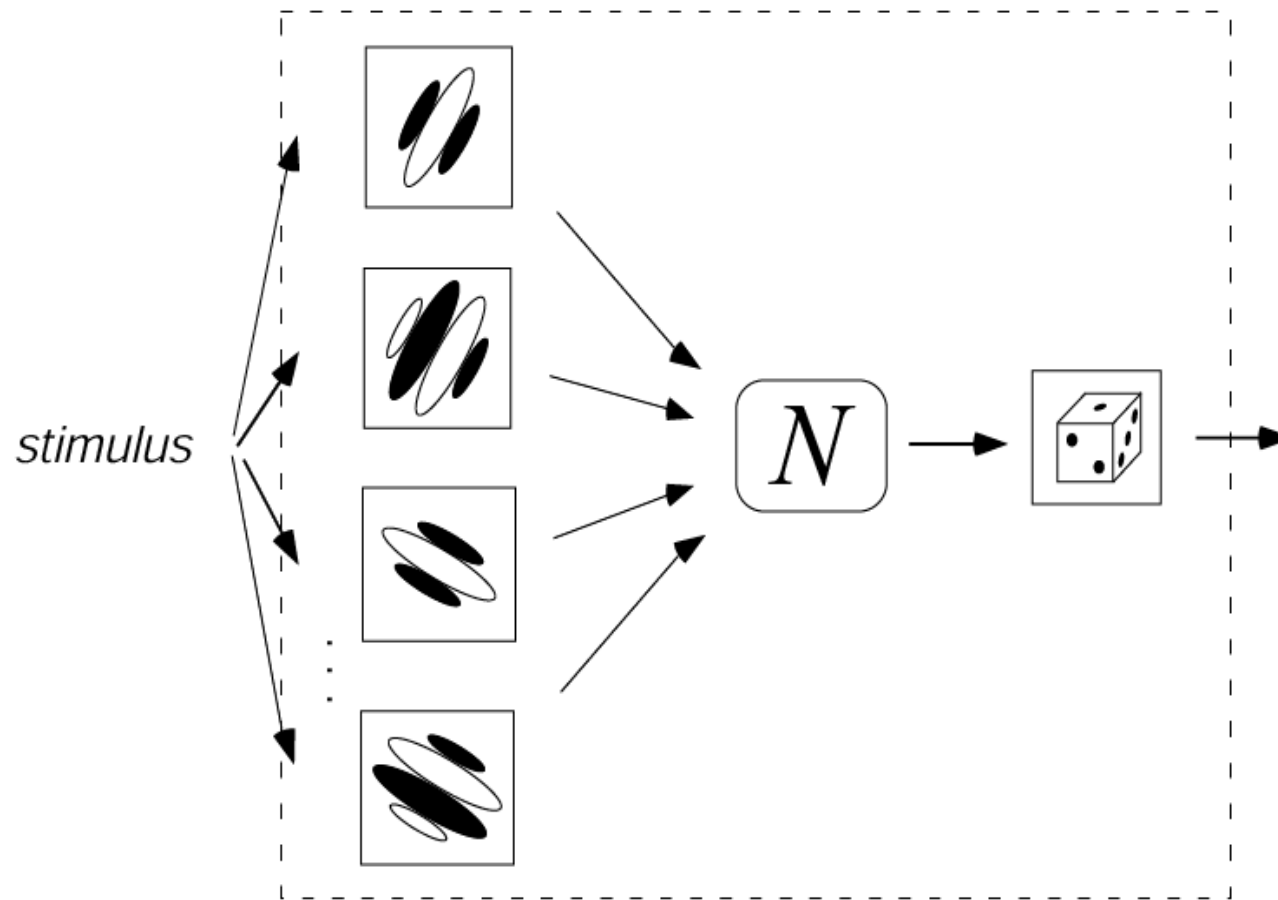


# Neural coding: Part 3

Odelia Schwartz

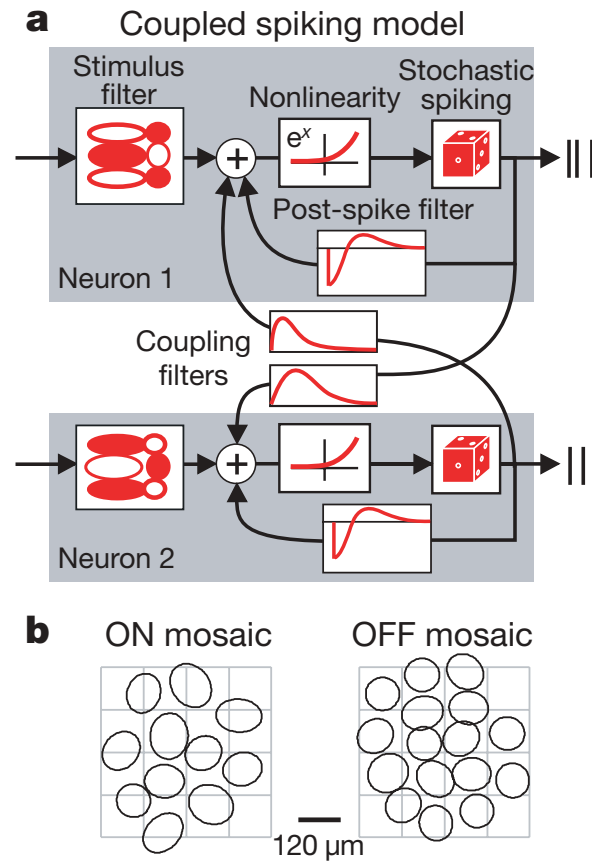
# Last time

*Generalized LNP response model*



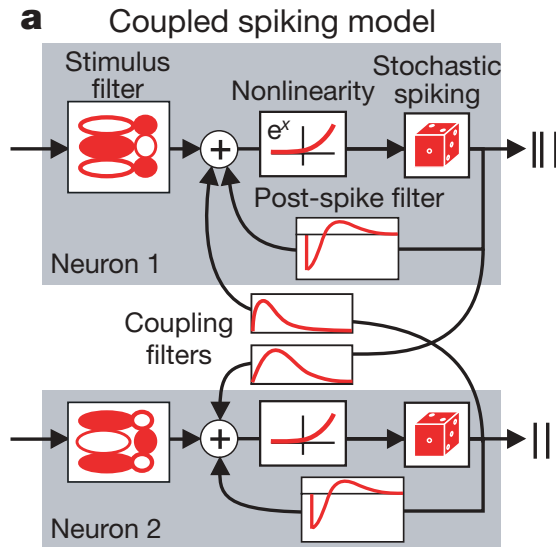
Methods paper on solving with Spike-triggered approaches:  
Schwartz, Pillow, Rust, Simoncelli 2006

# More complete visual system (e.g., retina)



Pillow et al., Nature, 2008

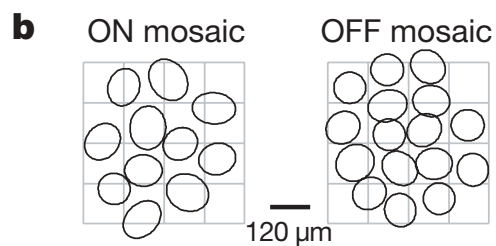
# More complete visual system (e.g., retina)



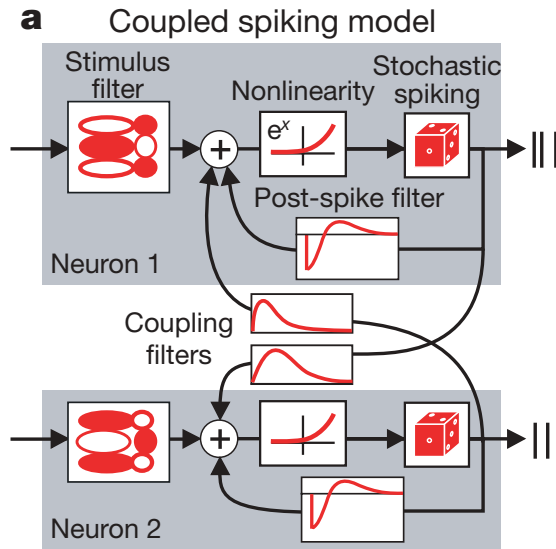
Stimulus filter: spatio-temporal light integration

Post-spike filter: Voltage-activated currents (time course of recovery after a spike)

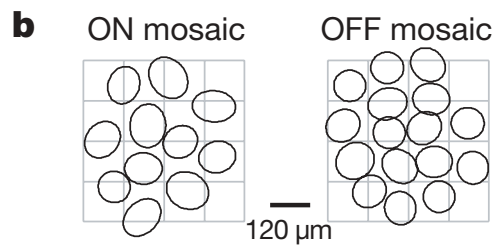
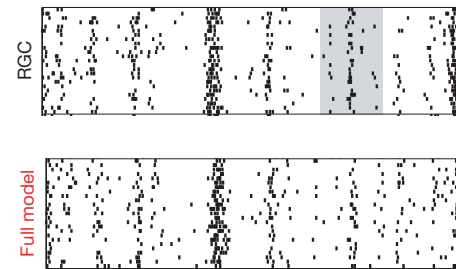
Coupling filters: e.g., synaptic interactions between cells



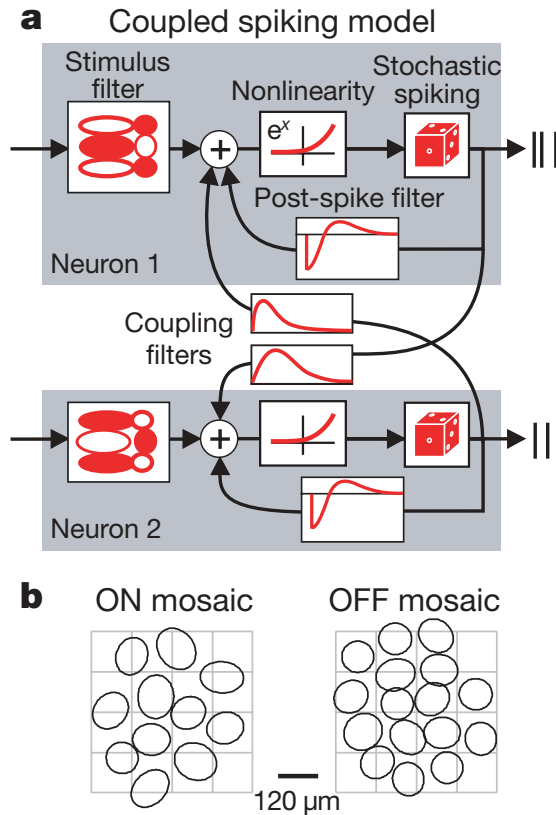
# More complete visual system (e.g., retina)



