Spike trains and spike codes

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Spike trains and spike codes

The zebra finch song system

The zebra finch.
The zebra finch auditory pathway.
Spike trains and spike codes

The zebra finch song system

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
  \[ d(a, b) \geq 0 \]
  \[ d(a, b) = 0 \iff a = b, \]

- 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 $\mathbb{R}^3$ say

\[
x = (x_1, x_2, x_3) \\
y = (y_1, y_2, y_3)
\]

- The dot product is given by

\[x \cdot y = x_1y_1 + x_2y_2 + x_3y_3\]

- The dot-product of a vector with itself is a norm, a measure of the length of the vector $|x| = \sqrt{x \cdot x}$.

- This norm induces a metric, called the $L^2$ metric

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

MacAdam ellipses in color space.
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 the 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.

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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 \( v \)

\[
d(u, v) = |\text{difference in the number of spikes}|
\]
The spike count distance:

$$d(u, v) = |m - n|$$

where $m$ is the number of spikes in $u$ and $n$ the number in $v$.

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 $u$ in the $i$th sub-interval.
- $n_i$ performs the same role for $v$.

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

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

- Probably the most common way to compare responses.
Segmented spike count distance - example.

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

$$d(u, v) = \sqrt{d_1^2 + d_2^2 + d_3^2 + d_4^2} = \sqrt{22} \approx 4.69$$
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 $u$ in $\delta(t)$.
  - $n(t)$ is the number of spikes in $v$ 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.
  $$d(u, v) = \sqrt{\int_0^T d(t)^2 dt}$$
- Smooths the segmented spike count distance.
Filtered spike count distance - example.

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

$$d(u, v) = \sqrt{\int_0^T d(t)^2 \, dt} \approx 7.91$$
The filtered distance can be rewritten as a filter: the van Rossum metric.

- A spike train is a list of spike times.
  \[ u = \{u_1, u_2, \cdots, u_m\} \]

- Map spike trains to functions of \( t \)
  \[ u \mapsto f(t; u) = \sum_{i=1}^{m} h(t - u_i) \]

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

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

**Gaussian**

\[ h(t) = \exp\left(-\frac{t^2}{2\delta_T^2}\right) \]
Filters

• Which filter is correct?
  ▶ 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 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.

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.
A is spike count distance. B boxcar, C Gaussian and D exponential. E – G are the same again but with site bests.
Average performance with the boxcar filter plotted against $\delta_T$. 
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.

\[ u \mapsto f(t; u) \]
- 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

\[ u \mapsto f(t; u) \]

where \( f(t; u) \) is modelled on the synaptic conductance.

- Unbinding of neurotransmitter.
  \[ \tau \frac{df}{dt} = -f \]

- Release of neurotransmitter.
  \[ f \rightarrow f + 1 \]

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 neurotransmitter.

\[ f \rightarrow (1 - \mu)f + 1 \]

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.
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The synapse metric

\[ f(t; u) \text{ for } \mu = 0 \text{ and } \mu = 0.7. \]
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.
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Synapse metric

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 $\mu$. 