

# NEPR 208 Lecture 3 Sensory Encoding

## Stephen Baccus

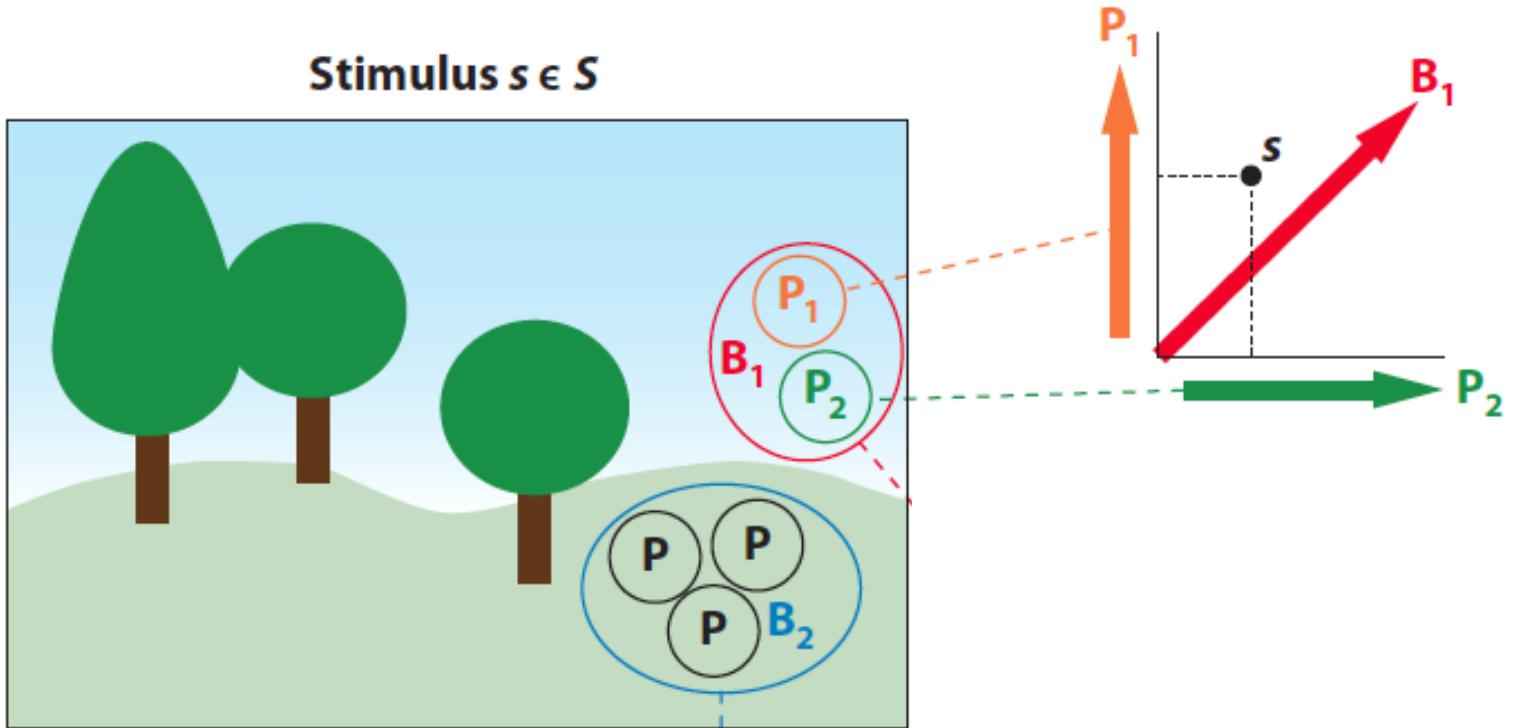
How does the nervous system represent sensory information?  
What stimuli drive neurons, let's call them sensory 'features'?

How are mechanisms used to construct a sensory representation?  
How can a neural code be decoded?  
How do properties of sensory neurons influence behavior?

Why is a particular neural code advantageous (or optimal)?  
Why are particular mechanisms advantageous?  
What design principles influence sensory systems, can they be used  
for artificial systems?

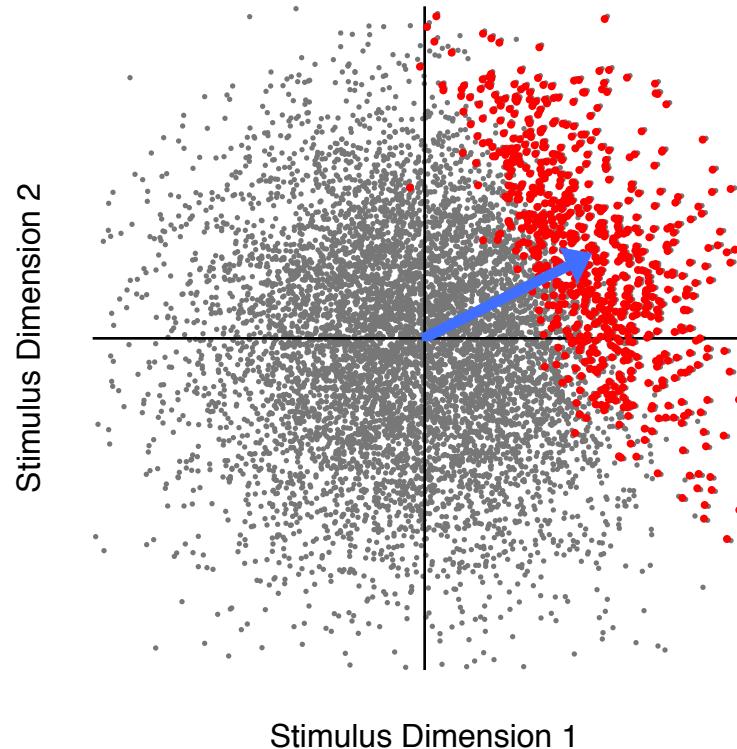
baccus@stanford.edu

# Stimulus space: A geometrical representation of input



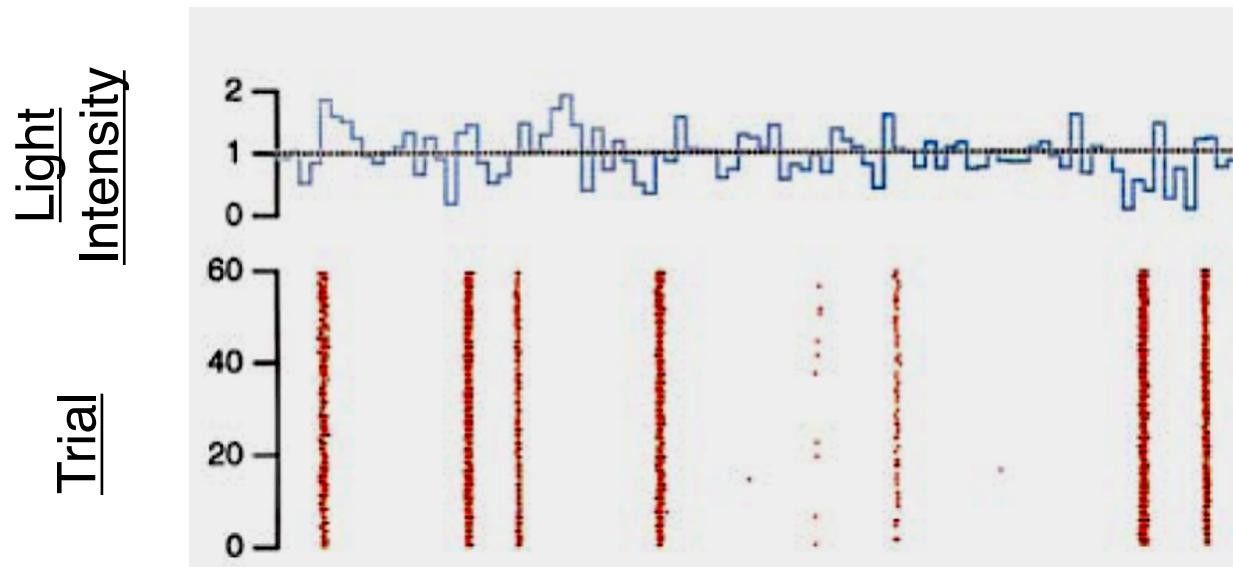
Not the same as “visual space”:  
receptors are *dimensions*, not points

Stimulus space: A geometrical representation of input  
Receptive field: a direction of sensitivity



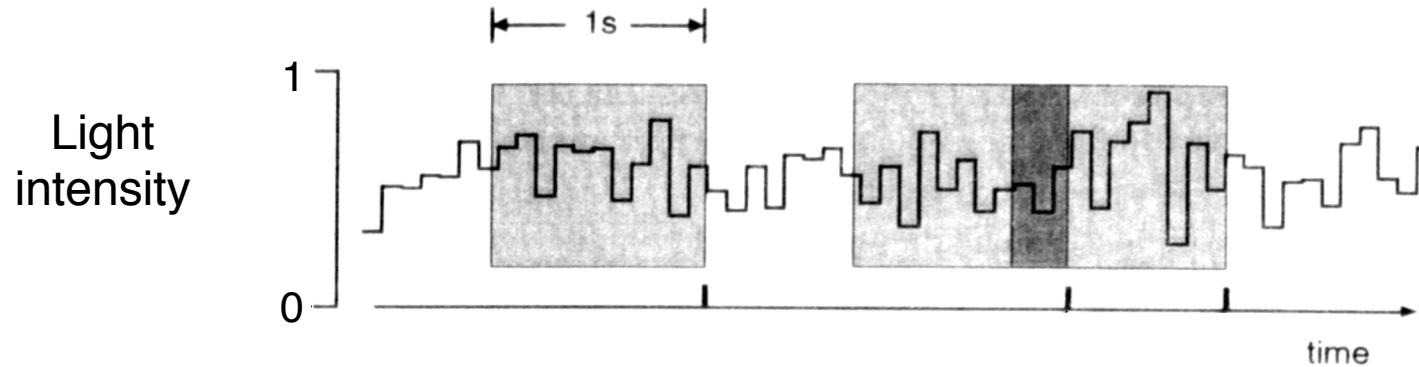
All stimuli  
Stimuli producing spikes  
Preferred direction in stimulus space

# Receptive field: What stimuli makes the neuron respond?

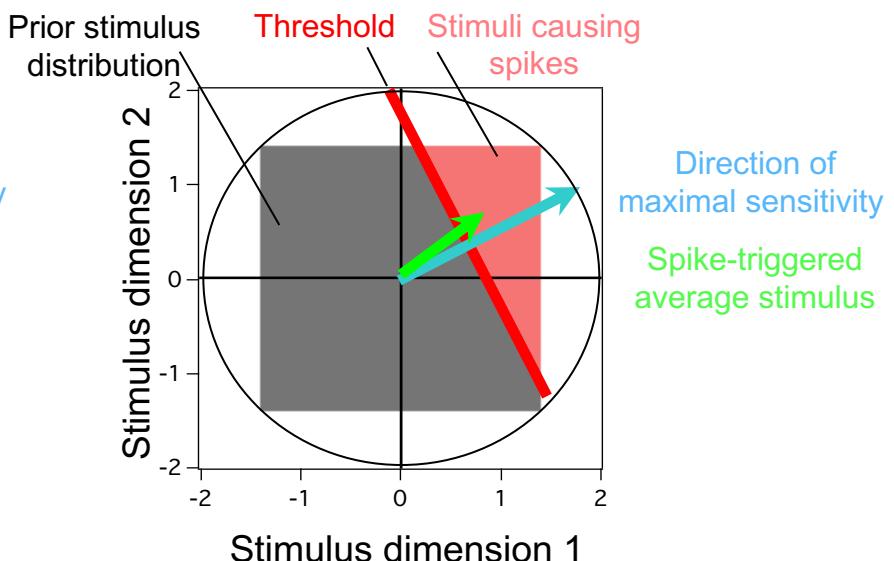
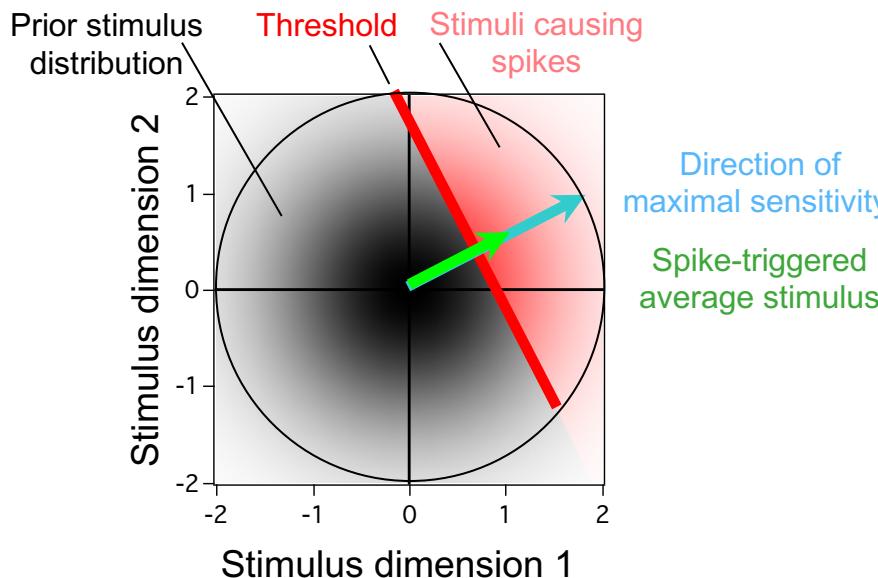


# Receptive field: What stimuli makes the neuron respond?

## Spike-triggered average for a spiking neuron



# Computing the most effective stimulus (Bussgang's theorem)



If an input is Gaussian white noise, correlation of the input with the output yields the most effective input , even if there is a distortion of the signal' s amplitude such as a threshold or saturation.

