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Realistic Spiking Neuron Statistics in a Population are Described by a Single Parametric Distribution

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Realistic Spiking Neuron Statistics in a Population are Described by a Single Parametric Distribution

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Introduction

Cortical neural activity in the form of **spikes** (action potentials) exhibit high levels of variability that have presented numerous challenges for scientists in uncovering how the brain functions. Random behavior of neurons in response to stimuli has led to complicated theories for the purpose of this randomness [4, 5].

Although the full spike train contains more details, we focus only on the time between spikes or interspike interval (ISI) because it is a common entity for many theorists and experimentalists in electrophysiology; it still has a great deal of information and provides an understanding of how likely a neuron is to respond at a given point in time.

Our study is focused on characterizing the probability distribution of the ISIs of a network of real neurons from in vivo recordings of awake adult macaque monkeys in area MT of the visual cortex [3]. Here, we employ a statistical framework based on parametric distribution fitting to characterize the random time between spikes using several goodness of fit criteria, including: maximum likelihood (ML) and Akaike Information Criteria (AIC) [1, 2].

Parametric Distributions

We use two common parametric probability distribution functions (PDF) as the basis for the class of models for modeling the ISI data, the exponential distribution and the gamma distribution:

$$f_{Exp}(x) = \frac{1}{\tau} e^{-x/\tau}, \text{ for } x > 0,$$

$$f_{Gam}(x) = \frac{1}{\beta^{\alpha}\Gamma(\alpha)} x^{\alpha-1} e^{-x/\beta}, \text{ for } x > 0.$$

These two families of PDFs are the most commonly utilized distributions for the ISI PDF. We also consider the three possible mixture distributions as candidate models:

$$f_{EE}(x) = c\left(\frac{1}{\tau_1} e^{-x/\tau_1}\right) + (1-c)\left(\frac{1}{\tau_2} e^{-x/\tau_2}\right) \text{ for } x > 0,$$

$$f_{EG}(x) = c\left(\frac{1}{\tau} e^{-x/\tau}\right) + (1-c)\left(\frac{1}{\beta^{\alpha}\Gamma(\alpha)} x^{\alpha-1} e^{-x/\beta}\right), \text{ for } x > 0,$$

$$f_{EG}(x) = c\left(\frac{1}{\beta_1^{\alpha_1}\Gamma(\alpha_1)} x^{\alpha_1-1} e^{-x/\beta_1}\right) + (1-c)\left(\frac{1}{\beta_2^{\alpha_2}\Gamma(\alpha_2)} x^{\alpha_2-1} e^{-x/\beta_2}\right), \text{ for } x > 0.$$

$$c \in [0, 1]$$

Goodness of Fit Procedure Details for Neural Recordings

•Maximum Likelihood (ML): For each neuron, the best model is the one with the largest log-likelihood value:

$$\log\left(L(\hat{\theta})\right) := \sum_{j=1}^{n} \log\left(f\left(t_j \mid \hat{\theta}\right)\Delta t\right),$$

where is t_j an ISI data point and n is the number of data points, and Δt is the width of the bin, which we set to two milliseconds.

•The finite size correction AIC [2]: This penalizes models with more parameters rather than simply considering the (log) likelihood. For each neuron, the best model is the one with the smallest AIC value:

$\text{AIC} := -2\frac{\log\left(L(\hat{\theta})\right)}{n} + 2k + \frac{2k(k+1)}{n-k-1}$, where k is the number of parameters in the model.

