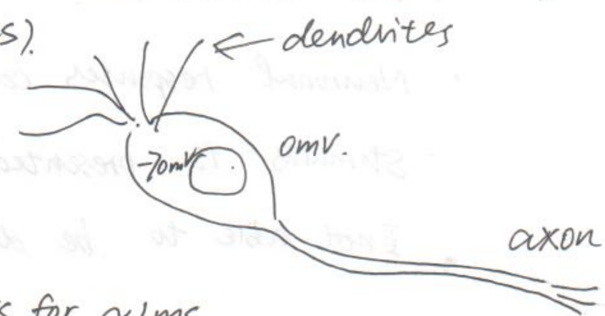
Theoretical Neuroscience. Reading Notes.

Ch 1. Firing Rate & Spike Statistics. Nov. 22nd, 2020.

1. Introduction.

- Neural coding: involves measuring how stimulus attributes (such as light or sound intensity) or motor actions (such as the direction of arm movement) are ~~repr~~ represented by action potentials.

- Stimulus $\xrightarrow{\text{encoding}}$ response. (how neurons respond to ~~stimulus~~ stimuli.)
  Stimulus $\xleftarrow{\text{decoding}}$ response. (reconstruct a stimulus from the spike sequence it ~~evoke~~ evokes).



- resting state: -70mV.

  action potential: 100mV. lasts for ~1ms.

  refractory period: for a few milliseconds just after an action potential has been fired, it may be virtually impossible to initiate another spike. (absolute refactory period)

  depolarization. hyperpolarization.

- Recording Neural Response.

intra-cellular	extra-cellular
sharp electrodes inserted through the cell	in vivo
patch electrodes. (seal).	only action potentials, not ~~subthre~~ subthreshold membrane potentials.

- usually soma.
  dendrites are ~~bef~~ becoming more and more.
- ~~invitro~~ in vitro

- From stimulus to response:
  - How do neurons respond to stimulus?

    producing complex sequences → refect
    - intrinsic dynamics of neurons
    - temporal characteristis of the stimulus.

  - challenges:
    - How to isolate features of the response that encode changes in the stimulus?
    - Neuronal responses can vary from trial to trial even when the stimulus is presented repeatedly. (trial-to-trial variability. not able to be described deterministically).

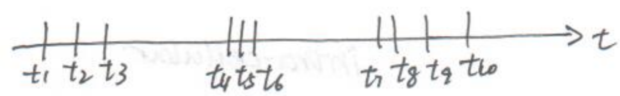
  - population coding:

    many neurons respond to the stimulus.

    - firing patterns of individual neurons
    - the relationships of these firing patterns to each other across the population.

2. Spike Trains and Firing Rates.

- spike time: t_i. $i = 1, 2, \dots, n$.



  $0 \le t_i \le T$. $\forall i = 1, 2, \dots, n$.

- Diract δ function:
  - properties:
    - approaches 0 everywhere except where the argument is 0.
    - infinite height & infinitesimal width.
    - $\int \delta(t)\,dt = 1$.

- $\int \delta(t-s) f(s)\, ds = f(t)$. f: continuous. (*).

- examples of possible $\delta(t)$ function:

  - $$\delta(t) = \lim_{\Delta t \to 0} \begin{cases} \frac{1}{\Delta t} & -\frac{\Delta t}{2} < t < \frac{\Delta t}{2} \\ 0 & \text{o.w.} \end{cases}$$

  - $$\delta(t) = \lim_{\Delta t \to 0} \frac{1}{\sqrt{2\pi}\Delta t} e^{-\frac{t^2}{2\Delta t^2}}$$

  - $$\delta(t) = \frac{1}{2\pi} \int_{-\infty}^{+\infty} \exp(i w t)\, dw. \quad \Leftarrow$$

- spike sequence: $\rho(t) = \sum_{i=1}^{n} \delta(t-t_i)$.

- According to (*): any $h(t)$ continuous;

$$h(t) = \int \delta(t-s)\, h(s)\, ds.$$

$$h(t-t_i) = \int \delta(t-s-t_i)\, h(s)\, ds.$$

$$\sum_{i=1}^{n} h(t-t_i) = \sum_{i=1}^{n} \int \delta(t-s-t_i)\, h(s)\, ds$$

$$= \int \underline{\sum_{i=1}^{n} \delta(t-s-t_i)}\, h(s)\, ds = \int \rho(t-s)\, h(s)\, ds$$

$$= \int \rho(t-s)\, h(s)\, ds.$$

- Spike-count rate:

$$r = \frac{n}{T} = \frac{1}{T} \int_0^T \rho(\tau)\, d\tau \qquad \left(n = \int_0^T \rho(\tau)\, d\tau \right).$$

- time-dependent firing rate. (averaged over trials).

