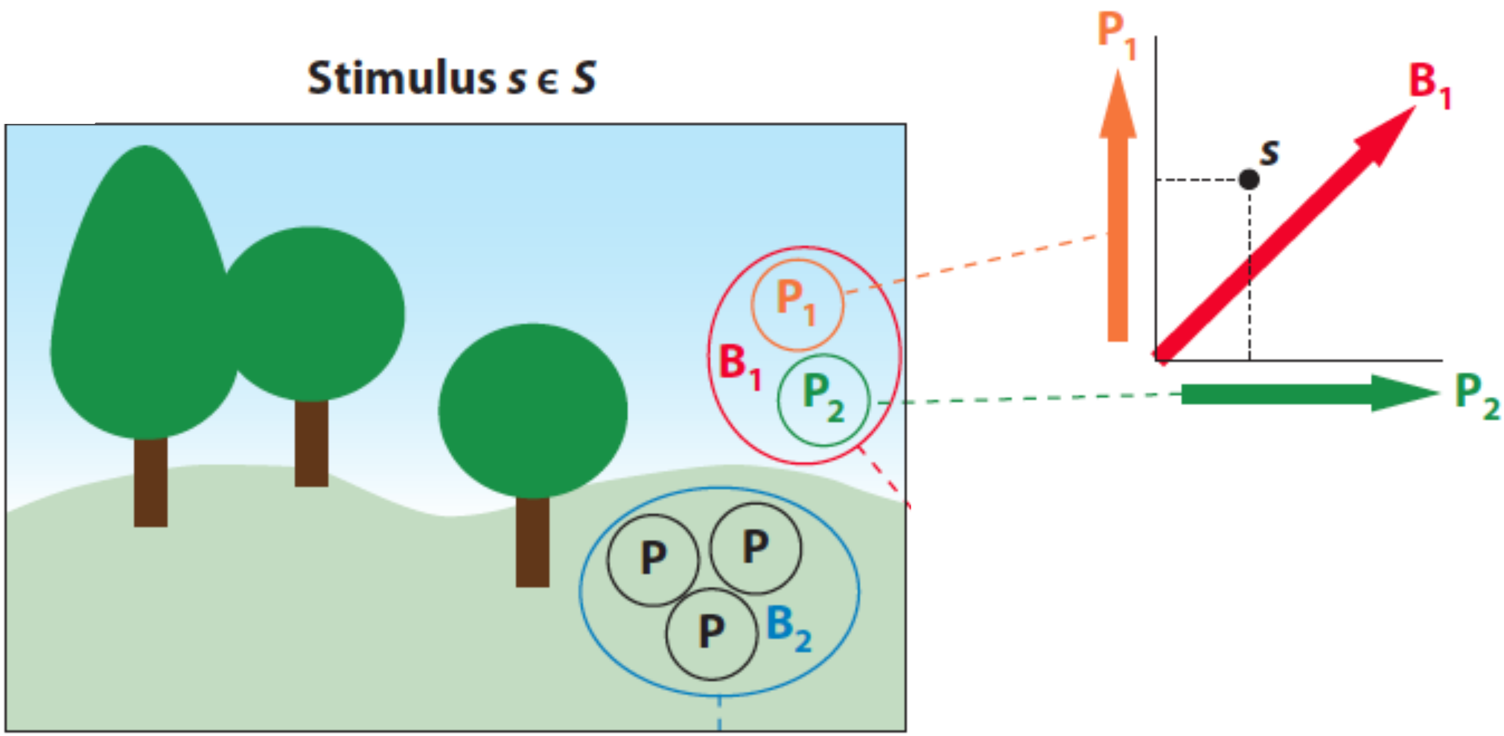
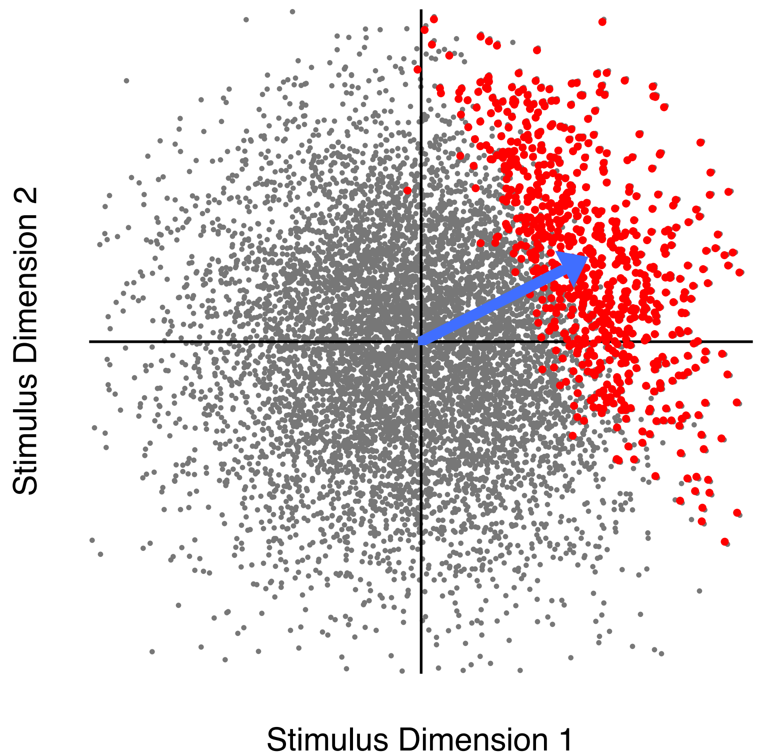
Lecture 3 encoding

Stimulus space: A geometrical representation of input



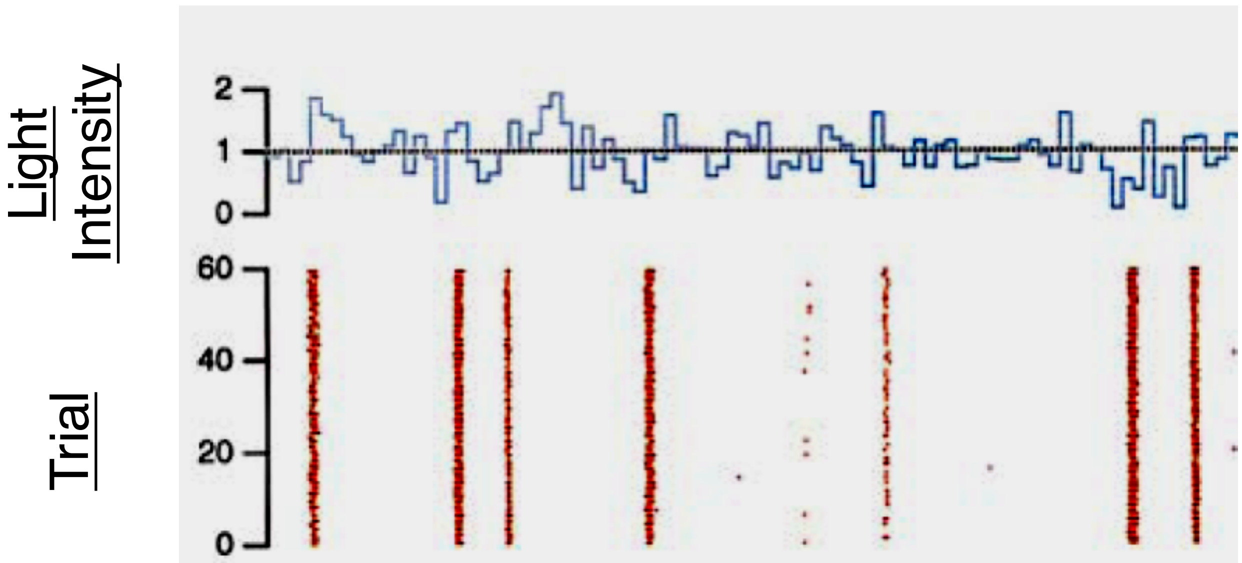
Not the same as "visual space":
receptors are *dimensions*, not points

