NEPR208 - Adaptation properties and mechanisms

Functional advantages in properties of a neural code and changes in those properties

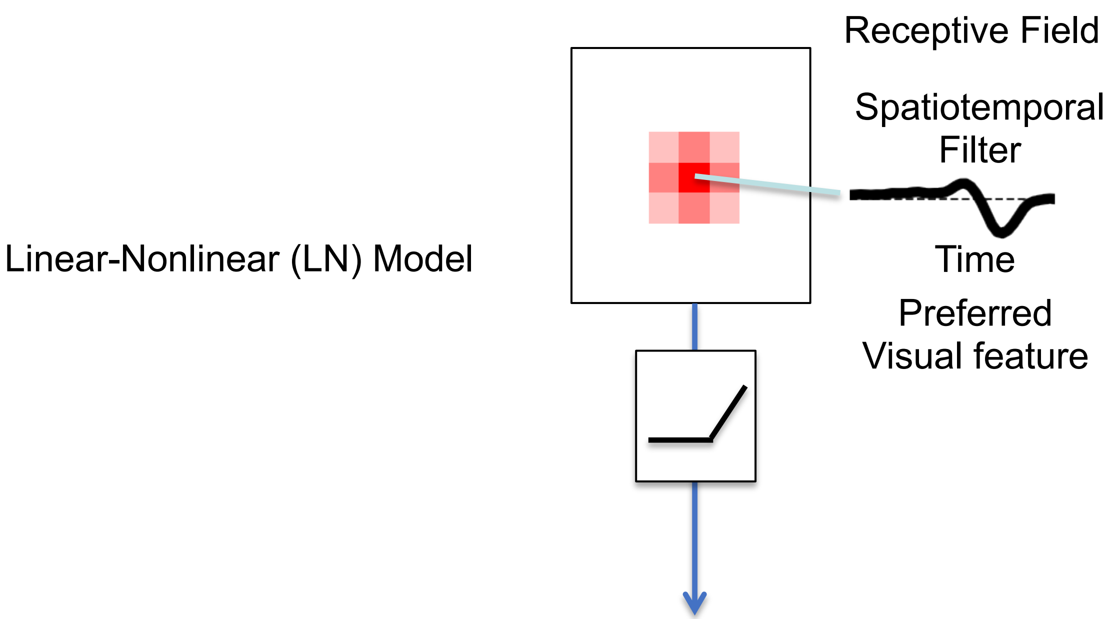
What is adaptation?

Why do neural systems have a particular nonlinear and filter?

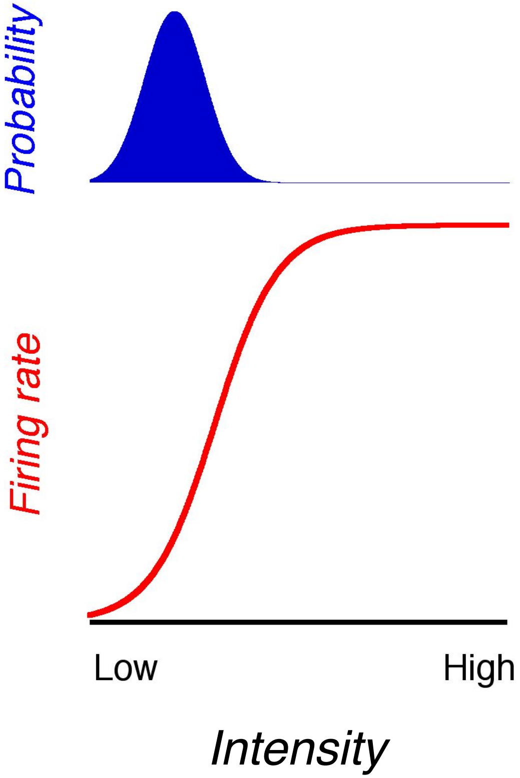
Why does the nonlinearity and filter change?

A hierarchy of systems

What biophysical mechanisms can cause adaptation?

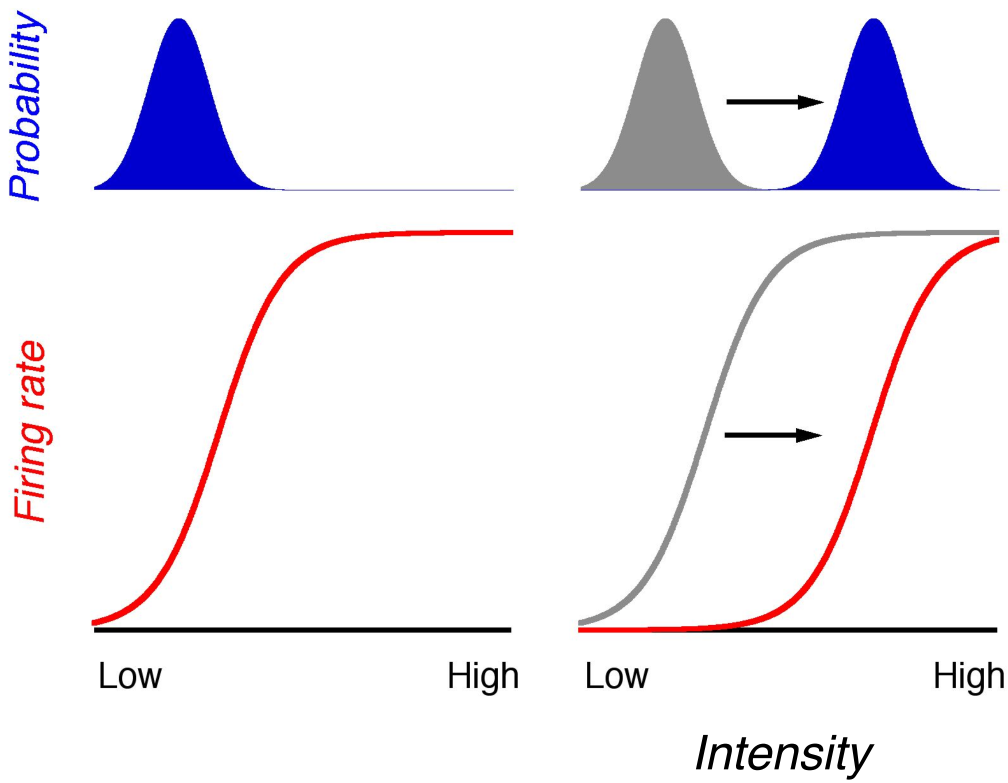


What happens when stimulus statistics change?

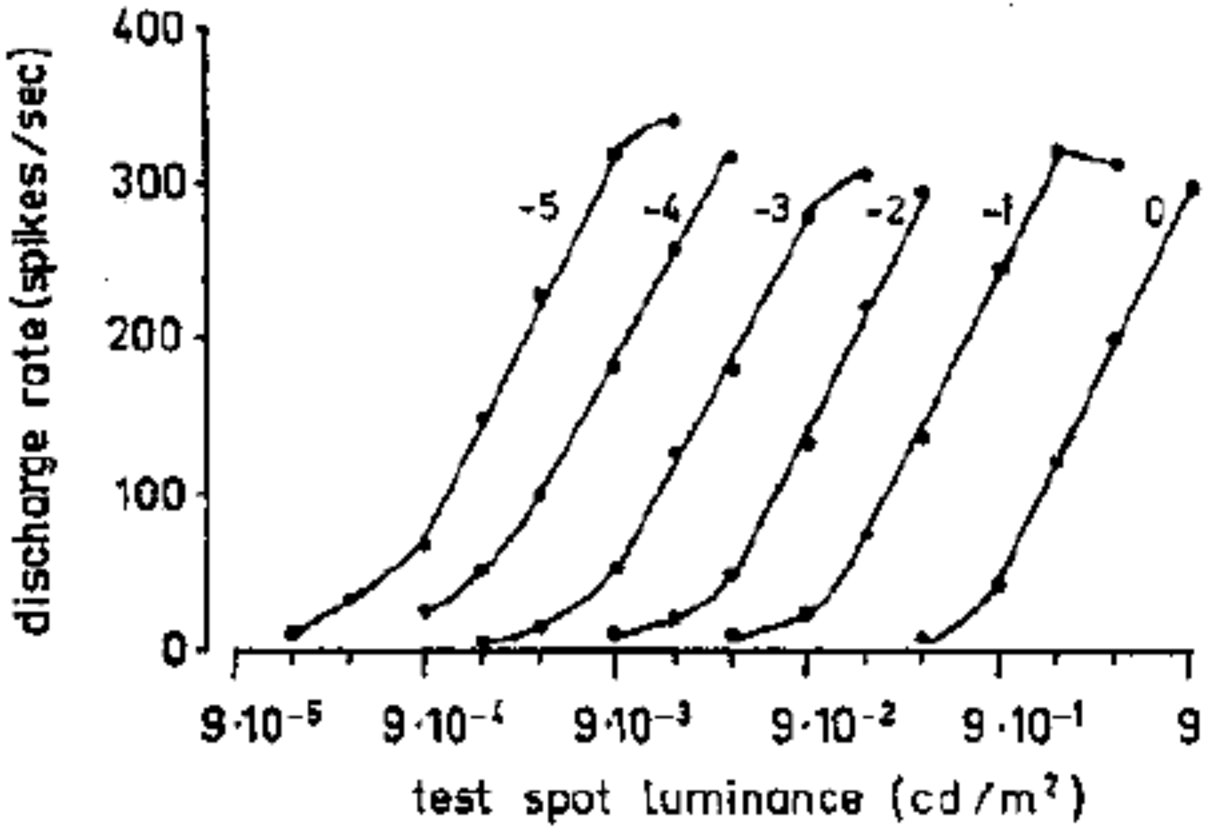


What happens when stimulus statistics change?