$\langle\ \rangle$: trial average.

$$r(t) = \frac{1}{\Delta t} \cdot \int_t^{t+\Delta t} \langle \rho(\tau) \rangle \, d\tau.$$

$$\cancel{\int dt} \int h(\tau) \langle \rho(t-\tau) \rangle d\tau = \int h(\tau) r(t-\tau) d\tau.$$

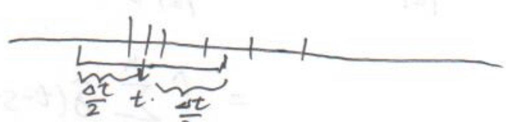
- average firing rate.

$$\langle r \rangle = \frac{\langle n \rangle}{T} = \frac{1}{T} \cdot \int_0^T \langle \rho(\tau) \rangle d\tau = \frac{1}{T} \int_0^T r(t) dt.$$

firing rate: $r(t)$. spike-count rate: r. average firing rate. $\langle r \rangle$.

Measuring Firing Rates.

- bin. count within bins
- sliding window.
- kernel.



sliding window:

$$r_{approx}(t) = \sum_{i=1}^{n} w(t-t_i). \qquad w(t) = \begin{cases} \frac{1}{\Delta t} & -\frac{\Delta t}{2} \le t \le \frac{\Delta t}{2} \\ 0. & \text{o.w.} \end{cases}$$

spike train convolve with ones(1, winSize) divided by winSize.

Kernel:

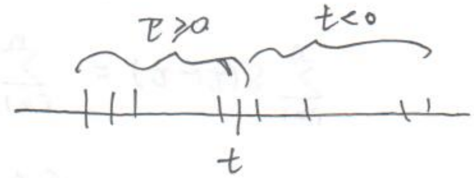
$$r_{approx}(t) = \int_{-\infty}^{+\infty} w(\tau) \rho(t-\tau) d\tau. \qquad \text{(linear filter)}.$$

$$w(\tau) = \frac{1}{\sqrt{2\pi}\,\sigma_w} e^{-\frac{\tau^2}{2\sigma_w^2}}$$

Causal: e.g. $w(\tau) = [\alpha^2 \tau e^{-\alpha\tau}]_+$.

$\tau < 0$: use spiking info after t:

$$[z]_+ = \begin{cases} z & z \geq 0. \\ 0 & \text{o.w.} \end{cases}$$



$$r_{approx}(t) = \int_{-\infty}^{+\infty} w(\tau)\,\rho(t-\tau)\,d\tau.$$

Tuning Curves..

$\langle r \rangle = f(s)$. neural response tuning curve.

3. What makes a neuron fire?

Spike-Triggered Average.

$C(\tau)$: Spike-triggered average Stimulus, the average of the stimulus a time interval τ before a spike is fired.

$$C(\tau) = \left\langle \frac{1}{n} \sum_{i=1}^{n} s(t_i - \tau) \right\rangle \approx \frac{1}{\langle n \rangle} \left\langle \sum_{i=1}^{n} s(t_i - \tau) \right\rangle \qquad (n \approx \langle n \rangle)$$

The response is typically affected by only the Stimulus in a window a few hundred milliseconds wide immediately preceding a spike.

$C(\tau) = 0.$ $(\tau < 0)$.