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



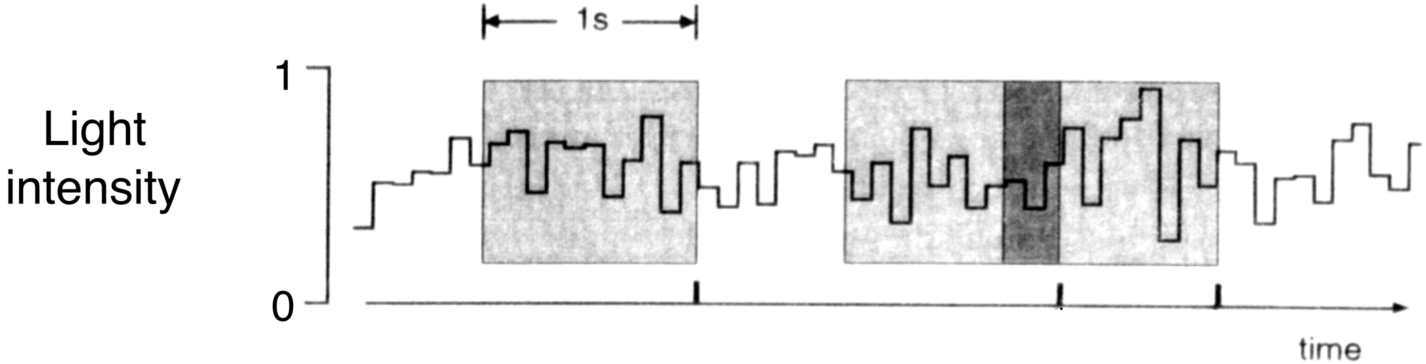
All stimuli
Stimuli producing spikes
Preferred direction in stimulus space

Receptive field: What stimuli makes the neuron respond?



Receptive field: What stimuli makes the neuron respond?

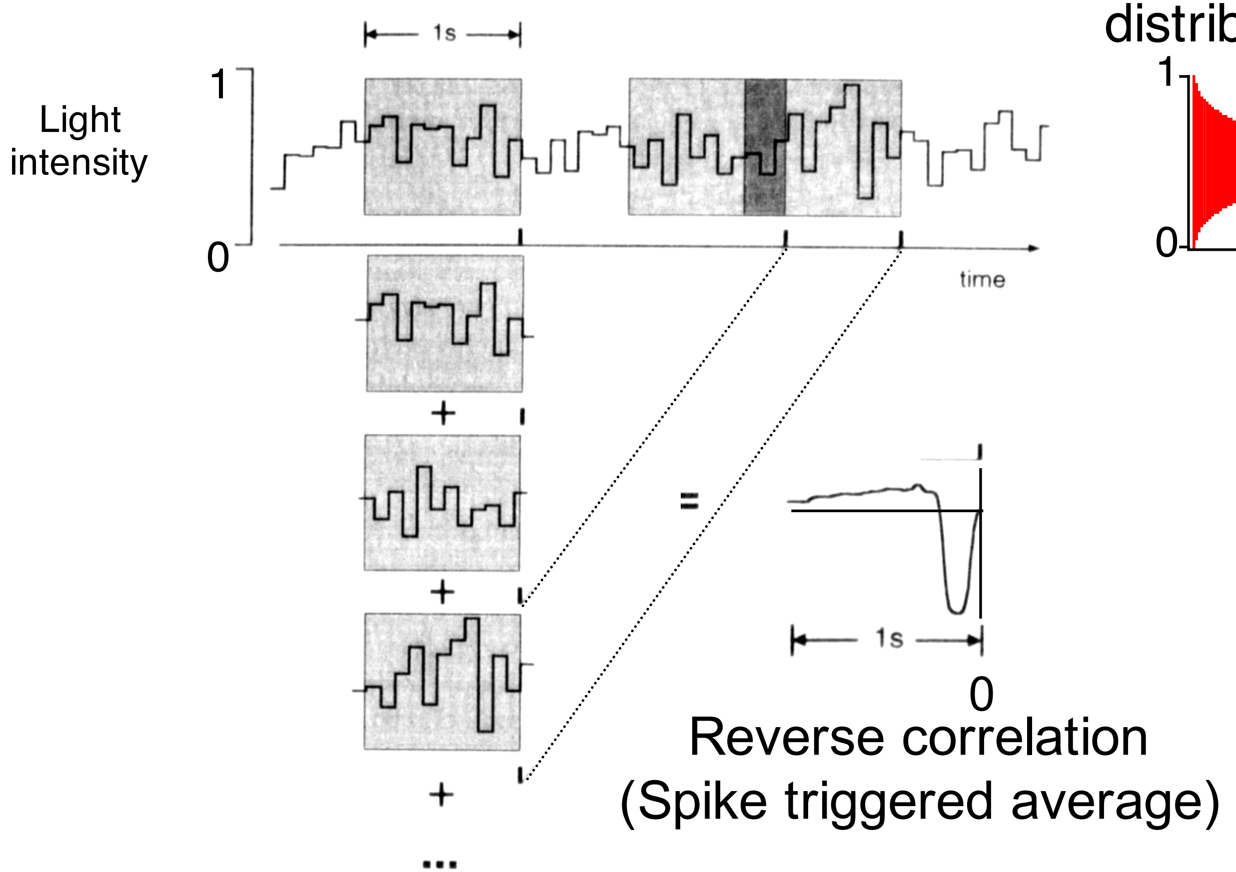
Reverse correlation for a spiking neuron

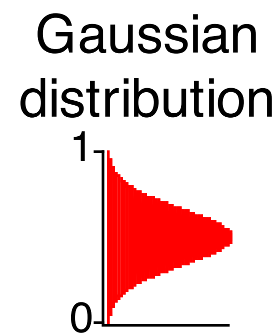


What stimulus makes the neuron respond?