Light adaptation

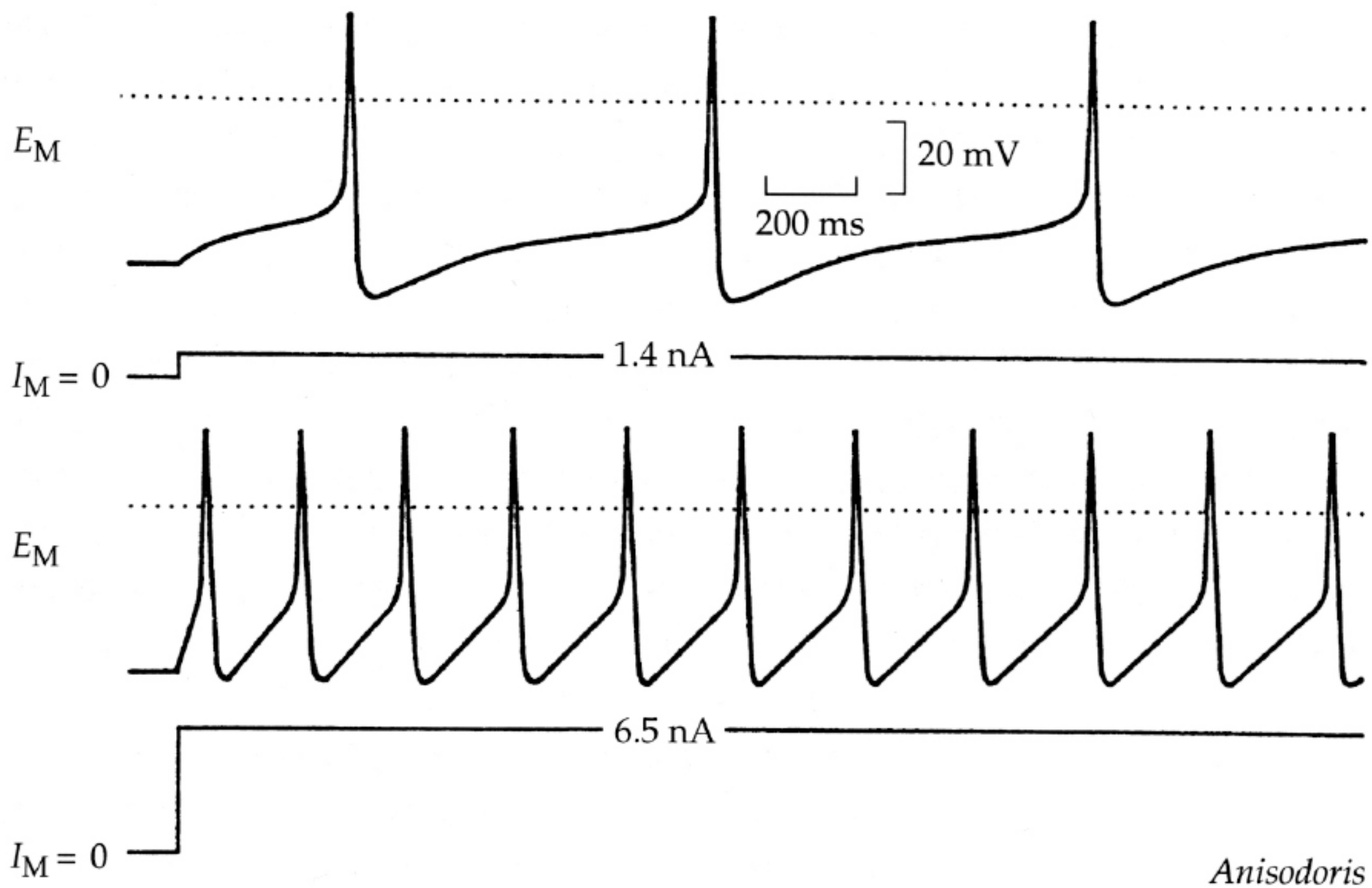


<u>Ganglion cell response curves shift to the mean light intensity</u>



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

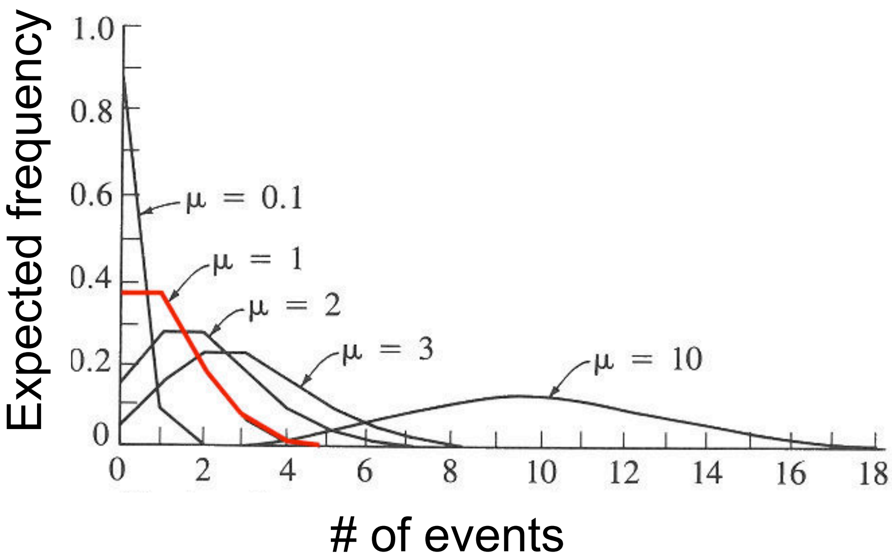


Events with Poisson statistics

$$P\left(X=n \mid E(X)=\mu\right)=\frac{e^{-\mu}\mu^{n}}{n!}$$

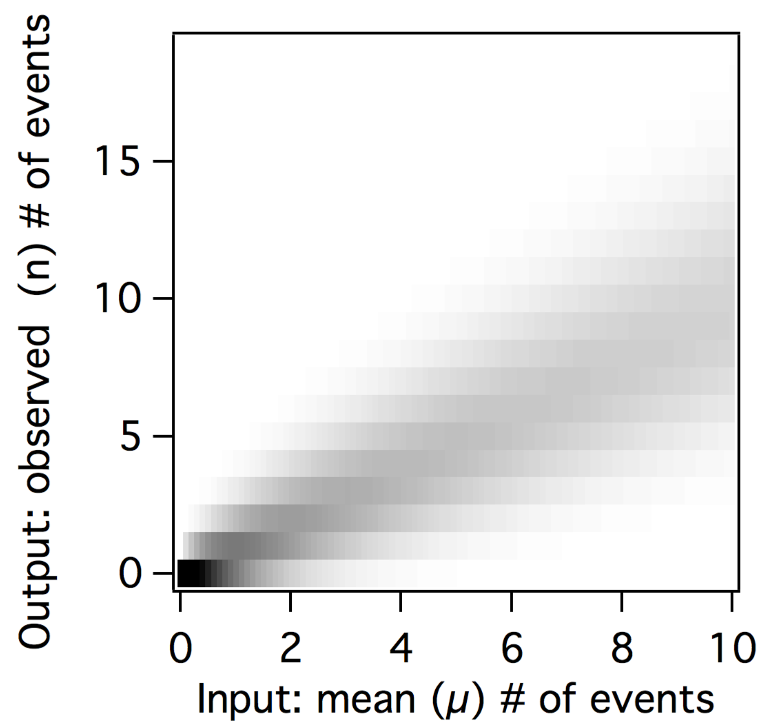
μ = mean # of events in a time interval

n = events in a time interval



variance=mean=μ

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



How to Model Noise?

Poisson distribution Independent events occurring at an average rate.

Photons
Spiking

$$\sigma^2 = \mu$$

Gaussian distribution Sum of many independent processes through central limit theorem.

Membrane potential noise

$$\sigma^2 = \text{constant parameter}$$

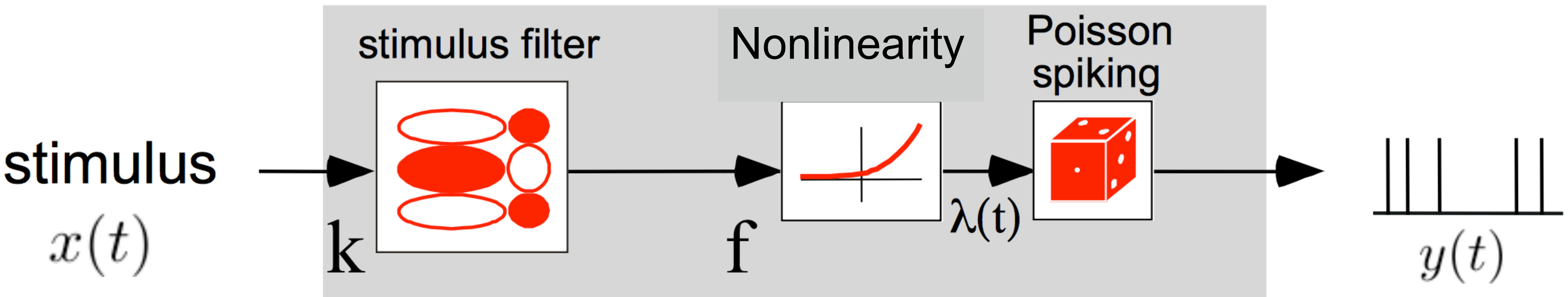
Binomial distribution *n* independent outcomes, each with probability p.

