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 propreties:

$$\int dt \delta(t) = 1$$

$$\int dt' \delta(t - t') f(t') = f(t)$$

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, 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 occured 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

$$\mathrm{r}(t) = \frac{1}{\Delta t} \int_t^{t+\Delta t} d\tau \langle \rho(\tau) \rangle.$$

- Spiking probability within interval $(t, t + \Delta t)$ is $\mathrm{r}(t) \Delta t$.

Average Neural Response and Firing Rate

- Average neural response can be represented in terms of firing rate:

$$\int d\tau h(\tau)\langle\rho(t-\tau)\rangle = \int d\tau h(\tau)\mathrm{r}(t-\tau)$$

- Average firing rate over multiple trials can then be defined as:

$$\langle r\rangle = \frac{\langle n\rangle}{T} = \frac{1}{T}\int_0^T d\tau\langle\rho(\tau)\rangle = \frac{1}{T}\int_0^T dt\,\mathrm{r}(t).$$

Summary of Different Firing Rates

- Single trial, entire trial duration:

$$r = \frac{n}{T} = \frac{1}{T}\int_0^T d\tau\rho(\tau).$$

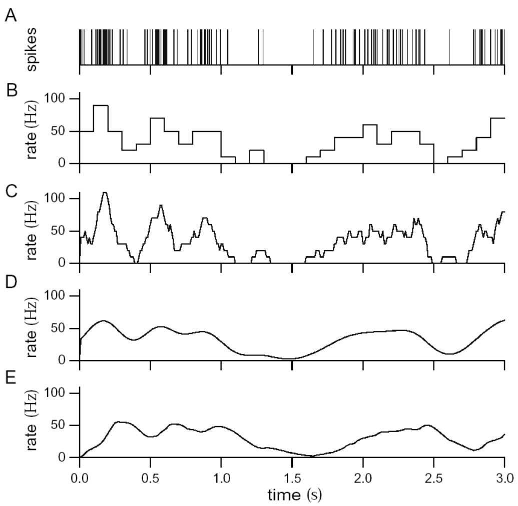
- Multiple trials, short time interval:

$$\mathrm{r}(t) = \frac{1}{\Delta t}\int_t^{t+\Delta t} d\tau\langle\rho(\tau)\rangle.$$

- Multiple trials, entire trial duration:

$$\langle r\rangle = \frac{\langle n\rangle}{T} = \frac{1}{T}\int_0^T d\tau\langle\rho(\tau)\rangle = \frac{1}{T}\int_0^T dt\,\mathrm{r}(t).$$

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

$$\mathrm{r}_{\mathrm{approx}}(t) = \sum_{i=1}^{n} w(t-t_i), \quad \text{where}$$

$$w(t) = \begin{cases} 1/\Delta t & \text{if } -\Delta t/2 \le t < \Delta t/2 \\ 0 & \text{otherwise.} \end{cases}$$

It can also be written as

$$\mathrm{r}_{\mathrm{approx}}(t) = \int_{-\infty}^{\infty} d\tau w(\tau)\rho(t-\tau)$$

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:

$$\mathrm{r}_{\mathrm{approx}}(t) = \int_{-\infty}^{\infty} d\tau w(\tau)\rho(t-\tau).$$

Compare to the definition of a convolution:

$$(f * g)(t) = \int_{-\infty}^{\infty} d\tau f(\tau) g(t-\tau) = \int_{-\infty}^{\infty} d\tau f(t-\tau) g(\tau).$$

- 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 σ_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.

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

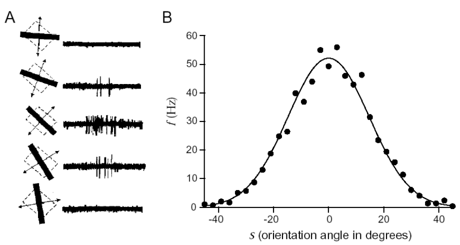
where $1/\alpha$ determines the temporal resolution of the estimate, and

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

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



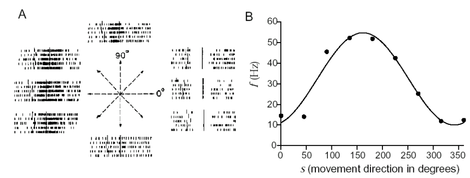
- Neurons are sensitive to stimulus attributes s: denote by s.
- The neural response tuning curve is a function of s is

$$\langle r \rangle = f(s).$$

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

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

Tuning Curve: M1, cos



- Motor cortex neurons:

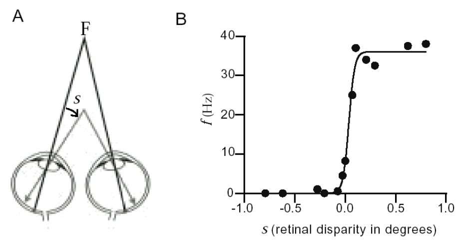
$$f(s) = r_0 + (r_{\max} - r_0)\cos(s - s_{\max}),$$

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

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

$$f(s) = [r_0 + (r_{\max} - r_0)\cos(s - s_{\max})]_+.$$

Tuning Curve: V1, sigmoid



- V1 disparity-sensitive neurons:

$$f(s) = \frac{r_{\max}}{1 + \exp\left((s_{1/2} - s)/\Delta_s\right)}.$$

where s is disparity and $s_{1/2}$ is where disparity response is half the max.