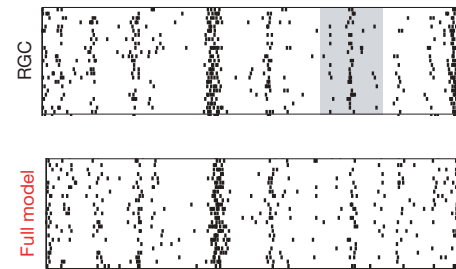
- Predict spike trains with coupled and uncoupled model



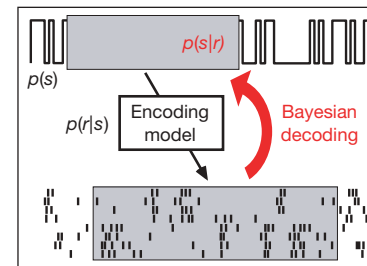
# More complete visual system (e.g., retina)



- Predict spike trains with coupled and uncoupled model



- Opposite direction: from spike train model, predict input stimuli



Pillow et al., Nature, 2008

Also used beyond vision, for instance:

Pillow et al., Nature Neuroscience 2014: Encoding and decoding in parietal cortex during sensorimotor decision-making

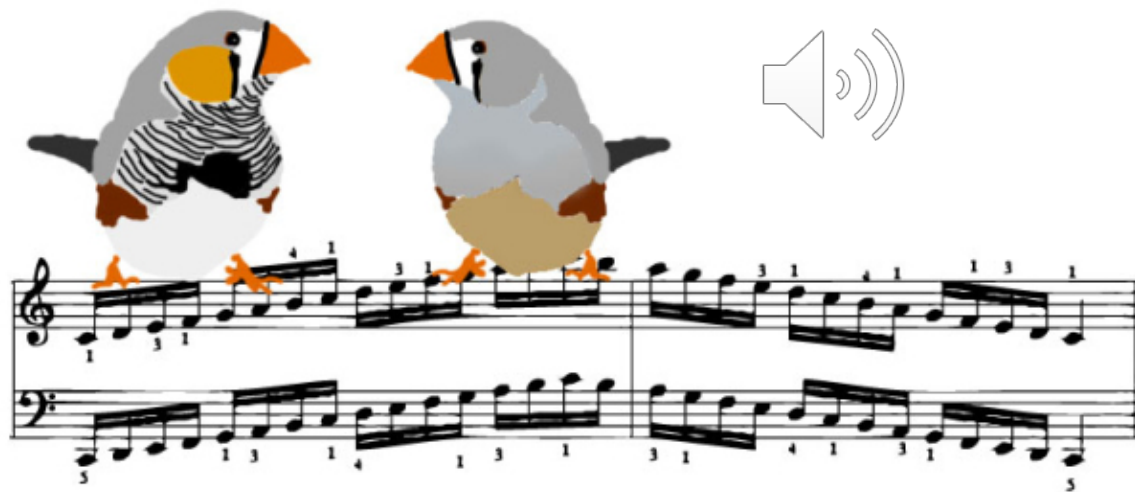
Another example  
system and coding

# Ultra Sparse Song Bird System





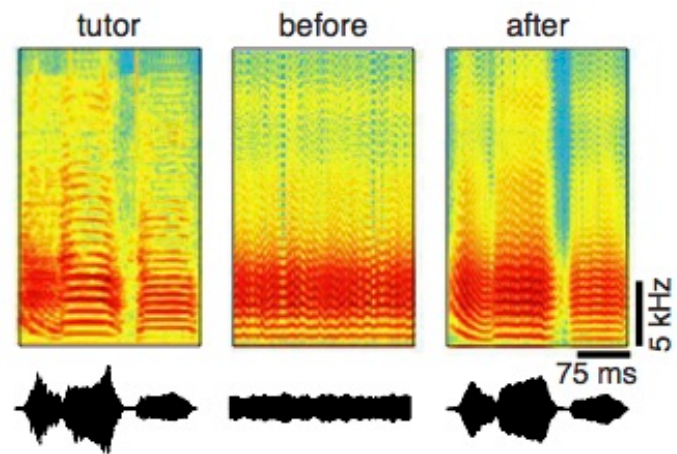
# Song before learning



# Song after learning

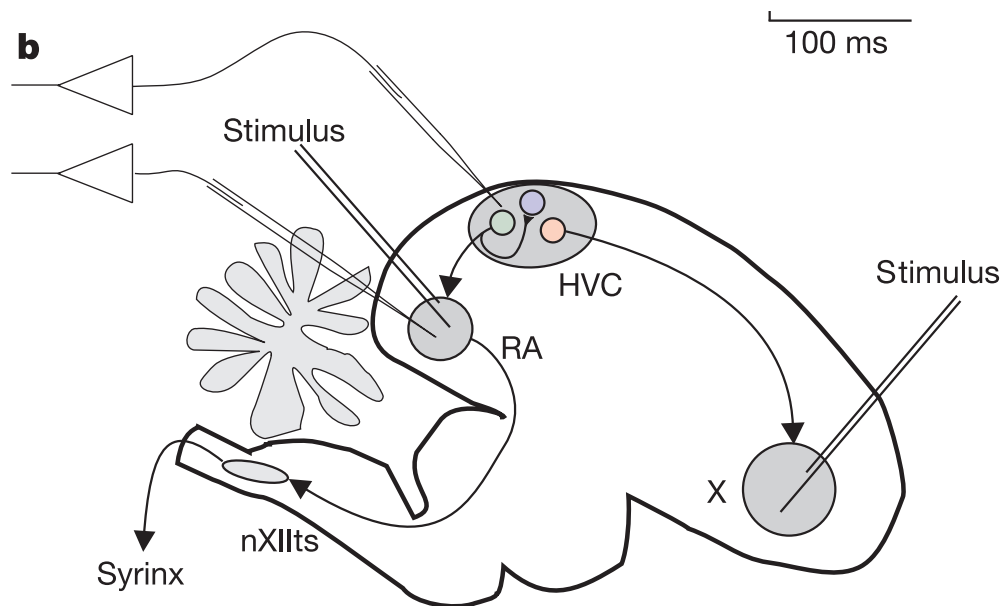


# Songbird



Fiete et al. 2009 review paper

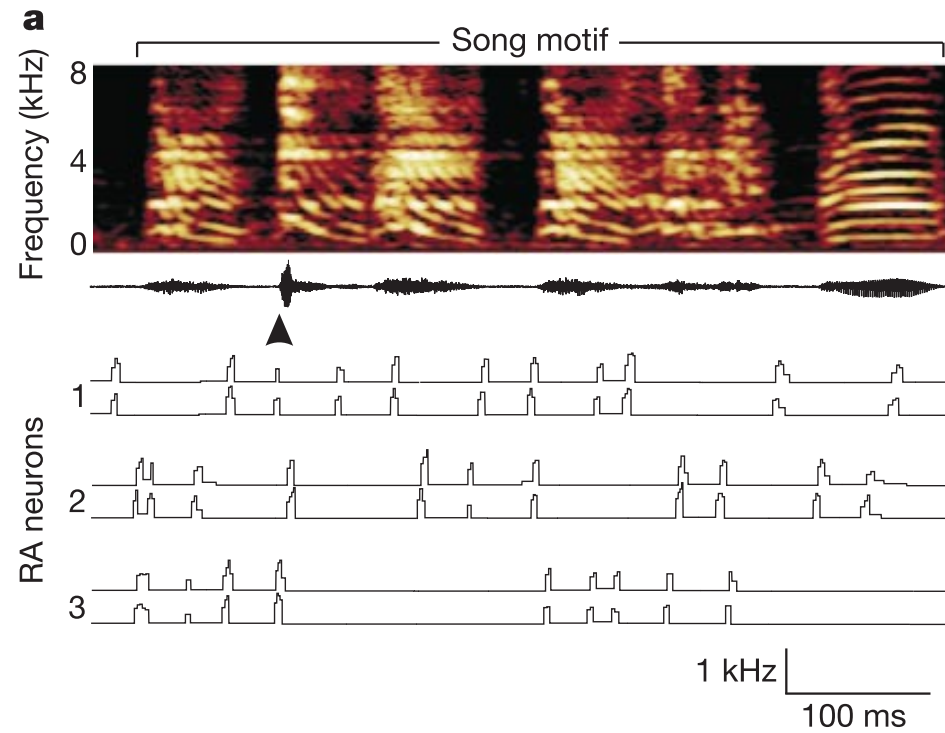
# Songbird



Hahnloser et al. 2002, Nature

HVC neurons connect to RA neurons, which control muscles

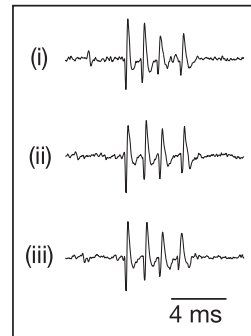
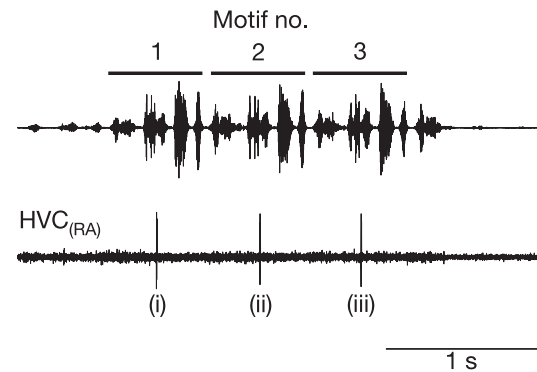
# Songbird



Hahnloser et al. 2002, Nature

RA neurons fire at multiple times during a song

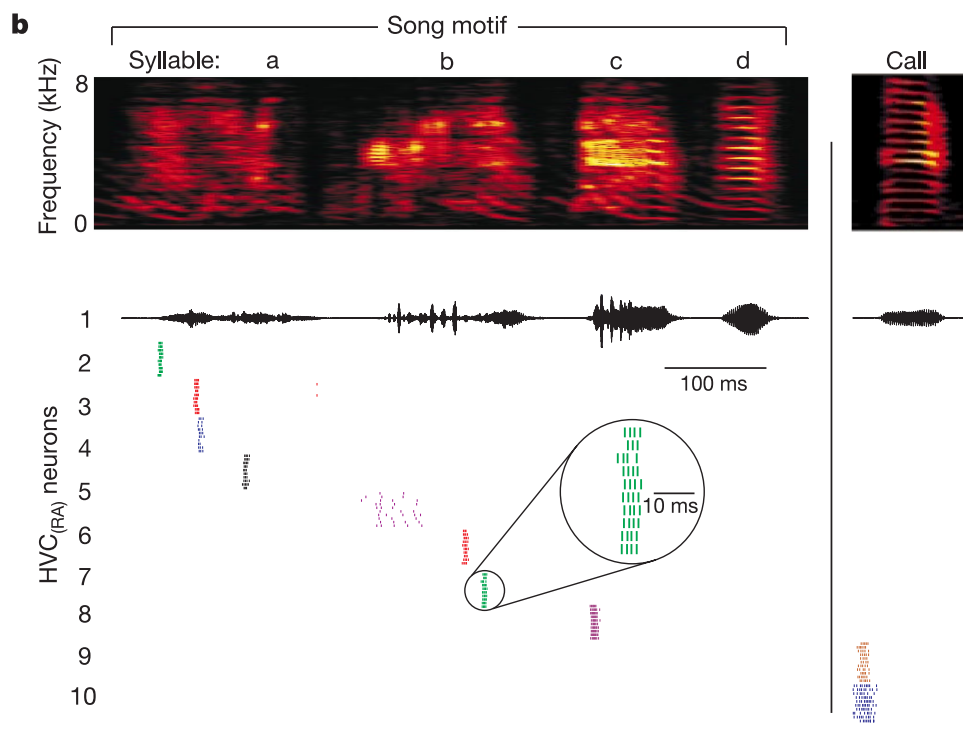
# Songbird



Hahnloser et al. 2002, Nature

HVC neurons burst reliably at a single precise time in the song or call!

