Lecture 4 – 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?

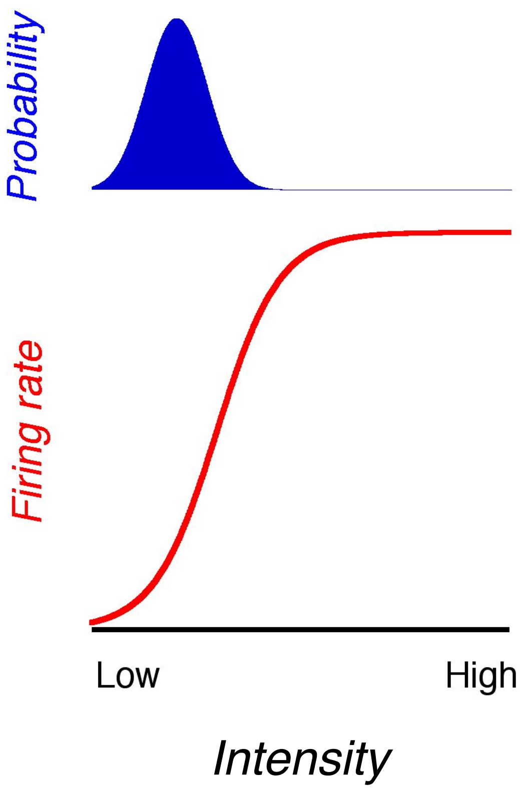
Why do cells have a certain duration filter?

Why do they have a certain shape filter?

Why does the filter change?

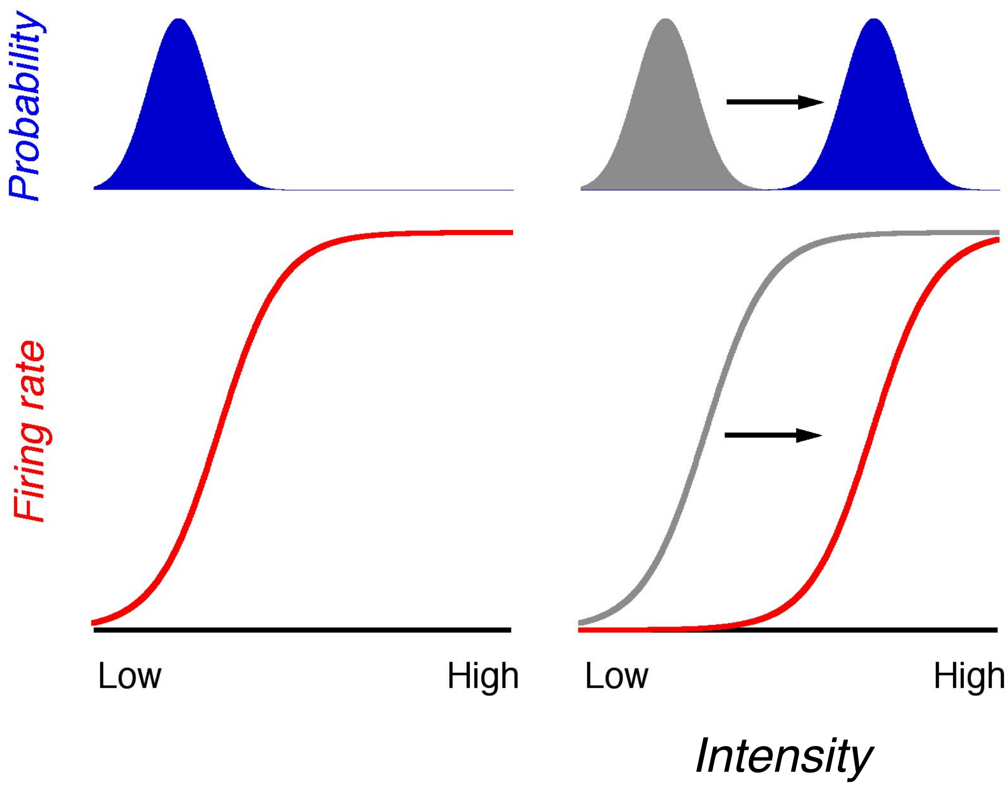
How can the nonlinearity and filter change?

Adaptation to the average input

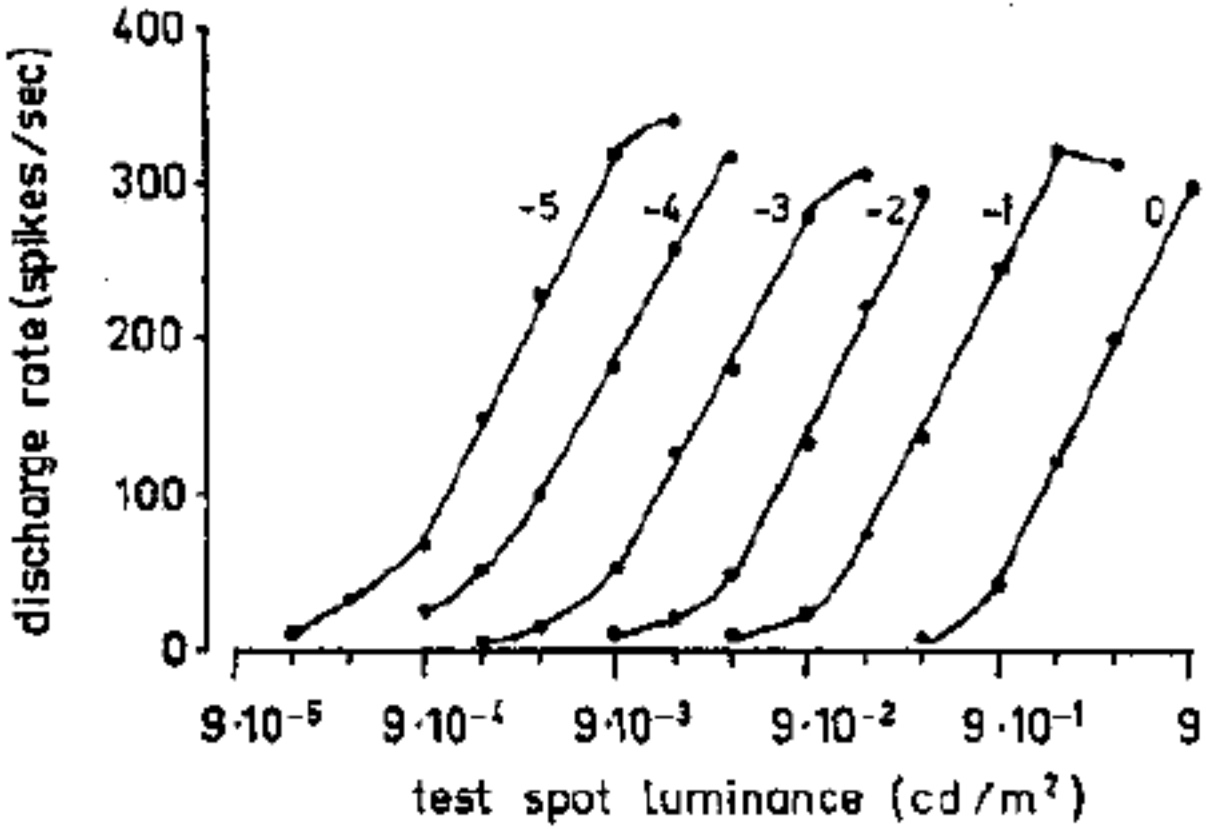


Adaptation to the average input

Light adaptation

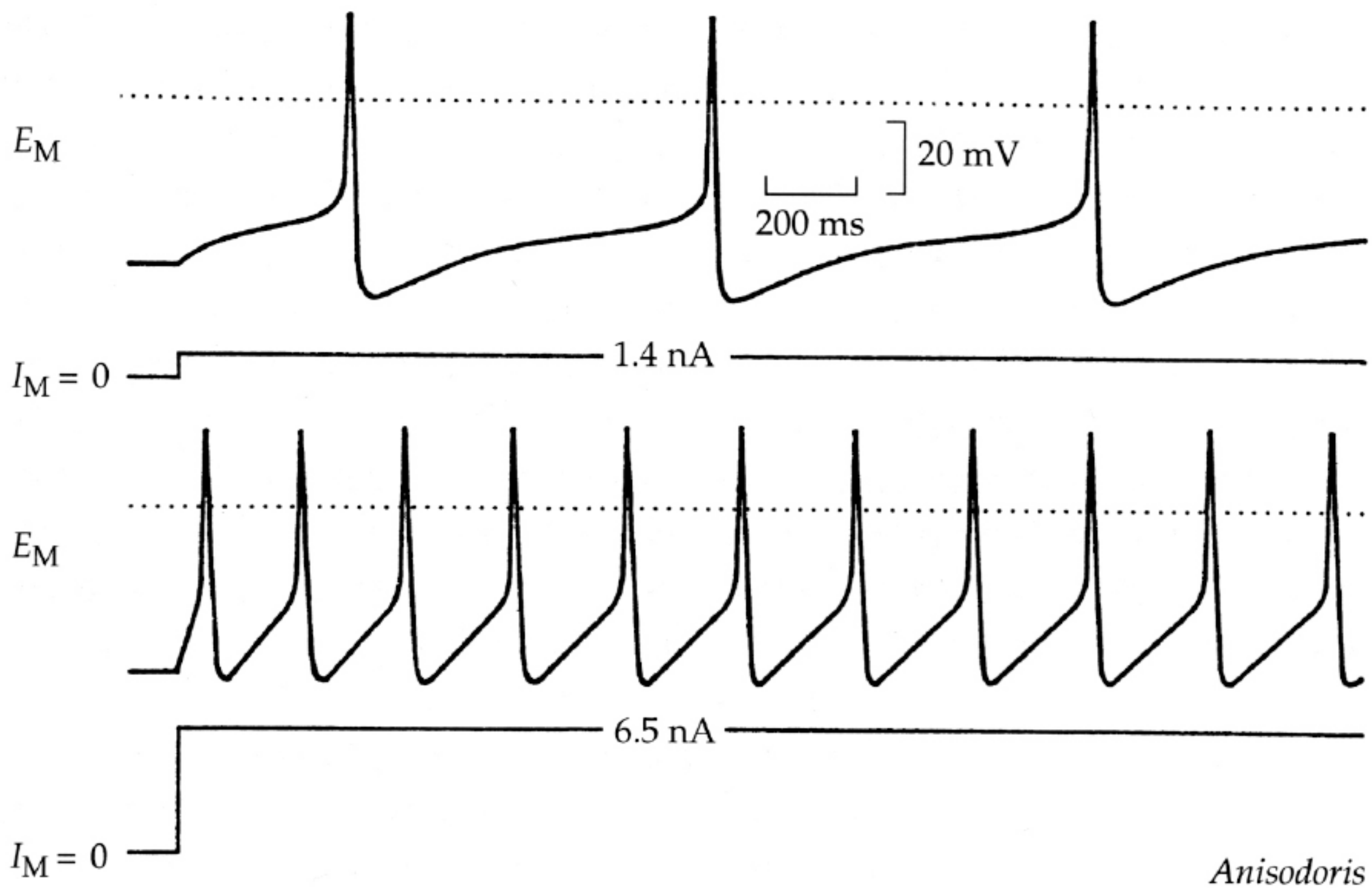


Ganglion cell response curves shift to the mean light intensity



Sakmann and Creuzfeldt, Scotopic and mesopic light adaptation in the cat's retina (1969)

