**Dynamic modeling of spike count data with Conway-Maxwell Poisson variability**

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# Abstract

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 (CMP) observations. The CMP distribution can flexibly describe firing patterns that are both under- and over-dispersed relative to the Poisson distribution. Here we track parameters of the CMP distribution as they vary over time. Using simulations, we show that a normal approximation can accurately track dynamics in state vectors for both the mean and dispersion parameters. We then fit our model to neural data from neurons in V1 area and “place cells” in the hippocampus. We find that this method out-performs previous dynamic model based on the Poisson distribution. This model provides a flexible framework for tracking time-varying non-Poisson count data and may also have applications beyond neuroscience.

# Introduction

The neural spiking activities will change across the time, even in the controlled settings with constant stimuli. There is growing evidence that not only mean of neural response is non-stationary, but the variability also varies. The drift in both mean and variance provide information about the external world. In most previous research, the neural variability is assumed to be Poisson distributed. However, many experiments suggest that the neurons can be substantially more or less variable than Poisson.

Variability appears to be an increasingly important aspect of the neural code and can act as a signature of decision making (Churchland et al. 2011), movement preparation (Churchland et al. 2006), or stimulus onset (Churchland et al. 2010). Although systems neuroscience has a long history of studying how external variables influence mean firing rates, much less is known about response variability. For instance, it is currently unknown how variability depends on stimulus intensity, how different cell types differ in their variability, and how differences in variability might impact the representation of external variables across populations of neurons. The primary roadblock to addressing these unknowns is a lack of statistical tools to accurately track the sources of variability within a given experiment. Neural activity changes on different timescales, and distinguishing changes in variability from changes in the mean response based on sparse, spike observations is a nontrivial challenge. Here we will develop probabilistic models with non-Poisson observations to characterize the effects of intrinsic noise and non-stationarity on neural variability. We will then fit these models to neural data to analyze the structure and timescales of variability in single neurons as well as neural populations.

To flexibly track time-varying neural response, in terms of both mean and variance, we developed a dynamic GLM with Conway-Maxwell-Poisson (CMP) observations. The CMP distribution can flexibly account for both over- and under-dispersion in spike count data. To get the closed-form posterior for state vectors with CMP likelihood, we fit the model using a global Gaussian approximation (the Laplace approximation). The procedure can be done efficiently because of the Markovian assumption in state space. We further provide an efficient way to estimate the process noise. After illustrating the proposed method by simulations, we applied it to neurons in V1 area and “place cells” in the hippocampus. The new method can not only capture more information, i.e., dynamics in mean and variance, but also outperforms previous methods based on Poisson assumptions.

Dynamic Poisson model has been developend (EDEN), static CMP model has been developed (Stevenson, Shmueli, Sellers). Here we do dynamic CMP…

Although Poisson adaptive filtering can model non-stationarity and the COM-Poisson model is able to describe non-Poisson noise, combining the two approaches will allow us to more accurately disentangle noise and non-stationarity. Non-stationarity appears as apparent over-dispersion if it is not modeled, and noise assumptions directly affect how accurately changes in firing can be tracked.

Drift…

(Rokni et al. 2007)

(Chestek et al. 2007)

(Stevenson et al. 2011)

(Tomko and Crapper 1974)

Stability…

(Dickey et al. 2009)

(Steinmetz et al. 2021) [shows that correcting for electrode drift reduces some instability]

[some amount of drift is functional] adaptation/plasticity…

(Lesica et al. 2007)

Variability…

(Ghanbari et al. 2019)

(Stevenson 2016)

(Fenton and Muller 1998)

(Barbieri et al. 2001)

(Maimon and Assad 2009)

(Churchland et al. 2010)

(Churchland et al. 2011)

(Eden et al. 2004)

(Brown et al. 2001)

(DeWeese and Zador 1998)

# Methods

Here we consider a dynamic GLM with Conway-Maxwell Poisson (CMP) observations to describe time-varying spike counts. We first introduce the model. Although the CMP distribution allows us to flexibly model non-Poisson variability, one major challenge with using this model is that there are no closed-form posteriors for the CMP likelihood. Here, we fit the model using a global Gaussian approximation, and we discuss several additional technical challenges that arise when using the CMP distribution with a dynamic GLM.

