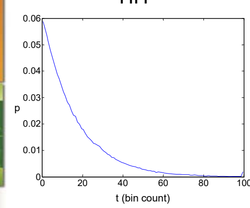
Homogeneous Poisson process

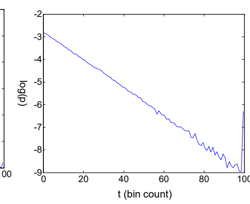
$$p(\tau) = re^{-r\tau}$$

$$\log(p(\tau)) = \log(r) - r\tau$$

TIH



log(TIH)



P=0.06, , bin size is 1ms

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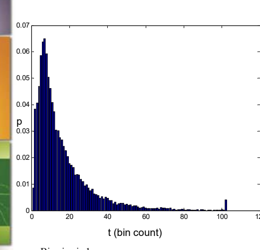
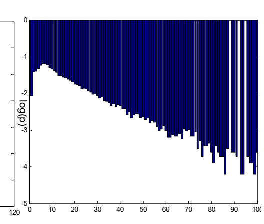
Experimentally recorded GPi neuron

TIH



log(TIH)



Bin size is 1ms

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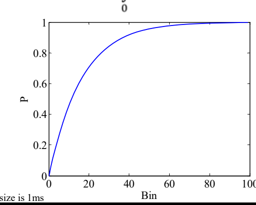
ISI: Other neuronal models

- Regular neuron
- Burster
- Non homogeneous Poisson

ISI cumulative distribution function

- The cumulative distribution is: $P[t_{i+1} - t_i < \tau]$
- For the Poissonian neurons:

$$P[t_{i+1} - t_i < \tau] = \int_0^\tau re^{-rt}\,dt = 1 - e^{-r\tau}$$



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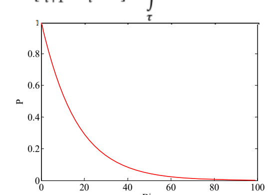
Survivor (survival) function

Survivor function = 1 - Cumulative sum of TIH

$$Survivor(t) = R(t) = 1 - \sum_{i=1}^{t} ISI(i)$$

$$P[t_{i+1} - t_i > \tau] = \int_\tau^\infty re^{-rt}\,dt = e^{-r\tau}$$



P=0.06, , bin size is 1ms

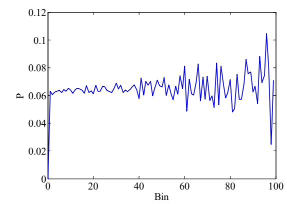
Hazard function

Hazard function reflect the independent probability to fire at any single point.

$$Hazard(t) = h(t) = \frac{ISI(t)}{Survivor(t)}$$

In the Poisson case

$$h(t) = \frac{p(\tau)}{R(\tau)} = \frac{re^{-r\tau}}{e^{-r\tau}} = r$$



Pitfall:
Very noisy for long ISIs

CV – refractory period

$$C_V = \frac{\sigma_t}{<t>}$$

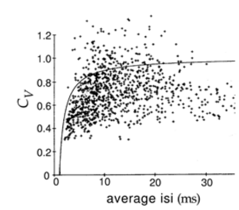
- Adding an absolute refractory period increases the mean by t_{ref} but the standard deviation remains the same

$$C_{Vref} = \frac{\sigma_t}{<t> + t_{ref}}$$

$$C_{Vref} = (1 - \frac{t_{ref}}{<t>}) \cdot C_V \qquad C_{Vnoref} = \frac{C_{Vref}}{1 - \frac{t_{ref}}{<t>}}$$

We record C_{Vref} but interested in C_{Vnoref}

Experimental validation of Poisson process: ISI (Coefficient of variation)



MT and V1 macaque $\quad C_V = \frac{\sigma_\tau}{t_{refr} + \langle\tau\rangle} \to 1$

Overview

- Single ISI measures
- Multiple ISI measures

Multiple ISIs

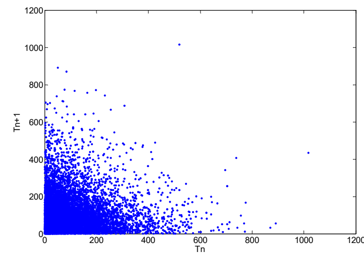
- In the Poissonian neuron, all the neuronal properties may be derived by the 1st order ISI.
- In other cases a measure of the 1st order ISI may be very different from a multi-ISI measure.
- For example CV vs. FF of a neuron firing doublets…

First order ISIs vs. Multi-ISI

- Shuffling → Permutation of the intervals.
- Compute the Fano factor before and after shuffling.
- If $F=F_{shuffle}$ all the irregularity may be explained by the ISIs.
- C_v remains the same...