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

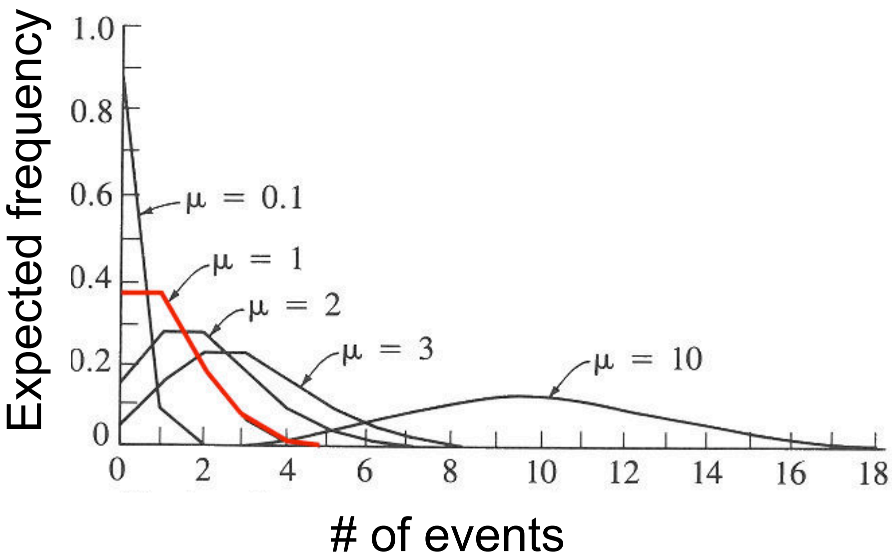


Events with Poisson statistics $\mathrm{P}[n,\mu]$

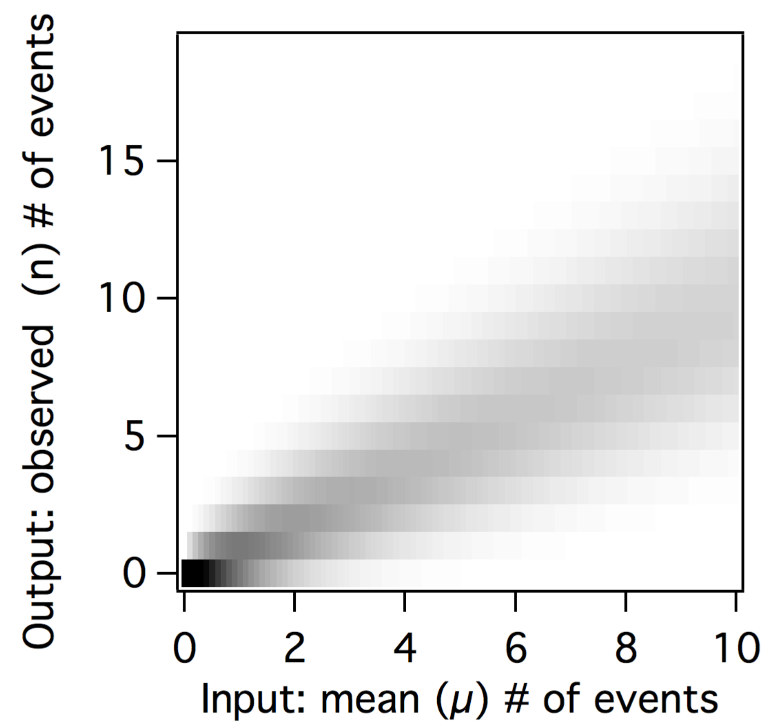
$$\frac{e^{-\mu}\mu^{n}}{n!}$$

μ = mean # of events in a time interval

n = events in a time interval

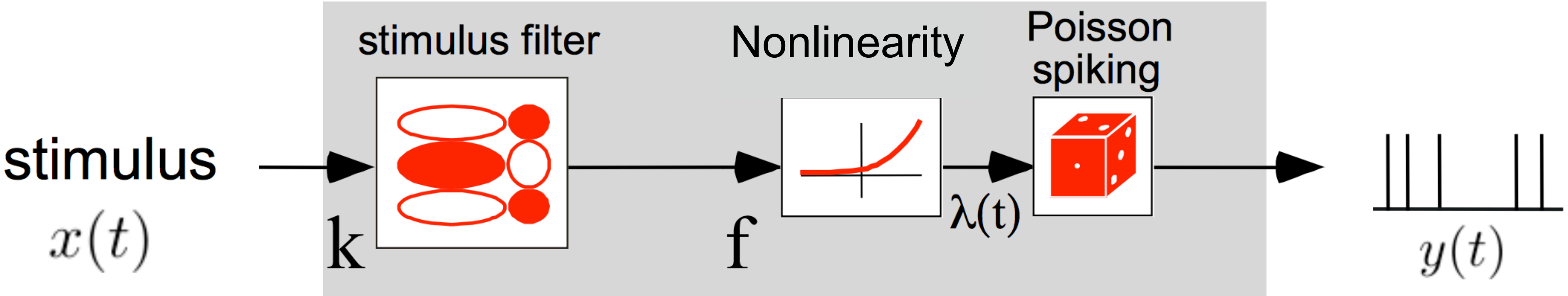


Joint probability distribution $\mathrm{P}[n,\mu]$

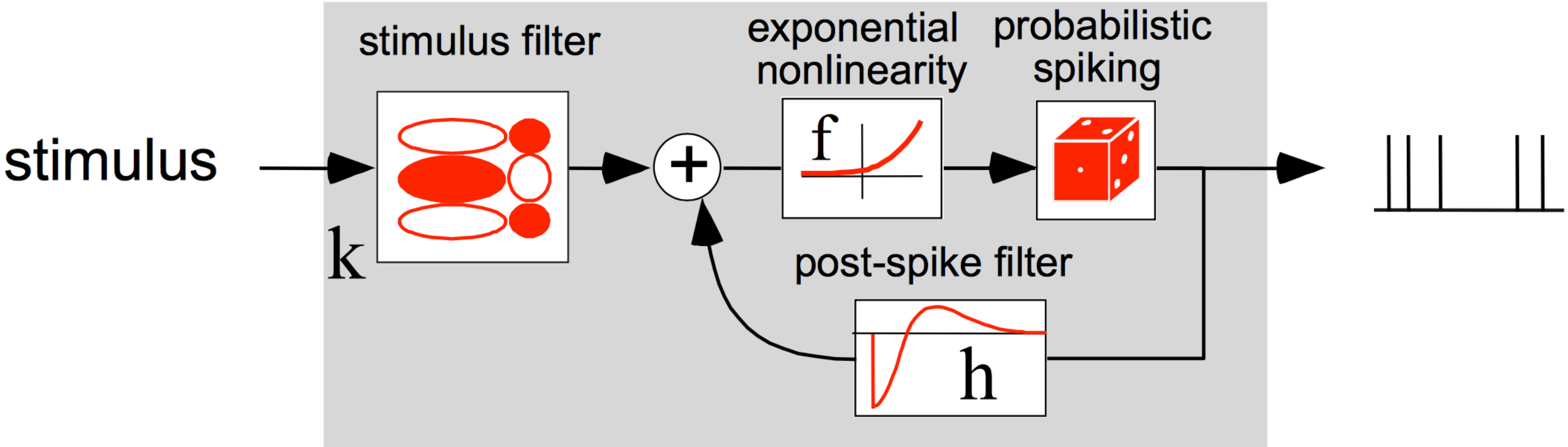


variance=mean=μ

Linear-Nonlinear-Poisson

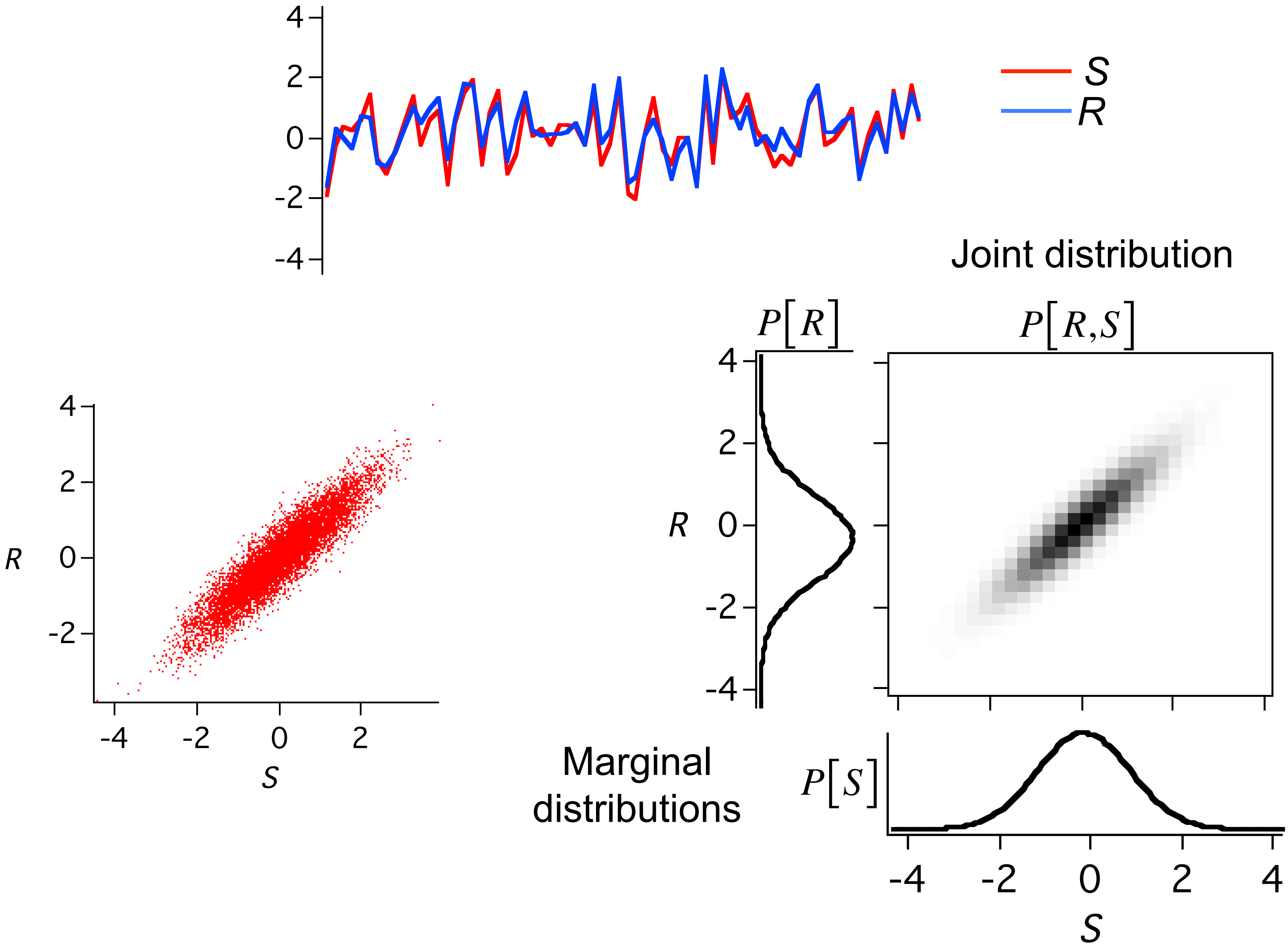


Generalized Linear Model



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

Primer on various encoding methods, Aljadeff et al., *Neuron,* 2016



S
R
Joint distribution
P[R]
P[R,S]
Marginal distributions
P[S]

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 =
- 1/2 log(1/2) - 1/2 log(1/2) = 1 bit

of an unfair coin =
- 3/4 log(3/4) - 1/4 log(1/4) = ~0.8 bits

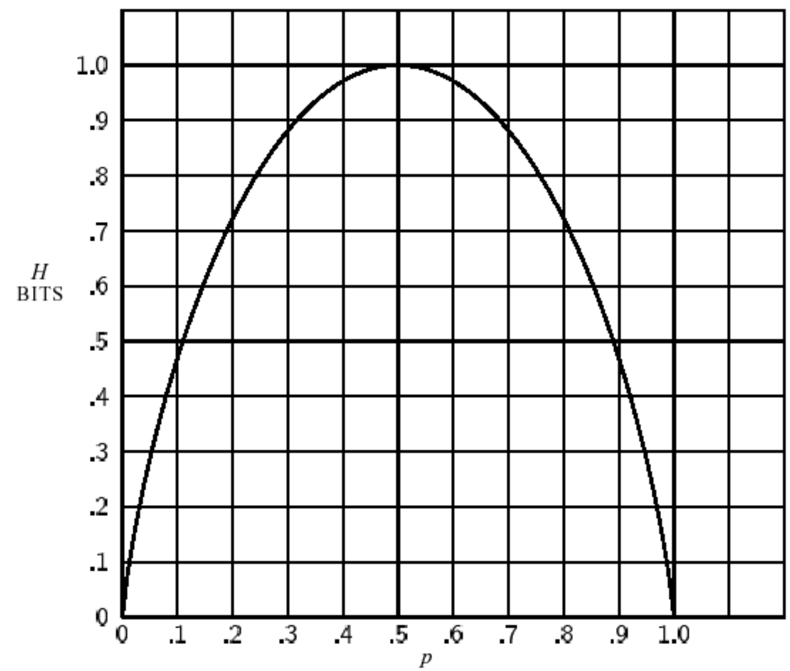


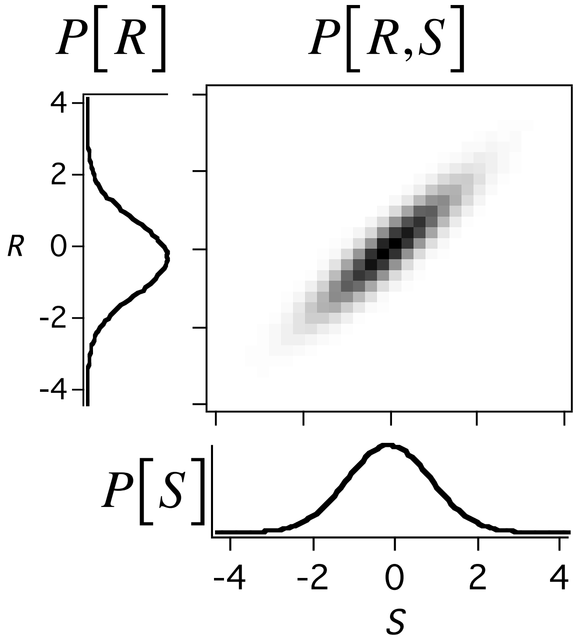
Fig. 7—Entropy in the case of two possibilities with probabilities p and $(1-p)$.

