

## NEPR208 - Adaptation / Plasticity

Functional advantages of response properties and changes in those properties

Why do cells have a particular nonlinear response function?

Why does the nonlinearity change?

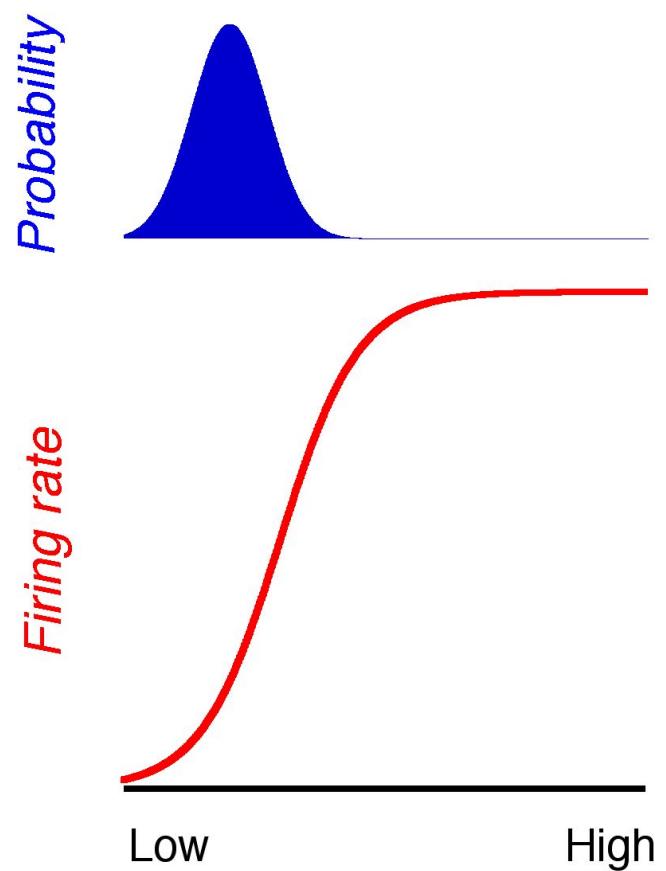
Why do cells have a certain duration filter?

Why do they have a certain shape filter?

Why does the filter change?

How can the nonlinearity and filter change?

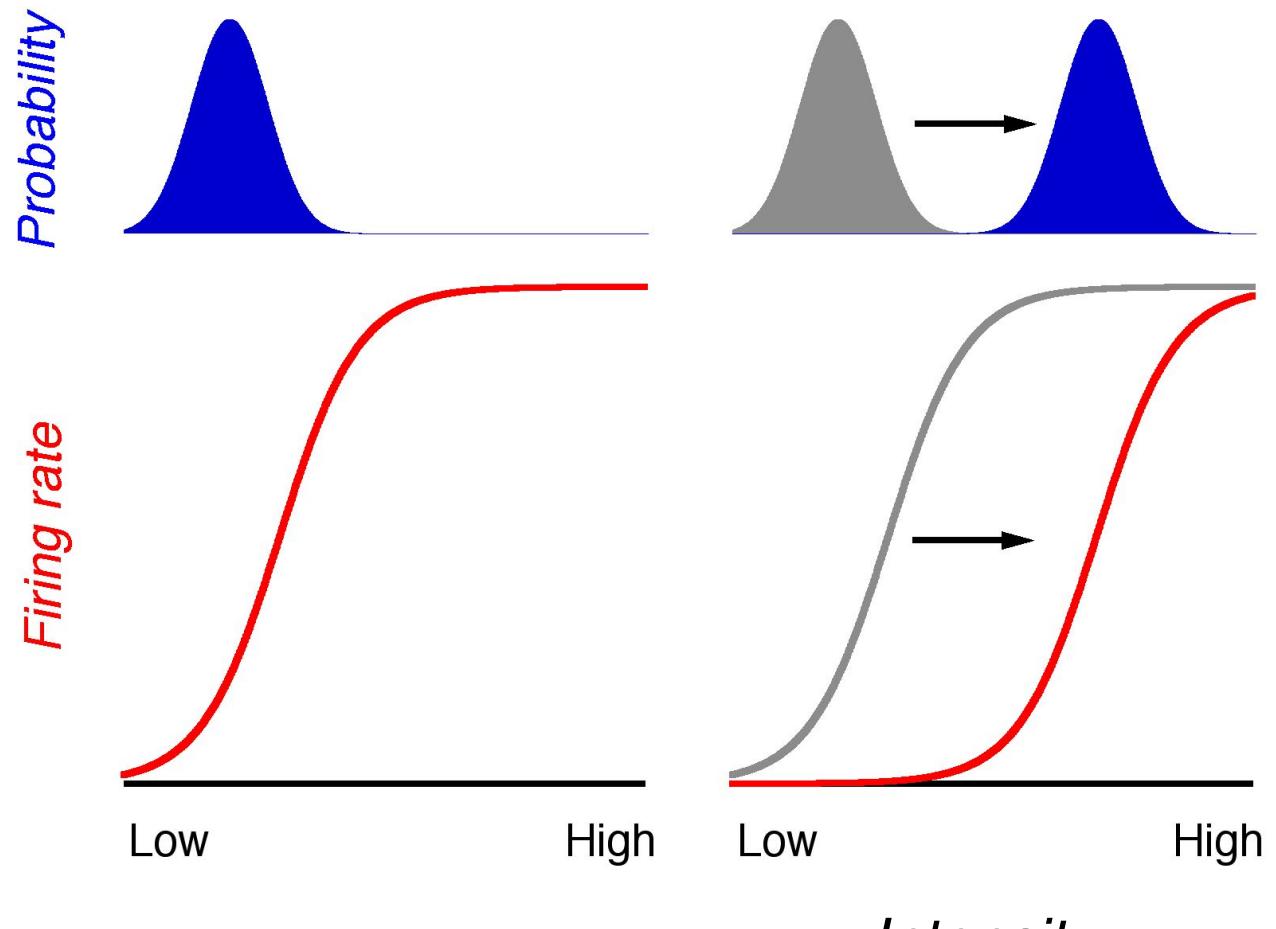
# Adaptation to the average input



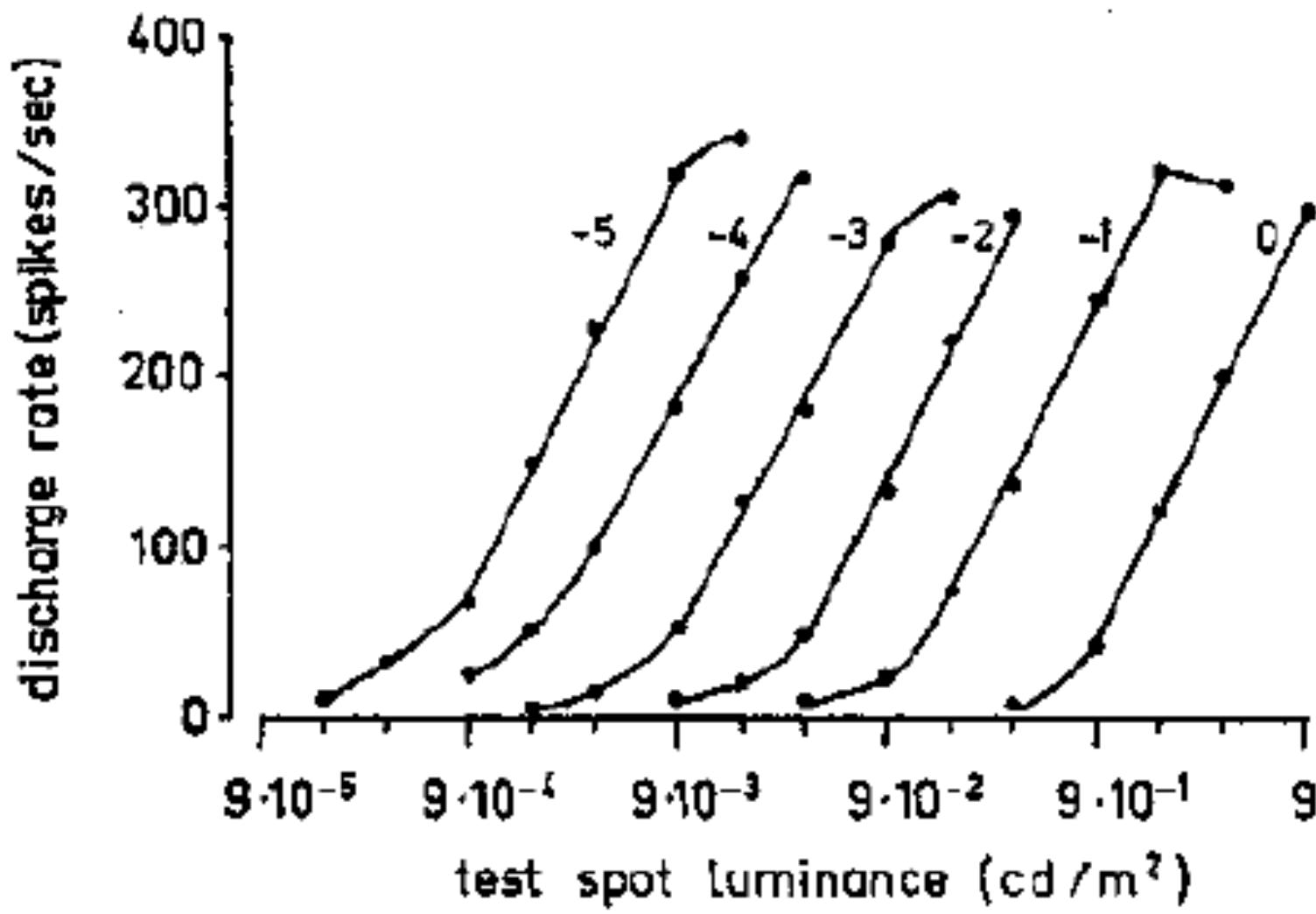
# Adaptation to the average input



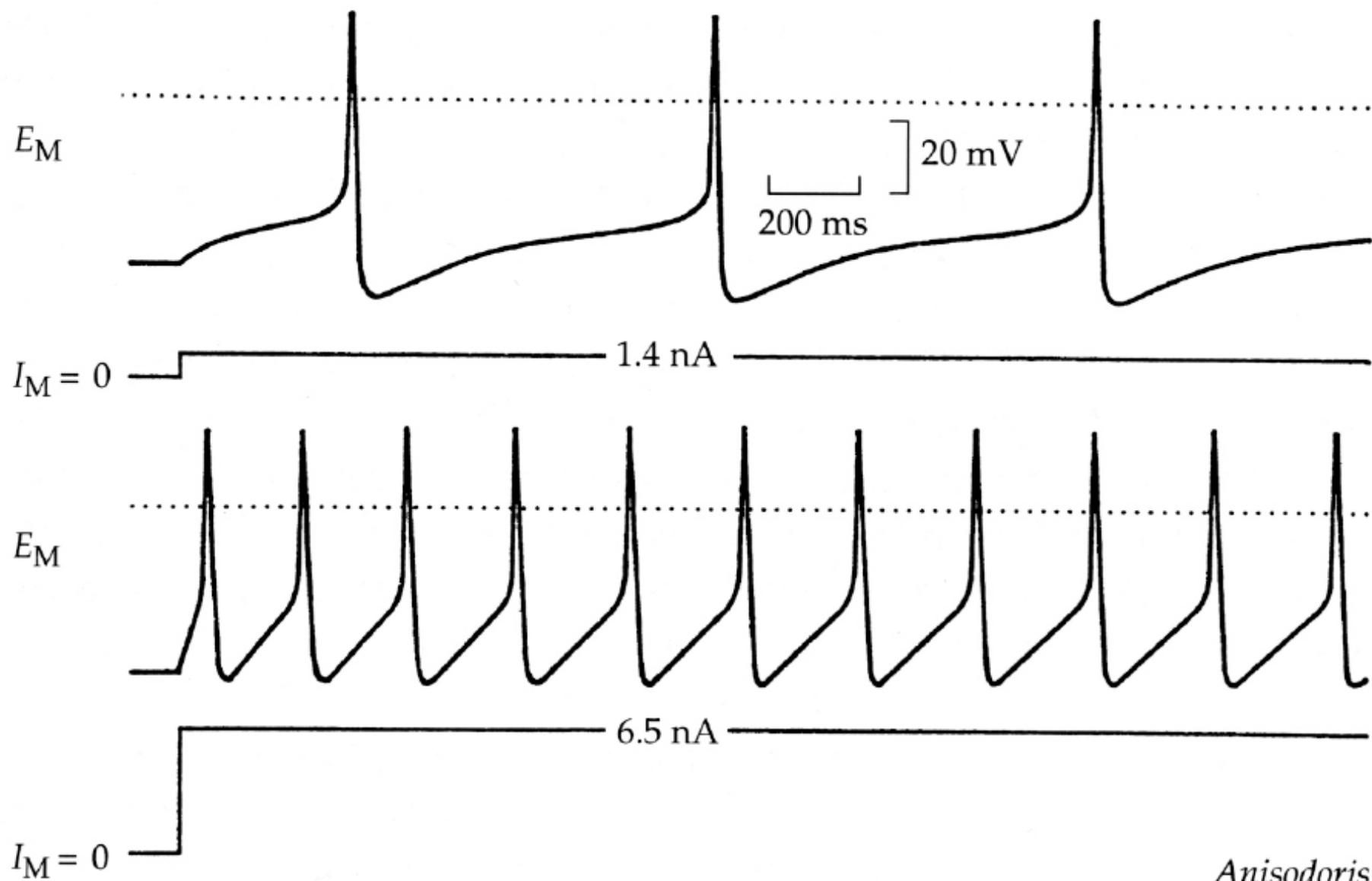
Light adaptation



## Ganglion cell response curves shift to the mean light intensity



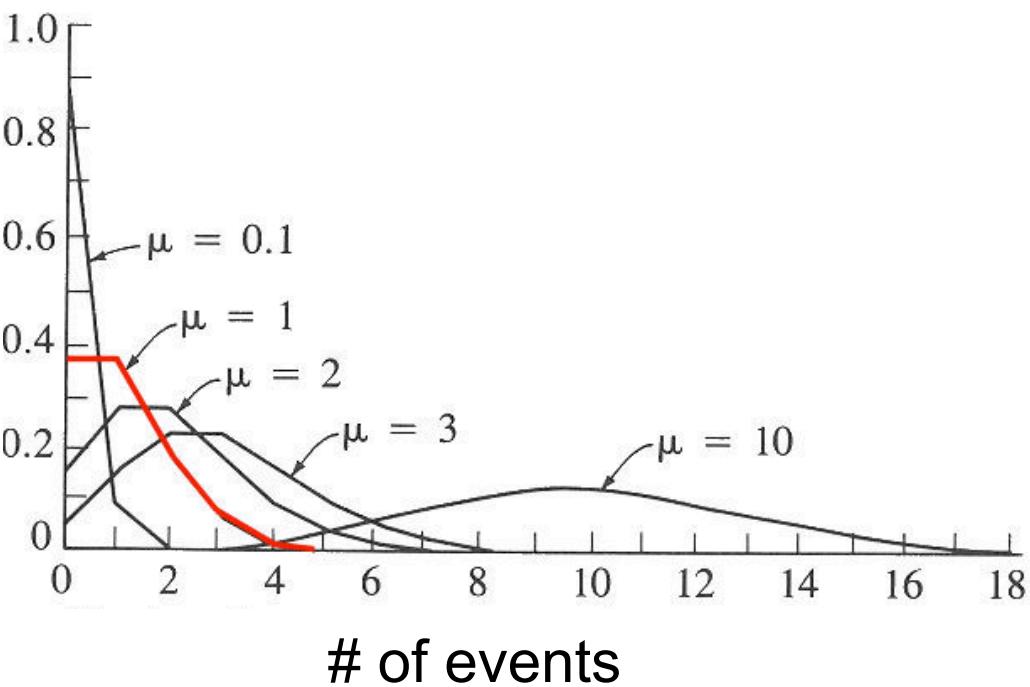
Neurons have a limited dynamic range set by maximum and minimum output levels, and by noise



