

Neuronal long-tails revisited

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The Poisson model is the standard model for describing cortical neuronal firing. We show that in spike data obtained along the visual pathway of cat and monkey (LGN, V1, MT). Based on our general framework of neuronal computation by locking [2,3], we predict that only a minority of neurons fire according to the Poisson model – namely those neurons, that provide an uncorrelated input for strongly coupled neurons. Neurons that are engaged in neuronal information processing through locking are expected to show a more complex firing behavior, e.g. power-law decaying probability distributions indicating the presence of long (time-)correlations. Furthermore, we expect the emergence of distinct classes of neuronal firing with respect to the occurrence of patterns [3]: I) Randomly firing neurons. II) Neurons that are unable to cope with a certain class of stimuli and show simple spike patterns embedded in a random background. III) Neurons that preferentially fire in patterns. We complement our analysis by measuring the occurrence of spike patterns in the data using correlation integral pattern discovery [4] in order to test the emergence of said three classes.

the majority show long-tail ISI distributions. Moreover, we confirm previous findings of the existence of three classes of neuronal firing. The results are consistent with the framework of neuronal computation by locking.

1. Introduction

The Poisson model with refractoriness is considered to provide a reasonable description for the firing of a majority of cortical neurons [1]. The model requires interspike interval (ISI) distribution of exponential decay type. We test this criterion for data obtained along the visual pathway of cat and macaque monkey (LGN, V1, MT). Based on our general framework of neuronal computation by locking [2,3], we predict that only a minority of neurons fire according to the Poisson model – namely those neurons, that provide an uncorrelated input for strongly coupled neurons. Neurons that are engaged in neuronal information processing through locking are expected to show a more complex firing behavior, e.g. power-law decaying probability distributions indicating the presence of long (time-)correlations. Furthermore, we expect the emergence of distinct classes of neuronal firing with respect to the occurrence of patterns [3]: I) Randomly firing neurons. II) Neurons that are unable to cope with a certain class of stimuli and show simple spike patterns embedded in a random background. III) Neurons that preferentially fire in patterns. We complement our analysis by measuring the occurrence of spike patterns in the data using correlation integral pattern discovery [4] in order to test the emergence of said three classes.

2. Methods

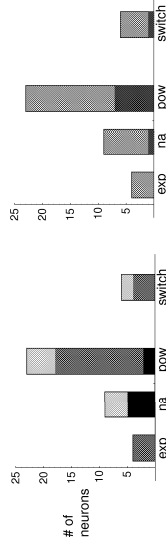
Our experimental data is from *in vivo* measurements obtained in anesthetized animals, as described in Refs. [5] (cat LGN), [6] (cat V1) and [7] (monkey). We quantify whether an experimentally derived distribution is closer to an exponential or a long tail type as follows: Let N_i be the number of ISI that fall into the i -th bin τ_i ($i = 1, \dots, m$) of the histogram: approximating the probability distribution. To avoid tampering effects of short ISI, the bin number m with $N_m = \max\{N_1, \dots, N_n\}$ is identified. A cut-off parameter $\kappa \in \mathbb{N}$ determines, up to which bin number κm the left side of the distribution is removed. For the remaining distribution, the best fits (minimizing mean square errors) of an exponential function $Exp(t) = e^{-\alpha t}$ and a power-law function $Pow(t) = t^{-\alpha}$ are calculated (α : fitting parameter). The fit coefficient is defined as:

$$\mathcal{F}(\kappa) = \frac{1}{\sqrt{2(n^* - \kappa m)}} \left(\sum_{i=\kappa m+1}^{n^*} (\text{Exp}(i\Delta\tau) - N_i)^2 - \sum_{i=\kappa m+1}^{n^*} (\text{Pow}(i\Delta\tau) - N_i)^2 \right)$$

n^* indicates that the sum only includes bins where $N_i \neq 0$ and $\Delta\tau$ is the binsize. The distribution is of long-tail type for $\mathcal{F}(\kappa) > 0$ and of exponential type for $\mathcal{F}(\kappa) < 0$. If $\mathcal{F}(\kappa) \approx 0$, neither function fits the distribution well. As one fit is usually far better than the other, we use the logarithm $\mathcal{F}_{\log}(\kappa) = \text{sig}(\mathcal{F}(\kappa)) \ln(\text{abs}(\mathcal{F}(\kappa)))$, for $-1 < \mathcal{F}(\kappa) < 1$; $\mathcal{F}_{\log}(\kappa) = 0$.

