What is a neuron's firing rate?

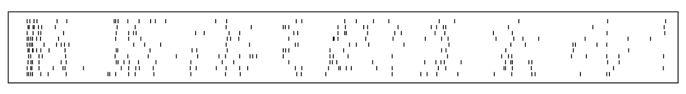
Úna Ní Éigeartaigh and Conor Houghton, Trinity College Dublin
nieigeau@tcd.ie and houghton@maths.tcd.ie

Abstract

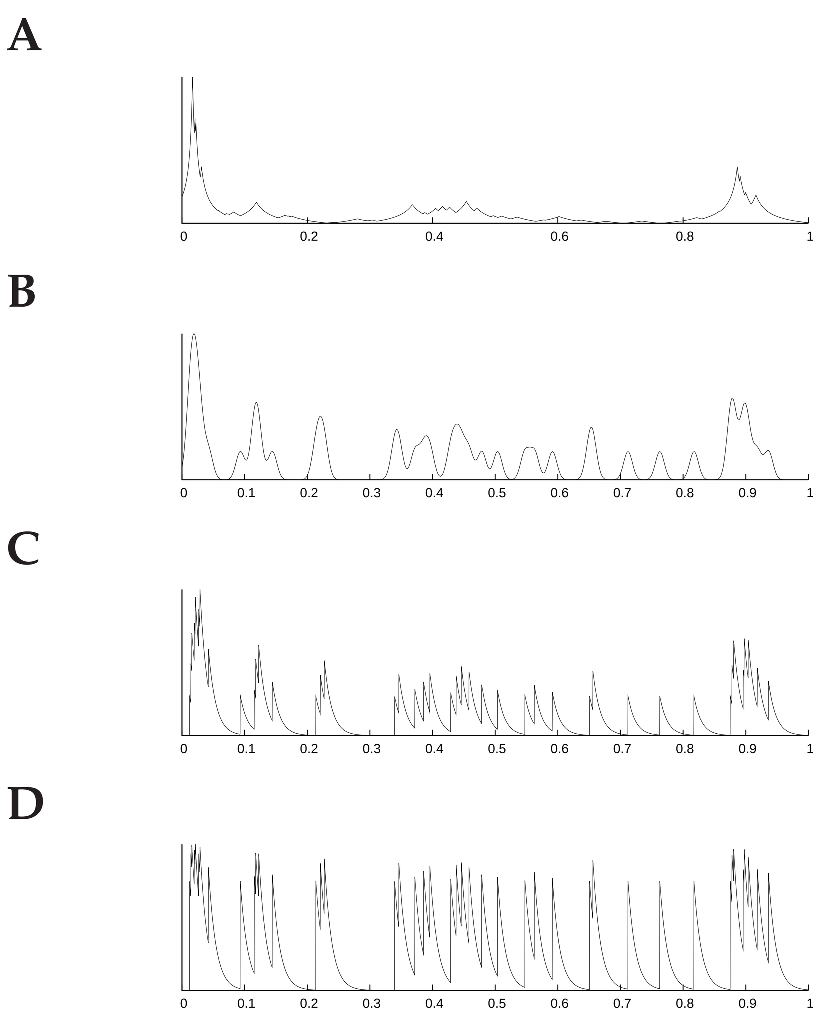
For such an obvious and commonly-used a concept, there is no clear, universally accepted, method for calculating the firing rate of a neuron in an experiment with a limited number of trials. While the spike count and histogram ignore the most striking features of neuronal signaling: the fine temporal structure. The common alternative; mapping spike trains to a rate function, appears to assume that spiking is a Poisson process, with the rate providing an intensity function. However, it is pointed out here that the normal methods for calculating an intensity function give a poor result compared with a mapping based on the dynamics of synapses. This is surprising and mysterious.

Rate functions

There are two common methods for reconstructing an intensity from a sample: kth nearest neighbour and symmetric kernel density estimation [5]. For spike trains these give plausible looking rate functions. Two other functions are given, these are based on the dynamics of synapses and look less plausible.



Raster plot. This shows ten trials for a single stimulus. The first trial was used to construct the four rate functions below.



Rate function. Four rate functions have been calculated.

- **A**: kth nearest neighbour with $k = 5$ [5].
- **B**: Gaussian filter with $\sigma = 7$ms.
- **C**: Exponential filter with $\tau = 12$ms [6].
- **D**: Synapse with $\tau = 12$ms and $\mu = 0.7$ [2].

The kth nearest neighbour is commonly used for density and intensity estimation:

$$f(t) \propto \frac{1}{k(t)}$$

where $k(t)$ is the distance to the kth closest spike to the time t. The two filter functions are calculated using a kernel

$$f(t) \propto \sum h(t - t_i)$$

where the t_i are the spike times and $h(t)$ is a Gaussian or causal decaying exponential. Optimal values for k, τ and μ are used with respect to the clustering test used below.