# Songbird



Hahnloser et al. 2002, Nature

HVC neurons burst reliably at a single precise time in the song or call

# Songbird model

Why ultra sparse responses in  
the songbird??



# Songbird model



Why ultra sparse responses in the songbird??

“Intuitively ... minimizing interference between different synapses during learning ... In this paper we make the intuitive argument more concrete.”

Fiete et al. 2004: Temporal Sparseness of the Premotor Drive Is Important for Rapid Learning in a Neural Network Model of Birdsong  
Also: Doya and Sejnowski 1995 (**considered sparseness in a model before known**)

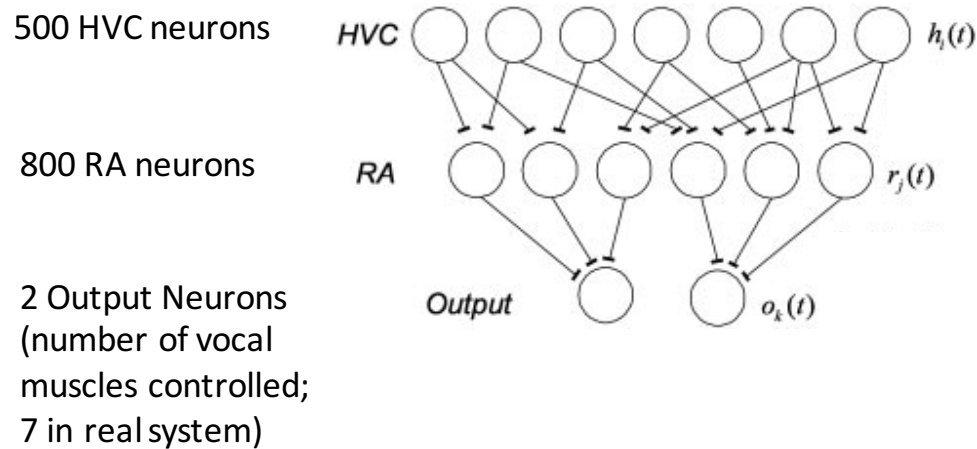
# Songbird model



Why ultra sparse responses in the songbird??

We'll look at modeling work, and also introduce network modeling approaches...

# Songbird model



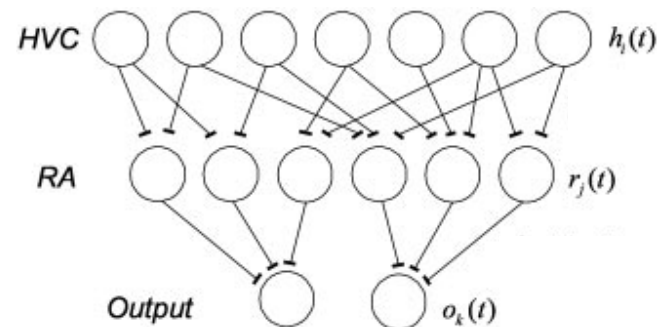
Fiete et al. 2004: Temporal Sparseness of the Premotor Drive  
Is Important for Rapid Learning in a Neural Network Model of Birdsong

# Songbird model

500 HVC neurons

800 RA neurons

2 Output Neurons  
(number of vocal  
muscles controlled;  
7 in real system)



**Input known** (binary burst pulses chosen randomly of either 1, 2, 4 or 8 bursts per motif)

**Hidden**

**Desired output known**

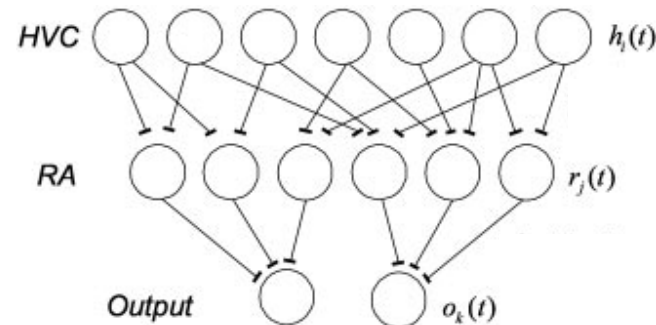
Fiete et al. 2004: Temporal Sparseness of the Premotor Drive Is Important for Rapid Learning in a Neural Network Model of Birdsong

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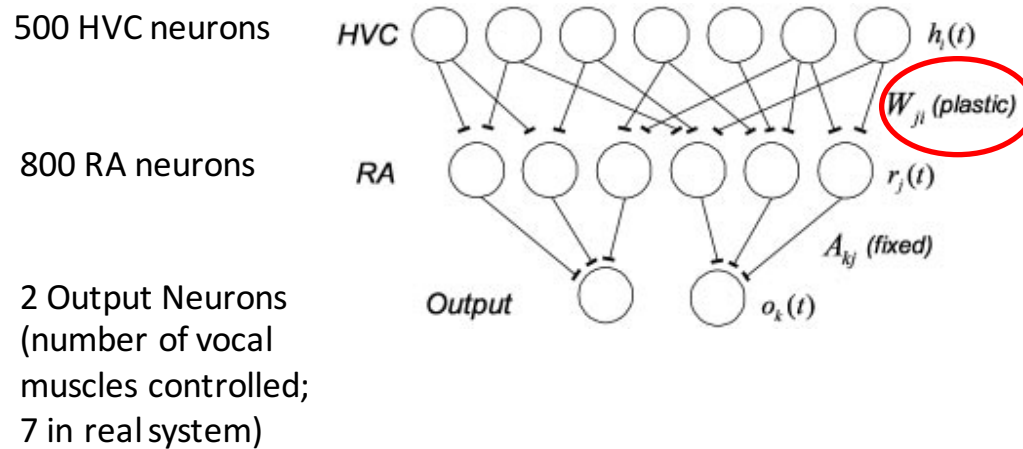
**Hidden**

**Desired output known**

**Goal: minimize error between network output and desired output**

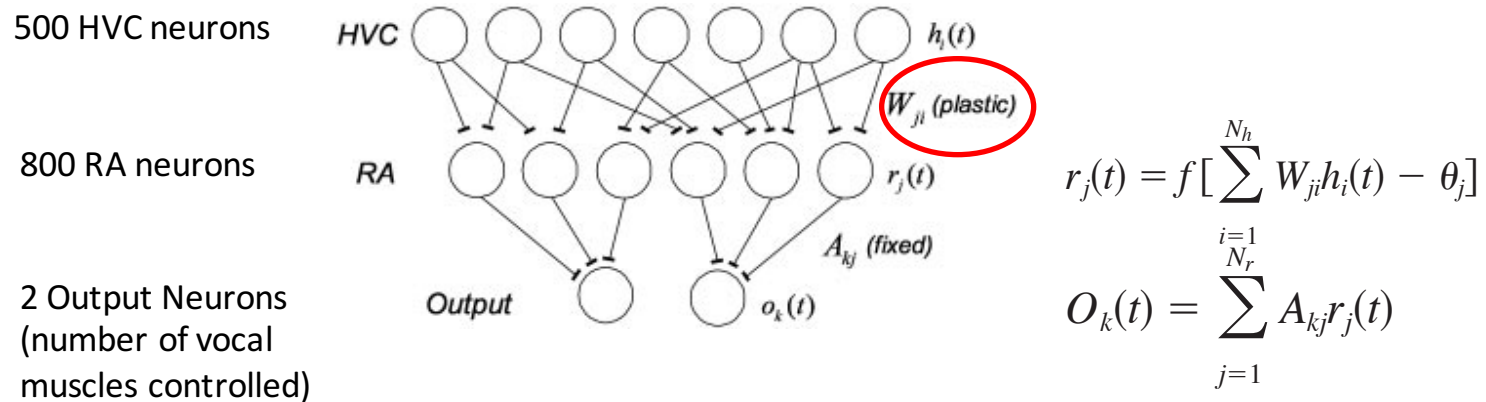
Fiete et al. 2004: Temporal Sparseness of the Premotor Drive Is Important for Rapid Learning in a Neural Network Model of Birdsong

# Songbird model



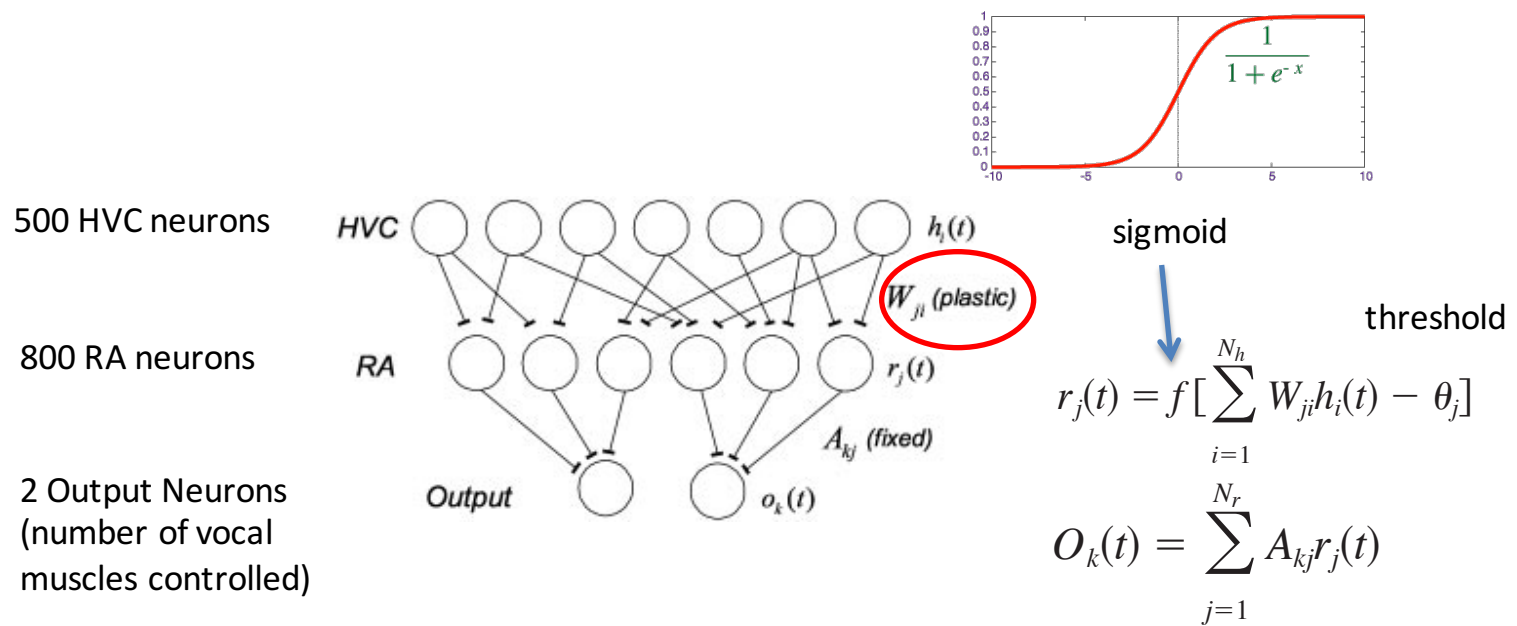
Fiete et al. 2004: Temporal Sparseness of the Premotor Drive  
Is Important for Rapid Learning in a Neural Network Model of Birdsong

