From today "Functional models"

Marr:

Computation

Algorithm

Implementation

Alternative division:

Anatomical ⟲ Functional

"bottom-up" "middle-out"

"Functional"?

Abstract neuronal activity from

- biophysics
    - spike trains
    - firing rates
    - abstract transformations
- details of network
    - feedforward perceptrons
    - no cell classes / Dale's Law

Link to function

- representation
- behaviour
- "computation"
    - "decision making"
    - control
    - adaptation + learning

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Tools ⟷ Science

1. statistical descriptions of spikes
2. Info theory

⟷

3. computational analysis
4. representational theory

6. Dynamical systems ⟷ 5. computation through dynamics

# Spike trains

All information is in which cell fired + when.

These things are extremely variable. $\Rightarrow$ need tools to characterise variability.

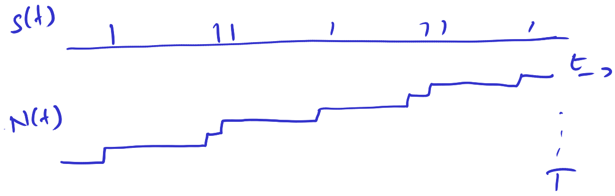
Different ways to represent spikes (in 1 cell)

$$S' = \{t_1, t_2, t_3 \cdot t_N\}$$

$$s(t) = \sum_{i=1}^{N} \delta(t - t_i)$$

$$N(t) = \int_0^{\to t} d\xi \, s(\xi)$$

$$N[t, t') = \int_t^{\to t'} d\xi \, s(\xi)$$




or discretizing time:

$$\underset{\sim}{s} = [s_1 \dots s_{T/\Delta t}]$$

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$$P(s(t)) \; ?$$

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Spike train constant avg rate: $\lambda$

otherwise unconstrained:

① $[s,t)$ $[s',t')$ disjoint $\Rightarrow N_\lambda[s,t) \perp\!\!\!\perp N_\lambda[s',t') \mid \lambda$

$\to$ max entropy (combination of many ind. processes)

② $\mathbb{E}[N_\lambda[s,t)] = (t-s)\lambda$

③ "conditional orderliness" $P(t_i = t_j) = 0$

Homogeneous Poisson Process.

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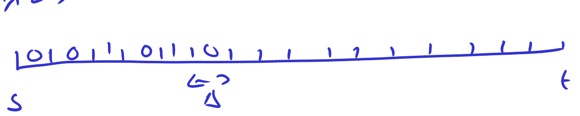
$$P(N_\lambda[s,t) = n) \; ?$$




$M$ bins, width $\Delta$   $t - s = T$

$$P(N_\lambda[s,t) = n) = \binom{M}{n} (\lambda\Delta)^n (1 - \lambda\Delta)^{M-n}$$

$$= \frac{M!}{n!\,(M-n)!} \left(\frac{\lambda T}{M}\right)^n \left(1 - \frac{\lambda T}{M}\right)^{M-n} \qquad \lambda T = \mu$$

$$= \frac{\mu^n}{n!} \cdot \frac{M(M-1)\dots(M-n+1)}{M^n} \left(1 - \frac{\mu}{M}\right)^{-n} \left(1 - \frac{\mu}{M}\right)^{M}$$

$\Delta \to 0 \Rightarrow$ $M \to \infty$

$$= \frac{\mu^n}{n!} \cdot 1 \cdot 1 \cdot e^{-\mu}$$

$$= \frac{\mu^n}{n!} e^{-\mu}$$

(5) $\text{Variance}[N_\lambda[s,t)] = \mu$

$\Rightarrow$ Fano factor $\dfrac{\mathrm{Var}[n]}{\mathbb{E}[n]} = 1$

only sensible for dimensionless RV

(6) ISI distribution

$\rightarrow$ all ISIs $\perp\!\!\!\perp$ | spike $i$ at $t_i$ $N[s,t_i) \perp N[t_i,t)$

