Adaptive Modeling of Neural Spikes with Non-Poisson Variability

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Introduction

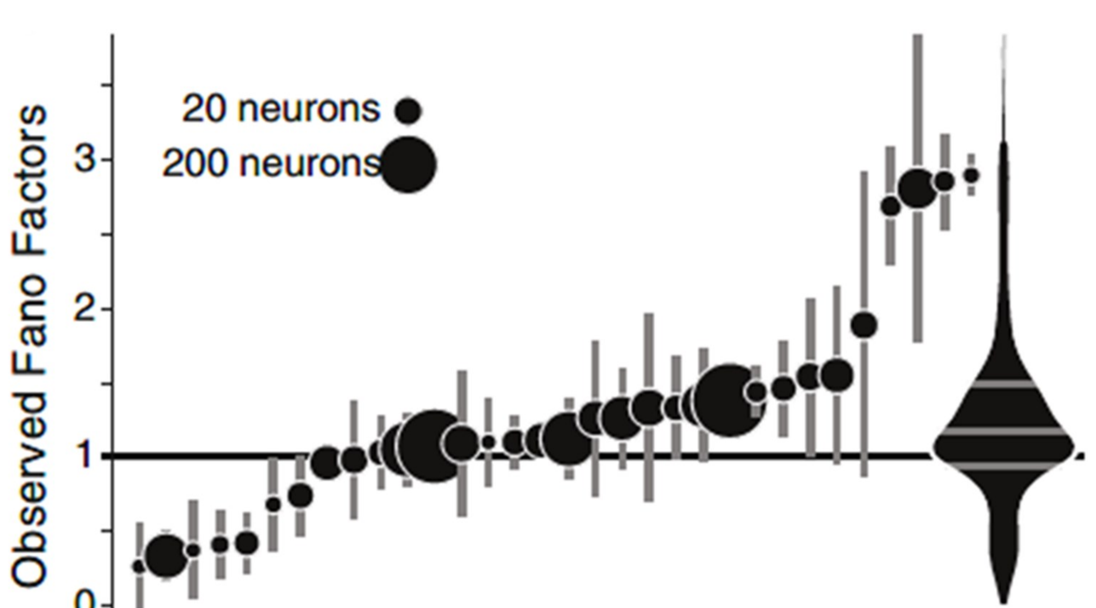
In many areas of the brain, neural spiking activity covaries with features of the external world, such as sensory stimuli or an animal's movement. Experimental findings suggest that the variability of neural activity changes over time and may provide information about the external world beyond the information provided by the average neural activity. To flexibly track time-varying neural response properties, here we developed a dynamic model with Conway-Maxwell-Poisson (COM-Poisson) observations.

Non-stationary and Non-Poisson Neural Spikes

Neurons respond and process stimulus from outside by rapid impulse response in membrane voltage, which is called as an action potential or a spike. The neural spiking data is a time series of count data, by calculating the number of spikes within each time bin. When the recording length is T, the spikes for a single neuron is $\{y_k\}_{k=0}^{T}, y_k \in \{0,1,2,\ldots\}$

To reflect the change of outside information, the spiking pattern will change along the time (**non-stationary**). Currently, most models focus only on the change in mean neural response. However, there is growing evidence that neural variability is not constant, but rather depends on an animal's alertness or motivation, as well as, the specific stimuli or behavior.

Moreover, these models assume the neural variability is Poisson distributed. However, even in controlled setting where the same stimulus can be repeatedly presented, neural responses often have **non-Poisson variability**.



Observed Fano Factor

When evaluating the observed variance-to-mean ratios, i.e. Fano factors, we see that most neurons are far from Poisson. If we further track the Fano factor along the time, we will see it is also non-stationary.

