NEURAL CODING
Single Cell Recording

dendrite

axon

15 mV

0.1 mV

100 mV

100 ms
Definitions

- **Neural response function**
  \[ \rho(t) = \sum_{i=1}^{n} \delta(t - t_i) \]

- **Spike-count rate**
  \[ r = \frac{n}{T} = \frac{1}{T} \int_0^T d\tau \rho(\tau) \]

- **Firing rate**
  \[ r(t) = \frac{1}{\Delta t} \int_t^{t+\Delta t} d\tau \langle \rho(\tau) \rangle \]

- **Average firing rate**
  \[ \langle r \rangle = \frac{n}{T} = \frac{1}{T} \int_0^T d\tau \langle \rho(\tau) \rangle = \frac{1}{T} \int_0^T d\tau r(t) \]
Estimating Firing Rate

Histogramming

\[ \hat{r}(t) = \int_{-\infty}^{\infty} d\tau w(\tau) \rho(t - \tau) \]

KDE (Rectangular)

\[ w(t) = \begin{cases} 
\frac{1}{\Delta t} & \text{if } -\Delta t / 2 \leq t \leq \Delta t / 2 \\
0 & \text{otherwise}.
\end{cases} \]

KDE (Gaussian)

\[ w(t) = \frac{1}{\sqrt{2\pi}\sigma_w} \exp\left(-\frac{\tau^2}{2\sigma_w^2}\right) \]

KDE (Causal)

\[ w(t) = \left[ \alpha^2 \tau \exp(-\alpha \tau) \right]_+ \]
Tuning Curves: Example 1

- Orientation selectivity

\[ f(s) = r_{\text{max}} \exp\left( -\frac{1}{2}\left( \frac{s - s_{\text{max}}}{\sigma_s} \right)^2 \right) \]
Tuning Curves: Example 2

- Movement direction selectivity in primary motor cortex of primate

\[
f(s) = r_0 + (r_{\text{max}} - r_0) \cos(s - s_{\text{max}})
\]
Tuning Curves: Example 3

- Binocular disparity tuning (Area 17 of cat)

\[ f(s) = \frac{r_{\text{max}}}{1 + \exp\left(\frac{s_{1/2} - s}{\Delta_s}\right)} \]
Spike-Triggered Averaging
Periodic Stimulus

- We analyze the relationship between stimulus and response over a finite interval of time \([0, T]\).
- However, it is sometimes mathematically convenient to consider the stimulus as extending beyond this interval, in periodic fashion, so that
  
  \[ s(T + \tau) = s(\tau) \] for any \( \tau \)

- As a result, integrals of any function \( h \) will be translationally-invariant:

\[
\int_0^T h(s(t + \tau)) \, dt = \int_0^{T+\tau} h(s(t)) \, dt = \int_0^{T} h(s(t)) \, dt
\]
The spike-triggered average $C(\tau)$ is the average value of the stimulus a time interval $\tau$ before the spike is fired:

$$C(\tau) = \left\langle \frac{1}{n} \sum_{i=1}^{n} s(t_i - \tau) \right\rangle$$

$$\approx \frac{1}{n} \left\langle \sum_{i=1}^{n} s(t_i - \tau) \right\rangle$$

$$= \frac{1}{n} \int_{0}^{T} r(t) s(t - \tau) dt$$

spike-triggered average
Correlation

- The spike-triggered average can be related to the firing-rate – stimulus correlation function $Q_{rs}$:

$$Q_{rs}(\tau) = \frac{1}{T} \int_0^T r(t)s(t + \tau) \, dt$$

- Thus

$$C(\tau) = \frac{1}{\langle n \rangle} \int_0^T r(t)s(t - \tau) \, dt$$

$$= \frac{T}{\langle n \rangle} Q_{rs}(-\tau)$$

$$= \frac{1}{\langle r \rangle} Q_{rs}(-\tau)$$

- Hence the spike-triggered average is often called the reverse correlation.
Autocorrelation

- We can also define the stimulus autocorrelation function $Q_{ss}(\tau)$:

$$Q_{ss}(\tau) = \frac{1}{T} \int_{0}^{T} s(t)s(t + \tau) \, dt$$

- If $s(t)$ is 0-mean white noise, then

$$Q_{ss}(\tau) = \sigma_s^2 \delta(\tau)$$
Multiple-Spike-Triggered Averages

- Blowfly H1 Neuron responding to moving visual image (de Ruyter & Bialek 1988)
  - Closely-spaced spikes can have a super-additive effect that is not identified by single-spike-triggered averaging.
  - This can be captured by triggering on pairs of spikes with specific inter-spike intervals.
Definitions

- **Point Process**
  - A stochastic process that generates a sequence of events.

- **Renewal Process**
  - The probability of an event occurring at a specified time is a function only of the time elapsed since the last event.