# Events with Poisson statistics $P[n,\mu]$

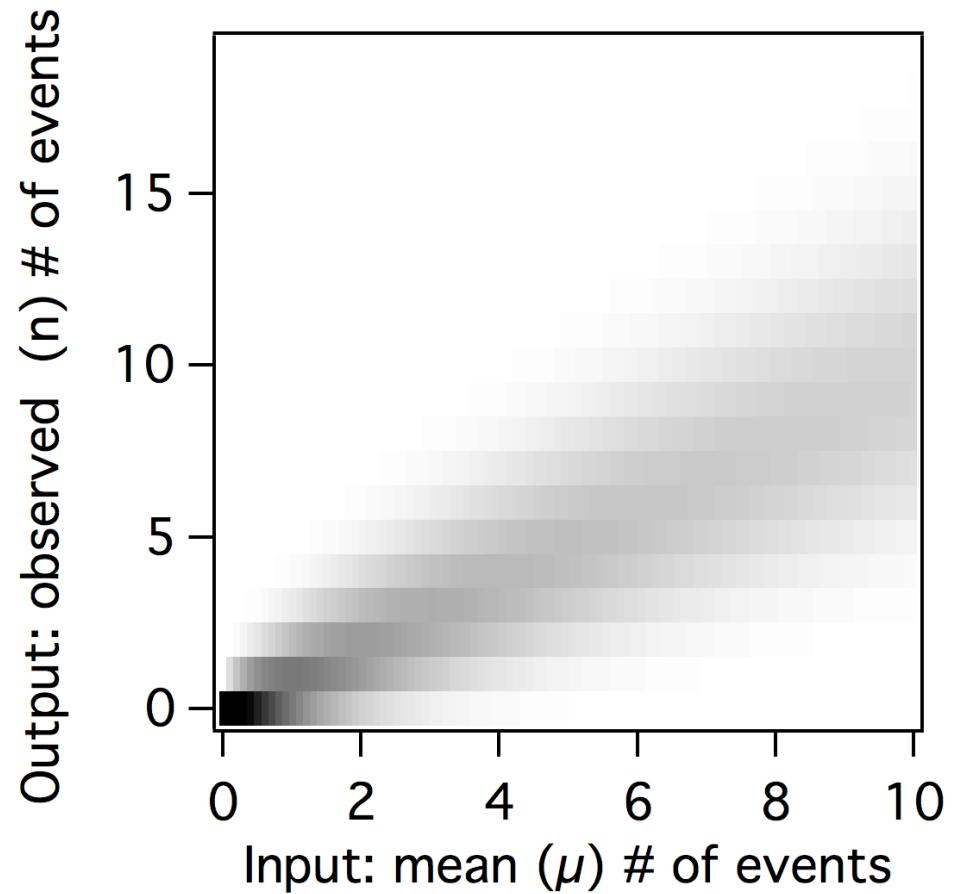
$$\frac{e^{-\mu} \mu^n}{n!}$$

$\mu$  = mean # of events in a time interval  
 $n$  = events in a time interval

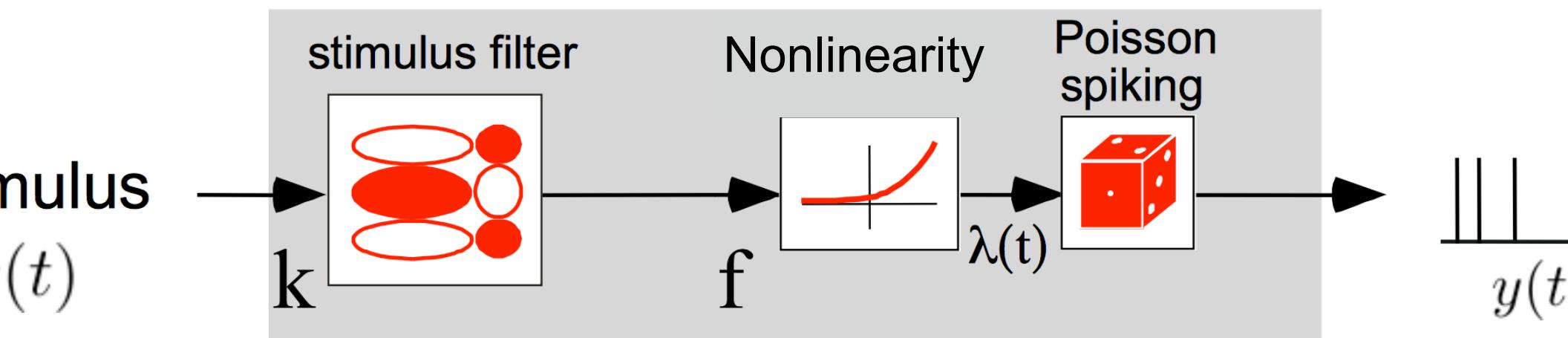


variance=mean= $\mu$

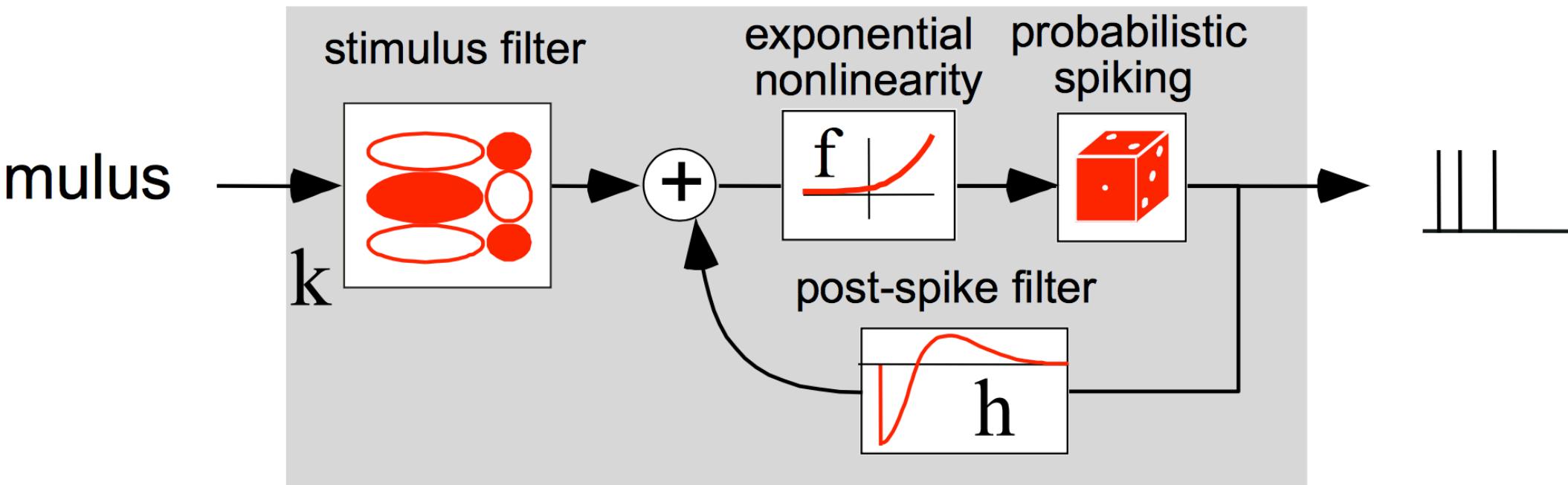
Joint probability distribution  $P[n,\mu]$



# Linear-Nonlinear-Poisson



# Generalized Linear Model

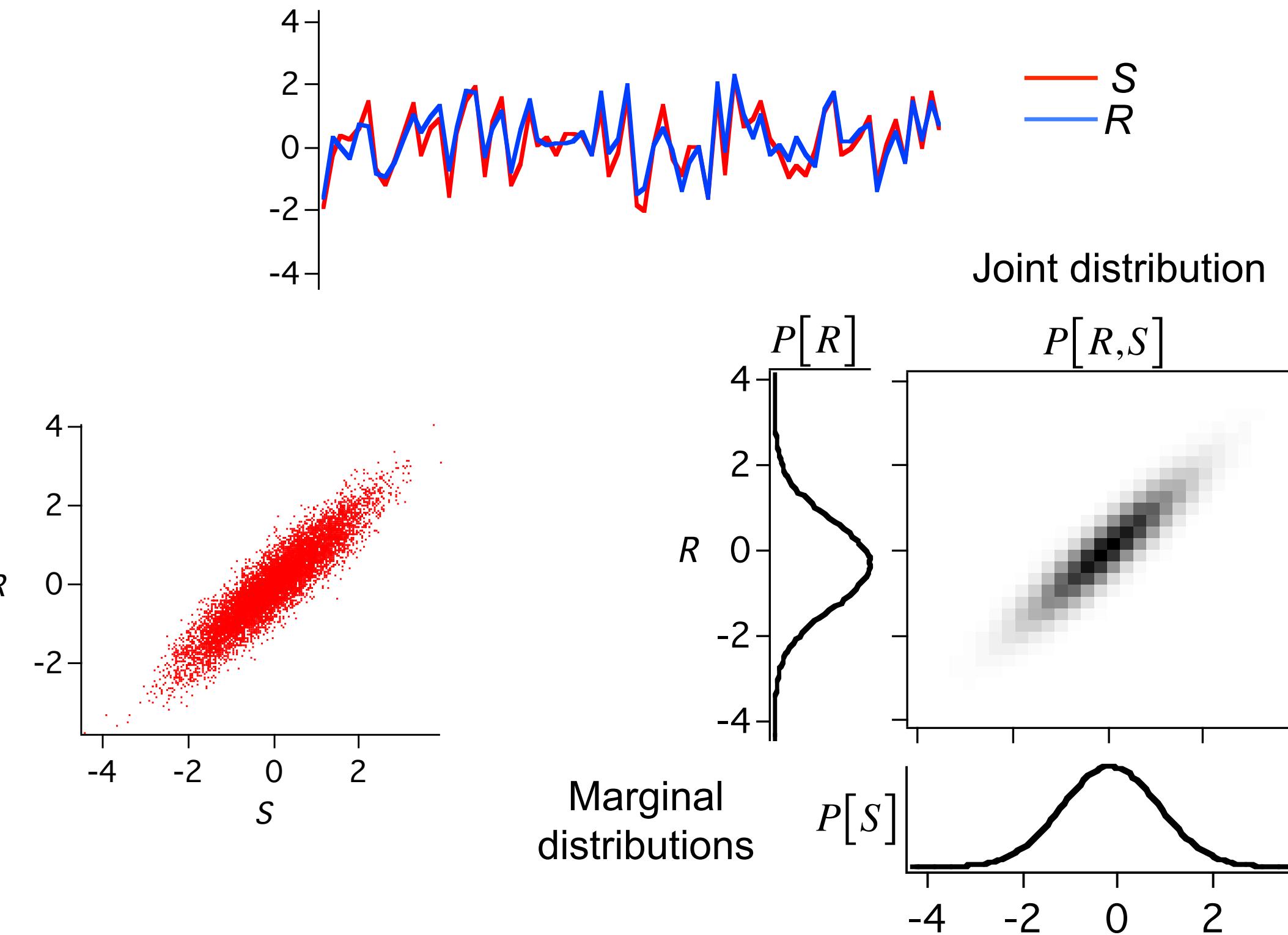


A form of LN model

Can be optimized, don't need Gaussian input

Is “convex”, meaning there are no local minima

Only works with “exponential family” distribution of responses, restricted nonlinearities



# A Mathematical Theory of Communication

## Claude Shannon (1948)

What is information?

### Entropy\*

A measure of uncertainty of a random variable in bits.

The maximum possible amount of information there is to be learned from a variable.

$$H(X) = - \sum_i P[x_i] \log P[x_i]$$

Entropy of a fair coin =

$$- \frac{1}{2} \log(1/2) - \frac{1}{2} \log(1/2) = 1 \text{ bit}$$

of an unfair coin =

$$- \frac{3}{4} \log(3/4) - \frac{1}{4} \log(1/4) = \sim 0.8 \text{ bits}$$

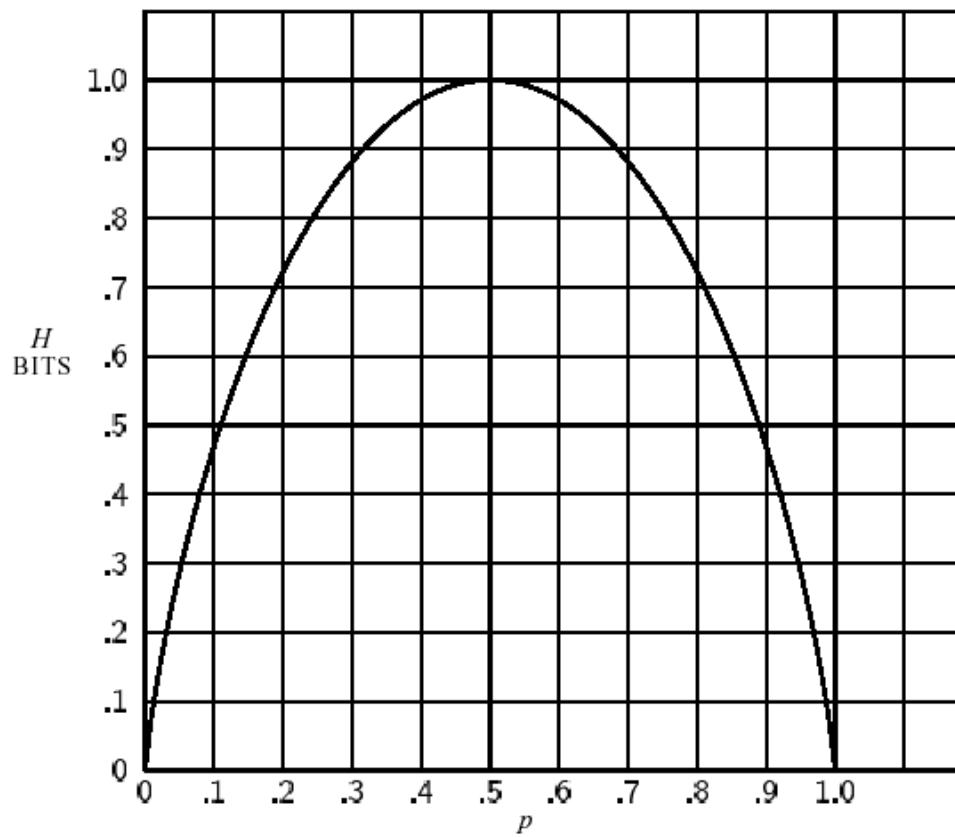
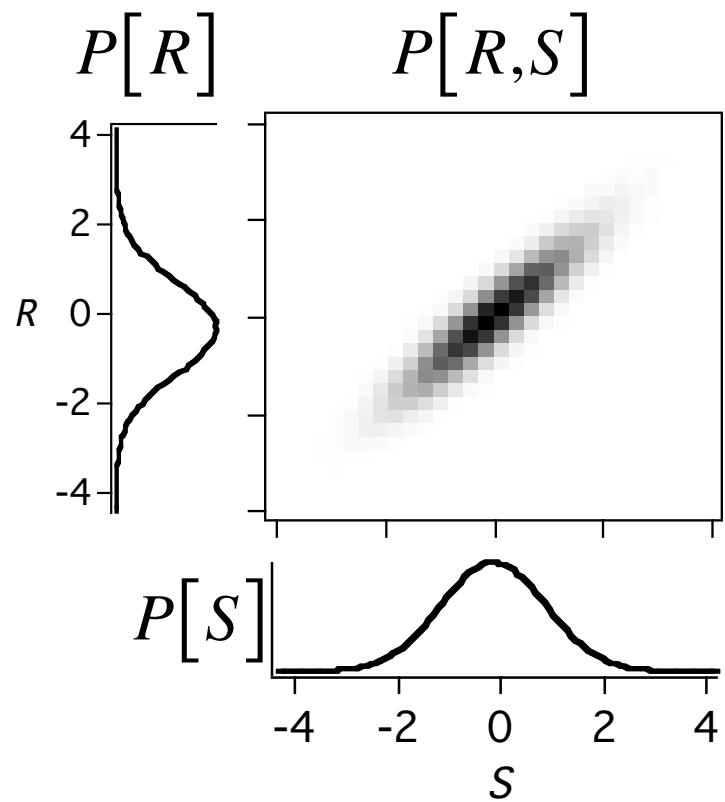


