# Dynamic modeling of neural spike count data with non-Poisson variability

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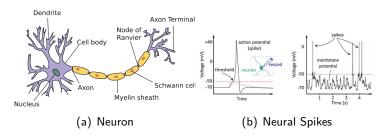
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### Introduction: Neuron and Neural Spikes

#### Neuron and Neural Spikes

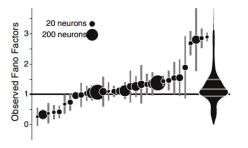
Spikes for single neuron:  $\{y_k\}_{k=0}^T$  for  $y_k \in \mathbb{N}_{\geq 0}$ 



Naturally, the spiking pattern (e.g. spiking rate & variance) will change along the time. These changes tell us how brain process information!

## Introduction: Neuron and Neural Spikes

Poisson (mean = Var)? NB (mean  $\leq$  Var)? **Unrealistic**! Fano factor = variance-to-mean ratio  $(\sigma^2/\mu)$ 



In summary, neural spikes:

- pattern (both mean & variance) changes along the time.
- non-Poisson, can be both over- and under-dispersed.

## Non-Poisson Counts: Conway-Maxwell Distribution

Goal: describe over- and under dispersed count data flexibly. **Conway-Maxwell Poisson** (CMP, jointly model **mean**& **variance**) p.m.f.  $(\lambda, \nu > 0 \text{ or } 0 < \lambda < 1, \ \nu = 0)$ 

$$P(X = x) = \frac{\lambda^x}{(x!)^{\nu}} \cdot \frac{1}{Z(\lambda, \nu)}$$

, for  $x=0,1,\ldots Z(\lambda,\nu)=\sum_{y=0}^{\infty}\frac{\lambda^{y}}{(y!)^{\nu}}$  is the normalizing constant. Parameter  $\nu$  controls the dispersion pattern:

- $\nu = 1$ : Poisson
- $\nu < 1$ : over-dispersed ( $\nu = 0$  Geometric)
- $\nu > 1$ : under-dispersed ( $\nu \to \infty$  Bernoulli)

## Track the Change: State Space Model

Jointly model parameters of the  $i^{th}$  neuron at step k:  $\log(\lambda_{ik}) = \mathbf{X}_{ik}\beta_k$  and  $\log(\nu_{ik}) = \mathbf{G}_{ik}\gamma_k$ . Denote  $\theta_k = (\beta'_k, \gamma'_k)'$ .

- ullet The prior (state equation):  $m{ heta}_k | m{ heta}_{k-1} \sim \textit{N}(m{ heta}_k m{ heta}_{k-1}, m{Q}_k)$
- The posterior:  $P\left(\theta_{k}\middle|\mathbf{Y}_{[k]}\right)\propto P\left(\mathbf{y}_{k}\middle|\theta_{k},\ \mathbf{Y}_{[k]}\right)P\left(\theta_{k}\middle|\mathbf{Y}_{[k-1]}\right)$

However, since the likelihood is CMP distributed  $\Rightarrow$  no closed posterior. Normal approximation: at recursive prior.

- Assume approximated (log-posterior) gradient & hessian are the equal to true values.
- fast: one-time calculation.

## Estimation: Filter by Normal Approximation (Original)

Normal approximation at recursive prior

Prior:

$$egin{aligned} oldsymbol{ heta}_{k|k-1} &= oldsymbol{F}_{k-1} oldsymbol{ heta}_{k-1|k-1} \ oldsymbol{\Sigma}_{k|k-1} &= oldsymbol{F}_{k-1} oldsymbol{\Sigma}_{k-1|k-1} oldsymbol{F}'_{k-1} + oldsymbol{Q}_k \end{aligned}$$

