Single neuron encoding

NEPR 208 lecture 3

What does a neuron do?

"The pattern of light and shade cast on the retina by the optical system of the eye gives rise to a pattern of nerve impulses in the optic nerve, but neither the temporal nor the spatial features of this pattern of impulses are accurate copies of the pattern of light."

"The present work was undertaken with the idea that these distortions might amount to some integrative action of the nervous layers of the retina analogous to the integrative action of the spinal cord studied by Sherrington."

Horace Barlow

Questions we would like to answer

How does the nervous system represent sensory information?

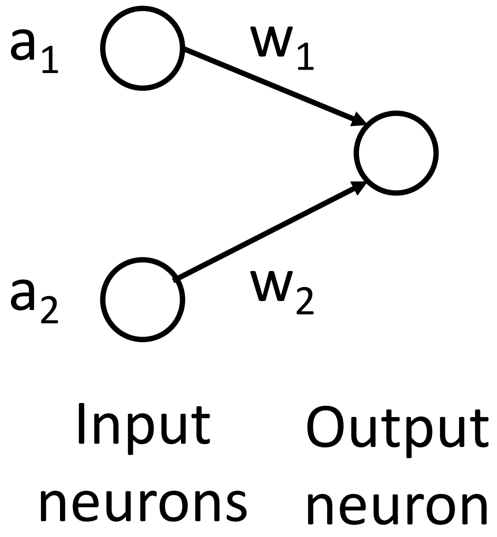
How are the set of important sensory features allocated to neurons?

Why is a particular neural code advantageous?

What design principles influence sensory systems, can they be used for artificial systems?

What does a neuron respond to?

Recall the perceptron model:



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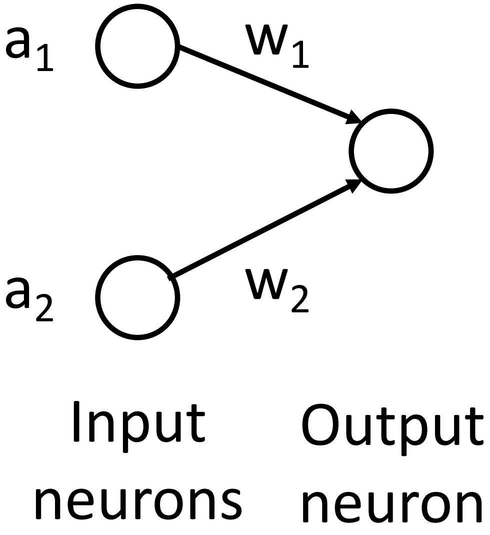

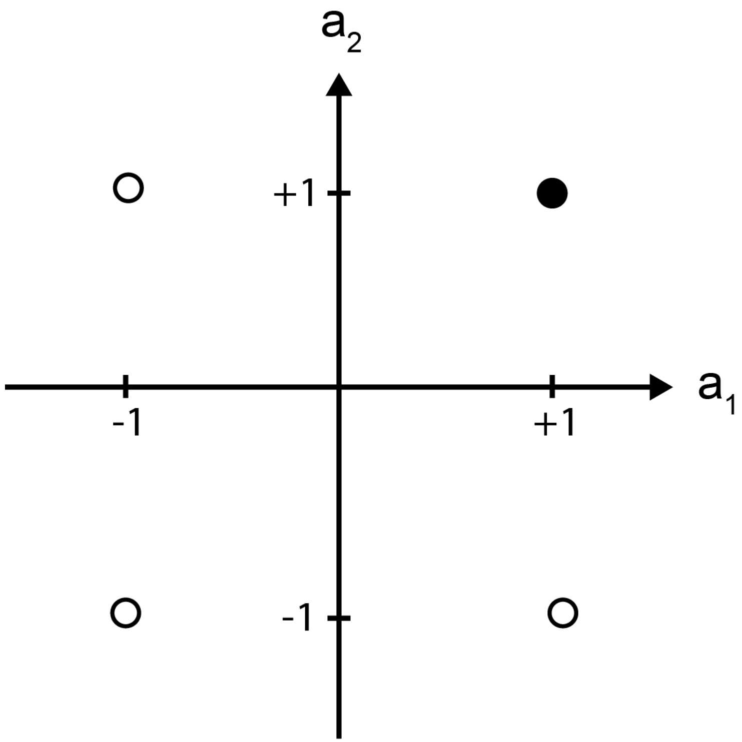

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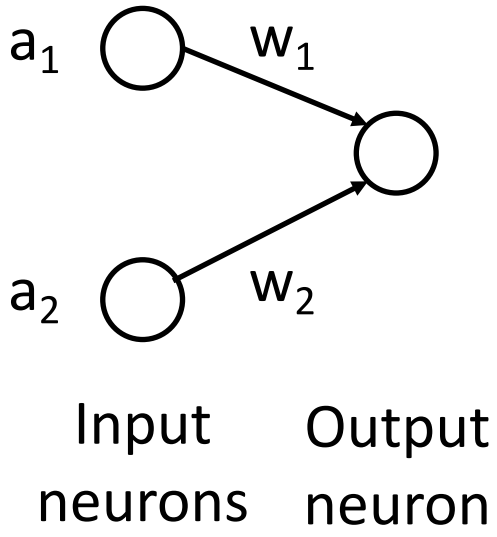

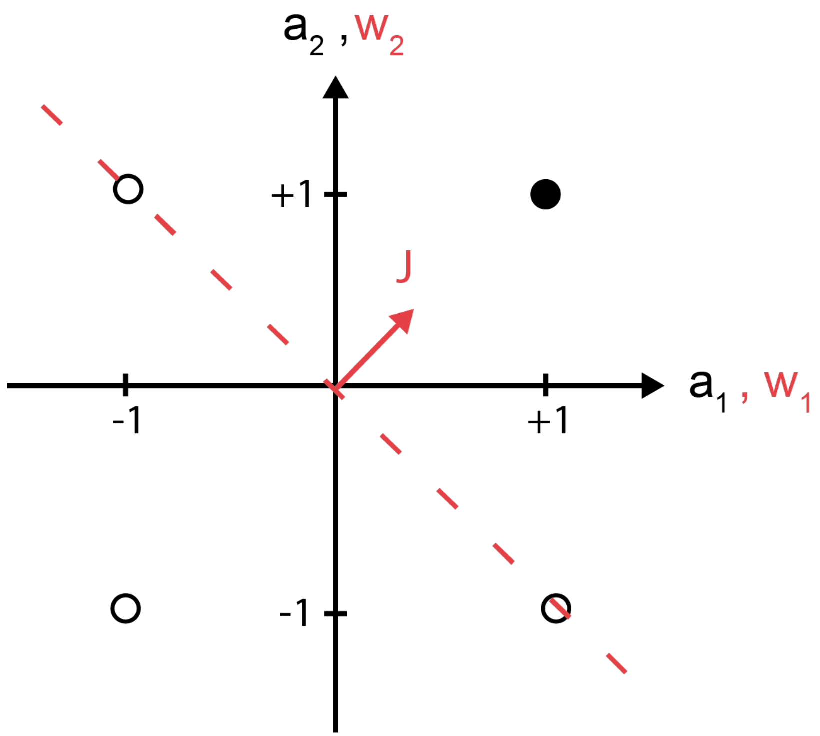

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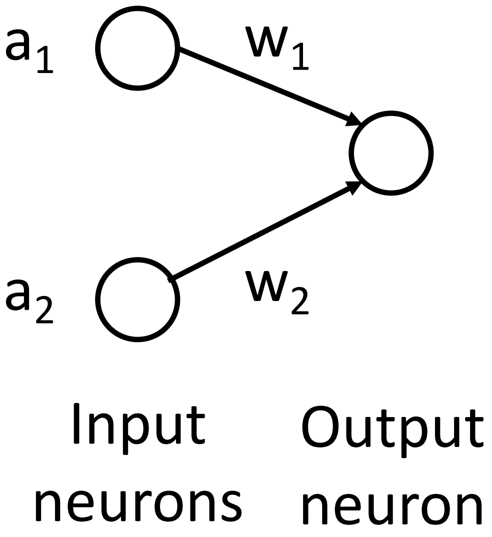