Fig. 7—Entropy in the case of two possibilities with probabilities  $p$  and  $(1-p)$

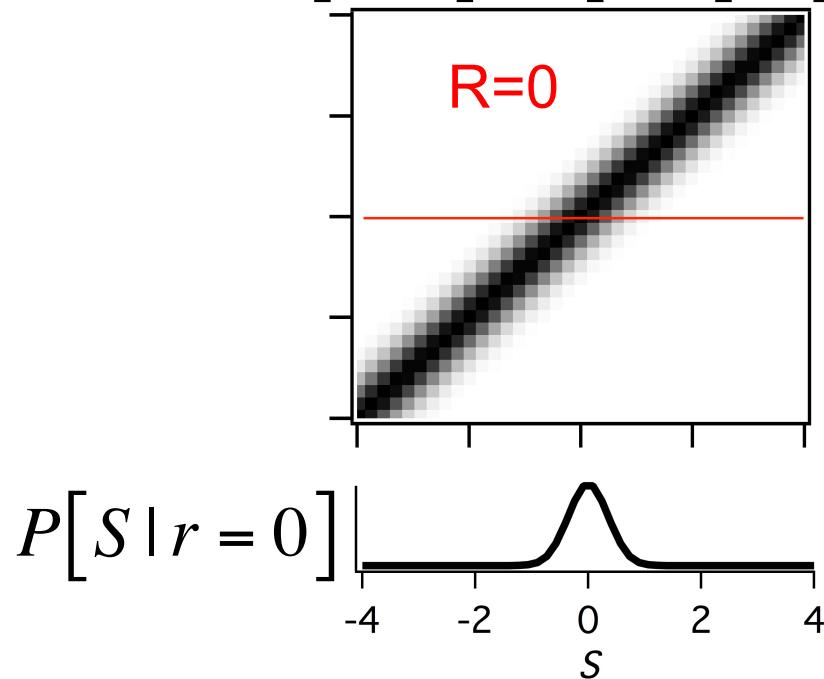
analogy to entropy in statistical mechanics,

$$S = k \log W$$

# Information is a reduction in entropy



Conditional distribution  
 $P[S|R] = P[R, S]/P[R]$



Conditional entropy

$$H(S|R) = - \sum_s \sum_r P(r,s) \log(P(s|r))$$

## Mutual information

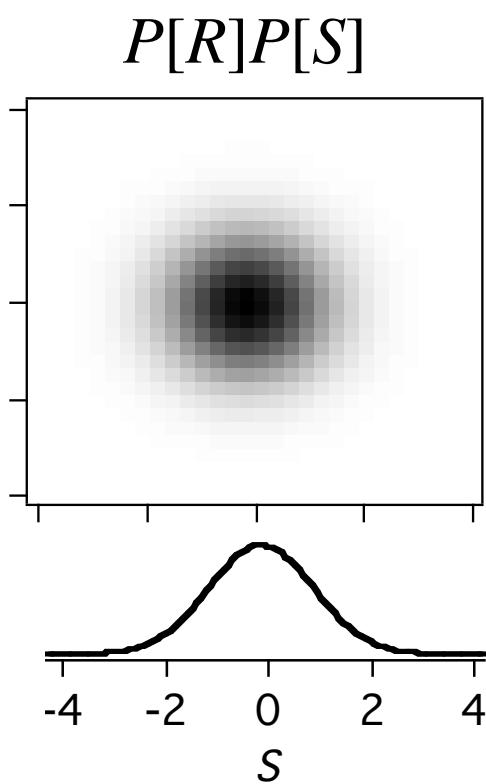
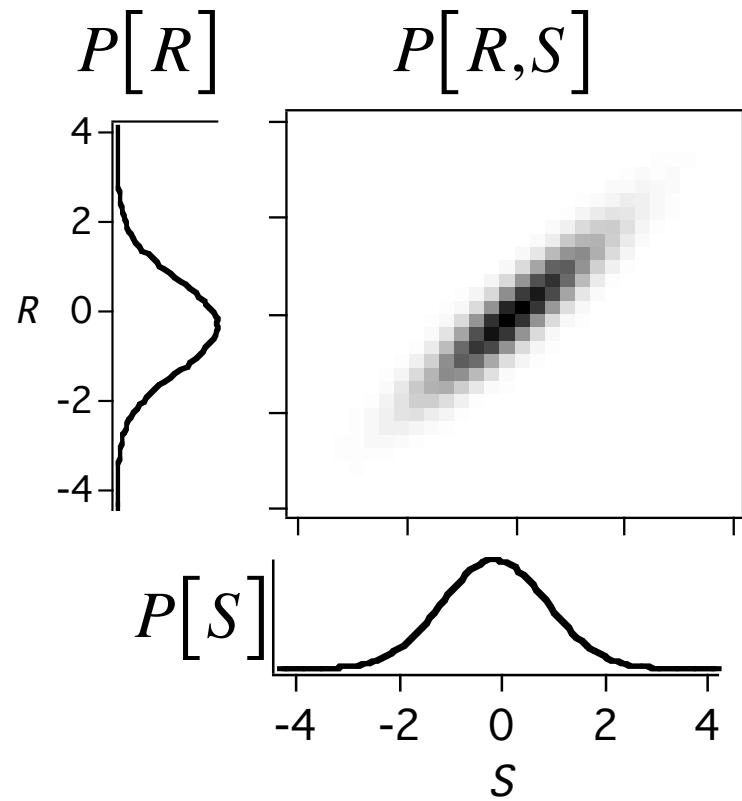
A measure, in bits, of how much information is conveyed by one random variable about another random variable. It is equal to the entropy minus the conditional entropy.

$$I(S;R) = H(S) - H(S|R)$$

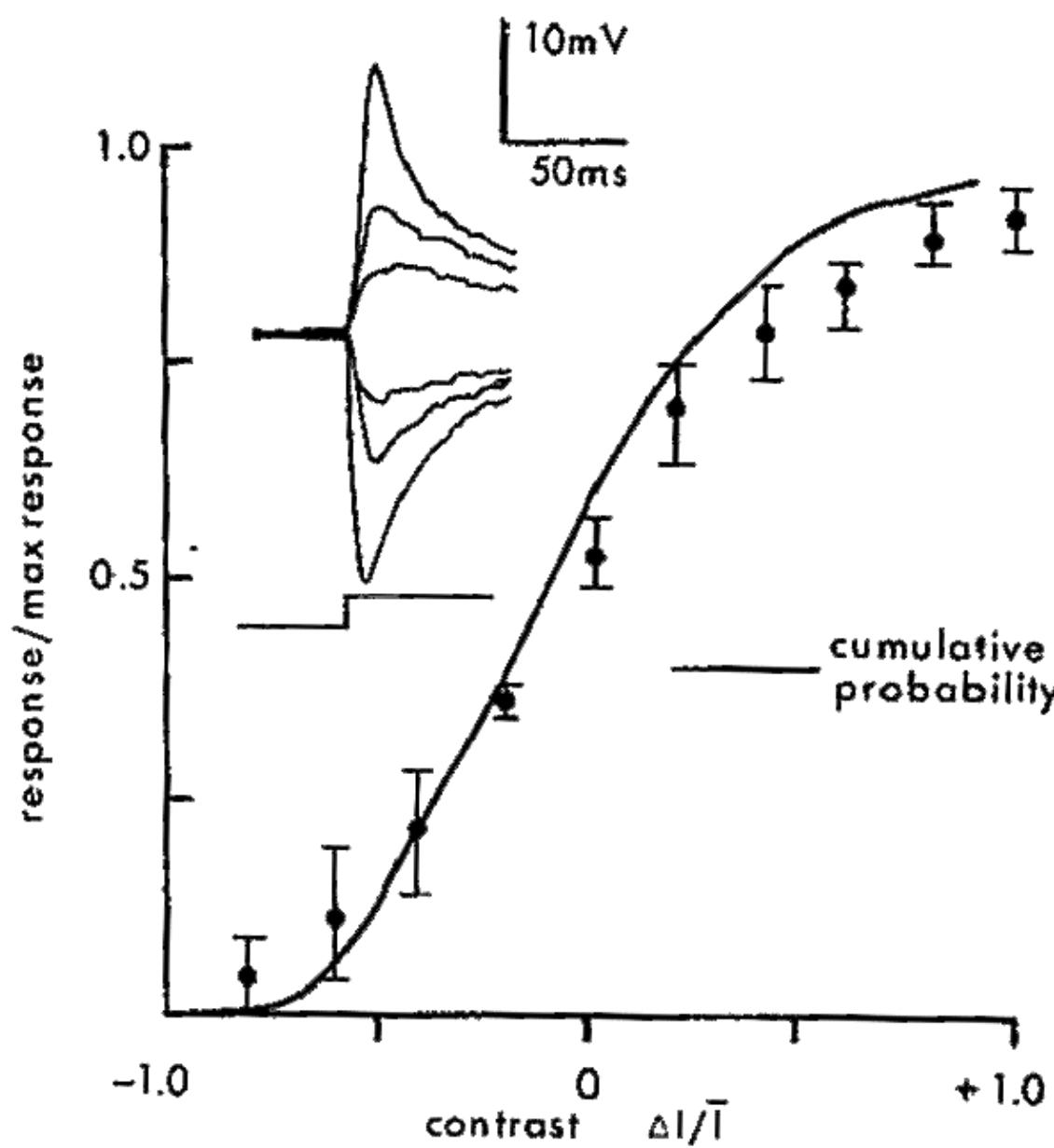
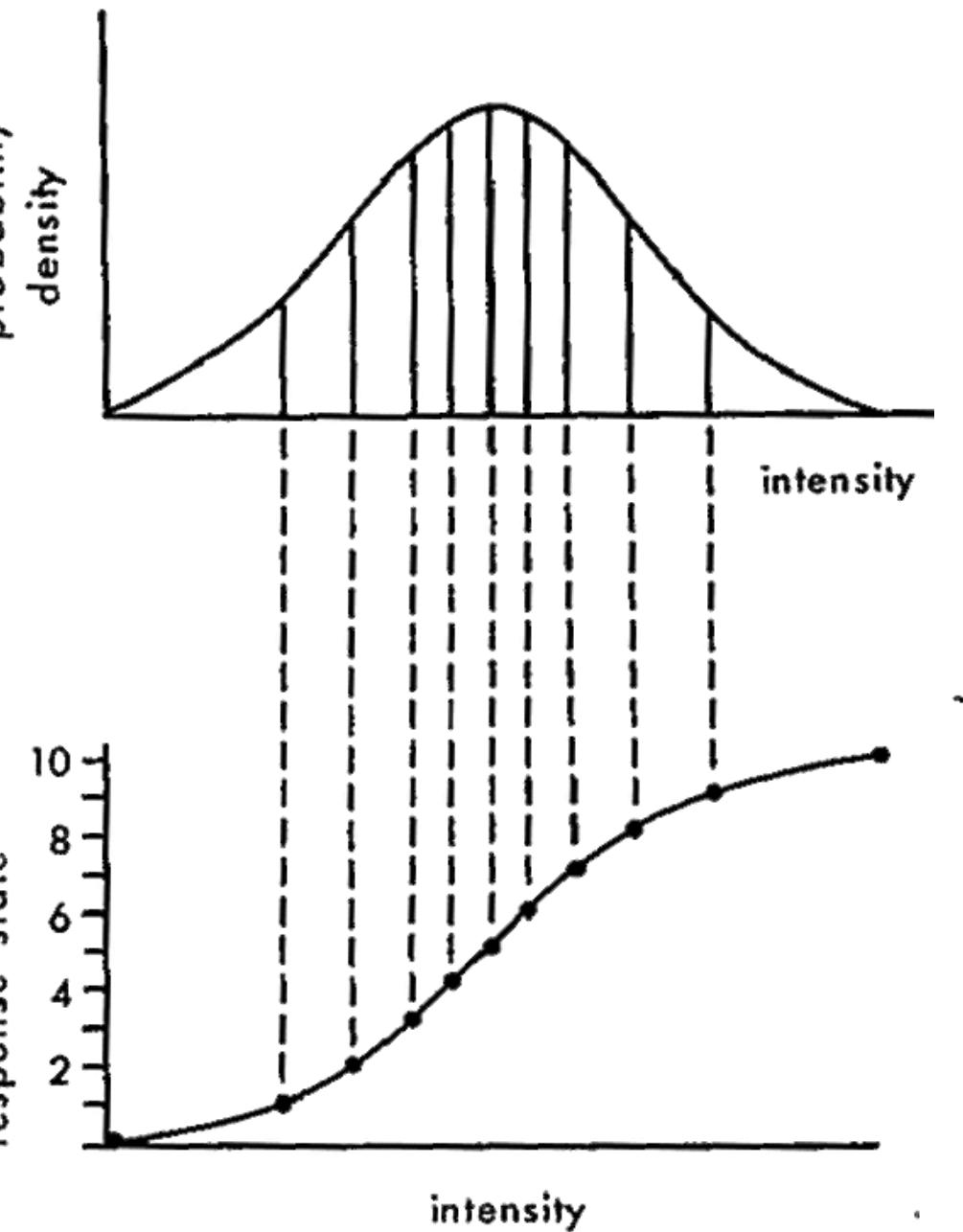
$$I(R;S) = I(S;R)$$

