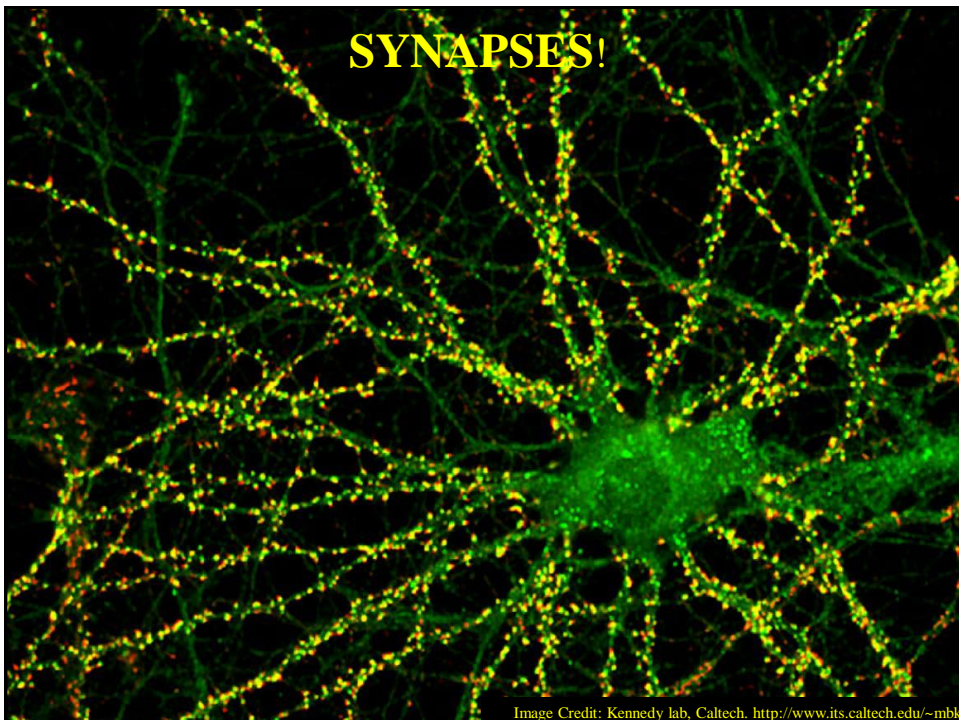


Course Summary (thus far)

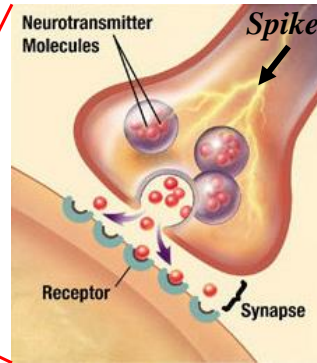
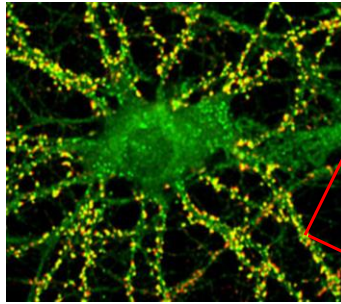
- ◆ Neural Encoding
 - ⇨ What makes a neuron fire? (STA, covariance analysis)
 - ⇨ Poisson model of spiking
- ◆ Neural Decoding
 - ⇨ Spike-train based decoding of stimulus
 - ⇨ Stimulus Discrimination based on firing rate
 - ⇨ Population decoding (Bayesian estimation)
- ◆ Single Neuron Models
 - ⇨ RC 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

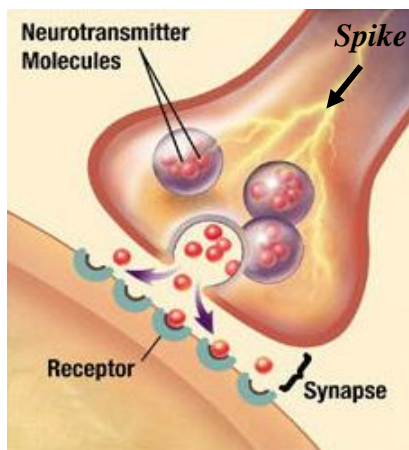


What do synapses do?