The synapse function

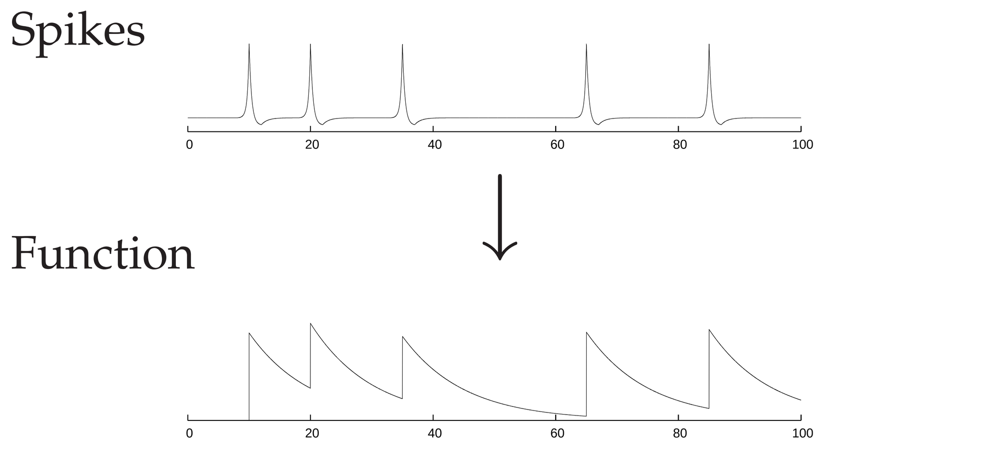
A new rate function is defined by filtering of the spike train with a new map [2]:

$$\text{spike train} \rightarrow f(t)$$

where $f(t)$ is the solution of

$$\tau \frac{d}{dt} f = -f$$

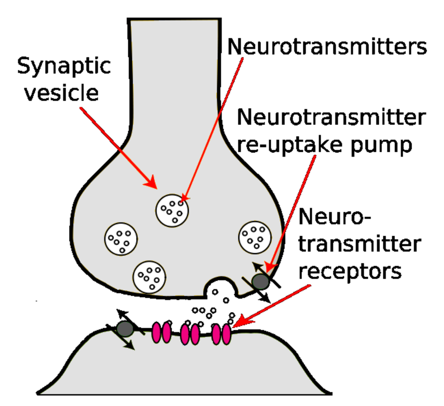
with discontinuities $f \rightarrow (1-\mu) f + 1$ at the spike times.



Motivation

This mapping mimicks the short term dynamics of synaptic conductance, modelling rapid binding and stochastic unbinding of neurotransmitter to gates in the synaptic cleft [1]

- τ is the time-scale for unbinding.
- μ quantifies the effect of the depletion of available binding sites.



When a spike arrives at the terminal button the synaptic cleft is rapidly flooded with neurotransmitter. The neurotransmitter binds to receptors in ligand gated channels, opening them and causing a change of the potential in the dendritic spine. The concentration of neurotransmitter falls quickly. Compared to the unbinding timescale, there is a only a significant concentration in the cleft for a short time. Modeling the rise profile of the conductance in a metric suggests it is not significant. However, the extent to which it rises does, this is what is modelled in the new metric.

References

[1] Dayan P, Abbott LF. *Theoretical Neuroscience*. MIT Press, 2001.
[2] Houghton C. *Journal of Computational Neuroscience*, 26: 149-155, 2009.
[3] Houghton C, Victor J. Spike codes and spike metrics. (Invite book chapter, to appear).
[4] Narayan R, Graña G, Sen K. *Journal of Neurophysiology*, 96:252–258, 2006.
[5] Silverman BW, Density Estimation (1986, Chapman and Hall, London).
[6] van Rossum M. *Neural Computation*, 13:751–763, 2001.
[7] Victor JD, Purpura KP. *Journal of Neurophysiology*, 76(2):1310–1326, 1996.