Mutual information as the ‘distance’ between two probability distributions

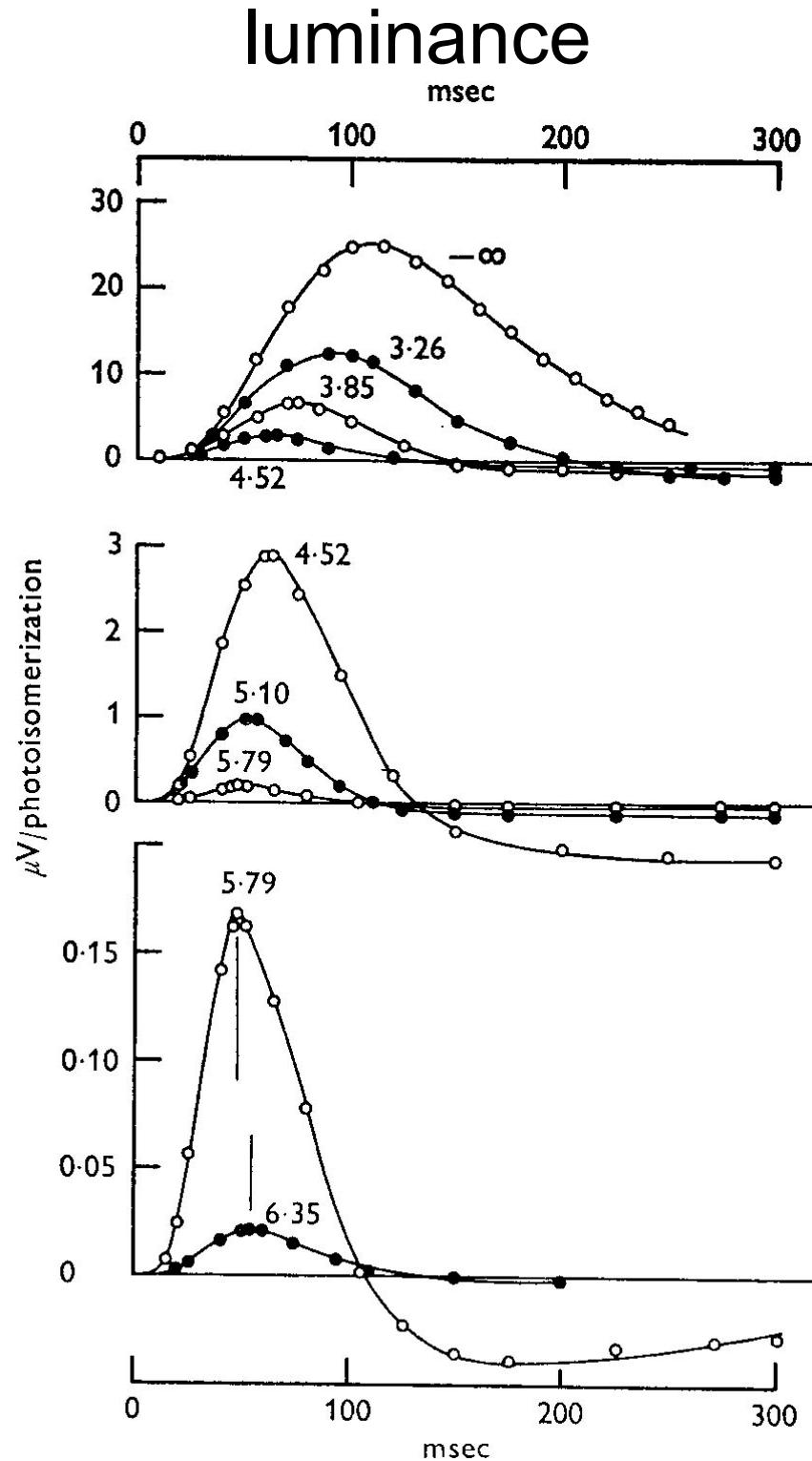
Product distribution – what things would  
look like with zero information



$$I(R;S) = \sum_i \sum_j P[R_i, S_j] \log \left( \frac{P[R_i, S_j]}{P[R_i]P[S_j]} \right)$$