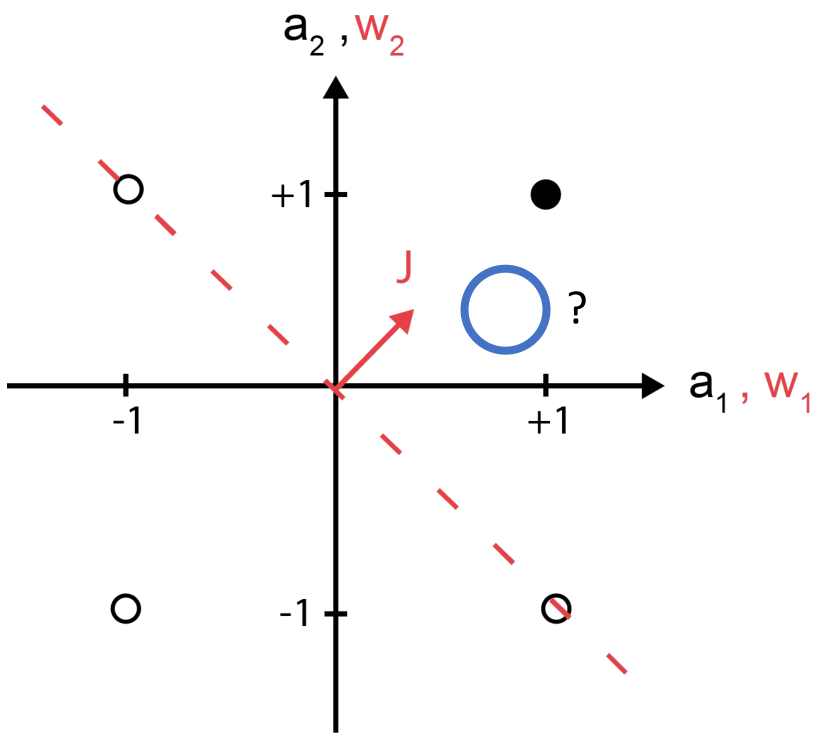

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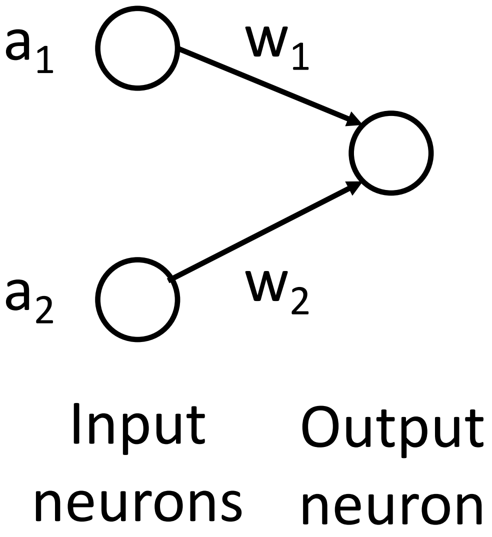

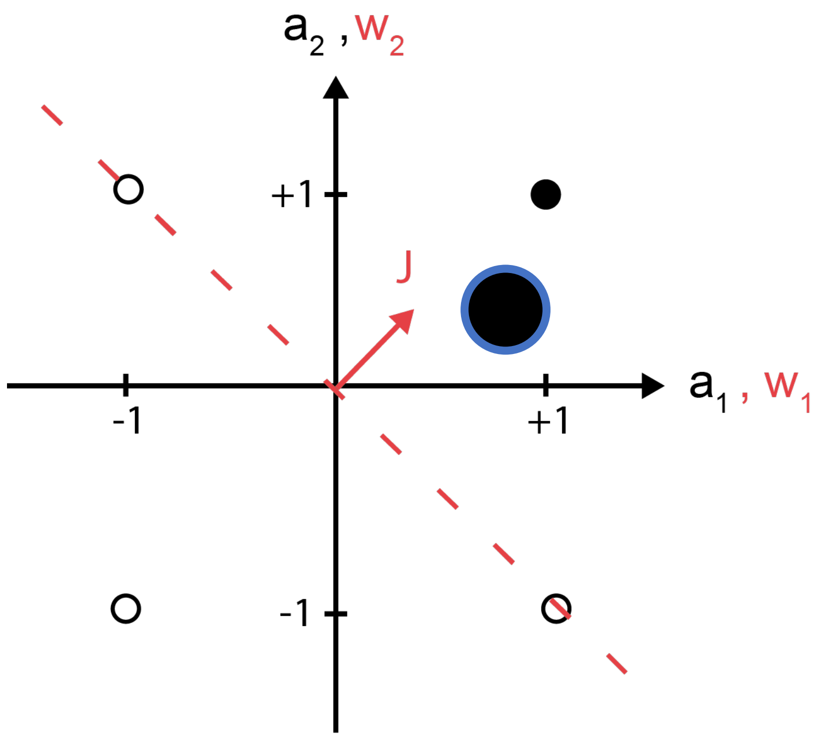

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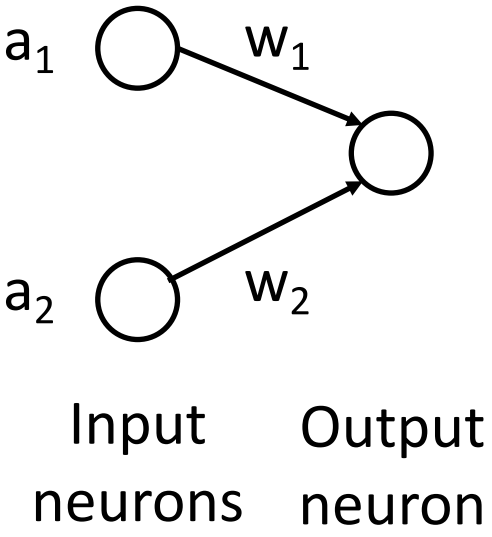