Channel gating
Vesicle fusion

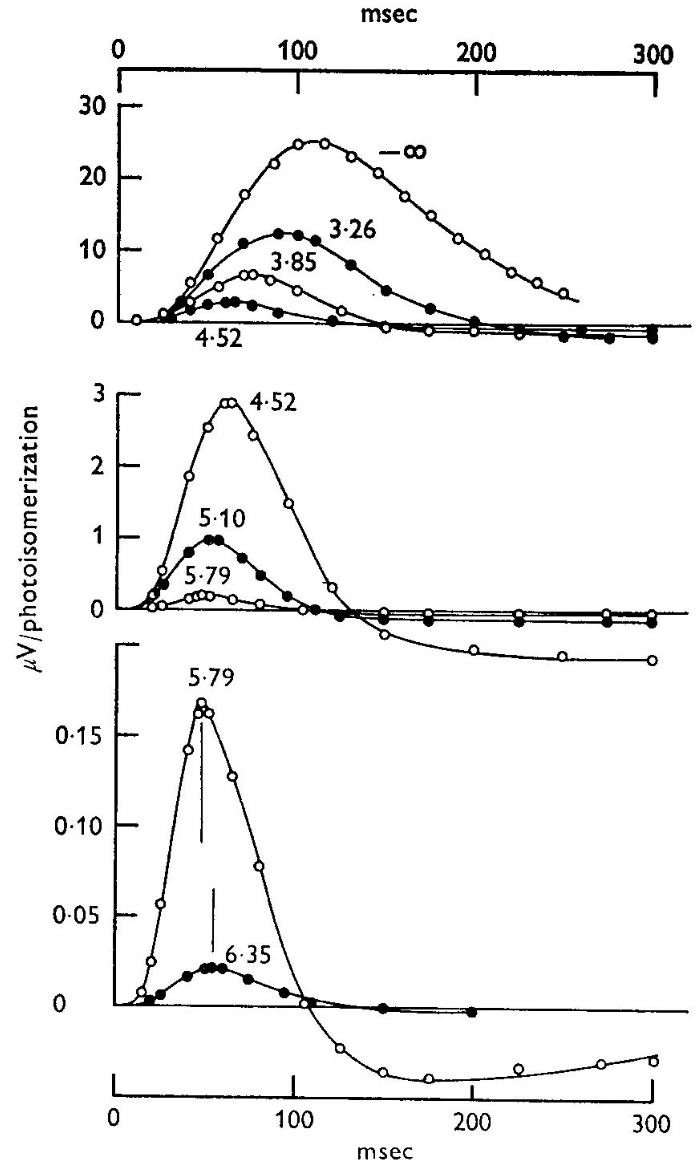
$$\sigma^2 = np(1-p)$$

Approximated by Poisson distribution at low probability p

Linear-Nonlinear-Poisson



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

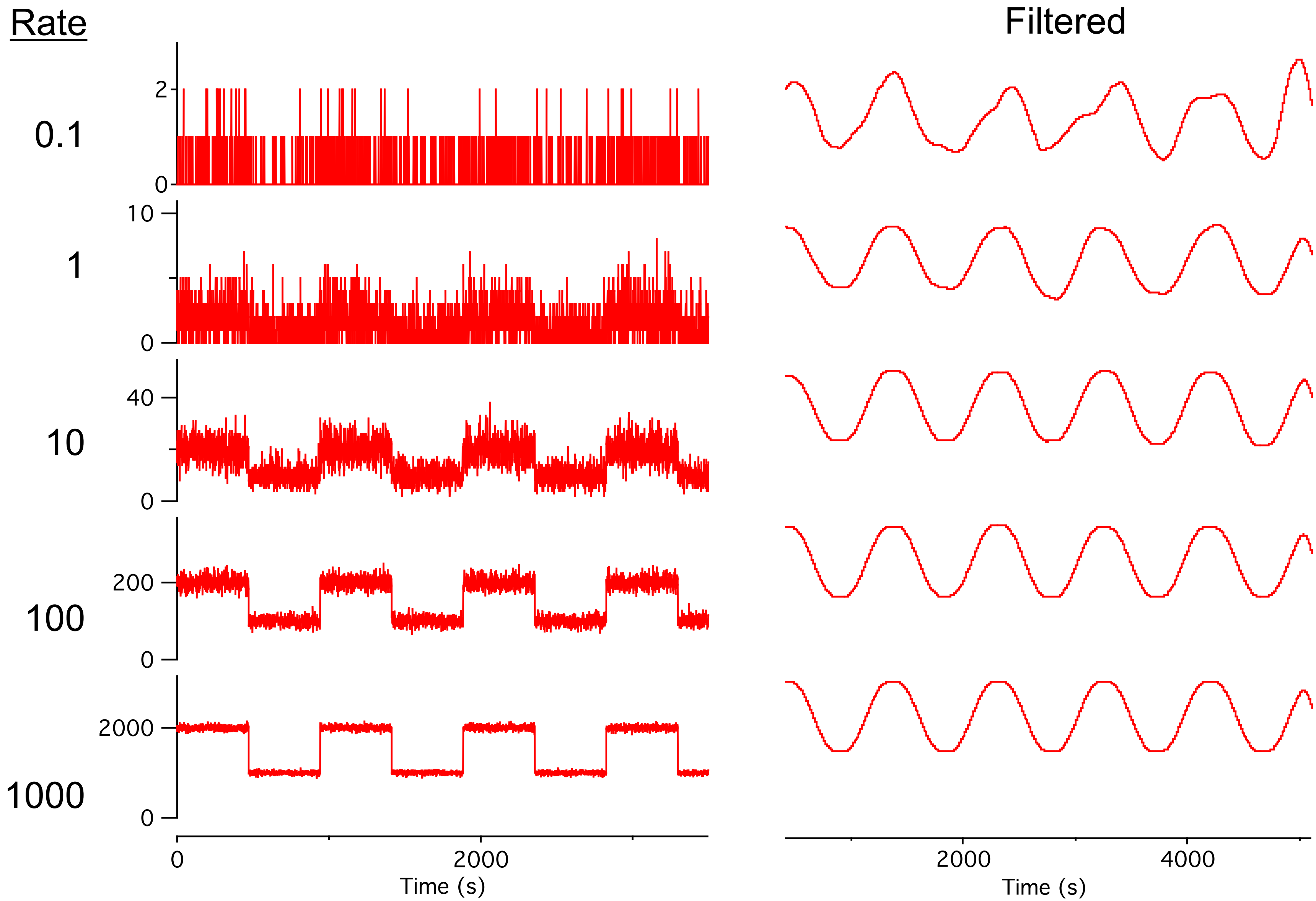


Dim background

Bright background

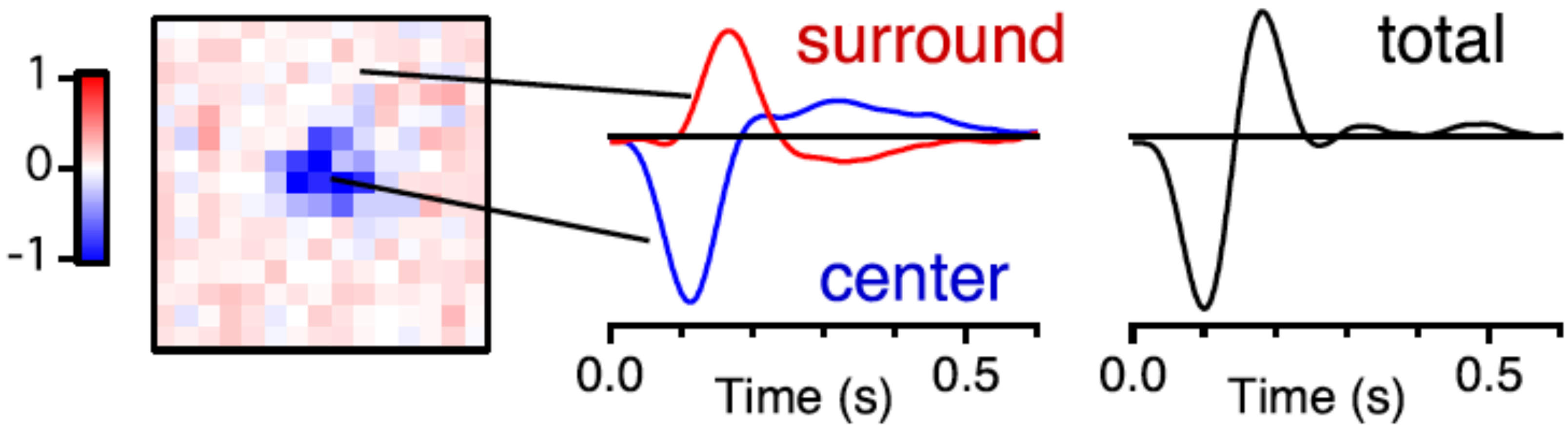
Baylor & Hodgkin 1974

Signal with poisson distribution



What receptive field maximizes information transmission?

Retinal bipolar cell receptive field



Baccus, Olveczky, Manu & Meister, 2008

A Mathematical Theory of Communication

Claude Shannon (1948)

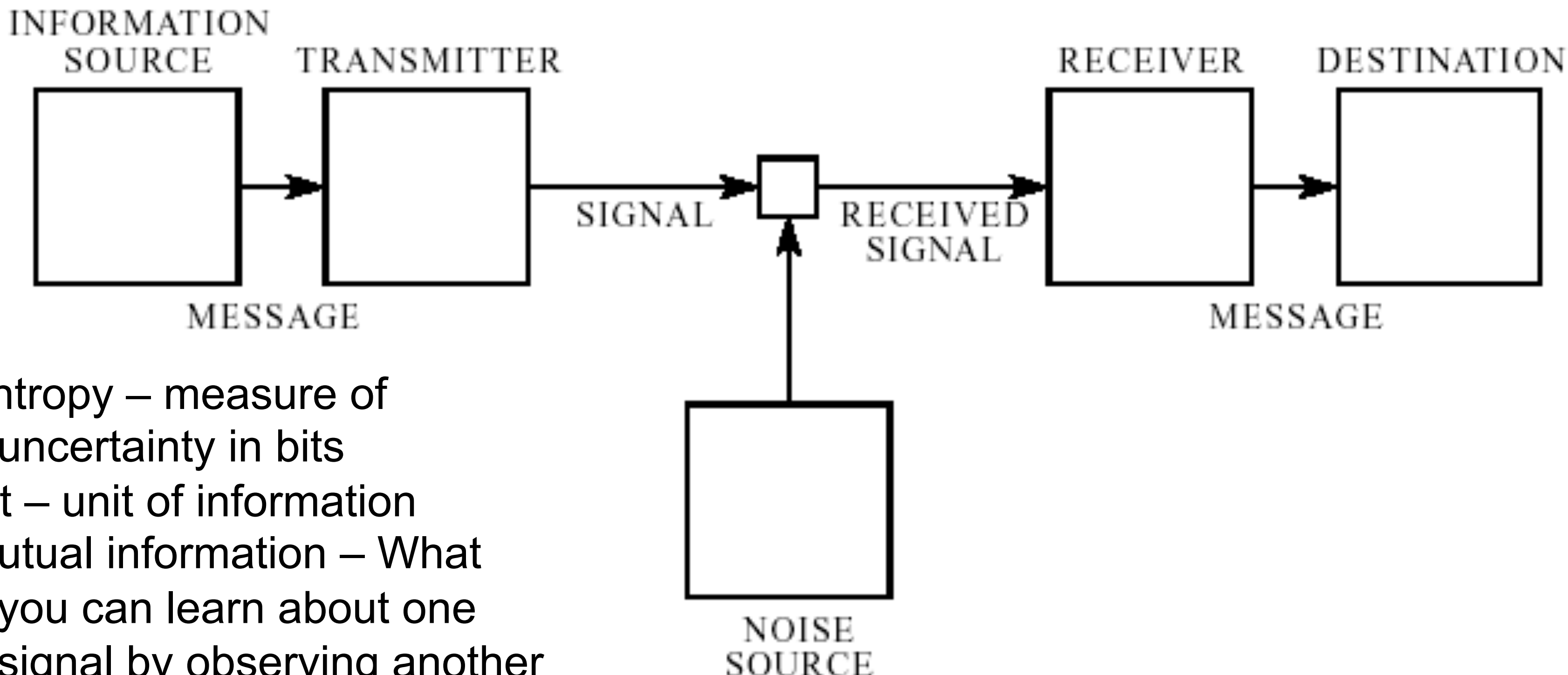


Fig. 1—Schematic diagram of a general communication system.

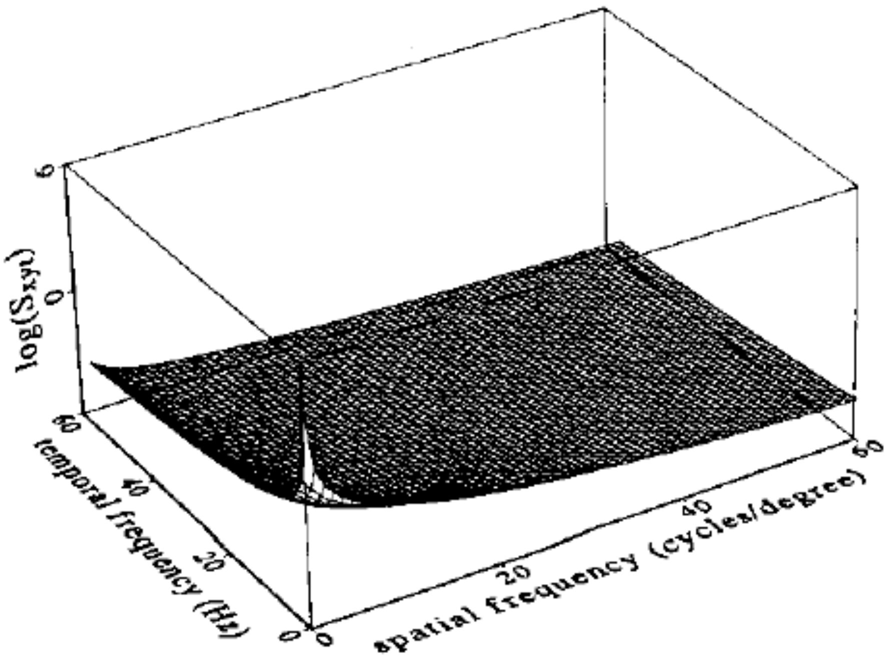
Entropy – measure of uncertainty in bits
Bit – unit of information
Mutual information – What you can learn about one signal by observing another

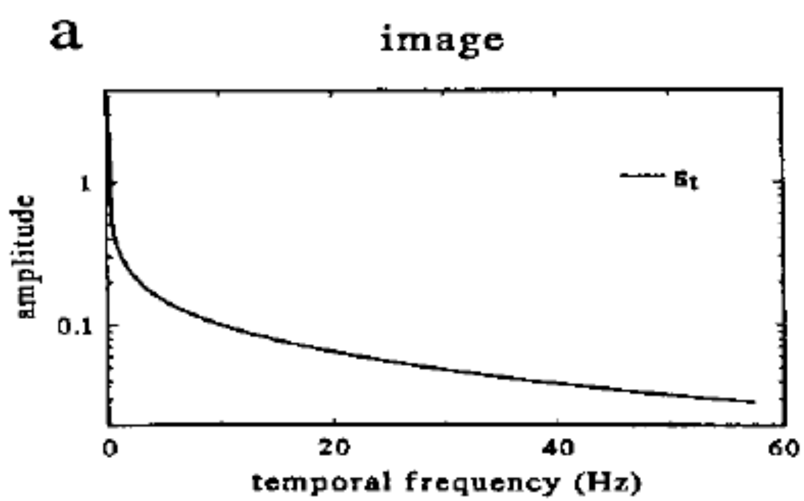
Bell System Technical Journal 27, 379-423