$$P[\Delta t_i \in [\tau, \tau+d\tau)] = P[\underset{N_\lambda(t_i,t_i+\tau)=0}{N_\lambda[t_i, t_i+\tau)=1} \mid t_i] \times P[N_\lambda[t_i+\tau, t_i+\tau+d\tau)=1]$$

$$= e^{-\tau\lambda}\, \lambda d\tau\, \underbrace{e^{-\lambda d\tau}}_{1-\lambda d\tau + \dots}$$

$$= \underbrace{\lambda e^{-\tau\lambda}}\, d\tau$$

ISI distribution : $\text{Exponential}[\lambda^{-1}]$

$\Rightarrow$ $\mathbb{E}[\tau] = 1/\lambda$

$\mathrm{Var}(\tau) = 1/\lambda^2$

$CV(\tau) = \dfrac{\mathrm{std}(\tau)}{\mu(\tau)} = 1$

Joint likelihood

$$\underline{P}(\{t_1, \dots t_n\}) \approx p(t_1 \dots t_n)\, dt_1 \dots dt_n \quad \text{in } (0,T)$$

$$= P[N[0,T)=n] \cdot \prod_i P[\text{ith spike} \in [t_i, t_i+dt) \mid n] \times \#\text{ordering}$$

$$= \frac{(\lambda T)^n e^{-\lambda T}}{n!} \prod_i \left(\frac{dt_i}{T}\right) \cdot n!$$

$$= \underbrace{\lambda^n e^{-\lambda T}} \cdot \prod_i dt_i$$

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## Inhomogeneous Poisson Process

rate $\lambda(t)$ $\quad \lim_{dt\to 0} \mathbb{E}[N[t,t+\Delta t)] = \lambda(t)\,dt$ $\quad$ intensity function

independence $\Rightarrow$

" $\Rightarrow$ " H. Poisson Process in $dt$

$$N[s,t) = \text{`}\textstyle\sum N[dt)\text{'} \sim \text{Poiss}\left[\int_s^t d\xi\, \lambda(\xi)\right]$$

$\Rightarrow$ Fano factor $= 1$

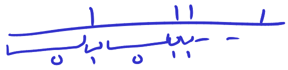
ISI ?

still have $\perp$

$$P[\Delta t_i \in [\tau, \tau+d\tau)] = \underbrace{e^{-\int_{t_i}^{t_i+\tau}\lambda(\xi)d\xi}\,\lambda(t_i+\tau)\,d\tau}\quad [e^{\cdots}]$$

CV doesn't make sense [ $CV_2$ instead]

Joint likelihood



$$P[\{t_1 \ldots t_n\}] = p(t_1 \ldots t_n)\,dt_1 \ldots dt_n$$

$$= e^{-\int_0^{t_1}\lambda}\,\lambda(t_1)dt_1\, e^{-\int_{t_1}^{t_2}\lambda}\,\lambda(t_2)dt_2 \cdots$$

$$= \prod_i \lambda(t_i)\,dt_i\; e^{-\int_0^T \lambda(\xi)d\xi}$$

Time rescaling

$$u(t) = \int_0^t \lambda(\xi)d\xi \qquad u_i = \int_0^{t_i}\lambda(\xi)d\xi \qquad t_i = t(u_i)$$

$$p(u_1 \ldots u_n) = p(t(u_1) \ldots t(u_n)) \Big/ \prod_i \frac{du_i}{dt_i}$$

$$= \prod_i \lambda(t_i)\, e^{-u(T)} \Big/ \prod_i \lambda(t_i)$$

$$= e^{-u(T)}$$

Self-exciting Point Processes

$$\lambda(t \mid \underbrace{N(t), t_1 \ldots t_{N-1}}_{H(t)})$$


$s_i \in \{0,1\}$

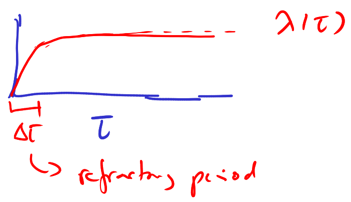
$$p(\underset{\sim}{s}) = p(s_1, s_2 \ldots s_n) = \prod_m \underbrace{p(s_m \mid s_1 \ldots s_{m-1})}$$

$$\to \lambda(t_m \mid H(t_m))$$

[note: time-rescaling by $\lambda(t \mid H(t))$ applies.]