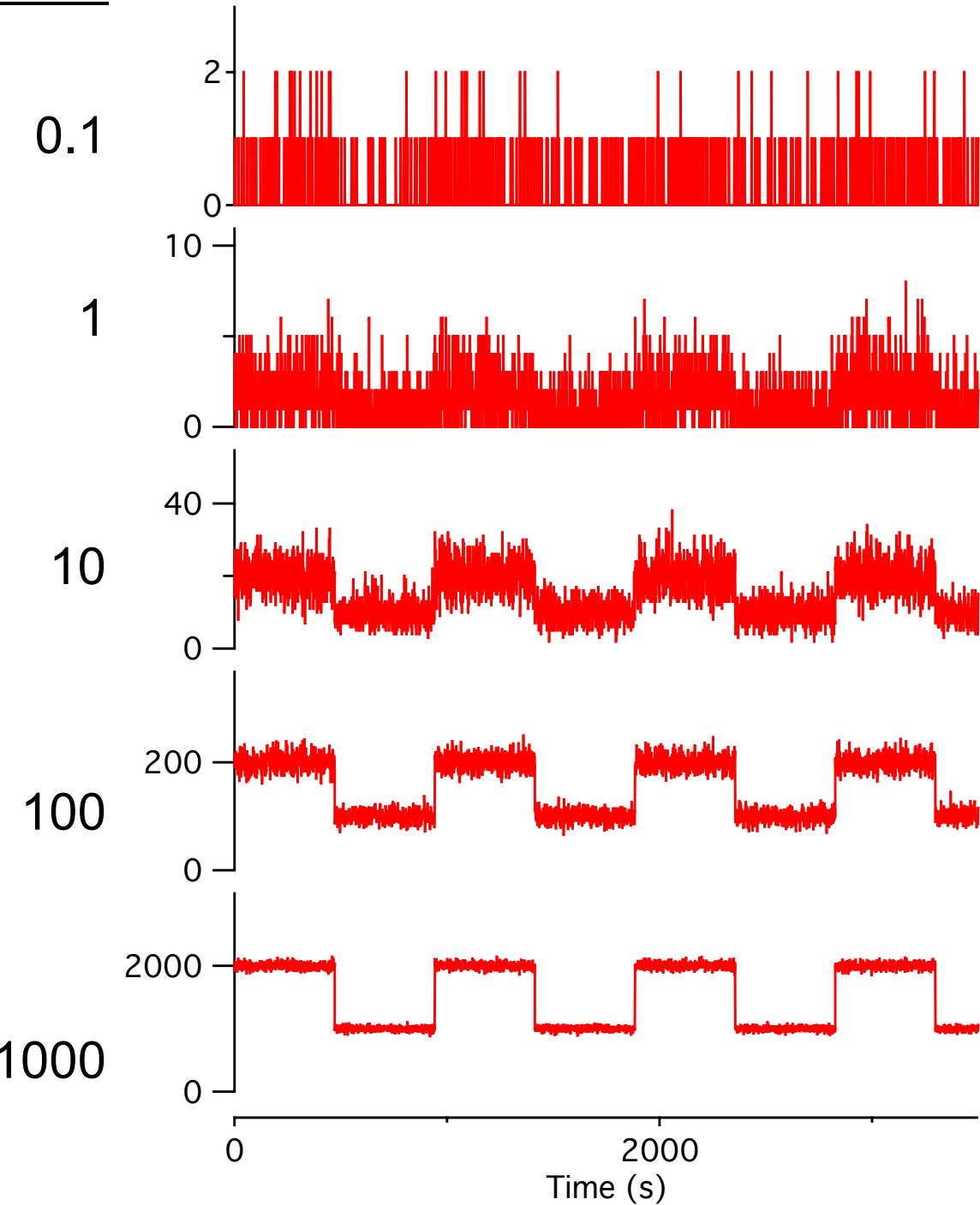


# Turtle Cones: Sensitivity and Kinetics change with mean luminance

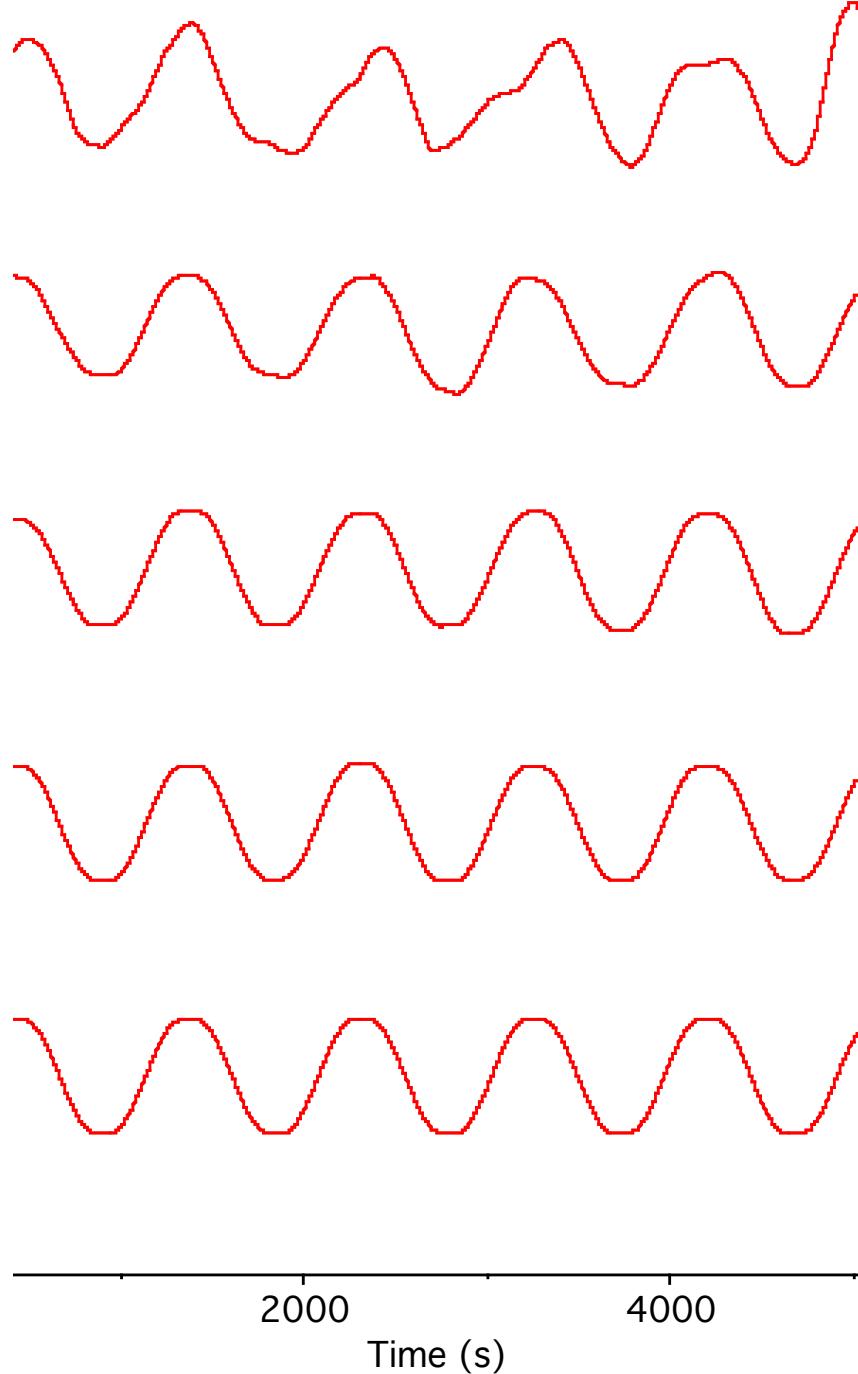


# Signal with poisson distribution

Rate

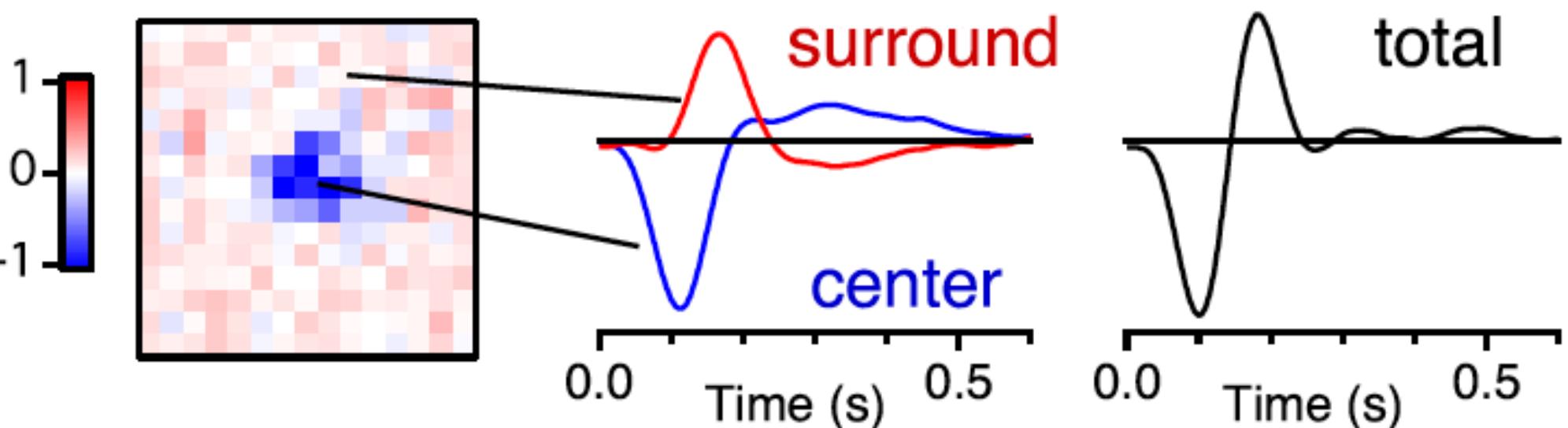


Filtered



# What receptive field maximizes information transmission?

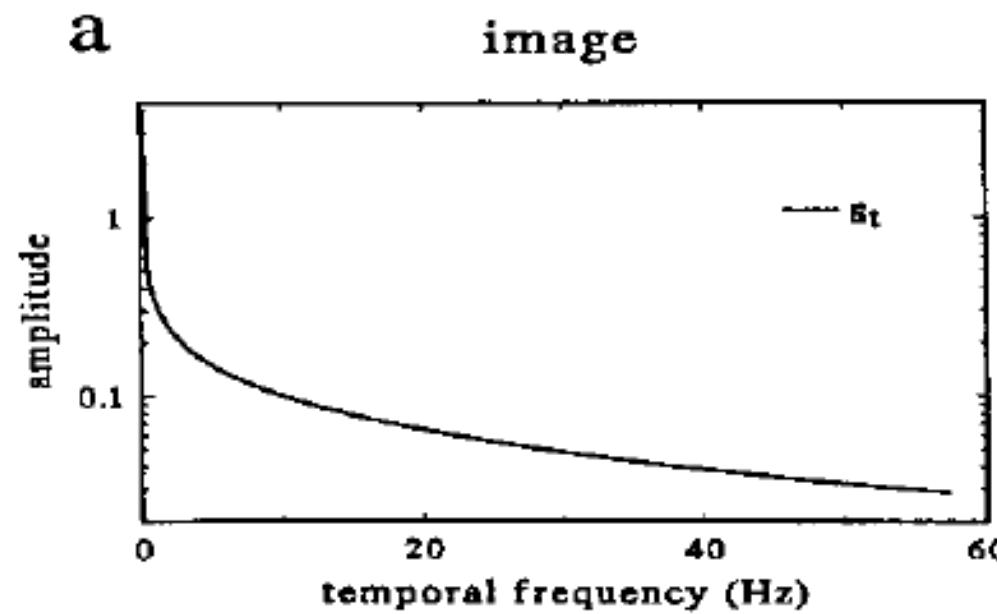
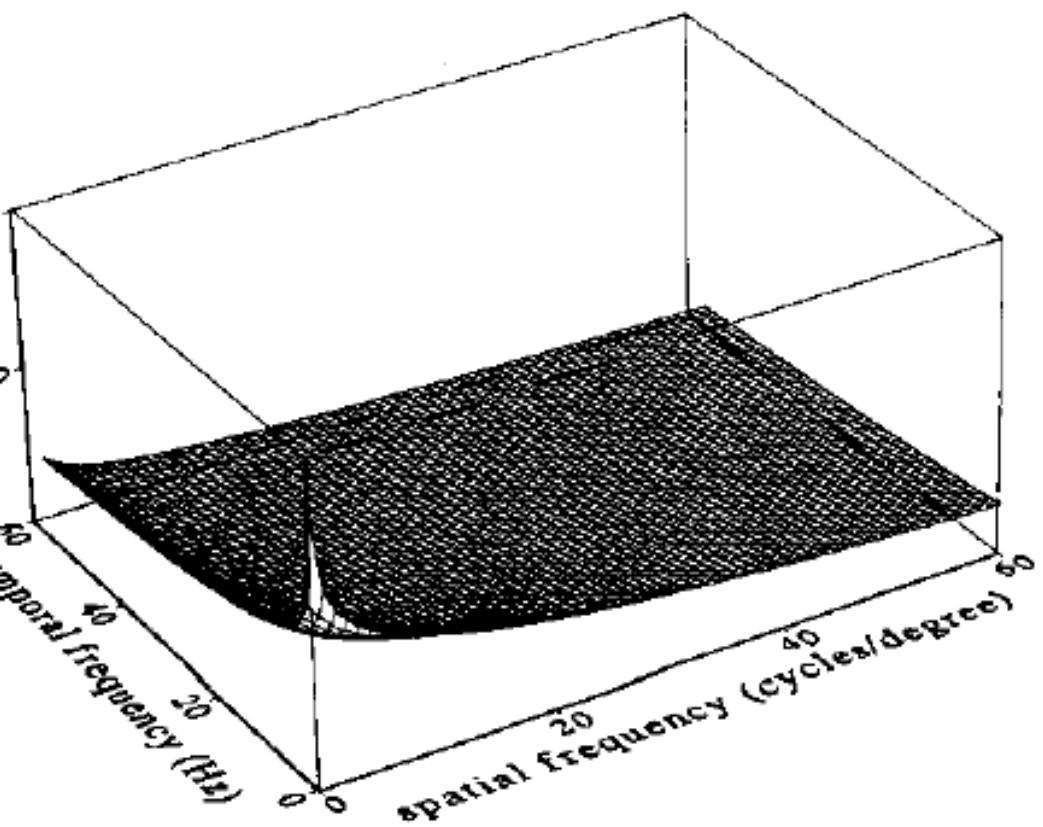
## Retinal bipolar cell receptive field



# Theory of maximizing information in a noisy neural system

'Efficient Coding' - Horace Barlow

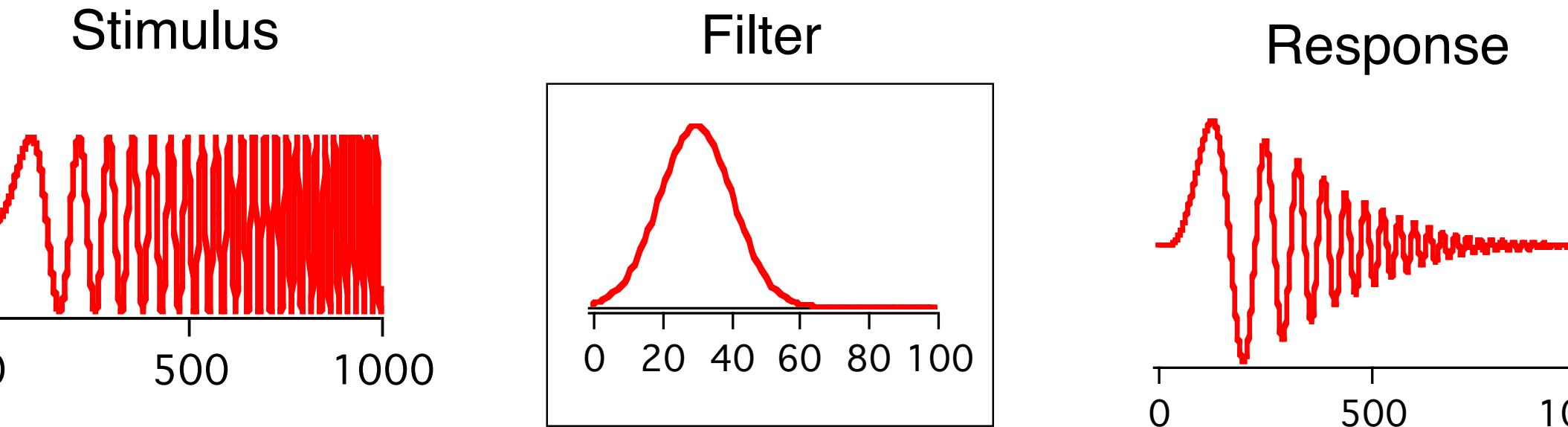
Natural visual scenes are dominated by low spatial and temporal frequencies



van Hateren. Real and optimal neural images in early vision. *Nature* 360:68-70 (1992)

van Hateren. Spatiotemporal contrast sensitivity of early vision. *Vision Res.* 33:257-67 (1993)

## Linear filter and frequency response



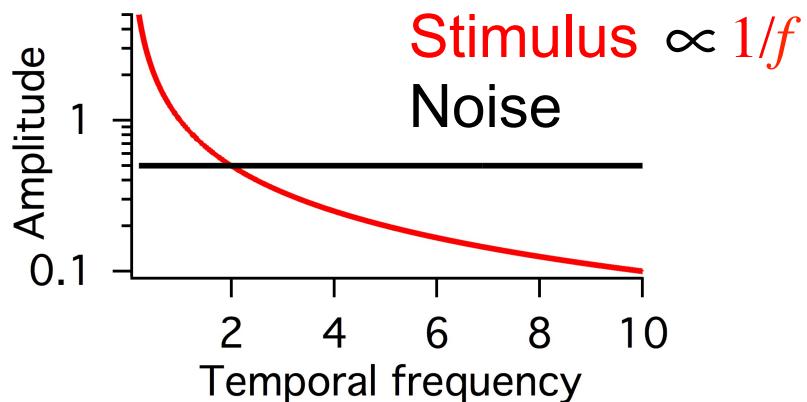
## Convolution theorem

$$h(t) = f(t) * g(t) \Leftrightarrow \tilde{h}(\omega) = \tilde{f}(\omega)\tilde{g}(\omega)$$

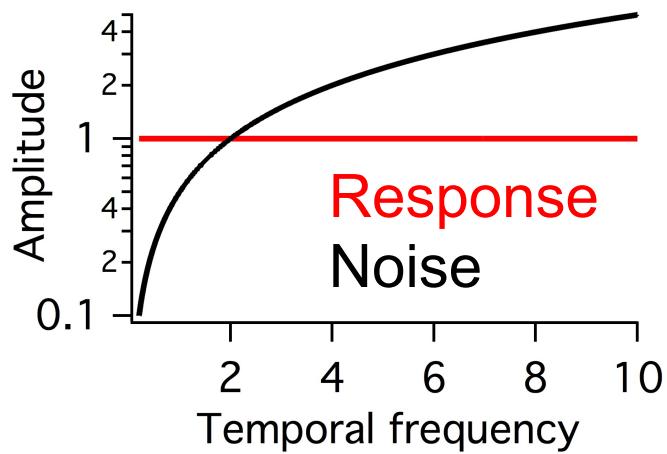
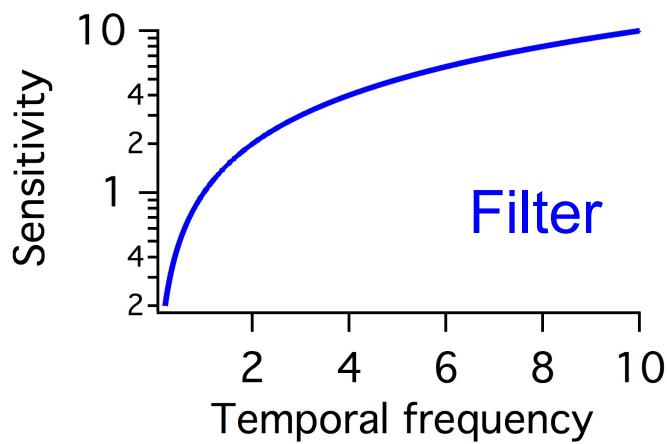
a convolution in the  
time domain

is a simple product in the  
frequency domain

# Optimal filter whitens but also cuts out noise



'Whitening' filter



## Filter to whiten in the presence of noise

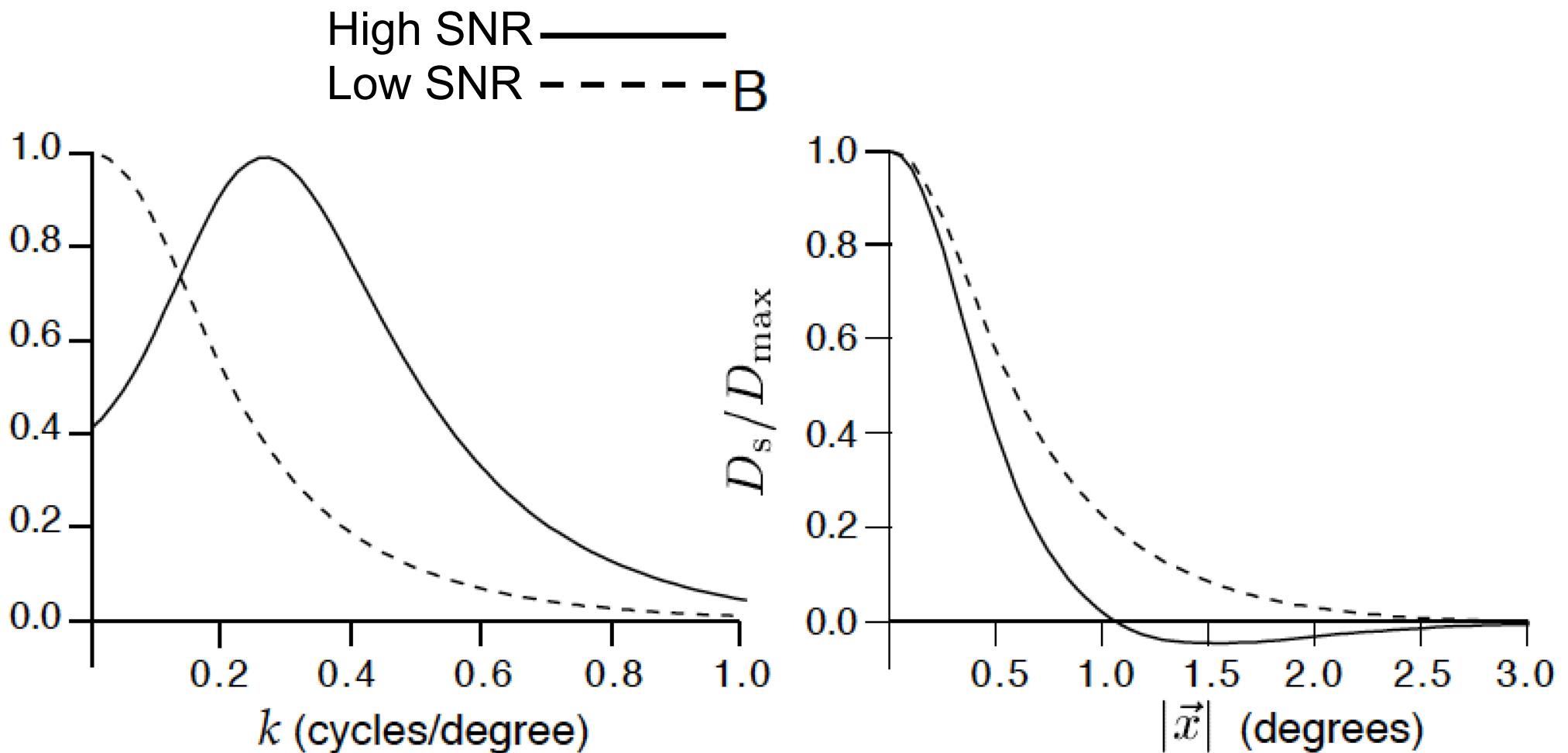
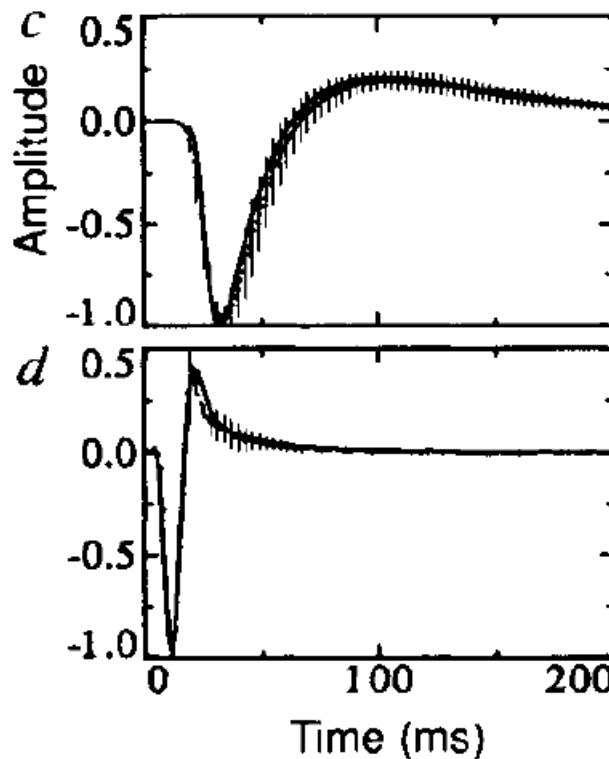


Figure 4.3: Receptive field properties predicted by entropy maximization and

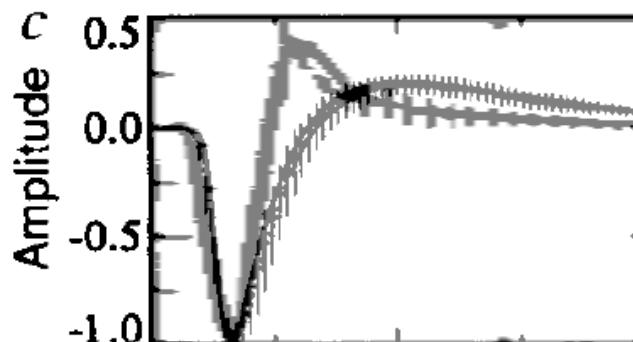
# Theory of maximizing information in a noisy neural system