Theory of maximizing information in a noisy neural system

‘Efficient Coding’ - Horace Barlow

Natural visual scenes are dominated by low spatial and temporal frequencies



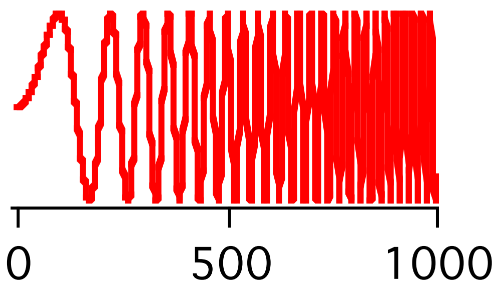


J.H. van Hateren. Real and optimal neural images in early vision. *Nature* 360:68-70 (1992)

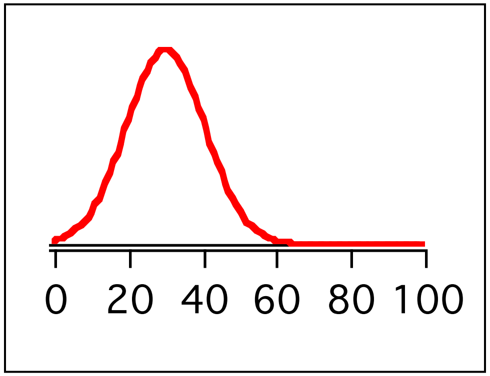
J.H. van Hateren, Spatiotemporal contrast sensitivity of early vision. *Vision Res.*, 33:257-67 (1993)

Linear filter and frequency response

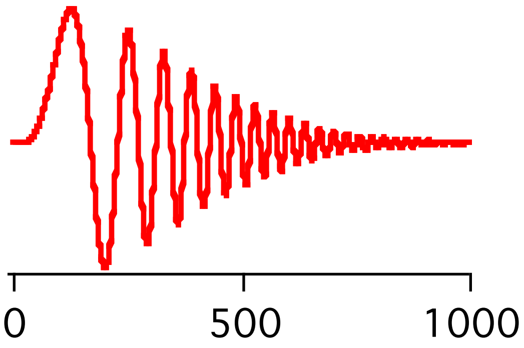
Stimulus



Filter



Response



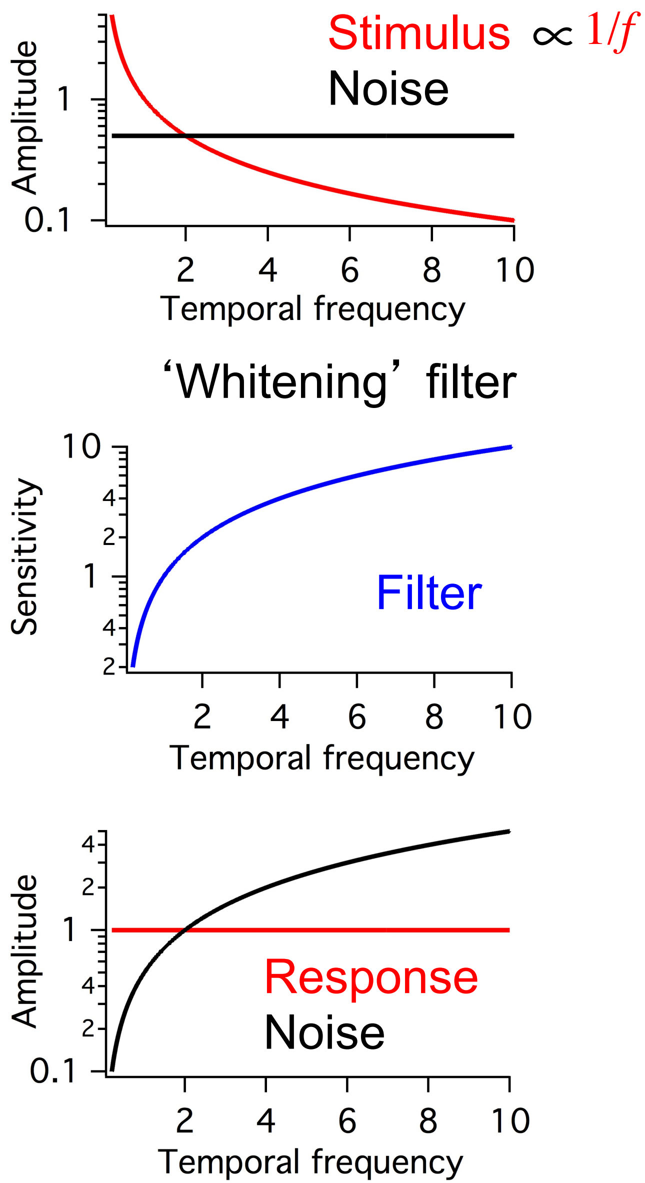
Convolution theorem

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

a convolution in the time domain

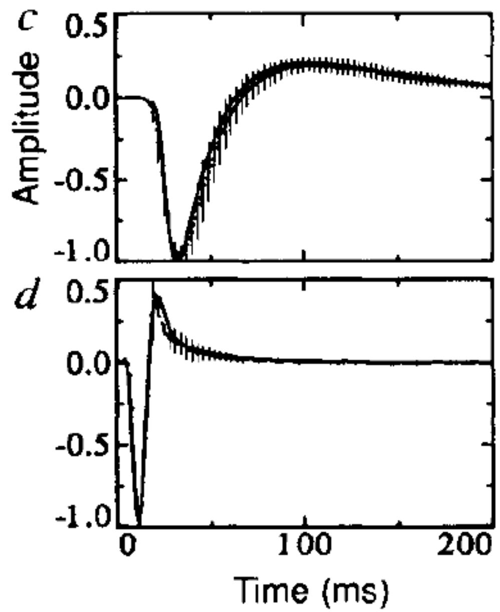
is a simple product in the frequency domain

Optimal filter whitens but also cuts out noise



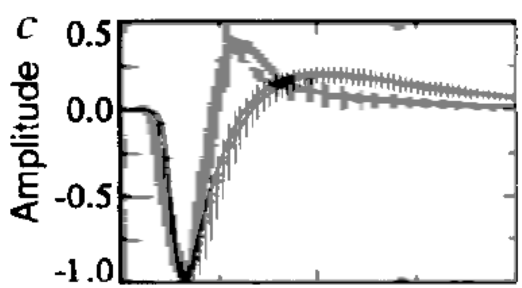
Theory of maximizing information in a noisy neural system

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



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

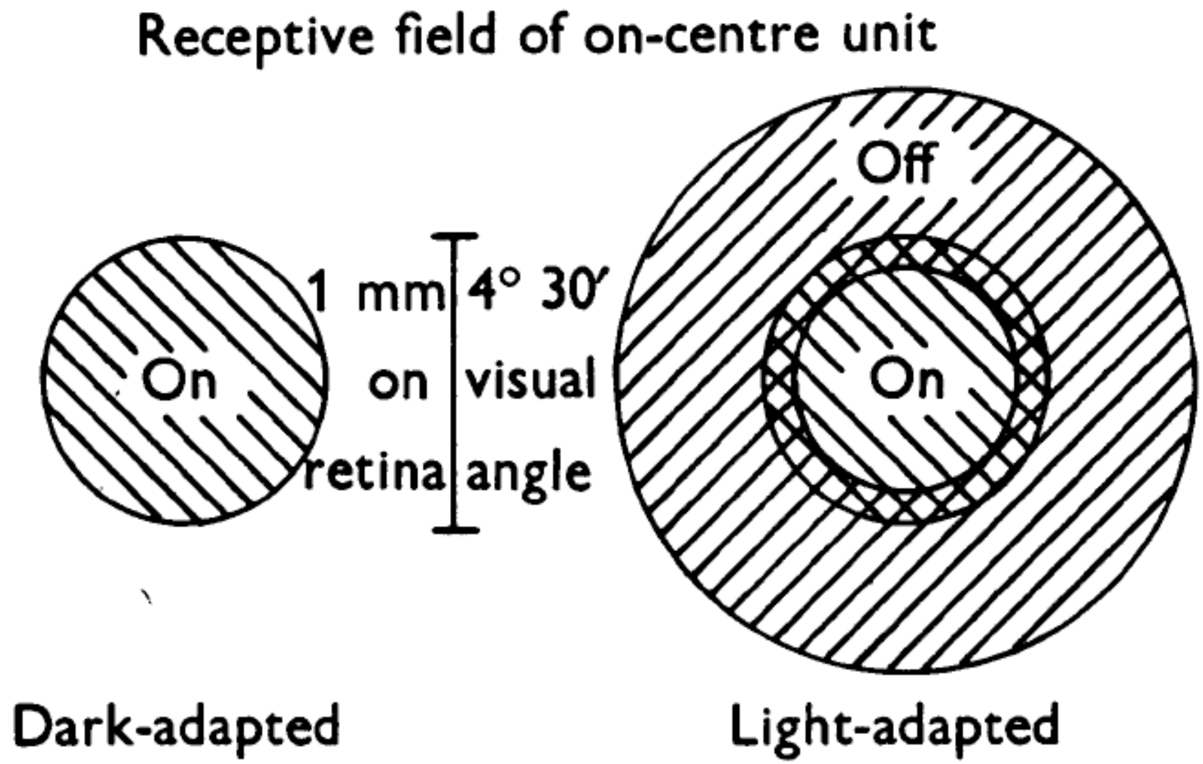
High background intensity
Emphasizes change, is more differentiating
(real and theoretical optimum)



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:

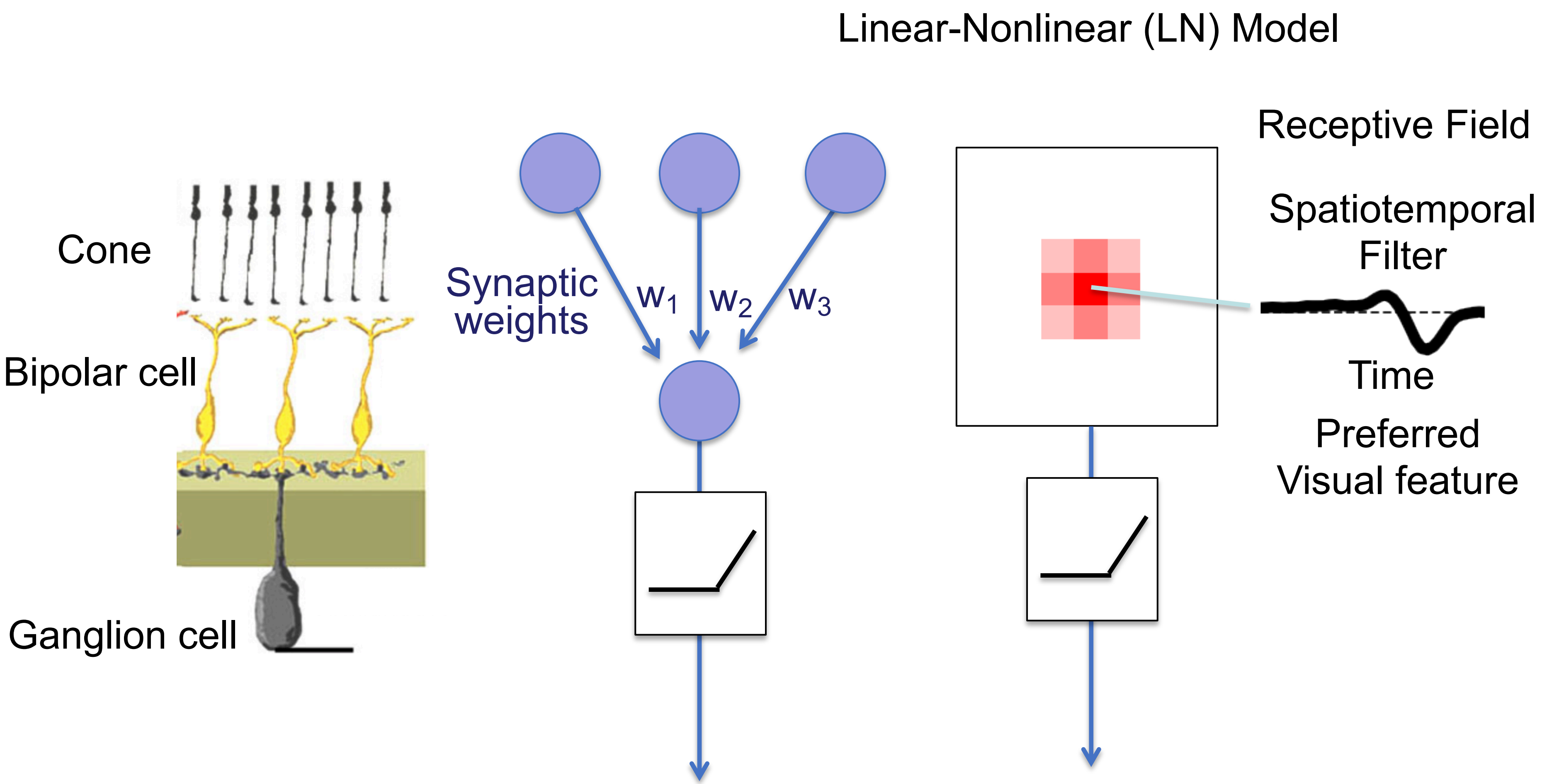
An ideal encoder should use all output values with equal probability