White noise analysis

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





What stimulus makes the neuron respond?

Reverse correlation

Continuous	Discrete
$C(\tau) = \int_0^T r(t)s(t-\tau)dt$	$C(\tau) = \sum_{t=0}^{T} r(t)s(t-\tau)\Delta t$

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

These equations give a mathematical definition for reverse correlation. If we think about signals as being continuous, then it is appropriate to use the integral. However in modern neuroscience, all continuous signals are sampled and digitized, and then integrals are computed by summing over digitized values. Even if you take a photograph on a film camera, the journal will digitize when they publish it. Thus it is appropriate to consider the ‘discrete’ form of this equation, where the summation (Σ) sign is used. This is also easier to translate into something like a computer program or spreadsheet.

r(t): the response as a function of time

s(t): the stimulus as a function of time

T: The length of the experiment

Δt: How much points are separated in time, for example 1 s, or 1 ms.

τ: The time delay of the stimulus relative to the response. When

0, the equation becomes:

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

In other words, for C(0), the response, r(t), is multiplied by the stimulus, s(t) that occurs at the same time for every time point. All results are then summed. Unless there is an instantaneous effect between s(t) and r(t), this C(0) should be close to zero.

Likewise, when τ = 1, the equation is:

$$C(1) = \sum_{t=0}^{T} r(t)s(t-1)\Delta t$$

In this case the response at time t, r(t), is multiplied with the stimulus that occurred one time point in the past, s(t-1), for every time point. In other words, the stimulus is shifted one time point before multiplying. If the stimulus caused the response with a delay of one time point, there will likely be a positive or negative correlation.

When τ = -1, the equation is:

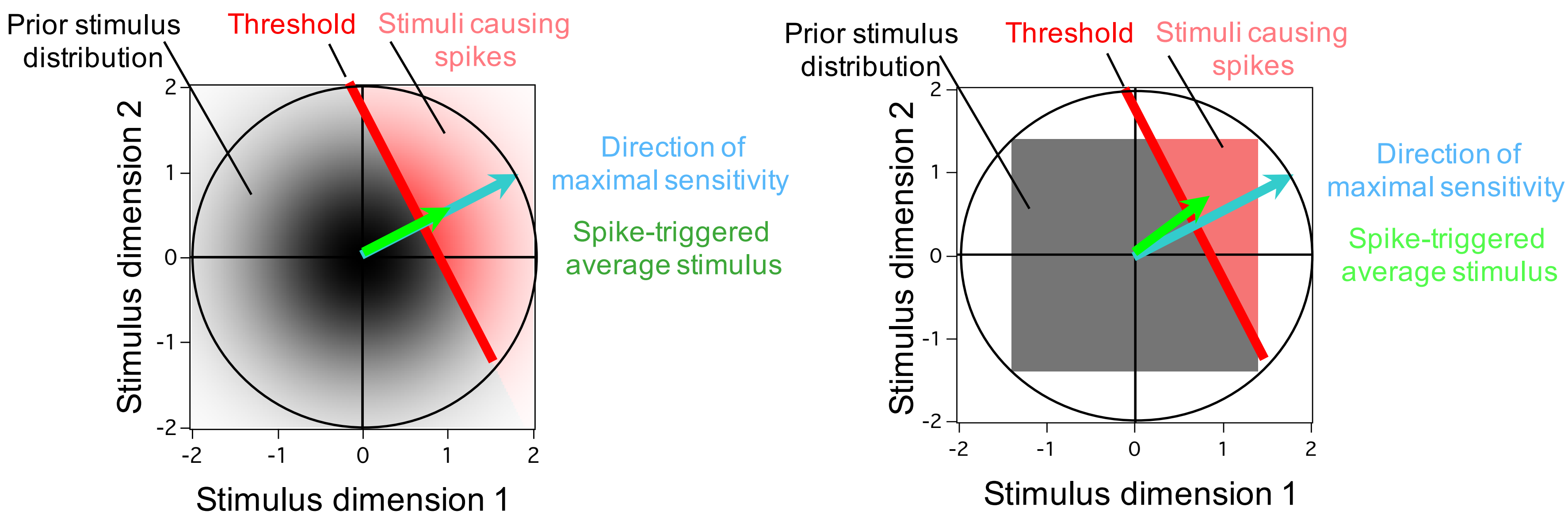
$$C(-1) = \sum_{t=0}^{T} r(t)s(t+1)\Delta t$$

If there is no correlation between the stimulus at one point of time and another point in time, the response should not be correlated with the stimulus in the future, and so the reverse correlation C(τ) for τ<0 should be close to zero. This is a good reality check on ones experiments and analysis.

Why correlation?

A correlation can be thought of as an average over many products. If two signals x(t) and y(t) are positively correlated, then x(t) will be positive when y(t) is positive, and x(t) multiplied by y(t) will be > 0. If x(t) and y(t) are unrelated, then on average, x(t) multiplied by y(t) will be zero. If x(t) and y(t) are negatively correlated, x(t) multiplied by y(t) will be < 0.