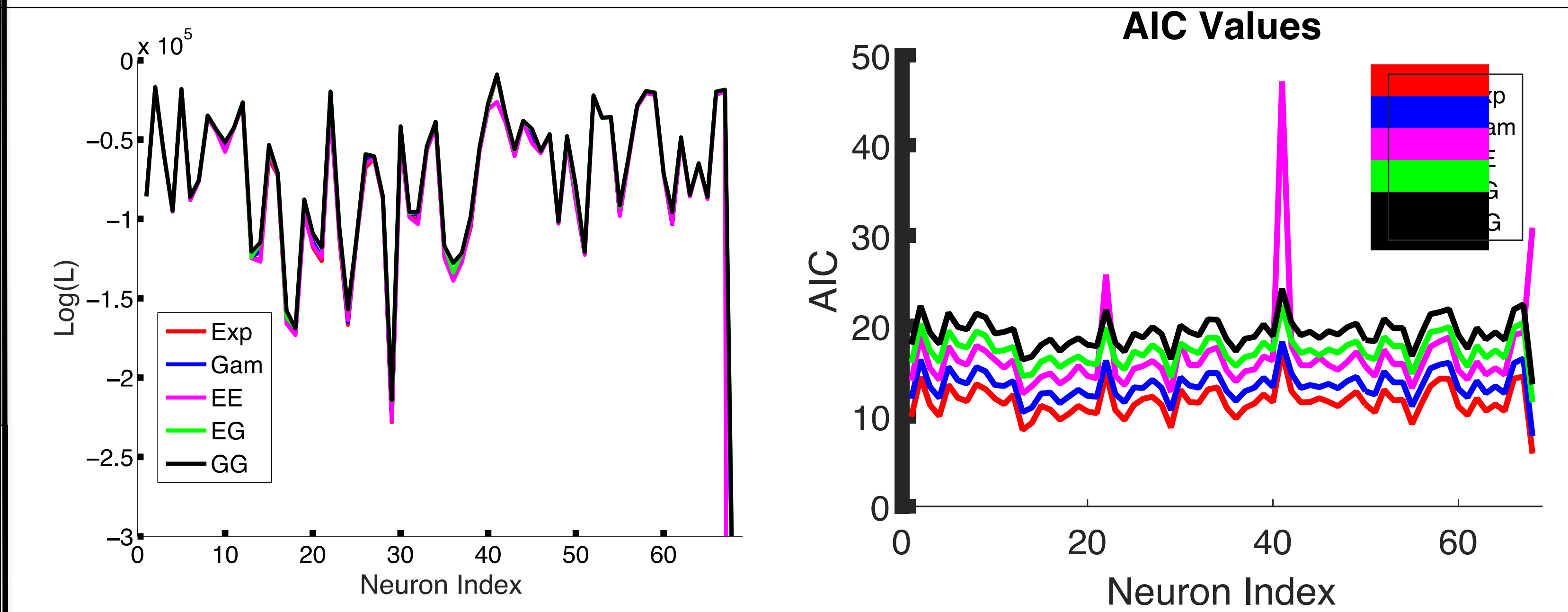


Fig. 1. (Left) Maximum Likelihood Goodness-of-Fit Criteria: a higher value indicates a better fit when using the ML criteria. For this dataset, the Gamma-Gamma mixture distribution f_{GG} is the best for all neurons. (Right) For AIC, a lower value indicates a better fit. As shown, the exponential distribution $f_{\exp}$ has the best fit for every neuron.