## Dynamic Conway-Maxwell Poisson Model

A count observation , such as the spike count for a neuron, is assumed to follow the CMP distribution, with parameters and . The probability mass function (pmf) of CMP is

, where is the normalizing constant. The parameter controls different dispersion patterns, i.e. equi- (), over- () or under-dispersion (). Three common distributions occur as special cases: 1) the Poisson (), 2) geometric (), and 3) Bernoulli ().

For multiple observations up to steps, such as simultaneous spike counts from neurons, denote the counts at time bin as , for The corresponding CMP parameters at are and . Previous work has examined the CMP-GLM (Chatla and Shmueli 2018; Sellers and Shmueli 2010), and here we focus on the dynamic version of this GLM. The CMP parameters at are modeled by two log-linear models, and , with and , and and denote known predictors. Under the CMP-GLM, the parameters are static. Here, we assume that they progress linearly with a Gaussian noise.

The observations follow conditionally independent CMP distributions, given the state vector .

While the state vector evolves linearly with Gaussian noise:

Given the initial state mean , covariance , linear dynamics and process covariance .

## Inference by Gaussian approximation

To fit the model to data we need to estimate the time-varying state vector In this section, we first assume **F** and **Q** are known. Since the observations are CMP distributed, we cannot estimate in closed form. Instead, here we approximate it by a multivariate Gaussian distribution, , with . The parameters of this Gaussian are found by a global Laplace approximation, i.e., and . The log-posterior is given by:

, where is the log-likelihood. The log-posterior is concave (Gupta et al. 2014), and the Markovian structure of the state vector dynamics makes it possible to optimize by Newton-Raphson (NR) in time (Paninski et al. 2010). After the Newton update, we can further quantify the uncertainty for the CMP parameters and the underlying rates (see Appendix).

There are several technical challenges involved with performing the Newton update with CMP observations. Firstly, in order to find the gradient and Hessian we need to calculate moments of and , which have no closed forms (Shmueli et al. 2005). We can calculate these moments by truncated summation. However, when and , truncated summation is computationally costly since we need many steps for accurate approximation. In this case, we approximate the moments using previous (Chatla and Shmueli 2018; Gaunt et al. 2019) asymptotic results (see Appendix). A second challenge is that the Hessian is not robust to outliers. Outliers often result in the Hessian being close to singular or even positive-definite (see details in Appendix). To ensure robustness, we use Fisher scoring where the observed information is replaced by the expected information. Finally, a third challenge is that the Newton updates take a long time to converge if the initial state estimate is far from the maximum of the posterior, especially when is large. To resolve this issue, we use a smoothing estimate with local Gaussian approximation as a “warm start”. Forward filtering for a dynamic Poisson model has been previously described (Eden et al. 2004), and, here we implement CMP filtering following the same rationale. Let and be the mean and variance for the one-step prediction density and and be mean and variance for the posterior density, then the filtering update for step is given by

Here, to again ensure robustness, we use Fisher scoring when updating the state covariance. We then find smoothed estimates using a backward pass ((Rauch et al. 1965)). Although doing smoothing is fast, the estimates can be inaccurate, especially when there are large changes in the state vectors. In the forward filtering stage, the Gaussian approximation at each step is conducted locally at the recursive prior . This will be statistically inefficient when the recursive prior is too far away from the posterior mode, or when there is a large change in the state vector. Moreover, Fisher scoring reduces the efficiency of the smoother even further. The smoother provides reasonable initial estimates, but estimation accuracy is substantially improved by using Newton’s method to find the global Laplace approximation for the posterior.

## Estimating process noise

For the applications to neural data examined here, we assume that . However, we still need to estimate the process noise . When is small, especially when , different values will have a substantial influence on estimation. One possible way to estimate is to use an Expectation Maximization (EM) algorithm (Macke et al. 2011). However, using the Laplace approximation for during the E-step breaks the usual guarantee of non-decreasing likelihoods in EM, and, hence, may lead to divergence. To avoid that, we could sample the posterior directly by MCMC. However, the lack of closed-form moments for the CMP distribution makes sampling computationally intensive. Here, to estimate robustly and quickly, we instead assume is diagonal and estimate it by maximizing the prediction likelihood in the filtering stage, as in (Wei and Stevenson 2021).