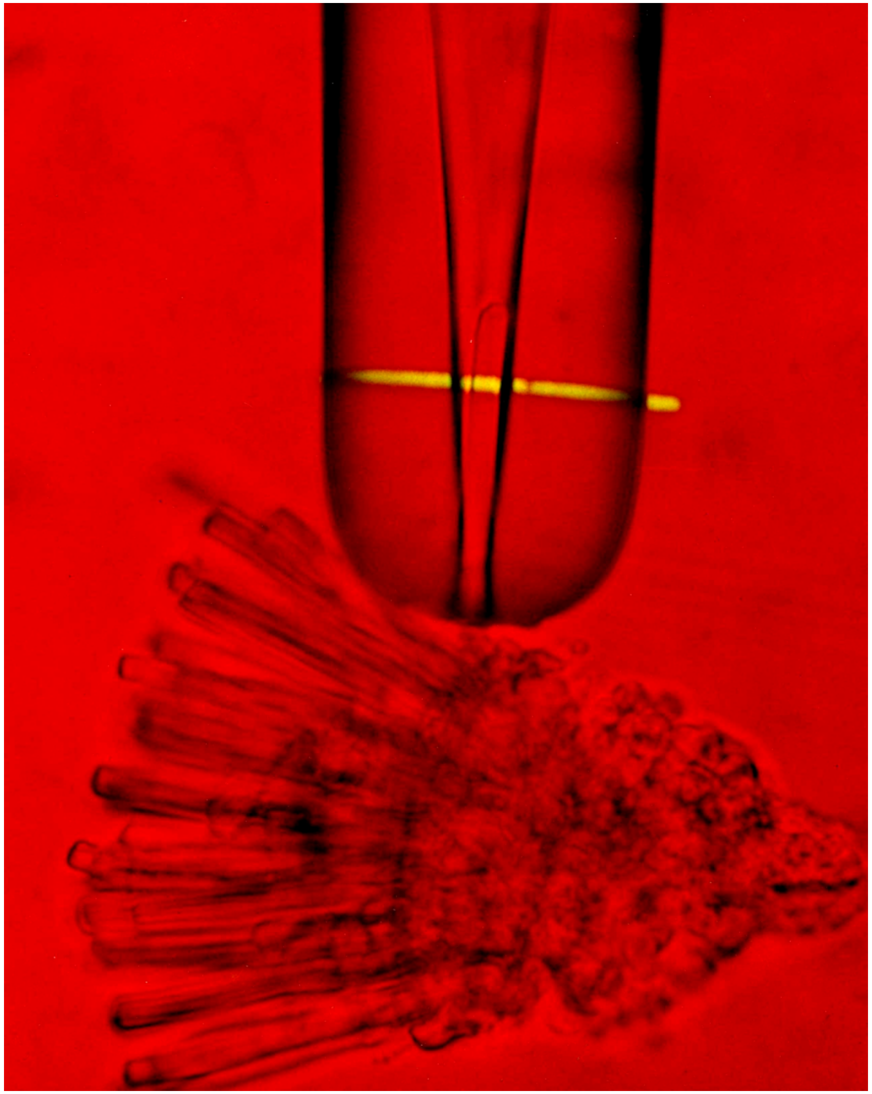
Computing the most effective stimulus (Bussgang's theorem)



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)

How will a neuron respond to a stimulus?

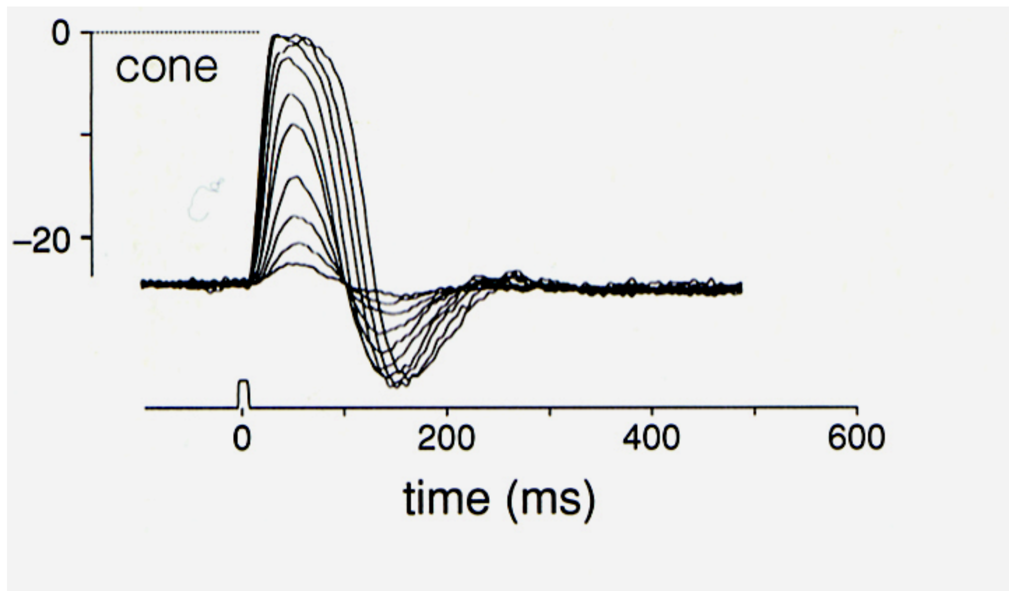


Baylor, Lamb and Yau (1979)

How will a neuron respond to a stimulus?

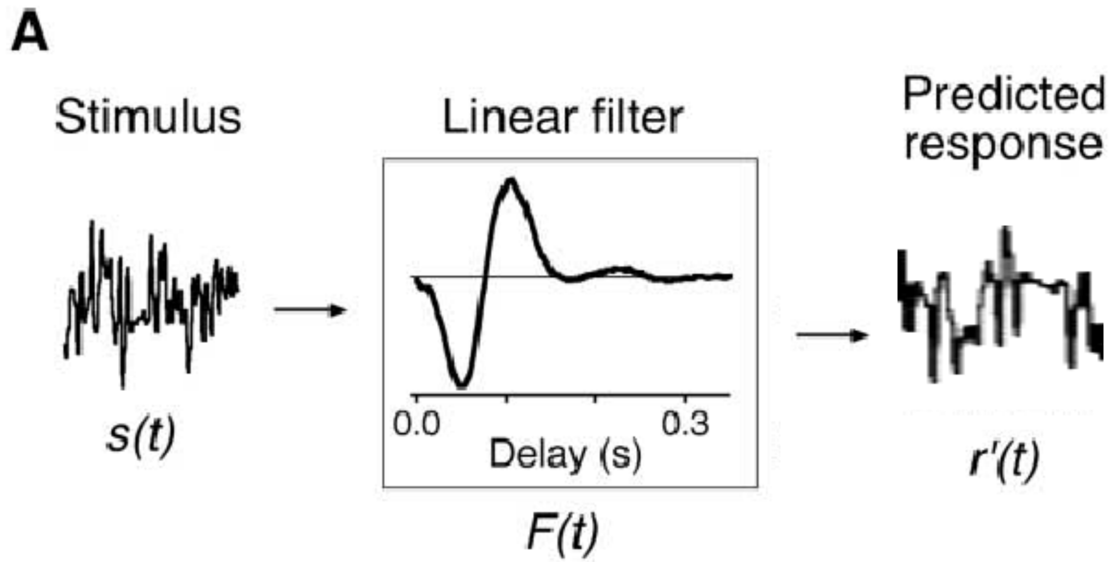
Single photoreceptor responses to a flash of light

Photocurrent
pA



Baylor (1987)

A linear model of the cell's response



Convolution

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

$$r'(t) = \sum s(\tau)F(t-\tau)\Delta\tau$$

$F(t)$ is called:

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

Like we did with the reverse correlation above, let's take the discrete convolution, it's easier to do calculations by hand. Here, we're considering that the length of the linear temporal filter is 1 second.

$$r'(t) = \sum_{t-1}^{t} s(\tau)F(t-\tau)\Delta\tau$$

t: time, the variable that indicates the time during the experiment, so if the experiment is 60 s long, t varies between 0 and 60 s.
τ: the summation variable that indicates time relative to the filter. Because the filter is 1 s long, τ varies between t-1 and t second.
r'(t): predicted response at time t
S(τ): stimulus at time point τ. Note that since τ varies between t-1 and t, s(τ) is summed over the previous one second to compute r'(t).
F(t- τ): The Filter at time t- τ. Since τ varies between t-1 and t, F(t-τ) is actually summed between F(1) and F(0).