$C(\tau) = 0.$ ($\tau > 0$ And. $\tau >$ correlation time between stimulus and the response).

$$\cancel{\sum_{i=1}^{n} S(t_i-\tau) = \int_{-\infty}^{+\infty}}$$

$$S(t_i-\tau) = \int \delta(t_i-\tau-t)\, S(t)\, dt.$$

$$\sum_{i=1}^{n} S(t_i-\tau) = \sum_{i=1}^{n} \int \delta(t_i-\tau-t)\, S(t)\, dt = \int \sum_{i=1}^{n} \delta(t_i-\tau-t)\, S(t)\, dt \quad \text{let } t = t'-\tau$$

$$= \int \sum_{i=1}^{n} \delta(t_i-t')\, S(t'-\tau)\, dt' = \int \sum_{i=1}^{n} \delta(t'-t_i)\, S(t'-\tau)\, dt'$$

$$= \int \rho(t')\, S(t'-\tau)\, dt' = \int_{-\infty}^{+\infty} \rho(t)\, S(t-\tau)\, dt.$$

$$= \int_0^T \rho(t)\, S(t-\tau)\, dt. \qquad S(t) = S(t+T). \quad \forall t.$$

$$C(\tau) = \frac{1}{\langle n \rangle} \left\langle \sum_{i=1}^{n} S(t_i-\tau) \right\rangle = \frac{1}{\langle n \rangle} \cdot \left\langle \int_0^T \rho(t)\, S(t-\tau)\, dt \right\rangle$$

$$= \frac{1}{\langle n \rangle} \int_0^T \langle \rho(t) \rangle\, S(t-\tau)\, dt. = \frac{1}{\langle n \rangle} \int_0^T r(t)\, S(t-\tau)\, dt.$$

Correlation Function:

determining how two quantities that vary over time are related to one another.

$$Q_{rs}(\tau) = \frac{1}{T} \int_0^T r(t) \cdot S(t+\tau)\, dt$$

$$\begin{cases} Q_{rs}(\tau) = \dfrac{1}{T} \displaystyle\int_0^T r(t)\, S(t+\tau)\, dt. \\ C(\tau) = \dfrac{1}{\langle n \rangle} \displaystyle\int_0^T r(t) \cdot S(t-\tau)\, dt. \Rightarrow C(-\tau) = \dfrac{1}{\langle n \rangle} \displaystyle\int_0^T r(t)\, S(t+\tau)\, dt \end{cases}$$

$$\Rightarrow \langle n \rangle \cdot C(-\tau) = T \cdot Q_{rs}(\tau). \Rightarrow C(\tau) = \frac{T}{\langle n \rangle} Q_{rs}(-\tau).$$

(reverse correlation function)

White power spectral density.

White-noise Stimuli:

its value at any one time is ~~uncorrelated~~ uncorrelated with its value at any other time.

Stimulus-Stimulus correlation function:

$$Q_{ss}(\tau) = \int_0^T s(t) \cdot s(t+\tau)\, dt.$$

For white-noise stimulus, $Q_{ss}(\tau) = 0$. $(\tau \neq 0)$. $Q_{ss}(\tau) = \sigma_s^2 \delta(\tau)$

~~$Q_{ss}(0)$:~~

4. Spike Train Statistics.

$p[\cdot]$: probability density. $P[\cdot]$: probability.

$$P[t_1, t_2, \ldots, t_n] = p[t_1, t_2, \ldots, t_n] \cdot (\Delta t)^n.$$

point process: a stochastic Process that generates a sequence of events. The prob. of an event occurring at any given time depend on the entire history.

Renewal Process: only on the ~~preceding~~ preceding event.

Poisson Process: no independence on ~~prec~~ preceding events.

Homogeneous Poisson Process.

- $r(t) = r$.

$S_n = \sum_{i=1}^{n} X_i$. $\cancel{\{N(t)\}}$ $\{N(t);\ t>0\}$.

$\{X_1, X_2, \dots\}$. $\{S_1, S_2, \dots\}$

$N(t)=n$. $S_n \le t < S_{n+1}$. $X_i = S_i - S_{i-1}$. $(i>1)$

↳ counting r.v. is defined. as the number of arrivals in interval $(0,t]$.

$\{S_n \le t\} = \{N(t) \ge n\}$.

$\{S_n > t\} = \{N(t) < n\}$

$\cancel{\{S_1\}}$ $\{S_1 > t\} = \{N(t) < 1\} = \{N(t) = 0\}$

- a renewal process is an arrival process for which the sequence of inter-arrival times is a sequence of iid r.v's.

- A Poisson Process is a renewal process in which the ~~inter-arrival~~ interarrivals have an exponential distribution function.

  i.e. for some $\lambda > 0$. $f_{X_i}(x) = \lambda e^{-\lambda x}$ $x \ge 0$.

  λ: rate of the process.

- Memoryless Property:

  X: r.v. $P(X>0)=1$. $\forall x \ge 0$ $t \ge 0$.