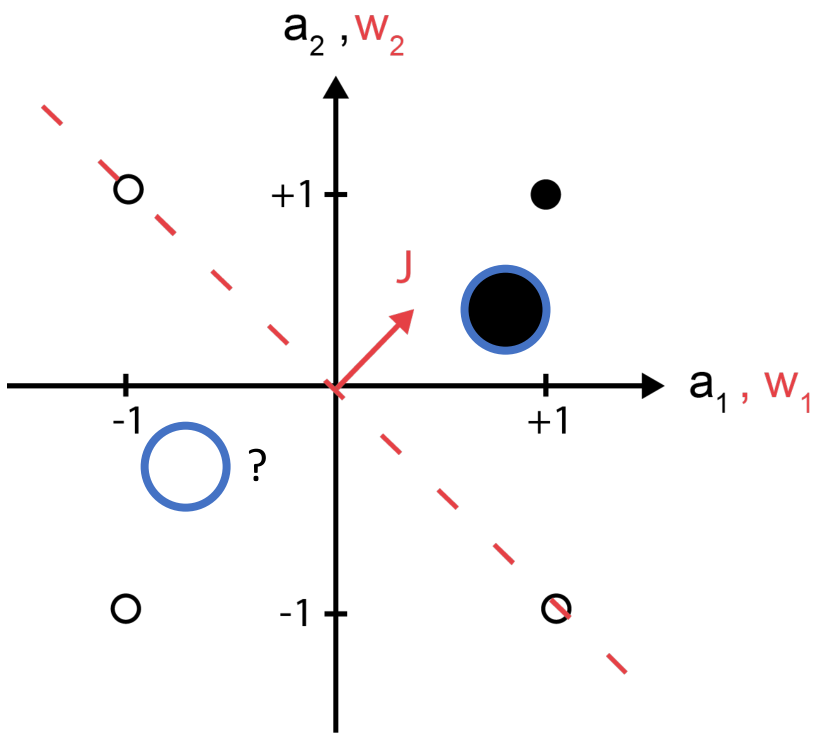

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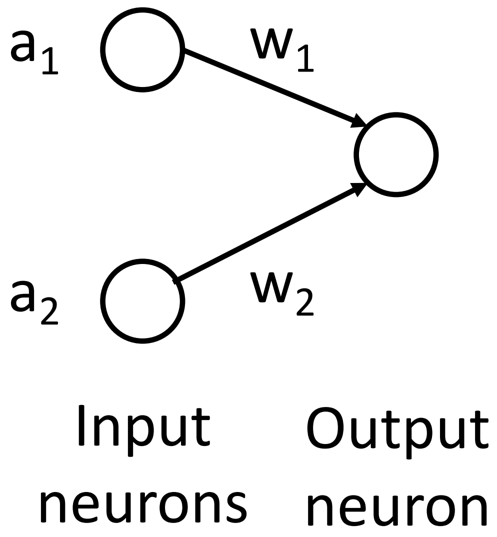

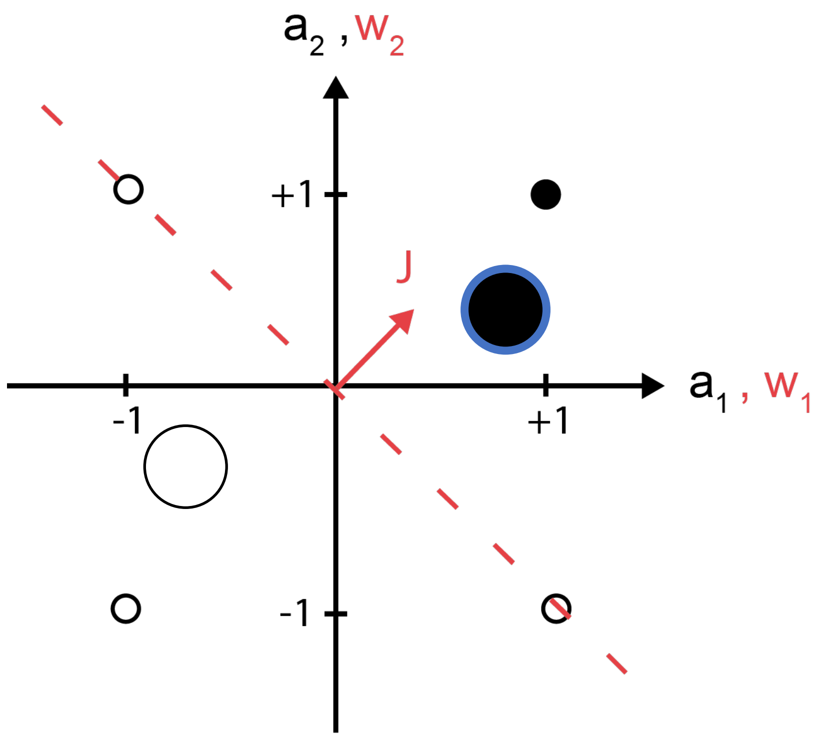

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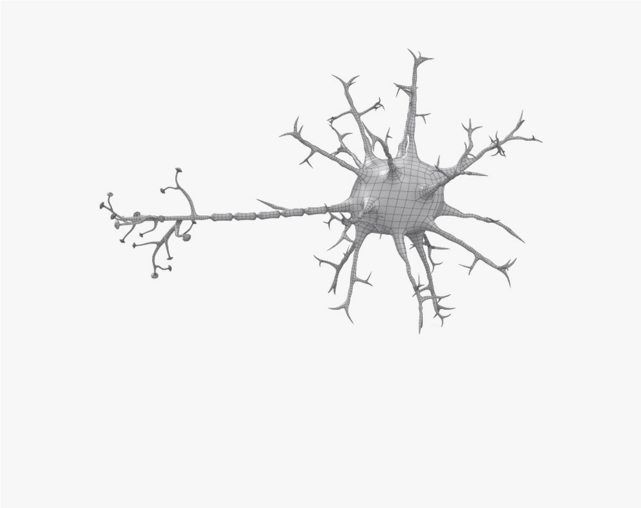

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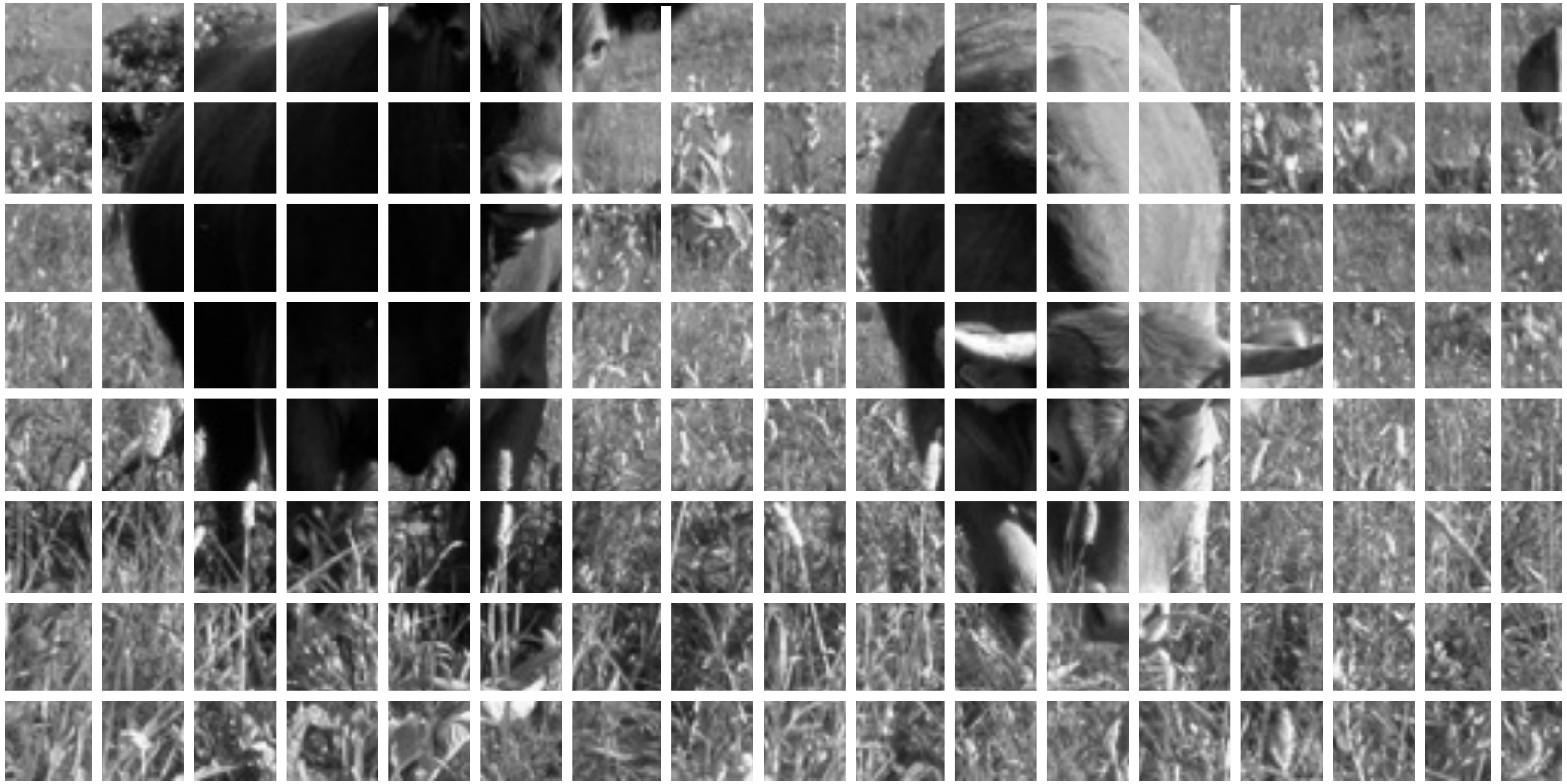