# Results

## Tracking the mean and dispersion of spike counts over time

To illustrate how the dynamic CMP model can track both time-varying mean and dispersion, we simulated a neuron with a time-varying tuning curve, where the response to hypothetical visual stimuli shifts over 100 trials. Here, the neuron’s tuning curve is determined by a linear combination of cubic B-spline basis functions with equally-spaced knots. The stimulus that evokes the highest average response – the “preferred orientation” – is initially ~80 deg, but shifts over the course of the experiment, and the response amplitude also increases over time (Fig. 1A). Meanwhile, the dispersion pattern also changes: the responses are initially over-dispersed relative to a Poisson distribution and then become under-dispersed (Fig. 1B). Noisy observations are sampled from the Conway-Maxwell Poisson distribution at each time (Fig. 1C), mimicking the types of experimental observations collected during adaptation experiments in primary visual cortex (Dragoi et al. 2000) . We then fitted the simulated spike observations using the same predictor variables as the generative model: the covariates for capture the tuning curve with as a 10-knot cubic spline basis expansion of the orientation, and the covariate for the dispersion parameter does not depend on the stimulus orientation . The fitted results match the ground truth well, for both the mean (Fig. 1C) and Fano factors (variance-to-mean ratio, Fig. 1D).

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| Chart, histogram  Description automatically generated with medium confidence |
| **Figure 1. A simulated neuron with a shifting firing and dispersion pattern.** (A) The tuning curve of the neuron shifts over time, with the preferred stimulus orientation changing and the response amplitude increasing. (B) At the same time, the variability in spiking changes from being over-dispersed relative to a Poisson distribution to under-dispersed. This leads to a decreasing Fano factor (variance-to-mean ratio) from 1.9 to 0.4 overall. (C) To illustrate the shifts, we show the tuning curve at two time points: Trial 20 (blue) and Trial 80 (red). Dots denote observed spike counts. The solid lines are the ground truth in mean firing rate, while the corresponding dashed lines are the fitted values. (D) To illustrate the shift in dispersion over time we show the true (solid) and estimated (dashed) Fano Factor for two specific stimuli as a function of time. The dispersion for the early preferred orientation is shown in cyan, while the dispersion for the late preferred orientation is shown in yellow. |

This model-based approach provides estimates of tuning curves and dispersion at each time point. In cases where the tuning curve and variability change simultaneously, this approach can efficiently track both. By using the model with CMP observations, rather than Poisson or negative-binomial observations, the Fano Factor can be both <1 (under-dispersed) and >1 (over-dispersed).

Changes in tuning have been widely documented in systems neuroscience both due to changing environment and spontaneous nonstationarity. Changes in variability also occur, but have been less well studied. With the CMP model, the mean and dispersion are both tracked and, thus, changes in variability can occur even when the mean is stable. To illustrate this potential, we simulated a neuron whose mean firing rate is controlled to be constant, but whose Fano factor varies over time. Here is a 5-knot cubic B-spline basis expansion of the orientation and . The model recovers the true mean firing rate (Fig. 2A) and capture the fluctuations in variance (Fig. 2B) at the same time. However, the estimated Fano factor is somewhat oversmoothed when the process noise is optimized by maximizing the predictive likelihood (see Methods).

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| **Figure 2. Constant mean with fluctuations in dispersion.** (A) The first two panels show the true mean firing rate and the simulated observations. The last panel show the fitted mean response. (B) Although the mean response is constant, the Fano factor varies across the trial (black line). The colored line show the fitted result. |

Although dynamic Poisson models have been applied in some neuroscientific settings, when spike counts are not Poisson distributed the model estimates can be biased. Since the dispersion influences estimates of the process noise , estimates of the mean in the dynamic Poisson model can be affected by over- or under-dispersion. To illustrate this interaction here we simulate a place cell from the hippocampus whose “place field” drifts over time. The true mean is determined by a Gaussian function where the preferred position varies over time. The spike counts are then generated by CMP distributions, here over-dispersed with constant dispersion parameter (). We fit 1000 observations randomly sampled from 100 “runs” of a linear track. We find that, in this data-limited regime, the dynamic Poisson model and the dynamic CMP model give substantially different estimates of the time-varying place field (Fig. 3A). The dynamic Poisson model, in this case, under-estimates the firing rate at the true preferred position and under-estimates the uncertainty (Fig. 3B).