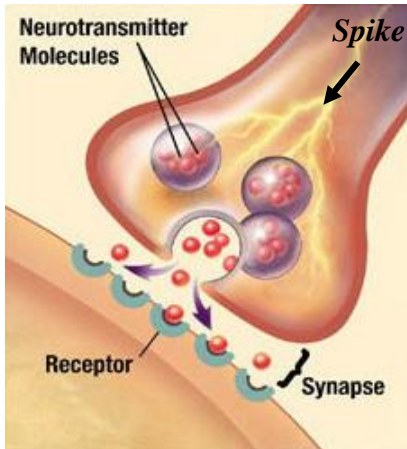
Increase or decrease postsynaptic membrane potential

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



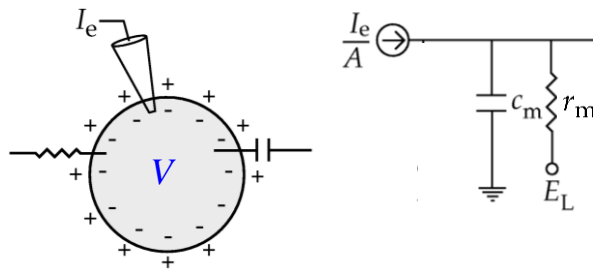
Input spike →
 Neurotransmitter
 release (e.g., GABA)
 → Binds to receptors
 → Ion channels open
 → positive ions (e.g.,
 K+) leave cell →
 Hyperpolarization due
 to IPSP (inhibitory
 postsynaptic potential)

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Image Source: Wikimedia Commons

Flashback Membrane Model



$\tau_m = r_m c_m = R_m C_m$
 membrane time
 constant

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

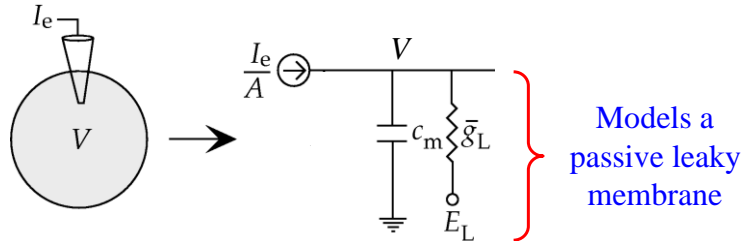
$$\tau_m \frac{dV}{dt} = -(V - E_L) + I_e R_m$$

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The Integrate-and-Fire Model



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

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

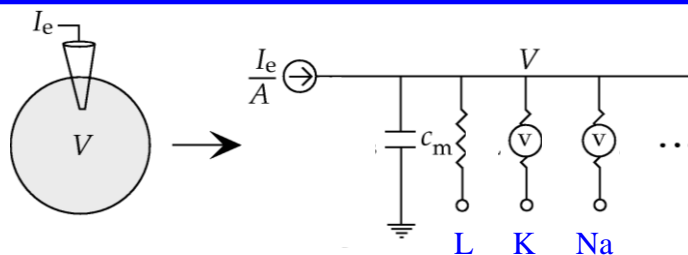
$E_L \approx -70 \text{ mV}$
 (resting potential)

$V_{\text{threshold}} \approx -50 \text{ mV}$

$V_{\text{reset}} \approx E_L$



Hodgkin-Huxley Model

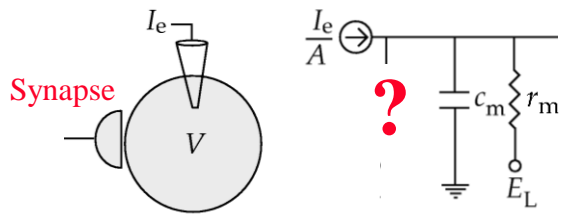
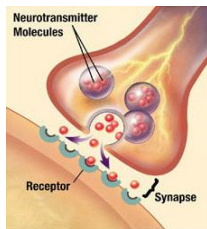