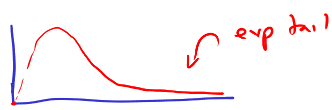
Renewal process

$$\lambda(t \mid H(t)) = \lambda(t - t_{N(t)})$$




alt. defn.

iid ISIs $\sim p(\tau)$



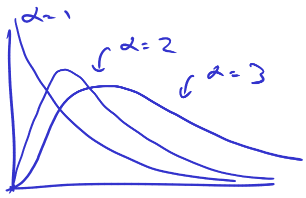
$$\lambda(t \mid t_{N(t)}) = \frac{p(t - t_{N(t)})}{1 - \int_0^{t - t_{N(t)}} d\tau \, p(\tau)}$$

$$p(\tau) = e^{-\int_0^{\tau} \lambda(t_N + s \mid t_N) ds} \qquad \lambda(t_N + \tau \mid t_N)$$

## Gamma-interval point process

$$\Delta t_i \overset{iid}{\sim} \underbrace{\text{Gamma}[\alpha, \beta]}$$

$$p(\tau) = \frac{\beta^{\alpha}}{\Gamma(\alpha)} \tau^{\alpha-1} e^{-\beta\tau}$$




H. Poisson process

keep every $\alpha$th event $\Rightarrow$ Gamma-Intvl $[\alpha, \beta)$

## Inhomogeneous Renewal?

① time rescaling

$$P(t_1 \ldots t_n) = \prod_i p_i(\Delta t_i) \big(1 - \underbrace{\int_{t_n}^{T} d\tau \, p(\tau)}_{\text{no spike after } t_n}\big)$$

$$\prod_i p(\Delta u_i) = \prod_i p\left(\int_{t_{i-1}}^{t_i} g(s) ds\right)$$

② 'spike-response'

$$\lambda(t \mid H(t)) = f(g(t), h(t - t_N)) \qquad \text{"IMI process"}$$

$$\text{often} = e^{g(t) + h(t - t_N)}$$

Difference?

Propose 2 ways for ISI dist to depend on $g(t)$

TR → higher rate ⇒ compressed ISI

SR / IMI → shape stays the "same", modulated by $g$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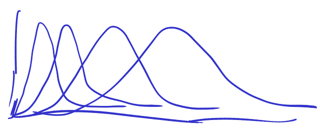
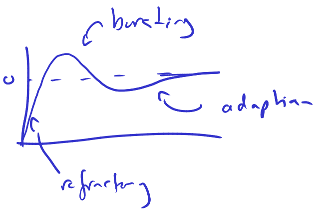
## (Generalised) Hawkes Process / Linear self-exciting process / "GLM"

$$\lambda(t \mid H(t)) = f\left(g(t) + \sum_j h(t - t_{N(t)-j})\right)$$



e.g. $h(\tau) =$




→ relatively easy to fit

Doubly stochastic point processes

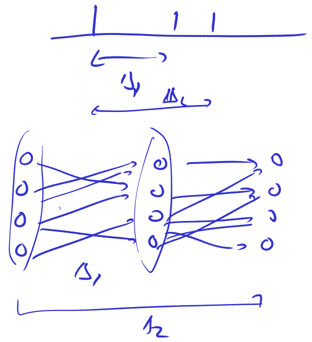
$\uparrow$

Poisson $\longrightarrow$ "Cox process"

