Course Summary (thus far)

- Neural Encoding
  - What makes a neuron fire? (STA, covariance analysis)
  - Poisson model of spiking

- Neural Decoding
  - Spike-train based decoding of stimulus
  - Stimulus Discrimination based on firing rate
  - Population decoding (Bayesian estimation)

- Single Neuron Models
  - RC circuit model of membrane
  - Integrate-and-fire model
  - Conductance-based Models
Today’s Agenda

- Computation in Networks of Neurons
  - Modeling synaptic inputs
  - From spiking to firing-rate based networks
  - Feedforward Networks
  - Linear Recurrent Networks

Image Credit: Kennedy lab, Caltech. http://www.its.caltech.edu/~mbk
What do synapses do?

Increase or decrease postsynaptic membrane potential

An **Excitatory** Synapse

Input spike →
Neurotransmitter release (e.g., Glutamate) →
Binds to receptors →
Ion channels open →
positive ions (e.g. Na+) enter cell →
**Depolarization** due to **EPSP** (excitatory postsynaptic potential)
An Inhibitory Synapse

Input spike → Neurotransmitter release (e.g., GABA) → Binds to receptors → Ion channels open → positive ions (e.g., K+) leave cell → Hyperpolarization due to IPSP (inhibitory postsynaptic potential)

Flashback

Membrane Model

\[ \tau_m = r_m c_m = R_m C_m \]

membrane time constant

\[ \frac{c_m}{A} \frac{dV}{dt} = - \frac{(V - E_L)}{r_m} + \frac{I_e}{A}, \text{ or equivalently} \]

\[ \tau_m \frac{dV}{dt} = -(V - E_L) + I_e R_m \]
**Flashback! The Integrate-and-Fire Model**

Models a passive leaky membrane

\[
\tau_m \frac{dV}{dt} = -(V - E_L) + I_e R_m
\]

If \( V > V_{\text{threshold}} \) \( \rightarrow \) Spike
Then reset: \( V = V_{\text{reset}} \)

- \( E_L \approx -70 \text{ mV} \)
- Resting potential
- \( V_{\text{threshold}} \approx -50 \text{ mV} \)
- \( V_{\text{reset}} \approx E_L \)

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**Flashback! Hodgkin-Huxley Model**

\[
c_m \frac{dV}{dt} = -i_m + \frac{I_e}{A}
\]

\[
i_m = g_{L,\text{max}} (V - E_L) + g_{K,\text{max}} n^4 (V - E_K) + g_{Na,\text{max}} m^3 h(V - E_{Na})
\]

- \( E_L = -54 \text{ mV} \)
- \( E_K = -77 \text{ mV} \)
- \( E_{Na} = +50 \text{ mV} \)
How do we model the effects of a synapse on the membrane potential $V$?

Modeling Synaptic Inputs

$$
\tau_m \frac{dV}{dt} = -(V - E_L) - r_m g_s (V - E_s) + I_e R_m
$$

$$
g_s = g_{s,\text{max}} P_{rel} P_s \quad \text{Probability of postsynaptic channel opening}
\quad \text{ (= fraction of channels opened)}
\quad \text{Probability of transmitter release given an input spike}
$$
Basic Synapse Model

- Assume $P_{\text{rel}} = 1$
- Model the effect of a single spike input on $P_s$
- Kinetic Model of postsynaptic channels:
  
  \[
  \frac{dP_s}{dt} = \alpha_s (1 - P_s) - \beta_s P_s
  \]

  - Opening rate
  - Closing rate
  - Fraction of channels closed
  - Fraction of channels open

What does $P_s$ look like over time?

Exponential function $K(t)$ gives reasonable fit to biological data
(other options: difference of exponentials, “alpha” function)
Linear Filter Model of Synaptic Input to a Neuron

Input Spike Train $\rho_b(t)$

Synaptic weight $w_b$

$\rho_b(t) = \sum_i \delta(t-t_i)$ \hspace{1em} ($t_i$ are the input spike times)

Filter for synapse $b$: $K(t) = \frac{1}{\tau_s} e^{\frac{-t}{\tau_s}}$

Synaptic current for $b$: $I_b(t) = w_b \sum_{t_i < t} K(t-t_i)$

$$= w_b \int_{-\infty}^{t} K(t-\tau) \rho_b(\tau) d\tau$$

Modeling Networks of Neurons

**Option 1:** Use *spiking* neurons

- **Advantages:** Model computation and learning based on:
  - Spike Timing
  - Spike Correlations/Synchrony between neurons
- **Disadvantages:** Computationally expensive

**Option 2:** Use neurons with *firing-rate outputs (real valued outputs)*

- **Advantages:** Greater efficiency, scales well to large networks
- **Disadvantages:** Ignores spike timing issues