$$C_m \frac{dV}{dt} = -i_m + \frac{I_e}{A}$$

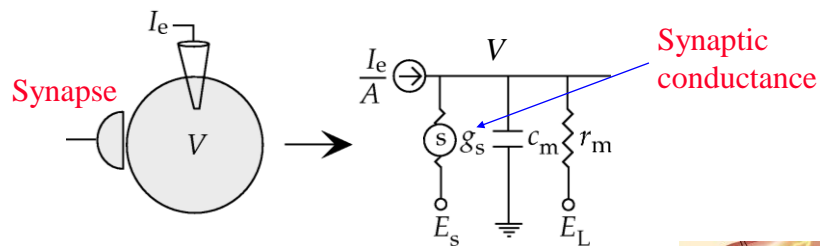
$$i_m = g_{L,\text{max}} (V - E_L) + g_{K,\text{max}} n^4 (V - E_K) + g_{Na,\text{max}} m^3 h (V - E_{Na})$$

$$E_L = -54 \text{ mV}, E_K = -77 \text{ mV}, E_{Na} = +50 \text{ mV}$$

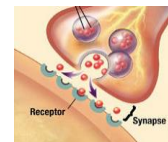
How do we model the effects of a synapse on the membrane potential V ?



Modeling Synaptic Inputs



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

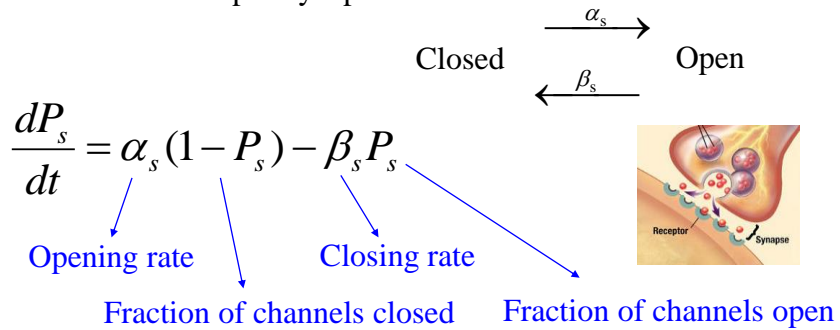


$$g_s = g_{s,\max} P_{rel} P_s$$

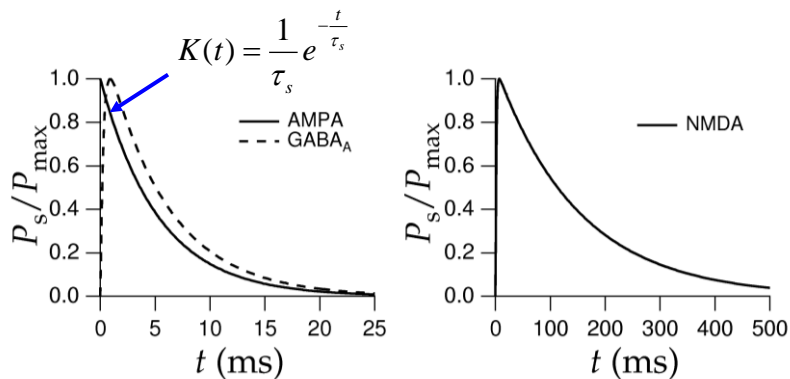
P_{rel} ← Probability of postsynaptic channel opening
 (= fraction of channels opened)
 P_s ← Probability of transmitter release given an input spike

Basic Synapse Model

- ◆ Assume $P_{rel} = 1$
- ◆ Model the effect of a single spike input on P_s fraction of channels opened
- ◆ Kinetic Model of postsynaptic channels:

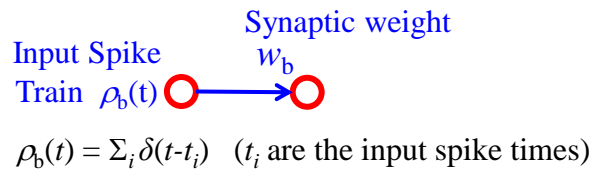


What does P_s look like over time?