*By analogy to entropy in statistical mechanics,

$$S = k \log W$$

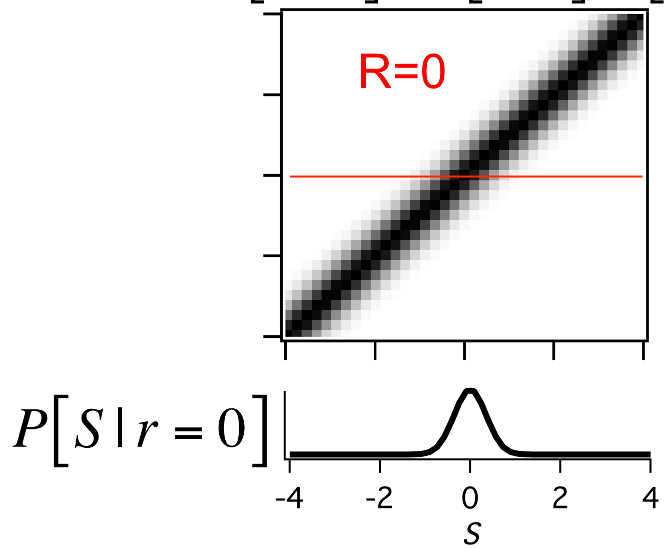
k: Boltzmann constant W: Number of possible microscopic states

Information is a reduction in entropy



Conditional distribution

$$P[S \mid R] = P[R,S]/P[R]$$



Conditional entropy

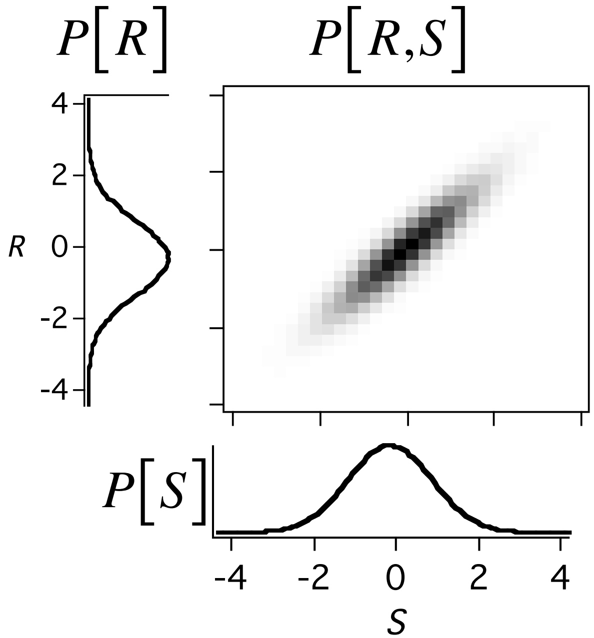
$$H(S \mid R) = -\sum_{s}\sum_{r} P(r,s)\log\left(P(s \mid r)\right)$$

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.

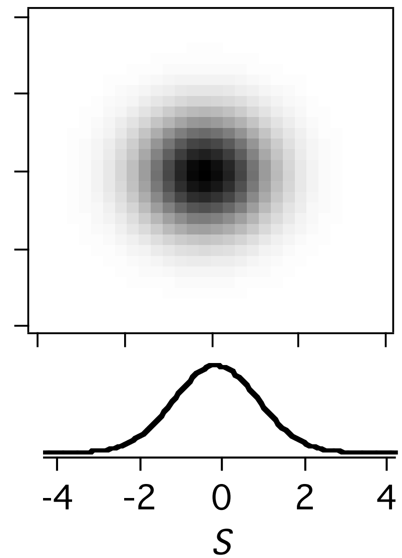
$$I(S;R) = H(S) - H(S \mid R) \qquad\qquad I(R;S) = I(S;R)$$

Mutual information as the ‘distance’ between two probability distributions

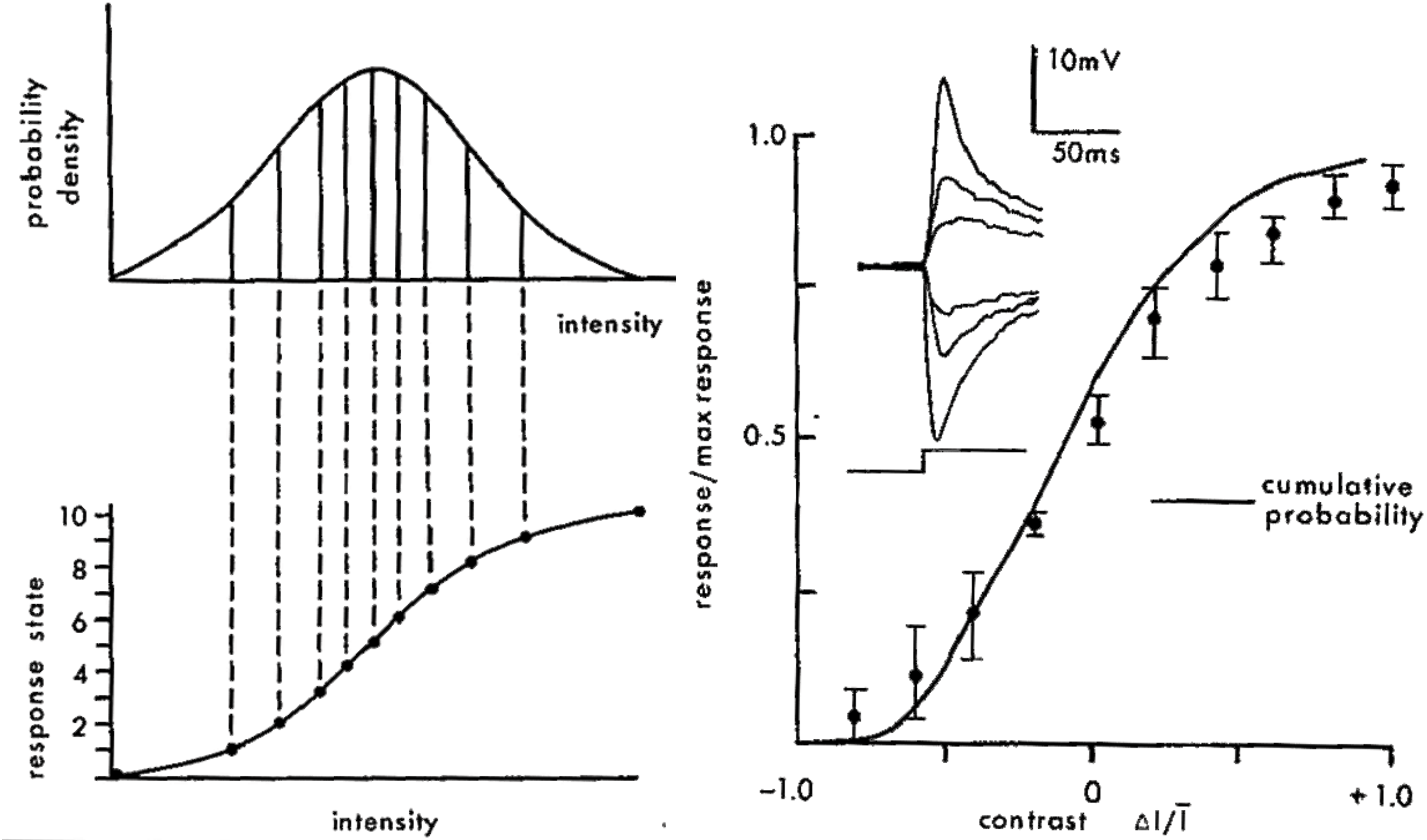


Product distribution – what things would
Look like with zero information

$P[R]P[S]$

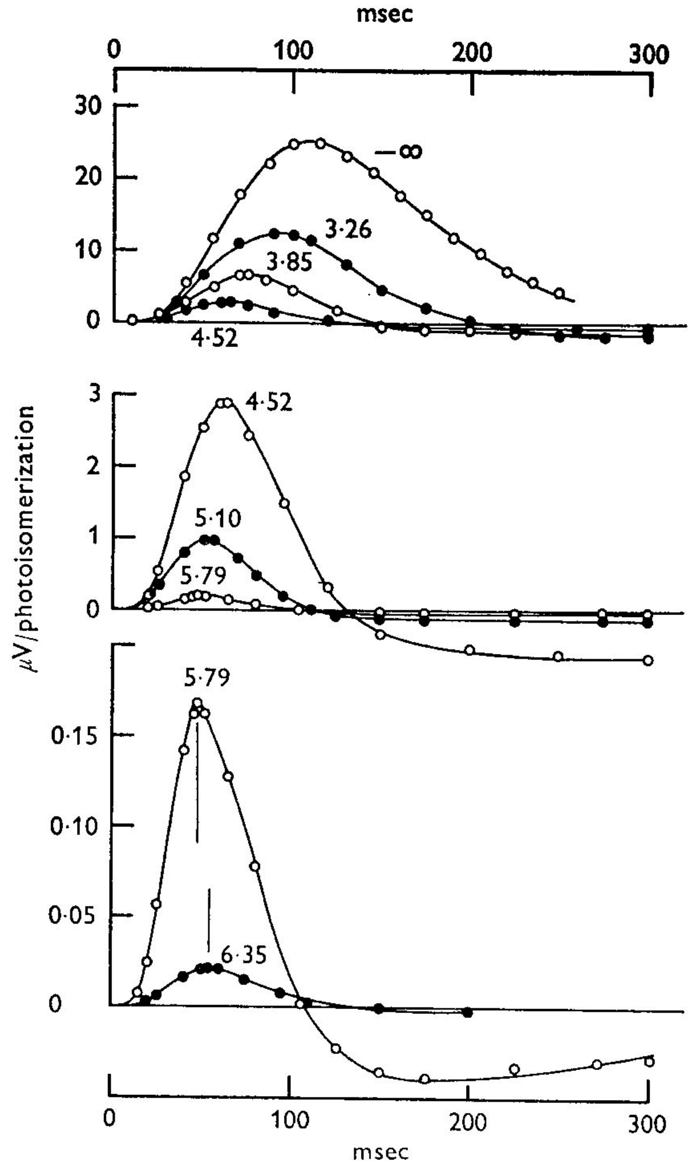


$$I(R;S) = \sum_i \sum_j P[R_i, S_j] \log\left(\frac{P[R_i, S_j]}{P[R_i]P[S_j]} \right)$$



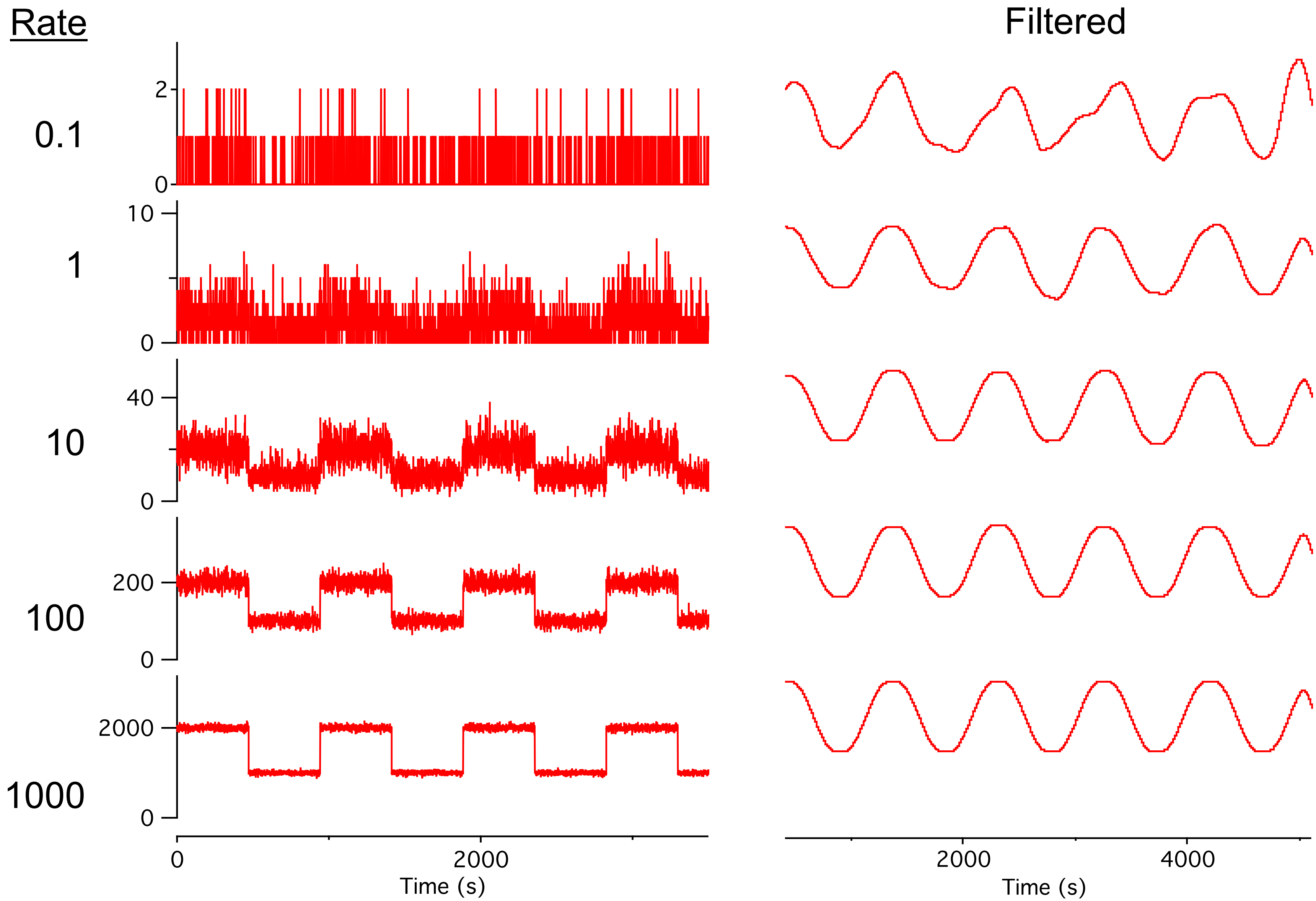
Simon Laughlin, A simple coding procedure enhances a neuron's information capacity Z. Naturforsch, 36c: 910-912 (1981)

Turtle Cones: Sensitivity *and Kinetics* change with mean luminance



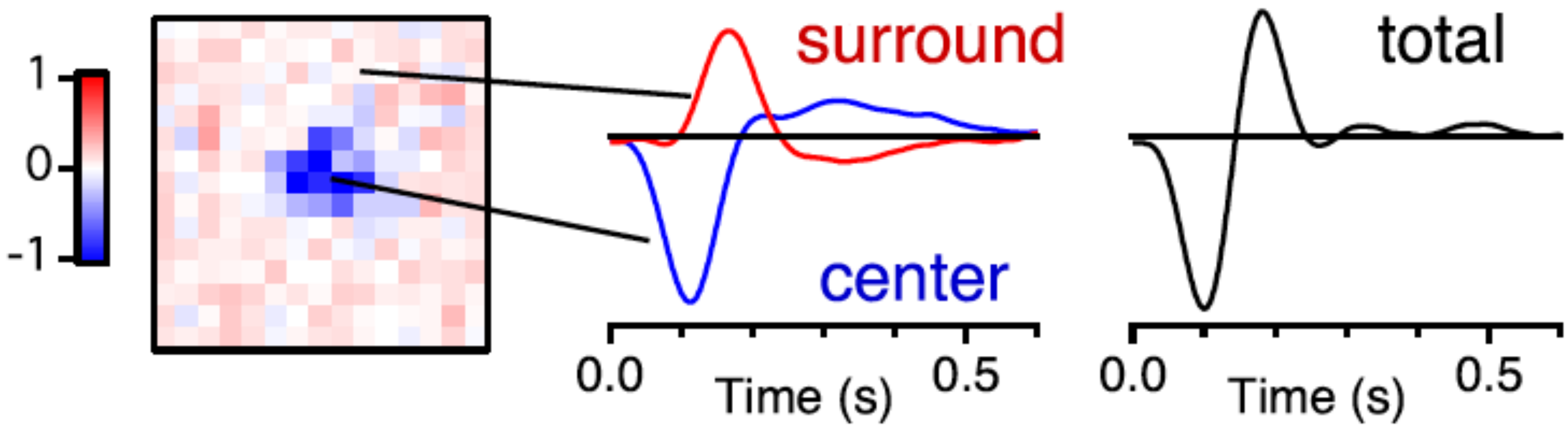
Baylor & Hodgkin 1974

Signal with poisson distribution



What receptive field maximizes information transmission?