  $P(X > t+x) = P(X>x) \cdot P(X>t)$.

  $P(X > t+s \mid X > t) = P(X > s)$.

• Stationary ~~incremental~~ increment property of ~~an~~ a counting process $\{N(t); t>0\}$.

$\forall t'>t>0$. $N(t')-N(t)$ has the same distribution function as $N(t'-t)$.

$\tilde{N}(t,t') = N(t') - N(t)$. the number of arrivals in the interval $(t, t']$. $(t'>t)$.

• independent increment property of a counting process $\{N(t); t>0\}$.

$\forall k \in \mathbb{N}_+$. $\forall$ k-tuple. $0<t_1<t_2<\cdots<t_k$. $N(t_1)$. $\tilde{N}(t_1,t_2), \ldots$ $\tilde{N}(t_{k-1}, t_k)$. are statistically independent.

• Poisson Process. has both stationary & independent increment. property(-ies)

X_1, X_2 · independent. $\Rightarrow$ $f_{X_1,X_2}(x_1,x_2) = f_{X_1}(x_1) \cdot f_{X_2}(x_2)$.

$X_1 + X_2 = S_2$. $\Rightarrow$ $f_{X_1,S_2}(x_1, S_2) = f_{X_1}(x_1) \cdot f_{X_2}(S_2 - x_1)$.

$$\Rightarrow f_{X_1,S_2}(x_1,S_2) = f_{X_1}(x_1) \cdot f_{X_2}(S_2-x_1) = \lambda \cdot e^{-\lambda x_1} \cdot \lambda e^{-\lambda(S_2-x_1)} = \lambda^2 \cdot e^{-\lambda S_2}. \quad 0 \le x_1 \le S_2.$$

$$\cancel{f_{X_1}(x_1)} \quad f_{S_2}(S_2) = \int_{x_1} f_{X_1,S_2}(x_1,S_2)\,dx_1 = \int_0^{S_2} \lambda^2 e^{-\lambda S_2}\,dx_1 = \lambda^2 S_2 \cdot e^{-\lambda S_2}.$$

$$f_{X_1,\ldots,X_n}(x_1,\ldots,x_n) = \prod_{i=1}^n f_{X_i}(x_i). = \lambda^n \cdot e^{-\lambda \sum_{i=1}^n x_i}. \quad S_n = \sum_{i=1}^n x_i.$$

$$\Rightarrow f_{X_1,\ldots,X_n}(x_1,\ldots,x_n) = \lambda^n \cdot e^{-\lambda S_n}$$

$$f_{X_1,\ldots,X_{n-1},S_n}(x_1,\ldots,x_{n-1},S_n) = f_{X_1}(x_1) \cdots f_{X_{n-1}}(x_{n-1}) \cdot f_{X_n}(S_n - x_1 - \cdots - x_{n-1})$$

$$= \lambda e^{-\lambda x_1} \cdots \lambda e^{-\lambda x_{n-1}} \cdot \lambda e^{-\lambda(S_n - x_1 - \cdots - x_{n-1})}$$

$$= \lambda^n \cdot e^{-\lambda x_1 - \lambda x_2 - \cdots - x_{n-1} + \lambda x_1 + \cdots + \lambda x_{n-1} - \lambda S_n}$$

$$= \lambda^n e^{-\lambda S_n}. \qquad \cancel{0 \le x_i \le S_n. \quad i=1,2,\ldots,n-1}$$

$$f_{S_n}(s_n) = \int_{x_1}\int_{x_2}\cdots\int_{x_{n-1}} f_{X_1,\dots,X_{n-1},S_n}(x_1,\dots,x_{n-1},s_n)\,dx_1\,dx_2\cdots dx_{n-1}$$

$x_i \geq 0$. $i = 1, 2, \dots, n-1$. $s_n - x_1 - \cdots - x_{n-1} \geq 0$.

$S_1 = X_1$. $S_2 = X_1 + X_2$. $S_3 = X_1 + X_2 + X_3$ $\cdots$ $S_n = X_1 + X_2 + \cdots + X_n$

$$S = (S_1 \; S_2 \; S_3 \; \cdots \; S_n)' = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ 1 & 1 & 0 & \cdots & 0 \\ 1 & 1 & 1 & & \vdots \\ \vdots & \vdots & & \ddots & \\ 1 & 1 & 1 & \cdots & 1 \end{pmatrix} \begin{pmatrix} X_1 \\ X_2 \\ \vdots \\ X_n \end{pmatrix}.$$

$S = AX$. The joint density of a non-singular linear transformation AX at $X = \alpha$. is $\cancel{f_X(\alpha)/|\det A|}$.