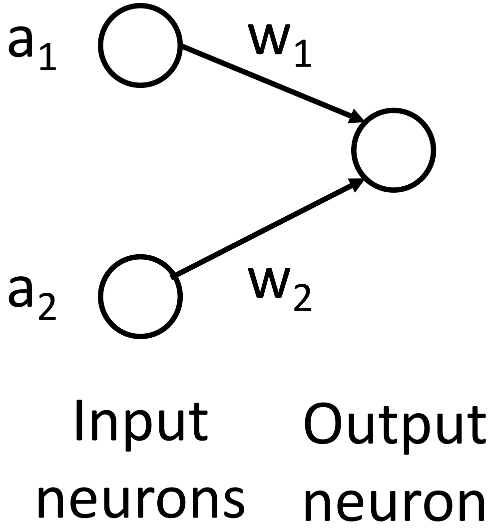

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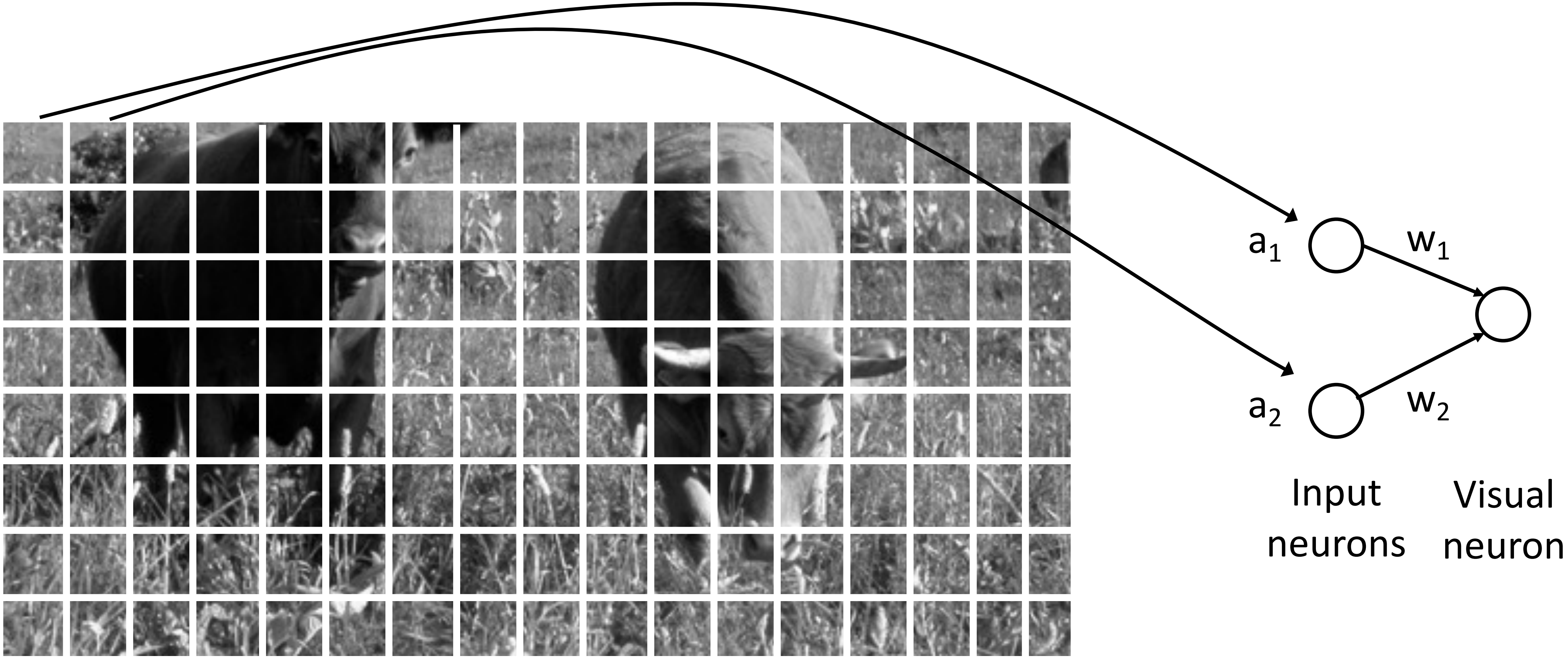