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



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

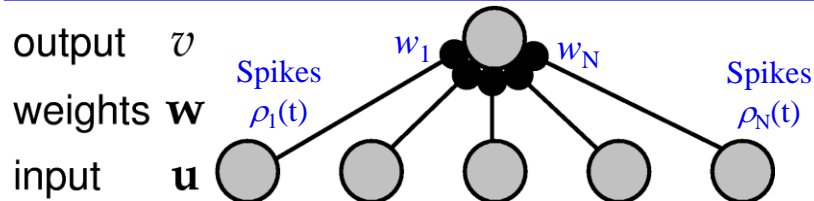
Synaptic current for b : $I_b(t) = w_b \sum_{t_i < t} K(t-t_i)$

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

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



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

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

$$\begin{aligned} \text{we get } \tau_s \frac{dI_s}{dt} &= -I_s + \sum_b w_b u_b \\ &= -I_s + \mathbf{w} \cdot \mathbf{u} \end{aligned}$$

Output Firing-Rate Dynamics

- ◆ How is the output firing rate ν related to synaptic inputs?

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

- ◆ Looks very much like membrane equation:

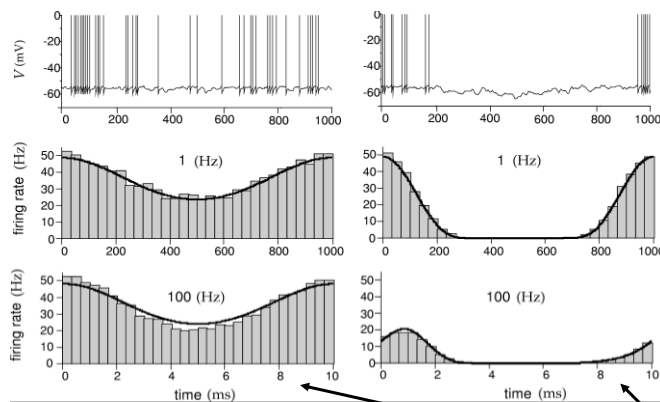
$$\tau_m \frac{dV}{dt} = -(V - E_L) + I_e R_m$$

- ◆ On-board derivations of special cases obtained from comparing the relative magnitudes of τ_r and $\tau_s \dots$

(see also pages 234-236 in the text)

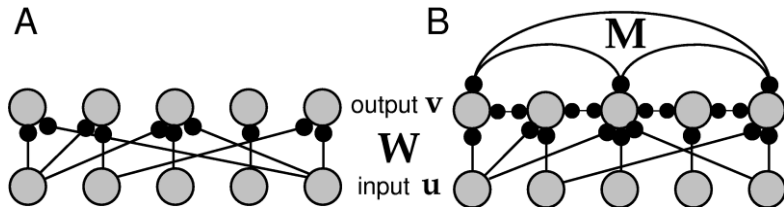
How good are Firing Rate Models?

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



Firing rate model $\nu(t) = F(I(t))$ describes this well but not this case

Feedforward versus Recurrent Networks

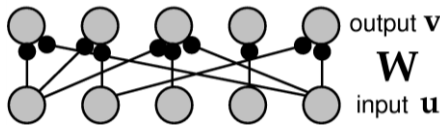


$$\tau \frac{d\mathbf{v}}{dt} = -\mathbf{v} + F(\mathbf{W}\mathbf{u} + \mathbf{M}\mathbf{v})$$

Output Decay Input Feedback

For feedforward networks, matrix $\mathbf{M} = 0$

Example: Linear Feedforward Network



Dynamics: $\tau \frac{d\mathbf{v}}{dt} = -\mathbf{v} + \mathbf{W}\mathbf{u}$

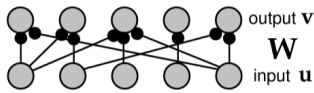
Steady State
(set $d\mathbf{v}/dt$ to 0): $\mathbf{v}_{ss} = \mathbf{W}\mathbf{u}$

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

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

What is \mathbf{v}_{ss} ?