Model Non-Poisson spiking counts: Conway-Maxwell Poisson

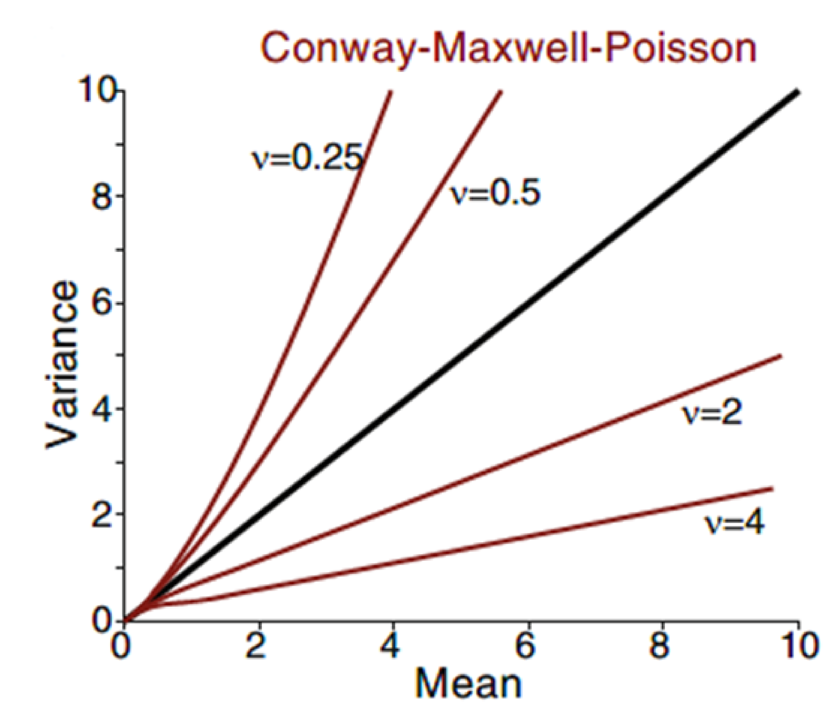
To flexibly describe over- and under-dispersed spiking counts, we assume the counts follow the Conway-Maxwell Poisson (CMP) distribution, which generalizes the Poisson distribution by adding a parameter to model overdispersion and underdispersion. The p.m.f. of CMP is:

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

, where $\lambda,\nu>0$ or $0<\lambda<1,\nu=0$ and $Z(\lambda,\nu)=\sum_{y=0}^{\infty}\frac{\lambda^y}{(y!)^\nu}$

CMP distribution can flexibly model dispersion with different ν

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



In this research, we further model the two parameters by two linear models:

$$\log(\lambda)=X\beta \quad \log(\nu)=G\gamma$$

Track the Change: State Space Model

We use the state-space model to track the change of CMP parameters.

At step k, the state vectors for neuron i is: $\boldsymbol{\theta}_k=(\boldsymbol{\beta}_k',\boldsymbol{\gamma}_k')'$, with

$$\log(\boldsymbol{\lambda}_{ik})=\boldsymbol{X}_{ik}\boldsymbol{\beta}_k \quad \log(\boldsymbol{\nu}_{ik})=\boldsymbol{G}_{ik}\boldsymbol{\gamma}_k$$

The state equation (or prior): $\boldsymbol{\theta}_k|\boldsymbol{\theta}_{k-1}\sim N(\boldsymbol{F}_k\boldsymbol{\theta}_{k-1},\boldsymbol{Q}_k)$

The posterior: $p(\boldsymbol{\theta}_k|\boldsymbol{Y}_{[k]})\propto p(\boldsymbol{y}_k|\boldsymbol{\theta}_k,\boldsymbol{Y}_{[k]})p(\boldsymbol{\theta}_k|\boldsymbol{Y}_{[k-1]})$

Approximate Posterior by Normal Distribution

The likelihood follows a CMP distribution, which breaks the Normal conjugacy and there's no closed posterior. However, since the likelihood is unimodal, we can use Normal approximation to update posterior efficiently. The fastest way is to evaluate the posterior at recursive prior, i.e. do adaptive filtering, at each step. More explicitly, we assume the approximated gradient and hessian are equal to true values at recursive prior. This leads to the one-time calculation for each step:

