# CSE/NEUBEH 528

Lecture 9: Computation by Networks (Chapter 7)

Image from http://clasdean.la.asu.edu/news/images/ubep2001/neuron3.jpg Lecture figures are from Dayan & Abbott's book

## 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

## Today's Agenda

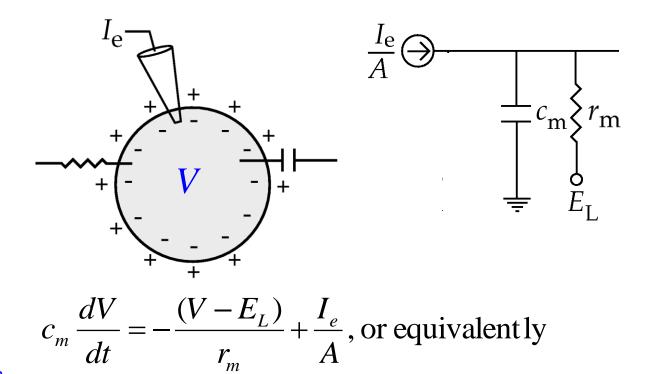
- Computation in Networks of Neurons
  - From spiking to firing-rate based networks
  - ⇒ Feedforward Networks

## 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?

# Flashback

#### Membrane Model

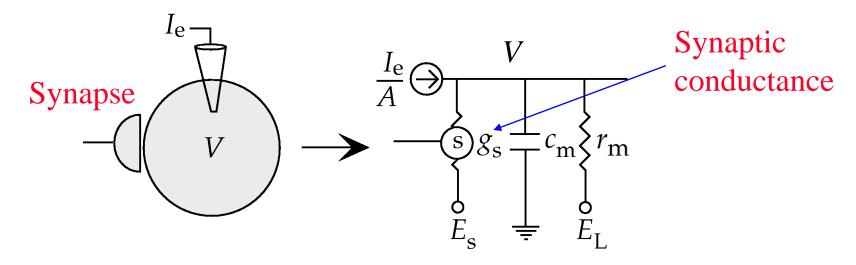


$$\tau_{m} = r_{m}c_{m} = R_{m}C_{m}$$
membrane time
constant

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



## Flashback Modeling Synaptic Inputs from other Neurons



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

 $g_s = g_{s, \max} P_{rel} P_s$  — Probability of postsynaptic channel opening (= fraction of channels opened)

Probability of transmitter release given an input spike

## Basic Synapse Model

- ightharpoonup Assume  $P_{rel} = 1$
- → Model the effect of a single spike input on P<sub>s</sub>

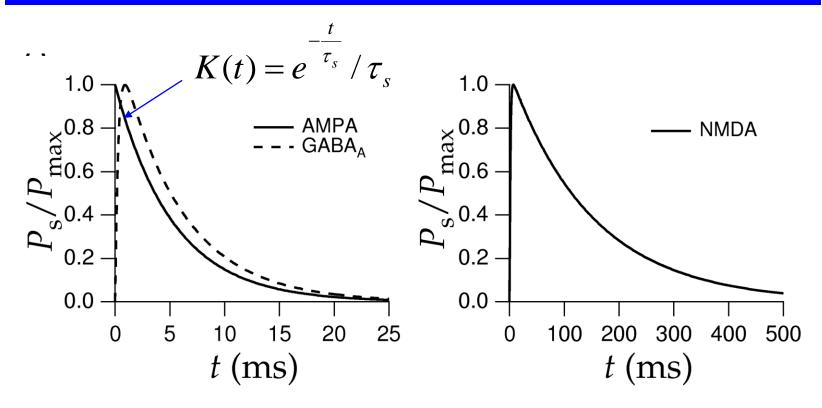
$$\frac{dP_s}{dt} = \alpha_s (1 - P_s) - \beta_s P_s$$
Opening rate

Closing rate

Closing rate

Fraction of channels closed

## Synaptic Filter and Postsynaptic Data



Exponential function K(t) gives reasonable fit to biological data (other options: difference of exponentials, "alpha" function)

## Modeling a Synaptic Input to a Neuron

Input Spikes 
$$w_b$$

$$\rho_b(t) \bigcirc \longrightarrow \bigcirc$$

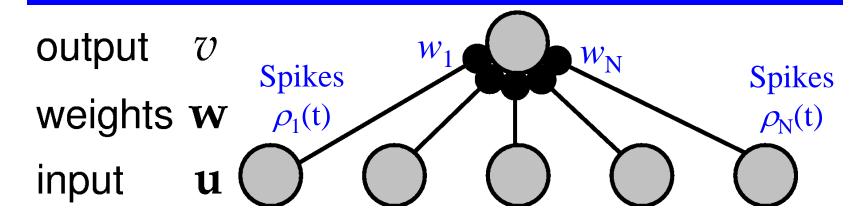
Filter for synapse *b*: 
$$K(t) = \frac{1}{\tau_s} e^{-\frac{t}{\tau_s}}$$

