On Overdispersion in Neuronal Evoked Activity

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One of the most commonly studied systems in neuroscience is the stimulus-response paradigm. A system, which could be a neuron or a population of neurons, is provided with an input and the resulting state change of the system is quantified in order to better characterize functional associations. A main problem in this approach is that the system response to repeated presentations of an identical visual stimulus often exhibits high variability, particularly in the spike count statistics. As a consequence, statistical methods are essential to characterize the information carried by neural populations and to understand the functional role of variability within neural activity.The Poisson model (PM) is the most commonly used assumption to model the trial-to-trial variability in neural evoked responses. Under this assumption, the variance of the spike count is constrained to be equal to the mean, irrespective to the considered time window. Numerous studies have shown that this relationship does not hold in many electrophysiological recordings which in majority show an "*overdispersion*", that is, where responses are more variable between trials than expected from a Poisson process. Our hypothesis is that the Poisson process only reflects the intrinsic noise induced by the spiking mechanism, i.e., the trial-to-trial variability only results from the stochastic properties of the neuron itself. Thus, the Poisson model could not account for other significant sources of variability such as hidden contextual variables or instantaneous cortical state, perceptual effects and overt behaviors (such as the precise eye's position).

Several models have been developed to account for overdispersion such as generalized Poisson, zero-inflated Poisson or quasi-Poisson models. Here, we bring into light an alternative stochastic model, called Negative-Binomial, that generalizes the Poisson distribution adding a dispersion parameter that directly controls the ratio between the mean and variance variance. Indeed, a Negative-binomial model depends on a distributional form equivalent to a compound stochastic process. It corresponds to a doubly stochastic process where the Poisson process has a parameter λ which is itself a random variable generated from a Gamma distribution with a shape parameter ϕ (known in the literature as the inverse dispersion parameter) and a scale parameter β. It converges to a Poisson model for large values of ϕ_i, but allows to reach larger variances than the Poisson for small ϕ_i values. This model is largely used and studied in a variety of domains but has only recently been applied to evoked neural responses [1]. We have particularly shown that this model could account for two main possible sources of overdispersion. The first, is extrinsic sensory noise. The second, is a population emergent noise that accounts for neuronal redundancy.

However, even if the Negative-binomial model has been considered as the model of choice allowing to account for overdispersion, several studies were interested on the special circumstances under which this claim is true. Thus, we would need to focus on testing overdispersion evidence. However, most of the methodological studies measuring trial-to-trial variability in firing rates do not take into account the estimation uncertainty induced by the limited number of trials. Indeed, the variability of spike counts is commonly quantified by the Fano factor (FF) given by the ratio between the variance and the mean of the number of spikes over multiple trials in a given time window. But considering only the FF value may induce errors in conclusions against the probability distribution assumption. Thus, we propose a statistical test for evaluating if the excess of variance in a given realization is significantly better described by the Negative-binomial model than the Poisson model. We applied this test to 3 data sets : the spiking responses of LGN neurons in the mouse to drifting gratings, V1 neurons in awake macaque monkeys to oriented moving bars and MT neurons in anesthetized macaque monkeys to drifting gratings.

Finally, To evaluate the gain in decoding when accounting for the overdispersion using NBM compared to PM, we extended the classical probabilistic decoding approach proposed by Jazayeri and Movshon (2006)[2] and tested the population decoder on the MT data set (presenting the highest overdispersion probability). We have shown that more knowledge about the tuning of dispersion tuning is necessary to have a significant gain, uncovering a possible feature of the neural spiking code

References

[1] R.L.T. Goris, J.A. Movshon and E.P. Simoncelli Partitioning neuronal variability, *Nature Neuroscience* 17 (6) pp. 858-865, 2014.

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