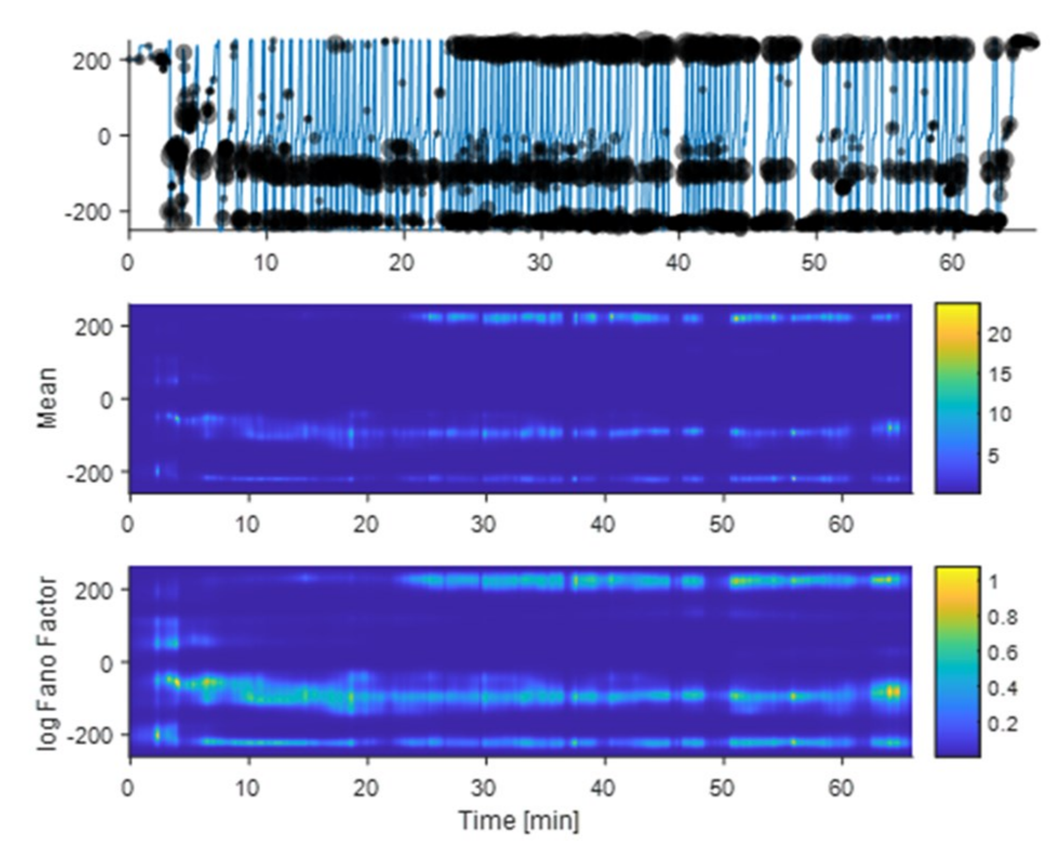
ones-step prediction:

$$\boldsymbol{\theta}_{k|k-1}=\boldsymbol{F}_{k-1}\boldsymbol{\theta}_{k-1|k-1}$$
$$\boldsymbol{\Sigma}_{k|k-1}=\boldsymbol{F}_{k-1}\boldsymbol{\Sigma}_{k-1|k-1}\boldsymbol{F}_{k-1}'+\boldsymbol{Q}_k$$

Posterior update:

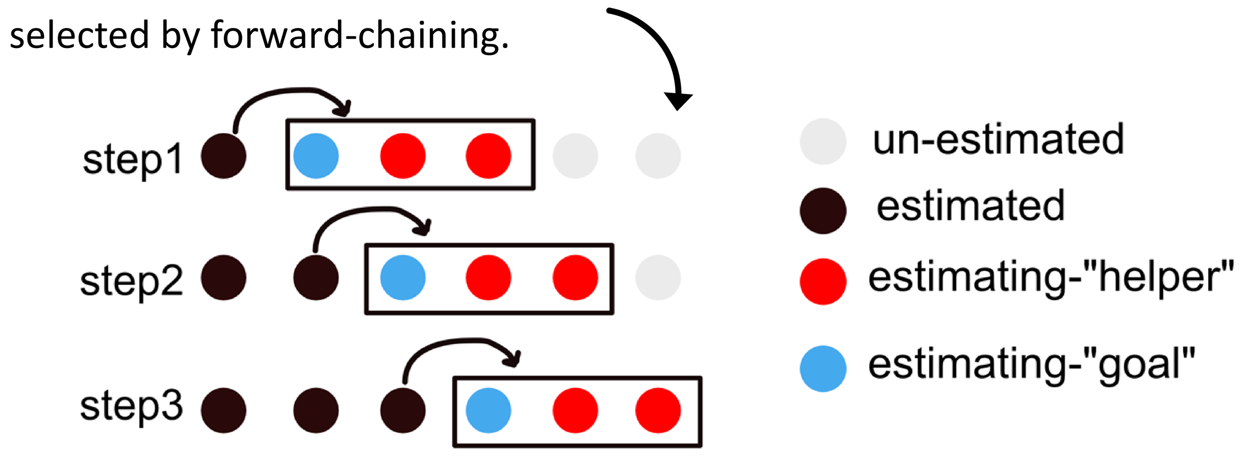
$$\boldsymbol{\theta}_{k|k}=\boldsymbol{\theta}_{k|k-1}+(\boldsymbol{\Sigma}_{k|k})\left[\frac{\partial l_k}{\partial\boldsymbol{\theta}_k}\right]_{\boldsymbol{\theta}_{k|k-1}}$$

$$(\boldsymbol{\Sigma}_{k|k})^{-1}=(\boldsymbol{\Sigma}_{k|k-1})^{-1}-\left[\frac{\partial^2 l_k}{\partial\boldsymbol{\theta}_k\partial\boldsymbol{\theta}_k'}\right]_{\boldsymbol{\theta}_{k|k-1}}$$