To compute r'(t), the sum is taken over τ=t-1 and τ=t. Thus the sum is computed across :

$$s(t-1)F(t-(t-1)) = s(t-1)F(1)$$

and

$$s(t)F(t-t) = s(t)F(0)$$

So the stimulus is multiplied by *the time-reverse of the filter*. Then all points are summed. In this way, the filter weights the stimulus over the previous one second, according to the filter's time course. It's instructive to work out a very simple example. Let's say the stimulus is five time points long s=(0,1,1,1,0), i.e. s(0)=0,s(1)=s(2)=s(3)=1,s(4)=0.
The filter is two time points long (1,-1), i.e. F(0)=1, F(1)=-1. τ goes from t-1 to t. Then,

Stimulus	Filter reversed in time	Response
s(0)=0	F(1)=-1	
s(1)=1	F(0)=1	r(1) = s(1)*F(0)+s(0)*F(1) = 1
s(2)=1		r(2) = s(2)*F(0)+s(1)*F(1) = 0
s(3)=1		r(3) = s(3)*F(0)+s(2)*F(1) = 0
s(4)=0		r(4) = s(4)*F(0)+s(3)*F(1) = -1

Note that this filter has essentially taken the derivative of the stimulus, taking (0,1,1,1,0) as an input, generating (1,0,0,-1) as an output

Filters and step responses
- Monophasic
- Biphasic

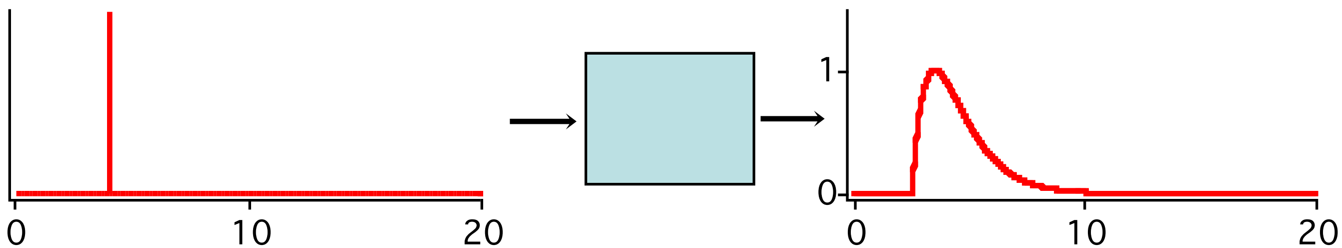
Two different algorithms for convolution
- Impulse response
- Dot product with time-reverse of filter

How do you find the filter?

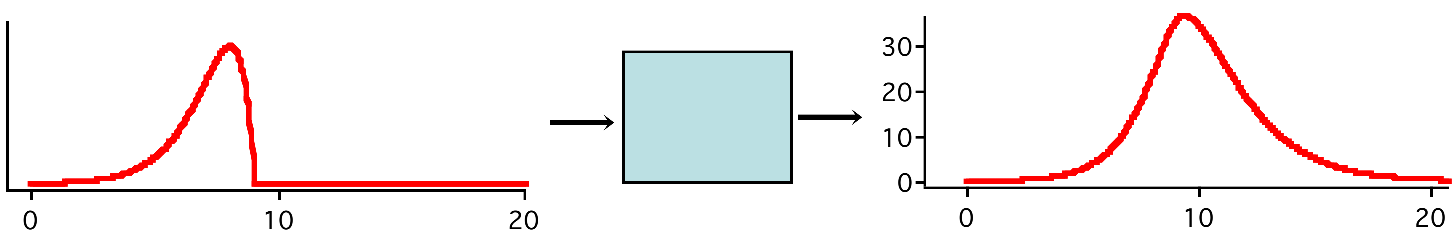
What stimulus produces the largest response?
- geometrical interpretation

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

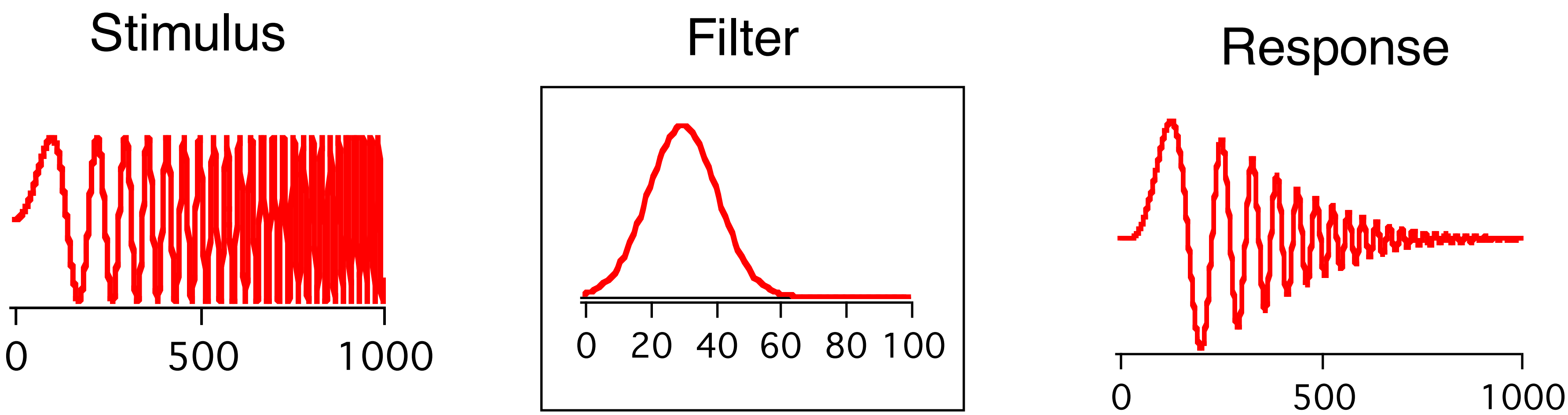
For a cell (or any system) responding in the linear range, the response to a brief input (an impulse):