Filter of fly Large Monopolar Cells,  
2nd order visual neuron



Low background intensity  
Integrates over time  
(real and theoretical optimum)

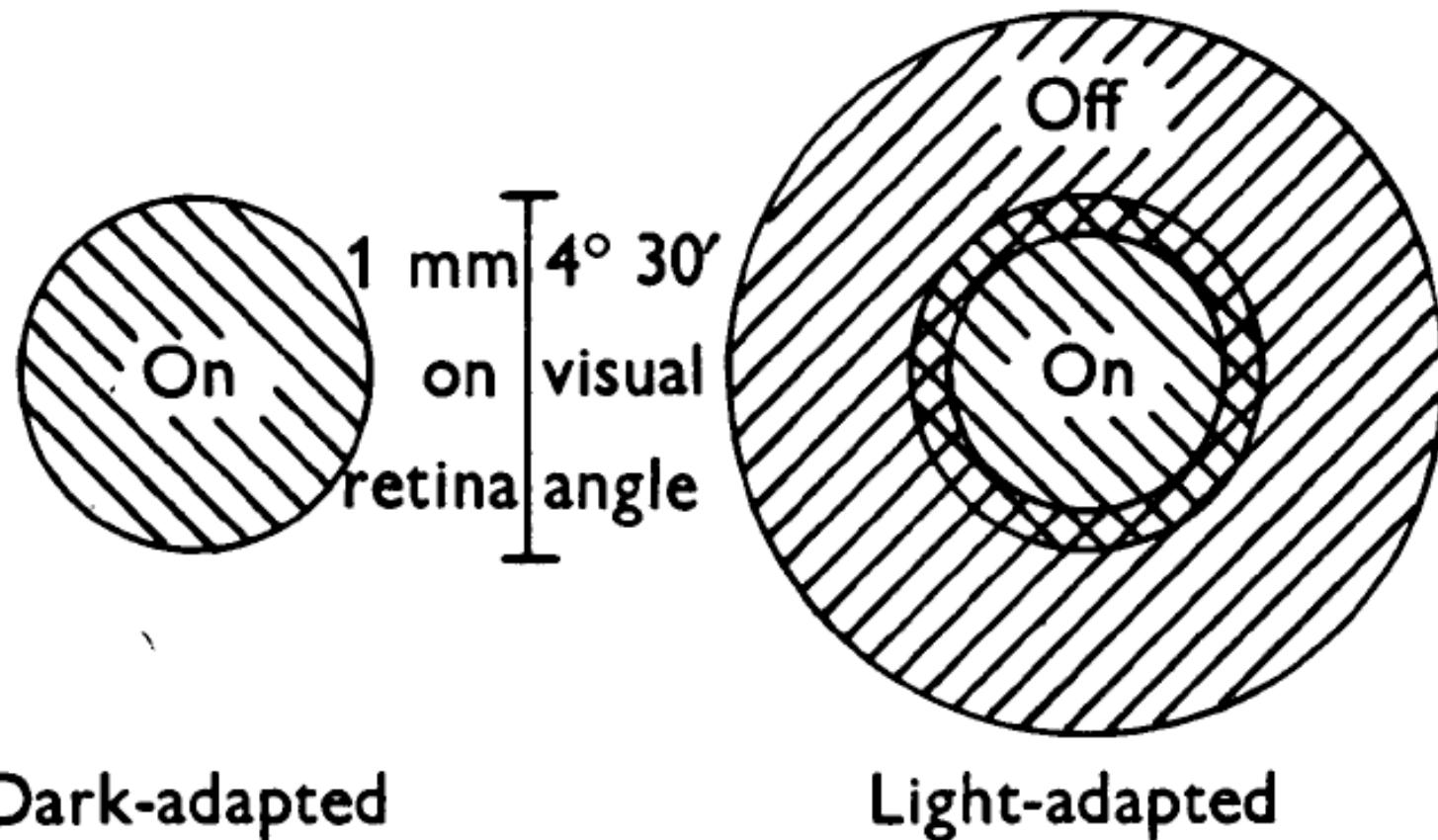
High background intensity  
Emphasizes change, is more  
differentiating  
(real and theoretical optimum)



Both, scaled in time to  
the first peak

# Spatial adaptation in retinal ganglion cells

Receptive field of on-centre unit



Theories of efficient coding:

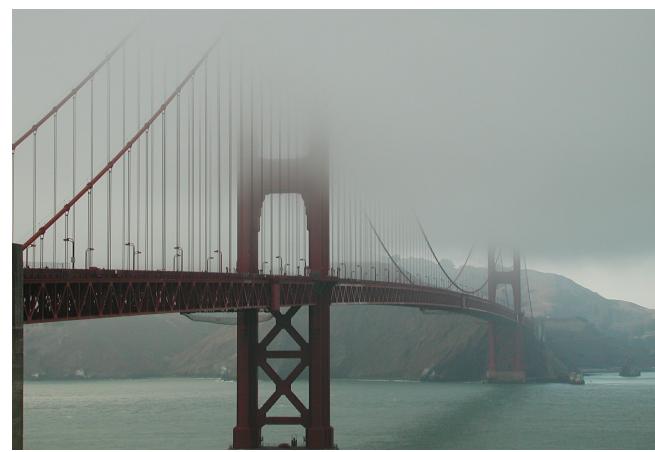
An ideal encoder should use all output values with equal probability

Low frequencies dominate in natural scenes

An efficient encoder should amplify higher frequencies more than low frequencies

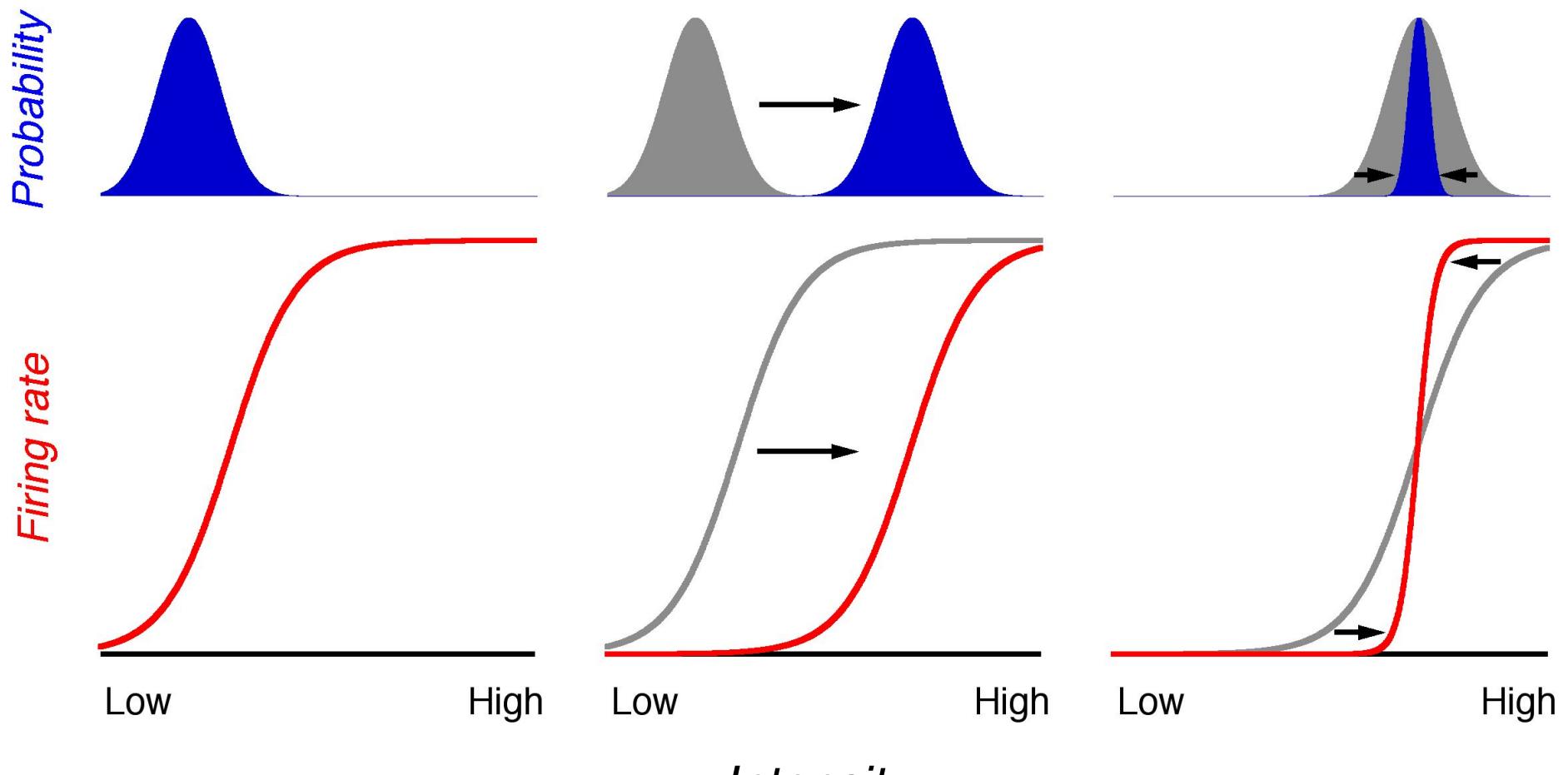
But when signals are more noisy, such as when the signal is weak, higher frequencies should be reduced, as they carry little information

# Adaptation to mean and variance



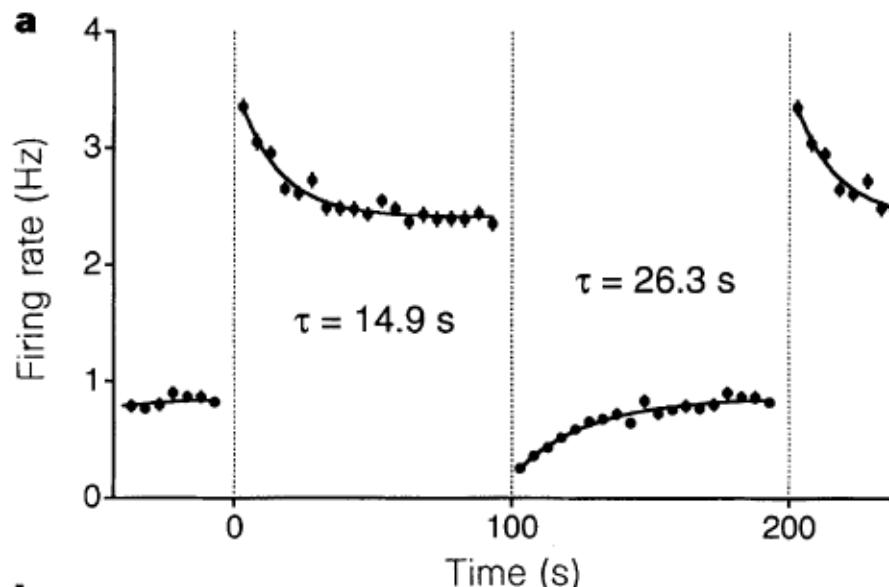
Light adaptation

Contrast adaptation

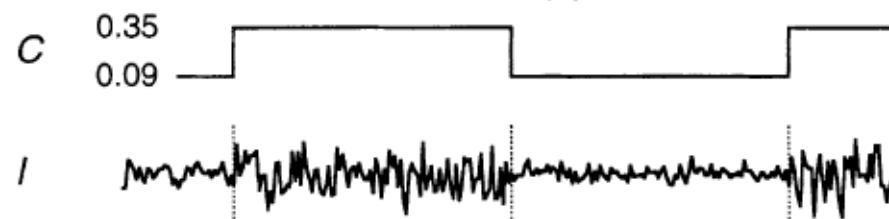
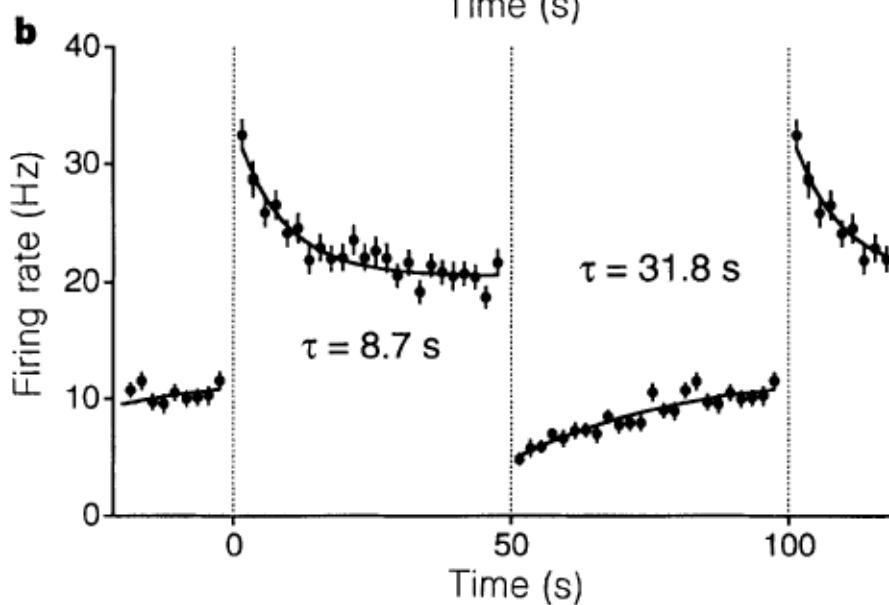