Improvement:

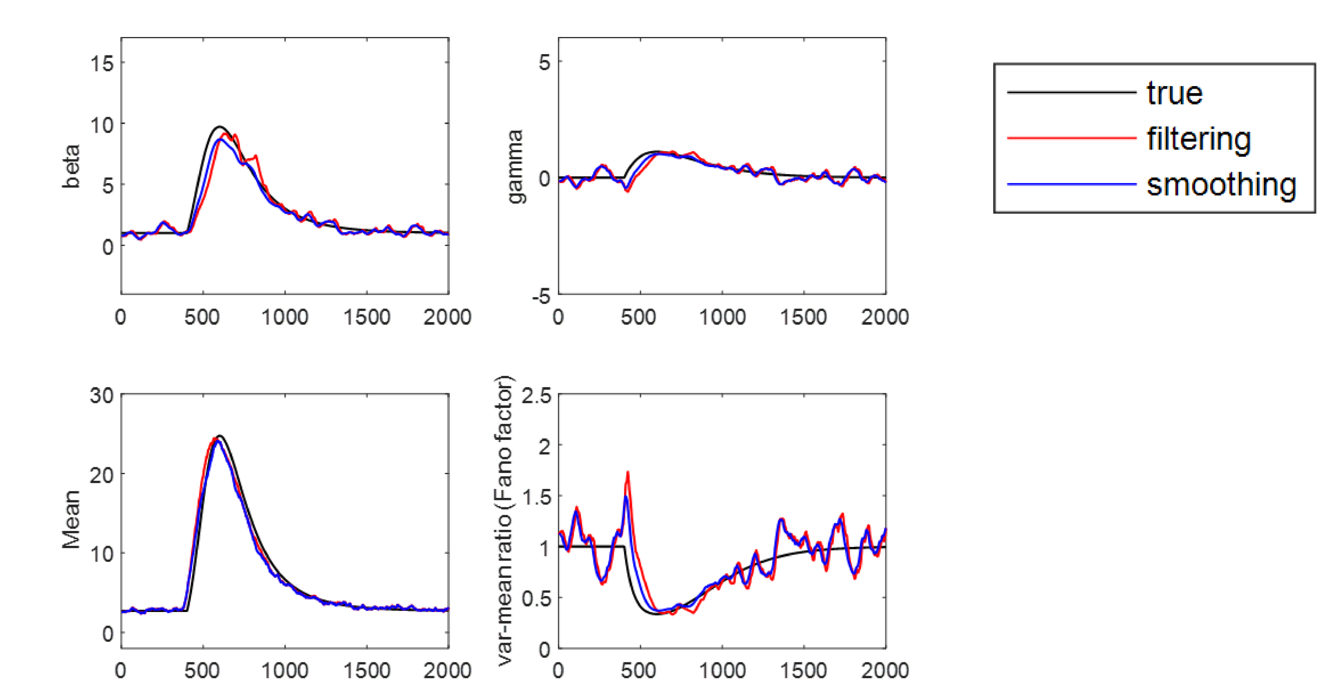
1. We can routinely improve adaptive filter by backward smoother.
2. The observed information matrix is not robust to the outliers. We can use expected hessian as in Fisher scoring.
3. When the true parameter is too far away from the recursive prior, the original method may not be accurate enough. Because of Markovian assumption, the hessian is tri-block diagonal, and we can directly use Newton-Raphson to do exact Laplace approximation (at posterior mode) efficiently in O(T), with adaptive filtering/smoothing estimates as the warm start.
4. We can also enlarge the local sample size at each step, by assuming stationary state vectors within pre-specified windows. The window size can be simply selected by forward-chaining.



* Both 3 and 4 have their own strength. Generally, when the spiking counts are sparse, improvement 4 is a bit better.

Simulation and Application

After implementation of the improvement 1, 2 and 4, we can recover the true values successfully.



We further implemented our model to neural data from "place cells" in the hippocampus. In this experiment, a rat ran back and forth along the linear track, and both changes in mean and Fano factor tell us the learning process of the rat.

References

Eden UT, Frank LM, Barbieri R, Solo V, Brown EN. Dynamic Analysis of Neural Encoding by Point Process Adaptive Filtering. *Neural Comput* 16: 971–998, 2004.

Stevenson IH. Flexible models for spike count data with both over- and under- dispersion. *J Comput Neurosci* 41: 29–43, 2016.