Low frequencies dominate in natural scenes

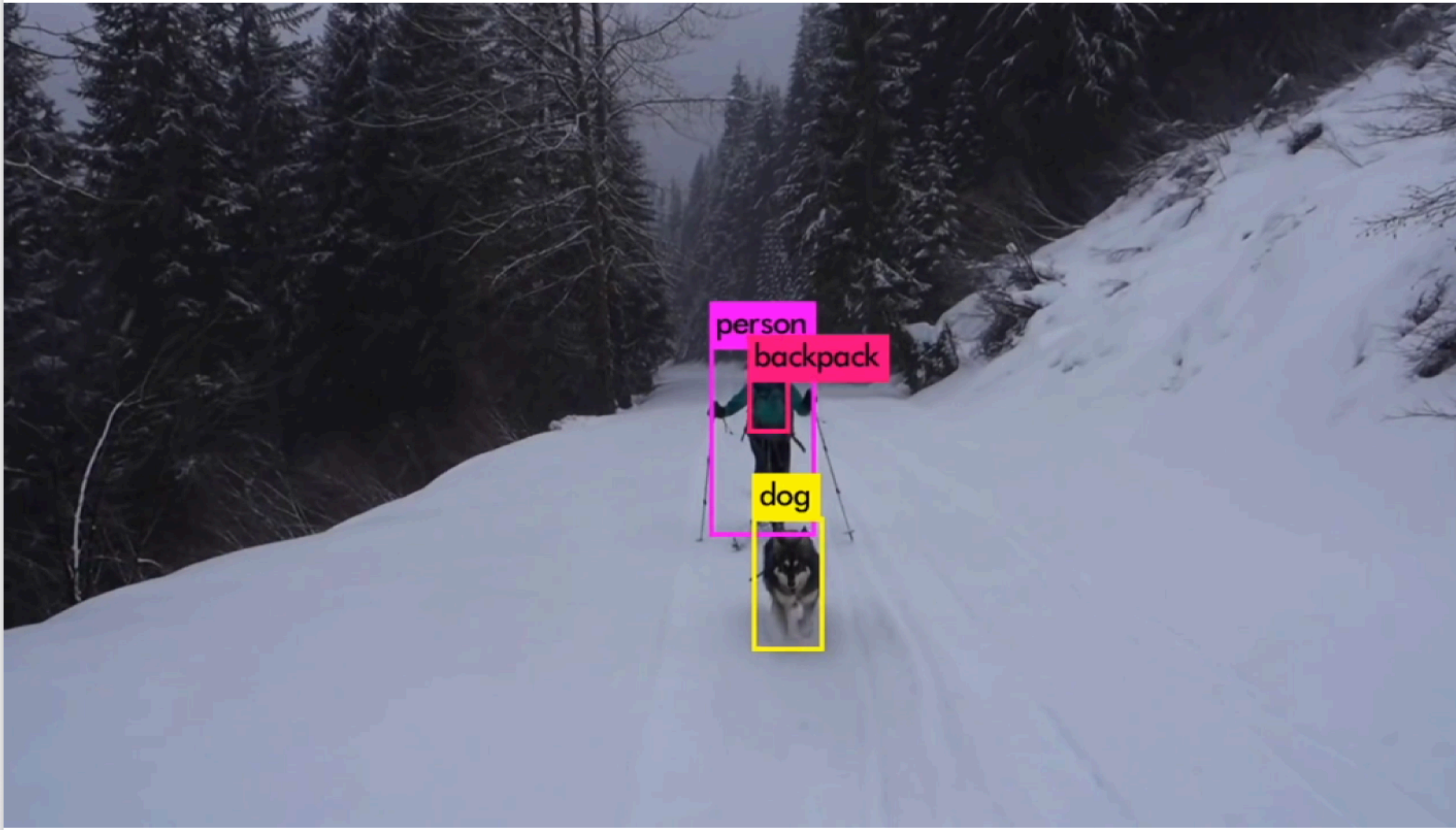
An efficient encoder should amplify higher frequencies more than low frequencies