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| **Figure 3. Dynamic CMP and dynamic Poisson estimates differ.** Simulated over-dispersed place cell spiking is generated by the dynamic CMP model with . (A) We then fit dynamic CMP and dynamic Poisson models with a 2-knot B-spline expansion for position ( for the CMP). (B) When evaluating the response at the true preferred position for each run, the dynamic Poisson estimates are biased (under-estimated) and the uncertainty is also underestimated. The solid line gives the MAP estimates of mean firing rate, and the dashed lines show one S.D. credible intervals. The standard deviations of dynamic CMP estimates are calculated using the truncated summations (see details in Appendix), while the standard deviations for the dynamic Poisson model are from a log-normal distribution. |

## Application to Experimental Data

We next applied our method to two publicly available datasets of extracellular spike recordings: 1) Utah array recordings of visually evoked activity from anesthetized macaque primary visual cortex (“V1 data”), and 2) multi-shank silicon probe recordings from hippocampus of a rat running back-and-forth on a linear maze (“HC data”).

### **V1 data**

In the V1 dataset. CRCNS pvc-11 (Kohn and Smith 2016), anesthetized macaque monkeys viewed full-field sinusoidal grating movies while neural activity was recorded by a 96-channel “Utah” array. Extracellular spiking activity was recording on each electrode, and spike waveform segments were sorted by hand with modified competitive mixture decomposition methods (Shoham et al. 2003). Here we use data from one animal (Monkey 1) viewing a movie of drifting sinusoidal gratings with ~100 different drift directions presented in pseudorandom order (300ms each, 30s movie in total), and the movie was repeated 120 times. Here we analyze spike counts following each stimulus presentation from the period 50-350ms after stimulus onset. For further details on how the data were obtained, see (Kelly et al. 2010; Smith and Kohn 2008).

As with many neurons in visual cortex, the responses of the neurons in this dataset are tuned to the stimulus direction. Neurons respond to some directions of stimuli more than others, but the spike counts from trial to trial are highly variable. Here, we are specifically interested in tracking changes tuning curves and changes in variability over time. Fig. 4A shows responses from one example neuron with a preferred direction around 240 deg. This neuron is somewhat direction insensitive, and responds preferentially to stimuli moving in the opposite direction, around 70 deg. After fitting the dynamic CMP model to these data, we find that the tuning curve itself appears mostly stable, but the overall firing rate increases over the course of the recording (Fig. 4B). At the same time, the Fano Factor decreases over the course of the recording (Fig. 4C).

Although the data here is structured in 120 “trials” the data are collected sequentially, and we model nonstationary at the level of individual observations. For the predictors and we use cubic B-spline basis functions with periodic boundary conditions over the grating directions. Results for the example neuron use 5 and 3 equally-spaced knots for and , respectively. Fitting the model with half of the data (in a speckled hold-out pattern) gives patterns for the mean response (Fig. 4B) and Fano Factor (Fig. 4C) that are similar to those using the full data. However, since the model-based approach provides a continuous estimate of the state vectors, the Fano Factor estimated by the dynamic CMP model differs from a simple estimate of the Fano Factor calculated using a sliding window (Fig. 4C).