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 variabilty is considered to be noise:
  - Noise distribution independent of $f(s)$: additive noise.
  - Noise distribution proportional to $f(s)$: multiplicative noise.

Stimuli that Makes a Neuron to Fire

- Weber's law: "just noticeable" difference in stimulus, Δs, 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:

$$\int_0^T dt \frac{s(t)}{T} = 0$$

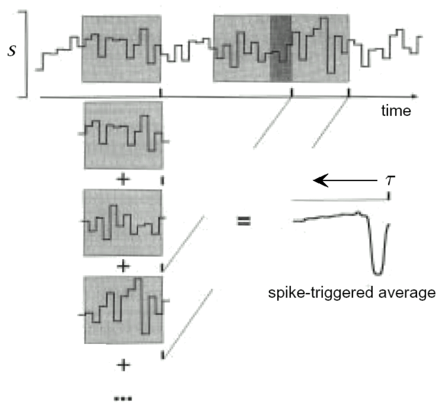
- Averages:
  - Over the same input, across trials: $\langle \cdot \rangle$.
  - Over different inputs: usually averaged over time as a single long stimulus.

Periodic Stimuli

- Given stimulus $s(t)$ from interval $0 \leq t \leq T$, we can replicate with a phase shift of τ.

$$\int_0^T dt\, h(s(t+\tau)) = \underbrace{\int_\tau^{T+\tau} dt\, h(s(t)) = \int_0^T dth(s(t))}_{\text{Holds when } s(T+\tau) = s(\tau) \text{ for any } \tau} .$$

Spike-Triggered Average



- Average stimulus (over trials), τ before spike occurred:

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

Spike Triggered Average and Stimulus-Response Correlation

- Spike-triggered average can be represented as:

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

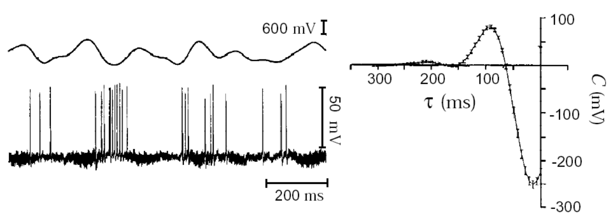
- The firing-rate stimulus correlation function is:

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

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:

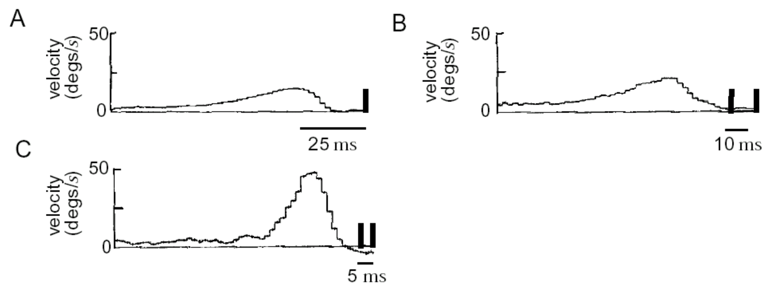
$$Q_{ss}(\tau) = \frac{1}{T} \int_0^T dt\, s(t) s(t+\tau).$$

- 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 σ_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 Δx,

$$P[x \leq z \leq x + \Delta x] \approx p[x]\Delta x.$$

- Probability of spike sequence given prob. density of spikes $p[t_1, t_2, ..., t_n]$ and a short interval Δt:

$$P[t_1, t_2, ..., t_n] = p[t_1, t_2, ..., t_n](\Delta t)^n.$$

Stochastic Process

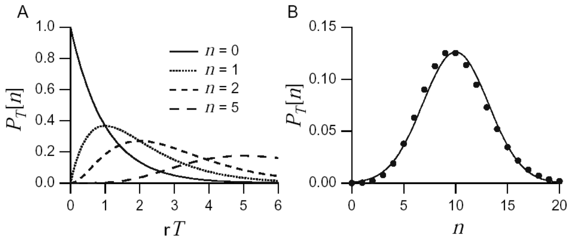
- Point process: stochastic process that generates a sequence of events, like action potentials.
- Probability of an event at time t is usually dependent on all past events.
- Renewal process: current event only depends on immediate past event so that intervals between successive events are independent.
- 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 that one event can occur in a very short interval is negligable.
- 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 $n \longrightarrow \infty$, $p \longrightarrow 0$, and $\mu = np$ stays fixed.