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

where  $w_s$  is a synaptic weight and  $\rho_b(\tau)$  is the input spike train:

$$\rho_{\rm b}(\tau) = \Sigma_{\rm i} \, \delta(\tau - t_{\rm i})$$
 (t<sub>i</sub> are the input spike times)

## From Spiking to Firing Rate Models



Current at synapse 
$$b$$
  $I_b(t) = w_b \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$  Spike train  $\rho_b(t)$   $\approx w_b \int_{-\infty}^{t} K(t-\tau)u_b(\tau)d\tau$  Firing rate  $u_b(t)$ 

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

## Synaptic Current Dynamics

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

Differentiating 
$$I_s(t) = \sum_b I_b(t) = \sum_b w_b \int_{-\infty}^t K(t-\tau)u_b(\tau)d\tau$$

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?

$$\tau_r \frac{dv}{dt} = -v + F(I_s(t))$$

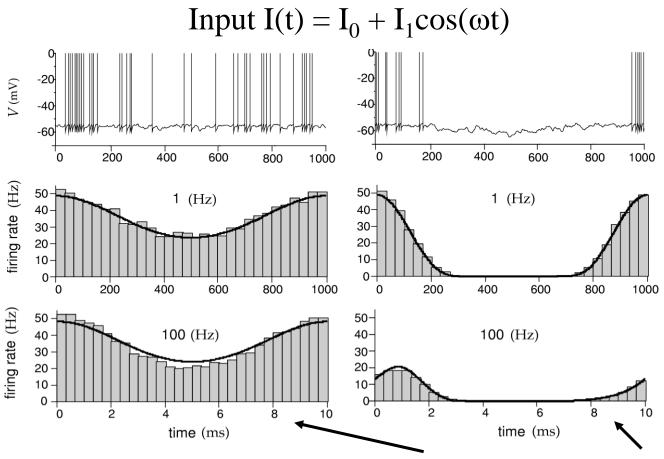
→ Looks very much like membrane dynamics equation:

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

• On-board derivations of special cases obtained from comparing  $\tau_r$  and  $\tau_s$  ...

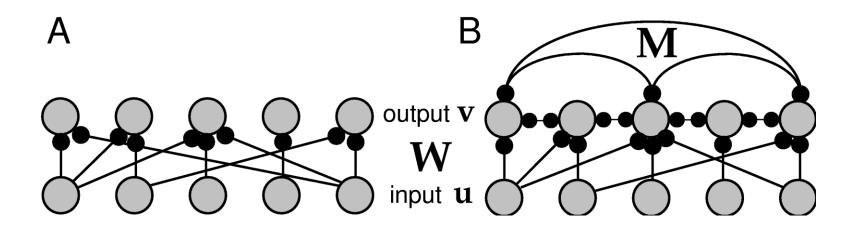
(see also pages 234-236 in the text)

## How good are the Firing Rate Models?



Firing rate model v(t) = F(I(t)) describes this well but not this case

#### Feedforward versus Recurrent Networks



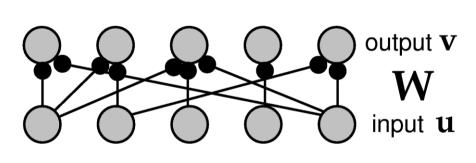
$$\tau \frac{d\mathbf{v}}{dt} = -\mathbf{v} + F(\mathbf{W}\mathbf{u} + \mathbf{M}\mathbf{v})$$

Output

Decay Input Feedback

For feedforward networks, matrix 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):  $\mathbf{v}_{ss} = \mathbf{W}\mathbf{u}$ 

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

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

$$\mathbf{u} = \begin{bmatrix} 1 \\ 2 \\ 2 \\ 2 \\ 1 \end{bmatrix}$$
 What is  $\mathbf{v}_{ss}$ ?

#### Linear Feedforward Network

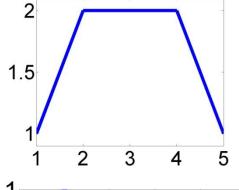
$$\mathbf{v}_{ss} = \mathbf{W}\mathbf{u} = \begin{bmatrix} 1 & 0 & 0 & 0 & -1 \\ -1 & 1 & 0 & 0 & 0 \\ 0 & -1 & 1 & 0 & 0 \\ 0 & 0 & -1 & 1 & 0 \\ 0 & 0 & 0 & -1 & 1 \\ 1 & 0 & 0 & 0 & -1 \end{bmatrix} \begin{bmatrix} 1 \\ 2 \\ 2 \\ 1 \end{bmatrix} = \begin{bmatrix} 0 \\ 1 \\ 0 \\ 0 \\ -1 \\ 0 \end{bmatrix}$$

What is the network doing?