We then compare the performance of multiple models on data from all 74 neurons in this recording (Fig. 4D). We assess four dynamic models: (1) dynamic CMP, with 5 knots for and 3 knots for , denoted as dCMP-(5,3); (2) dynamic CMP with , dCMP-(5,1); (3) dynamic CMP with constant , dCMP-(5)- (fit by coordinate descent) and (4) a dynamic Poisson model, dPoi-(5). Additionally, we assess three static models: (1) static CMP, sCMP-(5,3); (2) static CMP with , sCMP-(5,1) and (3) static Poisson, sPoi-(5). The held-out log-likelihoods relative to a homogeneous static Poisson model show that the CMP-based models, both dynamic and static, outperform the Poisson-based models (Fig. 4D). The dynamic models perform slightly better than the corresponding static models, on average. The best performance on test data comes from modeling nonstationarity and stimulus-dependence with the full dynamic CMP model dCMP-(5,3). However, the benefit of adding nonstationary dispersion parameter (dCMP-(5)- vs. dCMP-(5,1)) and of adding stimulus-dependent dispersion parameter (dCMP-(5,1) vs dCMP-(5,3)) tend to be small for these data.

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| **Figure 4. Modeling nonstationary spiking from visual cortex.** (A) The spike counts of one example neuron from V1 in response to drifting grating stimuli with different drift directions presented over 120 trials. Two preferred directions (estimated by the CMP model) are marked by the dashed lines. (B) Estimated mean for the dynamic CMP model dCMP-(5,3) when fit to all the data and only half of the observations (held out in a speckled pattern). (C) Fano factor estimates for the two models, along with a direct estimate from 15-trial sliding windows, at the two preferred directions. Dashed lines denote ±1 standard deviation around the window estimates, obtained by Bayesian bootstrapping. (D) Model comparison for all 74 neurons in the V1 dataset. In these models, 4 are dynamic and the remaining 3 are static, with different noise distributions (Poisson vs CMP) and bases. The training and test log-likelihood ratios (bits/spike) with respect to a homogeneous static Poisson model are shown for all neurons in grey lines. The solid orange lines and numbers denote the medians, and the dashed lines show the first and third quartiles. |

### Hippocampus data

In the HC dataset, CRCNS hc-3 (Mizuseki et al. 2013), a rat was running back and forth along a 250cm linear track. Extra cellular spiking activity was recorded in dorsal hippocampus using multi-shank silicon probes. Spikes were automatically sorting using KlustaKwik followed by manual adjustment (Rossant et al. 2016). Here we use data from one 66 min recording session (ec014-468) and analyze spike counts in 200ms bins. For further details on how the data were obtained, see (Mizuseki et al. 2014).

As with many neurons in hippocampus, the responses of the neurons in this dataset are tuned to the rat’s position along the track. Neurons spike at specific locations, but the place fields can also shift over time and the spike counts from run to run are highly variable. Fig. 5A shows an example from one neuron with two place fields where the location and firing within the place field vary over the course of the recording. Compared to the data from V1, neural responses of place cells in hippocampus tend to be sparser and more selective. Many place cells also tend to be direction tuned – spiking only when the animal is running in one direction down the track but not the other. We, thus, fit the data using a dynamic CMP model with 12 equally-spaced knots for with a circular representation of position, and let .

For this example neuron, the dynamic CMP model accurately tracks the time-varying place field (Fig. 5B). We then evaluate the fitted Fano factors at the peaks of the two place fields (Fig. 5C). Compared to example from the V1 data, the spiking of this example place cell is much more highly dispersed. The Fano factors vary over time and are also specific in both position and running direction. We then compare model performance on 78 neurons from this recording (19 neurons were excluded based on low firing rates). In these data, the dynamic models are generally better than the static models (Fig. 5D). Within groups of dynamic or static models, CMP-based models are consistently better than the Poisson-based models.

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| **Figure 5. Modeling nonstationarity in hippocampal spiking activity.** (A) Spike counts of an example neuron from the hippocampus recorded while a rat was running back-and-forth on a linear maze. The blue lines show the animal’s position over time. The black circles denote spike counts with the radius of each circle corresponding to number of spikes. (B) The heatmap shows fitted mean firing rate for the dynamic CMP model dCMP-(12,1). The colored lines show peaks for two place fields, chosen based on the model fit. (C) The estimated Fano factors at the two place field peaks, with each running direction (+ vs -) shown separately. (D) The training and test log-likelihood ratios (bits/spike) with respect to a homogeneous static Poisson model for 78 neurons (gray lines). Here the test set log-likelihood ratios are calculated using 5% of the data held-out in a speckled pattern. The red solid lines and numbers denote median values, while the dashed lines show the first and third quartiles. |

