Spike trains and spike codes

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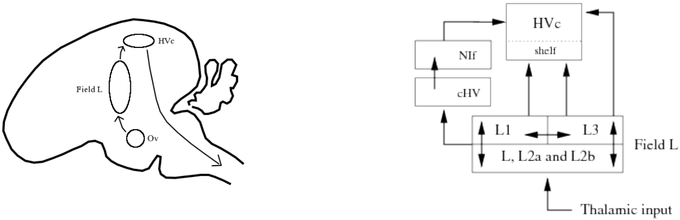
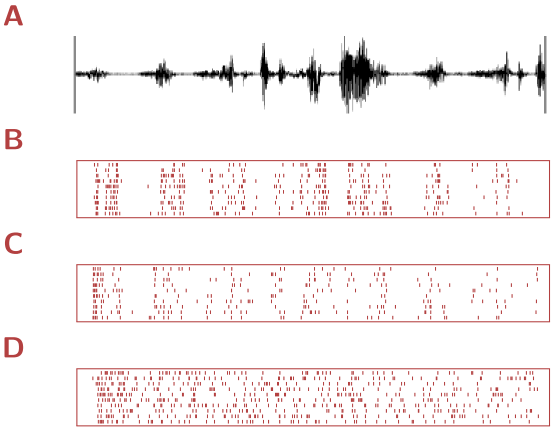
The zebra finch.

The zebra finch auditory pathway.



(a) (b)

Spike trains.



Spectro-temporal receptive fields.

$$\tilde{r}(t) = \int \sum_f h_f(\tau) s_f(t - \tau) d\tau$$

Questions about zebra finch spiking responses - rates.

- Is the song rate coded or is there information in temporal features?
  - How do you distinguish the effect of a time varying rate from a temporal feature?
  - How can the rate be calculated: this is both a practical and theoretical question.
  - What is that rate; are we to image there some platonic ideal rate for which the spike trains are derived statistically?

Questions about zebra finch spiking responses - information.

- How much information is carried in spike trains?
  - Should we use the discrete theory or the continuous one?
    - Spike times are not discrete and discrete calculations don't seem to give satisfactory answers.
    - The continuous theory assumes a continuous space, what is the space of spike trains?

Questions about zebra finch spiking responses - overall.

- How should we compare responses?
- What is the space of spike trains?

Metric spaces

A metric maps pairs of points a and b, to a real number $d(a, b)$ such that

- Positive and distinguishable

$$\begin{aligned} d(a,b) &\geq 0 \\ d(a,b) &= 0 \iff a = b, \end{aligned}$$

- Symmetric

$$d(a,b) = d(b,a).$$

- Triangle inequality

$$d(a,b) \leq d(a,c) + d(c,b).$$

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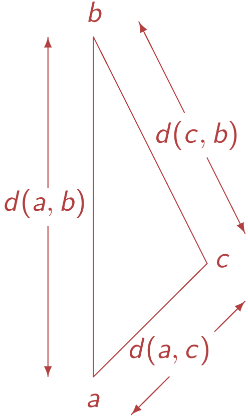
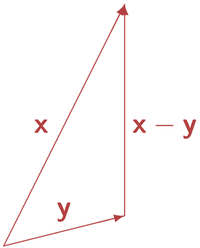


The triangle inequality

Euclidean metrics

- In $\mathbf{R}^3$ say

$$\begin{aligned} \mathbf{x} &= (x_1, x_2, x_3) \\ \mathbf{y} &= (y_1, y_2, y_3) \end{aligned}$$



- The dot product is given by $\mathbf{x}\cdot\mathbf{y} = x_1y_1 + x_2y_2 + x_3y_3$
- The dot-product of a vector with itself is *a norm*, a measure of the length of the vector $|\mathbf{x}| = \sqrt{\mathbf{x}\cdot\mathbf{x}}$.
- This norm induces a metric, called the *L^2 metric*

$$d(\mathbf{x},\mathbf{y}) = |\mathbf{x}-\mathbf{y}| = \sqrt{\sum_{i=1}^{3}(x_i - y_i)^2}.$$

Euclidean metrics on the space of functions.