Retinal bipolar cell receptive field

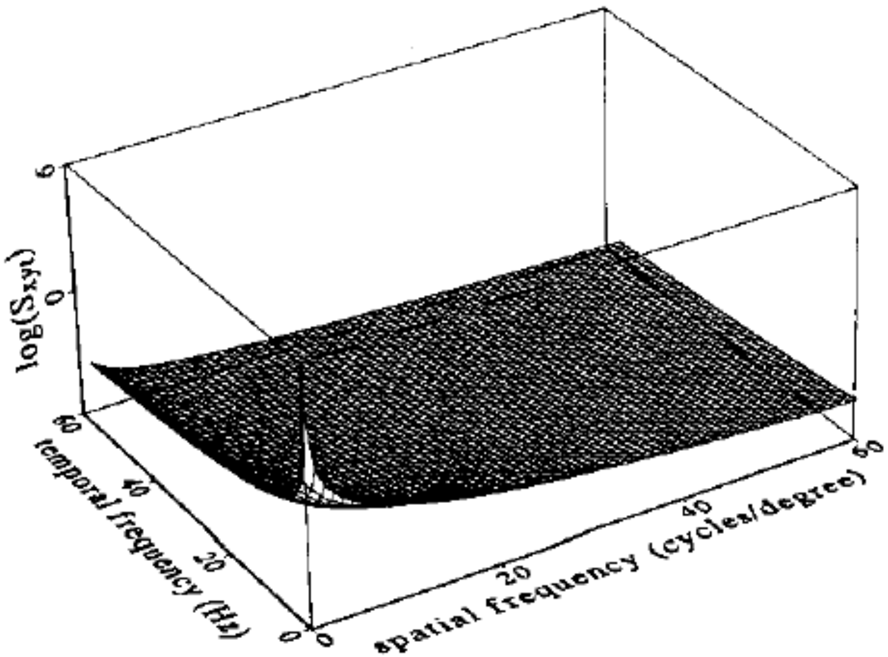


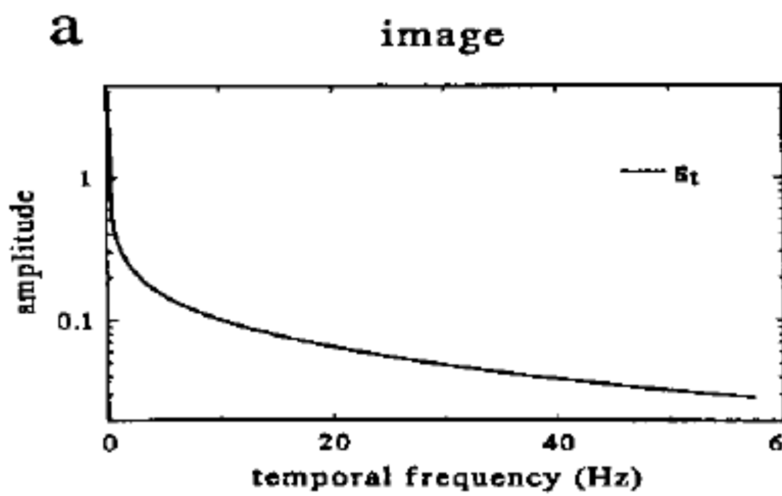
Baccus, Olveczky, Manu & Meister, 2008

Theory of maximizing information in a noisy neural system

'Efficient Coding' - Horace Barlow

Natural visual scenes are dominated by low spatial and temporal frequencies



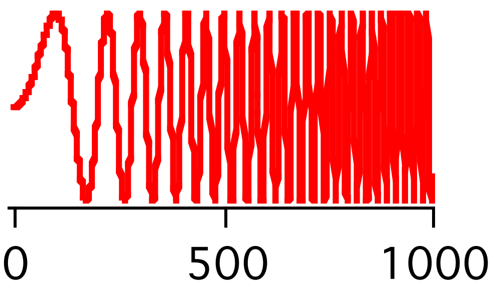


J.H. van Hateren. Real and optimal neural images in early vision. *Nature* 360:68-70 (1992)

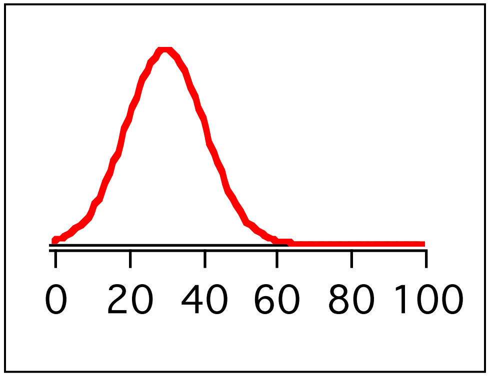
J.H. van Hateren, Spatiotemporal contrast sensitivity of early vision. *Vision Res.*, 33:257-67 (1993)

Linear filter and frequency response

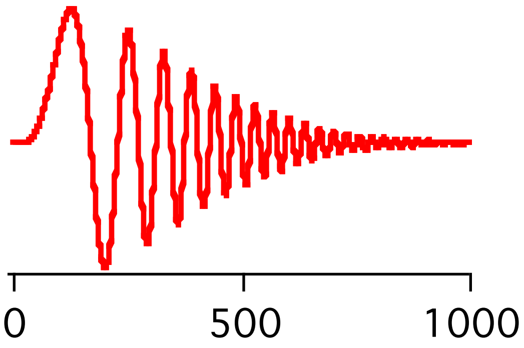
Stimulus



Filter



Response



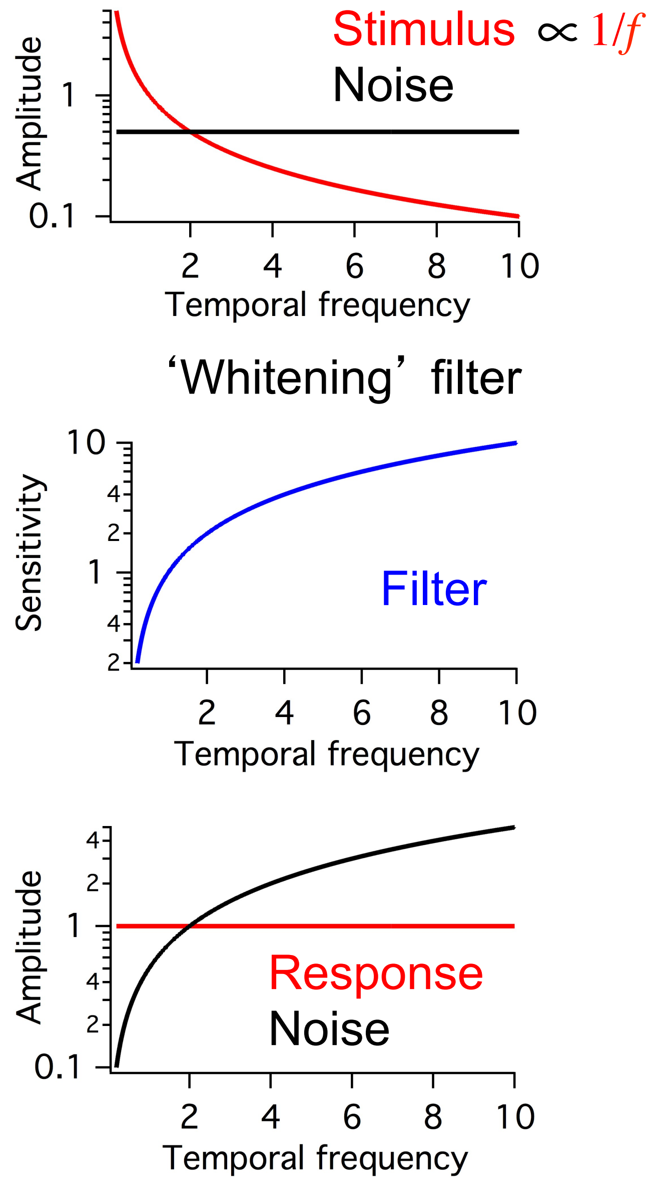
Convolution theorem

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

a convolution in the time domain

is a simple product in the frequency domain

Optimal filter whitens but also cuts out noise



Filter to whiten in the presence of noise

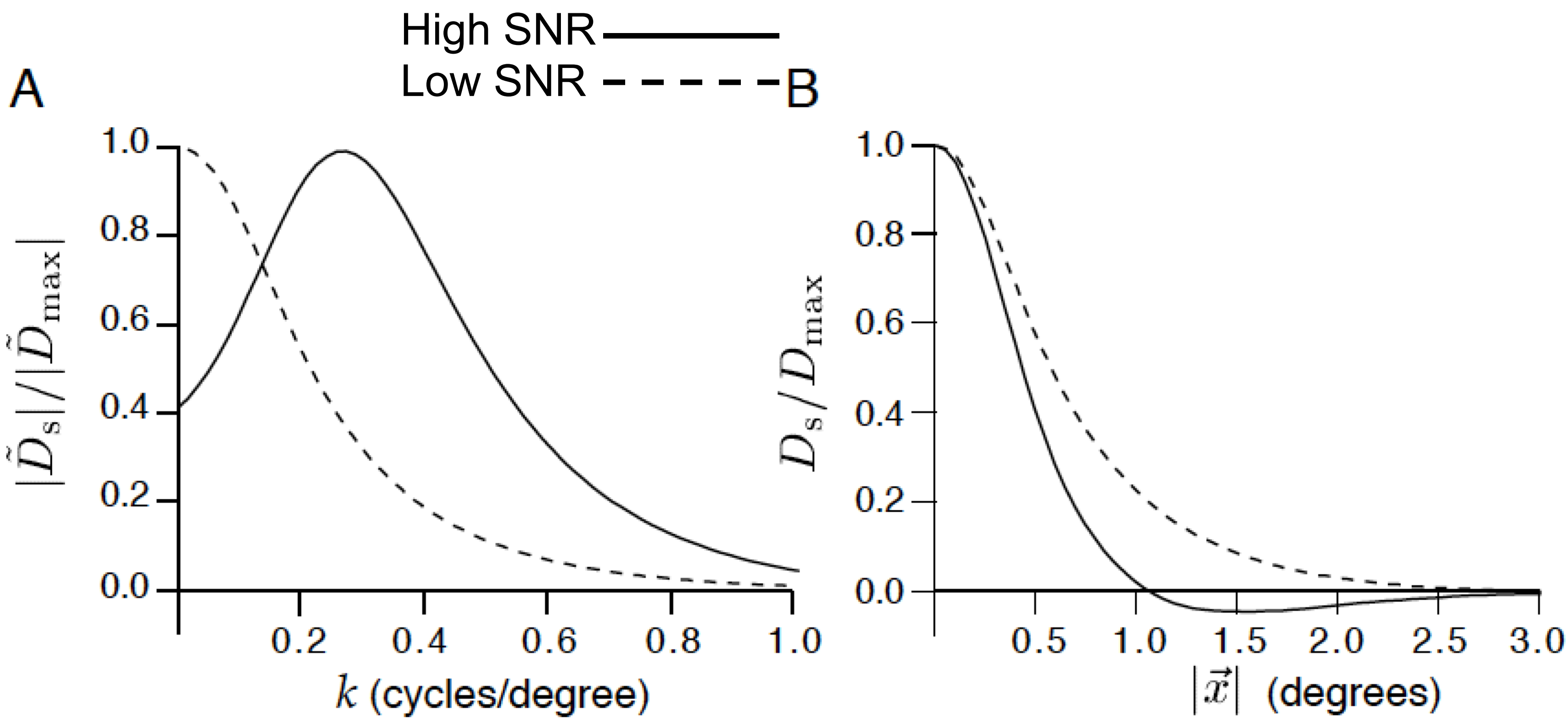
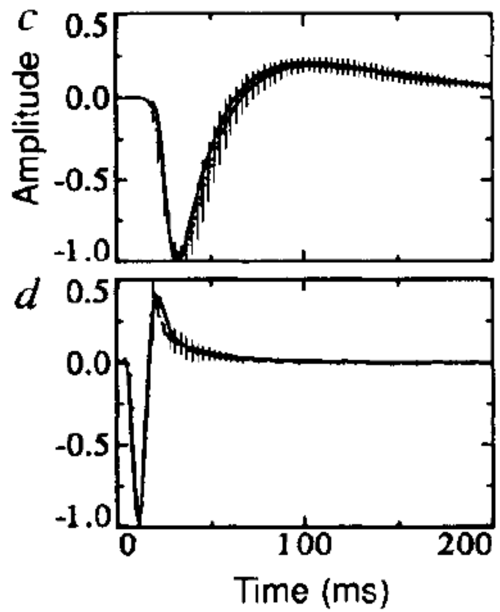