Bussgang (1952)

# What stimulus makes the neuron respond?

## Reverse correlation

Continuous

$$C(\tau) = \int_0^T r(t)s(t - \tau)dt$$

Discrete

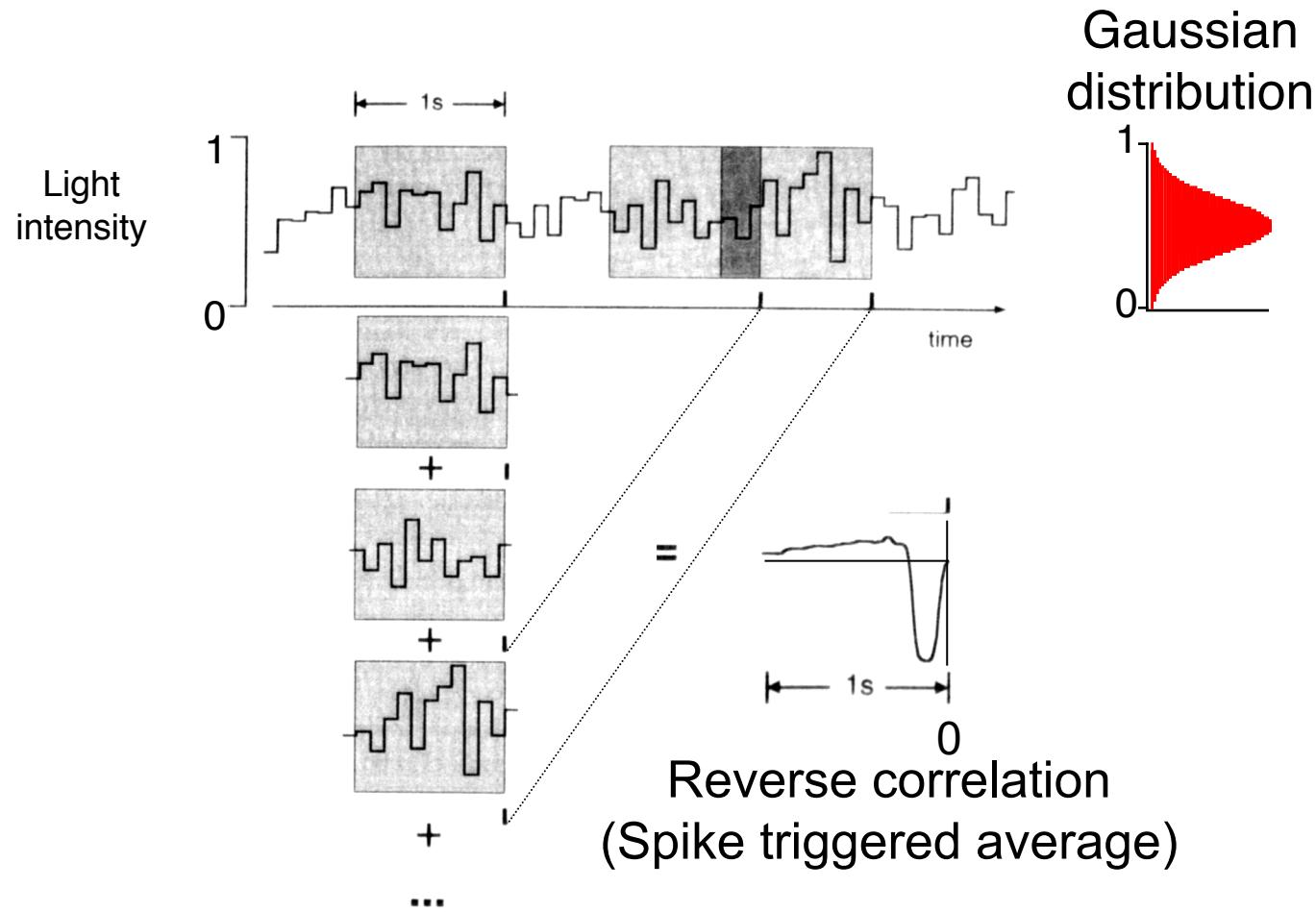
$$C(\tau) = \sum_{t=0}^T r(t)s(t - \tau)\Delta t$$

For spikes, this is proportional to the spike-triggered average

# What stimulus makes the neuron respond?

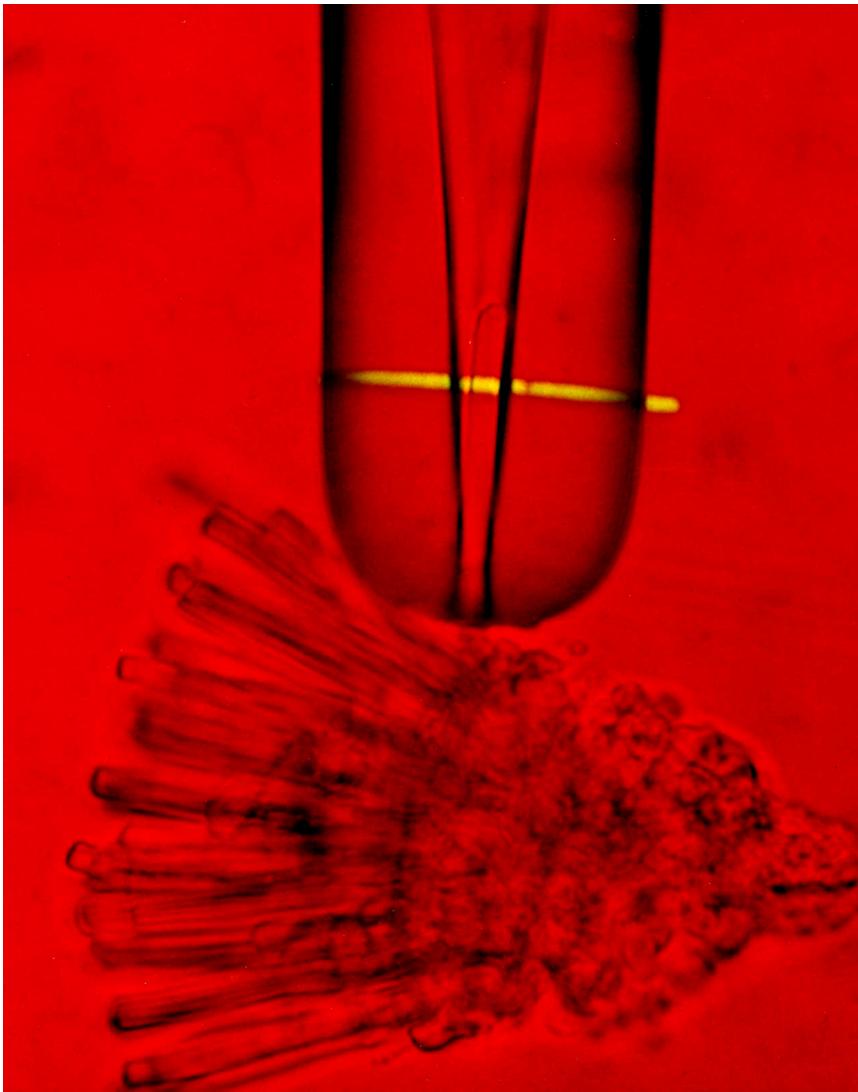
## White noise analysis

For a Gaussian white-noise stimulus, the reverse correlation gives the input that is transmitted with greatest sensitivity



# How will a neuron respond to a stimulus?

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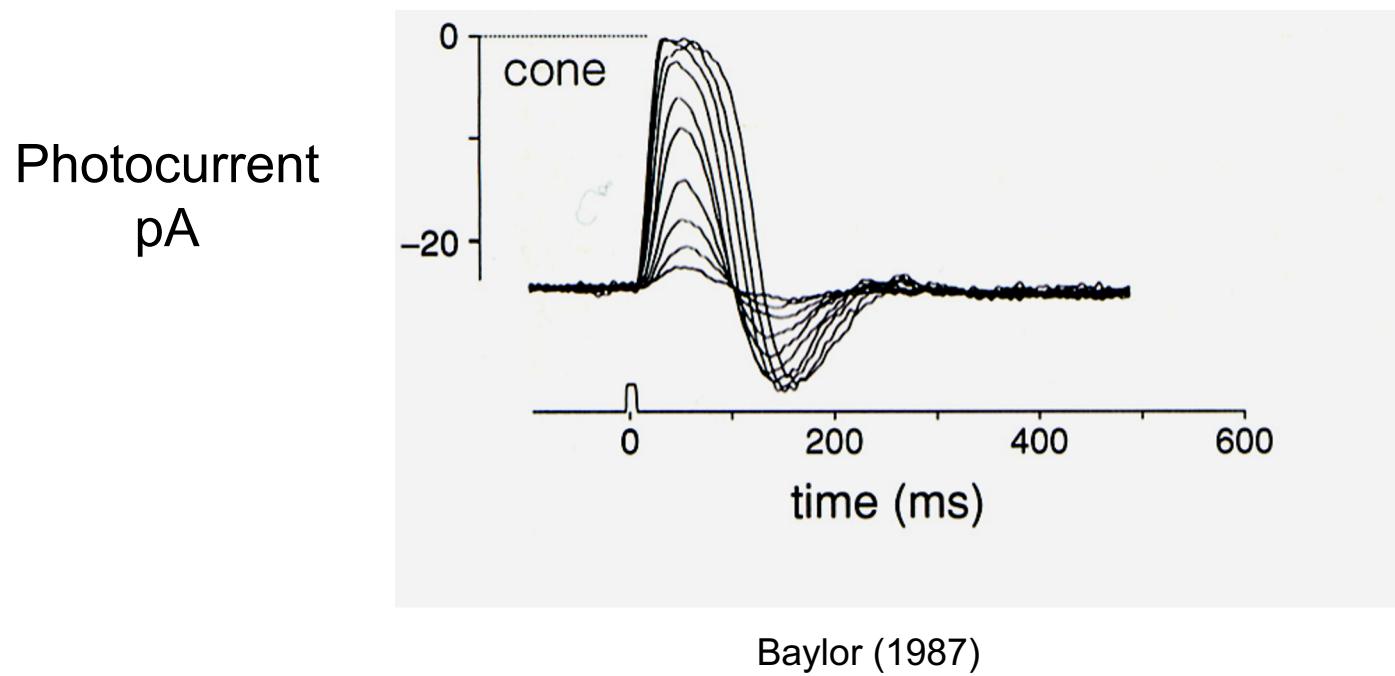


Baylor, Lamb and  
Yau (1979)

