Neural Encoding: Firing Rates and Spike Statistics

- Dayan and Abbott (2001) Chapter 1

Instructor: Yoonsuck Choe; CPSC 644 Cortical Networks

Background: Dirac δ Function

- Dirac δ function has the following properties:
  \[ \int dt \delta(t) = 1 \]
  \[ \int dt' \delta(t - t') f(t') = f(t) \]
  and it will be used a lot in the following.

Spike Trains

- Action potentials can be represented as a sequence of spike timing:
  \[ t_i, i = 1, 2, 3, ..., n, \text{ and } 0 \leq t_i \leq T \]
- The spike sequence can be represented as:
  \[ \rho(t) = \sum_{i=1}^{n} \delta(t - t_i) \]
- For any well-behaved function \( h(t) \),
  \[ \sum_{i=1}^{n} h(t - t_i) = \int_{-\infty}^{\infty} d\tau h(\tau) \rho(t - \tau). \]

Firing Rate

"Firing rate" can mean many different quantities.

- Spike count rate is defined as
  \[ r = \frac{n}{T} = \frac{1}{T} \int_{0}^{T} d\tau \rho(\tau), \]
  where \( n \) spikes occurred within a time interval of \( 0 \leq t \leq T \), which is the entire trial period of a single trial.
- Trial average \( \langle z \rangle \) means the average of the same quantity \( z \) at the same time point over multiple trials.
- Firing rate is defined as
  \[ r(t) = \frac{1}{\Delta t} \int_{t}^{t+\Delta t} d\tau \langle \rho(\tau) \rangle. \]
- Spiking probability within interval \((t, t + \Delta t)\) is \( r(t) \Delta t \).
Average Neural Response and Firing Rate

- Average neural response can be represented in terms of firing rate:
  \[
  \int d\tau h(\tau) \langle \rho(t - \tau) \rangle = \int d\tau h(\tau) r(t - \tau)
  \]

- Average firing rate over multiple trials can then be defined as:
  \[
  \langle r \rangle = \frac{\langle n \rangle}{T} = \frac{1}{T} \int_0^T d\tau \langle \rho(\tau) \rangle = \frac{1}{T} \int_0^T dt \, r(t).
  \]

Summary of Different Firing Rates

- Single trial, entire trial duration:
  \[
  r = \frac{n}{T} = \frac{1}{T} \int_0^T d\tau \rho(\tau).
  \]

- Multiple trials, short time interval:
  \[
  r(t) = \frac{1}{\Delta t} \int_t^{t+\Delta t} d\tau \langle \rho(\tau) \rangle.
  \]

- Multiple trials, entire trial duration:
  \[
  \langle r \rangle = \frac{\langle n \rangle}{T} = \frac{1}{T} \int_0^T d\tau \langle \rho(\tau) \rangle = \frac{1}{T} \int_0^T dt \, r(t).
  \]

Measuring Firing Rates

- A: spikes
- B: Binned count
- C: Sliding window
- D: Sliding Gaussian kernel
- E: Sliding causal kernel

Measuring Firing Rates w/ Sliding Windows

- Fixed-size sliding window
  \[
  r_{\text{approx}}(t) = \sum_{i=1}^n w(t - t_i), \quad \text{where}
  \]
  \[
  w(t) = \begin{cases} 
  1/\Delta t & \text{if } -\Delta t/2 \leq t < \Delta t/2 \\
  0 & \text{otherwise}.
  \end{cases}
  \]
  It can also be written as
  \[
  r_{\text{approx}}(t) = \int_{-\infty}^{\infty} d\tau w(\tau) \rho(t - \tau)
  \]
  which is a linear filter with kernel \(w\).
Measuring Firing Rates w/ Sliding Windows (II)

- The equation below is basically a convolution of spike train with a kernel function:

\[ r_{\text{approx}}(t) = \int_{-\infty}^{\infty} d\tau w(\tau) \rho(t - \tau). \]

Compare to the definition of a convolution:

\[ (f \ast g)(t) = \int_{-\infty}^{\infty} d\tau f(\tau) g(t - \tau) = \int_{-\infty}^{\infty} d\tau f(t - \tau) g(\tau). \]

- A smooth window function (or kernel) \( w \) can be used (here, a Gaussian):

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

where the std of the Gaussian \( \sigma_w \) controls the window size.

Measuring Firing Rates w/ Sliding Windows (III)

- Instead of looking at both sides of a time point \( t \), we can also look at only spikes in the past.

\[ w(\tau) = [\alpha^2 \tau \exp(-\alpha \tau)]_+, \]

where \( 1/\alpha \) determines the temporal resolution of the estimate, and

\[ [x]_+ = \begin{cases} 
  x & \text{if } x \geq 0 \\
  0 & \text{otherwise}
\end{cases} \]

This kernel is called a causal kernel.