Figure 4.3: Receptive field properties predicted by entropy maximization and

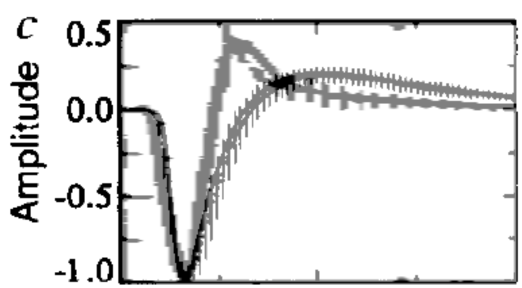
Theory of maximizing information in a noisy neural system

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



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

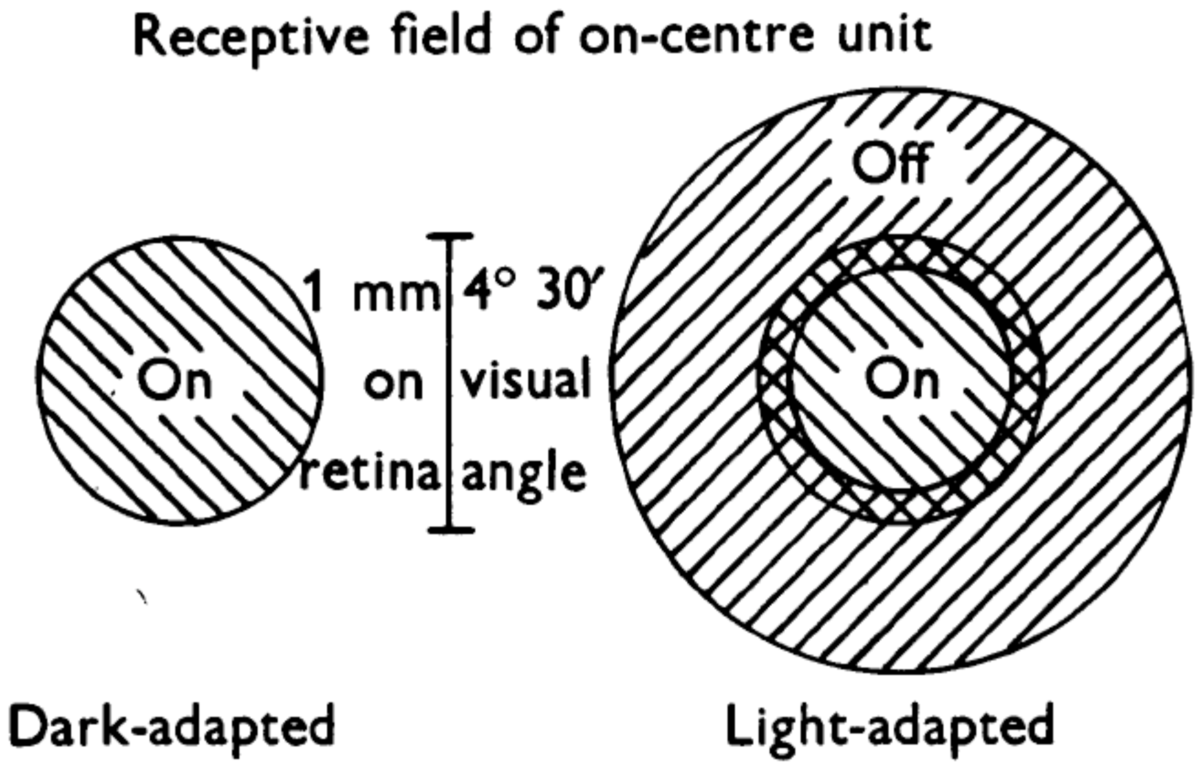
High background intensity
Emphasizes change, is more differentiating
(real and theoretical optimum)



Both, scaled in time to the first peak

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

Spatial adaptation in retinal ganglion cells



Barlow, Fitzhugh & Kuffler (1957)

Theories of efficient coding:

An ideal encoder should use all output values with equal probability

Low frequencies dominate in natural scenes

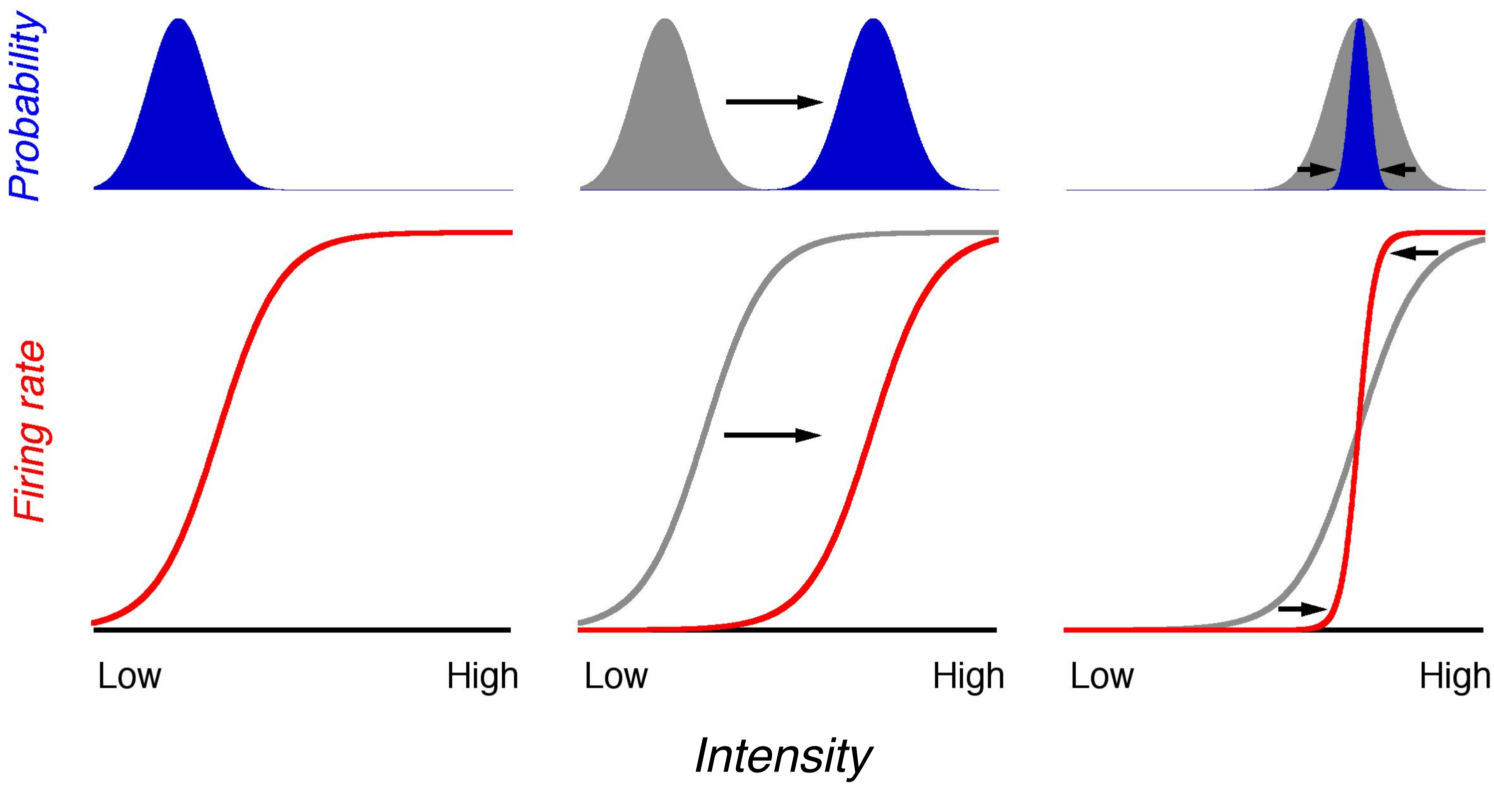
An efficient encoder should amplify higher frequencies more than low frequencies

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

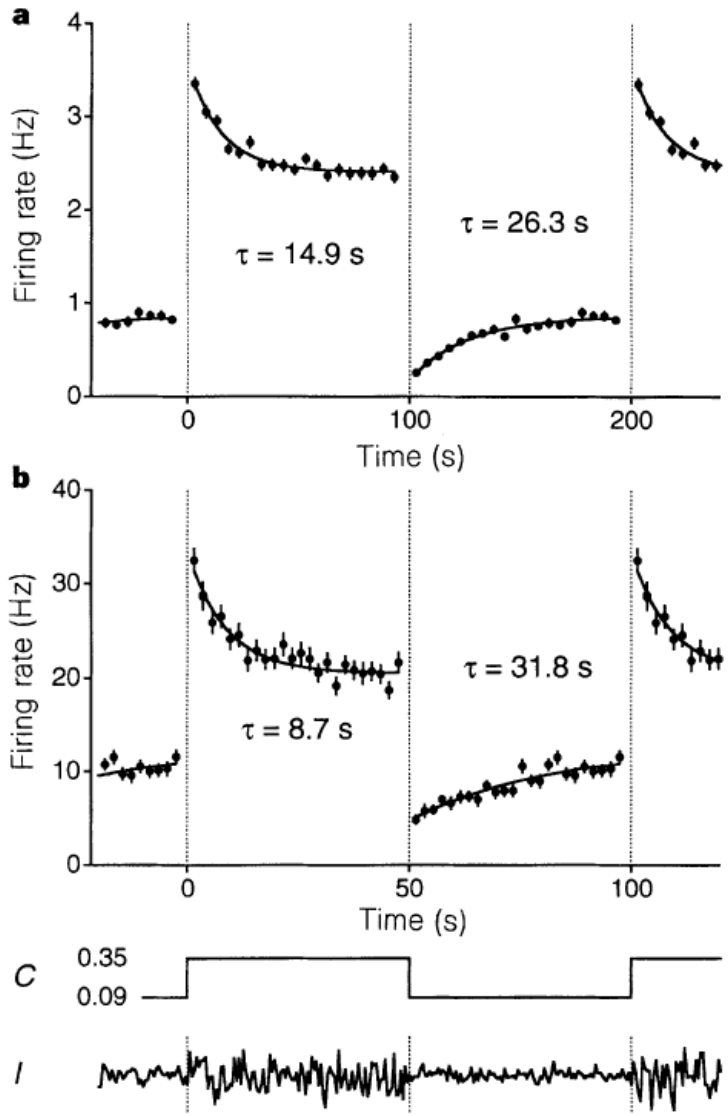
Contrast adaptation



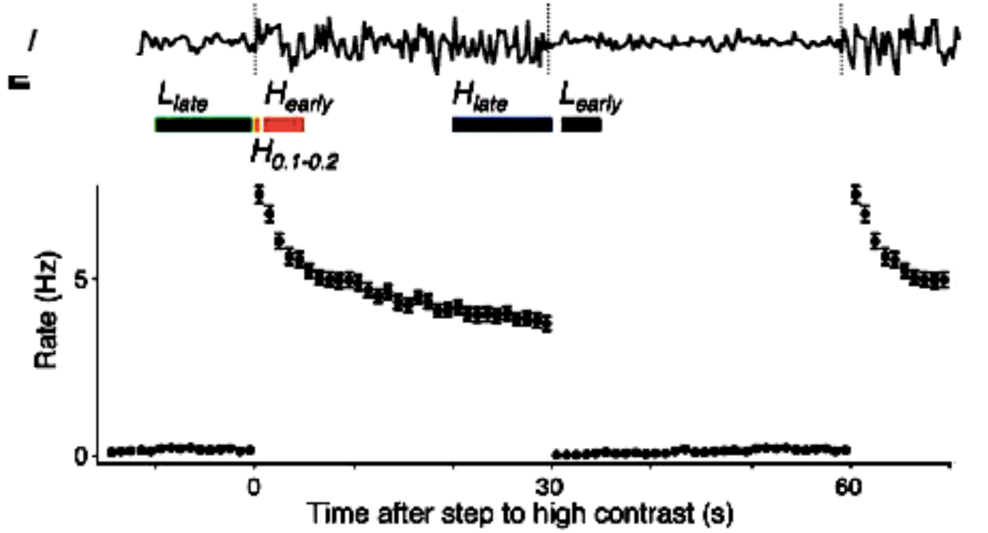
Retinal contrast adaptation

Salamander

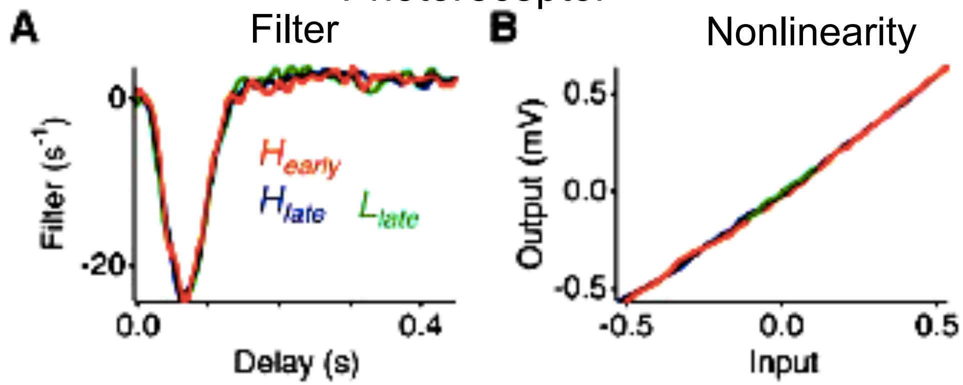
Rabbit



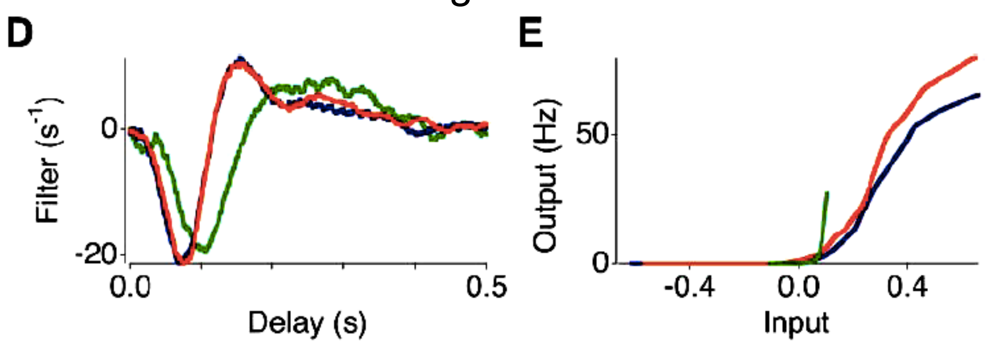
Smirnakis et al., Adaptation of retinal processing to image contrast and spatial scale. *Nature,* 386:69-73 (1997).