For the analysis, we took the measurement files (spike trains transformed in ISI sequences) deriving from the three most responsive stimulus conditions (166 files). Inappropriate files due to non-stationarity, bimodal distributions and a cut-dependent ($\kappa = 2, 3$) classification (see below) were excluded.

Classification of ISI-distributions



Classification of firing patterns

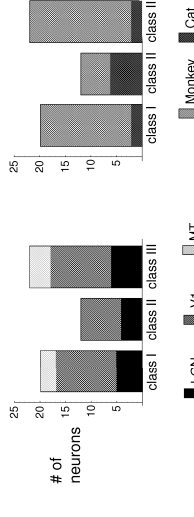


Figure 1: Above: Classification of neurons as exponential firing (exp), not attributable (na), long-tail firing (pow) and switches. Below: classification of neurons according to firing patterns in classes I, II, III (see text). Left: classified according to area / right: classified according to species.

For the remaining 125 files, $\mathcal{F}_{\log}(2)$ has been calculated. Based on this results, we classified the **ISI-distributions** as follows:

- Exponential (exp): $\mathcal{F}_{\log}(2) < -2$
- Not attributable (na): $-2 \leq \mathcal{F}_{\log}(2) \leq 2$
- Power-law (pow): $\mathcal{F}_{\log}(2) > 2$

In most cases, all files assigned to one neuron fell in the same class and the neuron was classified accordingly. If spike trains classified as ‘exp’ as well as ‘pow’ emerged from the same neuron, then the neuron was classified as ‘switch’.

Correlation integral pattern discovery [4] has been applied to all files with a minimum ISI number of 500 (embedding dimensions $m = 1, \dots, 10$). The result led to a classification of the files according to **firing patterns**:

- Class I: smooth correlation plots for all m , indicating absence of patterns.

- Class II: pronounced steps in the correlation plots only for small m , indicating short-, unstable patterns.

- Class III: pronounced steps for all embedding dimensions, indicating stable patterns.

In most cases, all files assigned to one neuron fell in the same class and the neuron was classified accordingly. Otherwise, the classification of the majority of the files determined the attribution.

3. Results

We find, that the majority of the neurons have long-tail ISI distributions. About 10% are clearly identified as ‘exp’ (Fig. 1 above). The coefficient of variation of the ISI obtained from ‘exp’ neurons was ~ 1 and correlation-integral pattern discovery did not indicate any preferred serial ISI order. Thus, only a minority of neurons fulfill all criteria of the Poisson model – as predicted by our general framework. Neurons with exponential distributions in all three stimulus conditions are not found in LGN and MT, although ‘switchers’ are present in both LGN and V1. Pattern discovery analysis (Fig. 1 below) corroborates previous findings of three distinct neuronal firing classes. The two ways of classification do not – as expected – lead to similar class sizes. The discrepancy between the number of ‘exp’-neurons and class-I-neurons results from the fact that more neurons have been excluded for the fit-coefficient analysis, and that, in principle, also neurons classified as ‘ind’ or ‘pow’ may fall into class I.

4. Conclusions

We find, that the Poisson model does not cope with the majority of the data we investigated. Furthermore, previous studies [3,4] showing the existence of three distinct classes of neuronal firing have been confirmed. The result is compatible with the predictions of our general framework of neuronal computation with locking. This supports the need for extended experimental studies for investigating this framework.

References: [1] Dayan P, and LF Abbott: *Theoretical neuroscience*. MIT Press, Cambridge, London, 2001. [2] Stoop R, K Schindler, and LA Bunimovich. *Nonlinearity* 13(5): 1515-1529, 2000. [3] Stoop R, DA Blank, A Kern, J-J van der Vyver, M Christen, S Leechini, and C Wagnor. *Cognitive Brain Research* 13: 293-304, 2002. [4] Christen M, A Kern, A Nikitchenko, W-H Steeb, and R Stoop. *Physical Review E* 70: 011901-1-7, 2004. [5] Freeman TC, S Durand, DC Kiper, and M Carandini. *Neuron of Computational Neuroscience* 380(2): 230-242, 1997. [7] Kohn A, and MA Smith. *The Journal of Neuroscience* 25(14): 3661-3673, 2005.

The authors thank M. Carandini, A. Kohn, V. Mantle and K. Martin for the data used in this analysis.