This is because the transformation A carries an incremental cube, δ on each side, into a parallelpiped of volume $\delta^n |\det A|$. $\det A = 1$ here.

$$f_{S_1,\dots,S_n}(s_1,\dots,s_n) = \lambda^n \cdot \exp(-\lambda s_n). \qquad 0 \leq s_1 \leq s_2 \leq \cdots \leq s_n.$$

- For a Poisson Process of rate λ, and for any $t > 0$. the PMF for $N(t)$ (i.e. the number of arrivals in $(0,t]$) is given by:

$$P_{N(t)}(n) = \frac{(\lambda t)^n e^{-\lambda t}}{n!}.$$

· Non-homogeneous Poisson Process.

$$P(\tilde{N}(t,t+\delta)=0) = 1-\delta\lambda(t)+o(\delta).$$

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

$$P(\tilde{N}(t,t+\delta)=2) = o(\delta) \qquad \tilde{N}(t,t+\delta) = N(t+\delta)-N(t).$$

does not have stationary increment property.

· $Y = g(x).$

$$F_Y(y) = P(Y \le y) = P(g(X) \le y) = P(X \in g^{-1}(y)).$$
$$= F_X(g^{-1}(y))$$

$$\Rightarrow f_Y(y) = F_Y'(y) = \frac{dF_X(g^{-1}(y))}{dy} = \frac{dF_X(g^{-1}(y))}{dg^{-1}(y)} \cdot \frac{dg^{-1}(y)}{dy}.$$

$$= f_X(g^{-1}(y))\frac{dg^{-1}(y)}{dy}.$$

(Random):

$S_n = X_1 + X_2 + \cdots + X_n$. $\quad S = AX.$ $\quad A$ invertible.

$S = g(X).$

$$f_{S_1,\dots,S_n}(s_1,\dots,s_n) = f_{X_1,\dots,X_n}(A^{-1}s)\frac{dg^{-1}(s)}{ds}.$$

$$= f_{X_1,\dots,X_n}(x_1,\dots,x_n) \cdot 1$$

$\cancel{dA}$

$$\cancel{\lim_{\delta\to 0}\frac{A(x+\delta)-Ax}{\delta}}$$

$$\cancel{=\lim_{\delta\to 0}}.$$

$$P_T[n] = \frac{(rT)^n}{n!} e^{-rT}.$$

$n \uparrow . \to$ Gaussian.

Mean: $$\sum_{n=0}^{\infty} n \cdot P_T[n] = \sum_{n=1}^{\infty} P_T[n] = \sum_{n=1}^{\infty} n \cdot \frac{(rT)^n}{n!} e^{-rT} = e^{-rT} \sum_{n=1}^{\infty} \frac{(rT)^n}{(n-1)!}$$

$$= (rT) e^{-rT} \sum_{n=1}^{\infty} \frac{(rT)^{n-1}}{(n-1)!} = (rT) \cdot e^{-rT} \sum_{n=0}^{\infty} \frac{(rT)^n}{n!} = rT \cdot e^{-rT} e^{rT}$$
$$= rT.$$

Variance: $$\sum_{n=0}^{\infty} n^2 P_T[n] - (rT)^2$$

$$= \sum_{n=0}^{\infty} n^2 \frac{(rT)^n e^{-\lambda T}}{n!} - (rT)^2 = \sum_{n=1}^{\infty} n^2 \frac{(rT)^n e^{-\lambda T}}{n!} - (rT)^2.$$

$$= rTe \sum_{n=1}^{\infty} n \frac{(rT)^{n-1}}{(n-1)!} - (rT)^2 = (rT) \cdot e^{-rT} \sum_{n=1}^{\infty} n \cdot \frac{(rT)^{n-1}}{(n-1)!} - (rT)^2$$

$$= (rT) e^{-rT} \sum_{n=0}^{\infty} (n+1) \cdot \frac{(rT)^n}{n!} - (rT)^2$$

$$= (rT) e^{-rT} \left[\sum_{n=0}^{\infty} \frac{(rT)^n}{n!} + \sum_{n=1}^{\infty} \frac{(rT)^n}{(n-1)!} \right] - (rT)^2$$

$$= (rT) e^{-rT} \left[e^{rT} + rT \cdot e^{rT} \right] - (rT)^2$$

$$= rT + (rT)^2 - (rT)^2 = rT.$$

$\square$

- Fano Factor: $\frac{\sigma_n^2}{\langle n \rangle}$

~~Fano Factor = 1 $\Leftrightarrow$ homogeneous Poisson Process~~.

