Modeling dispersion improves decoding of population neural responses

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Abstract: Neural responses to repeated presentations of an identical stimulus often show substantial trial-to-trial variability. Although the mean firing rate in response to different stimuli or during different movements (tuning curves) have been extensively modeled, the variability of neural responses can also have clear tuning independent of the tuning in the firing rate. This suggests that the variability carries information regarding the stimulus/movement beyond what is encoded in the mean firing rate. Here we demonstrate how taking variability into account can improve neural decoding.

In a typical neural coding model spike counts are assumed to be Poisson with the mean response depending on an external variable, such as a stimulus/movement direction. Bayesian decoding methods then use the probabilities under these Poisson tuning models (the likelihood) to estimate the probability of each stimulus given the spikes on a given trial (the posterior). However, under the Poisson model, spike count variability is always exactly equal to the mean (Fano Factor = 1). Here we use the Conway-Maxwell-Poisson (COM-Poisson) model to more flexibly model how neural variability depends on external stimuli. This model contains the Poisson distribution as a special case, but has an additional parameter that allows both over- and under-dispersed data, where the variance is greater than (Fano Factor >1) or less than (Fano Factor <1) the mean, respectively.

We find that neural responses in both primary motor cortex (M1) and primary visual cortex (V1) have diverse tuning in both their mean firing rates and response variability. These tuning patterns can be accurately described by the COM-Poisson model, and, in both cortical areas, we find that a Bayesian decoder using the COM-Poisson models improves stimulus/movement estimation by 4-8% compared to the Poisson model. The additional layer of information in response variability thus appears to be an important part of the neural code.

Methods: The COM-Poisson distribution takes the form $p(y|\lambda,\nu) = \frac{\lambda^y}{y!^\nu}\frac{1}{Z(\lambda,\nu)}$ with normalization $(\lambda,\nu) = \sum_{n=0}^{\infty}\frac{\lambda^n}{y!^\nu}$. For spike counts y the distribution is a function of the intensity and dispersion parameters λ and ν with $\nu < 1$ describing over-dispersion and $\nu > 1$ describing under-dispersed data. Note that with $\nu = 1$ the COM-Poisson is exactly the Poisson distribution. Here we use the COM-Poisson distribution as the noise model for a GLM [1] to estimate both the mean and variance of neural responses to varying stimuli/movement. In particular, we estimate parameters β and γ that map stimulus/movement covariates $X(\theta)$ and $G(\theta)$ to neural responses using the link functions $\log(\lambda(\theta)) = X(\theta)\beta$ and $\log(\nu(\theta)) = G(\theta)\gamma$. This framework is in effect a dual-link GLM where both the mean and the variance depend on the stimulus/movement direction θ.

Here we estimate the tuning curves using spline bases and maximum a posteriori (MAP) estimation with L2 regularization. Importantly, this approach allows us to model neural responses that are under-dispersed, over-dispersed, or that contain intermingled under- and over-dispersed counts [2]. Using the tuning curve models to describe the likelihood of spike responses, Bayesian decoding approaches then estimate the posterior distribution over stimuli/movement directions given spiking: $p(\theta|y_{1\ldots n}) \propto p(y_{1\ldots n}|\theta)p(\theta)$ for a population of n neurons. Here we make a common assumption that the neurons are conditionally independent $p(y_{1\ldots n}|\theta) = \prod p(y_i|\theta)$ and compare the accuracy of our Bayesian decoder under Poisson and COM-Poisson noise assumptions.

Results: After taking dispersion into account in the Bayesian decoding framework, under-dispersion results in more precise posterior distributions compared to the Poisson assumption, while over-dispersion results in less precise posterior distributions. Assuming Poisson noise when in fact spike counts are under- or over-dispersed can thus results in under- or over-confidence in the decoding results as well as biases (Fig 1). In data from V1 (CRCNS pvc-11) and M1 (CRCNS dream-stevenson) we find that the correlation between mean firing rate and Fano Factor tuning curves spans the whole range from -1 to 1. This diversity is in conflict with the Poisson assumption where Fano Factor is constant (1) and thus would have zero correlation with the tuning curve for the mean. The COM-Poisson approach, on the other hand, accurately describes both mean and variability curves and results in improved accuracy for the Bayesian decoder.

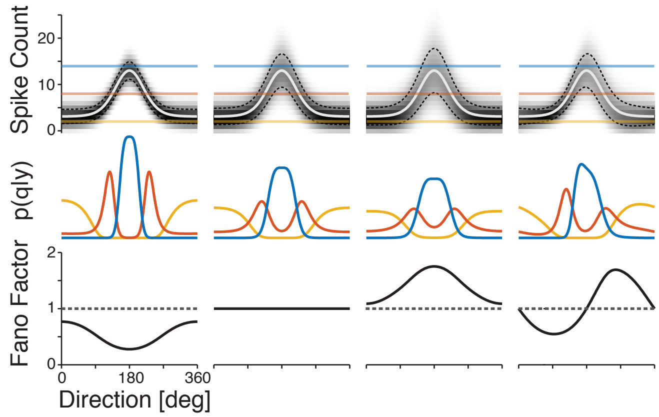

Figure 1: Four simulated neurons with identical mean tuning curves and different types of dispersion. From left to right, spike counts are under-dispersed, equi-dispersed, over-dispersed, and both under- and over-dispersed depending on the stimulus. Note that although the encoding distributions (top) are similar, the decoding distributions for different spike counts (middle) show substantial differences. Middle plot shows tuning curves for low (yellow), medium (red) and high (blue) firing rates. Spike count variability is directly reflected by uncertainty in the stimulus, and if the spike count variability is not one-to-one with the spike count mean the maxima of the posterior may also be different (right-most neuron).