Ref: Walpole and Myers, *Probability and Statistics for Engineers and Scientists*, 3rd ed. Macmillan (1985)

Poisson Distribution (II)



- The number of events n in a given interval T is

$$P_T[n] = \frac{\exp(-\mu)\mu^n}{n!},$$

where μ is the average number of events in that interval. Note, if firing rate is r and the interval is T, $\mu = \mathrm{r}T$.

- The probability of an ordered sequence of spikes is:

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

Properties of Poission Distribution

- Variance and mean of spike count is the same:

$$\sigma_n^2 = \langle n^2 \rangle - \langle n \rangle^2 = \mathrm{r}T = \mu.$$

- Fano factor:

$$\frac{\sigma_n^2}{\langle n \rangle}$$

is 1 for homogeneous Poisson process.

- Coefficient of variation:

$$C_V = \frac{\sigma_n^2}{\langle \tau \rangle},$$

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

Interspike Interval

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

$$P[t_i + \tau \leq t_{i+1} \leq t_i + \tau + \Delta t] = \underbrace{\mathrm{r}\Delta\mathrm{t}}_{\text{Firing within } \Delta t} \overbrace{\exp(-\mathrm{r}\tau)}^{\text{No spike within } \tau}.$$

- Mean and variance of interspike interval:

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

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

Spike-Train Auto- and Crosscorrelation Function

- ISI distribution describes τ between two successive spikes.
- Generalizing this to times between any two pair of spikes in a spike train is spike-train autocorrelation function:

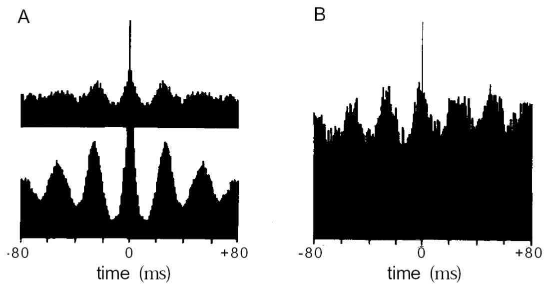
$$Q_{\rho\rho}(\tau) = \frac{1}{T}\int_0^T dt\, \langle (\rho(t) - \langle r \rangle)(\rho(t+\tau) - \langle r \rangle) \rangle.$$

Property:

$$Q_{\rho\rho}(\tau) = Q_{\rho\rho}(-\tau).$$

- Do the above across two spike trains to get the crosscorrelation function.

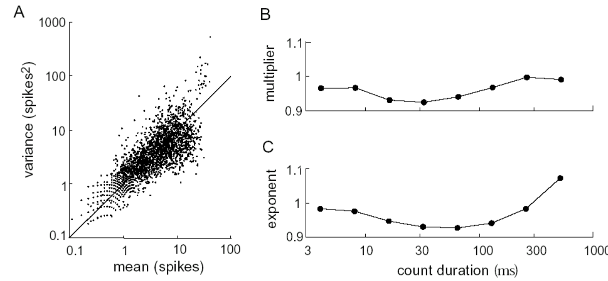
Auto- and Crosscorrelation Histogram

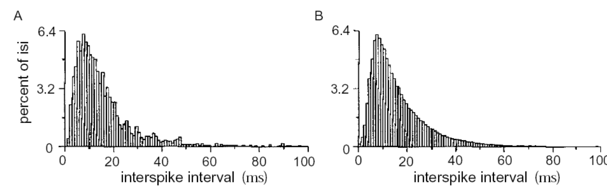


- Lag m.
- Number of spike-pairs with distance within $m \pm 1/2\Delta t$: N_m.
- Normalize N_m by the number of intervals in each bin $n^2\Delta t/T$ and duration of trial T:

$$H_m = \frac{N_m - n^2\Delta t/T}{T}.$$

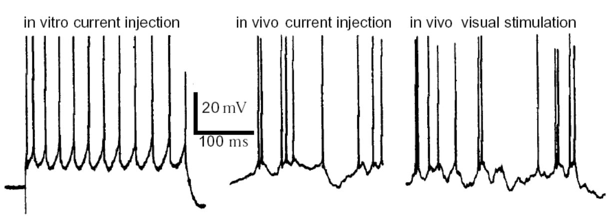
Comparison of Poisson Model and Data





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

Neuronal Response Variability



- Poission model does not account for neuronal repsonse 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