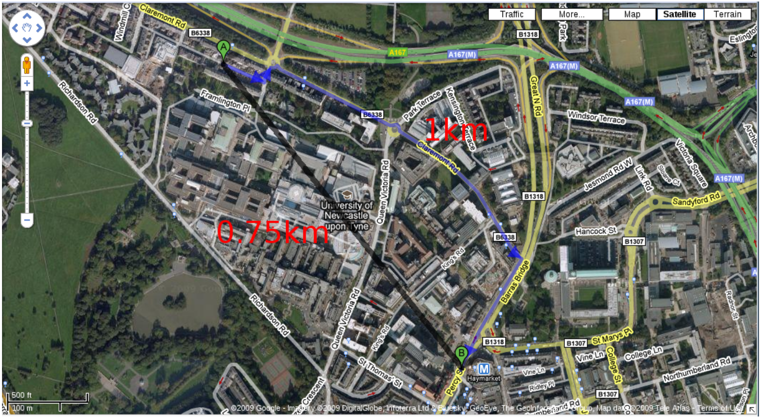
This generalizes to functions, if $f(t)$ and $g(t)$ are both real functions on the same interval, $[0, T]$ say, then the L^2-metric is

$$d(f,g) = \sqrt{\int_0^T dt(f-g)^2}.$$

Spike trains aren't a vector space.

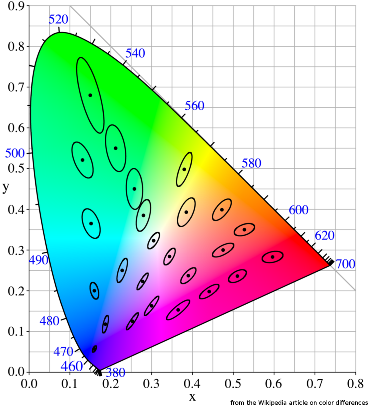
- While it might be possible to define the addition of two spike trains by superposition, it isn't at all obvious how to define the difference.
- There is no reason to expect spike trains to be Euclidean.

A non-Euclidean metric: Metrics in towns.



'As the crow flies' distance versus route distance.

A non-Euclidean metric: Color perception.



from the Wikipedia article on color differences

MacAdam ellipses in color space.

Metrics and spike trains.

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Metrics and spike trains.

- Perhaps spike train metrics will allow us to find the salient features of spike trains without the need to discuss spike rates.
- The framework for continuous version of information theory is a manifold, but perhaps that isn't needed, perhaps it can be rephrased in terms of metric spaces.
- Obviously this leaves open the question of how to find a spike train metric.
- Maybe we are wrong in using a metric space, maybe a semimetric is more natural in this context.

The spike count distance.

- The influence of stimulus strength on a neuron's firing rate is perhaps the most broadly observed principle in the sensory systems.
  - Somatosensory receptor cells fire with a rate that depends on the stimulus strength.
  - V1 cells in the mammalian visual cortex fire with a rate that depends on how well the stimulus matches a receptive field.
  - Auditory cells are tuned to show a rate response to particular features in sound.

This gives the spike count distance between spike trains **u** and **v**

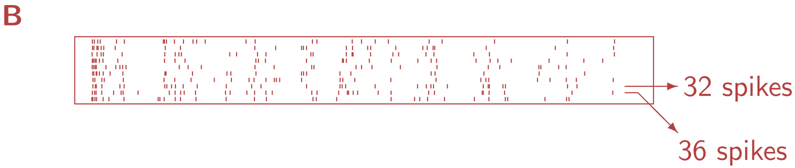
$$d(\mathbf{u}, \mathbf{v}) = |\text{difference in the number of spikes}|$$

Example.