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



Linear filter and frequency response



Convolution theorem

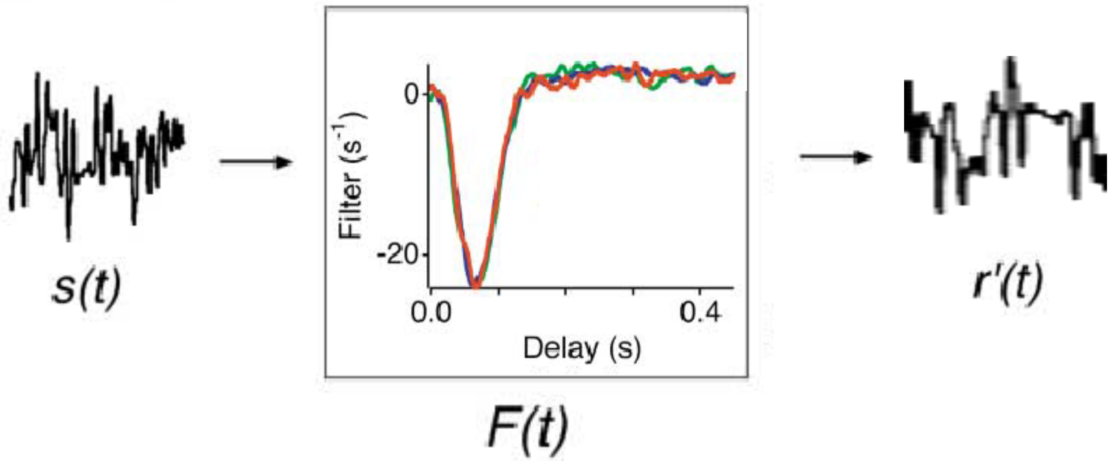
$$h(t) = f(t) * g(t) \quad \Leftrightarrow \quad \tilde{h}(\omega) = \tilde{f}(\omega)\tilde{g}(\omega)$$

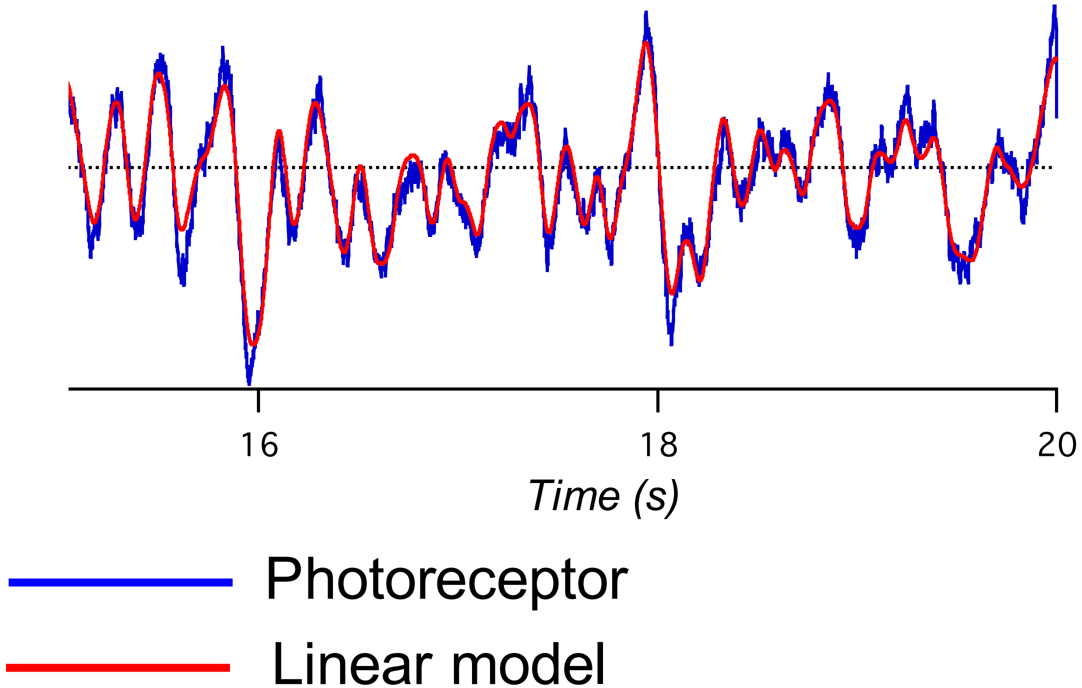
a convolution in the time domain

is a simple product in the frequency domain

A linear model of the cell's response

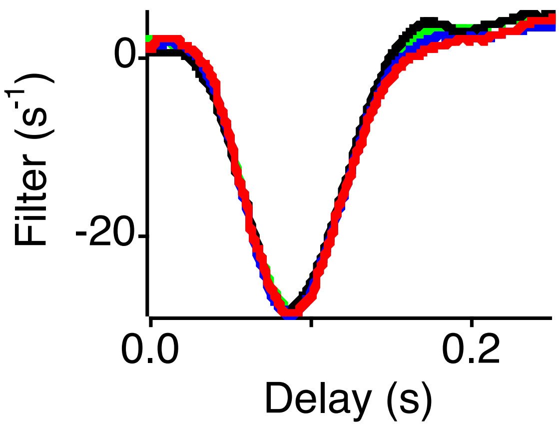
Stimulus Linear filter Predicted response