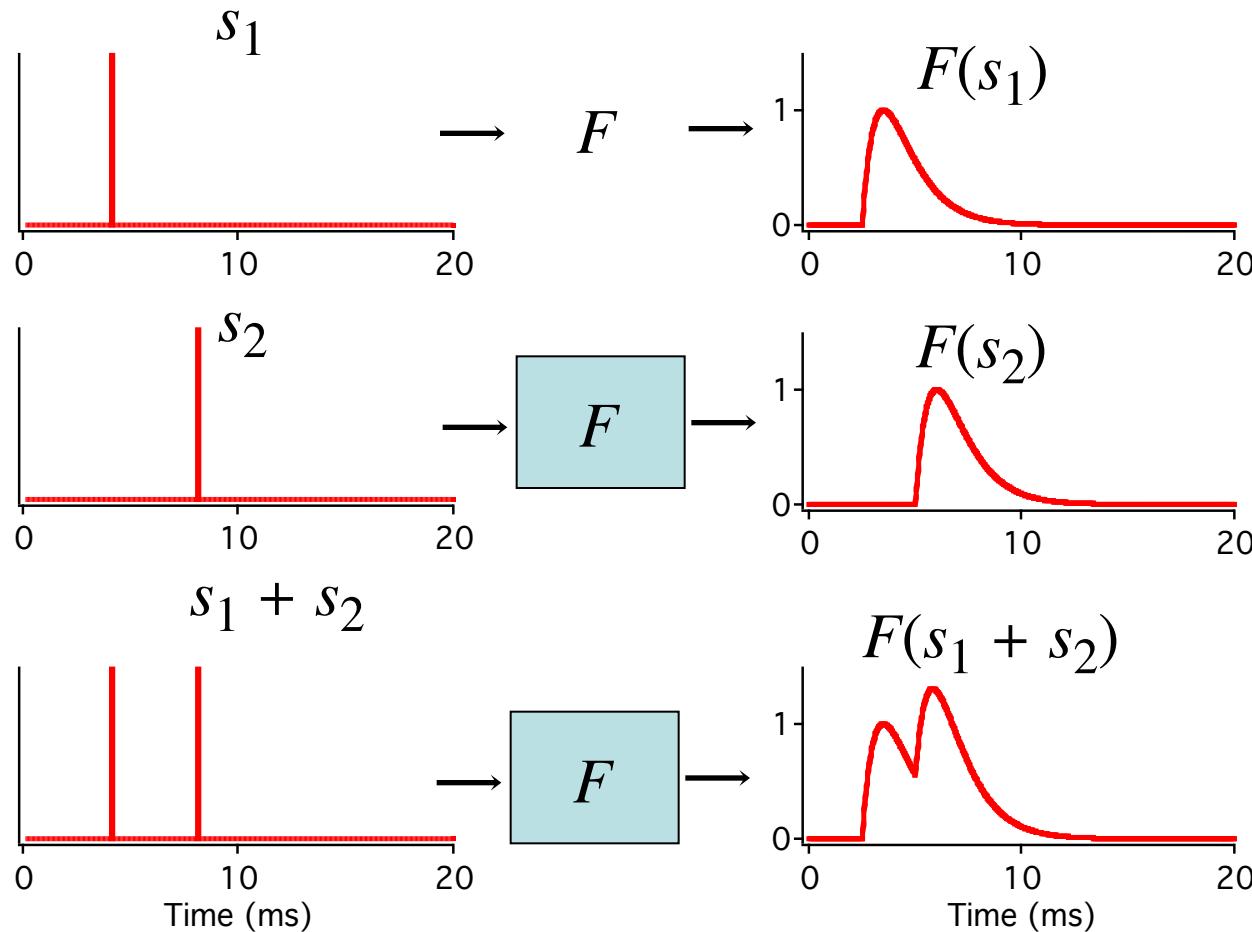
# How will a neuron respond to a stimulus?

## Single photoreceptor responses to a flash of light

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## A linear system



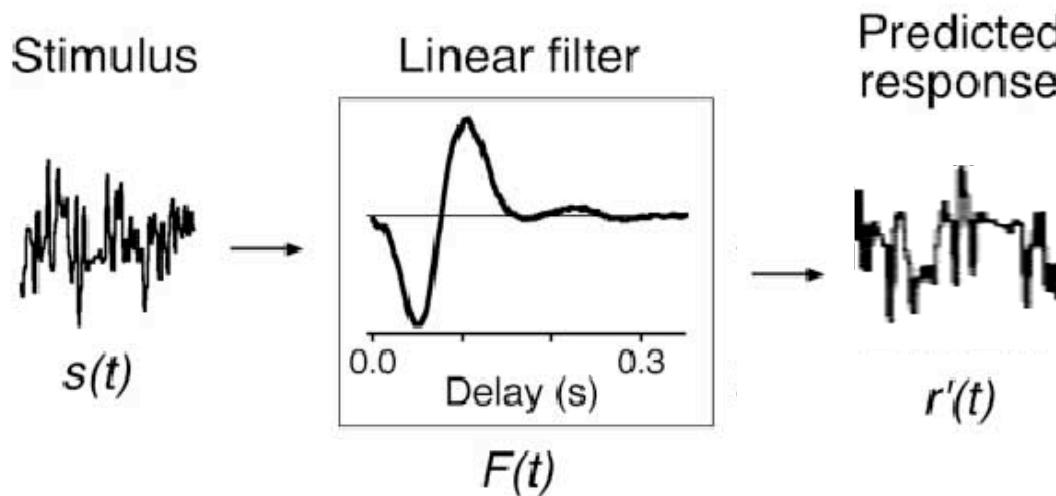
## The Superposition Principle

When two inputs are presented to a linear system, their effects sum.

$$F(s_1 + s_2) = F(s_1) + F(s_2)$$

# A linear model of the cell's response

**A**



## Convolution

$$r'(t) = \int s(\tau)F(t - \tau)d\tau = F * s$$

$F(t)$  is called:

- Impulse response function
- Linear kernel
- First-order kernel
- First-order Wiener kernel

Filters and step responses

Monophasic

Biphasic

Two different concepts for convolution

Dot product with time-reverse of filter

Impulse response

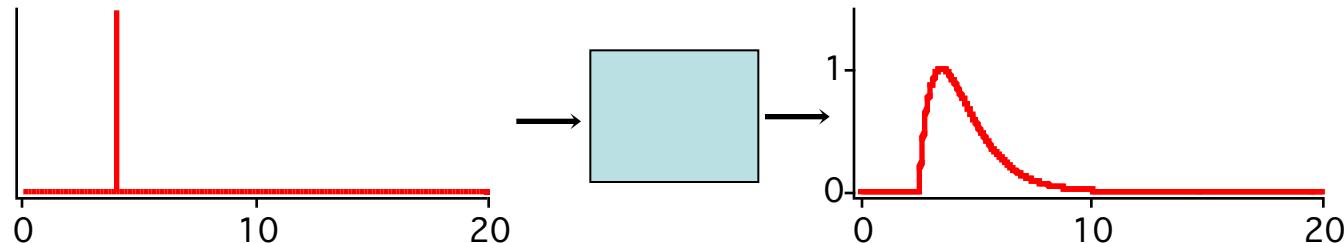
How do you find the filter?

What stimulus produces the largest response?

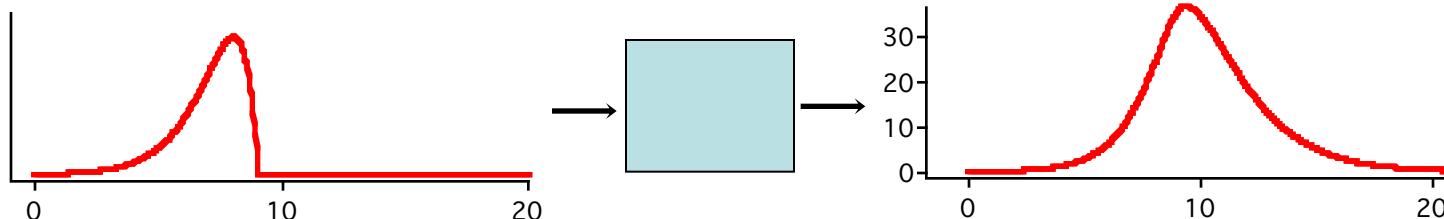
geometrical interpretation

Summary of relationship between the response to an impulse and the most effective input.

For a cell (or any system) responding in the linear range, the response to a brief input (an impulse):

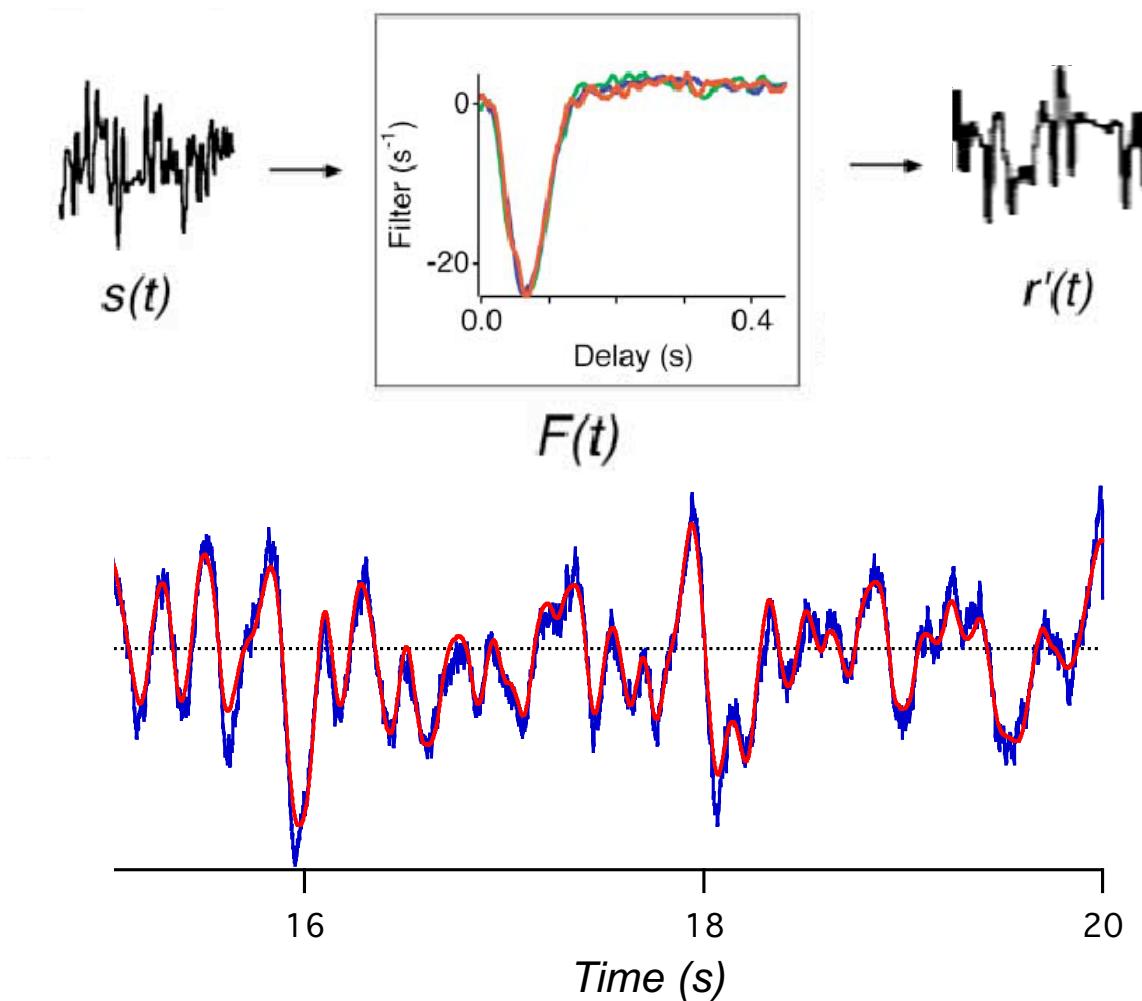


yields the time-reverse of the input that the cell is most sensitive to:



## A linear model of the cell's response

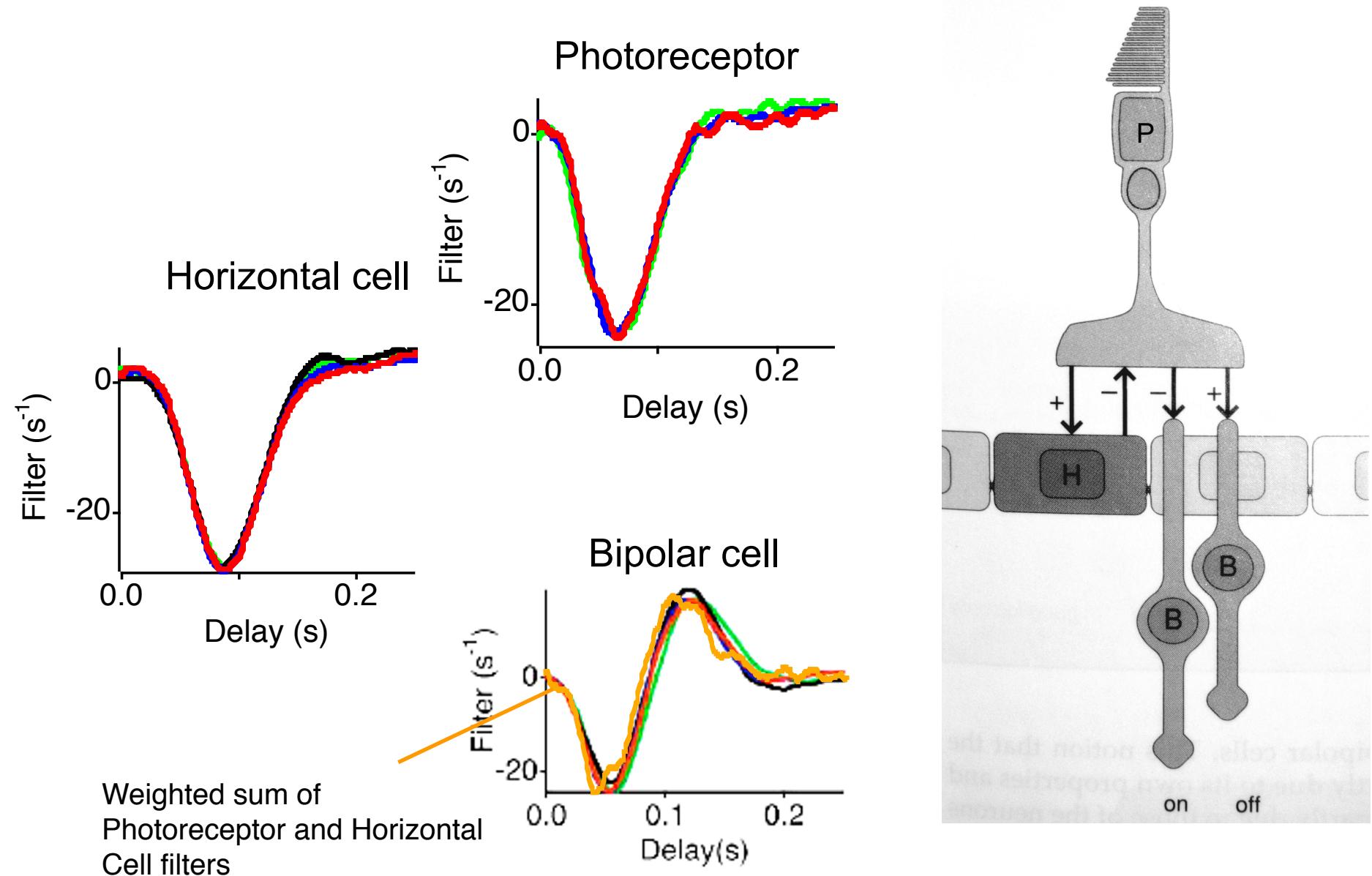
Stimulus      Linear filter      Predicted response