The spike count distance:

$$d(\mathbf{u}, \mathbf{v}) = |m - n|$$

where m is the number of spikes in $\mathbf{u}$ and n the number in $\mathbf{v}$.



Here the distance between the two spike trains would be four.

Segmented spike count distance.

- Divide the interval into N sub-intervals of length $\delta_T = T/N$.
- Take the spike count distance in each sub-interval

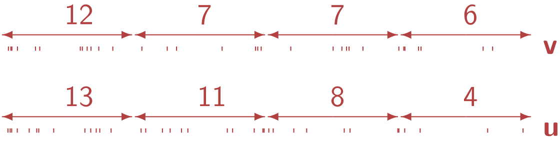
$$d_i = |m_i - n_i|$$

  - m_i is the number of spikes in $\mathbf{u}$ in the ith sub-interval.
  - n_i performs the same role for $\mathbf{v}$.
- The distance between the two spike trains is the Pythagorean sum of all these sub-interval distances.

$$d(\mathbf{u}, \mathbf{v}) = \sqrt{\sum_{i=1}^{N} d_i^2}$$

- Probably the most common way to compare responses.

Segmented spike count distance - example.



$d_1 = 1$ $d_2 = 4$ $d_3 = 1$ $d_4 = 2$

Here, with $\delta_T = .25$s, the distance between the two spike trains is

$$d(\mathbf{u}, \mathbf{v}) = \sqrt{d_1^2 + d_2^2 + d_3^2 + d_4^2} = \sqrt{22} \approx 4.69$$

Filtered spike count distance.

- Use a moving interval: $\delta(t) = [t - \delta_T/2, t + \delta_T/2]$
  - $m(t)$ is the number of spikes in $\mathbf{u}$ in $\delta(t)$.
  - $n(t)$ is the number of spikes in $\mathbf{v}$ in $\delta(t)$.
- Take the spike count distance in each sub-interval

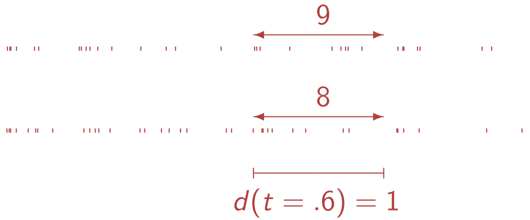
$$d(t) = |m(t) - n(t)|$$

- The distance between the two spike trains is the Pythagorean integral all these sub-interval distances.

$$d(\mathbf{u}, \mathbf{v}) = \sqrt{\int_0^T d(t)^2 dt}$$

- Smooths the segmented spike count distance.

Filtered spike count distance - example.



Here, with $\delta_T = .25$s, the distance between the two spike trains is

$$d(\mathbf{u}, \mathbf{v}) = \sqrt{\int_0^T d(t)^2 dt} \approx 7.91$$

The filtered distance can be rewritten as a filter: the van Rossum metric.

- A spike train is a list of spike times.

$$\mathbf{u} = \{u_1, u_2, \cdots, u_m\}$$

- Map spike trains to functions of t

$$\mathbf{u} \mapsto f(t; \mathbf{u}) = \sum_{i=1}^{m} h(t - u_i)$$

- $h(t)$ is a kernel, here, it is a boxcar function

$$h(t) = \begin{cases} 1 & -\delta_T/2 < t < \delta_T/2 \\ 0 & \text{otherwise} \end{cases} .$$

- Now

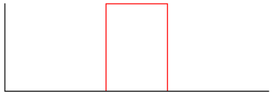
$$d(\mathbf{u}, \mathbf{v}) = \sqrt{\int dt [f(t; \mathbf{u}) - f(t; \mathbf{v})]^2}.$$

The van Rossum metric.

Two steps

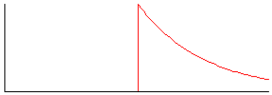
- Maps from spike trains to functions using a filter.
- Use the metric on the space of functions.