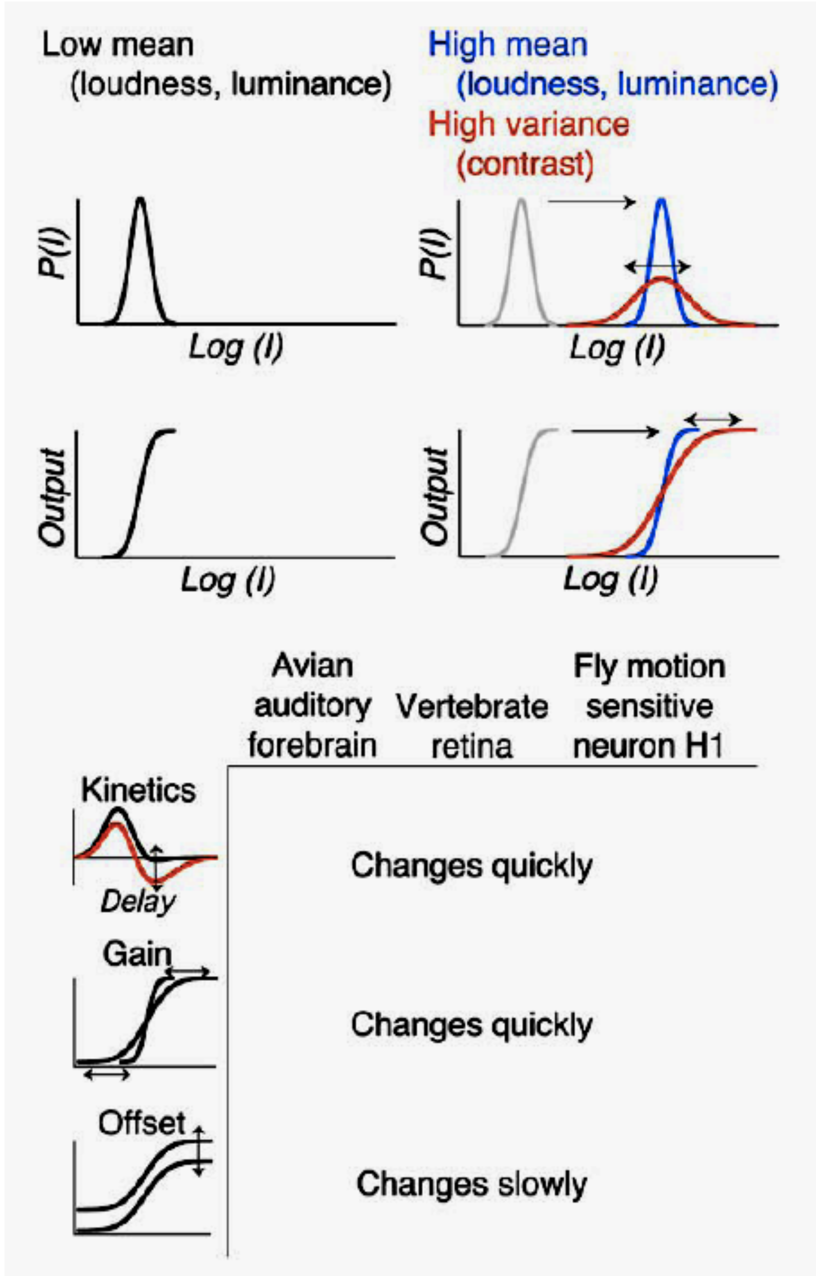
Photoreceptor



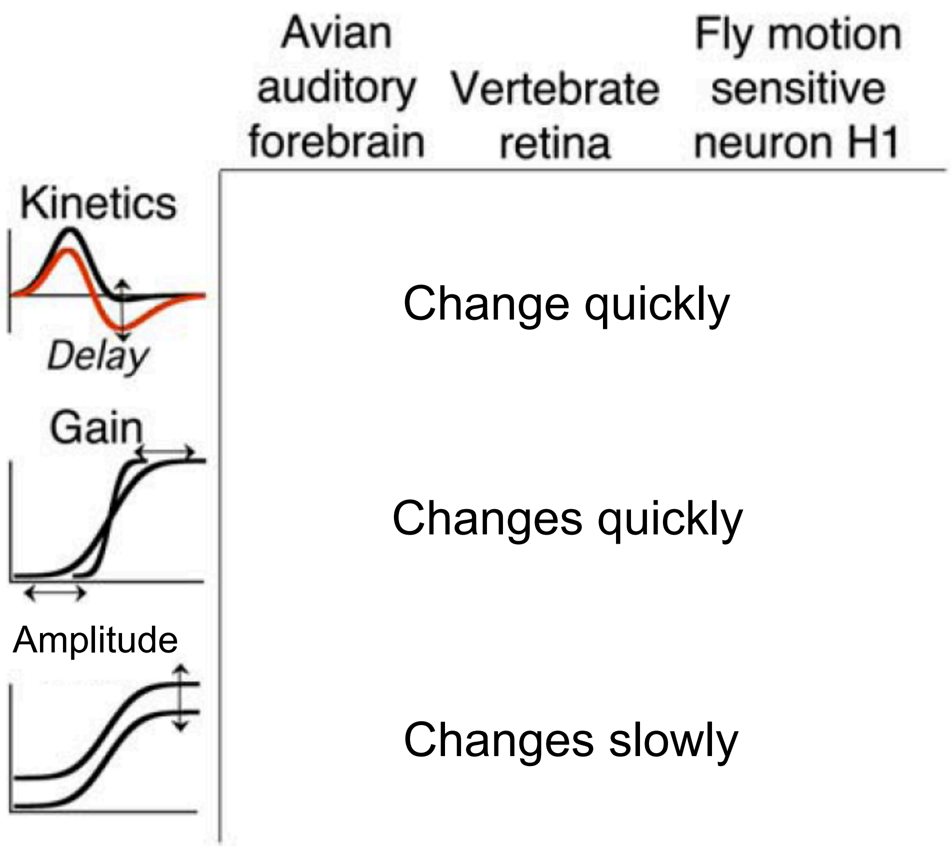
Ganglion cell



Baccus & Meister. Fast and slow contrast adaptation in retinal circuitry. (2002).


Low mean
(loudness, luminance)
High mean
(loudness, luminance)
High variance
(contrast)
P(I)
Log (I)
P(I)
Log (I)
Output
Log (I)
Output
Log (I)
Avian auditory forebrain
Vertebrate retina
Fly motion sensitive neuron H1
Kinetics
Delay
Changes quickly
Gain
Changes quickly
Offset
Changes slowly

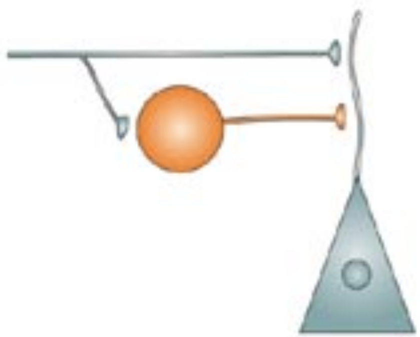
Common properties of contrast adaptation