# Songbird model



Fiete et al. 2004: Temporal Sparseness of the Premotor Drive  
Is Important for Rapid Learning in a Neural Network Model of Birdsong

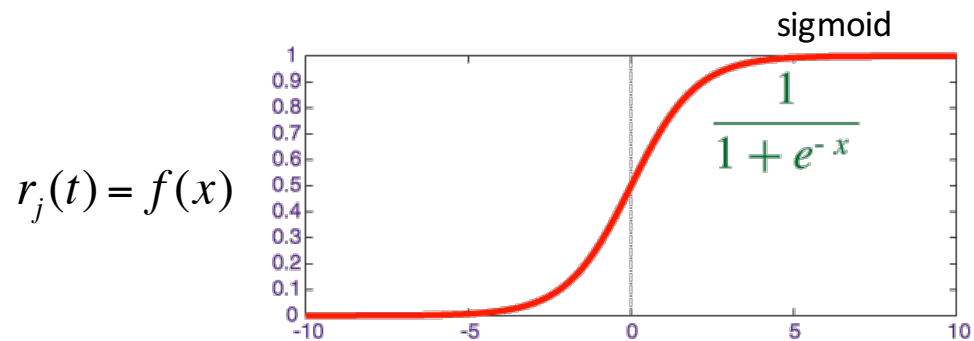
# Songbird model



Fiete et al. 2004: Temporal Sparseness of the Premotor Drive  
Is Important for Rapid Learning in a Neural Network Model of Birdsong



# Sigmoid curve

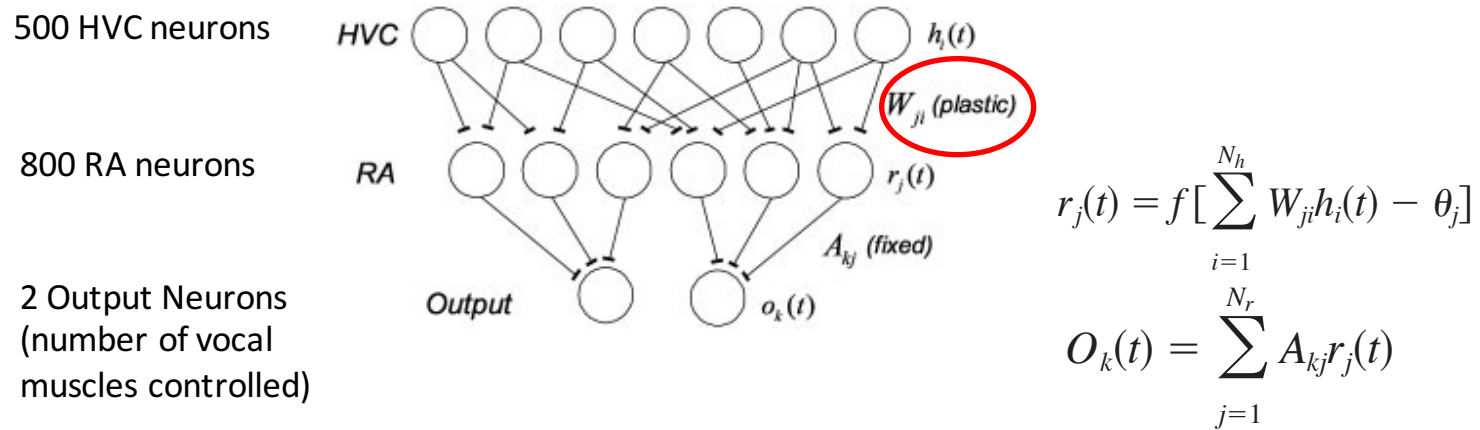


$$x = \sum_{i=1}^{N_h} w_{ji} h_i(t) - \Phi_j$$

$$r_j(t) = f\left[\sum_{i=1}^{N_h} W_{ji} h_i(t) - \theta_j\right]$$

Fiete et al. 2004: Temporal Sparseness of the Premotor Drive  
Is Important for Rapid Learning in a Neural Network Model of Birdsong

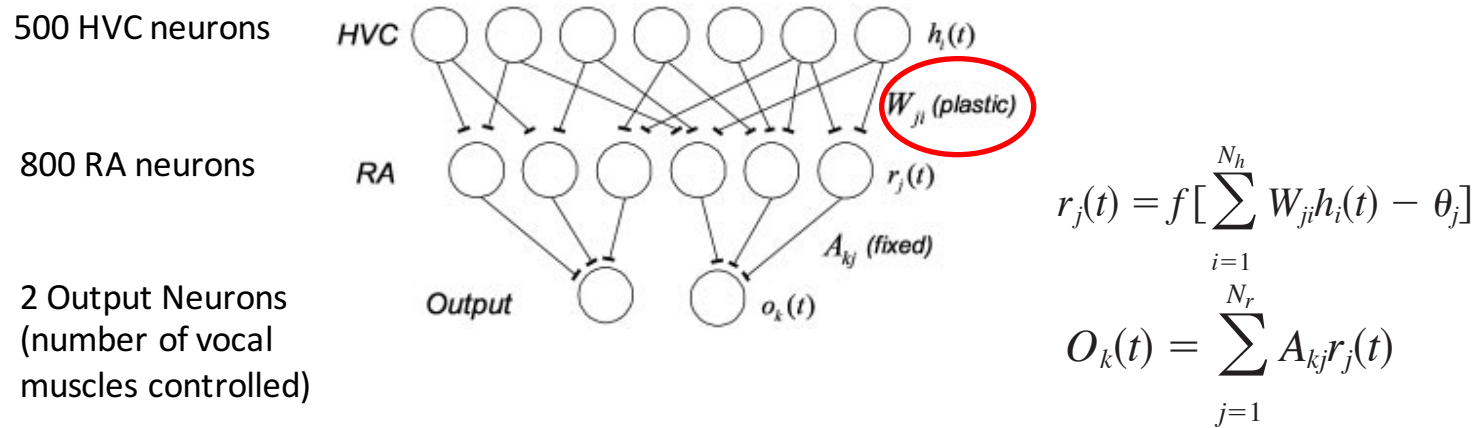
# Songbird model



**We know inputs and desired outputs**

Back Propagation: 1970s; Rumelhart, Williams, Hinton, Nature, 1986; and prominent again today in deep networks

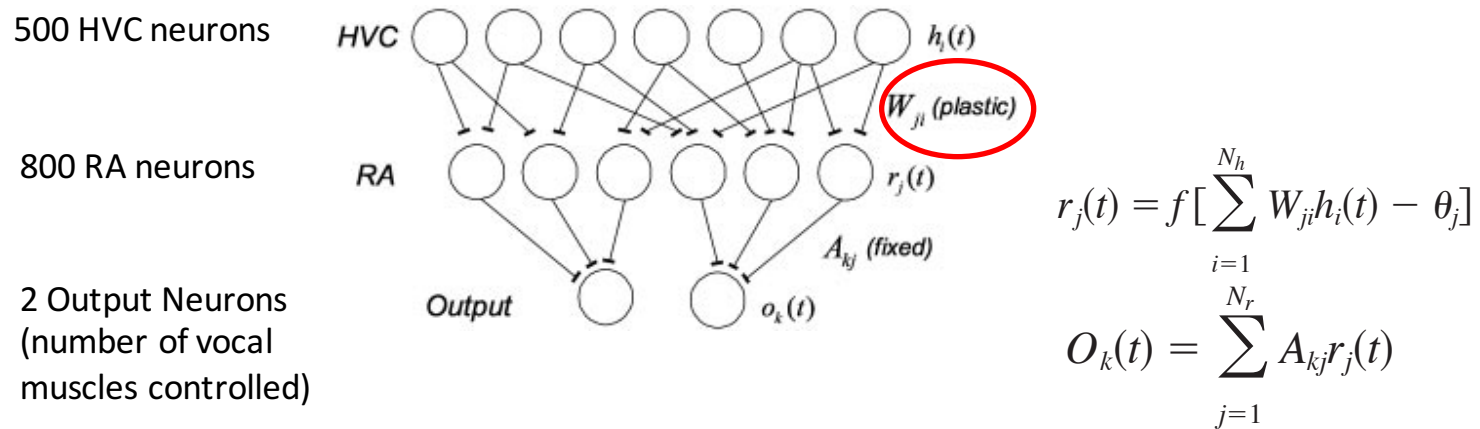
# Songbird model



**Back propagation:**  
Compare outputs with correct answer to get error

Back Propagation: 1970s; Rumelhart, Williams, Hinton, Nature, 1986; and prominent again today in deep networks

# Songbird model

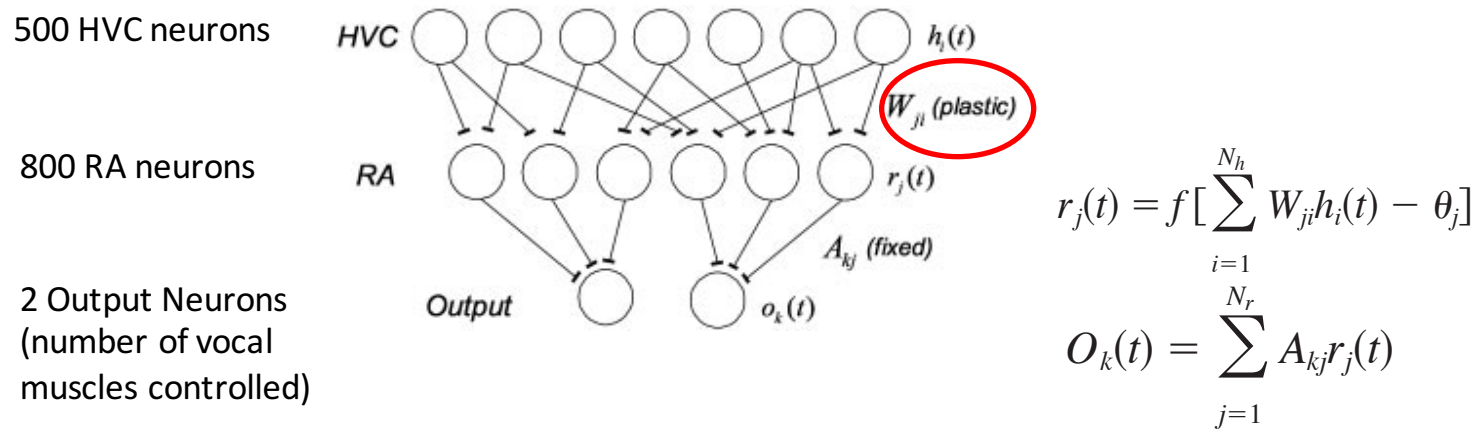


## Back propagation:

Compare outputs with correct answer to get error  
What kind of machine learning approach is this??