Posterior:

$$egin{aligned} oldsymbol{ heta}_{k|k} &= oldsymbol{ heta}_{k|k-1} + \left(oldsymbol{\Sigma}_{k|k}
ight) \left[rac{\partial I_k}{\partial oldsymbol{ heta}_k}
ight]_{oldsymbol{ heta}_{k|k-1}} \ &\left(oldsymbol{\Sigma}_{k|k}
ight)^{-1} = \left(oldsymbol{\Sigma}_{k|k-1}
ight)^{-1} - \left[rac{\partial^2 I_k}{\partial oldsymbol{ heta}_k \partial oldsymbol{ heta}_k'}
ight]_{oldsymbol{ heta}_{k+1}} \end{aligned}$$

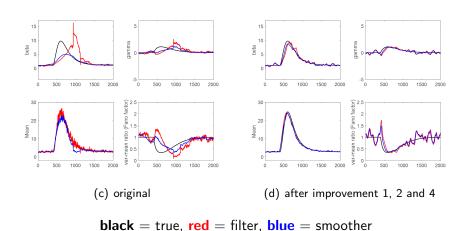
Great, fast 1-time calculation, but...

- Hessian is not robust to outliers.
- Evaluate things at recursive prior: may bias too much if true values are far from priors.

### **Improvement**

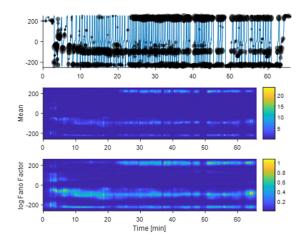
- Routinely improve filter by backward RTS smoother
- Ensure positive-definite covariance (robustness): use expected information (like Fisher scoring).
- ① Do exact Laplace approximation at the posterior mode: Because of Markovian assumption, the hessian for log-posterior is tri-block diagonal  $\Rightarrow$  can update efficiently in  $\mathcal{O}(T)$  by Newton-Raphson, starting with smoother estimates.

#### Simulation



## Application: "place cell" in hippocampus

Experiment: a rat run back and forth along the linear track.



## Appendix 1: Evaluation at Recursive Prior

Posterior:

$$\begin{split} P(\boldsymbol{\theta}_{k}|\boldsymbol{Y}_{[k]}) &\propto L_{k} \cdot P(\boldsymbol{\theta}_{k}|\boldsymbol{Y}_{[k-1]}) \\ &= L_{k} \cdot \exp\left(-\frac{1}{2}\left(\boldsymbol{\theta}_{k} - \boldsymbol{\theta}_{k|k-1}\right)'\left(\boldsymbol{\Sigma}_{k|k-1}\right)^{-1}\left(\boldsymbol{\theta}_{k} - \boldsymbol{\theta}_{k|k-1}\right)\right) \\ &\propto \exp\left(-\frac{1}{2}\left(\boldsymbol{\theta}_{k} - \boldsymbol{\theta}_{k|k}\right)'\left(\boldsymbol{\Sigma}_{k|k}\right)^{-1}\left(\boldsymbol{\theta}_{k} - \boldsymbol{\theta}_{k|k}\right)\right) \end{split}$$

Take 1st and 2nd derivatives, w.r.t.  $\theta_k$ :

$$\begin{split} \left(\frac{\partial l_{k}}{\partial \boldsymbol{\theta}_{k}}\right)^{'} - \left(\boldsymbol{\Sigma}_{k|k-1}\right)^{-1} \left(\boldsymbol{\theta}_{k} - \boldsymbol{\theta}_{k|k-1}\right) &= -\left(\boldsymbol{\Sigma}_{k|k}\right)^{-1} \left(\boldsymbol{\theta}_{k} - \boldsymbol{\theta}_{k|k}\right) \\ \frac{\partial^{2} l_{k}}{\partial \boldsymbol{\theta}_{k} \partial \boldsymbol{\theta}_{k}^{\prime}} - \left(\boldsymbol{\Sigma}_{k|k-1}\right)^{-1} &= -\left(\boldsymbol{\Sigma}_{k|k}\right)^{-1} \end{split}$$