- $$F_X(x) = \int_0^x \lambda e^{-\lambda t} dt = -\int_0^x e^{-\lambda t} d\lambda t = -e^{-\lambda t} \Big|_0^x = -(e^{-\lambda x} - 1) = 1 - e^{-\lambda x}.$$

$$P(X > x) = e^{-\lambda x}.$$

$P[\tau \le t_{i+1} - t_i < \tau + \Delta t]$

$$= \frac{(r\tau)^0 e^{-r\tau}}{0!} \cdot \frac{(r\Delta t)^1 \cdot e^{-r\Delta t}}{1!} = r\Delta t \cdot e^{-r\tau} \underbrace{e^{-r\Delta t}}_{1}$$

$$= r\Delta t e^{-r\tau}$$

$$\sum_{n=0}^{\infty} \frac{(-r\Delta t)^n}{n!} = 1 - r\Delta t + \frac{(r\Delta t)^2}{2!} + \cdots$$

τ: interspike interval.

$$\tau \sim \begin{cases} r e^{-r\tau} & \tau \ge 0 \\ 0 & \text{o.w.} \end{cases}$$

$$\langle \tau \rangle = \int_0^{+\infty} \tau \cdot r e^{-r\tau} d\tau \cancel{= -\int_0^{+\infty} e^{-r\tau} d{-r\tau} = -e^{-r\tau}\Big|_0^{+\infty} = -(0-1) = 1}$$

$$= -\int_0^{+\infty} \tau d e^{-r\tau} = -\left(\tau e^{-r\tau}\Big|_0^{+\infty} - \int_0^{+\infty} e^{-r\tau} d\tau\right)$$

$$= -\left(0 - 0 + \frac{1}{r}\int_0^{+\infty} d e^{-r\tau}\right)$$

$$= -\frac{1}{r} e^{-r\tau}\Big|_0^{+\infty} = -\frac{1}{r}(0-1) = \frac{1}{r}.$$

$$\sigma_\tau^2 = \int_0^{+\infty} \tau^2 \cdot r e^{-r\tau} \cdot d\tau - \frac{1}{r^2} = -\int_0^{+\infty} \tau^2 d e^{-r\tau} - \frac{1}{r^2}.$$

$$= -\left(\tau^2 e^{-r\tau}\Big|_0^{+\infty} - \int_0^{+\infty} e^{-r\tau} 2\tau d\tau\right) - \frac{1}{r^2}.$$

$$= 2\int_0^{+\infty} e^{-r\tau} \tau d\tau - \frac{1}{r^2}$$

$$= \frac{2}{r}\int_0^{+\infty} r\tau e^{-r\tau} d\tau - \frac{1}{r^2} = \frac{2}{r} \cdot \frac{1}{r} - \frac{1}{r^2} = \frac{1}{r^2}.$$

Coefficient of variation

$$C_V = \frac{\sigma_\tau}{\langle \tau \rangle} = \frac{\frac{1}{r}}{\frac{1}{r}} = 1$$

$C_V = 1 \Leftarrow$ Homogeneous Poisson Process.

Spike-Train Autocorrelation Function.

useful for detecting patterns in a spike train, most ~~notbo~~ notably, oscillations.

$$\langle r \rangle = \frac{\langle n \rangle}{T}.$$

$$\cancel{Q_{\rho\rho}(\tau) = \frac{1}{T}\int_0^T \langle \rho(t) \langle r \rangle \rangle}$$

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

Inhomogeneous Poisson Process.

$$0 \le t_1 \le t_2 \le \cdots \le t_n \le T.$$

$$p[t_1, t_2, \ldots, t_n] = \exp\left(-\int_0^T r(t)\,dt\right) \prod_{i=1}^{n} r(t_i).$$