- **Poisson Process**
  - The probability of an event occurring at a specified time is independent of all other events.
Homogeneous Poisson Processes

- The firing rate \( r(t) = r \) is constant.
- Any sequence of \( n \) spikes over a finite interval \([0, T]\) is equally likely.
- Thus the probability of an observed spike train depends only upon the number \( n \) of spikes in the train:

\[
P[t_1, t_2, \ldots, t_n] = n! P_T[n] \left( \frac{\Delta t}{T} \right)^n
\]

where
\[
0 \leq t_1 \leq t_2 \leq \ldots \leq t_n \leq T
\]

and

\( P_T[n] \) is the probability of observing \( n \) spikes over a trial of length \( T \).

and we have divided the interval \([0, T]\) into \( M \) bins of duration \( \Delta t = T / M \).
Homogeneous Poisson Processes

Number of orderings in which the n spikes can be selected

Probability of observing n spikes

Probability that a particular spike will be placed in a particular bin

\[ P[t_1, t_2, \ldots, t_n] = n! P_T[n] \left( \frac{\Delta t}{T} \right)^n \]
Homogeneous Poisson Processes

\[ P_T[n] = \lim_{\Delta t \to 0} \frac{M!}{(M-n)!n!} (r\Delta t)^n (1-r\Delta t)^{M-n} \]

- Number of ways to choose \( n \) bins from a total of \( M \) bins
- Probability that the process will not generate a spike in a particular bin
- Probability that the process will generate a spike in a particular bin
Homogeneous Poisson Processes

\[ P_T[n] = \lim_{\Delta t \to 0} \frac{M!}{(M-n)!n!} (r\Delta t)^n (1-r\Delta t)^{M-n} \]

- Taking the limit...

\[ P_T[n] = \frac{(rT)^n}{n!} \exp(-rT) \]
Homogeneous Poisson Process

$T =$ Duration of trial

$r =$ Constant firing rate

$n =$ Number of spikes observed during trial

Approaches a Gaussian distribution as $rT \to \infty$
Moments of the Homogeneous Poisson Process

Mean \( E[n] = \langle n \rangle = rT \)

Variance \( \sigma_n^2 = E\left[ (n - E[n])^2 \right] = E\left[ n^2 \right] - E[n]^2 = \langle n^2 \rangle - \langle n \rangle^2 = rT \)

Fano Factor \( \triangleq \frac{\sigma_n^2}{\langle n \rangle} = 1 \) for a homogeneous Poisson process.
Interspike Interval Distribution

Given a spike at time $t_i$, the probability that the next spike will occur in the time slice $t_i + \tau \leq t_{i+1} \leq t_i + \tau + \Delta t$ is (for small $\Delta t$)

$$P\left[ \tau \leq t_{i+1} - t_i \leq \tau + \Delta t \right] = r\Delta t \exp(-r \tau)$$

Thus the probability density of the interspike interval is

$$P[\tau] = r \exp(-r \tau)$$

And

$$\langle \tau \rangle = \frac{1}{r}$$

$$\sigma_{\tau}^2 = \frac{1}{r^2}$$

Coefficient of variation $C_v = \frac{\sigma_{\tau}}{\langle \tau \rangle} = 1$ for a homogeneous Poisson process.
Spike-Train Autocorrelation Function

\[ Q_{pp}(\tau) = \frac{1}{T} \int_{0}^{T} dt (\rho(t) - \langle r \rangle)(\rho(t + \tau) - \langle r \rangle) \]

- Measures the distribution of times between any two spikes in a train.
- Actually a covariance (mean subtracted before correlation computed)
- Useful for analyzing oscillation
- For a homogeneous Poisson process,
  \[ Q_{pp}(\tau) = r \delta(\tau) \]
Oscillations & Synchrony

- Area 17 of Cat

A

Right Hemisphere

Left Hemisphere

Spike-Train Autocorrelations

B

Spike-Train Cross-Correlation
Generative Poisson Model

- Exponential ISIs can be generated by transforming a uniform distribution:

Suppose $x_{\text{rand}}$ is uniformly-distributed on $[0, 1]$.

Let $\tau = -\log(x_{\text{rand}})/r$

\[ \rightarrow x_{\text{rand}} = \exp(-r\tau) \]

The distribution of $\tau$ is given by

\[ p(\tau) = \left| \frac{dx}{dy} \right| p(x) = -r \exp(-r\tau) \]
Generative Poisson Model
Example: Primate MT Neurons

\[ \sigma_n^2 = A \langle n \rangle^B \]

\[ \text{variance (spikes}^2) \]
\[ \text{mean (spikes)} \]

\[ \langle n \rangle \]

\[ \text{multiplier} \]
\[ \text{count duration (ms)} \]

\[ \text{exponent} \]
Example: Primate MT Neurons

Data

Poisson model with stochastic refractory period
Meta-Analysis of Primate V1 and MT Neurons

\[ C_V = \frac{\sigma_\tau}{\langle \tau \rangle} \]
Correlations in Population Codes

Example: Place-cells in rat hippocampus

- Timing of action potentials relative to theta-rhythm of population depends upon position of animal.
Temporal Coding Example

- Primate MT neural response to noisy motion stimuli