**Question:** How are these two approaches related?
From Spiking to Firing Rate Models

output $\mathbf{v}$
weights $\mathbf{w}$
input $\mathbf{u}$

Total synaptic current $I_s(t) = \sum_b I_b(t)$

$$I_s(t) = \sum_b w_b \int_{-\infty}^{t} K(t - \tau) \rho_b(\tau) \, d\tau \quad \text{Spike train } \rho_b(t)$$

$$\approx \sum_b w_b \int_{-\infty}^{t} K(t - \tau) u_b(\tau) \, d\tau \quad \text{Firing rate } u_b(t)$$

Synaptic Current Dynamics in Firing Rate Model

- Suppose synaptic kernel $K$ is exponential: $K(t) = \frac{1}{\tau_s} e^{-t/\tau_s}$

Differentiating $I_s(t) = \sum_b w_b \int_{-\infty}^{t} K(t - \tau) u_b(\tau) \, d\tau$ w.r.t. time $t$,

we get

$$\tau_s \frac{dI_s}{dt} = -I_s + \sum_b w_b u_b$$

$$= -I_s + \mathbf{w} \cdot \mathbf{u}$$
Output Firing-Rate Dynamics

- How is the output firing rate $v$ related to synaptic inputs?

$$\tau_r \frac{dv}{dt} = -v + F(I_s(t)) \quad \tau_s \frac{dI_s}{dt} = -I_s + w \cdot u$$

- Looks very much like membrane equation:

$$\tau_m \frac{dV}{dt} = -(V - E_l) + I_m R_m$$

- On-board derivations of special cases obtained from comparing the relative magnitudes of $\tau_r$ and $\tau_s$ …

(see also pages 234-236 in the text)

How good are Firing Rate Models?

Input $I(t) = I_0 + I_1 \cos(\omega t)$

Firing rate model $v(t) = F(I(t))$ describes this well but not this case
Feedforward versus Recurrent Networks

$$\tau \frac{dv}{dt} = -v + F(Wu + Mv)$$

Output Decay Input Feedback

For feedforward networks, matrix $M = 0$

Example: Linear Feedforward Network

$$W = \begin{bmatrix}
1 & 0 & 0 & 0 & -1 \\
-1 & 1 & 0 & 0 & 0 \\
0 & -1 & 1 & 0 & 0 \\
0 & 0 & -1 & 1 & 0 \\
0 & 0 & 0 & -1 & 1 \\
1 & 0 & 0 & 0 & -1
\end{bmatrix}$$

$$u = \begin{bmatrix}
1 \\
2 \\
2 \\
1
\end{bmatrix}$$

What is $v_{ss}$?
Linear Feedforward Network

\[ v_{ss} = W u = \begin{bmatrix} 1 & 0 & 0 & 0 & -1 \\ -1 & 1 & 0 & 0 & 0 \\ 0 & -1 & 1 & 0 & 0 \\ 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & -1 & 1 \\ 1 & 0 & 0 & 0 & -1 \end{bmatrix} \begin{bmatrix} 1 \\ 2 \\ 2 \\ 2 \\ 1 \end{bmatrix} = \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ -1 \\ 0 \end{bmatrix} \]

What is the network doing?

Linear Filtering for Edge Detection

Filter = \[ \begin{bmatrix} 0 & -1 & 1 & 0 & 0 \end{bmatrix} \]
(and shifted versions in W)

Input = \[ \begin{bmatrix} 1 \\ 2 \\ 2 \\ 2 \\ 1 \end{bmatrix} \]
Output = \[ \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ -1 \\ 0 \end{bmatrix} \]
Example of Edge Detection in a 2D Image

Edge detectors in the visual system

Examples of receptive fields in primary visual cortex (V1)

(From Nicholls et al., 1992)
Filtering network is computing derivatives!

\[ \frac{df}{dx} = \lim_{h \to 0} \frac{f(x + h) - f(x)}{h} \]

Discrete approximation \( \approx f(x + 1) - f(x) \)

\[ \frac{d^2f}{dx^2} = \lim_{h \to 0} \frac{f'(x + h) - f'(x)}{h} \]

Disc. approx. \( \approx (f(x + 1) - f(x)) - (f(x) - f(x - 1)) \)
\[ = f(x + 1) - 2f(x) + f(x - 1) \]

Feedforward Networks: Example 2

Coordinate Transformation

Output: Premotor Cortex Neuron with \textit{Body-Based Tuning Curves}

Input: Area 7a Neurons with \textit{Gaze-Dependent Tuning Curves}

(From Section 7.3 in Dayan & Abbott)
Output of Coordinate Transformation Network

Head fixed; gaze shifted to $g_1$, $g_2$, $g_3$

Same tuning curve regardless of gaze angle
Premotor cortex neuron responds to stimulus location relative to body, not retinal image location

(See section 7.3 in Dayan & Abbott for details)

Linear Recurrent Networks

\[ \tau \frac{dv}{dt} = -v + Wu + Mv \]

Output Decay Input Feedback
Next Class: Recurrent Networks

✦ To Do:
  ➜ Homework 2
  ➜ Find a final project topic and partner(s)