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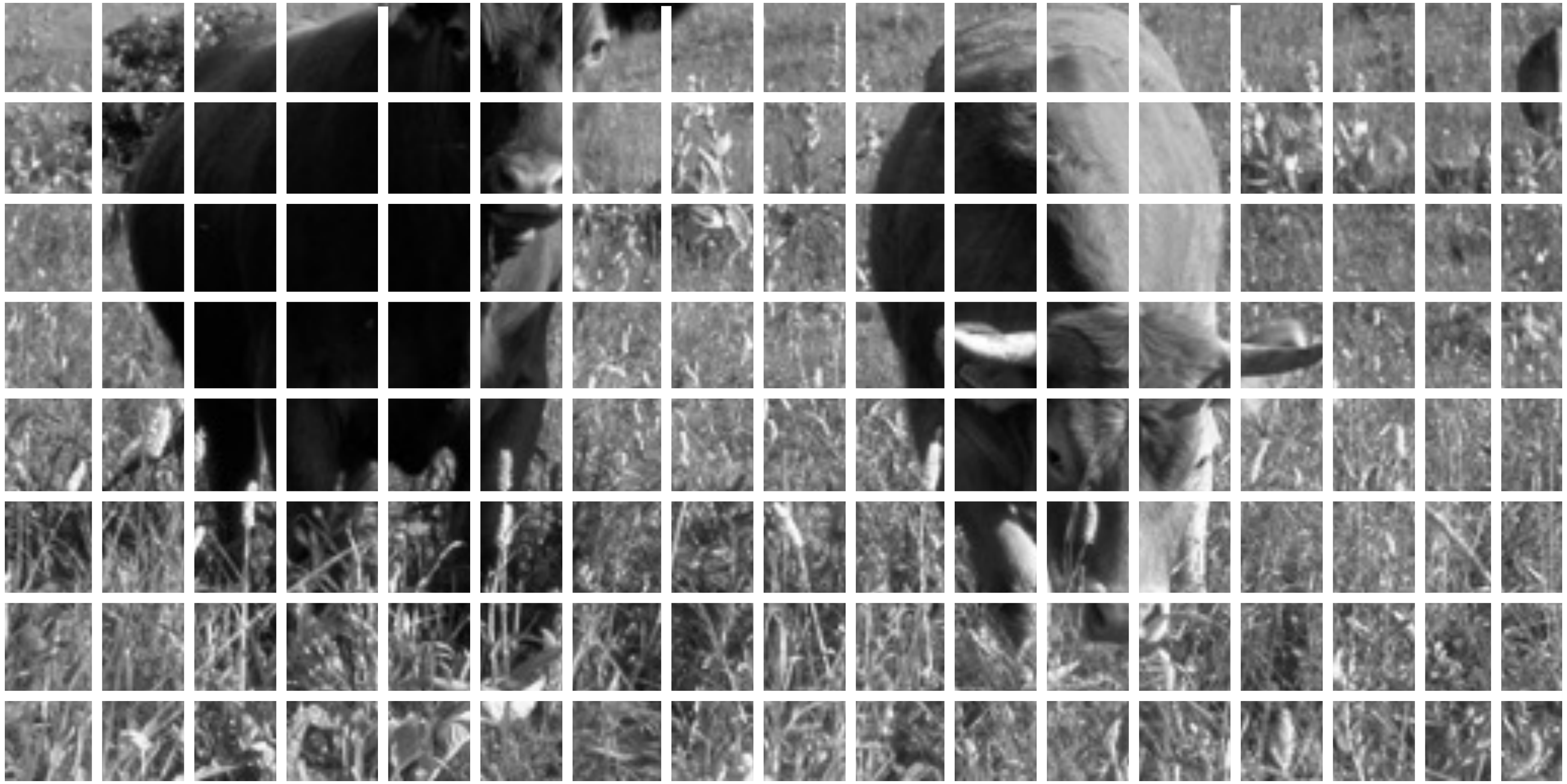

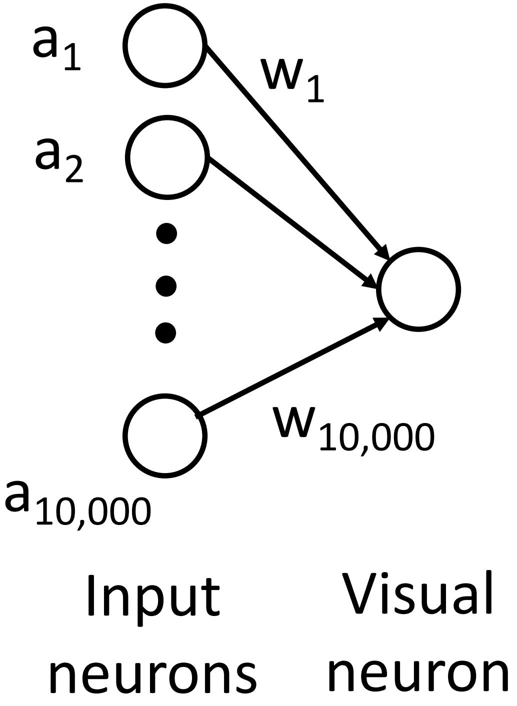

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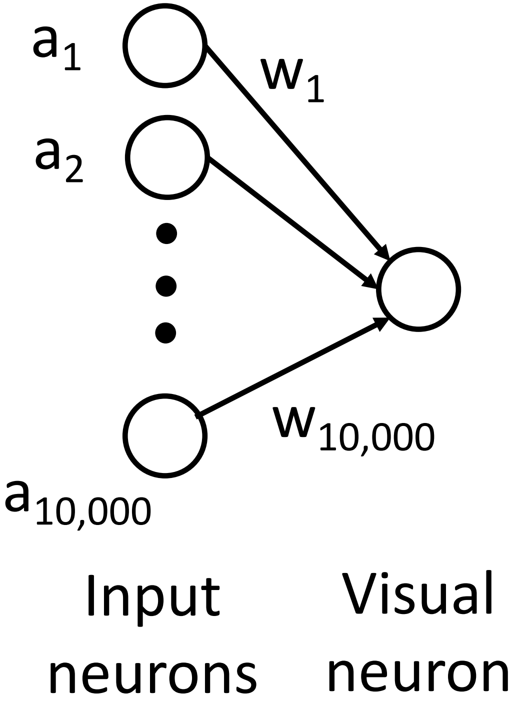
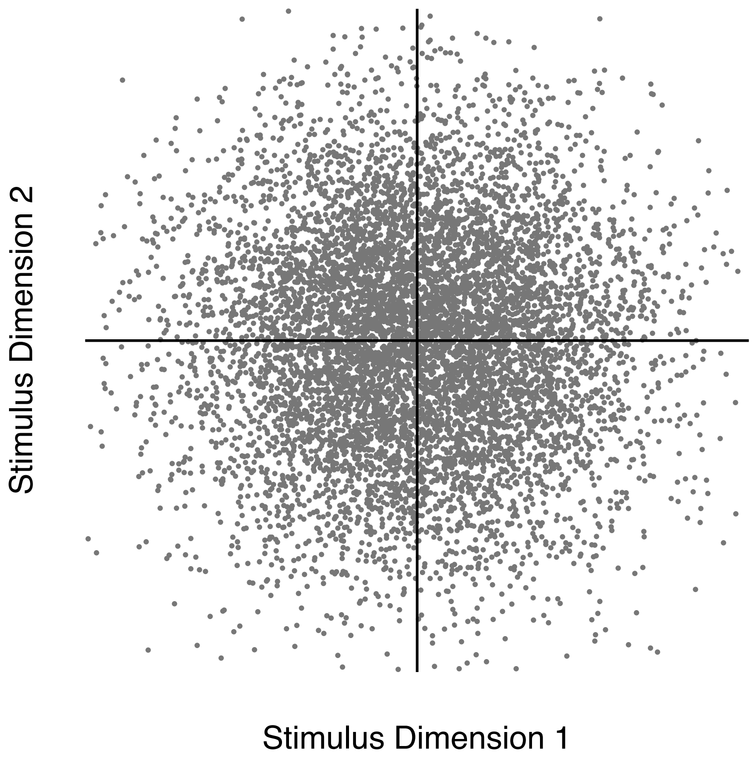
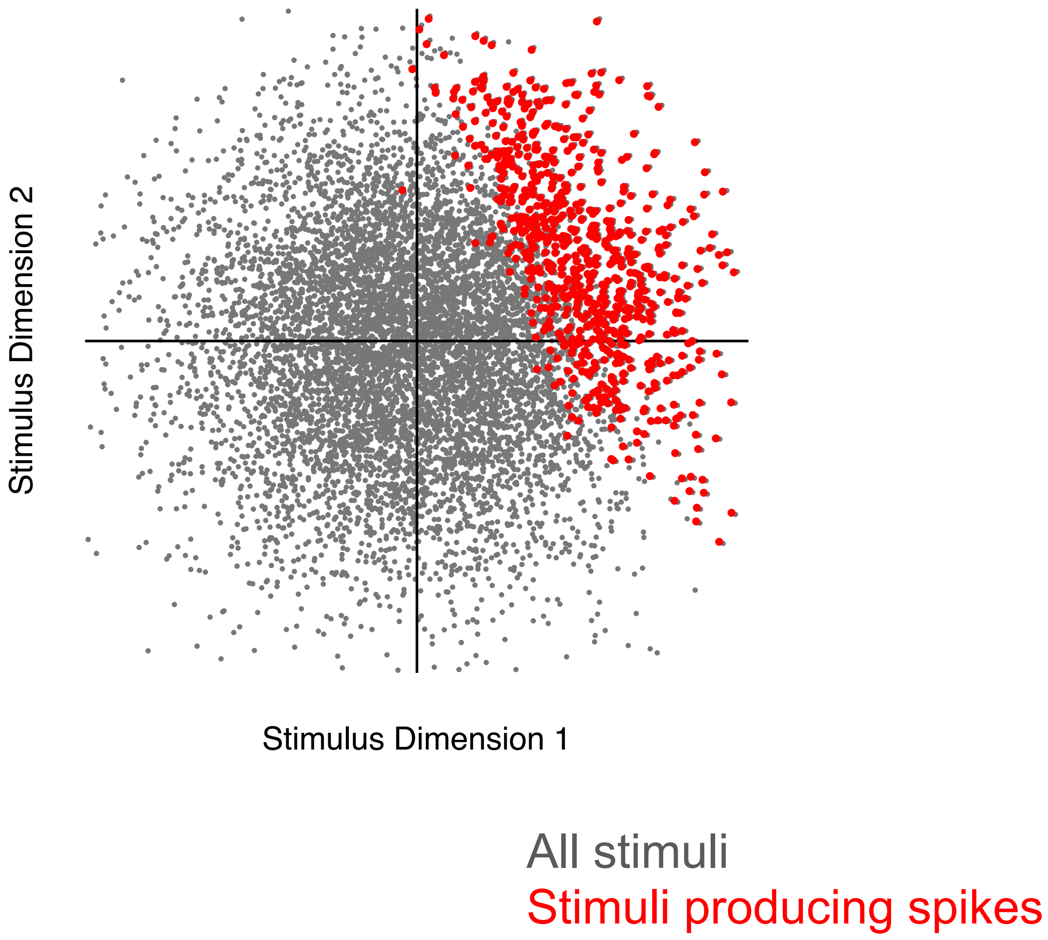