Results

The performance of each function is measured by using it to cluster the spiking responses. The distance between two functions is measured using the L^2 metric

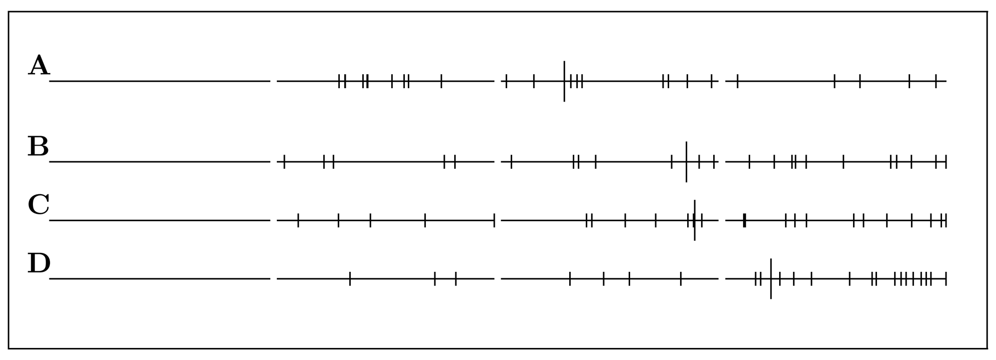
$$d = \sqrt{\int dt[\delta f(t)]^2}$$

on the space of functions. Now, the better this clustering matches a clustering by stimulus, the better the function reflects the content of the stimulus.

Clustering accuracy is measured using transmitted information [7].

$$\tilde{h} = \frac{1}{n} \sum_{ij} N_{ij} \left(\ln N_{ij} - \ln \sum_k N_{kj} - \ln \sum_k N_{ik} + \ln n \right) / \ln s.$$

where N is the confusion matrix, a square matrix whose ijth entry, N_{ij}, is the number of responses from stimulus i which are closest, on average, to the responses from stimulus j. n is the number of responses and s the number of stimuli. $\tilde{h} = 1$ for perfect clustering.



Evaluating various rate functions.

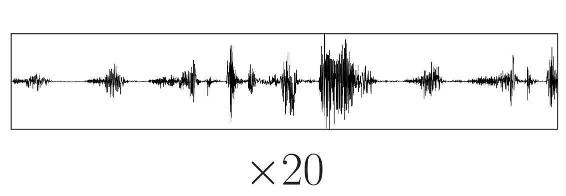
- **A**: kth nearest neighbour with $k = 5$.
- **B**: Gaussian filter with $\sigma = 7$ms.
- **C**: Exponential filter with $\tau = 12$ms.
- **D**: Synapse with $\tau = 12$ms and $\mu = 0.7$.

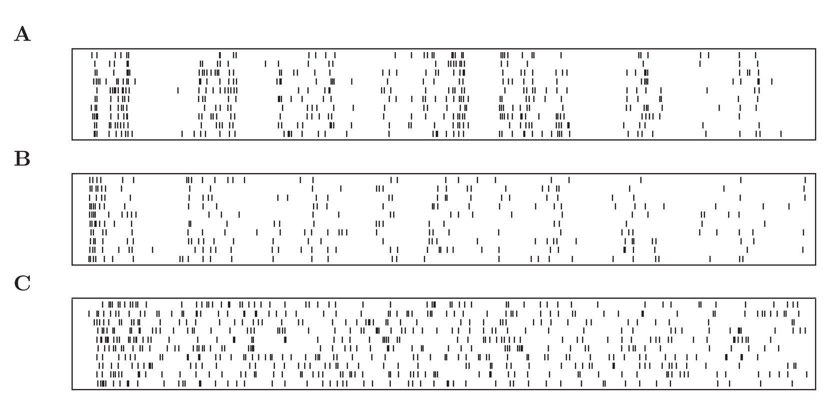
In this figure the value of $\tilde{h}$ has been plotted for each of the 24 sites in the zebra finch data. Each horizontal line corresponds to the performance of a single metric, the line runs from zero to one, as a visual aid a tiny gap is left at 0.25, 0.5 and 0.75. Along each line a small stroke corresponds to a single site, the long stroke corresponds to the average value.

- A good function should reflect the way the neuronal signal encodes information. Here, the clustering of responses to repeated stimuli is used as a test of this.
- The synapse function does best.
- kth nearest neighbour, the most robust method of estimating intensity, is the worst.
- What is the firing rate if it is not a Poisson intensity?
- Synapses appear to extract salience from neuronal signals.

Data

The metrics have been applied electrophysiological data recorded from the primary auditory area of zebra finch during playback of conspecific songs [4].





Ten responses are recorded to each song; responses for three different cells are shown here.

The recordings were taken from field L of anesthetized adult male zebra finch and data was collected from sites which showed enhanced activity during song playback. In the ascending auditory pathway, area field L is afferent to the song system and is considered the oscine analogue of the primary auditory cortex. 24 sites are considered here; of these, six are classified as single-unit sites and the rest as consisting of two to five units. The average spike rate during song playback is 15.1 Hz with a range of across sites of 10.5-33 Hz.

Acknowledgements: Thanks to Science Foundation Ireland for grants 08/RFP/MTH1280, to Trinity College Dublin School of Mathematics for supporting an internship for ÚNíÉ and to Kamal Sen for the use of the data analysed here.

MNLab