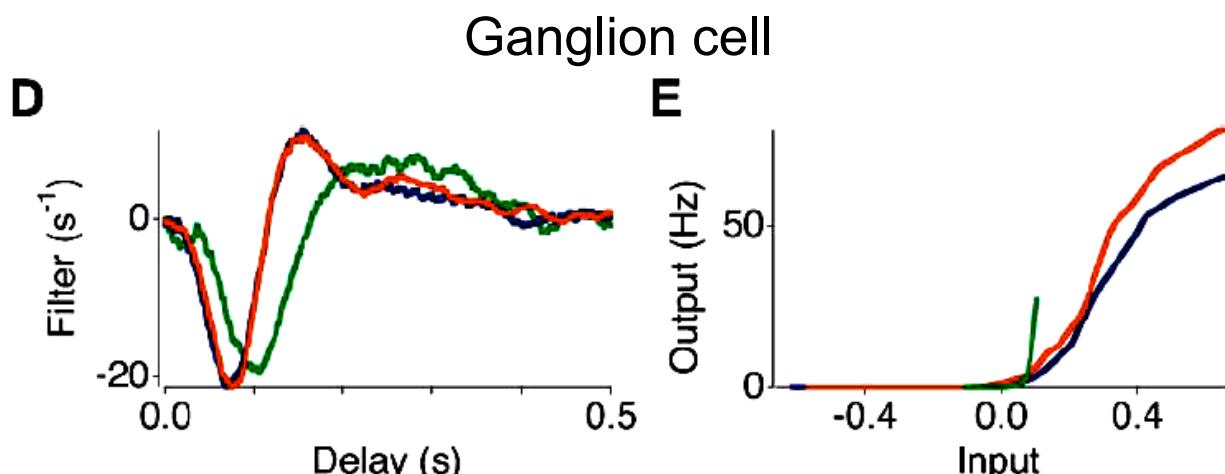
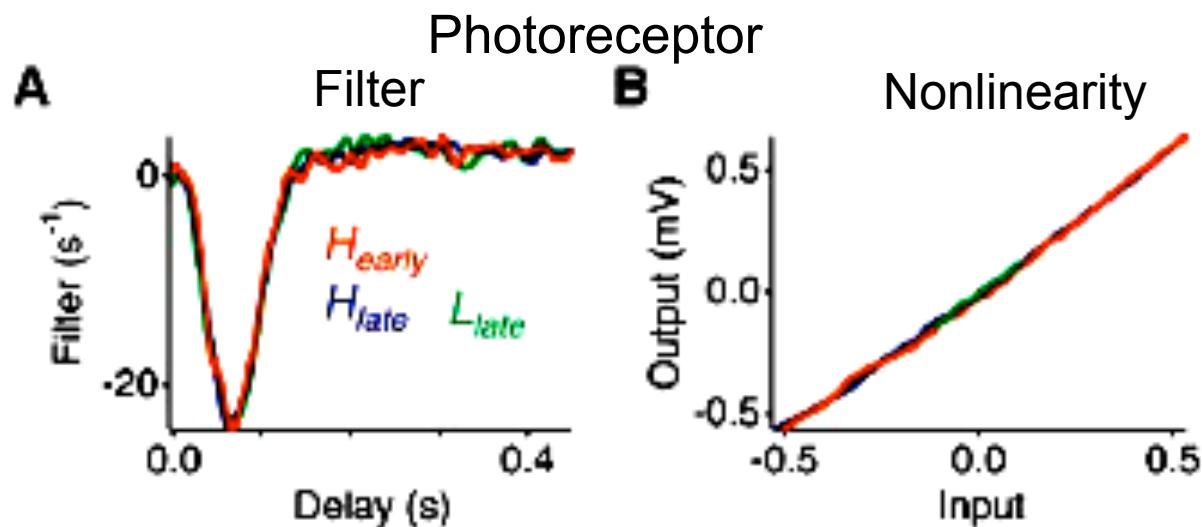
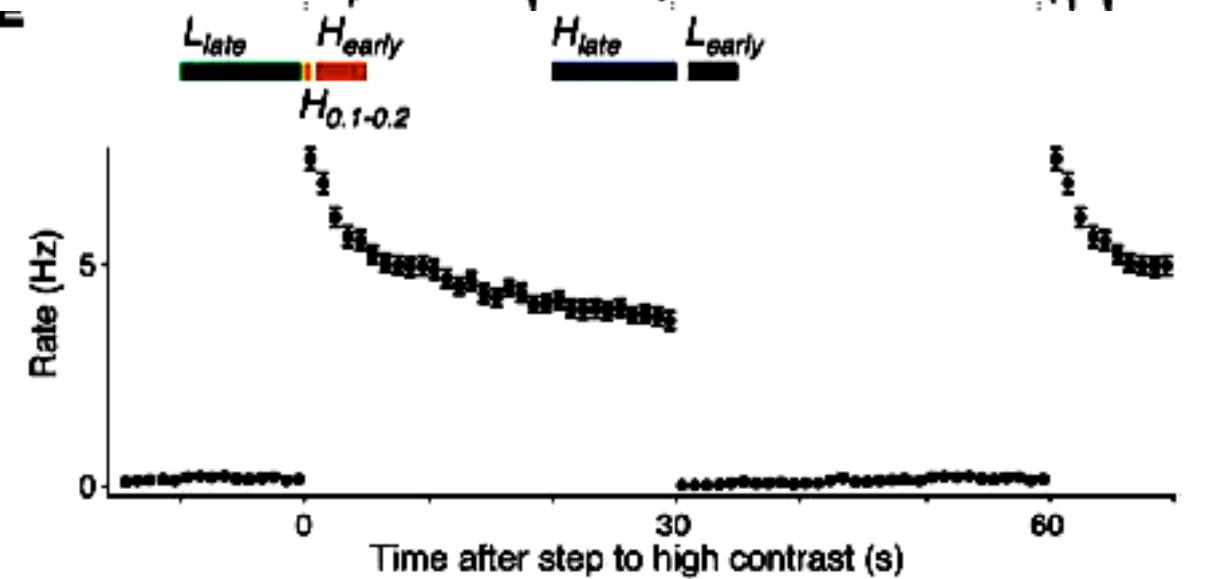
# Retinal contrast adaptation

Salamander

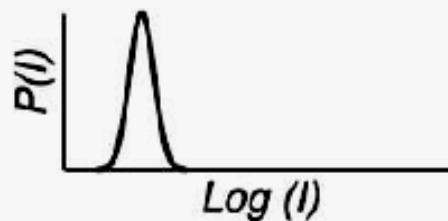


Rabbit

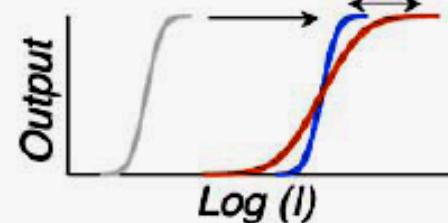
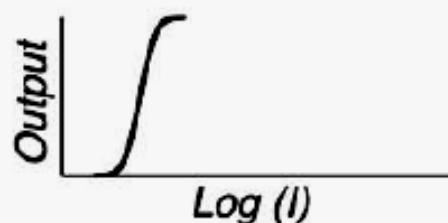
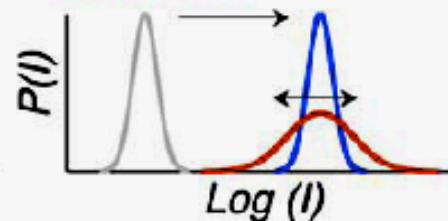




Low mean  
(loudness, luminance)



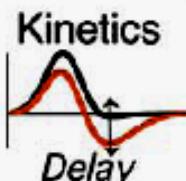
High mean  
(loudness, luminance)  
High variance  
(contrast)