Responses in stimulus space

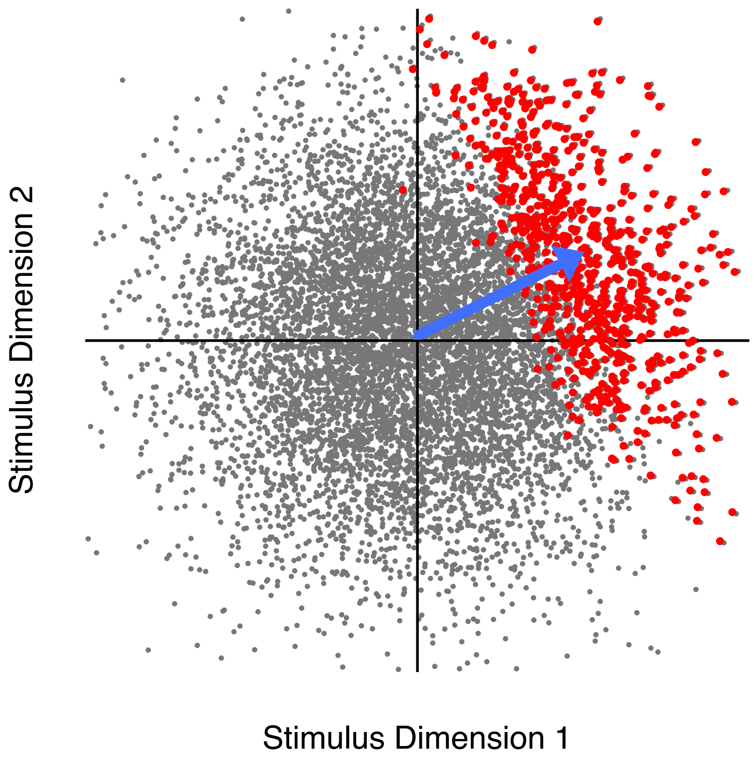


All stimuli

Responses in stimulus space



Receptive field: a direction of sensitivity



All stimuli
Stimuli producing spikes
Preferred direction in stimulus space

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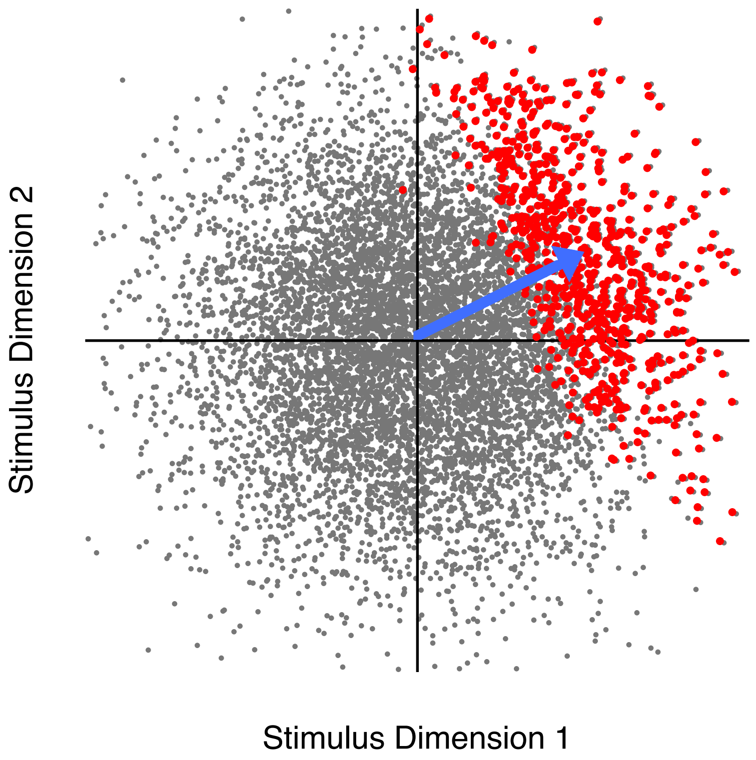

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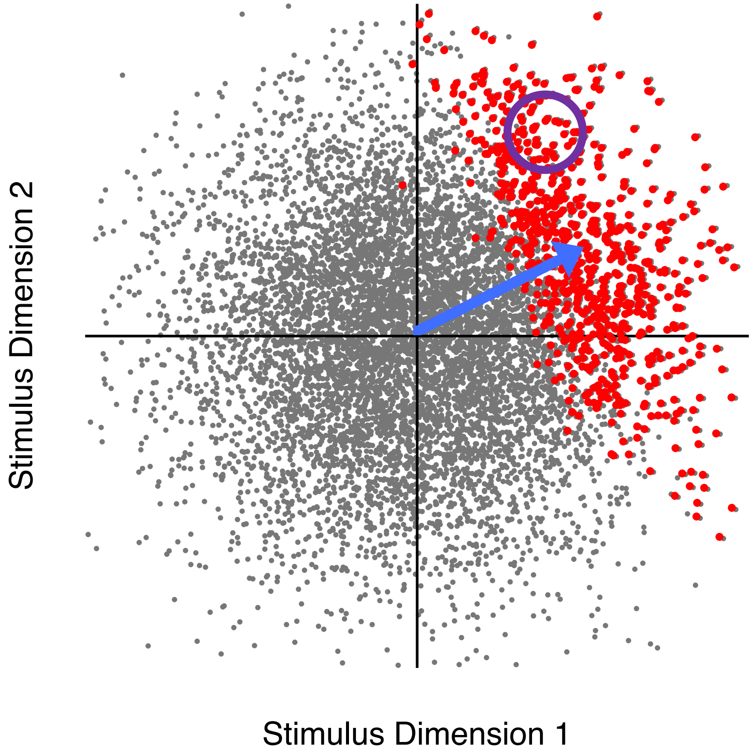

