Adaptation in the ventral cochlear nucleus in the presence of constant-amplitude tone bursts is determined by ordered inter-spike interval statistics

ISH 2012

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Introduction

The VCN is the first sound processing station in the mammalian brain
Understand sound coding in the VCN would allow a better understanding of all aspects of hearing
VCN neurons show various different physiological and morphological aspects.

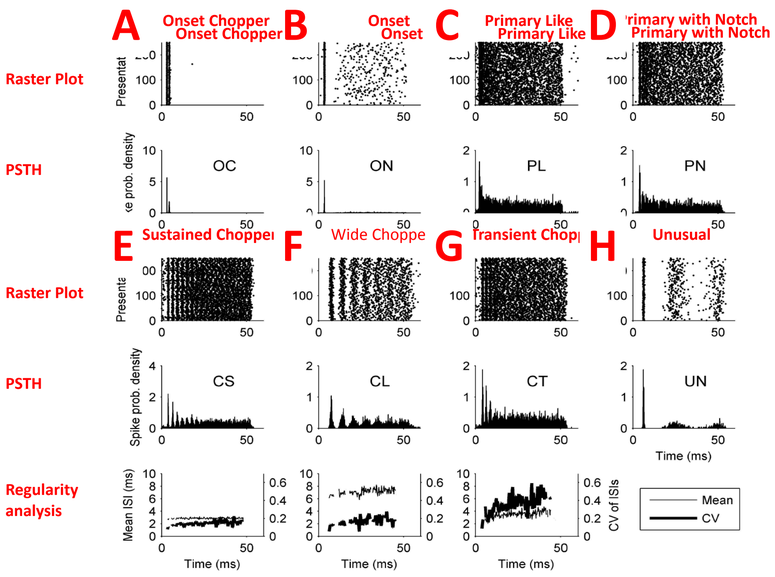

Figure 1 Raster plots (top) and derived Post Stimulus Time Histograms (PSTHs, below) for typical neurons evoked by a 50 ms tone burst at the ear, 20 dB above the threshold of hearing. For the chopper cells E—G a third trace shows the regularity analysis consisting of the mean and coefficient of variation respectively of inter-spike intervals commencing at each time.

Research questions:

1. **Can we understand the neurons response better using *INTERVAL* statistics (instead of spike times)?**
2. **Are spikes (intervals) independent of each other? (necessary for modelling and reconstruction of PSTH)**
3. **Can we reconstruct (model) neuronal responses compactly?**
4. **Can we define response class distinctions better?**

Methods

extracellular single cell recordings from the ventral cochlear nucleus of the urethane anaesthetized guinea pig (Cavia porcellus).
50 ms tone-bursts (5 ms rise/fall time and randomized starting phase) at the unit's best frequency (BF) at 20 dB and at 50 dB (in a subset of neurons) above its threshold.
Response types at both levels were classified by the third author according to the classification scheme by (Blackburn and Sachs 1989) into one of the following classes: 273 CS; 527 CT; 29 CL; 276 PN; 106 PL; 156 ON.
Excluding 361 units showing phase locking
After exclusions 1015 different units at 20 dB of which 833 units were also measured at 50 dB, totalling 1376 measurements in which we obtained 250 repeats