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

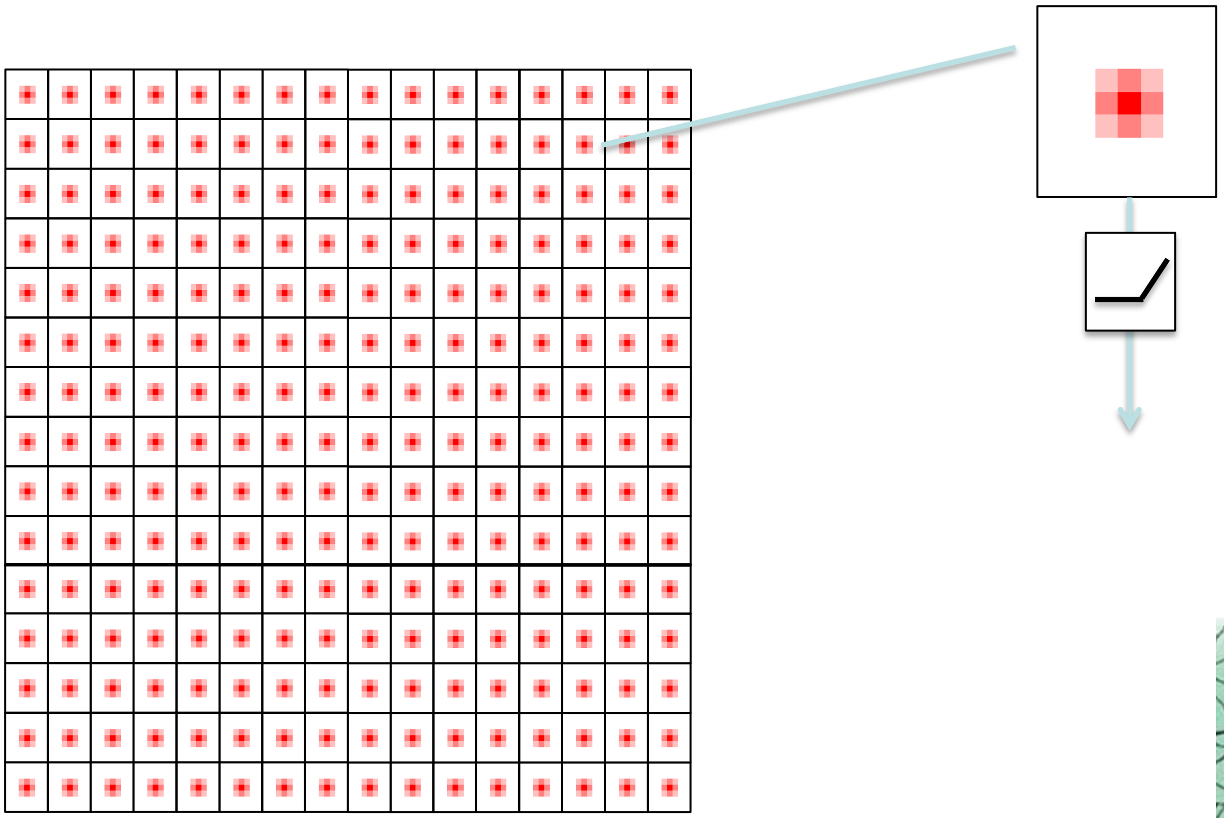
A Simple Model of Visual Responses



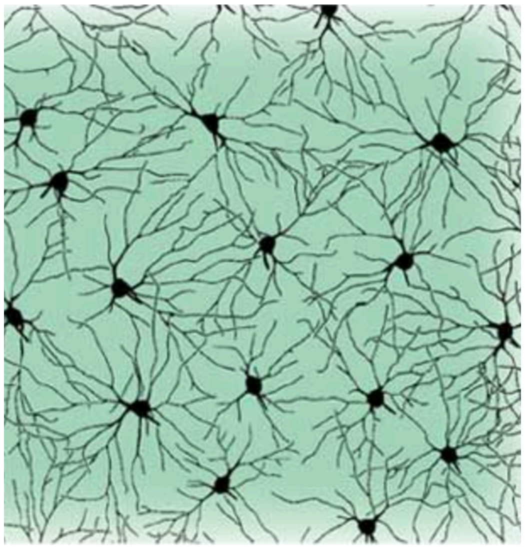
Deep Learning Object Recognition



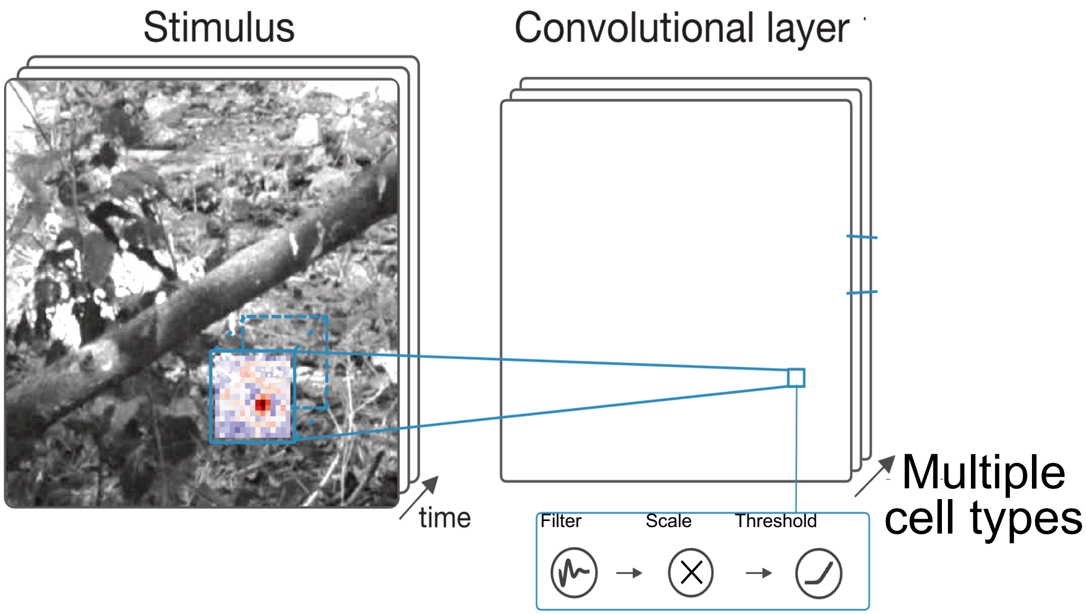
“Convolutional” layer



Like a mosaic
of retinal neurons

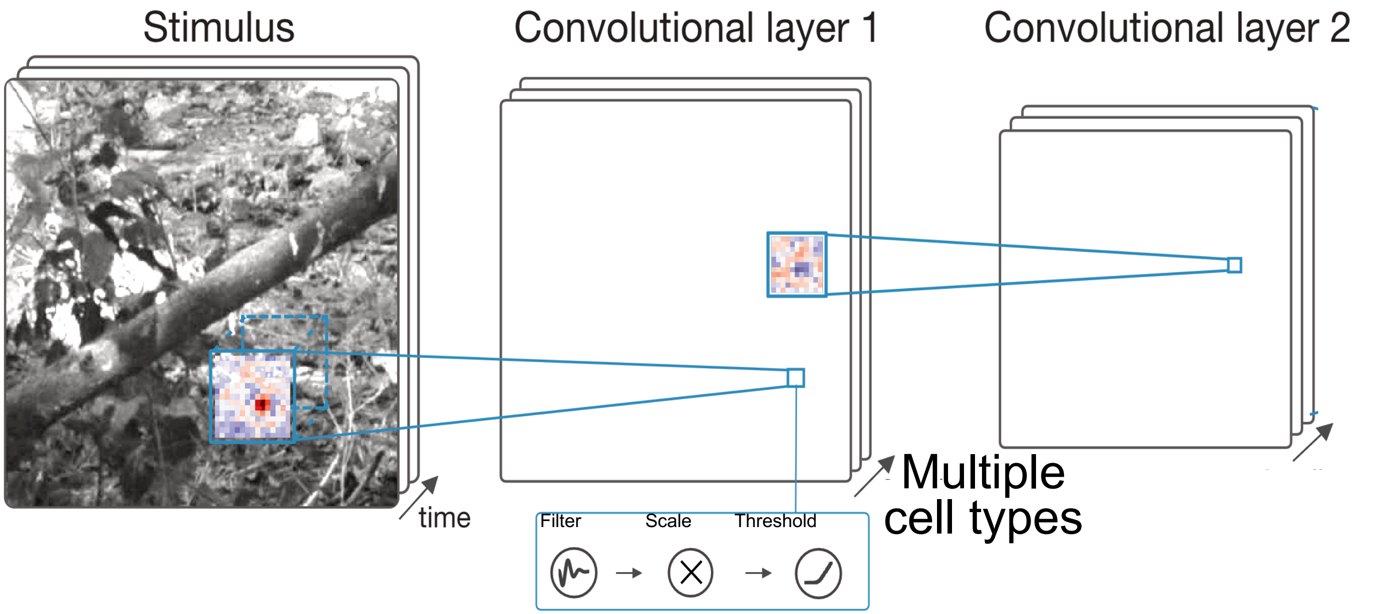


Multiple cell types



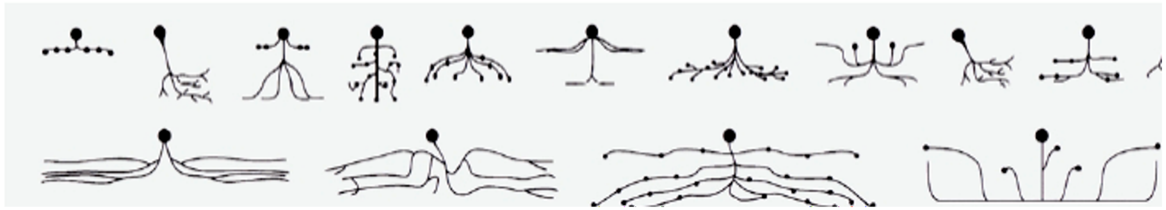
Like the multiple cell
types in the retina