Nagel & Doupe, 2006
Fairhall et al., 2001

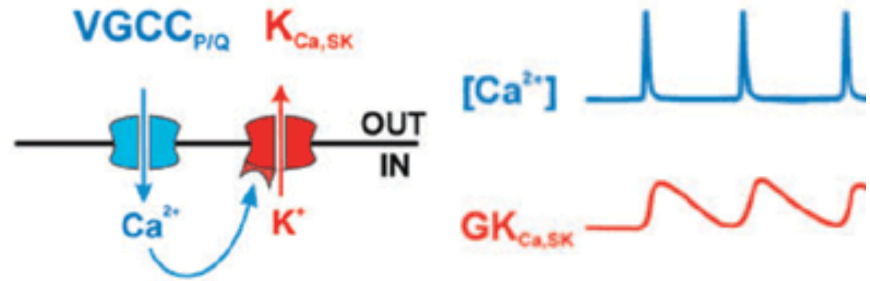
Change in sensitivity by *modulation*

Feedforward inhibition



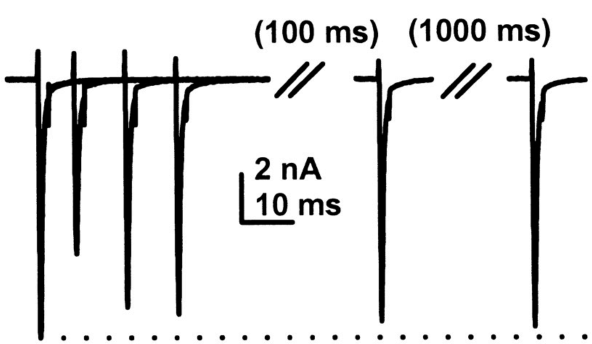
Feedback inhibition

Spike dependent conductances

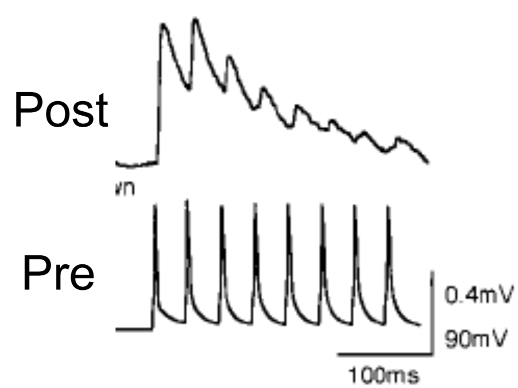


Change in sensitivity by *depletion*

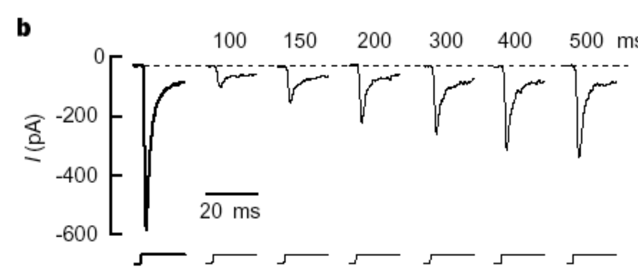
Ion channel inactivation



Short-term synaptic plasticity synaptic depression



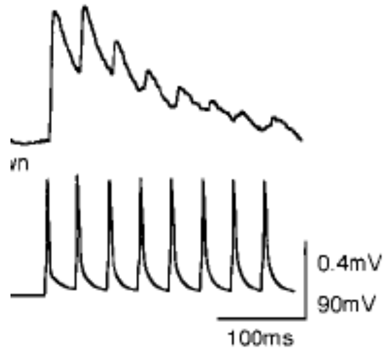
Receptor desensitization

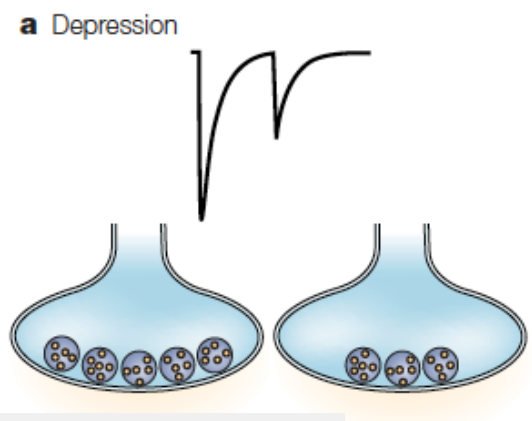


Short-term synaptic plasticity – synaptic depression

Post

Pre





Depletion of available vesicles as a mechanism for depression

n: Number of vesicle
p: Probability of vesicle release

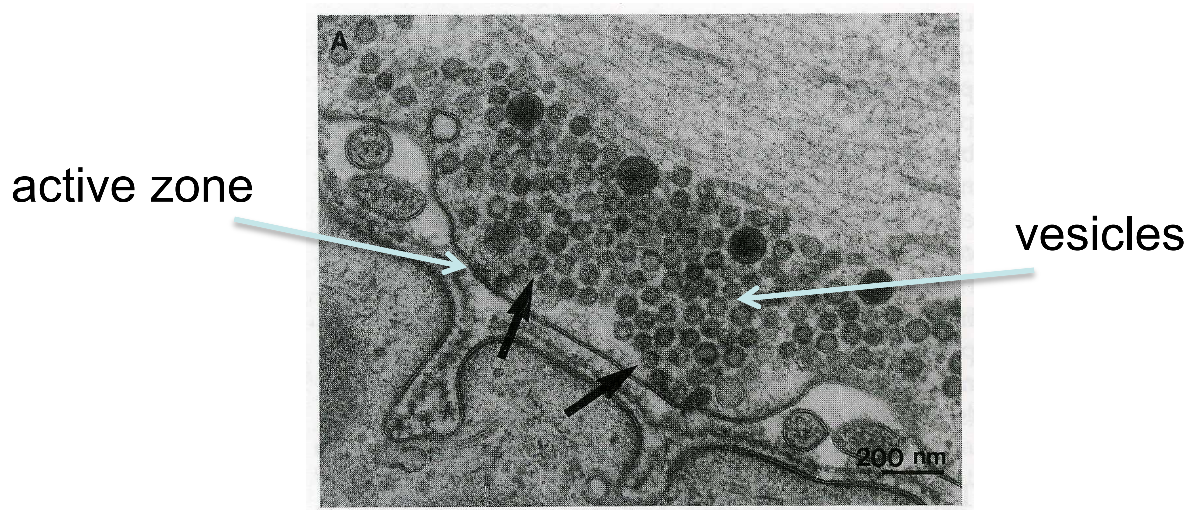
Release = n x p

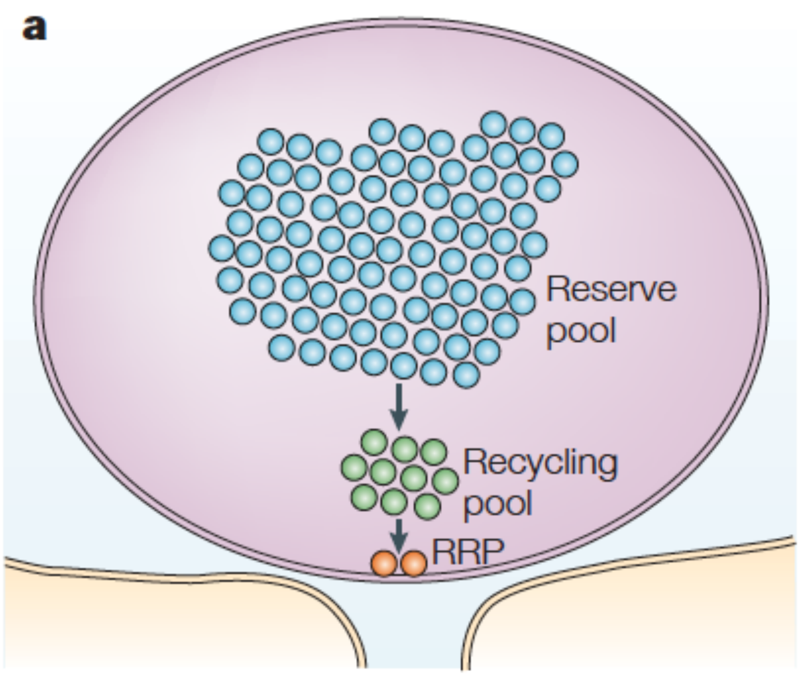
$$\frac{dn(t)}{dt} = \underbrace{\frac{1 - n(t)}{\tau_r}}_{\text{replenishment}} - \underbrace{\sum_j \delta(t - t_j) \cdot p \cdot n(t)}_{\text{release}}$$

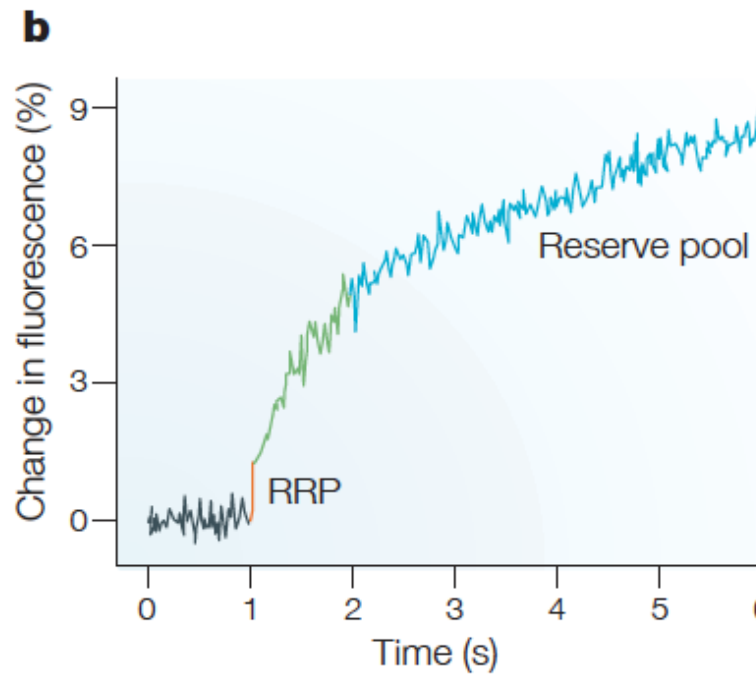
Hennig, 2013. Theoretical models of synaptic short term plasticity

Chance FS, Nelson SB, Abbott LF. (1998)
Ozuysal & Baccus (2012)

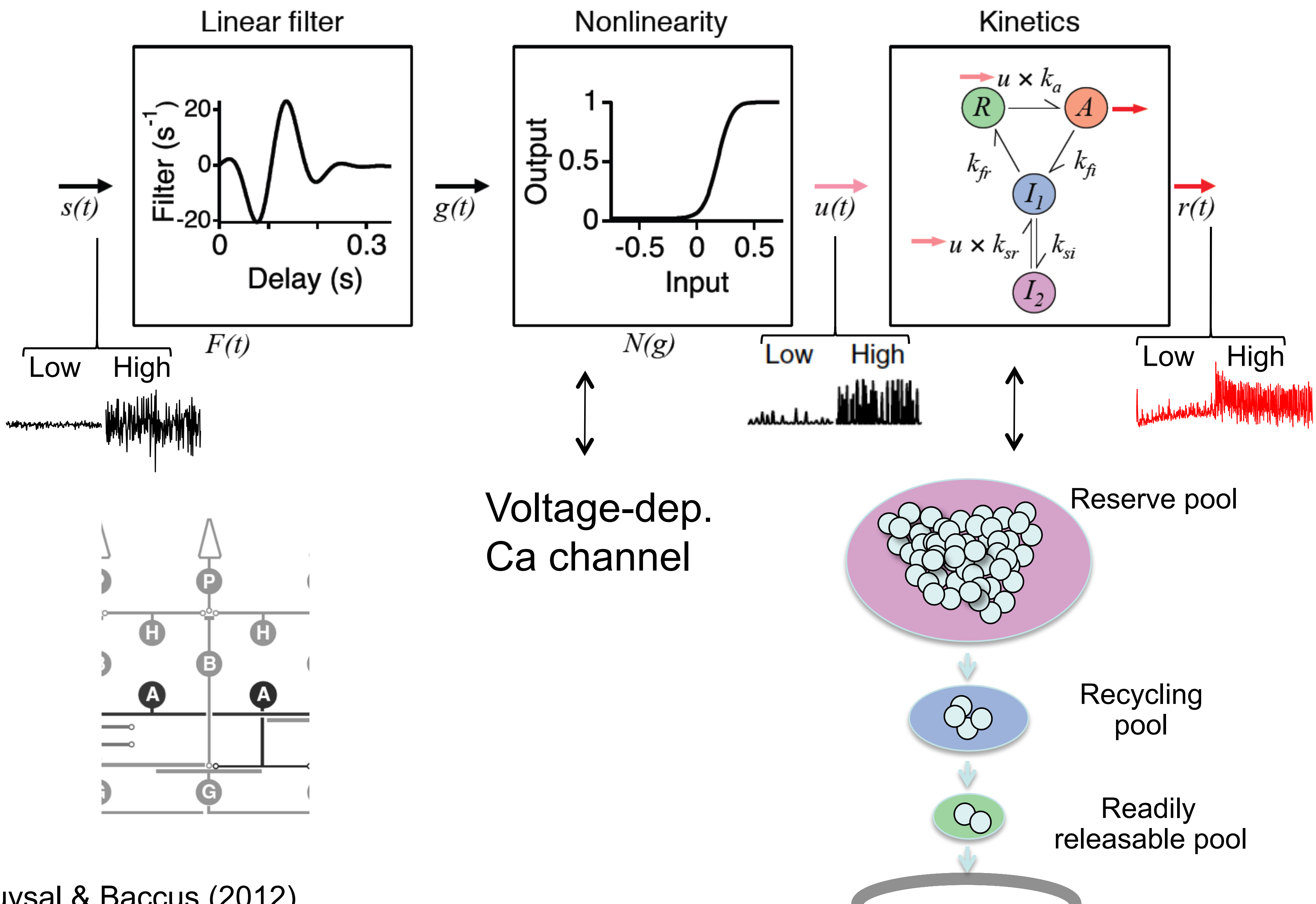
Vesicle release has dynamics over multiple timescales



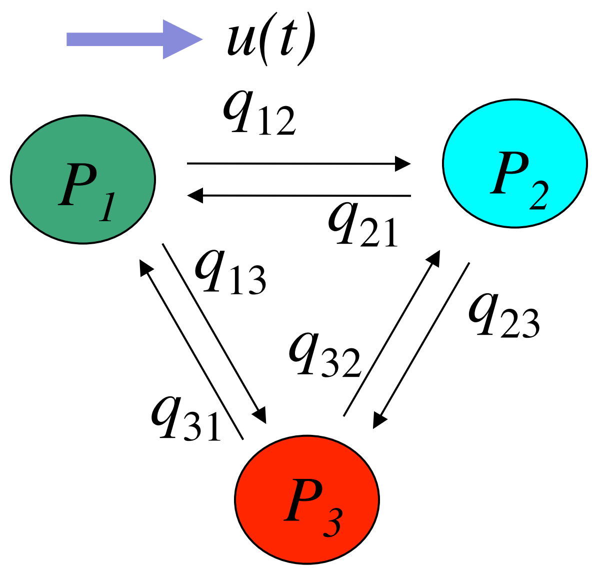




Linear-Nonlinear-Kinetic (LNK) model of adaptation



Ozuysal & Baccus (2012)



Linear time-varying,
n-1 eigenvalues

State vector

$$\mathbf{P} = \begin{bmatrix} P_1 \\ P_2 \\ P_3 \end{bmatrix}$$

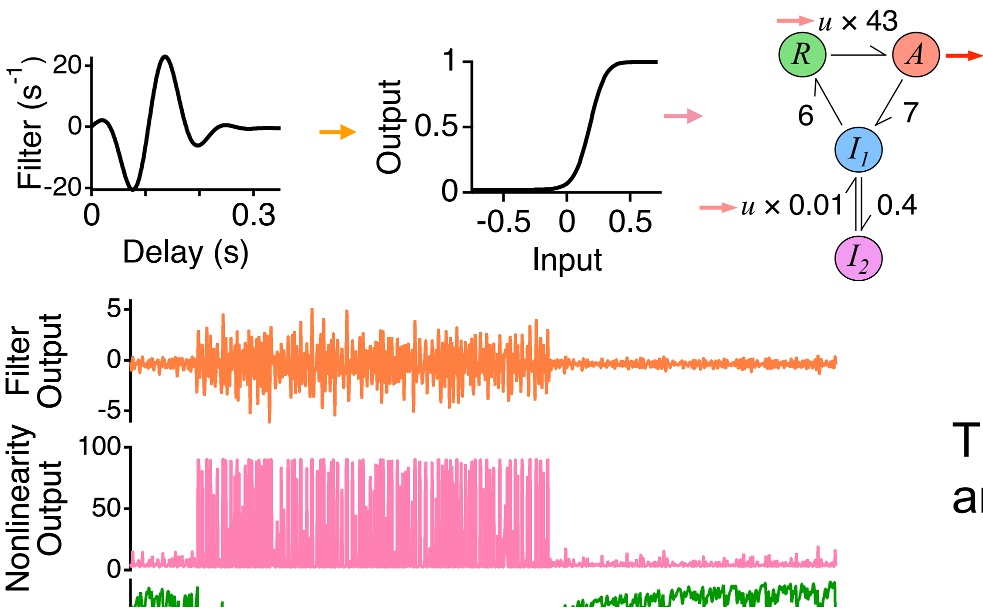
Transition matrix

$$\mathbf{Q} = \begin{bmatrix} -\sum_{j\neq 1} q_{1j} & u(t) & q_{13} \\ q_{21} & -\sum_{j\neq 2} q_{2j} & q_{23} \\ q_{31} & q_{32} & -\sum_{j\neq 3} q_{3j} \end{bmatrix}$$