- Note that \( w(t - t_i) \) is summed up, so any spikes in the future will have a negative value plugged into \( w(\cdot) \).

Tuning Curve: V1, Gaussian

- Neurons are sensitive to stimulus attributes \( s \); denote by \( s \).

- The neural response tuning curve is a function of \( s \) is

\[ \langle r \rangle = f(s). \]

- A typical example is that of V1 neurons (figure above), a Gaussian tuning curve:

\[ f(s) = r_{\text{max}} \exp\left(-\frac{1}{2} \left(\frac{s - s_{\text{max}}}{\sigma_f}\right)^2\right). \]

Tuning Curve: M1, cos

- Motor cortex neurons:

\[ f(s) = r_0 + (r_{\text{max}} - r_0) \cos(s - s_{\text{max}}), \]

where \( s \) is the arm reach angle, and \( r_0 \) the baseline response and \( r_{\text{max}} \) the max response.

- \( f(s) \) reaches min at \( 2r_0 - r_{\text{max}} \), which can be a negative value, which should not exist, so:

\[ f(s) = [r_0 + (r_{\text{max}} - r_0) \cos(s - s_{\text{max}})]_+. \]
**Tuning Curve: V1, sigmoid**

- V1 disparity-sensitive neurons:
  \[ f(s) = \frac{r_{\text{max}}}{1 + \exp\left(\frac{(s_{1}/2 - s)}{\Delta s}\right)} . \]
  where \( s \) is disparity and \( s_{1}/2 \) is where disparity response is half the max.

**Stimuli that Makes a Neuron to Fire**

- Weber’s law: “just noticeable” difference in stimulus, \( \Delta s \), has the property:
  \[ \frac{\Delta s}{s} = \text{constant}. \]
- Fechner’s law: Noticeable differences set the scale for perceived stimulus intensities. Perceived intensity of stimulus of absolute intensity \( s \) varies as \( \log s \).
- Zero mean stimulus:
  \[ \int_0^T dt \frac{s(t)}{T} = 0 \]
- Averages:
  - Over the same input, across trials: \( \langle \cdot \rangle \).
  - Over different inputs: usually averaged over time as a single long stimulus.

**Periodic Stimuli**

- Given stimulus \( s(t) \) from interval \( 0 \leq t \leq T \), we can replicate with a phase shift of \( \tau \).
  \[
  \int_0^T dt \ h(s(t+\tau)) = \int_0^{T+\tau} dt \ h(s(t)) = \int_0^T dth(s(t)) .
  \]
  Holds when \( s(T + \tau) = s(\tau) \) for any \( \tau \).

**Tuning Curves: Spike-Count Variability**

- Tuning curves gives average firing rate, but do not describe the spike count variability around the mean firing rate \( \langle r \rangle = f(s) \) across trials.
- Spike-count rate can be from a probability distribution where \( f(s) \) is the mean.
- The variability is considered to be noise:
  - Noise distribution independent of \( f(s) \): additive noise.
  - Noise distribution proportional to \( f(s) \): multiplicative noise.
Spike Triggered Average and Stimulus-Response Correlation

- Spike-triggered average can be represented as:
  \[
  C(\tau) = \frac{1}{\langle n \rangle} \int_0^T dt \langle \rho(t) \rangle s(t-\tau) = \frac{1}{\langle n \rangle} \int_0^T dt r(t)s(t-\tau).
  \]
- The firing-rate stimulus correlation function is:
  \[
  Q_{rs}(\tau) = \frac{1}{T} \int_0^T dt r(t)s(t+\tau).
  \]
  Thus,
  \[
  C(\tau) = \frac{1}{\langle r \rangle} Q_{rs}(-\tau).
  \]

Spike Triggered Average Example

- Neuron of the electrosensory lateral-line lobe of the weakly electric fish *Eigenmannia*.
- Input $I$, spikes, and spike-triggered average shown.

Stimulus Autocorrelation and White-Noise Stimuli

- White noise stimulus: any one time point of the stimulus is uncorrelated with any other time point.
- Stimulus autocorrelation function:
  \[
  Q_{ss}(\tau) = \frac{1}{T} \int_0^T dt s(t)s(t+\tau).
  \]
- For white noise stimulus,
  \[
  Q_{ss}(\tau) = \begin{cases} 
  0 & \text{if } -T/2 < \tau < T/2, \tau \neq 0 \\
  \sigma_s^2 \delta(\tau) & \text{if } \tau = 0 
  \end{cases},
  \]
  where $\sigma_s^2$ is the stimulus variance.
Multiple-Spike-Triggered Averages

- Instead of a single spike, you can look for stimuli triggering a pattern of spikes.
- Blowfly H1 neuron data are shown above.