Multiple Layers

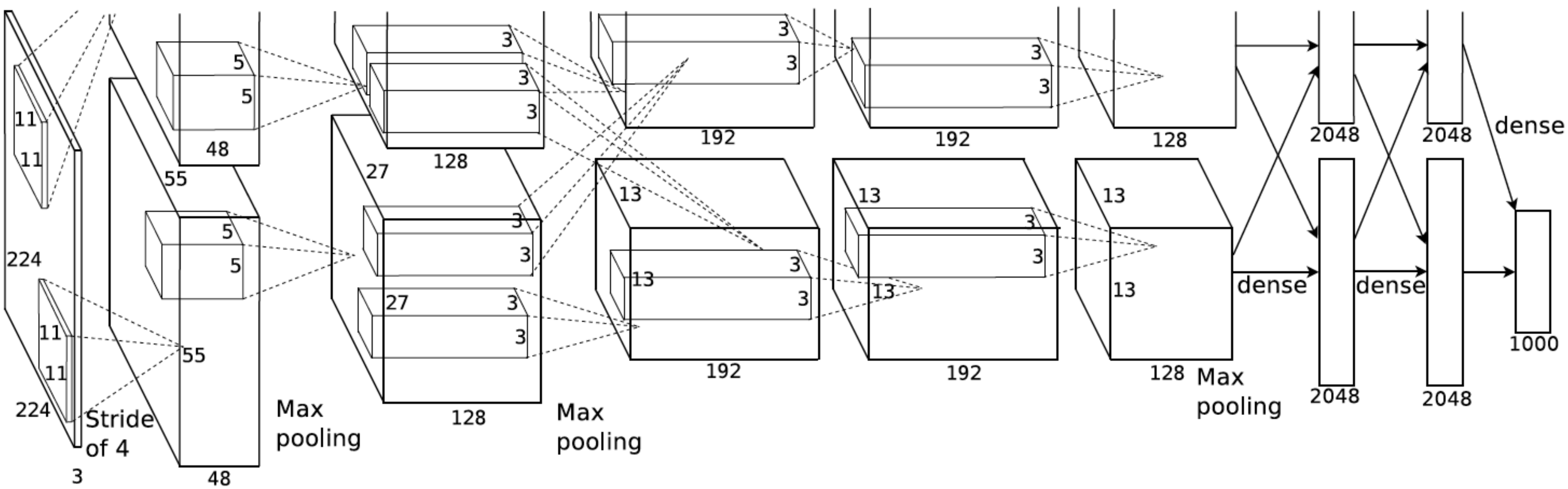


Like the multiple cell types in the retina

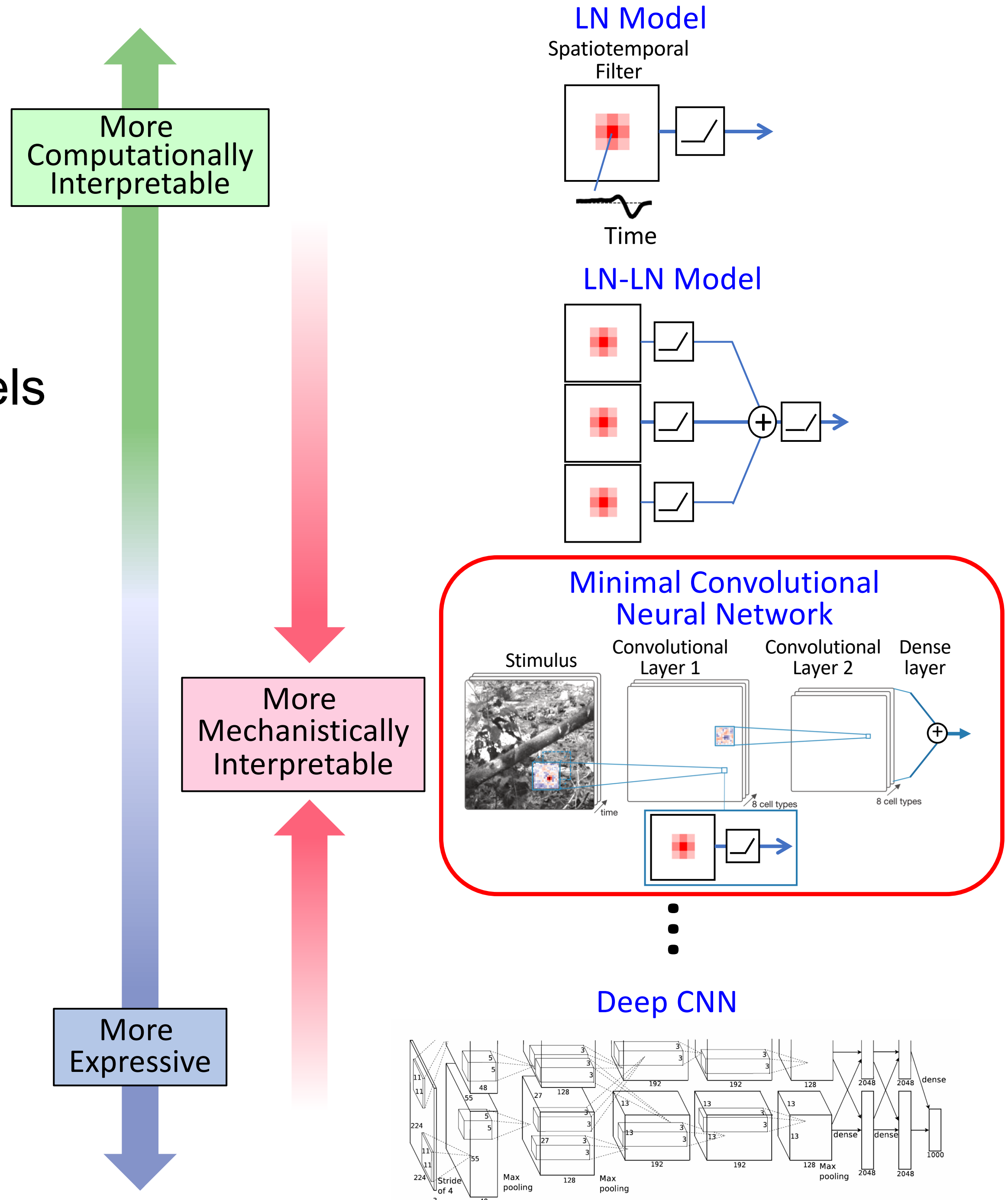
Like the hierarchy of retinal circuitry



Object Recognition Deep Network

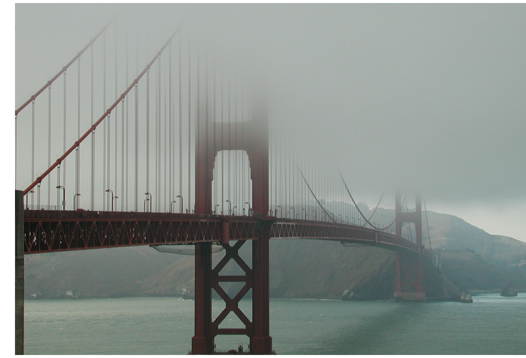


Different sensory models for different questions

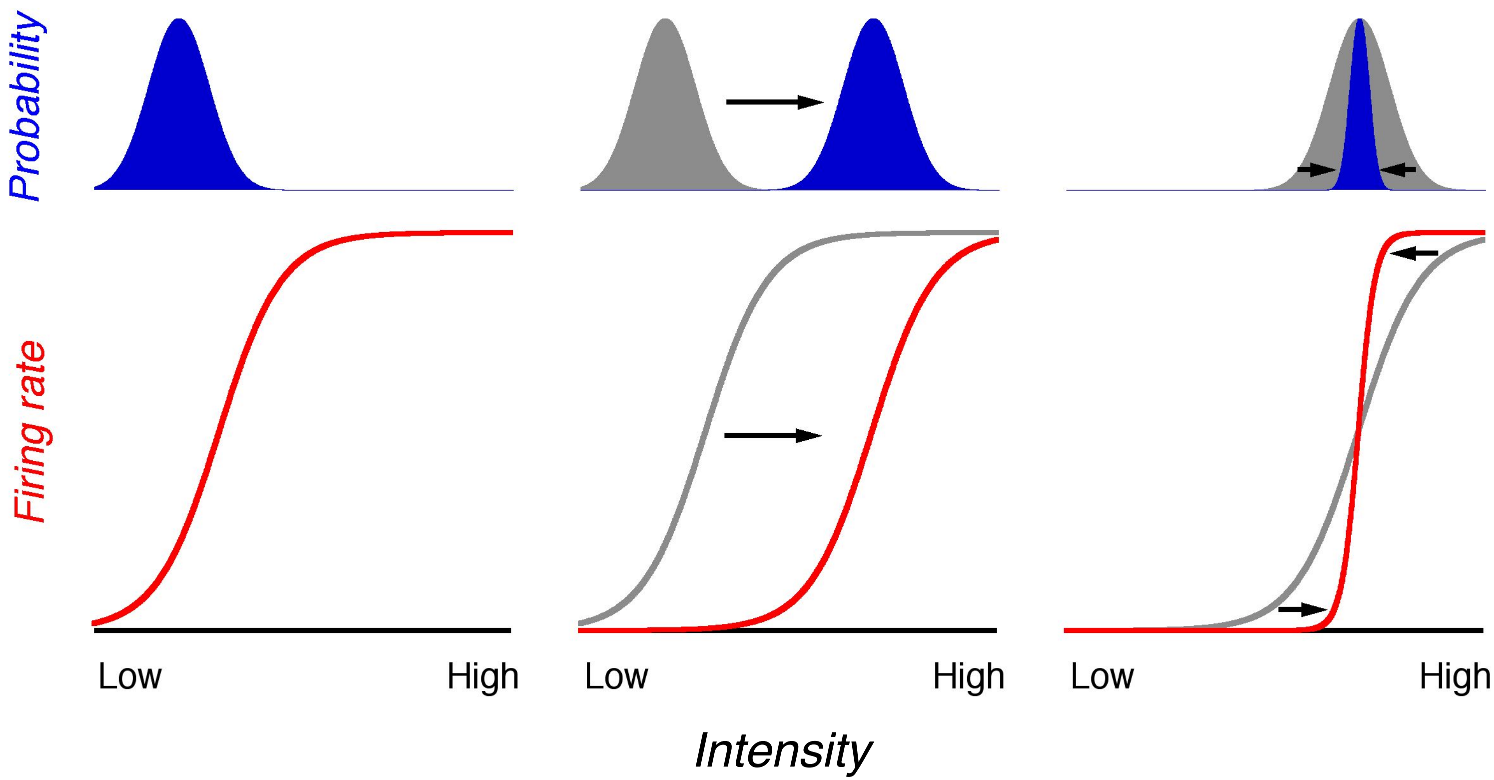


Adaptation to mean and variance

Light adaptation



Contrast adaptation



Why study biophysical mechanisms?

Biophysics provides constraints

Biophysics provides a tool kit

Function

Mechanisms

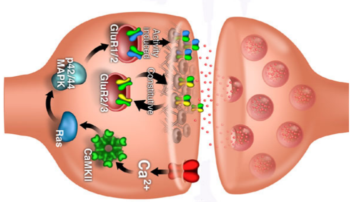
Computations

Theory

Higher level function

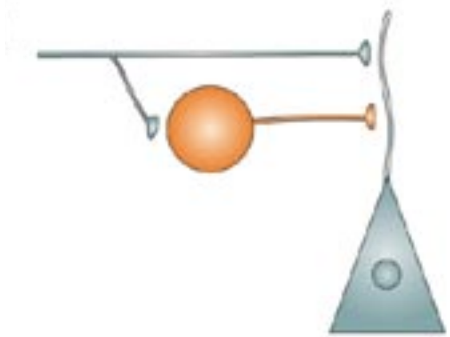
↕

Lower level mechanisms



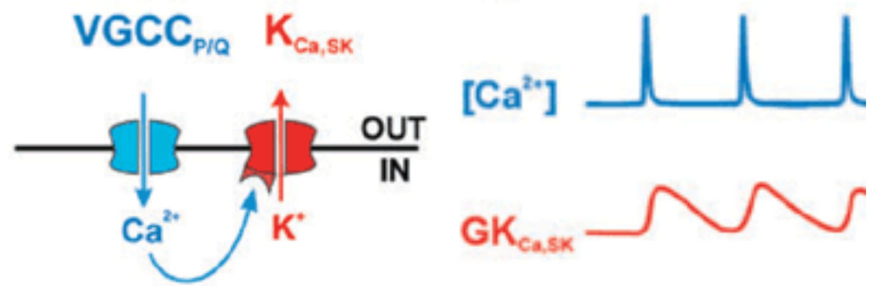
Change in sensitivity by *modulation*

Feedforward
inhibition



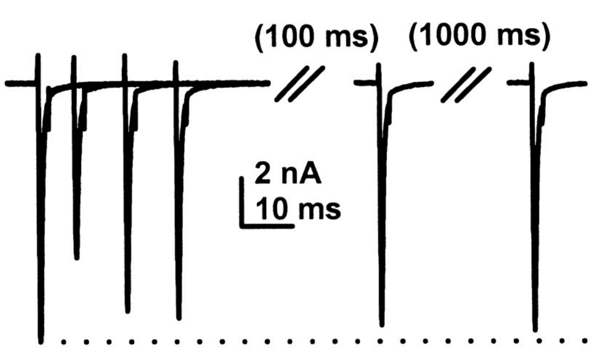
Feedback
inhibition

Spike dependent conductances

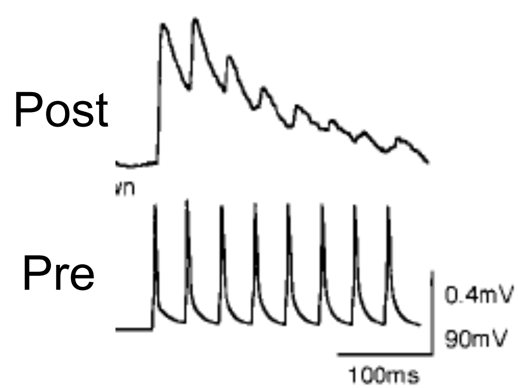


Change in sensitivity by *depletion*

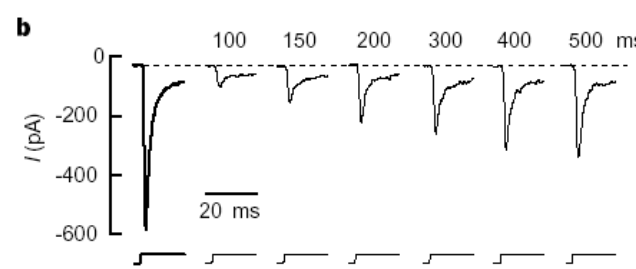
Ion channel
inactivation



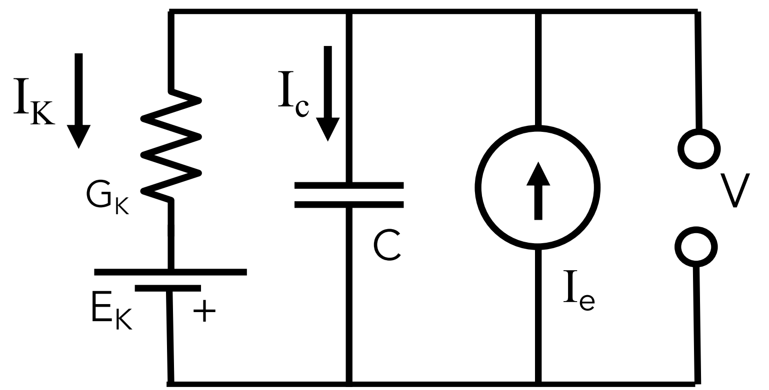
Short-term synaptic plasticity
synaptic depression



Receptor
desensitization



‘Equivalent’ circuit model of a neuron

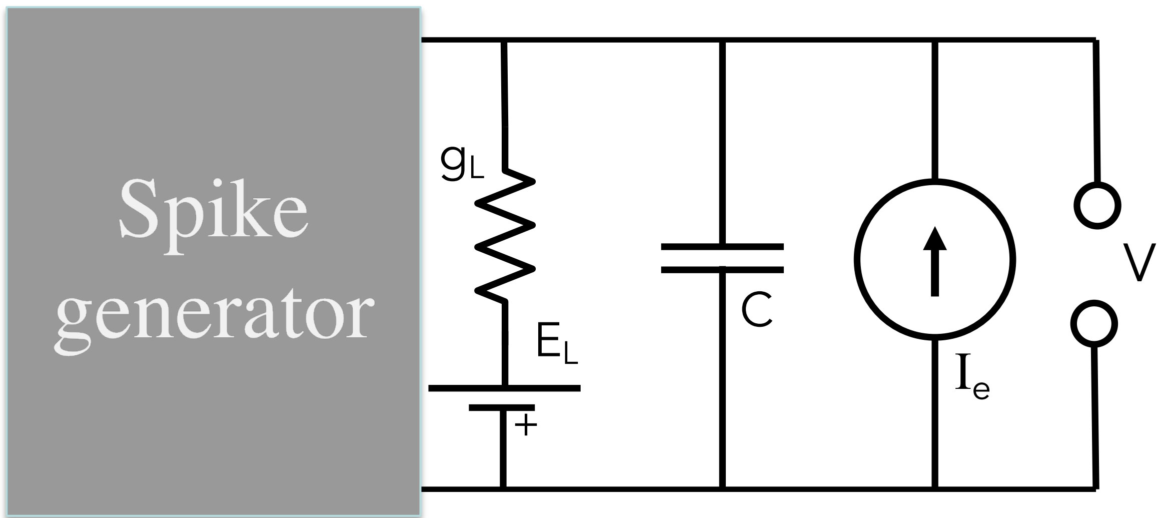


$$I_K + I_c = I_e$$

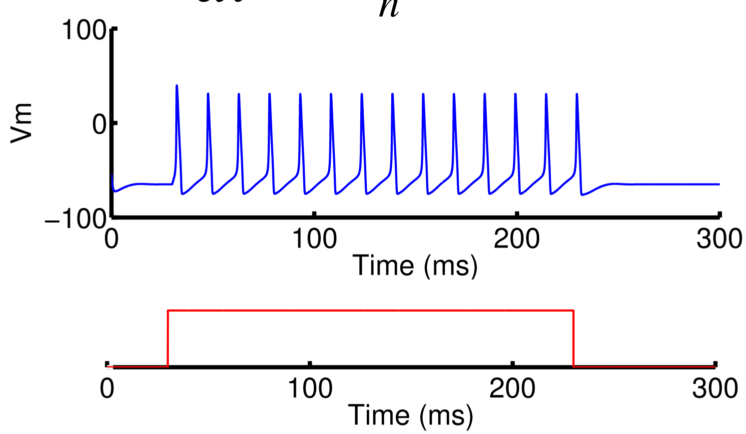
$$C\frac{dV}{dt} = I_e - G_K(V - E_K)$$

$$G_K = 1/R_K$$

A mathematical model of a neuron

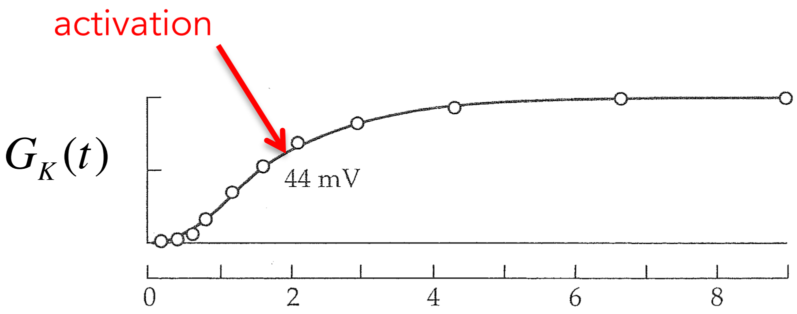


$$C\frac{dV}{dt} = \sum_n I_n(t) = I_e(t) - \sum_i g_i(V - E_i)$$

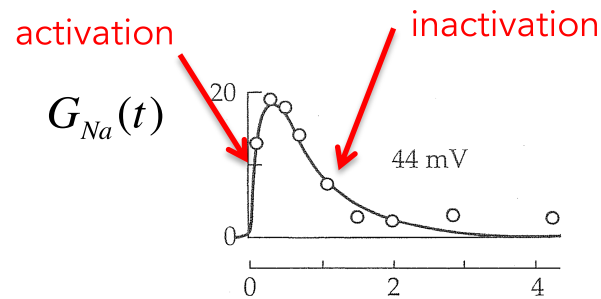


Alan Hodgkin
Andrew Huxley, 1952

Ionic currents (Time dependence)