Linear Feedforward Network



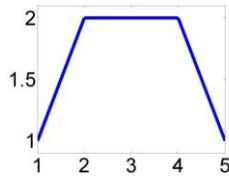
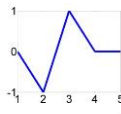
$$\mathbf{v}_{ss} = \mathbf{W}\mathbf{u} = \begin{bmatrix} 1 & 0 & 0 & 0 & -1 \\ -1 & 1 & 0 & 0 & 0 \\ 0 & -1 & 1 & 0 & 0 \\ 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & -1 & 1 \\ 1 & 0 & 0 & 0 & -1 \end{bmatrix} \begin{bmatrix} 1 \\ 2 \\ 2 \\ 2 \\ 1 \end{bmatrix} = \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ -1 \\ 0 \end{bmatrix}$$

What is the network doing?

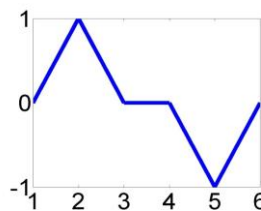
Linear Filtering for Edge Detection

Filter = $[0 \ -1 \ 1 \ 0 \ 0]$
(and shifted versions in \mathbf{W})

$$\text{Input} = \begin{bmatrix} 1 \\ 2 \\ 2 \\ 2 \\ 1 \end{bmatrix} \quad \text{Output} = \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ -1 \\ 0 \end{bmatrix}$$

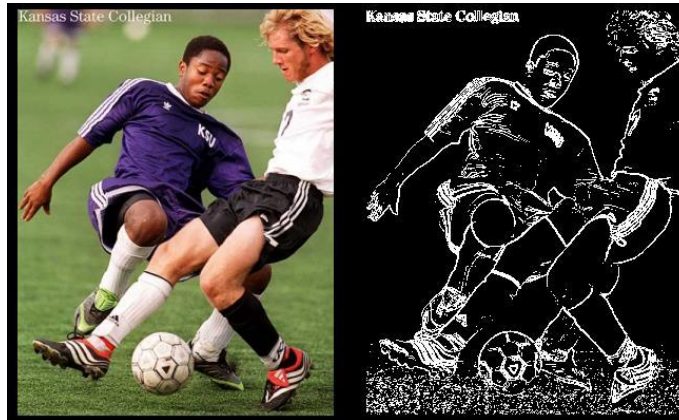


Input



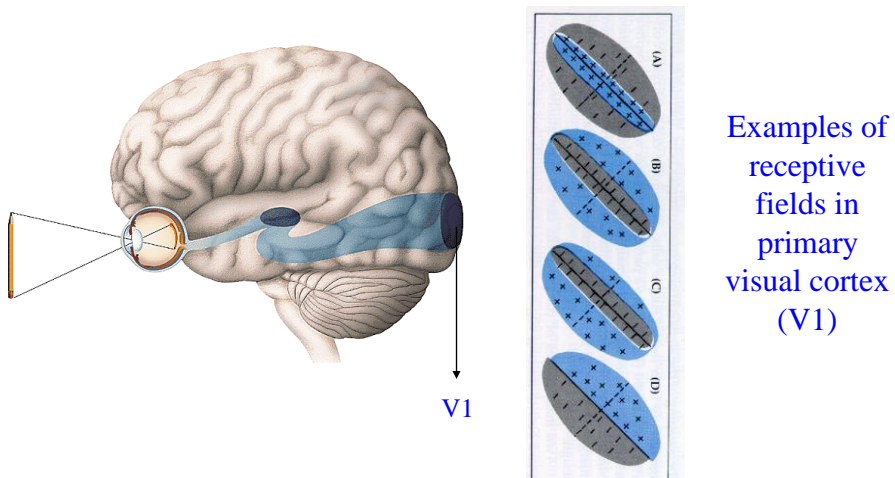
Output

Example of Edge Detection in a 2D Image

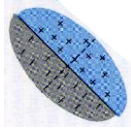


<http://www.alexandria.nu/ai/blog/entry.asp?E=51>

Edge detectors in the visual system

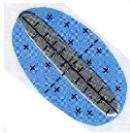


Filtering network is computing derivatives!