Back Propagation: 1970s; Rumelhart, Williams, Hinton, Nature, 1986; and prominent again today in deep networks

# Songbird model



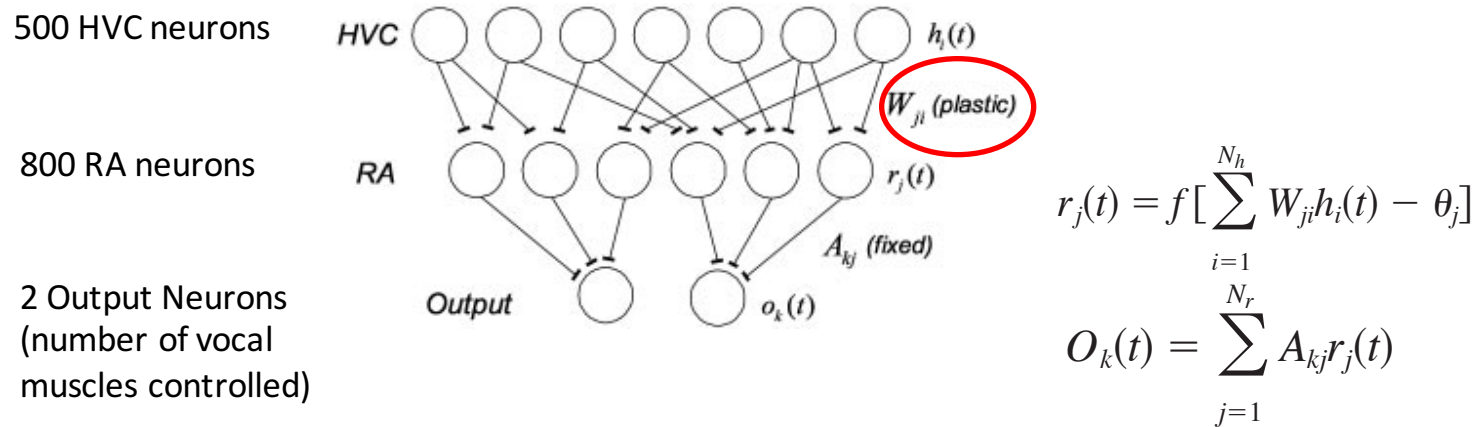
## Back propagation:

Compare outputs with correct answer to get error

What kind of machine learning approach is this?? Supervised learning

Back Propagation: 1970s; Rumelhart, Williams, Hinton, Nature, 1986; and prominent again today in deep networks

# Songbird model



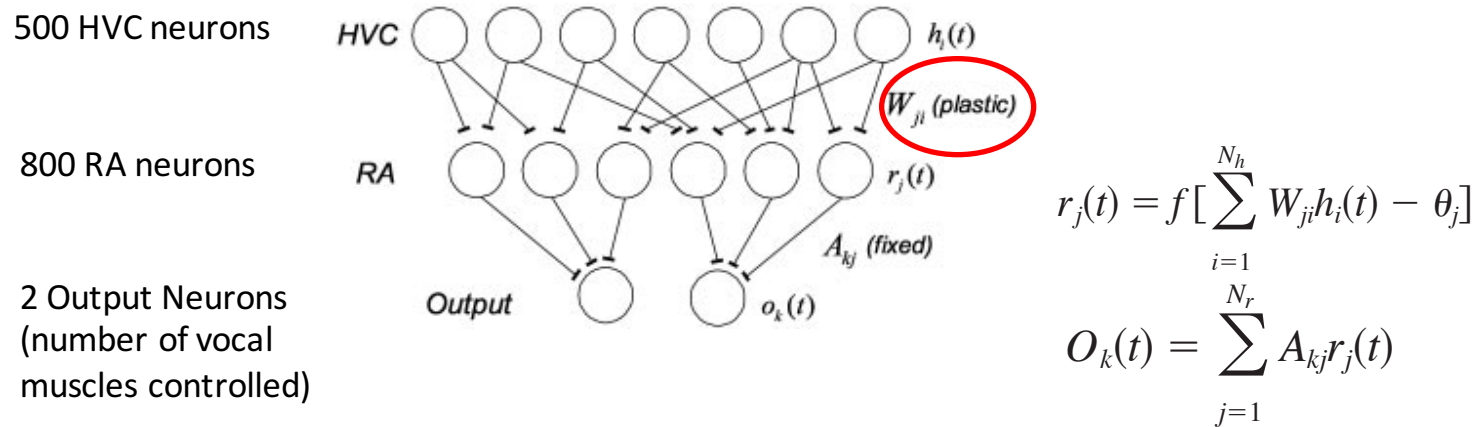
## Back propagation:

Compare outputs with correct answer to get error

(What other approach could be relevant here??)

Back Propagation: 1970s; Rumelhart, Williams, Hinton, Nature, 1986; and prominent again today in deep networks

# Songbird model



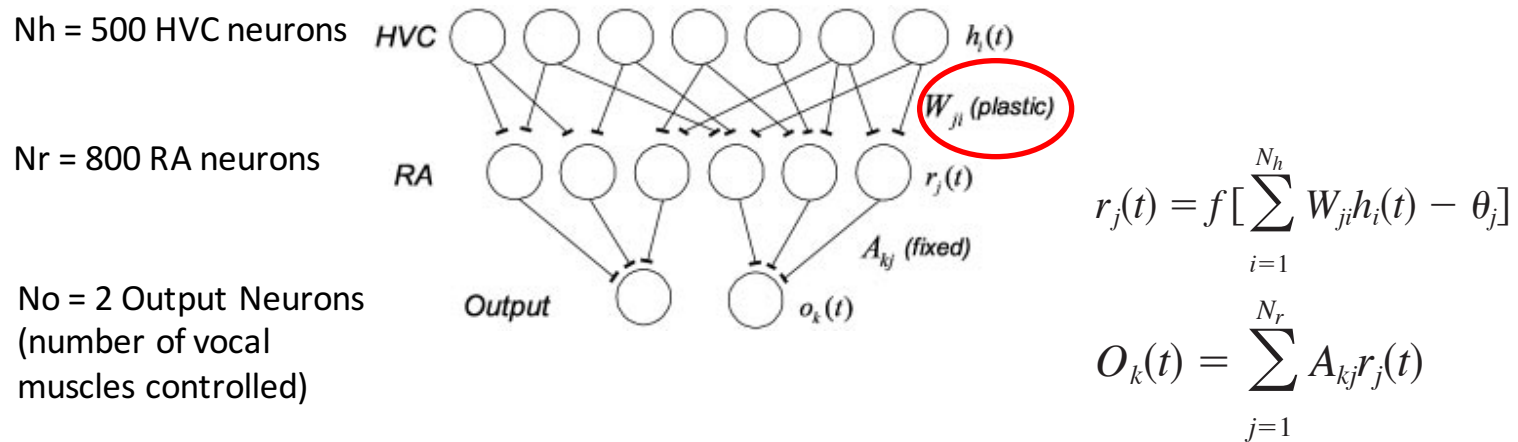
## Back propagation:

Compare outputs with correct answer to get error

(What other approach could be relevant here?? Reinforcement learning)

Back Propagation: 1970s; Rumelhart, Williams, Hinton, Nature, 1986; and prominent again today in deep networks

# Songbird model



## Back propagation:

- Compare current outputs with correct desired answer to get error
- Update weights by small step down gradient

Back Propagation: 1970s; Rumelhart, Williams, Hinton, Nature, 1986; and prominent again today in deep networks



# Back propagation

Error:

$$C = \int_0^T dt \sum_{k=1}^{N_o} [d_k(t) - o_k(t)]^2$$

Desired minus actual outputs

$$r_j(t) = f \left[ \sum_{i=1}^{N_h} W_{ji} h_i(t) - \theta_j \right]$$

Back Propagation Gradient descent:

$$\Delta W_{ji} = -\eta \frac{\partial C}{\partial W_{ji}} = \eta \int_0^T dt \sum_{k=1}^{N_o} 2[d_k(t) - o_k(t)] A_{kj} f'_j h_i$$

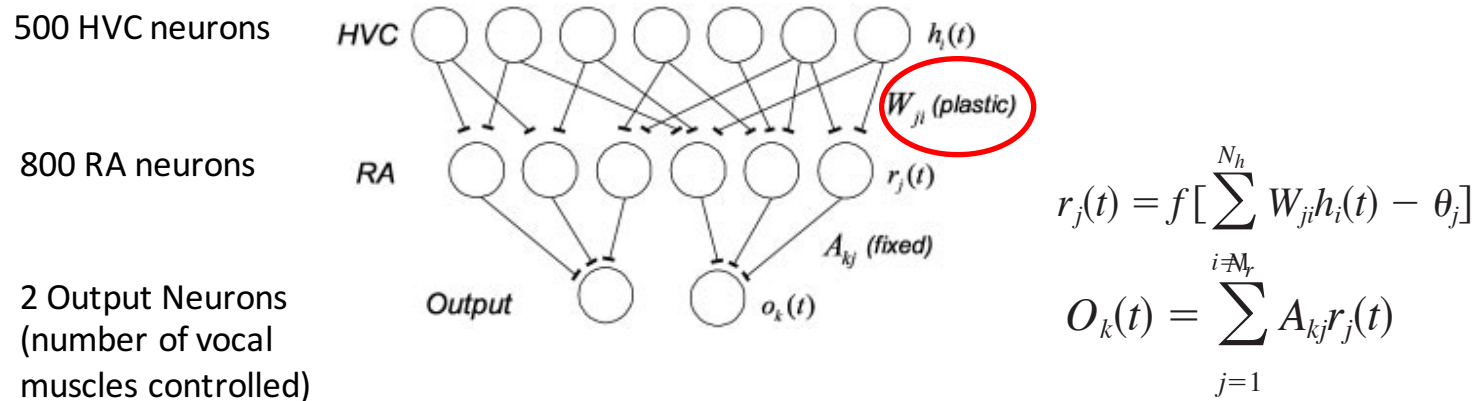
Learning rate

Derivative of RA neuron  $r_j$   
with respect to weights

Back Propagation: 1970s; Rumelhart, Williams, Hinton,  
Nature, 1986; and prominent again today in deep networks