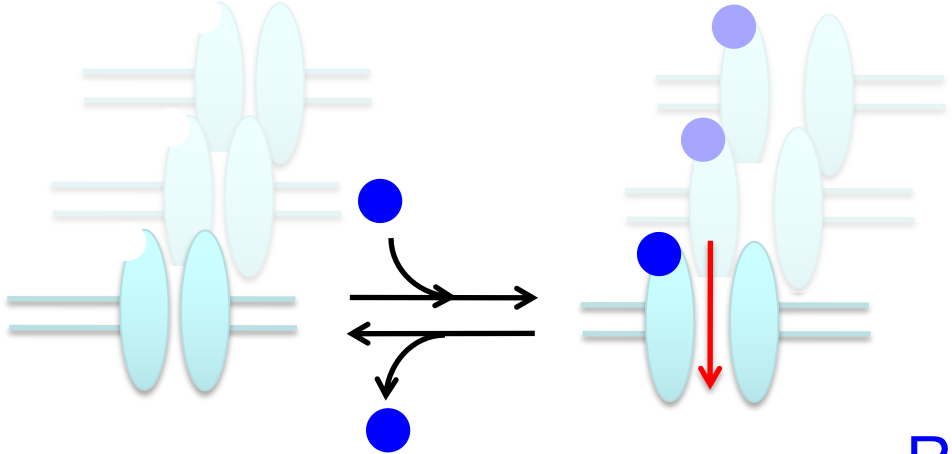


Time after start
of pulse (ms)



Time after start
of pulse (ms)

$$I_K(t) = G_K(V,t) \cdot \left(V - E_K\right) \qquad I_{Na}(t) = G_{Na}(V,t) \cdot \left(V - E_{Na}\right)$$



Rate constants

Closed $\qquad$ Open

$$R \underset{k_{\text{off}}}{\overset{[L]k_{\text{on}}}{\rightleftharpoons}} A$$

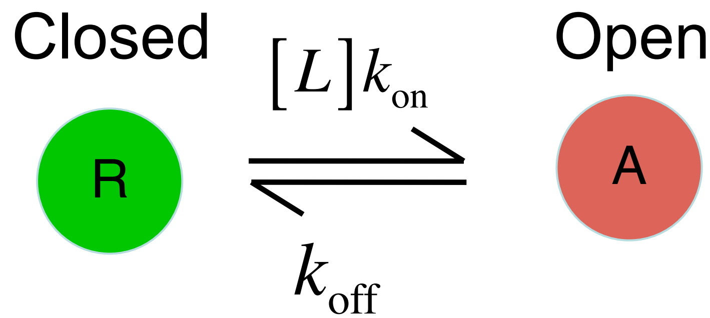
State Occupancies (sum to 1)

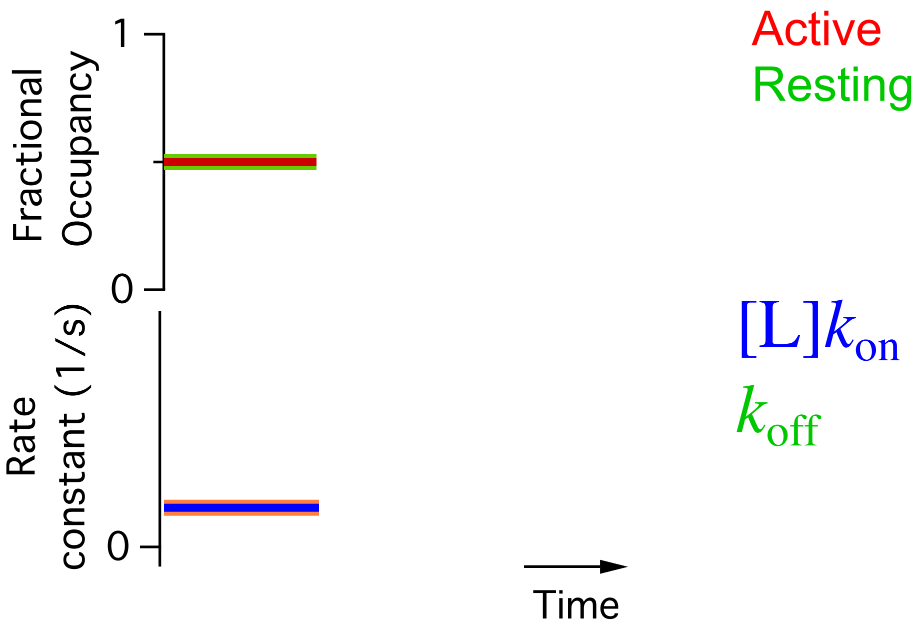
Change in activity = Inflow – Outflow

$$\frac{dA}{dt} = R[L]k_{\text{on}} - Ak_{\text{off}}$$

Kinetic model

Input and output in a kinetic model





Steps for computing the model, focusing on K+ current:

$$C\frac{dV(t)}{dt} = I_e(t) - \bar{G}_K n^4\left(t, \alpha_n, \beta_n\right)\cdot(V - E_K)\ldots$$

Max cond. state variable

Closed Open

$$1\text{-}n \underset{\beta(V)}{\overset{\alpha(V)}{\rightleftharpoons}} n$$

$$dn/dt = \alpha(V)(1-n) - \beta(V)n$$

Steps for computing the model, focusing on K+ current:

$$C\frac{dV(t)}{dt} = I_e(t) - \bar{G}_K n^4\left(t, \alpha_n, \beta_n\right)\cdot(V - E_K)\ldots$$

Closed $\quad$ Open

$$1\text{-}n \underset{\beta(V)}{\overset{\alpha(V)}{\rightleftharpoons}} n \qquad dn/dt = \alpha(V)(1-n) - \beta(V)n$$

Start with V_m at time step t

Compute rate constants as a function of V_m

Compute $\frac{dn}{dt}$ and integrate one time step to get $n(t)$

Compute K current: $\quad I_K = \bar{G}_K n^4 (V - E_K)$

Compute total membrane current: $I_m = I_K + I_{Na} + I_L$

Integrate $\frac{dV_m}{dt}$ to get V_m at next time step

Hodgkin Huxley Model

Voltage state variable (membrane equation):

$$C\frac{dV}{dt} = I(t) - \bar{g}_K n^4 (V - E_K) - \bar{g}_{Na} m^3 h (V - E_{Na}) - \bar{g}_l (V - E_l)$$

Conductance state variables:

$$\begin{aligned} dn/dt &= \alpha_n(V)(1-n) - \beta_n(V)n \\ dm/dt &= \alpha_m(V)(1-m) - \beta_m(V)m \\ dh/dt &= \alpha_h(V)(1-h) - \beta_h(V)h \end{aligned}$$

Rate "constants":

$$\begin{aligned} \alpha_n(V) &= \frac{10-V}{100\left(\exp\left((10-V)/10\right)-1\right)} \\ \alpha_m(V) &= \frac{25-V}{10\left(\exp\left((25-V)/10\right)-1\right)} \\ \alpha_h(V) &= 0.07\exp(-V/20) \end{aligned}$$

$$\begin{aligned} \beta_n(V) &= 0.125\exp(-V/80) \\ \beta_m(V) &= 4\exp(-V/18) \\ \beta_h(V) &= \frac{1}{\exp\left((30-V)/10\right)+1} \end{aligned}$$

Constants:

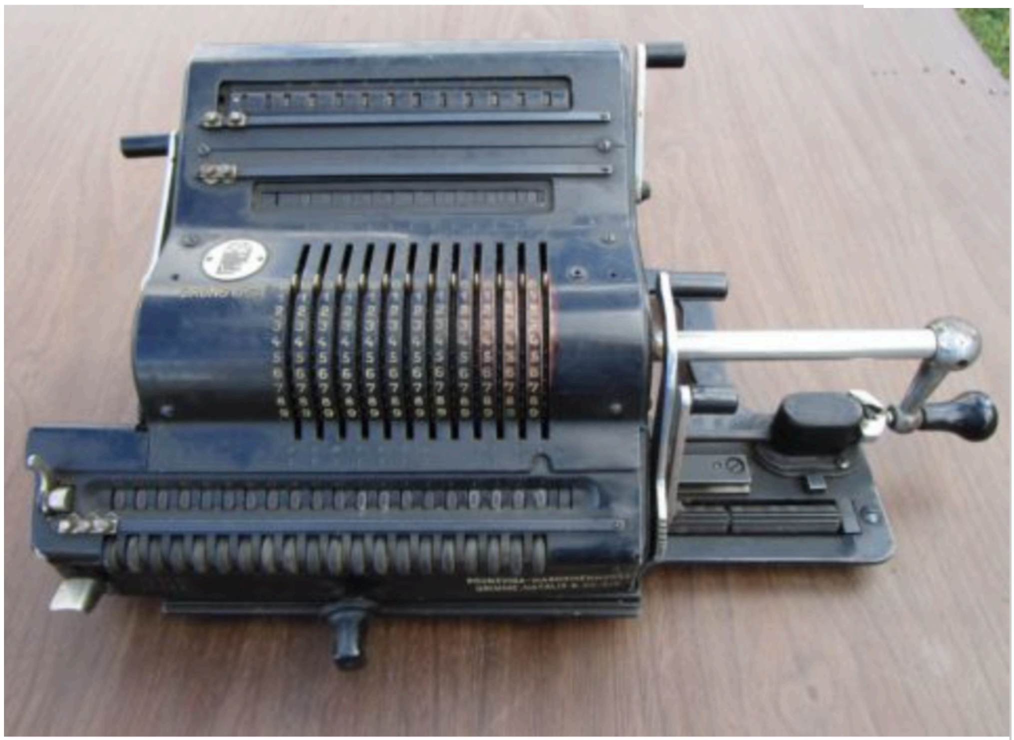
$$C = 1\,\mu\mathrm{F/cm^2}$$

$$\begin{aligned} \bar{g}_{\mathrm{K}} &= 36\,\mathrm{mS/cm^2} \\ \bar{g}_{\mathrm{Na}} &= 120\,\mathrm{mS/cm^2} \\ \bar{g}_l &= 0.3\,\mathrm{mS/cm^2} \end{aligned}$$

$$\begin{aligned} E_K &= -12\,\mathrm{mV} \\ E_{Na} &= +115\,\mathrm{mV} \\ E_l &= +10.613\,\mathrm{mV} \end{aligned}$$

Note: these are given in the original form, relative to V_{rest} =~ -66 mV

Vintage Brunsviga 20 Mechanical Pinwheel Calculator Made In Germany Read!



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Adaptation to the mean and variance of signals are similar in a number of systems

The kinetics and gain of the response change when the stimulus statistics change

These adaptive properties can be interpreted as avoiding saturation and maximizing information in the presence of noise

Many mechanisms can contribute these adaptive nonlinear properties at different timescales