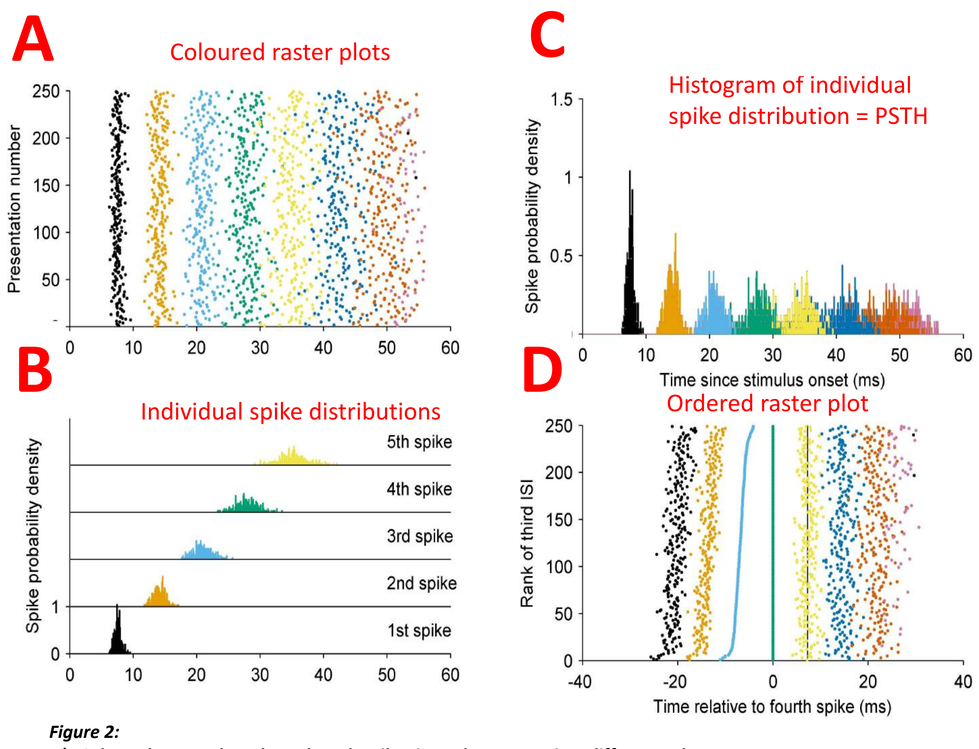

Figure 2:
A) Coloured raster plots show the nth spikes in each response in a different colour.
B) Individual spike distributions show gradual widening histograms
C) The sum of all individual spike distributions is equal to the overall PSTH.
D) All presentations ordered relative to the interval between 3rd and 4th spike: the fifth spike seems to be independent of the 4th.

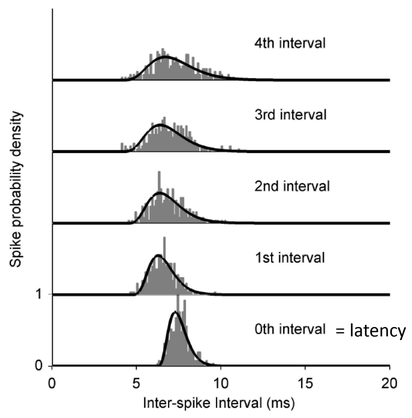

Figure 3:
Interval distributions offer an alternative representation of the same neuronal response. Black lines show best fits using a Gamma-distribution with dead time

Are neurons 'clocks' or 'counters'?

$$f(t;\lambda,k,\tau_0) = x^{k-1}\frac{\exp(-(t-\tau_0)/\lambda)}{\Gamma(k)\,\lambda^k}$$

Gamma distribution: λ=scale parameter, k=shape parameter, τ₀ = dead time

Results

Independence

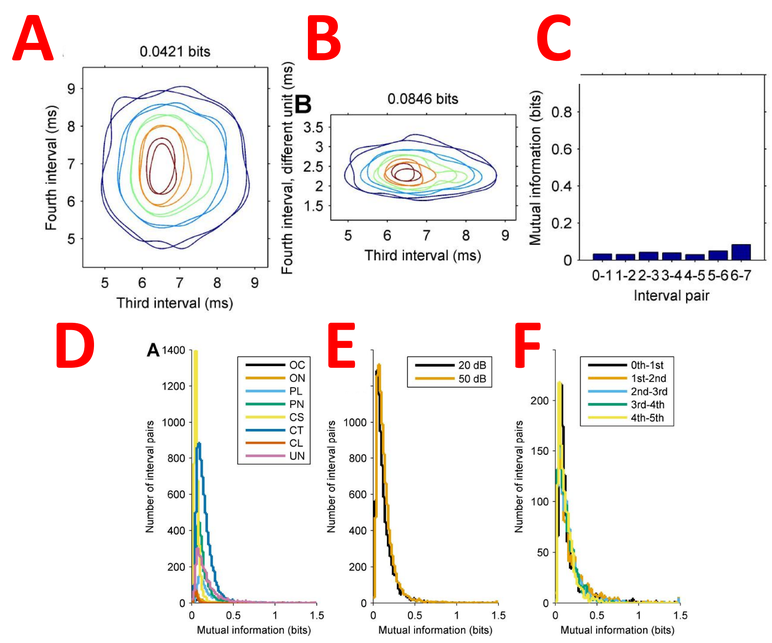

Figure 4: A-C: mutual information $\iint_{X,Y} p_{X,Y}(x,y)\log_2\left(\frac{p_{X,Y}(x,y)}{p_X(x)p_Y(y)}\right)\mathrm{d}x\,\mathrm{d}y,$

A) kernel density estimates of one interval against previous one
B) one interval of one neuron against another neuron (presumed 0)
C) Mutual information of all intervals for this neuron
D) - F) Mutual information for different response types, amplitudes and interval numbers

PSTH reconstruction

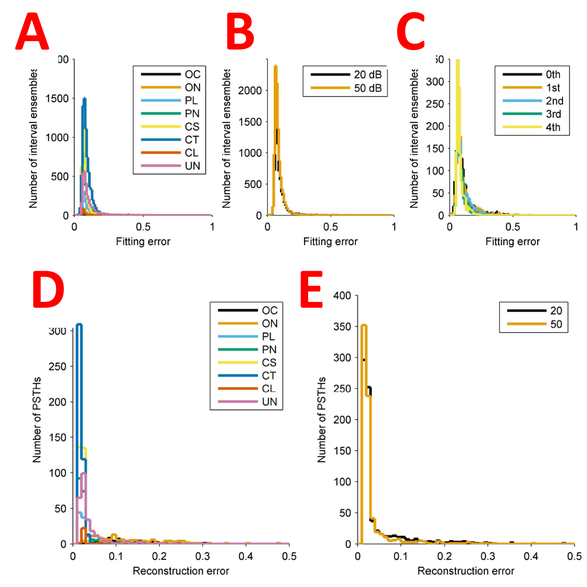

Figure 5:
A-C) histogram of fitting errors of intervals (Gamma fit)
D-E) histogram of fitting errors of PSTH reconstructions
PSTHs are reconstructed by convoluting successive interval distributions:

$$p_{X+Y}(z) = (p_X * p_Y)(z) = \int_{-\infty}^{\infty} p_X(x)p_Y(x-z)\mathrm{d}x \qquad P(t) = \sum_{j=1}^{N} f_j(t) \qquad f_n(t) = (g_0 * g_1 * g_2 * \cdots * g_{n-1})(t)$$