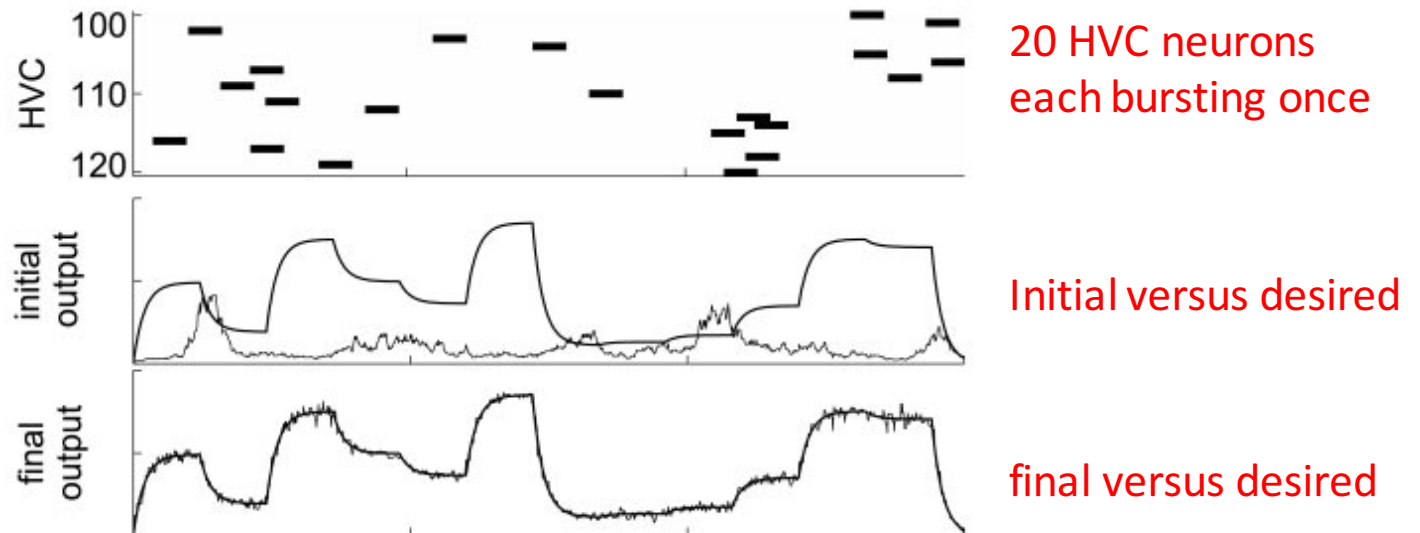
# Songbird model

Do sparse HVC responses help learning??



Fiete et al. 2004: Temporal Sparseness of the Premotor Drive  
Is Important for Rapid Learning in a Neural Network Model of Birdsong

# Songbird model



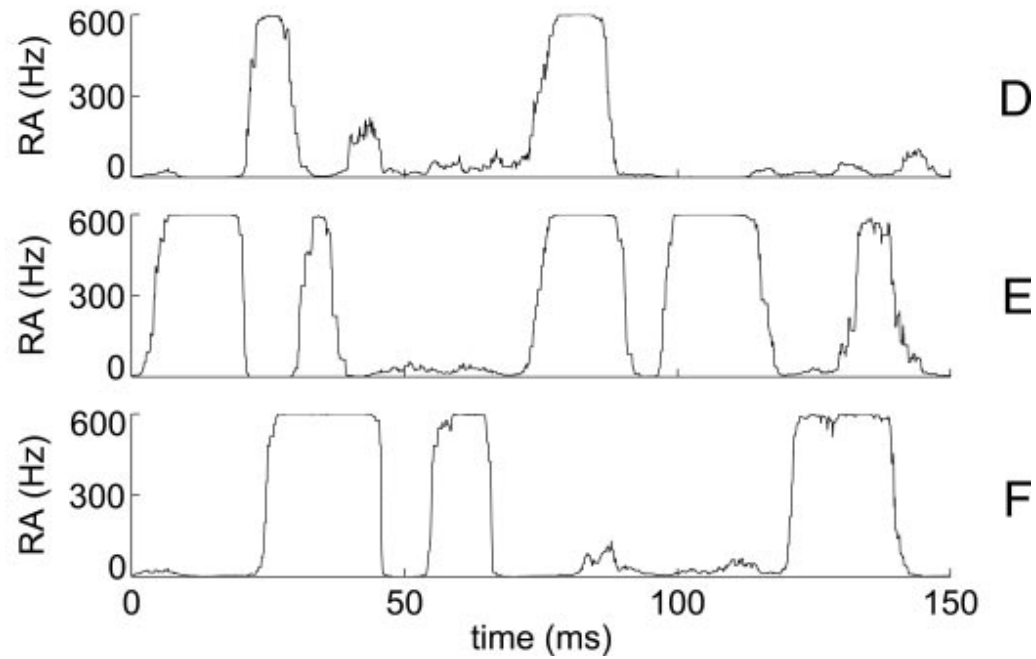
Top: HVC units; middle: initial network output; and  
bottom: final network output matching desired output  
for one of the two output units

output units

Fiete et al. 2004: Temporal Sparseness of the Premotor Drive

Is Important for Rapid Learning in a Neural Network Model of Birdsong

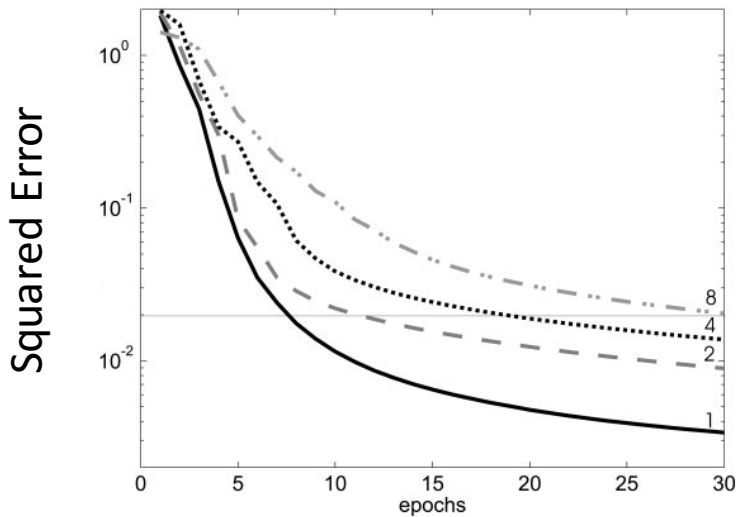
# Songbird model



3 RA units after learning

Fiete et al. 2004: Temporal Sparseness of the Premotor Drive Is Important for Rapid Learning in a Neural Network Model of Birdsong

# Songbird model

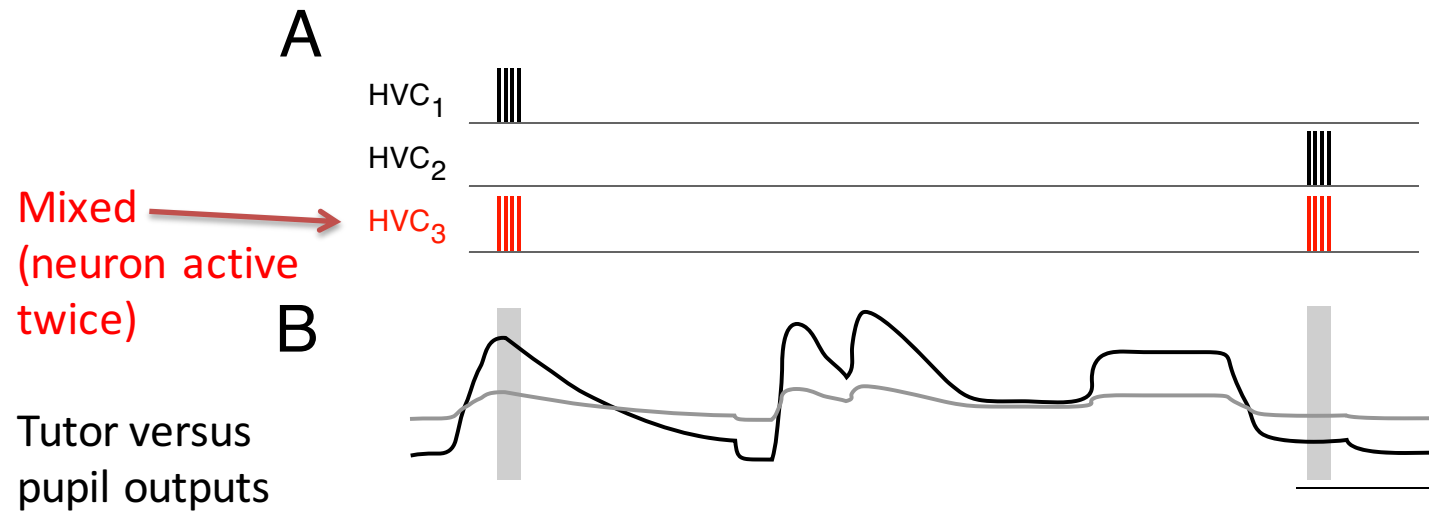


Each line plot: Varying number of bursts per motif of simulated HVC neurons.  
Lowest error for 1 burst per motif.