# Appendix 2: Fisher Scoring

gradient and hessian of log-likelihood:

$$\left[\frac{\partial I_{k}}{\partial \theta_{k}}\right]_{\theta_{k|k-1}} = \sum_{i=1}^{n_{k}} \binom{(y_{ik} - E(Y_{ik})) \mathbf{x}_{ik}}{\nu_{ik} (E(\log Y_{ik}!) - \log y_{ik}!) \mathbf{g}_{ik}}_{\theta_{k|k-1}}$$

$$\left[-\frac{\partial^{2} I_{k}}{\partial \theta_{k} \partial \theta_{k}'}\right]_{\theta_{k|k-1}} = \sum_{i=1}^{n_{k}} \binom{A_{ik} B_{ik}}{B_{ik}' C_{ik}}$$

, where

$$\begin{aligned} &A_{ik} = Var(Y_{ik}) \mathbf{x}_{ik} \mathbf{x}'_{ik} \\ &B_{ik} = -\nu_{ik} Cov(Y_{ik}, \log Y_{ik}!) \mathbf{x}_{ik} \mathbf{g}'_{ik} \\ &C_{ik} = \nu_{ik} (\nu_{ik} Var(\log Y_{ik}!) - E(\log Y_{ik}!) + \log y_{ik}!) \mathbf{g}_{ik} \mathbf{g}'_{ik} \end{aligned}$$

 $C_{ik}$  is not robust to outliers. Replace it by the expected value:

$$C_{ik}^* = \nu_{ik}^2 Var(\log Y_{ik}!) \mathbf{g}_{ik} \mathbf{g}'_{ik}$$



## Appendix 3: Tri-block Diagonal Hessian

Hessian for log-posterior:

$$H = \frac{\partial^2 \log P(\boldsymbol{\theta}|\mathbf{Y})}{\partial \boldsymbol{\theta} \partial \boldsymbol{\theta}'} = \begin{pmatrix} \frac{\partial^2 \log P(\boldsymbol{\theta}|\mathbf{Y})}{\partial \theta_1 \partial \theta_1'} & \mathbf{F}_2' \mathbf{Q}_2^{-1} & \cdots & 0 \\ \mathbf{Q}_2^{-1} \mathbf{F}_2 & \frac{\partial^2 \log P(\boldsymbol{\theta}|\mathbf{Y})}{\partial \theta_2 \partial \theta_2'} & \cdots & \vdots \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & \cdots & \frac{\partial^2 \log P(\boldsymbol{\theta}|\mathbf{Y})}{\partial \theta_T \partial \theta_T'} \end{pmatrix}$$

,where

$$\begin{split} \frac{\partial^2 \log P(\boldsymbol{\theta}|\boldsymbol{Y})}{\partial \boldsymbol{\theta}_1 \partial \boldsymbol{\theta}_1'} &= \frac{\partial^2 l_1}{\partial \boldsymbol{\theta}_1 \partial \boldsymbol{\theta}_1'} - \boldsymbol{\Sigma}_0^{-1} - \boldsymbol{F}_2' \boldsymbol{Q}_2^{-1} \boldsymbol{F}_2 \\ \frac{\partial^2 \log P(\boldsymbol{\theta}|\boldsymbol{Y})}{\partial \boldsymbol{\theta}_k \partial \boldsymbol{\theta}_k'} &= \frac{\partial^2 l_k}{\partial \boldsymbol{\theta}_k \partial \boldsymbol{\theta}_k'} - \boldsymbol{Q}_k^{-1} - \boldsymbol{F}_{k+1}' \boldsymbol{Q}_{k+1}^{-1} \boldsymbol{F}_{k+1} \\ \frac{\partial^2 \log P(\boldsymbol{\theta}|\boldsymbol{Y})}{\partial \boldsymbol{\theta}_T \partial \boldsymbol{\theta}_T'} &= \frac{\partial^2 l_T}{\partial \boldsymbol{\theta}_T \partial \boldsymbol{\theta}_T'} - \boldsymbol{Q}_T^{-1} \end{split}$$