Filters



Boxcar

$$h(t) = \begin{cases} 1 & t \in [-\delta_T/2, \delta_T/2] \\ 0 & \text{otherwise} \end{cases}$$



Causal exponential

$$h(t) = \begin{cases} \exp\left(-t/\delta_T\right) & t > 0 \\ 0 & t \leq 0 \end{cases}$$

Gaussian

$$h(t) = \exp\left(-t^2/2\delta_T^2\right)$$

Filters

- Which filter is correct?
- Each filter has a different motivation.
  - Boxcar - rate difference.
  - Exponential - neuronal and synaptic dynamics.
  - Gaussian - statistical models.
- Probably best considered as an experimental question.

Comparing metrics

The basic idea is to use the candidate metric to cluster a set of spike trains, and to compare this clustering with a “gold standard”, namely, clustering the spike trains according to the stimuli that elicited them.

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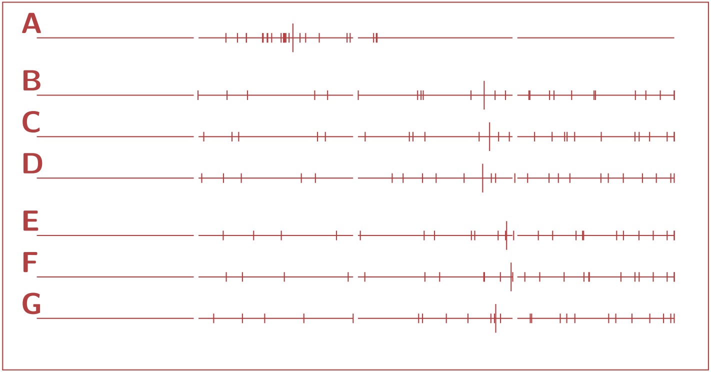
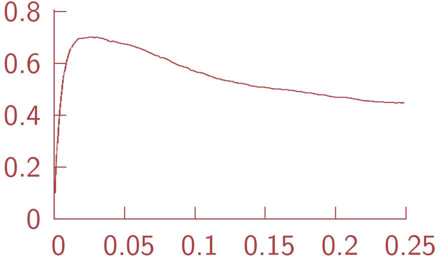
The scheme we will use here is a jack-knife calculation of a confusion matrix. The transmitted information $\tilde{h}$ is used to score clustering with one, the highest, corresponding to perfect clustering.

Comparing metrics



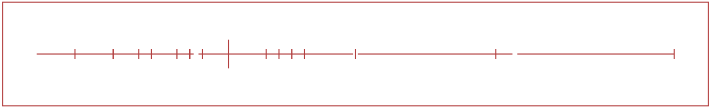
A is spike count distance. **B** boxcar, **C** Gaussian and **D** exponential. **E** – **G** are the same again but with site bests.

Metrics - boxcar timescale.



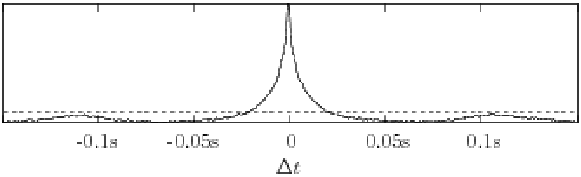
Average performance with the boxcar filter plotted against δ_T.

Comparing metrics - exponential timescales.



Optimal timescales plotted from 0 to 50ms. The average is 15ms.

Ideal filter.



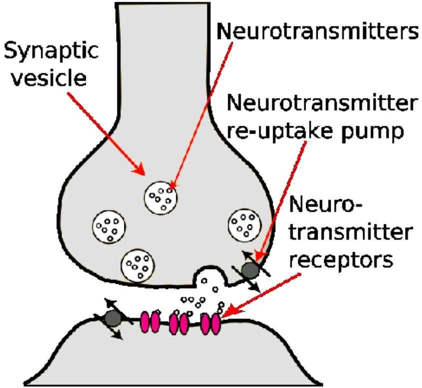
Learning the best filter.