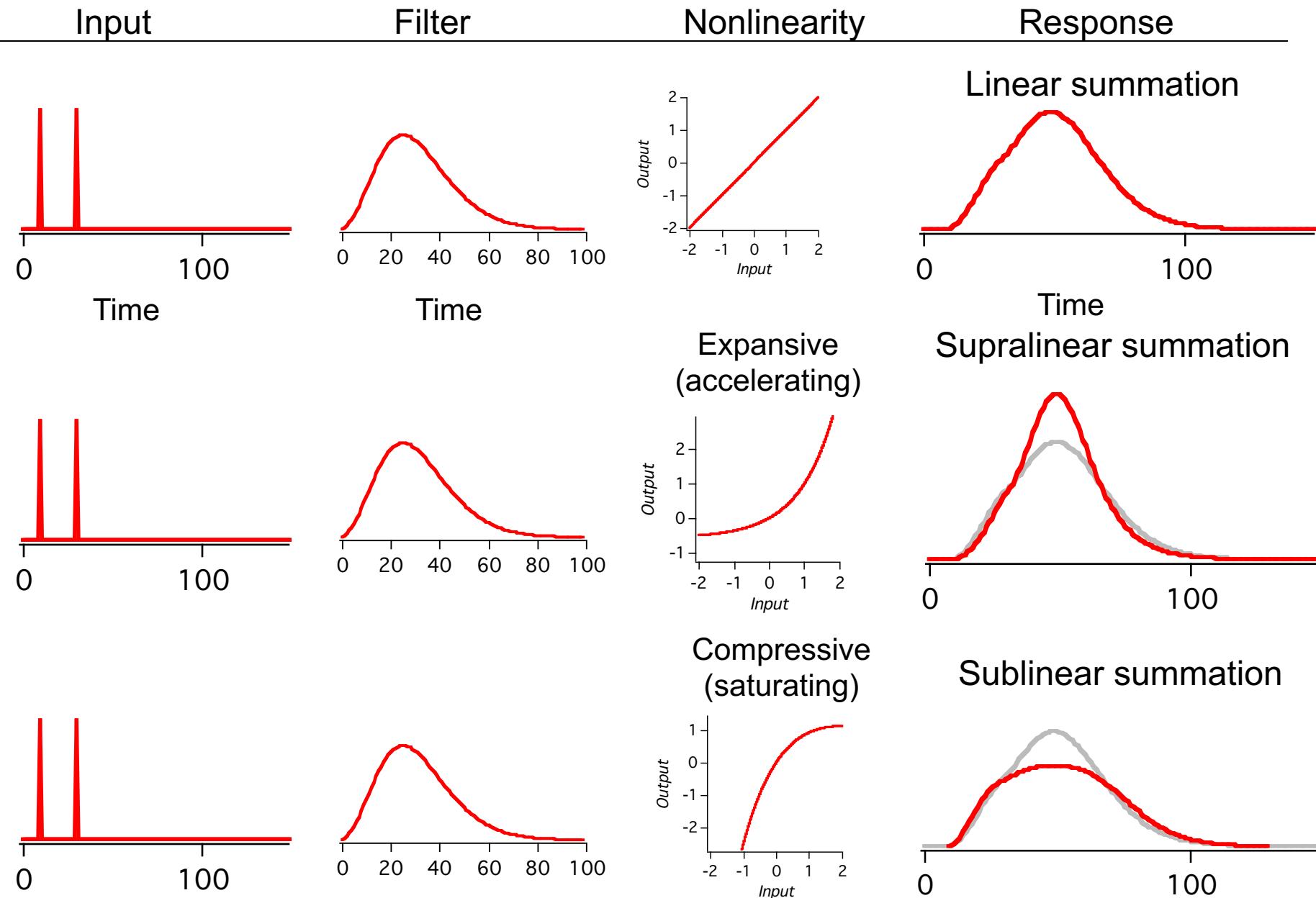
— Photoreceptor

— Linear model

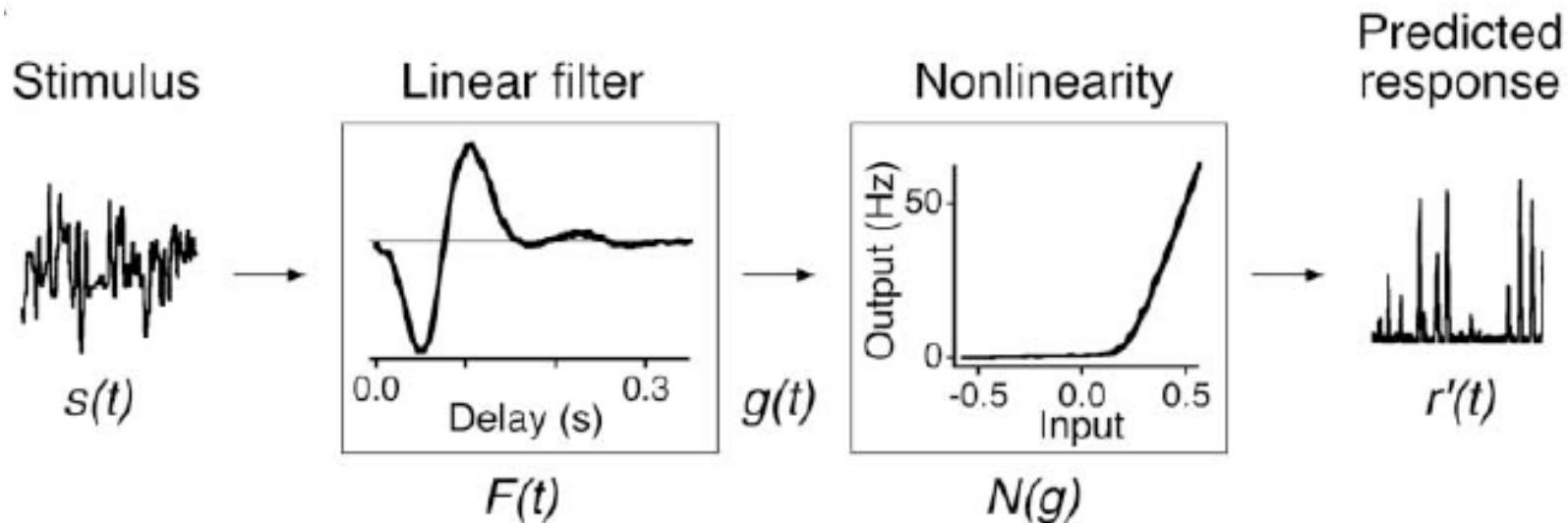
# Linear filters in the early visual system



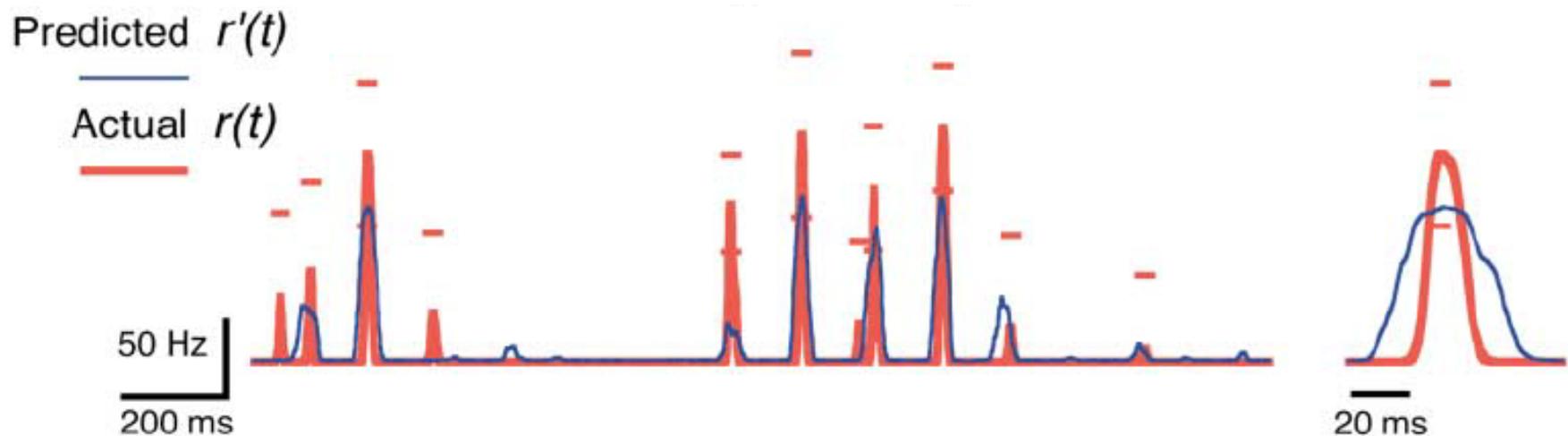
## Nonlinear summation of inputs by a static nonlinearity



# Linear - Nonlinear “LN” model of a “Feature Selective Neuron”



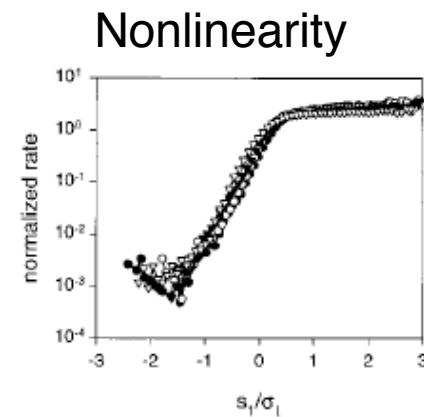
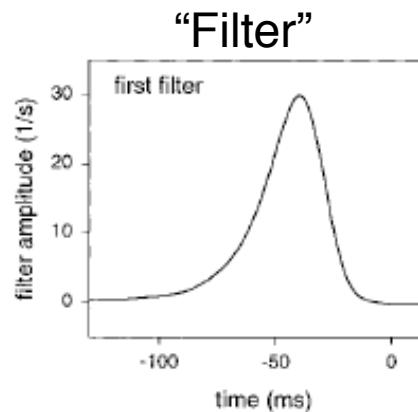
Retinal ganglion cell firing rate and LN model



# LN models in the nervous system

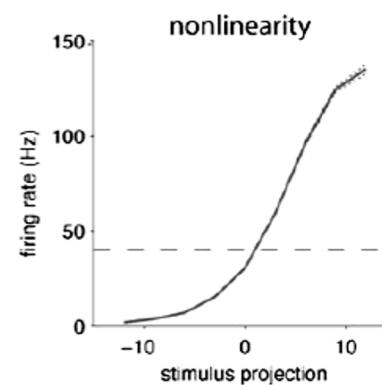
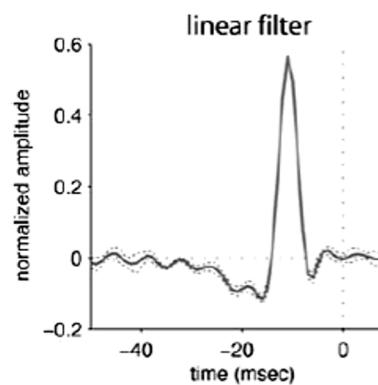
Fly H1 Motion sensitive neuron

Brenner et al., *Neuron* (2000)