$$[0 \quad -1 \quad 1 \quad 0 \quad 0] \quad \frac{df}{dx} = \lim_{h \rightarrow 0} \frac{f(x+h) - f(x)}{h}$$

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



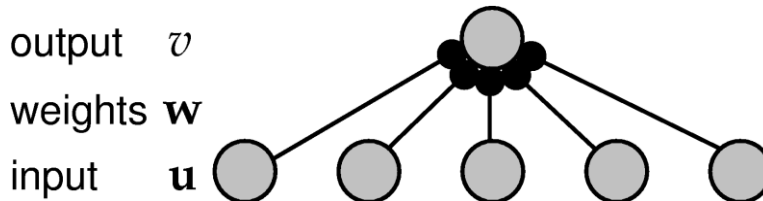
$$[0 \quad 1 \quad -2 \quad 1 \quad 0] \quad \frac{d^2 f}{dx^2} = \lim_{h \rightarrow 0} \frac{f'(x+h) - f'(x)}{h}$$

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

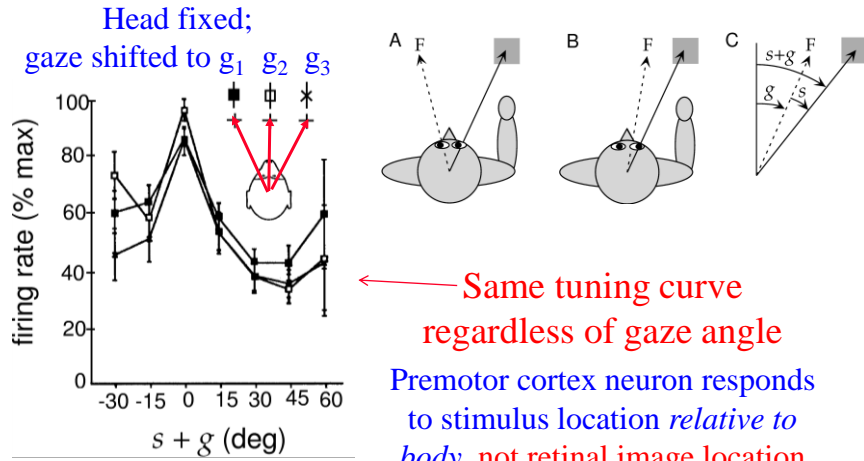
Coordinate Transformation

Output: Premotor Cortex Neuron with Body-Based Tuning Curves



Input: Area 7a Neurons with Gaze-Dependent Tuning Curves

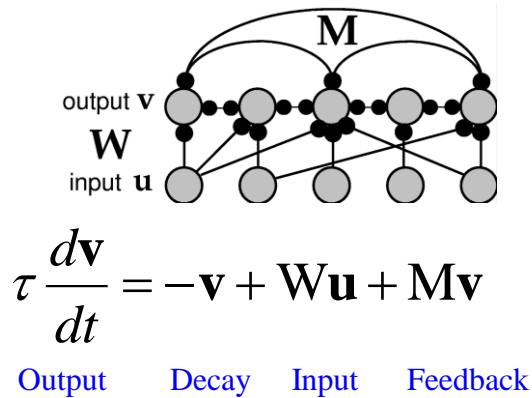
Output of Coordinate Transformation Network



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(See section 7.3 in Dayan & Abbott for details)

Linear Recurrent Networks



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Next Class: Recurrent Networks

- ◆ To Do:
 - ⇒ Homework 2
 - ⇒ Find a final project topic and partner(s)