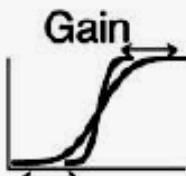
Avian  
auditory  
forebrain

Vertebrate  
retina

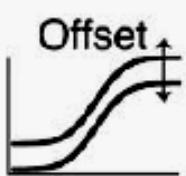
Fly motion  
sensitive  
neuron H1



Changes quickly

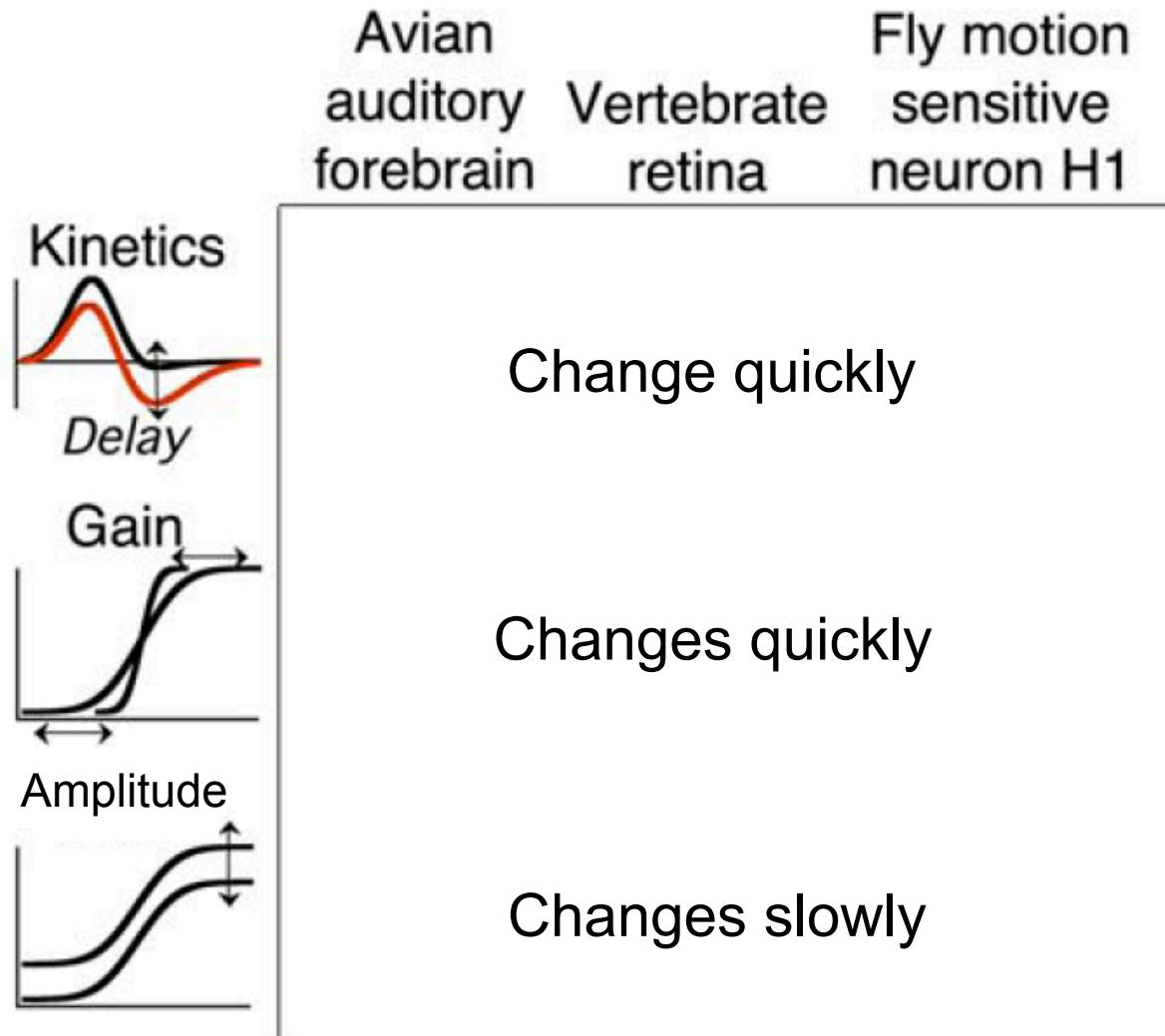


Changes quickly



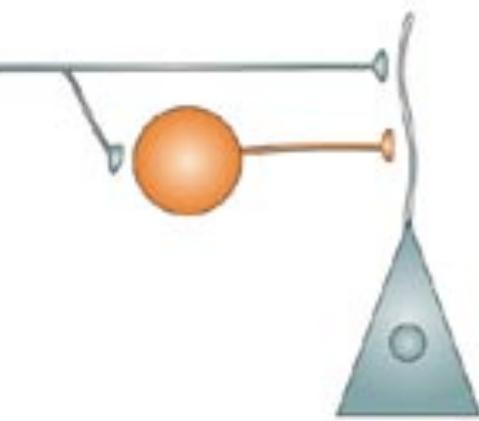
Changes slowly

# Common properties of contrast adaptation

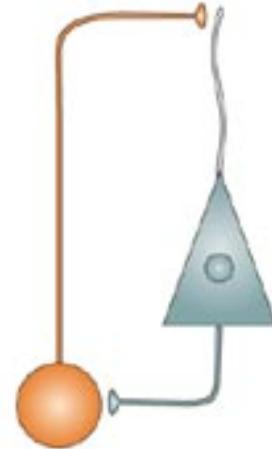


# Change in sensitivity by *modulation*

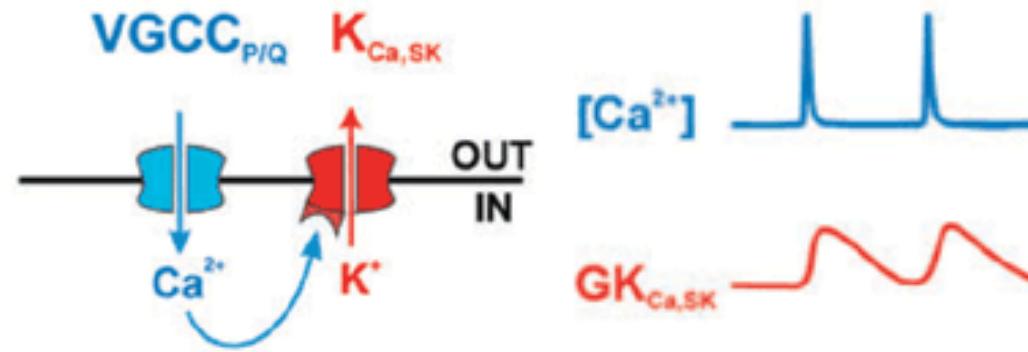
Feedforward inhibition



Feedback inhibition

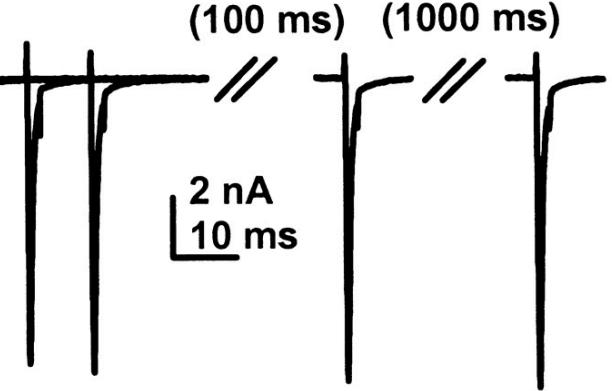


Spike dependent conductances

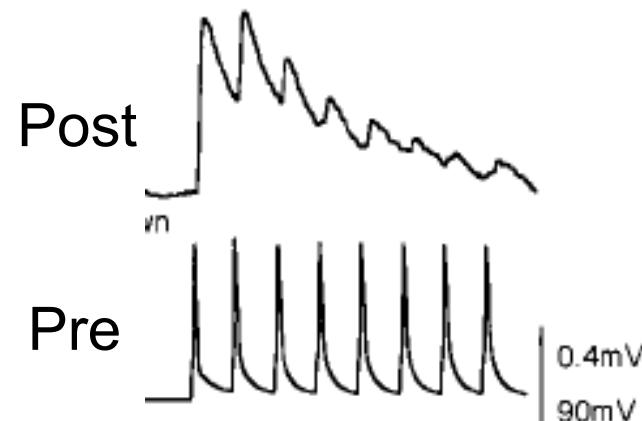


# Change in sensitivity by *depletion*

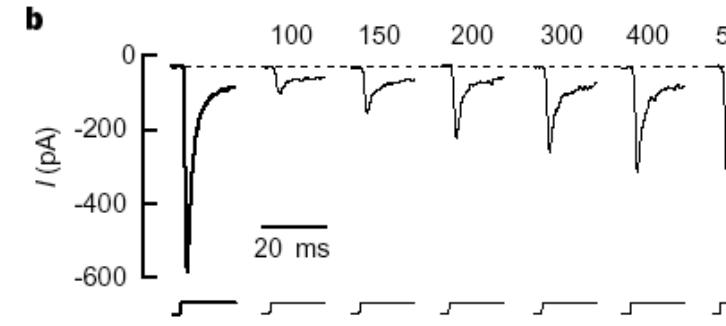
Ion channel inactivation



Short-term synaptic plasticity  
synaptic depression

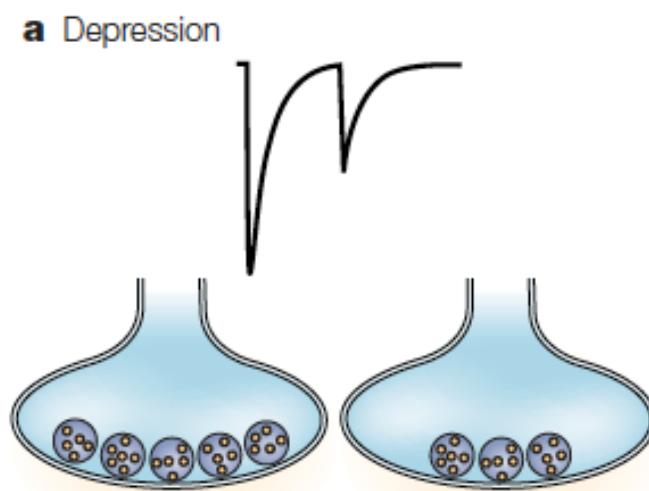
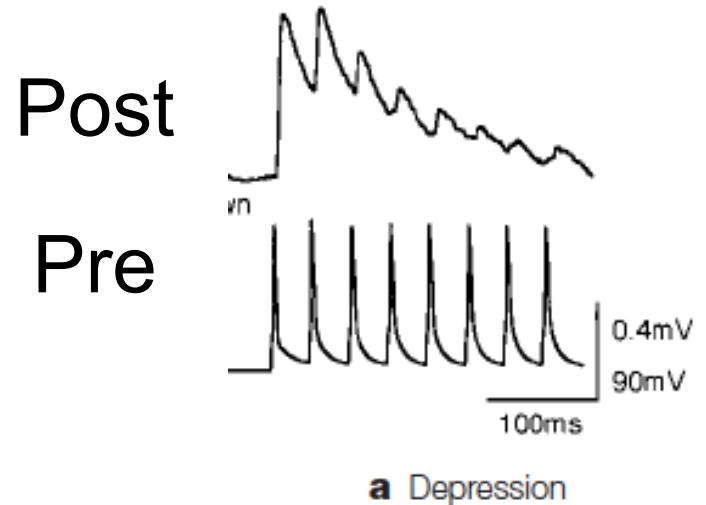


Receptor desensitization



# Short-term synaptic plasticity – synaptic depression

Number of vesicle  
Probability of vesicle release  
 $\text{Release} = n \times p$

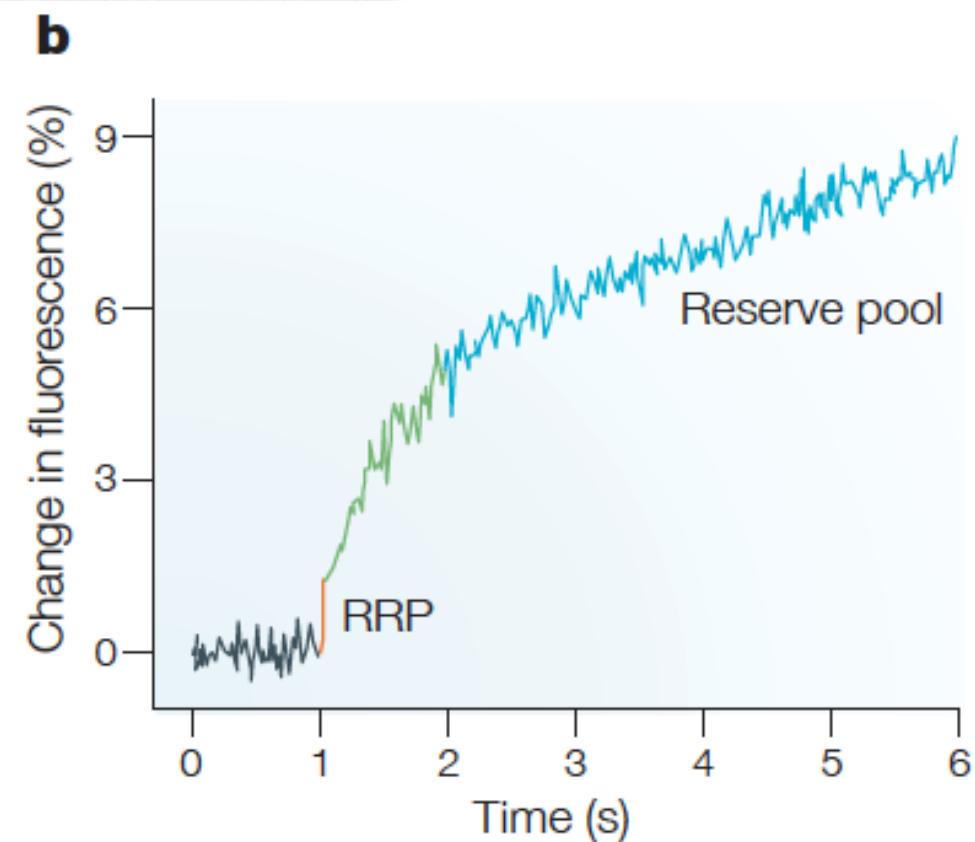
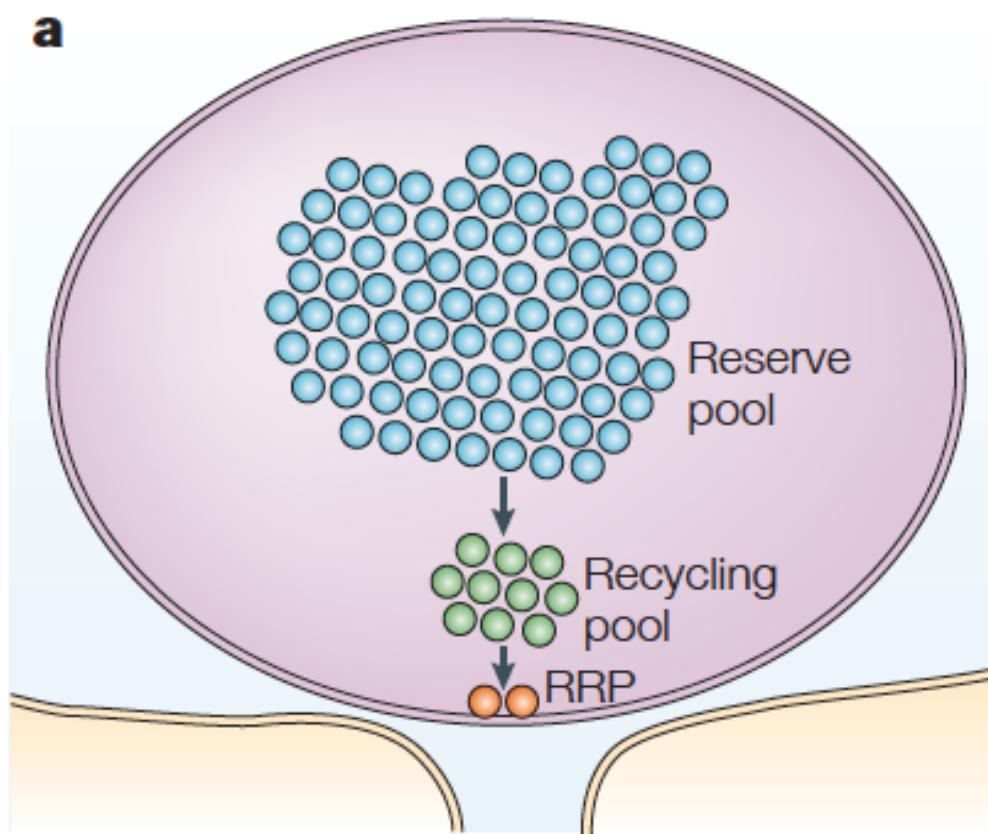
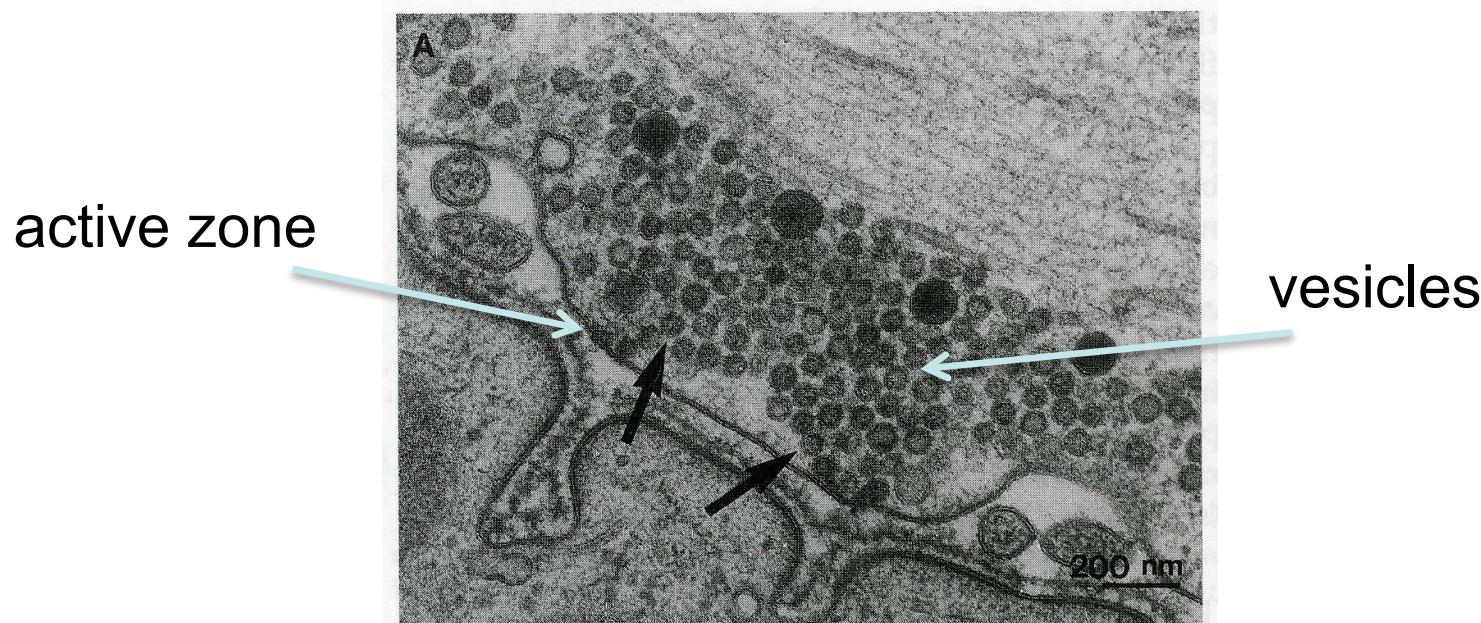


$$\frac{dn(t)}{dt} = \underbrace{\frac{1 - n(t)}{\tau_r}}_{\text{replenishment}} - \underbrace{\sum_j \delta(t - t_j) \cdot p \cdot n(t)}_{\text{release}}$$

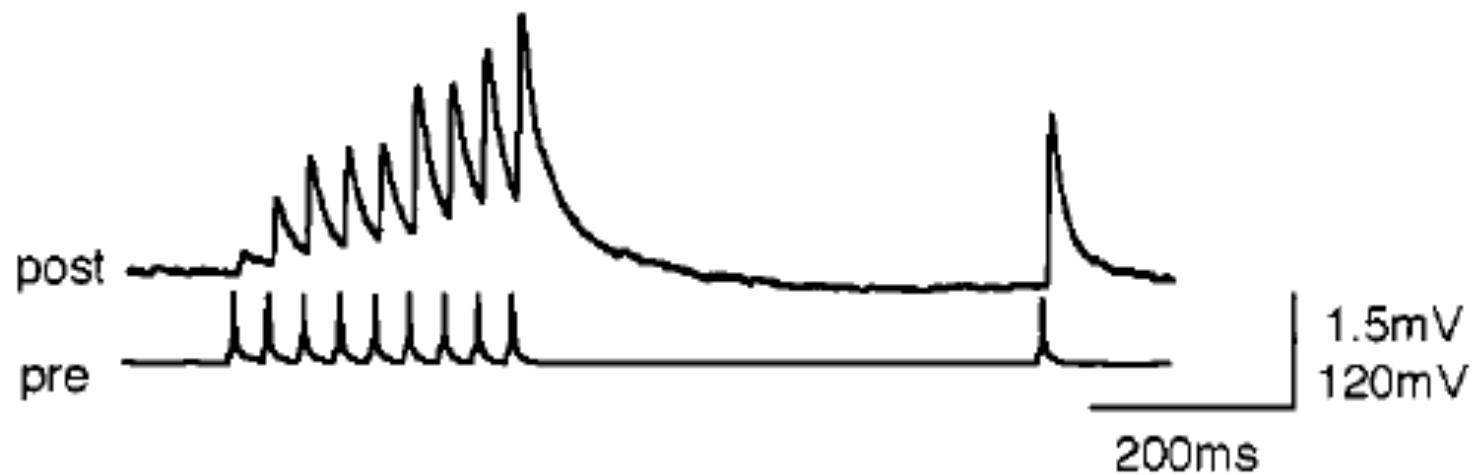
Depletion of available vesicles  
a mechanism for depression

Hennig, 2013. Theoretical model of synaptic short term plasticity

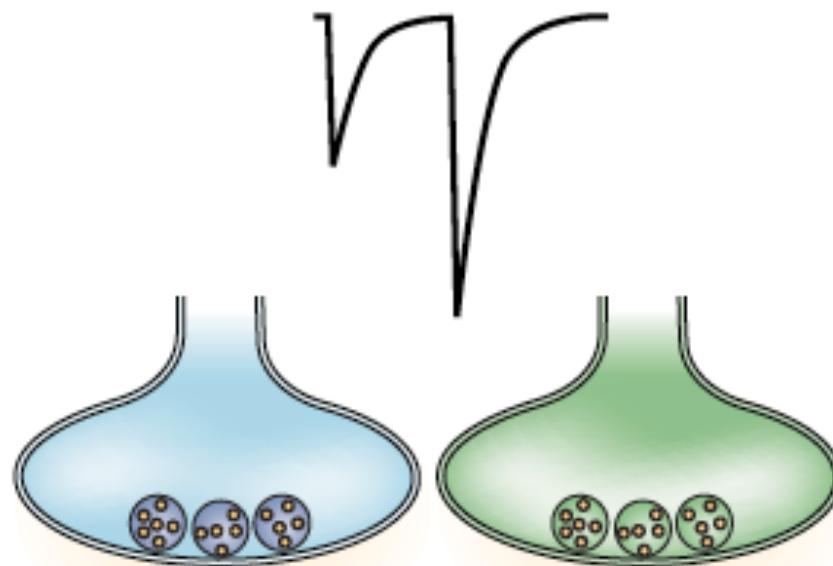
# Vesicle release has dynamics over multiple timescales



# Short-term synaptic plasticity – synaptic facilitation



**b** Facilitation



Residual calcium  
as a mechanism  
for increased  
release

$$\frac{dp(t)}{dt} = \frac{p_0 - p(t)}{\tau_f} + \sum_j \delta(t - t_j) \cdot a_f \cdot (1 - p(t))$$