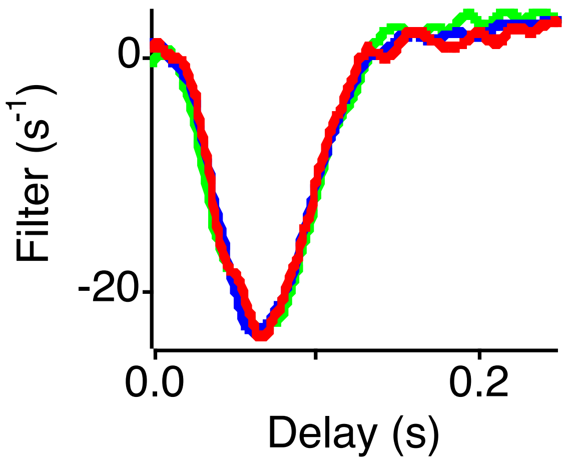


Linear filters in the early visual system

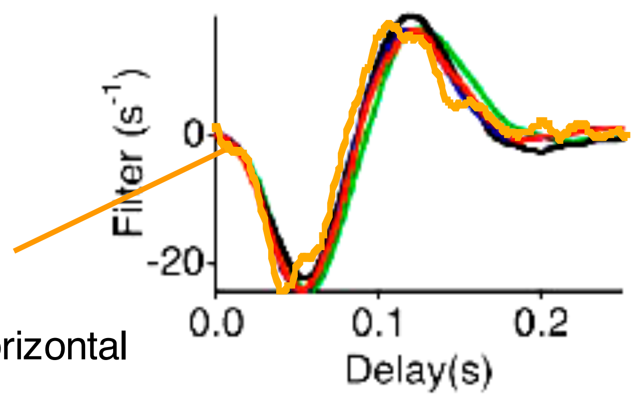
Horizontal cell



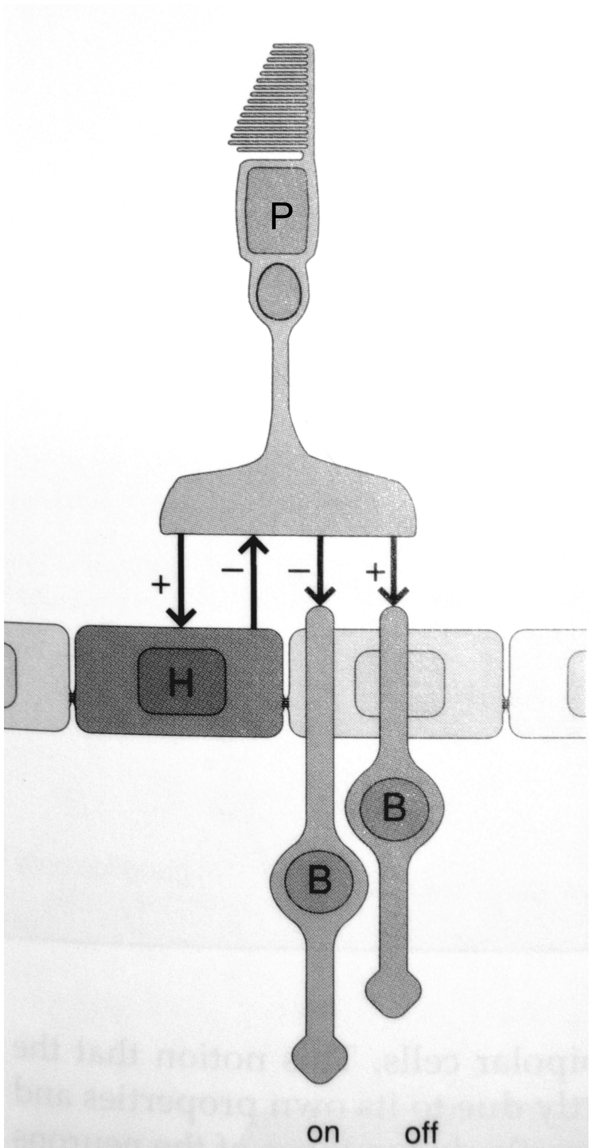
Photoreceptor

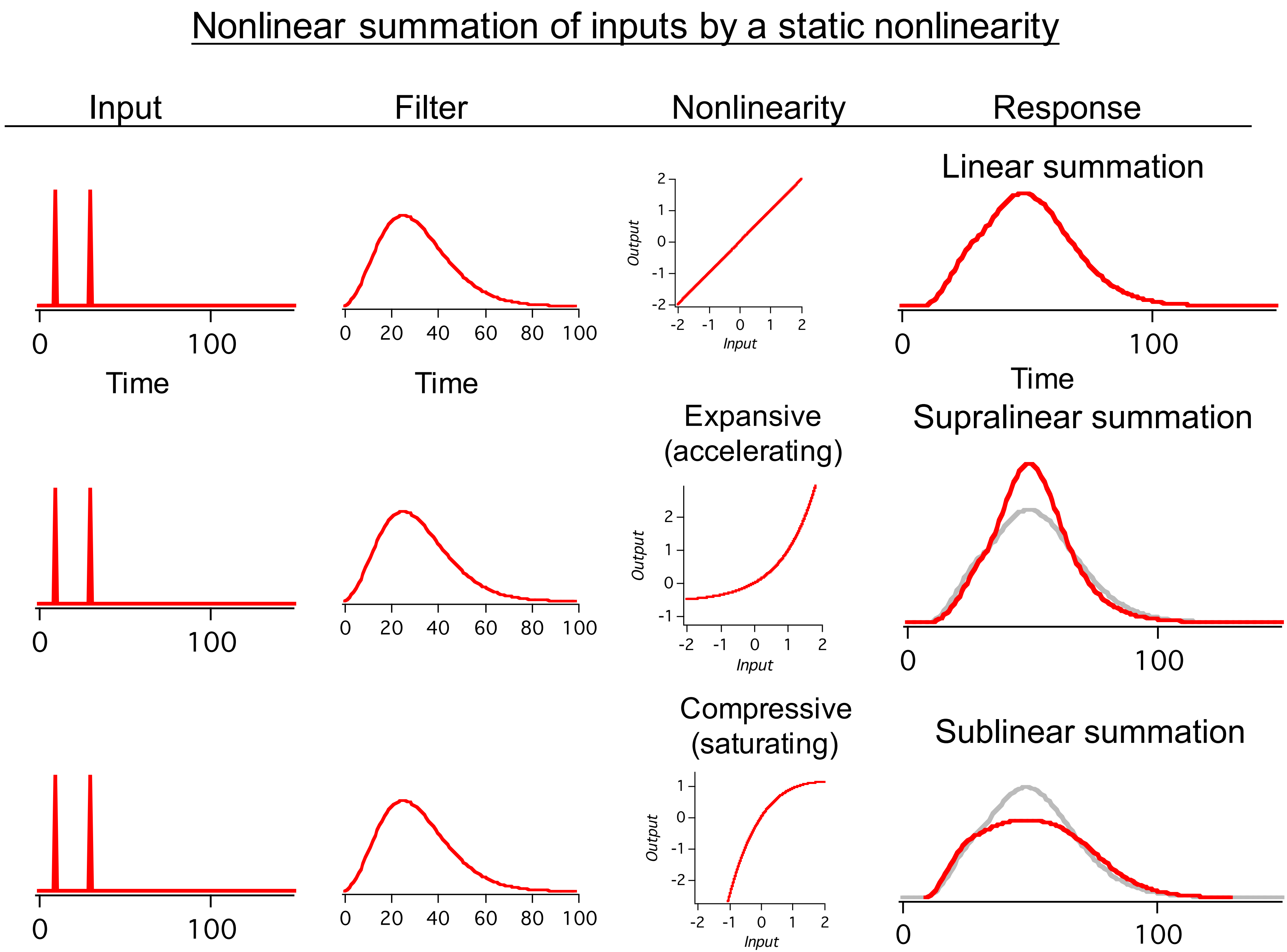


Bipolar cell



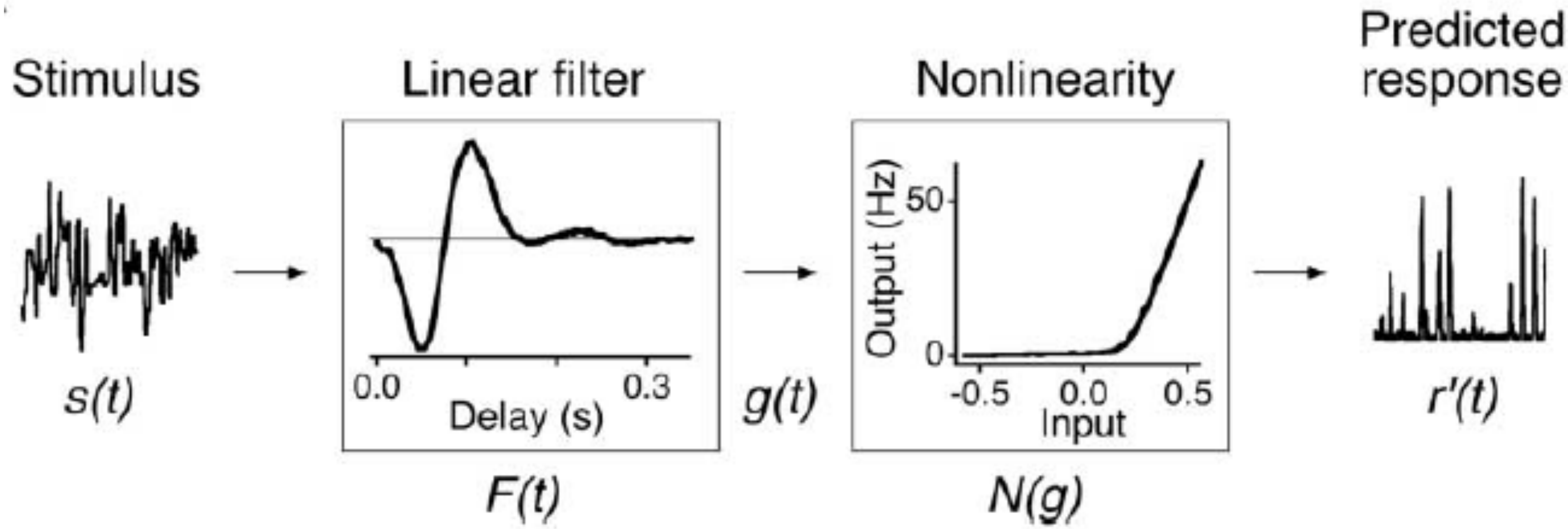
Weighted sum of
Photoreceptor and Horizontal
Cell filters



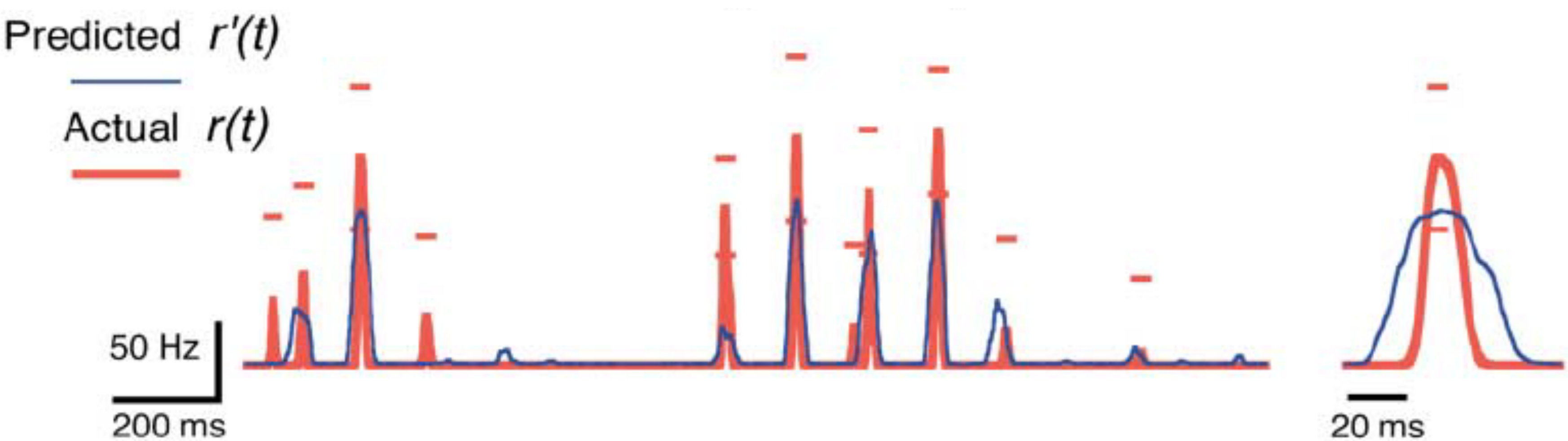


Nonlinear summation of inputs by a static nonlinearity
Input
Filter
Nonlinearity
Response
Linear summation
0
100
Time
0 20 40 60 80 100
Time
2
1
0
-1
-2
Output
-2 -1 0 1 2
Input
0
100
Time
Expansive
(accelerating)