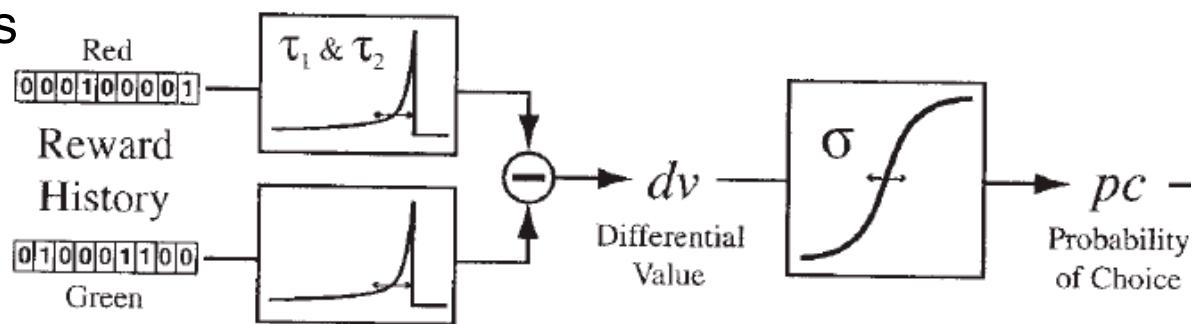
Songbird auditory forebrain neuron

Nagel & Doupe, *Neuron* (2007)



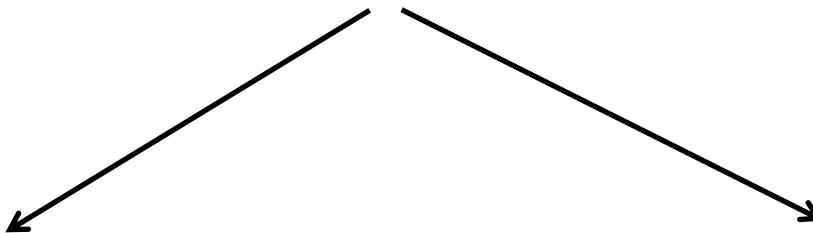
Whole monkey making decisions

Corrado, Sugrue, Seung & Newsome, *J. Exp. Anal. Behav.* (2005)



# How do we study more complex responses to sensory input?

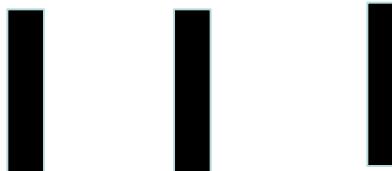
## Properties of feature detection



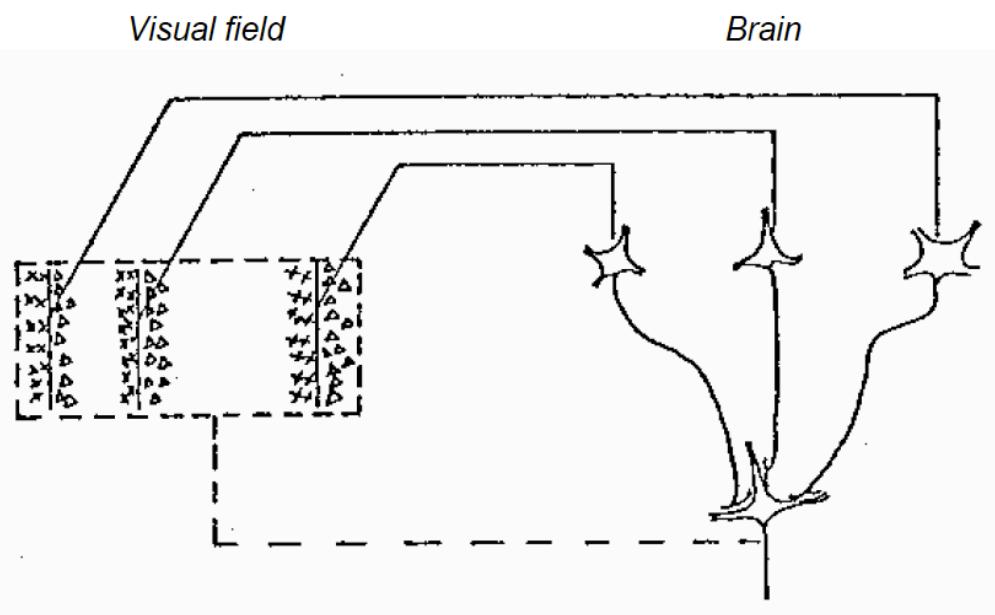
Selectivity



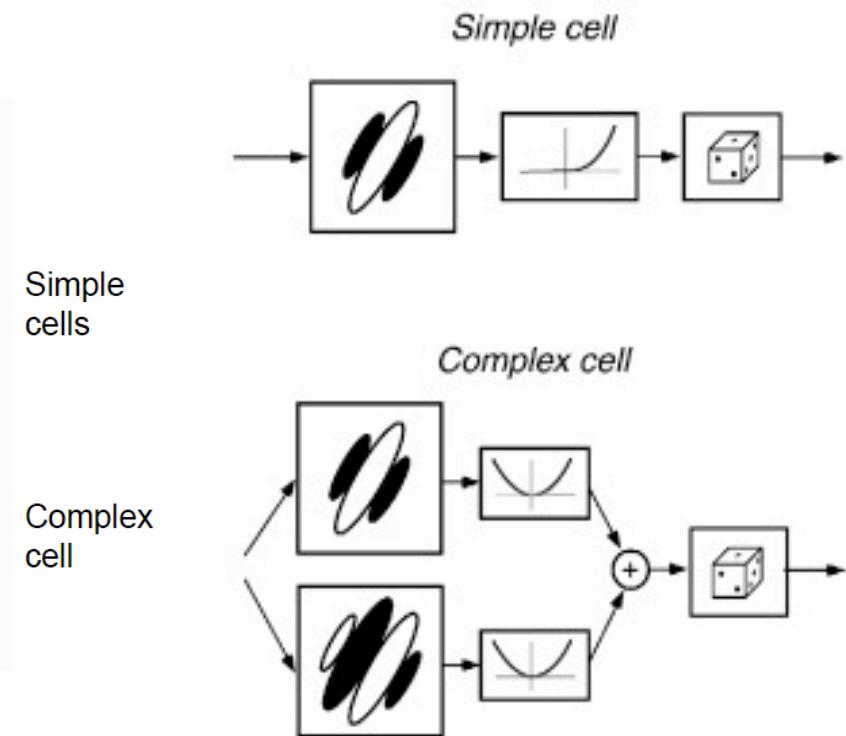
Invariance



# Models of selectivity and invariance in primary visual cortex

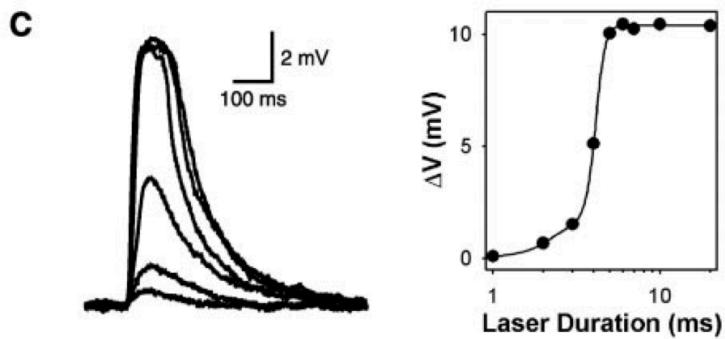
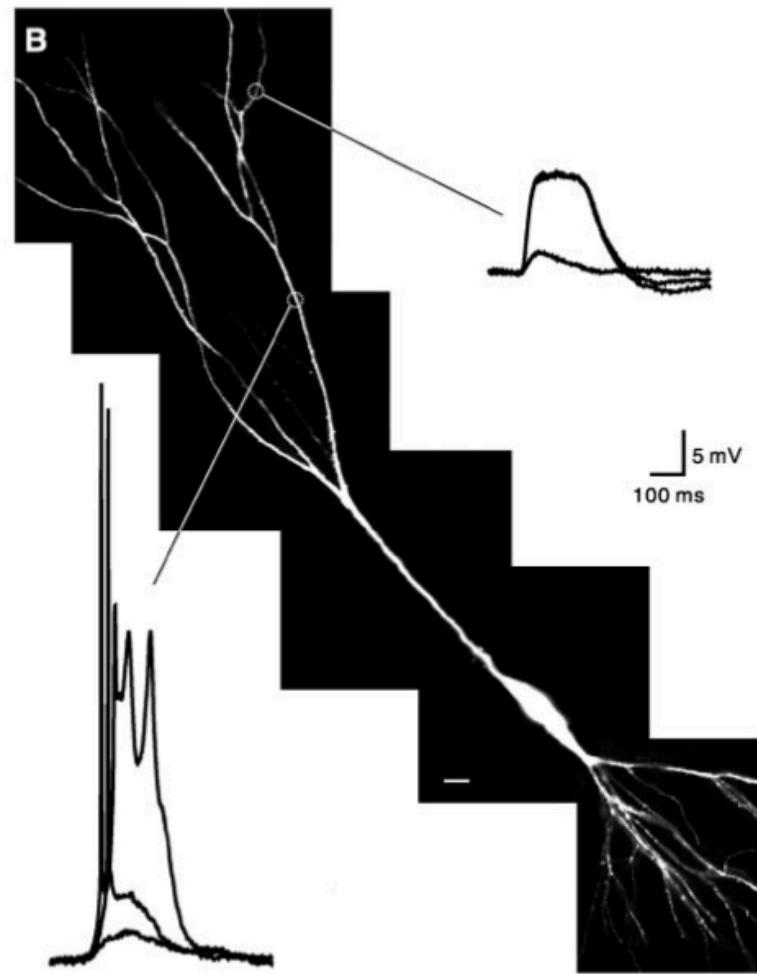
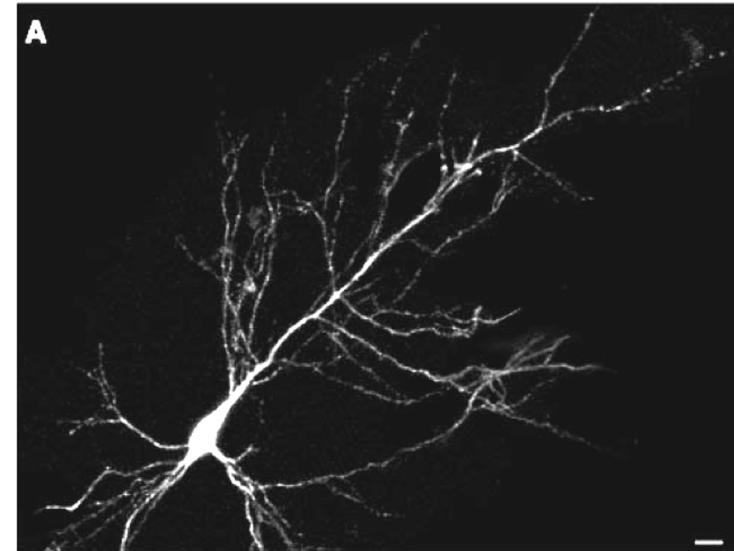