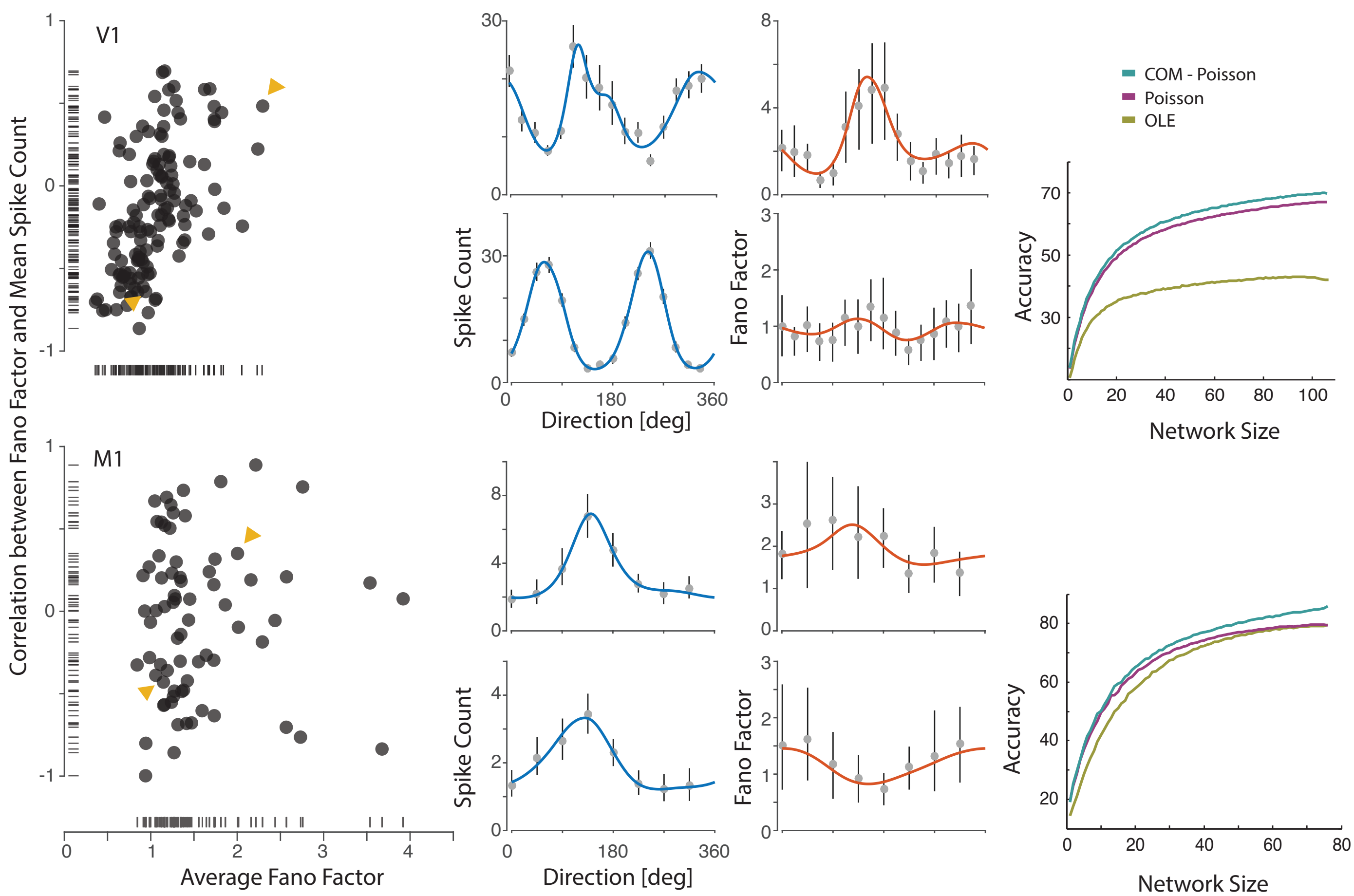

Figure 2: Diversity in tuning curve dispersion. Left, Fano factors and correlation between Fano factor and mean spike count tuning curve for V1 (top, data from CRCNS pvc-11) and M1 (bottom, data from CRCNS dream-stevenson). Note that the Fano factors are not well described as constant close to 1 (as would be the case for Poisson firing) or even well correlated with the spike count (as would be the case for a fixed mean-variance relationship). Two example neurons from V1 and M1 are shown at middle and correspond to the arrows at left. Curves show fits from COM-Poisson models; dots and error bars denote observed means and 95% confidence intervals (estimated by Bayesian bootstrapping). Decoding accuracy increases as more neurons are modeled for the Bayesian decoders with Poisson and COM-Poisson assumptions as well as for optimal linear estimation (OLE).

Reference:

[1] Guikema, S. D., & Goffelt, J. P. (2008). A flexible count data regression model for risk analysis. *Risk analysis*, *28*(1), 213-223.

[2] Stevenson, I. H. (2016). Flexible models for spike count data with both over-and under-dispersion. *Journal of Computational Neuroscience*, *41*(1) 29-43.