Total inflow = total outflow,
rows sum to zero

Dynamics

$$\frac{d\mathbf{P}^{\mathrm{T}}}{dt} = \mathbf{P}^{\mathrm{T}}\mathbf{Q}(u)$$



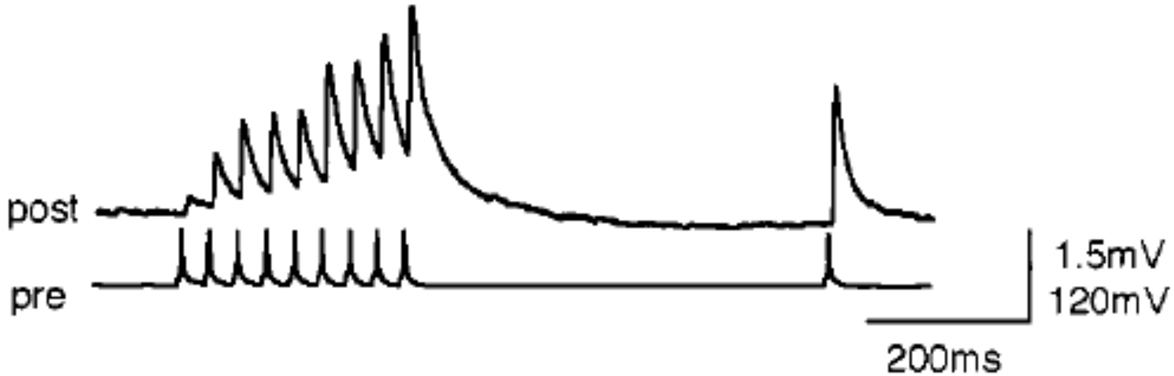
Threshold converts amplitude to mean

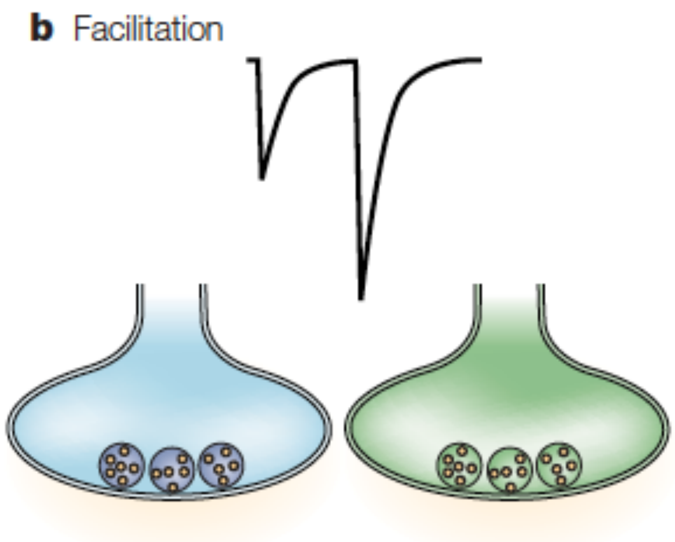
Change in rate constants change kinetics

Depletion of resting state changes sensitivity

Inactivated states act as buffers

Short-term synaptic plasticity – synaptic facilitation

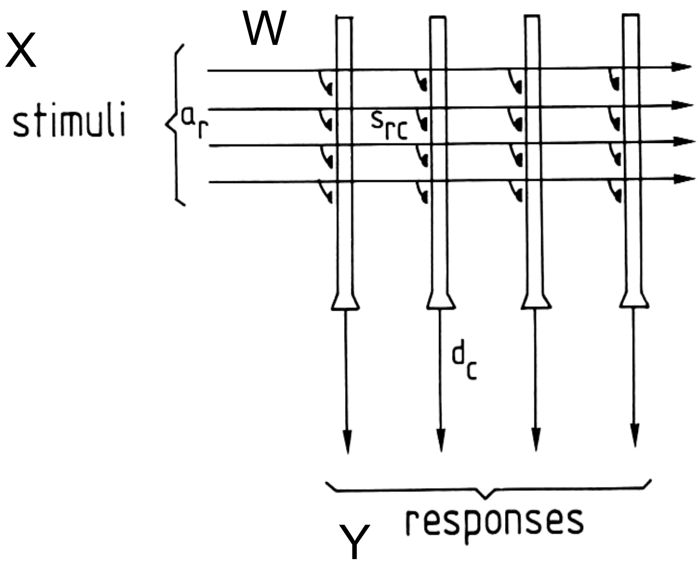




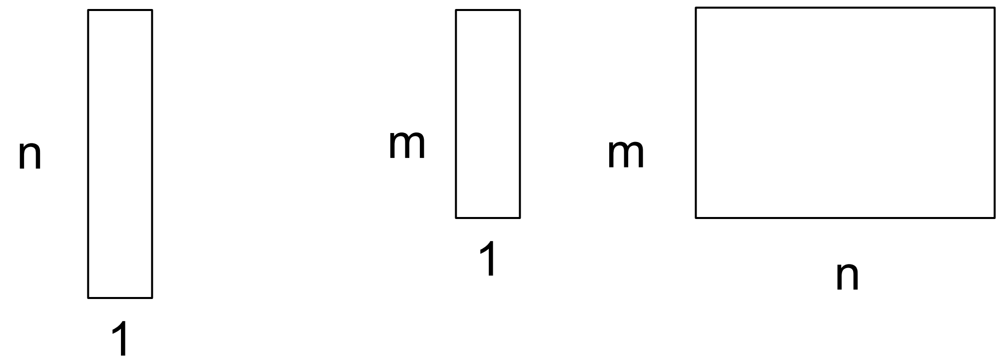
Residual calcium as a mechanism for increased release

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

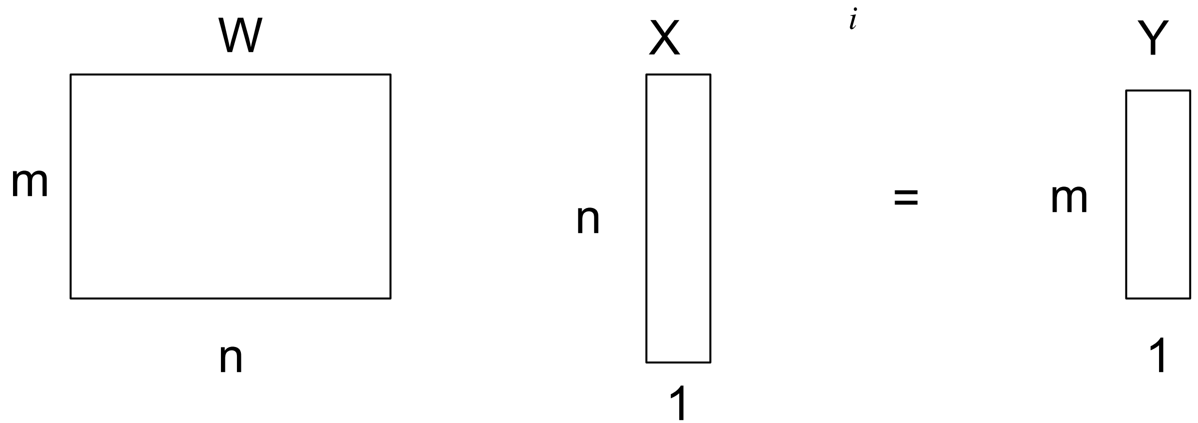
Synaptic transmission as a matrix multiplication



Input X, column vector | Output Y, column vector | Matrix of synapses W



$$WX = Y \qquad \sum_i w_{ji} x_i = y_j$$



The Hebb rule for synaptic plasticity

$$A \xrightarrow{w_{BA}} B$$

When an axon of cell A is near enough to excite cell B or repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased.

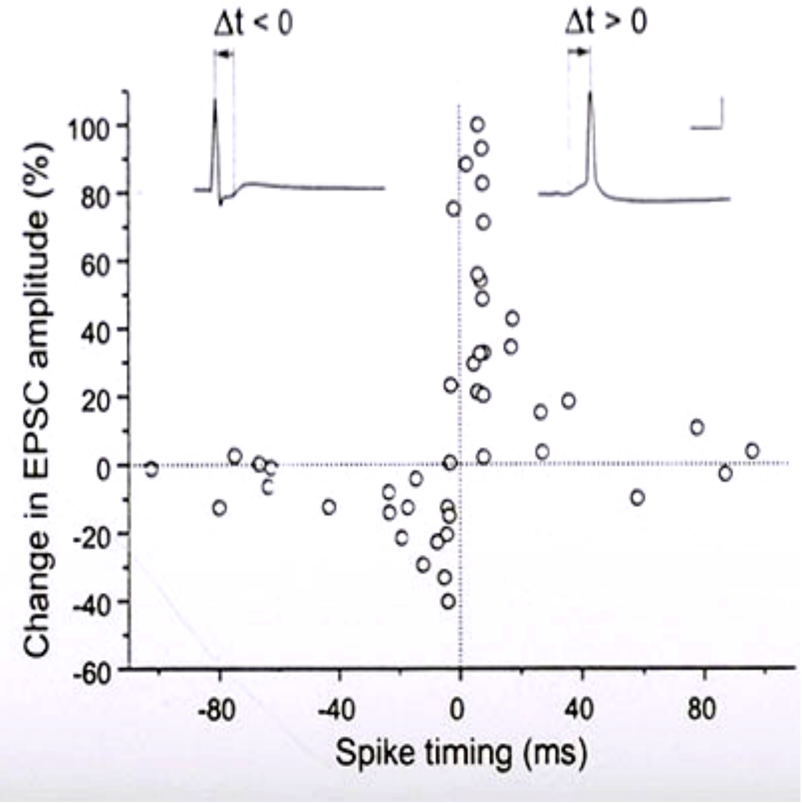
Hebbian plasticity

A excites B: Coincidence leads to greater release

$$\frac{dw_{BA}}{dt} = \langle AB \rangle$$

Hebbian spike timing plasticity (STDP)

hippocampal neurons



Pre before Post

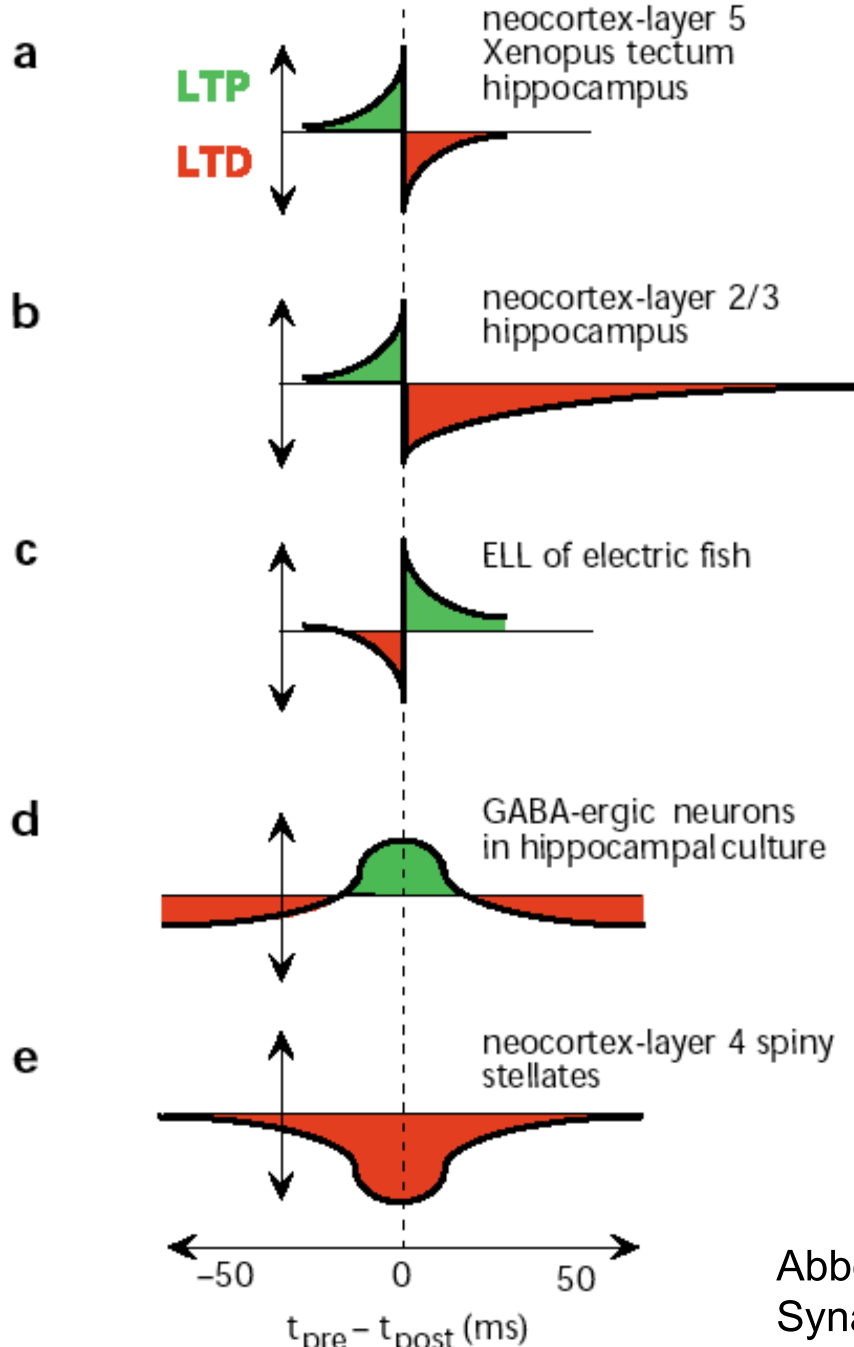
$$\frac{dw_{ba}}{dt}(t) = f(\tau)a(t)b(t-\tau)$$

Bi & Poo (1998)

Simplified: $$\frac{dw_{ba}}{dt}(t) = a(t)b(t-1) - a(t-1)b(t)$$

Okubo et al., (2015)

Different varieties of Spike-timing dependent plasticity



Abbott L. and Nelson S.
Synaptic plasticity: taming the beast (2000)