# Discussion

While many studies have characterized noise (DeWeese et al. 2003; Deweese and Zador 2004; Taouali et al. 2016) or non-stationarity (Tomko and Crapper 1974; Wu and Hatsopoulos 2008) separately, modeling both terms will allow us to examine how they together impact the neural code. The models and results developed here will build on several previous findings, including findings that cortical neurons are highly non-Poisson (Amarasingham et al. 2006; DeWeese et al. 2003; Kara et al. 2000), that hippocampal place fields appear to drift over time (Brown et al. 2001), and that neurons in visual cortex rapidly adapt (Lesica et al. 2003; Lesica and Stanley 2005) to changing image statistics.

Omitted variables can increase the apparent variability of observations via the law of total variance. For example, in the hippocampus, place cell firing is highly variable on different passes through the field (cite Fenton). This may be partially due to joint selectivity to position, speed, and head direction, as well as the influence of theta phase. Here, rather than model these distinct covariates assuming Poisson observations, we allow the variability to be non-Poisson and introduce a dynamic GLM model with CMP observations. The proposed model can track the fluctuations in mean and dispersion for neural spiking activities simultaneously. The global Laplace approximation with smoothing estimates initialization provide an accurate and computational efficient model estimates. After validating our method by simulations, we further applied it to neurons in V1 area and “place cells” in the hippocampus. All these examples show that our model can successfully capture dynamics in response mean and dispersion, and the proposed method outperforms models based on Poisson observations or static parameters.

Although the current model works well for fitting the neural spikes, there are some potential improvements. First, the state transition matrix is currently assumed to be known and fixed to be identity for convenience. This doesn’t allow for interactions between state vectors and may limit the usage in some situation. Because the state vectors progress linearly with a Gaussian noise, the estimation of is straightforward. The EM algorithm for Poisson linear dynamics system (PLDS), a modified model for Poisson factor analysis model can be found in (Macke et al. 2011). Secondly, although the CMP distribution can flexibly model over- and under-dispersed data, the assumed mean-variance relationship may not be appropriate in some cases. To give a more flexible modeling of the dispersion, we can instead consider the generalized count (GC) distribution(del Castillo and Pérez-Casany 2005), which is a further generalization of CMP distribution. Combining the idea of dynamical factor analysis, (Gao et al. 2015) proposed GC linear dynamical system (GCLDS) model. However, in their GCLDS, the dispersion function is static. To track the fluctuations in dispersion, we can further model dynamically as for in the proposed dynamic CMP model.

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[Some references are not correct, but they are fixed in LaTeX]

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# Appendix

## Quantifying Uncertainties

After convergence, we have an approximation of the log-posterior , and we can use this approximation to quantify he uncertainty about the CMP parameters, as well as about the mean rate at each time.

The CMP parameters are log-normal distributed. Let , then . Denote the variance of CMP parameters as . The variance can be easily found in Wiki. If I write it out, I need to define some useless notations. . and .

The conditional mean firing rate is , whose variance can be calculated by the Delta method:

We can calculate the moments as in the first section of the appendix, or we can use a simpler approximation when or . Then and .

## Moments approximation for Conway-Maxwell Poisson distribution

To estimate the state-vector for the dynamic CMP model, we need to find first and second moments for and . For ,

Generally, these moments can be calculated by truncated summation.

However, when and , we need many steps for accurate approximation. In this case, we make use of a previous asymptotic results for efficient calculation. Let , and

Then the moments are (The highlights can be found in the reference, the covariance is calculated by myself):

## Gradient and Hessian of the log-posterior

We estimate the state vector by maximizing the log-posterior with Newton-Raphson updates. Denote , the -th update of NR algorithm is .

The gradient is:

The Hessian:

, where

When , the Hessian may be ill-conditioned or even positive-definite. To ensure the robustness, do Fisher scoring, i.e. replace the observed information by the expected information , so that .