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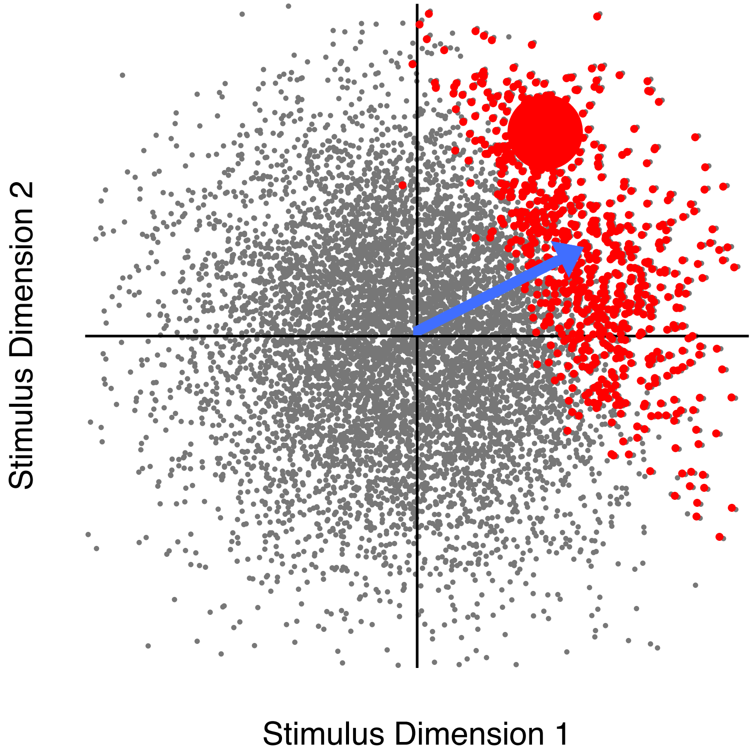

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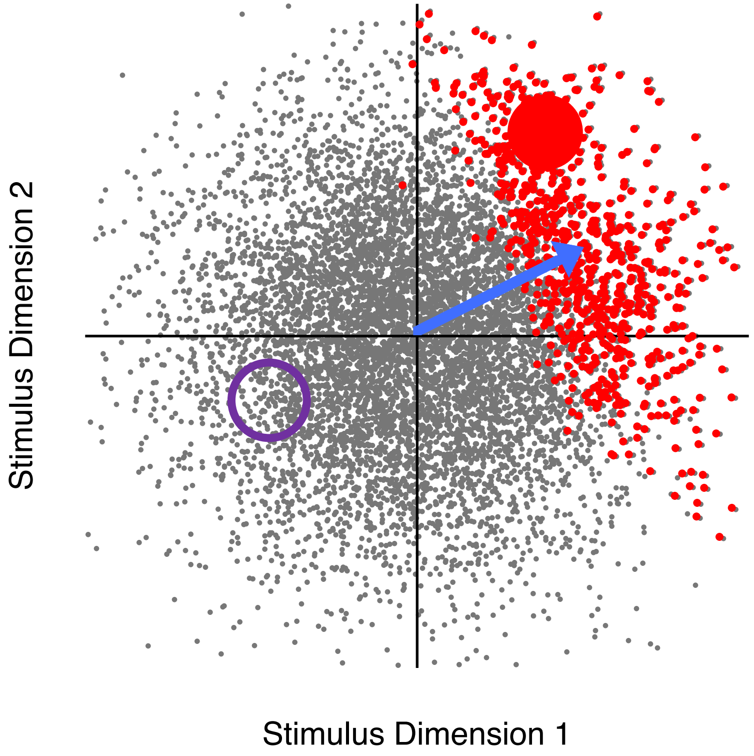

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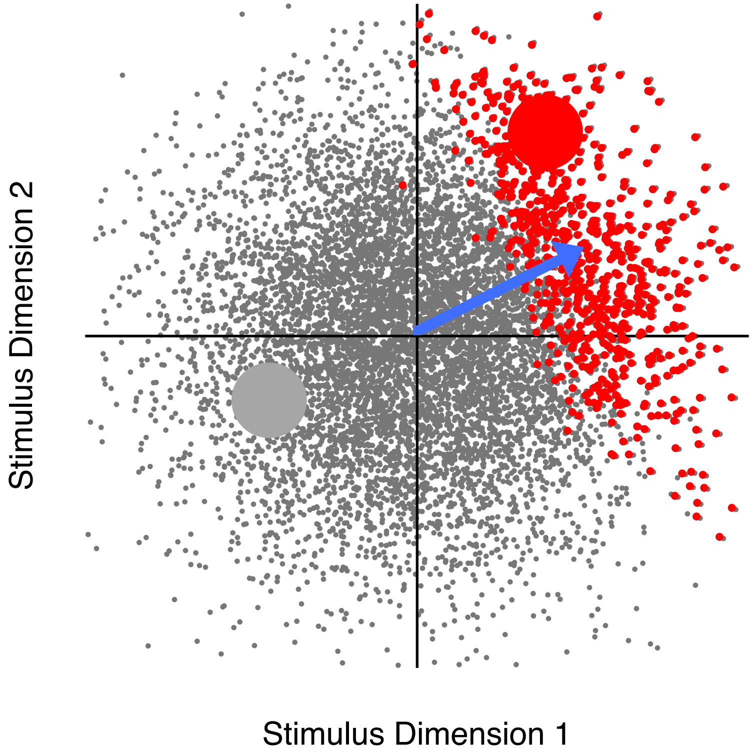

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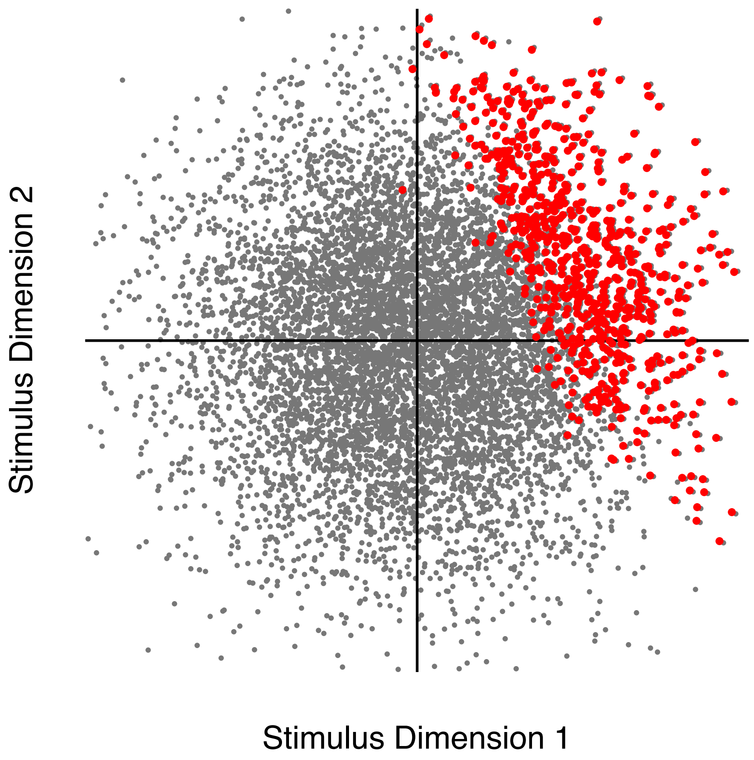
Finding receptive fields from recordings