[ FF for DS Poisson P. $> 1$

$$\lambda(t)|\rho = f(\rho(t)) \qquad \rho(t) \sim \text{random process}$$

$$\lambda(t|H(t)) = \int d\rho \; \lambda(t|\rho) \, p(\rho | H(t))$$



Random scale

$$\rho \sim \text{Gamma}(\alpha, \beta)$$

$$\lambda(t|\rho) = \rho \cdot \sigma(t)$$

Log-normal Cox process

$$\rho(t) \sim GP(\mu(t), K(t,t'))$$

$$\lambda(t|\rho) = e^{\rho(t)} + \sigma(t)$$

GPFA

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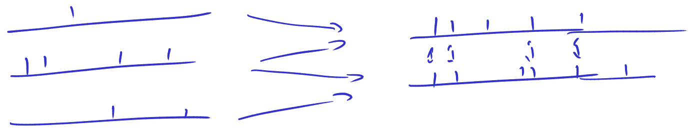
Joint models

- 2D point process? $\times$ $\Rightarrow$ each "spike" had coordinates in both cells ($N$ … $N$)
- superposition



$\Rightarrow$ infinitely divisible processes

- Hawkes processes

$$\lambda^{(c)}(t \,|\, \underline{H}(t)) = f\left( \sum_{j,c'} h^{c,c'}(t - t_j^{c'}) + \rho(t) \right)$$

multivariate GLM

easy to fit

as models nonlinearities $\Rightarrow$ difficult to analyse dynamics

- Doubly stochastic

$$\lambda^{(c)}(t \,|\, \rho(t))$$ common to cells

GPFA: $\rho_i(t) \sim GP(\mu_i(t), K_i)$

$$\lambda^{(c)}(t) = f(\underset{\sim}{c} \cdot \underset{\sim}{\rho}(t))$$

# Measuring Point Processes

$\lambda(t \mid H(t'))$ can be fit assuming a model

nonparametric descriptions ?

$$\bar{\lambda}(t) = \langle \lambda(t \mid H(t)) \rangle_{H(t)} \quad \text{2-- PSTH}$$

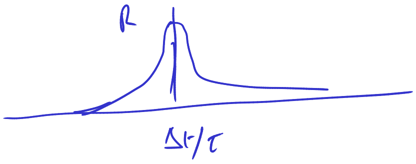
$$\approx \rho(t)$$

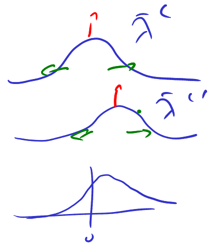
$$R^{c,c'}(t,t') = \langle s^{c}(t)\, s^{c'}(t') \rangle$$

$$= \langle \lambda^{c}(t \mid H)\, \lambda^{c'}(t' \mid H) \rangle_{H} \qquad \text{cross-correlation}$$

Assume stationary ( function of $t - t'$ )

$$R^{c,c'}(\tau) :$$




$$R^{c,c'}(\tau) = \frac{1}{T}\int dt \left( \left\langle \left(\lambda^{c}(t \mid H) - \bar{\lambda}^{c}(t)\right)\left(\lambda^{c'}(t+\tau \mid H) - \bar{\lambda}^{c'}(t+\tau)\right)\right\rangle + \underbrace{\bar{\lambda}^{c}(t)\,\bar{\lambda}^{c'}(t+\tau)}_{\text{"shift/shuffle correction"}} \right)$$

Covariance , $Q^{cc'}(\tau)$

$$\rightarrow \frac{1}{T}\int dt \Big( \left(\lambda^{c}(t \mid H,\rho) - \langle \lambda^{c}(t \mid \rho)\rangle_{H}\right)\left( \;\; c' \;\; \right)$$

$$+ \left(\langle \lambda^{c}(t \mid \rho)\rangle_{H} - \bar{\lambda}^{c}(t)\right)\left( \;\; c' \;\; \right) \leftarrow$$

$$+ \bar{\lambda}^{c}(t)\,\bar{\lambda}^{c'}(t+\tau) \Big)$$