Two methods for time-resolved inter-spike interval analysis

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1 Introduction

Neurons observed in a living organism typically exhibit temporal changes in their spike train statistics in response to sensory input. Most obvious are changes in firing rate, while changes of other properties, like for example the variability of inter-spike intervals (ISIs), are more difficult to detect.

Here we propose two complementary methods A and B for the time resolved analysis of the interspike-interval distribution and compare their performance on two different data sets.

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2 Method A

In each single trial \(i\) collect all intervals \(D_1^i, D_2^i, \ldots, D_m^i\) in the interval \((a, b]\) with \(a < b\) of fixed duration \(T = b - a\).

\[\Rightarrow \text{Coefficient of variation:} \]
\[CV^i := \sqrt{\frac{\text{Var}(\Delta^i)}{E(\Delta^i)}}.\]

and the trial average \(CV = \langle CV^i \rangle_i\).

Bias for short observation window

We can only observe intervals \(\Delta \leq T\). For all values \(\Delta \in (0, T)\) the likelihood of observation is proportional to \(T - \Delta\) and the empiric distribution is given by

\[\hat{p}_T(x) = \begin{cases} \eta^{-1} \cdot (T - x) \cdot p(x) & \text{for } x \in [0, T] \\ 0 & \text{otherwise} \end{cases},\]

where \(\eta\) re-normalizes to unit area.

This introduces a bias of estimation for the mean interval, the standard deviation of intervals and for the CV. For large \(T \gg \langle \Delta \rangle\) this bias is negligible.

Non-stationary rate

Temporal changes of firing rate impair the second order statistics of ISIs. We therefore perform a non-linear transformation of real time. For a given rate profile \(\lambda(t)\) we define operational time

\[t' = \Lambda(t) = \int_0^t \lambda(s) ds.\]
The resulting process exhibits constant unit rate $\lambda' = 1$. This procedure requires a reliable estimate of the spike rate.

3 Method B

Take all ISIs of length $\Delta_1(t), \Delta_2(t), \ldots, \Delta_M(t)$ from the $M$ trials that contain a particular time $t$.

The ISI distribution $\tilde{p}(\Delta)$ we obtain by directly binning the ISIs $\Delta_i(t)$ into a histogram in general fails to retrieve the true ISI distribution $p(T)$, since

$$\tilde{p}(T) \propto \int_{t-T}^{t} p(T)r(t')dt', \quad (3)$$

with the probability of observing a spike at time $t$ given by the firing rate $r(t) = \lim_{\Delta \rightarrow 0} N/M/\Delta t$, where $N$ is the number of spikes observed in the time window of width $\Delta t$ centered at $t$.

Ordinary Renewal Process

If all spikes before the observation time $t$ occur at the same time, then $r(t) = \delta(t)$ and the ISI distribution estimated directly from the ISIs $\tilde{p}(T)$ equals the true ISI distribution $p(T)$:

$$p(T) = \tilde{p}(T). \quad (4)$$

Equilibrium Renewal Process

Here $r(t) = r = \text{const.}$ and

$$p(T) = \eta^{-1} \cdot \tilde{p}(T)/T. \quad (5)$$

Thus, sampling ISIs at a given time $t$ overestimates the presence of long ISIs.
⇒ Mean ISI:

\[
\langle T \rangle_p = \frac{1}{\langle \frac{1}{T} \rangle_p} = \frac{N}{\sum_{i=1}^{N} 1/T_i}, \tag{6}
\]

where we average over the reciprocal ISIs \(1/T_i\) of all \(N\) trials.

⇒ Coefficient of variation:

\[
CV = \sqrt{\langle T \rangle_p \langle 1/T \rangle_p^{-1}} - 1. \tag{7}
\]

⇒ Spike frequency:

\[
f = \frac{1}{\langle T \rangle_p} = \frac{1}{\langle \frac{1}{T} \rangle_p} = \frac{N}{\sum_{i=1}^{N} 1/T_i}. \tag{8}
\]

For Poisson spike trains \(1/(T)_p\) underestimates the true rate by exactly a factor of two.

4 Data I: Locust Auditory Receptor

![Graphs and plots related to data I: Locust Auditory Receptor]
5 Data II: Honeybee Mushroom Body Extrinsic Neurons

Data courtesy by Eugenio Urdapilleta and Jan Benda.
6 Summary

Method A

+ Only few trials needed
+ Good sampling of short ISIs
- Time resolution is fixed and long
- Undersampling of long ISIs

Method B

+ Best possible time resolution
+ Time resolution adaptively given by instantaneous ISI distribution
- Many trials needed
- Undersampling of short ISIs

⇒ Use both methods!

Data courtesy by Martin Strube and Randolf Menzel.