## Linear Filtering for Edge Detection

Filter =  $\begin{bmatrix} 0 & -1 & 1 & 0 & 0 \end{bmatrix}$  (and shifted versions)

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



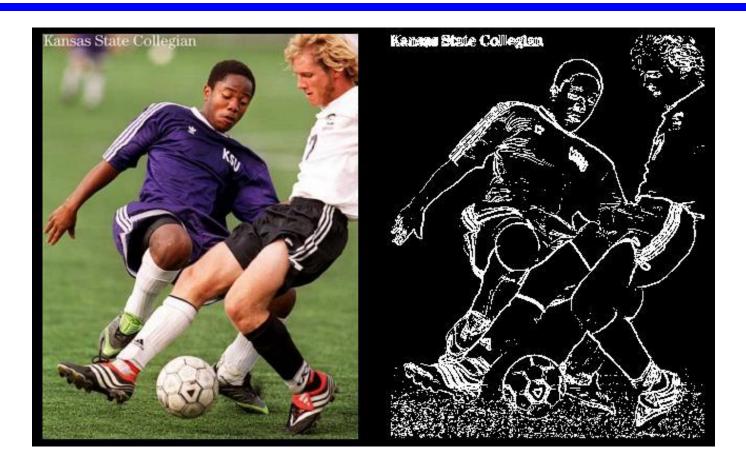
Input

Output

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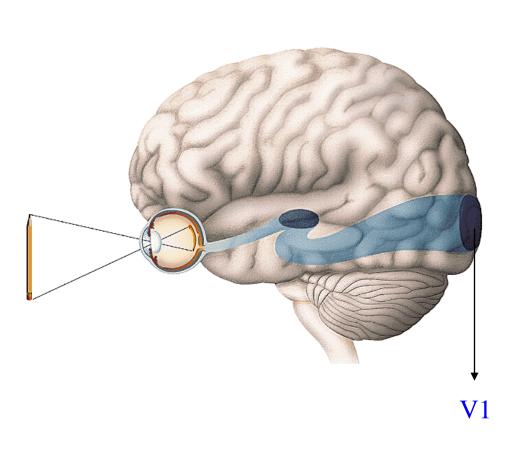
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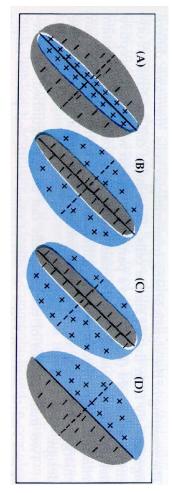
## Example of Edge Detection in a 2D Image



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

## 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!

$$[0 -1 \ 1 \ 0 \ 0] \qquad \frac{df}{dx} = \lim_{h \to 0} \frac{f(x+h) - f(x)}{h}$$
Discrete approximation  $\approx f(x+1) - f(x)$ 

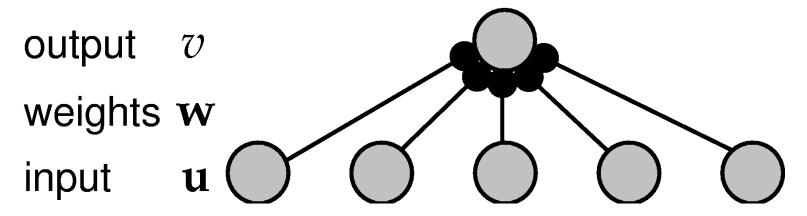
[0 1 -2 1 0] 
$$\frac{d^2 f}{dx^2} = \lim_{h \to 0} \frac{f'(x+h) - f'(x)}{h}$$
Disc. approx.  $\approx (f(x+1) - f(x)) - (f(x) - f(x-1))$ 

$$= f(x+1) - 2f(x) + f(x-1)$$

## Feedforward Networks: Example 2

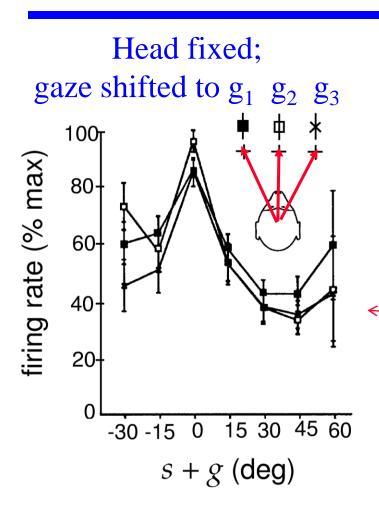
#### Coordinate Transformation

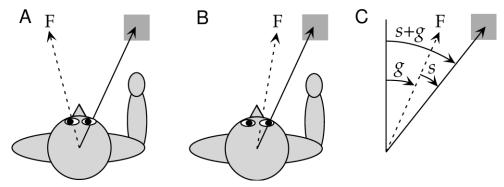
Output: Premotor Cortex Neuron with Body-Based Tuning Curves



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

## Output of Coordinate Transformation Network





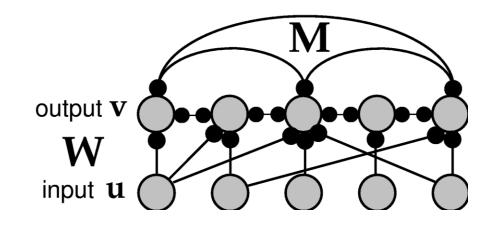
—Same tuning curve regardless of gaze angle

Premotor cortex neuron responds to stimulus location *relative to body*, not retinal image location

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(See section 7.3 in Dayan & Abbott for details)

## Linear Recurrent Networks



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

Output Decay Input Feedback

#### Next Class: Recurrent Networks

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