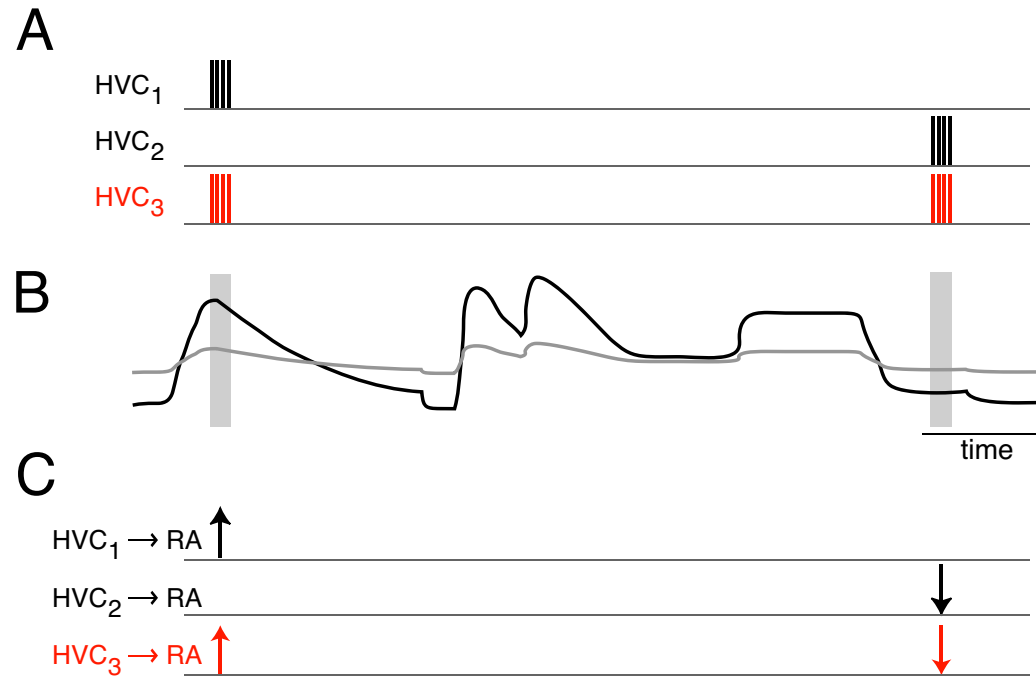
Most sparse

Fiete et al. 2004: Temporal Sparseness of the Premotor Drive Is Important for Rapid Learning in a Neural Network Model of Birdsong

# Songbird model



# Songbird model

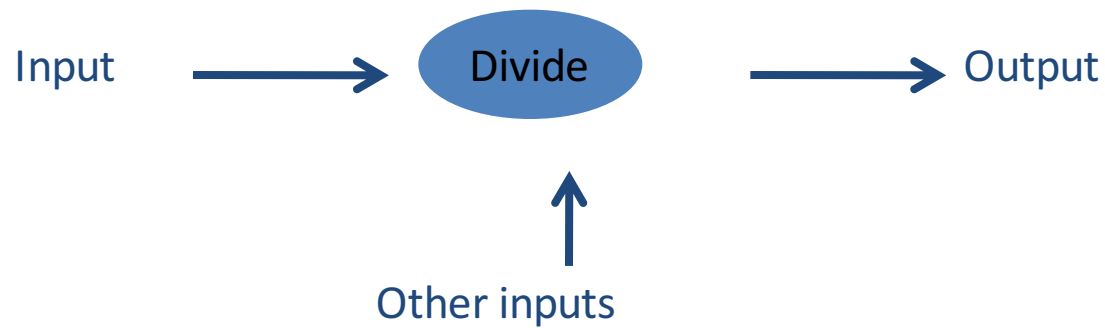


Synapse should be strengthened and weakened -> Conflicting demands causes slowdown of learning

Canonical computations in the brain??

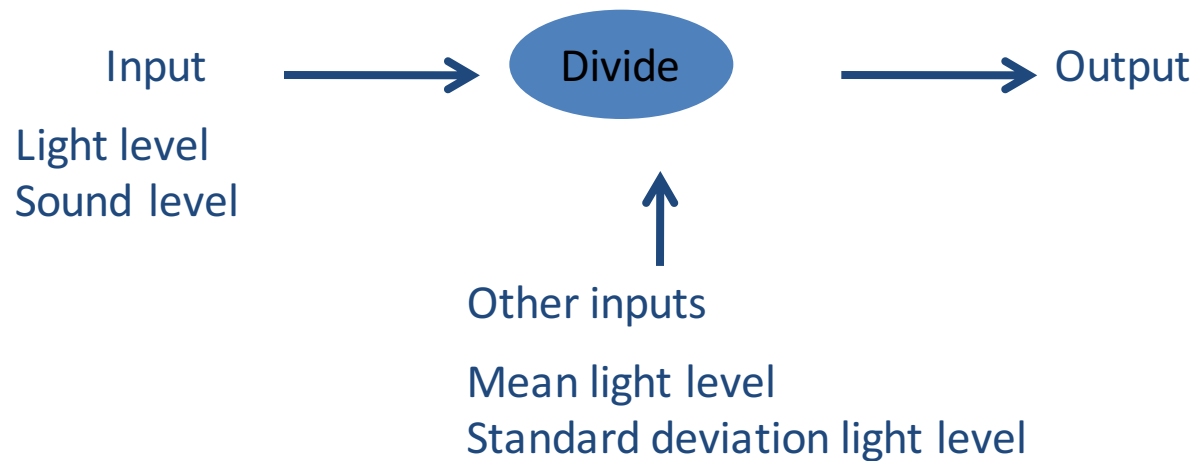


# Divisive normalization model



- **Descriptive neural model**
- Canonical computation (Carandini, Heeger, Nature Reviews, 2012)
- Has mechanistic and interpretive versions
- Related to gain control in engineering

# Divisive normalization model



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# Divisive normalization model

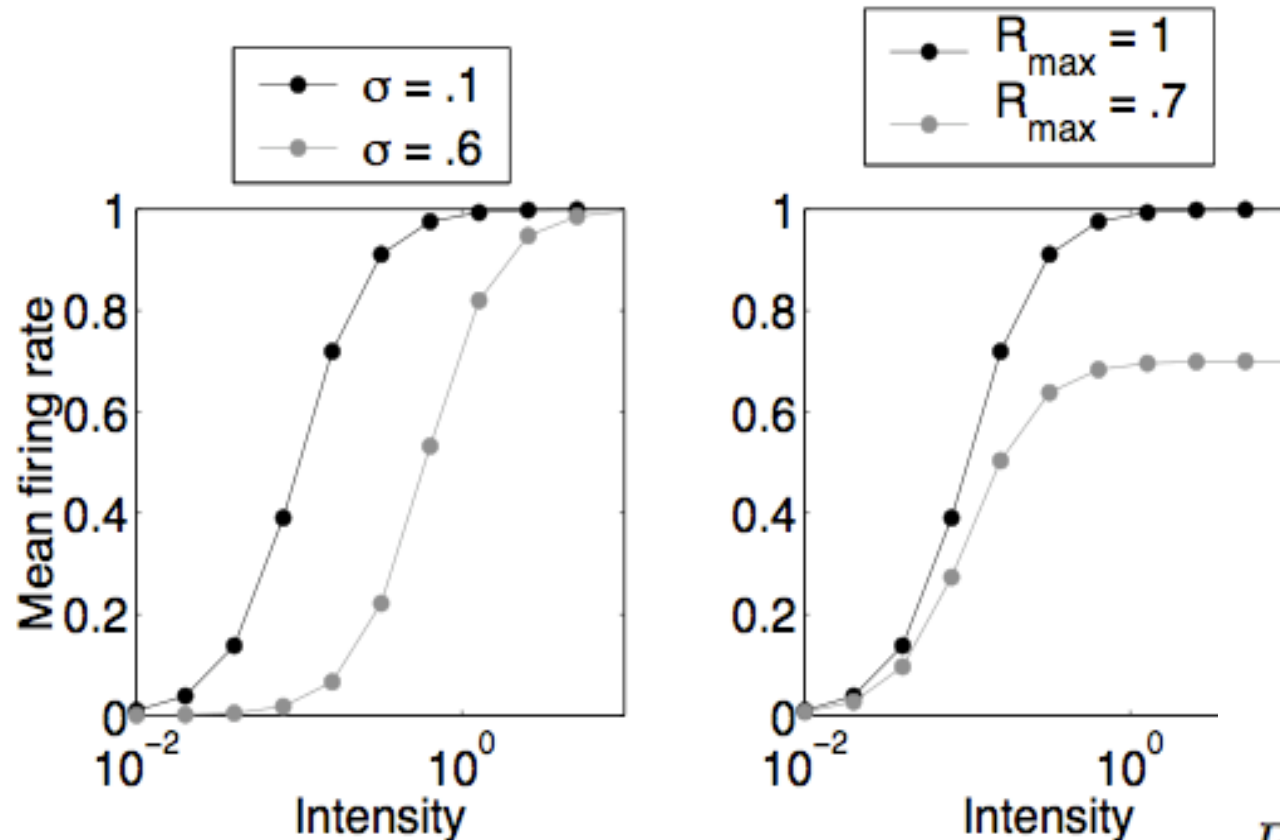
Simple version of **descriptive** model:

$$R = \frac{R_{max}K^2}{K^2 + \sigma^2}$$

K corresponds to illumination, contrast,  
sound intensity, etc.

# Divisive normalization model

Simple version of **descriptive** model:

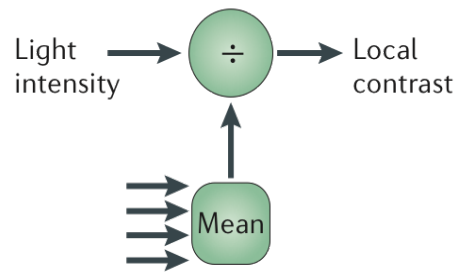


$$R = \frac{R_{max}K^2}{K^2 + \sigma^2}$$

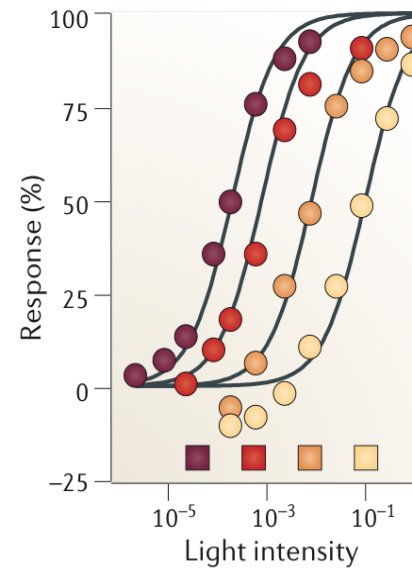
Figure 1.3. Behavior of Naka-Rushton equation. Left, The Naka-Rushton equation for a constant  $R_{max} = 1$  and variable  $\sigma$ . Note that higher values of  $\sigma$  shift the response curve to the right on a log axis. Right, The Naka-Rushton equation for a constant  $\sigma = .1$  and variable  $R_{max}$ . Note that lower values of  $R_{max}$  reduce the saturation level of the response curve.