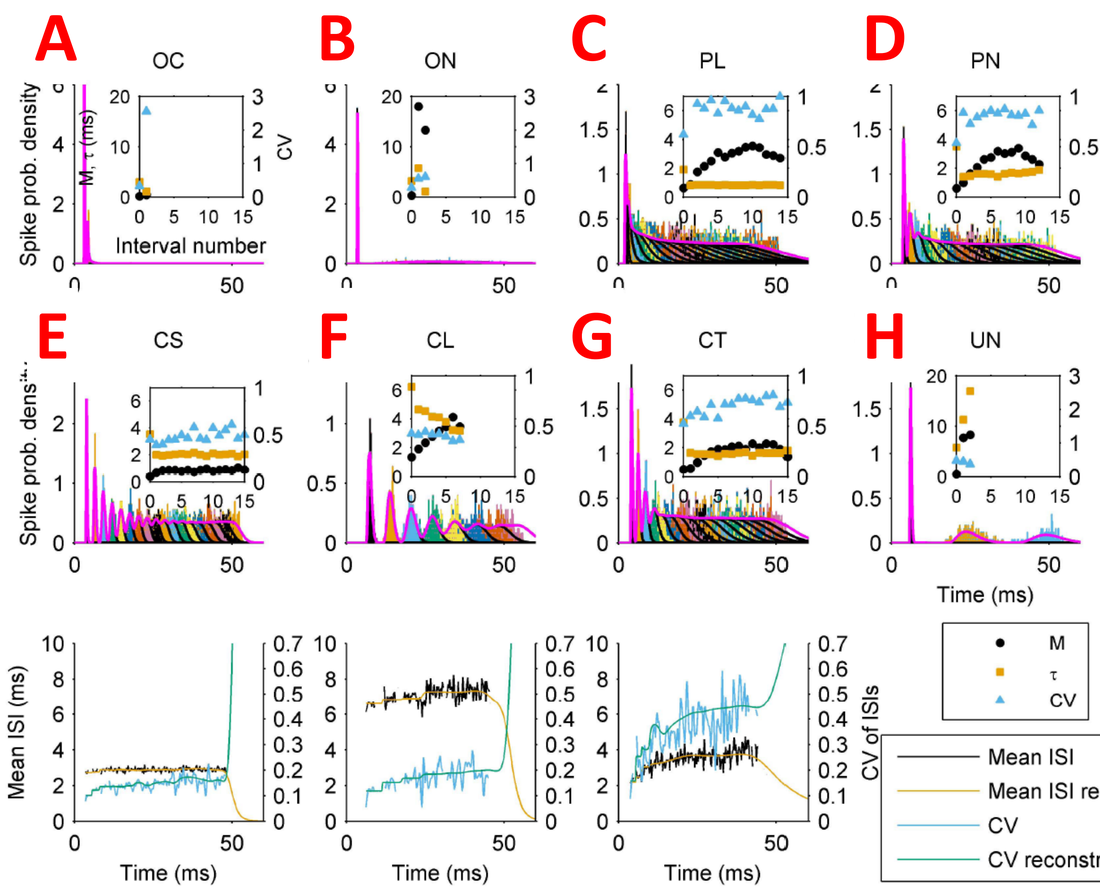

Figure 6: summary: PSTH's of all response classes can be reconstructed using simple interval statistics. Insets show for each reconstruction all parameters necessary: means dead times and CVs.

Conclusions

- Interspike Intervals statistics are useful
  - They offer a good description for the whole response
  - They contain the information to recreate every spike train, not just the PSTH
  - They allow to reconstruct the PSTH simple and exact.
- Intervals are independent to all intents and purposes. A spike erases the memory of the previous interval. This is different from the LSO (Johnson, 1986)!
  - Neurons are counters (not clocks): adaptive behaviour depends more on the number of spikes than on the time since tone onset.
- Class distinctions are nebulous when observed in the context of ISI statistics. A small change in one of the statistics can move a response from one class to another.
- ISI description provides the means to describe ('model') responses very simply and compactly (3n parameter, can be modelled with fewer)
- First spikes are different from subsequent intervals.
- We are now in a position to examine:
  - To what extent are the classes truly distinct?
  - Why do choppers chop?
  - What rules allow us to go from ISI statistics to response types? (automatic classification)
  - How does response depend on different stimulus attributes (amplitude, etc)