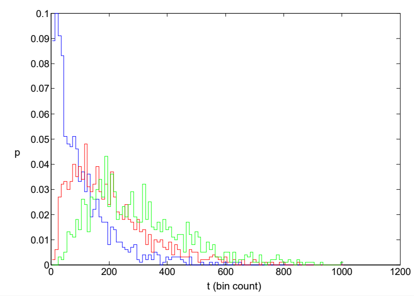
Consecutive intervals

If consecutive interval are independent the density resembles
An exponential multiplication.



Multiple intervals

1st (blue), 2nd (red), 3rd (green) intervals



Correlation

- Covariance

$$Cov(X,Y) = E[(X-\mu_x)\cdot(Y-\mu_y)]$$

- Pearson correlation coefficient

$$R(X,Y) = \frac{E[(X-\mu_x)\cdot(Y-\mu_y)]}{\sigma_x \cdot \sigma_y}$$

Autocorrelation function

- General definition

$$R(t_1,t_2)=\frac{E[(X_{t_1}-\mu_{x_{t_1}})\cdot(X_{t_2}-\mu_{x_{t_2}})]}{\sigma_{x_{t_1}}\cdot\sigma_{x_{t_2}}}$$

- Wide-sense stationary (WSS) process

$$R(\tau)=\frac{\mathrm{E}[(X_t-\mu)(X_{t+\tau}-\mu)]}{\sigma^2}$$

- A common definition for spike trains (Dayan & Abbott)

$$Q_\rho(\tau)=\frac{1}{T}\int_0^T(\rho(t)-r)\cdot(\rho(t+\tau)-r)dt$$

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Autocorrelation practicalities

- Count $Q_C(\tau)=\sum_{i=1}^{n}\rho(t_i)\cdot\rho(t_i+\tau)$
- Probability $Q_P(\tau)=\frac{1}{n}\cdot\sum_{i=1}^{n}\rho(t_i)\cdot\rho(t_i+\tau)$
- Rate $Q_R(\tau)=\frac{1}{n\cdot\Delta t}\cdot\sum_{i=1}^{n}\rho(t_i)\cdot\rho(t_i+\tau)$
- Value at t=0
- Symmetry

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Autocorrelation practicalities

- Rate normalized version
- Count $Q_C(\tau)=\sum_{i=1}^{n}[\rho(t_i)-r]\cdot[\rho(t_i+\tau)-r]$
- Probability $Q_P(\tau)=\frac{1}{n}\cdot\sum_{i=1}^{n}[\rho(t_i)-r]\cdot[\rho(t_i+\tau)-r]$
- Rate $Q_R(\tau)=\frac{1}{n\cdot\Delta t}\cdot\sum_{i=1}^{n}[\rho(t_i)-r]\cdot[\rho(t_i+\tau)-r]$
- Not as common…

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Relating to standard correlation

- Covariance $C(\tau) = \frac{1}{n} \cdot \sum_{i=1}^{n} [\rho(t_i) - r] \cdot [\rho(t_i + \tau) - r]$
- Pearson $R(\tau) = \frac{1}{n \cdot (r - r^2)} \cdot \sum_{i=1}^{n} [\rho(t_i) - r] \cdot [\rho(t_i + \tau) - r]$

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Autocorrelation practicalities

- Normalization to rate / probability / count
- Normalization to 0 vs. absolute value
- Calculating the autocorrelation:
  - All spikes at distance τ from each spike.
  - Summation of ISI of all orders.