Hubel & Wiesel, 1963



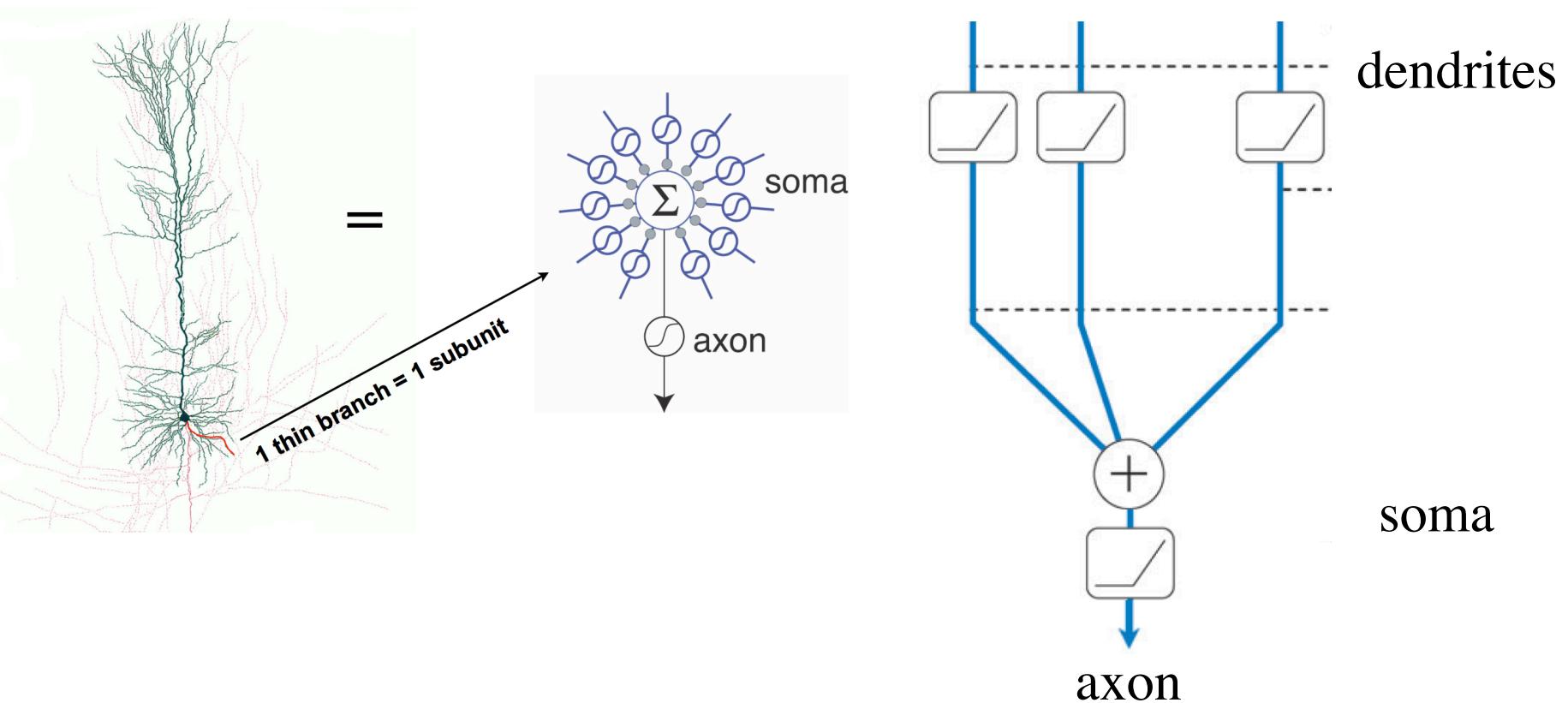
Rust et al., 2005

# All or none calcium action potentials in pyramidal cell dendrites



Wei et al., 2001. Compartmentalized and Binary Behavior of Terminal Dendrites in Hippocampal Pyramidal Neurons

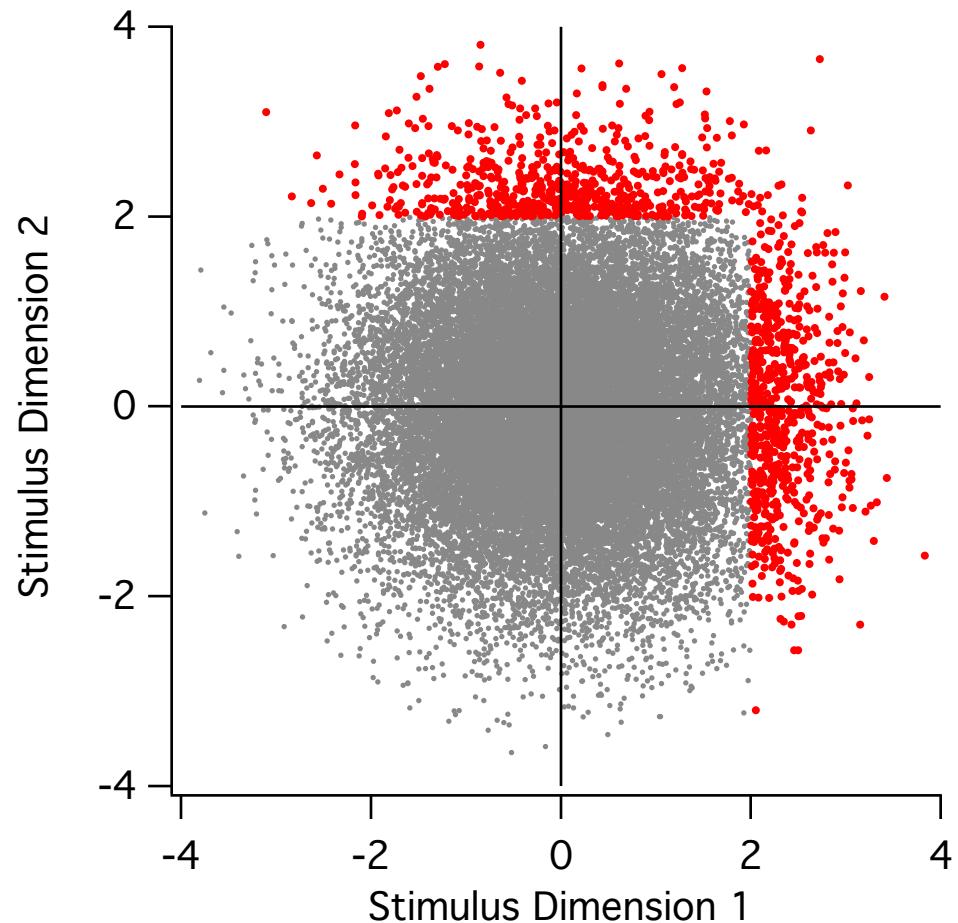
# “Two layer” model of active dendrites



Poirazi, Brannon & Mel, 2003

Bartlett Mel

## Sensitivity to multiple stimulus dimensions



All stimuli  
Stimuli producing spikes

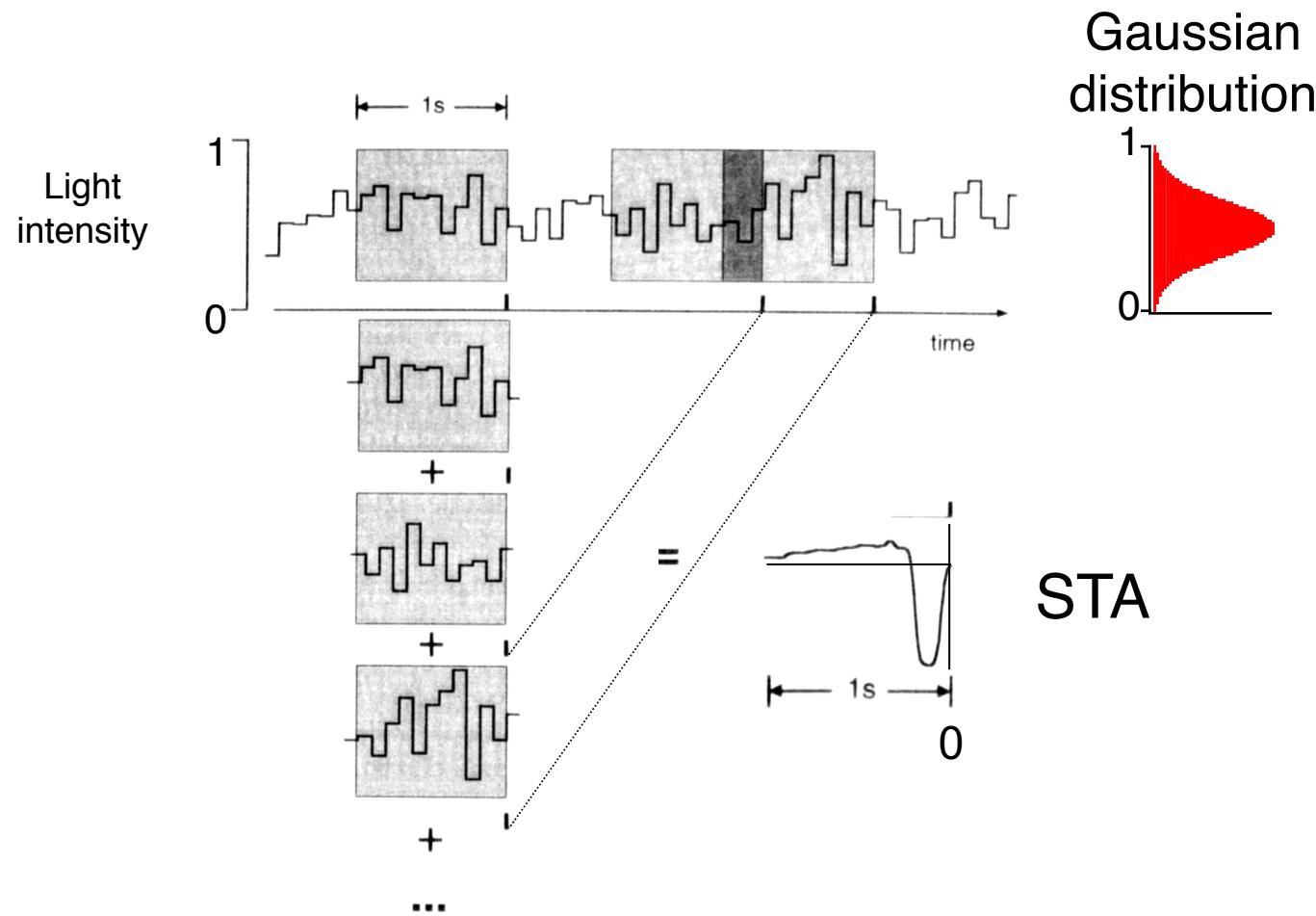
## Spike-triggered Covariance

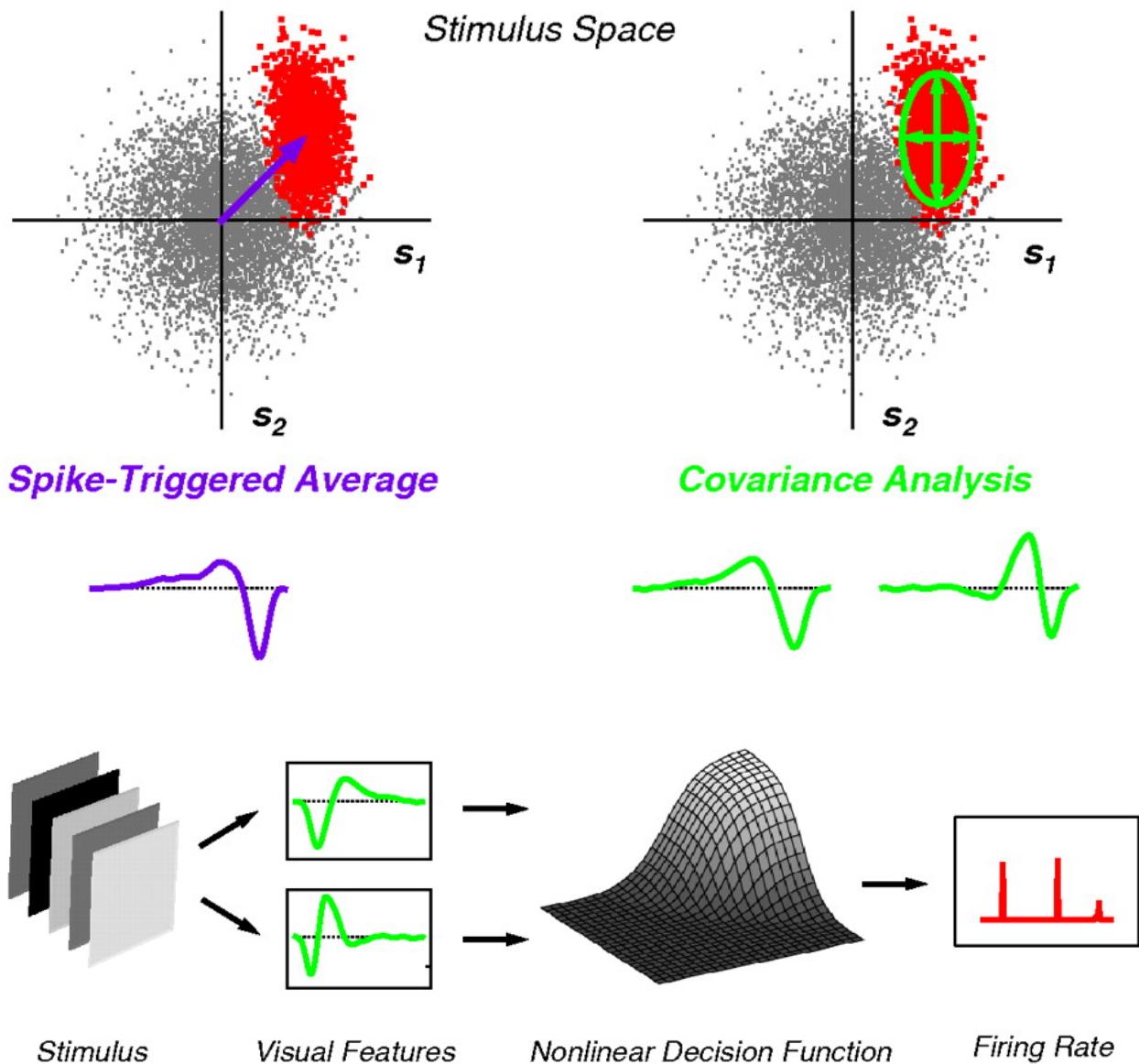
What are special directions in stimulus space that influence the response?

What are the stimulus directions where the spike triggered ensemble “differs” from the original stimulus distribution?