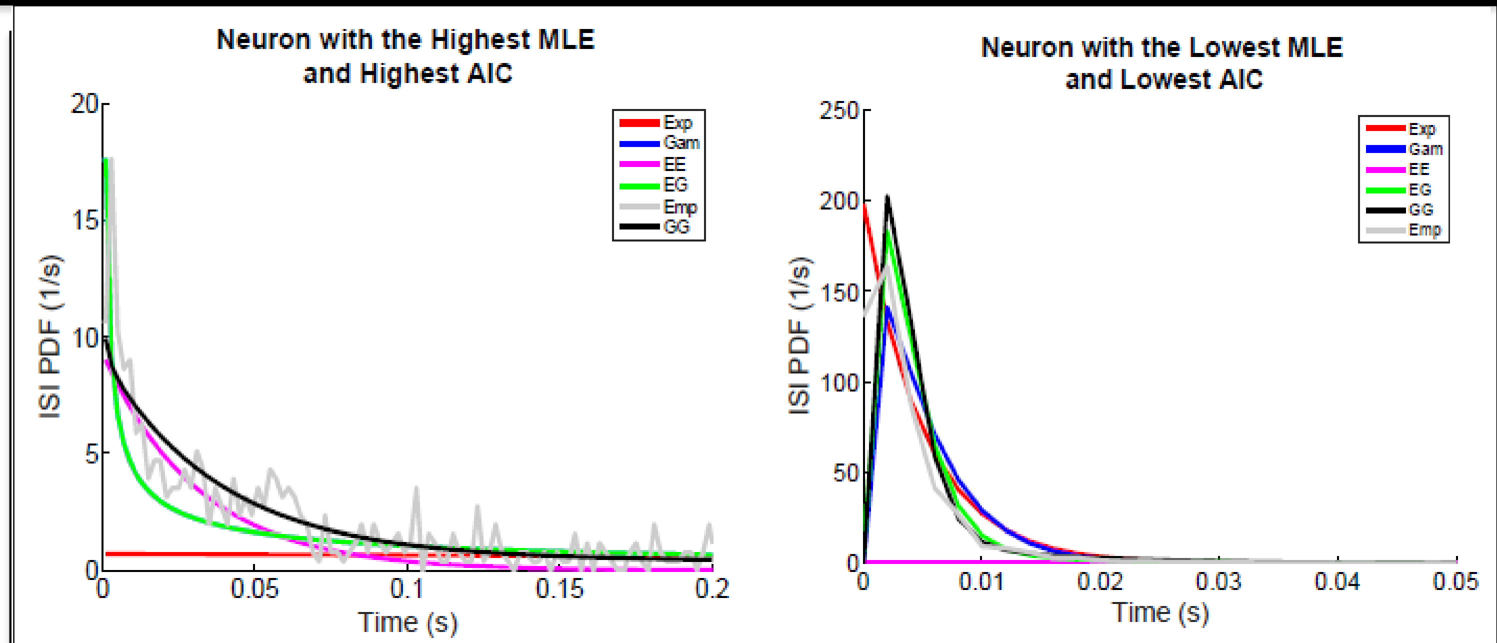
AIC Parameter Penalty is Severe

There were some clear examples where AIC was not able to properly capture the spikes from the model, while ML consistently resulted in a better fitting distribution. This motivated further investigation. Consider comparing two models with k [model A] and (k+1) [model B] parameters respectively. Assuming that n is much greater than k, the last term can be ignored.

In order for Model B to have a lower AIC, we need $\frac{-2l_2}{n} + 2(k+1) < \frac{-2l_1}{n} + 2k.$

Or equivalently: $e^{l_2 - l_1} > e^n$, where $e^{l_2-l_1} = \frac{\prod_{j=1}^{n} \rho_2(\theta_2)}{\prod_{j=1}^{n} \rho_1(\theta_1)}$.

Adding an extra parameter, the ratio of the likelihoods has to increase by **a huge number** (e^n) for Model B to be selected.



(a) Neuron 41 with a Firing Rate of 0.71 Hz (b) Neuron 68 with a Firing Rate of 199.75 Hz

Fig. 3. ISI PDFs and corresponding fits for the extreme (best and worst) cases using ML and AIC. With ML, f_{GG} is always the better fit. The highest (best) likelihood is shown in a), corresponding to neuron 41, and lowest likelihood (worst) is shown in b), corresponding to neuron 68. With AIC, $f_{\exp}$ is always the better fit, so the lowest AIC (best) is shown in b), corresponding to neuron 68 and the highest AIC (worst) is shown in a), corresponding to neuron 41.

Conclusions:

We applied statistical methods and goodness of fit criteria to spiking neural data obtained from monkeys to better understand the variability of neural activity in a representative population of neurons. Using a formal statistical framework to characterize spiking neural data is under-utilized by computational neuro-scientists, who often use a single goodness-of-fit criteria (often ML). Our work gives a better understanding for how different goodness-of-fit criteria yield different results.

We found that only one family of parametric distributions was selected as the best for all goodness-of-fit criteria (although it depended on which criteria). According to ML criterion, the Gamma-Gamma mixture distribution consistently had the best fit and according to AIC criterion, the Exponential distribution consistently had the best fit. Since this dataset contains many generic features of cortical neural networks, some of these results may have wider applicability beyond these 68 recorded neurons. Indeed, we applied the framework to a bursting spiking model with a multimodal ISI PDF, and found that the results still hold.

References

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