A more general map.

The van Rossum metric filters the spike train to get a function and then uses the metric on the space of functions. It can be easily generalized by allowing any map.

$$\mathbf{u} \mapsto f(t; \mathbf{u})$$

Synapses.



- Neurotransmitter floods the cleft.
- The neurotransmitter binds to the gated channels.
  - Conductance in the dendritic membrane causes a PSP.
- The neurotransmitter unbinds.

The van Rossum metric

$$\mathbf{u} \mapsto f(t; \mathbf{u})$$

where $f(t; \mathbf{u})$ is modelled on the synaptic conductance.

- Unbinding of neurotransmitter.

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

- Release of neurtransmitter.

$$f \rightarrow f + 1$$

  whenever a spike arrives.

Equivalent to the van Rossum map with exponential filter.

A metric based on a (slightly) more realistic synapse model.

- Unbinding of neurotransmitter.

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

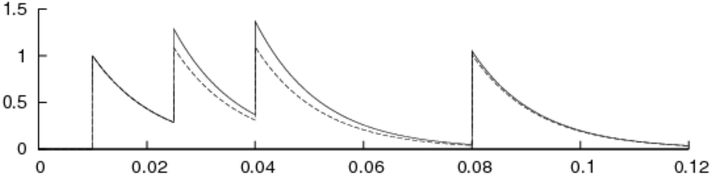
- Release of neurtransmitter.

$$f \to (1-\mu)f + 1$$

whenever a spike arrives. The extra factor of $(1-\mu)$ models the depletion of binding sites.

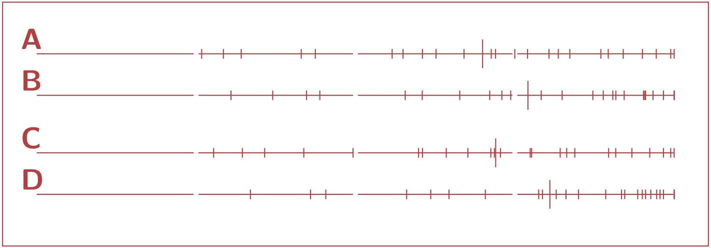
  - If $\mu = 0$ this is the original van Rossum map.
  - If $\mu = 1$ a spike arriving resets f to one; this is the case if all binding sites are used up when a spike arrives.

The synapse metric



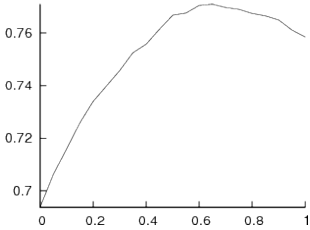
$f(t; \mathbf{u})$ for $\mu = 0$ and $\mu = 0.7$.

Comparing metrics - synapse metric.



A is van Rossum with exponential filter, **B** the synapse metric.
C – **D** are the same again but with site bests.

Comparing metrics - synapse metric.

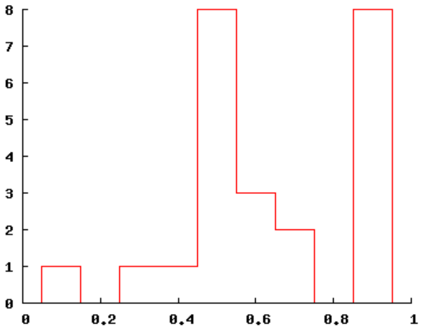


Average performance plotted against $\tilde{h}$.

Synapse metric - properties.

- The only adjustment that seems to produce an improvement for these data.
  - All sorts of synapse dynamics can be modelled: depression and facilitation, a continuous response to spikes.
- Spike times and spike count more salient when there are fewer spikes.

Synapse metric - physiology?



Values of μ.