# Example: light adaptation

a



b



$$R = \frac{R_{max}K^2}{K^2 + \sigma^2}$$

Light adaptation to mean intensity in the retina

(in figure: turtle cone photoreceptor)

Carandini and Heeger, Nature Review Neuroscience, 2012

# Example: primary visual cortex

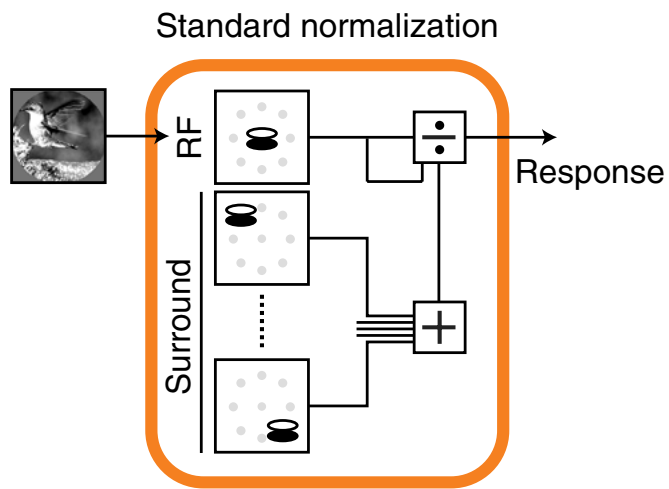
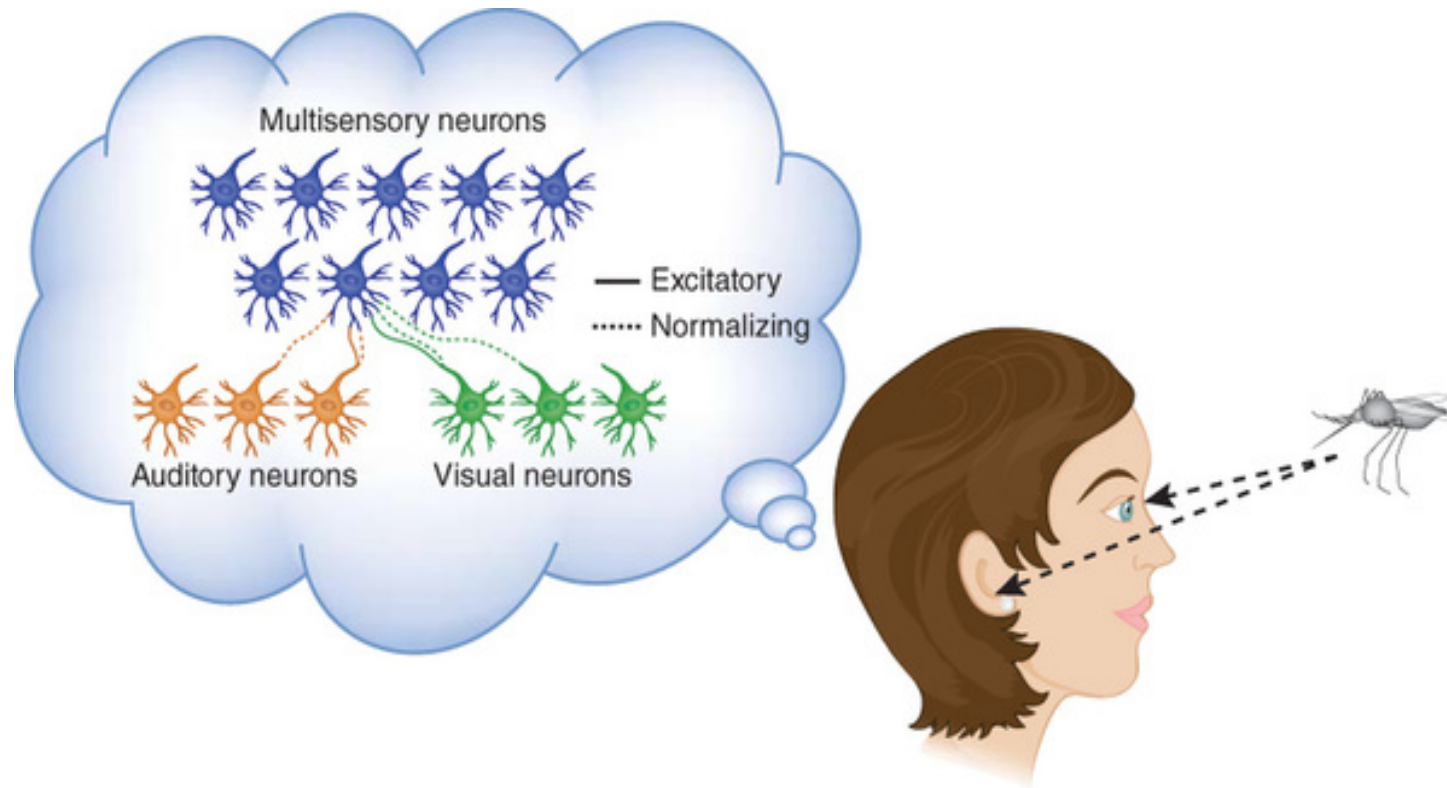


Figure from:  
Cagli, Kohn, Schwartz, Nature Neuroscience 2015

# Example: multisensory integration

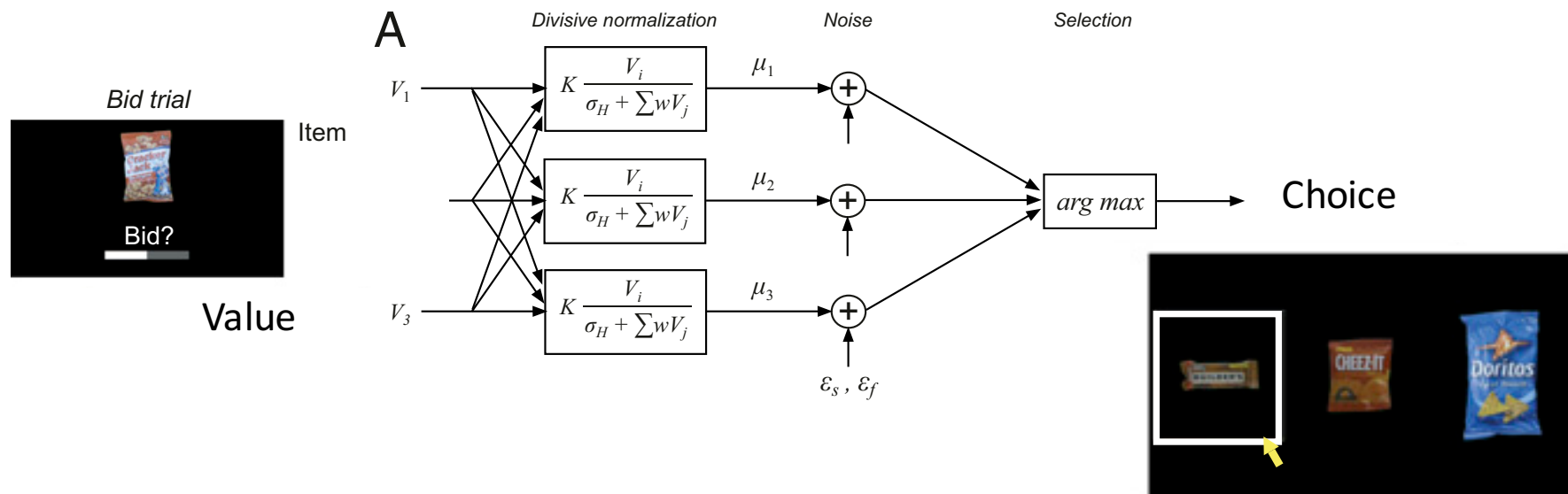


Multisensory integration (eg, can explain change in neural responses with cue reliability)

Ohshiro, Angelaki, DeAngelis, Nature Neuroscience 2011

Figure from Churchland News and Views.

# Example: decision making



“Context-dependent choice behavior is of particular interest in economics because it violates one of the fundamental assumptions of many rational-choice theories, namely, that decisions reflect absolute valuations assigned to individual options” .. Distractors can reduce or even reverse choice“

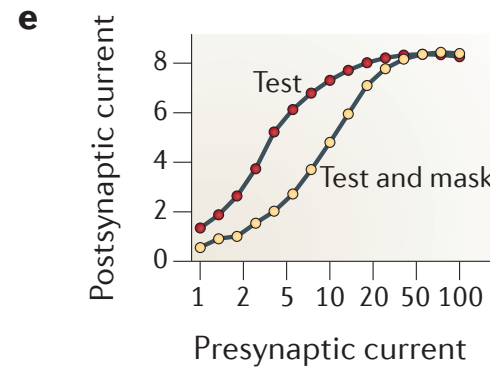
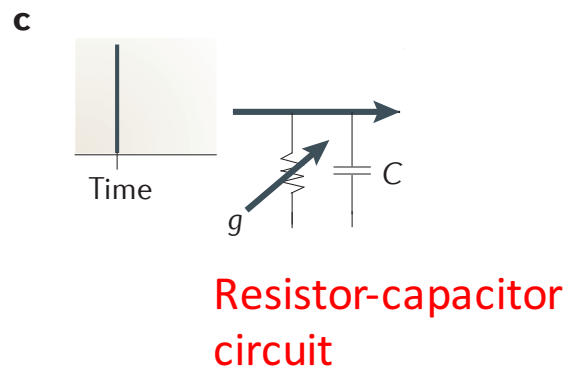
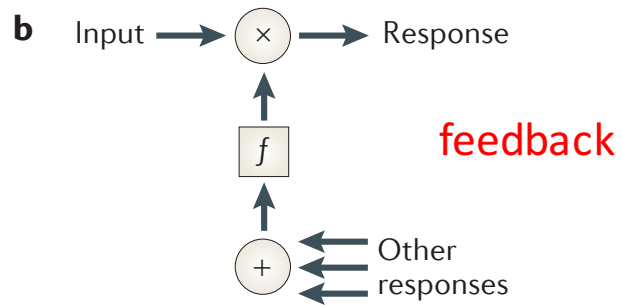
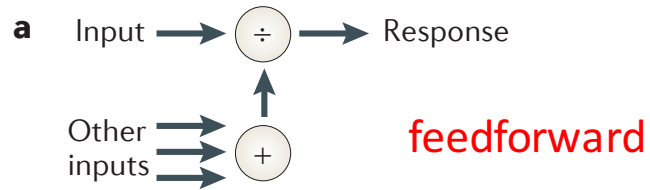
Louie, Khaw and Glimcher, PNAS 2013: Normalization is a general neural mechanism for context-dependent decision making



# Alterations in Divisive Normalization?

- Rosenberg, Patterson, Angelaki, PNAS 2015: A computational perspective on autism
- Tibber MS, et al. (2013) Visual surround suppression in schizophrenia. *Front Psychol* 4:88.
- Betts LR, Taylor CP, Sekuler AB, Bennett PJ (2005) Aging reduces center-surround antagonism in visual motion processing. *Neuron* 45(3):361–366

# Mechanism of divisive normalization model



**Synaptic depression**