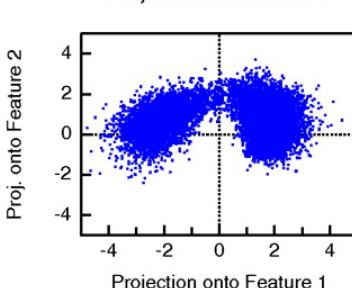
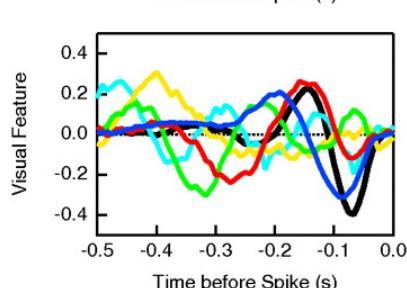
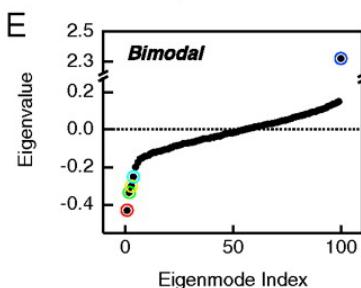
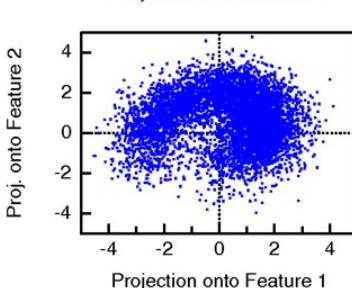
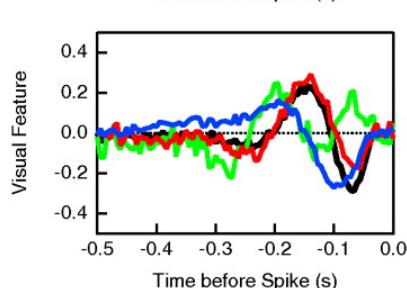
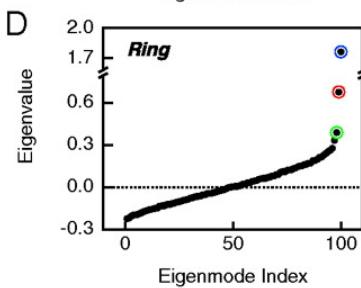
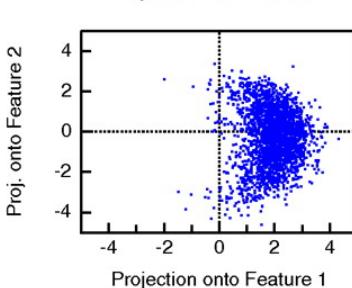
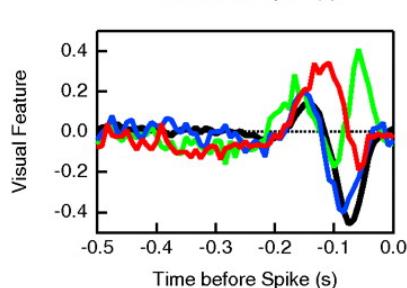
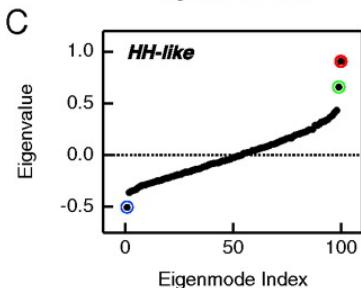
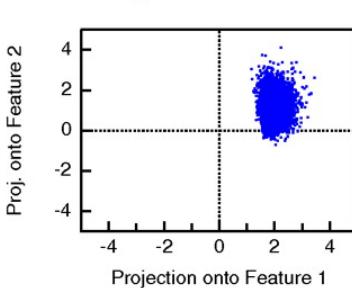
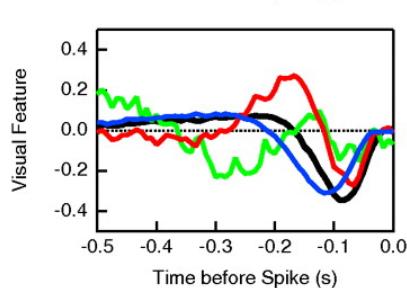
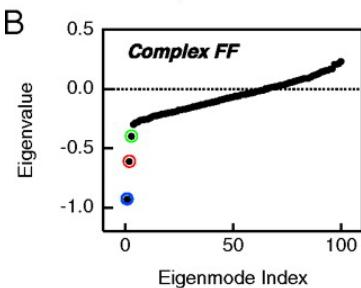
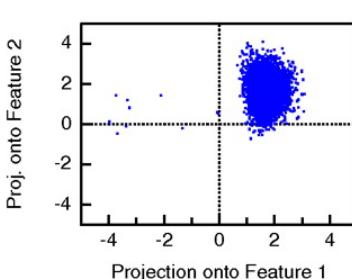
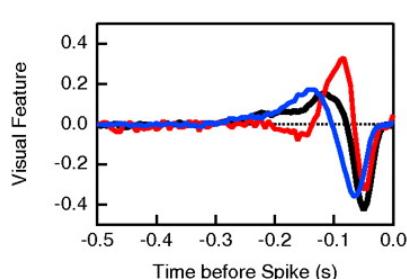
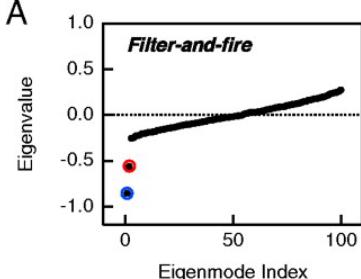
What are the stimulus directions where the spike triggered ensemble *has a different covariance* from the original stimulus distribution?