Supralinear summation
Compressive
(saturating)
Sublinear summation

Linear - Nonlinear "LN" model of a "Feature Selective Neuron"



Retinal ganglion cell firing rate and LN model



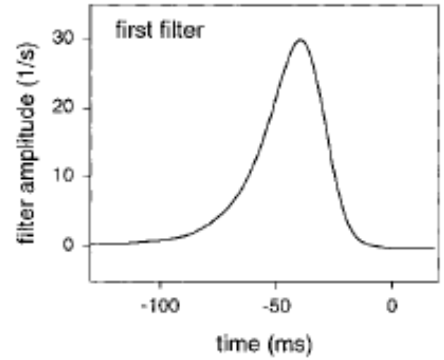
LN models in the nervous system

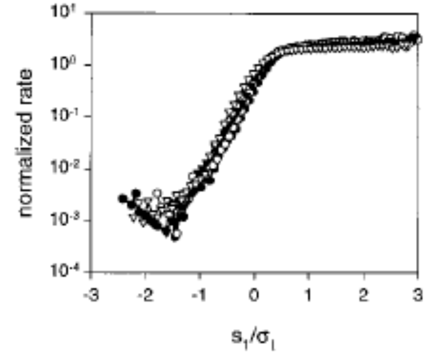
Filter

Nonlinearity

Fly H1 Motion sensitive neuron

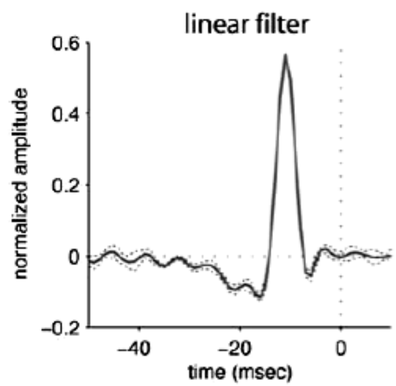
Brenner et al.,, *Neuron* (2000)

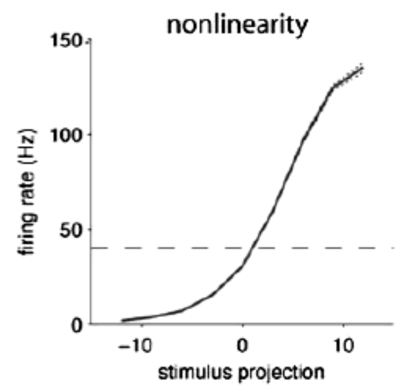




Songbird auditory forebrain neuron

Nagel & Doupe, *Neuron* (2007)





Whole monkey making decisions

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