Spike-Train Statistics

- The probability density of a random variable $z$ is $p[z]$.
  $$\int_{-\infty}^{\infty} dz \, p[z] = 1.$$
- Probability of $z$ taking a value between $a$ and $b$:
  $$P[a \leq z \leq b] = \int_a^b dz \, p[z].$$
- For small $\Delta x$,
  $$P[x \leq z \leq x + \Delta x] \approx p[x] \Delta x.$$
- Probability of spike sequence given prob. density of spikes $p[t_1, t_2, \ldots, t_n]$ and a short interval $\Delta t$:
  $$P[t_1, t_2, \ldots, t_n] = p[t_1, t_2, \ldots, t_n](\Delta t)^n.$$  

Stochastic Process

- Point process: stochastic process that generates a sequence of events, like action potentials.
- Probability of an event at time $t$ is usually dependent on all past events.
- Renewal process: current event only depends on immediate past event so that intervals between successive events are independent.
- Poisson process: All events are statistically independent.
  - Homogenous: firing rate is constant over time.
  - Inhomogeneous: firing rate is dependent on time.

Poisson Distribution

- Poisson experiment:
  - Number of events in one time interval is independent of that in another non-overlapping interval.
  - Probability of a single event during a short interval is proportional to the length of the interval, and is independent of events outside that interval.
  - Probability that more than one event can occur in a very short interval is negligible.
- The number $X$ of outcomes in such an experiment (in a specific time interval) has the Poisson distribution.
- Binomial random variable with distribution $b(x; n, p)$ approaches Poisson distribution as $n \to \infty, p \to 0$, and $\mu = np$ stays fixed.

Poisson Distribution (II)

- The number of events \( n \) in a given interval \( T \) is
  \[
P_T[n] = \frac{\exp(-\mu)\mu^n}{n!},
  \]
  where \( \mu \) is the average number of events in that interval. Note, if firing rate is \( r \) and the interval is \( T, \mu = rT \).

- The probability of an ordered sequence of spikes is:
  \[
P[t_1, t_2, ..., t_n] = n!P_T[n]\left(\frac{\Delta t}{T}\right)^n.
  \]

Interspike Interval

- Probability of two successive spikes at \( t_i \) and \( t_{i+1} \) with \( t_i + \tau \leq t_{i+1} + \tau + \Delta t \) is
  - No spike within \( \tau \) (interspike interval) and,
  - Spike within a short period \( \Delta t \) immediately following that.

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

- Mean and variance of interspike interval:

  \[
  \langle \tau \rangle = \int_0^\infty d\tau \, \tau \exp(-r\tau) = \frac{1}{r}.
  \]

  \[
  \sigma_\tau^2 = \int_0^\infty d\tau \, \tau^2 \exp(-r\tau) - \langle \tau \rangle^2 = \frac{1}{r^2}.
  \]

Properties of Poisson Distribution

- Variance and mean of spike count is the same:

  \[
  \sigma_n^2 = \langle n^2 \rangle - \langle n \rangle^2 = rT = \mu.
  \]

- Fano factor:

  \[
  \frac{\sigma_n^2}{\langle n \rangle} = 1
  \]

  is 1 for homogeneous Poisson process.

- Coefficient of variation:

  \[
  CV = \frac{\sigma_n^2}{\langle \tau \rangle},
  \]

  is 1 for homogeneous Poisson process (\( \tau \) is the interspike interval).

Spike-Train Auto- and Cross-correlation Function

- ISI distribution describes \( \tau \) between two successive spikes.

- Generalizing this to times between any two pair of spikes in a spike train is spike-train autocorrelation function:

  \[
  Q_{\rho\rho}(\tau) = \frac{1}{T} \int_0^T dt \langle (\rho(t) - \langle \rho \rangle) (\rho(t + \tau) - \langle \rho \rangle) \rangle.
  \]

  Property:

  \[
  Q_{\rho\rho}(\tau) = Q_{\rho\rho}(-\tau).
  \]

- Do the above across two spike trains to get the crosscorrelation function.
Auto- and Crosscorrelation Histogram

- Lag $m$.
- Number of spike-pairs with distance within $m \pm 1/2\Delta t$: $N_m$.
- Normalize $N_m$ by the number of intervals in each bin $n^2\Delta t/T$ and duration of trial $T$:
  \[
  H_m = \frac{N_m - n^2\Delta t/T}{T}.
  \]

Comparison of Poisson Model and Data

- Fano factor and ISI distribution show close match between Poisson model and experimental data.

Neuronal Response Variability

- Poisson model does not account for neuronal response variability in in vivo (alive animal) experiments as compared to in vitro (in isolated tissue).

The Neural Code

- How is information coded by spikes?
- A matter of intense debate: Rate coding or temporal coding?
- Other perspectives: Independent or dependent spikes?
  - Independent-spike code
  - Correlation code
  - Independent-neuron code
  - Synchrony and oscillations