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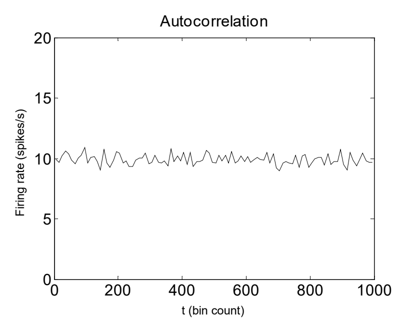
Example - Poisson



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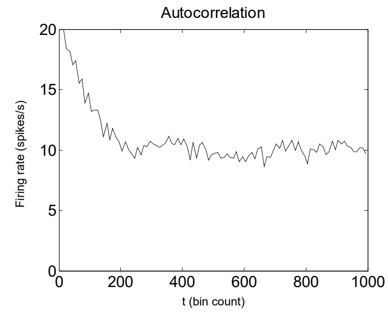
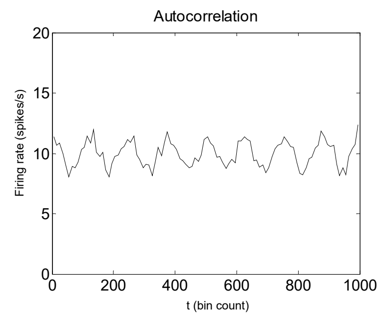
Example - Burster

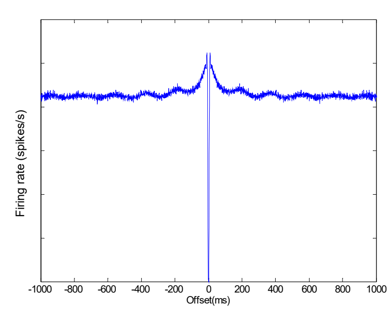


- What about a pauser?

Example - Oscillator



Example – GP neuron during Parkinson's disease



Long term phenomena

- Firing rate fluctuates over time.
- It is crucial to examine the process on multiple timescales.
- Rate fluctuations will reflect as changes in the autocorrelation function.

Single spike train measures

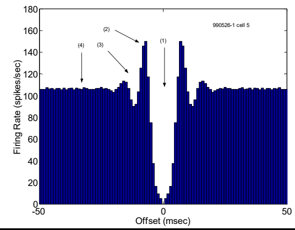
- The ISI is typically a good measure on the regularity of firing and its fit to the Poisson distribution.
- The hazard function is a good measure of short term phenomena but cannot be used on long timescales.
- The autocorrelation function is a good measure for identifying long-term phenomena.

Appendix

The results of different measures are not as simple as they seem…

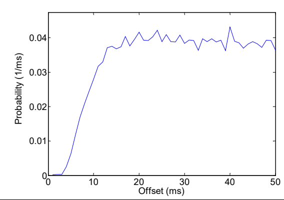
Typical autocorrelation in the pallidum

Multiple phases:
1) Refractory phase
2) Elevated phase
3) Oscillatory phase
4) Steady state

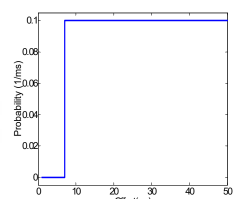


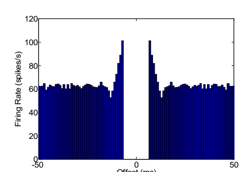
So is the neuron bursting/oscillating ?

- The spike trains do not reveal any evident bursts or an obvious oscillation.
- The hazard function is (almost) flat (!?)



Simulations – simple case





p=0.1 and τ_r=6ms

Firing rate without refractory period: 1000/10=100 spikes/s
Firing rate with refractory period: 1000/(10+6)=62.5 spikes/s

Intuition ☺

- The key is observing the probability of being in a refractory period (RP).
- Assuming RP of length τ_r . If at any time during the last τ_r ms there was a RP than the probability for a new RP is reduces since there couldn't have been a spike during the RP.
- The autocorrelation which reflects the firing rate behave as a negative reflection of the RP probability.

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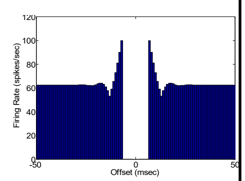
Analysis – simple case

(1) $$h_t = \begin{cases} 0 & t \le \tau_r \\ p & t > \tau_r \end{cases}$$

(2) $$a_t = \begin{cases} 0 & t \le \tau_r \\ (1 - \sum_{i=1}^{\tau_r} a_{t-i}) \cdot p & t > \tau_r \end{cases}$$



(3) $$a_{\tau_r+1} = p$$

(4) $$a_\infty = (1 - \tau_r \cdot a_\infty) \cdot p \qquad t \to \infty \qquad \Rightarrow \qquad a_\infty = \frac{p}{1 + p \cdot \tau_r}$$

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