# Analyzing the spike-triggered stimulus ensemble



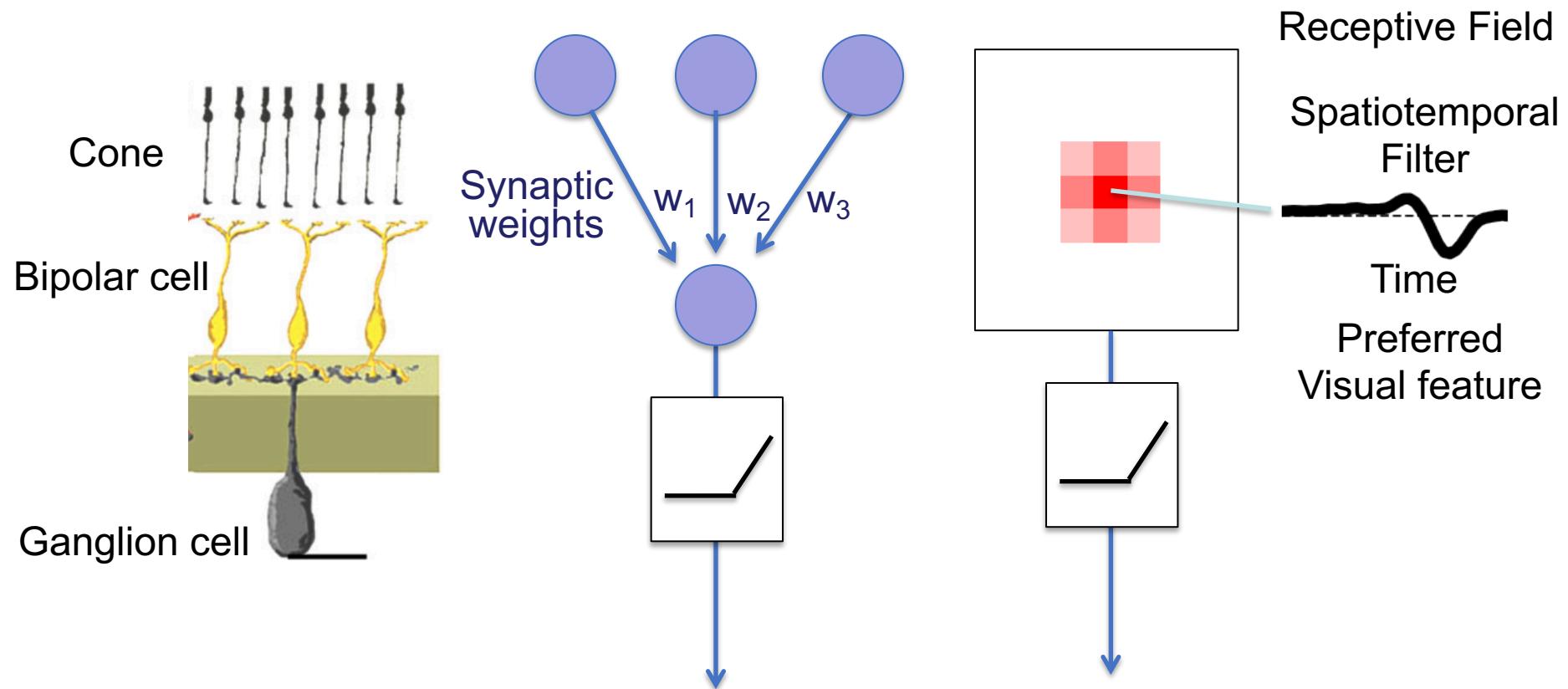


Fairhall et al, 2006

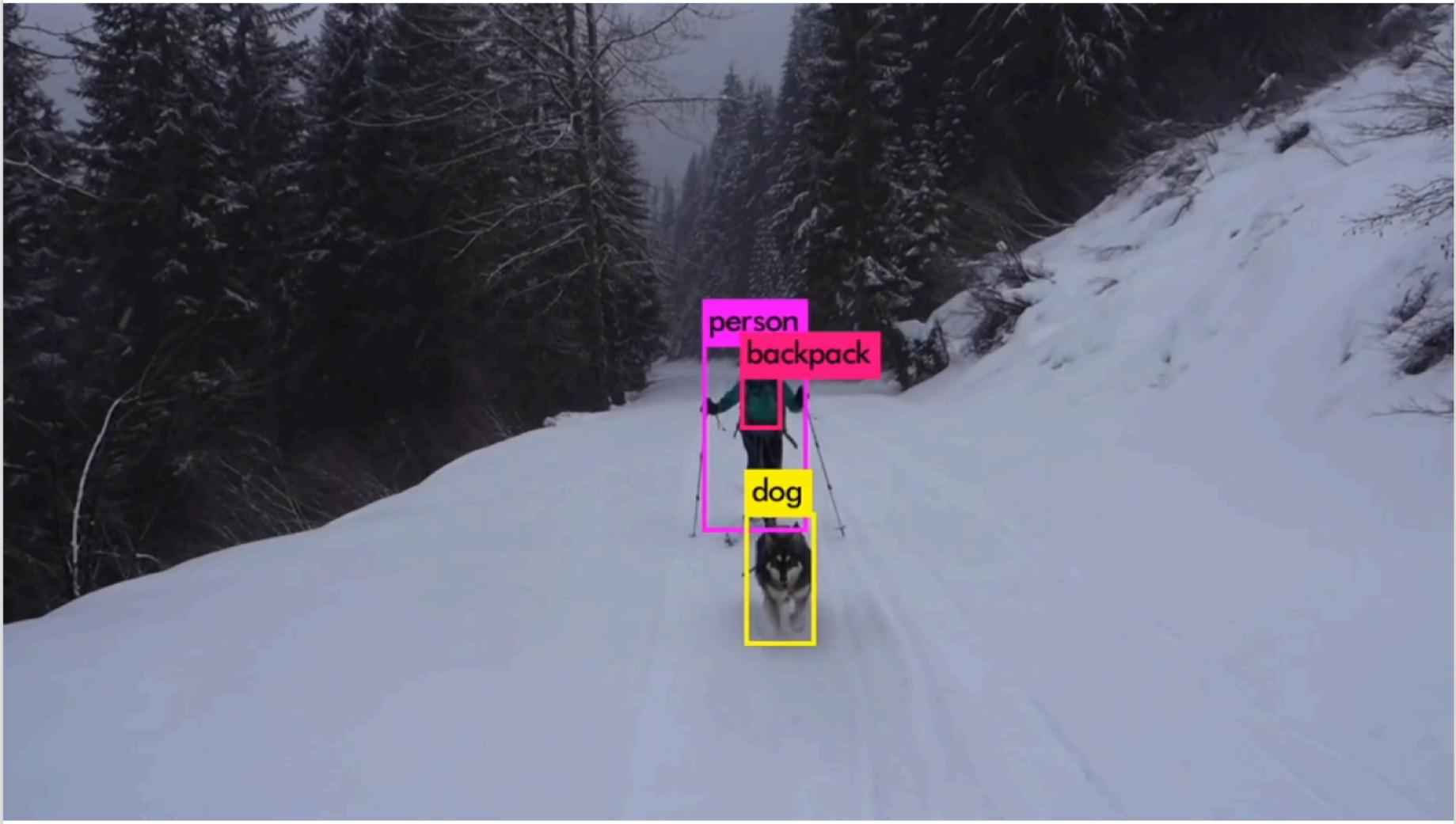


# A Simple Model of Visual Responses

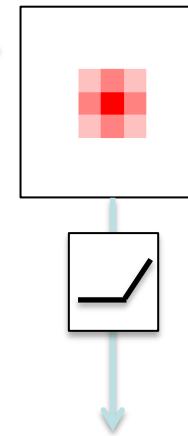
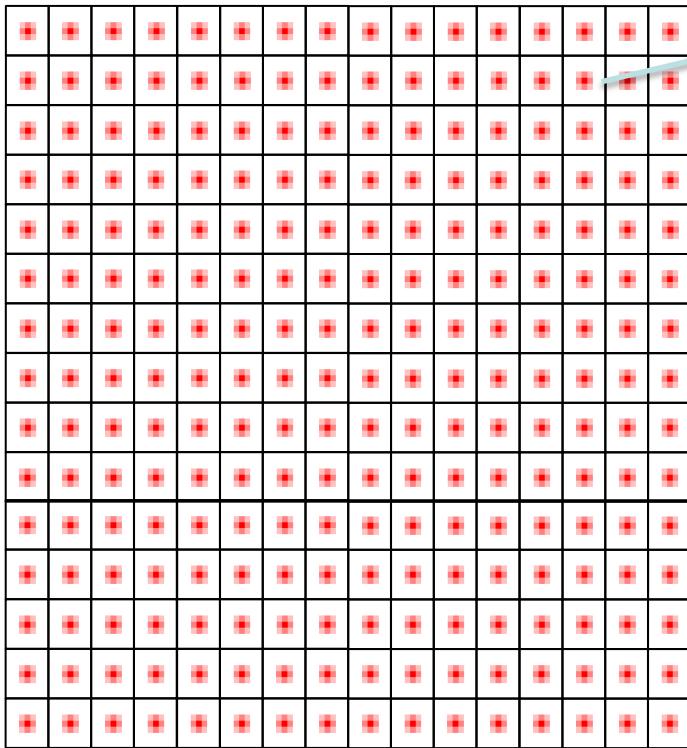
Linear-Nonlinear (LN) Model



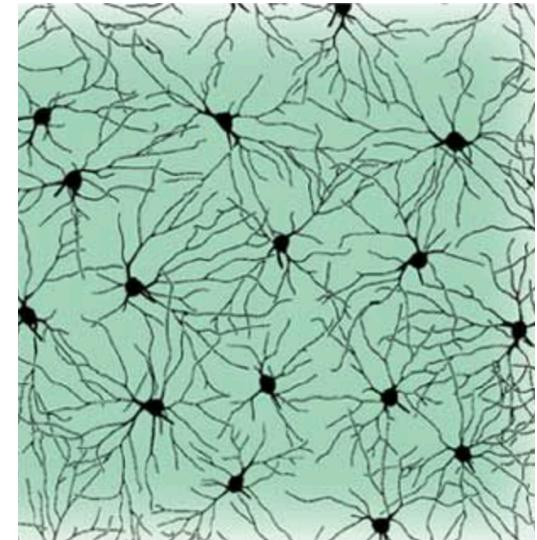
# Deep Learning Object Recognition



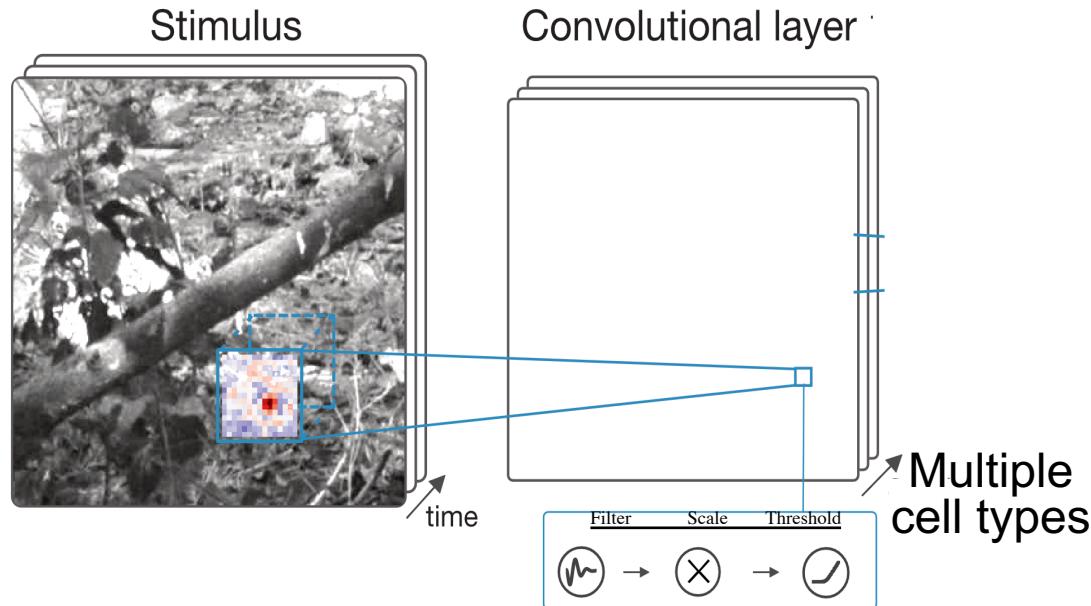
## "Convolutional" layer



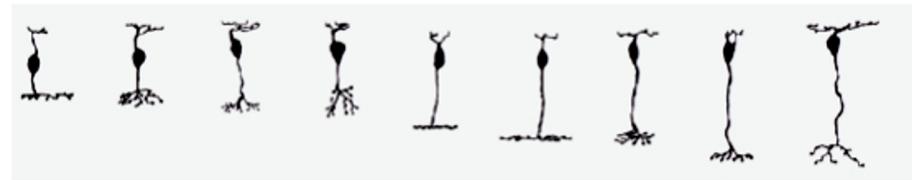
Like a mosaic  
of retinal neurons



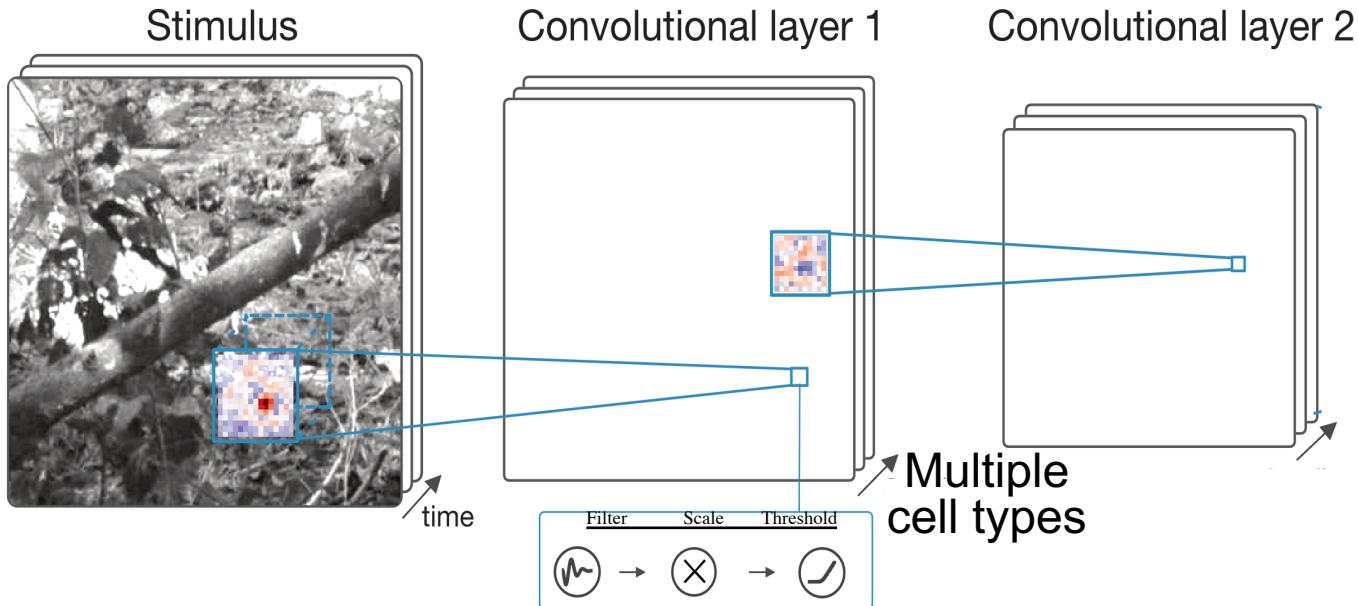
# Multiple cell types



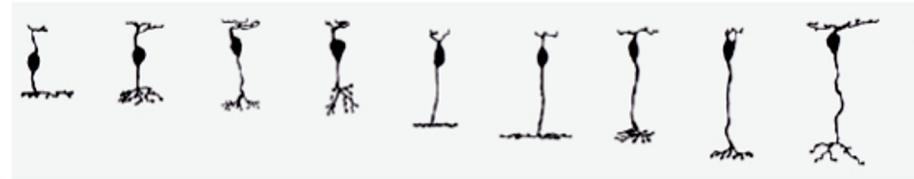
Like the multiple cell types in the retina



# Multiple Layers



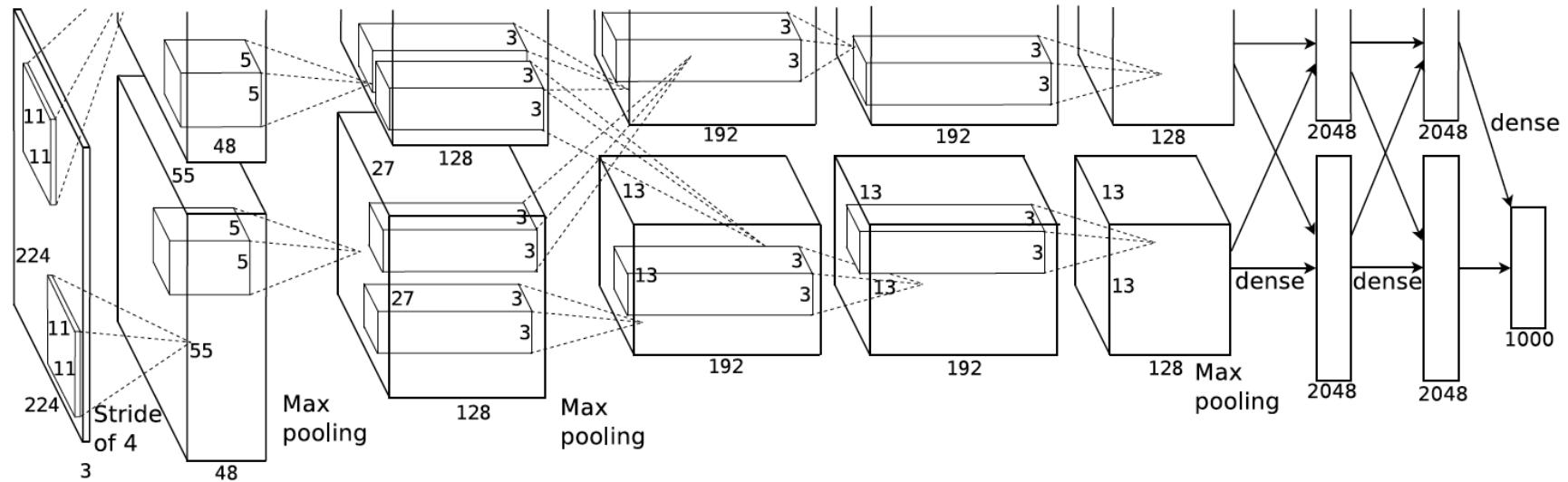
Like the multiple cell types in the retina



Like the hierarchy of retinal circuitry



# Object Recognition Deep Network

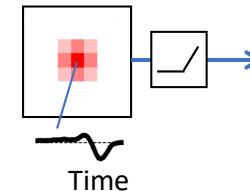


Different sensory models  
for different questions

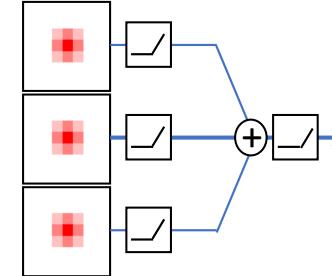
More  
Computationally  
Interpretable

LN Model

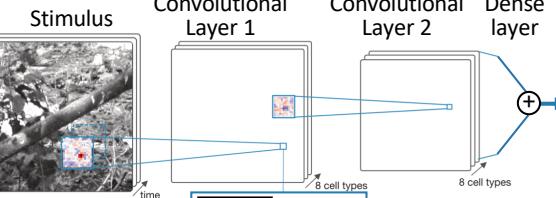
Spatiotemporal  
Filter



LN-LN Model



Minimal Convolutional  
Neural Network



More  
Expressive

Deep CNN