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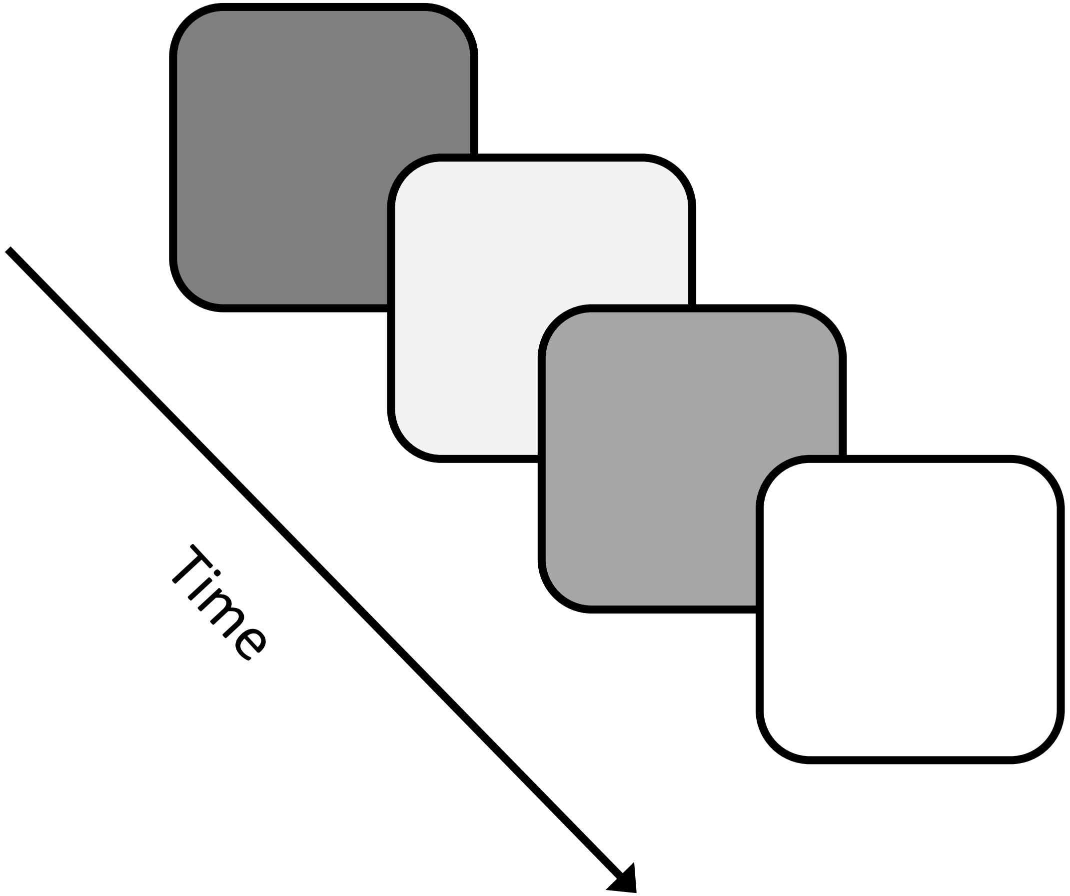

Full-field flicker stimuli,
recordings from salamander retina

Spikes, MIT press Rieke et al. (1997)

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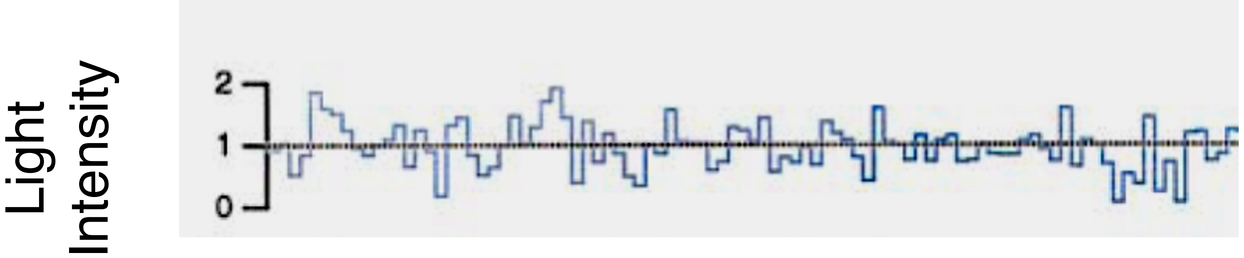

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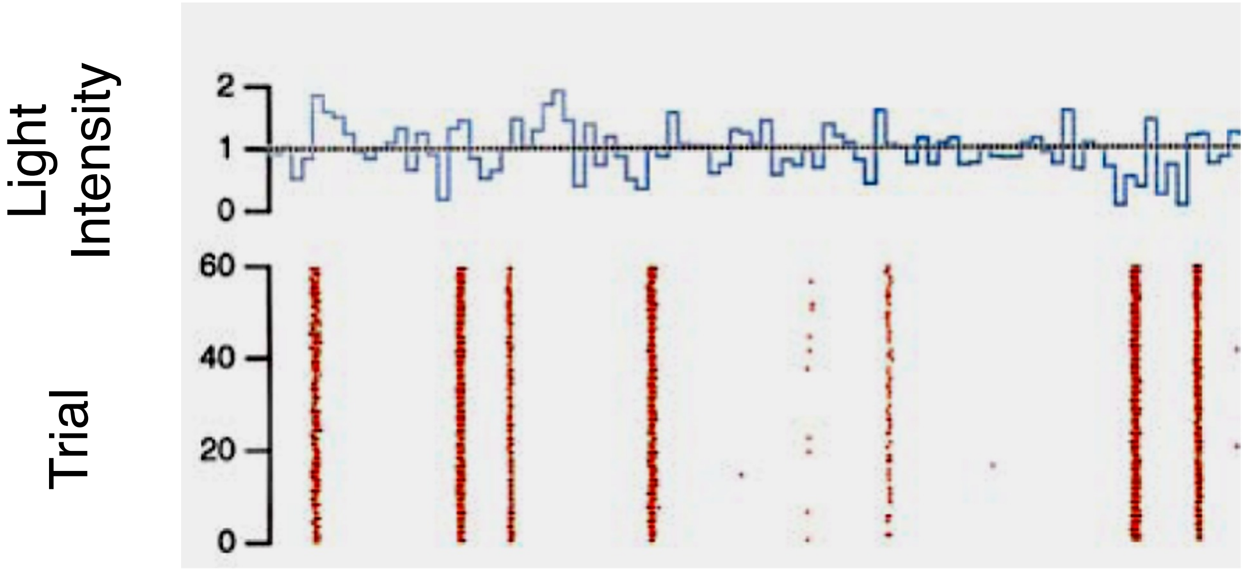

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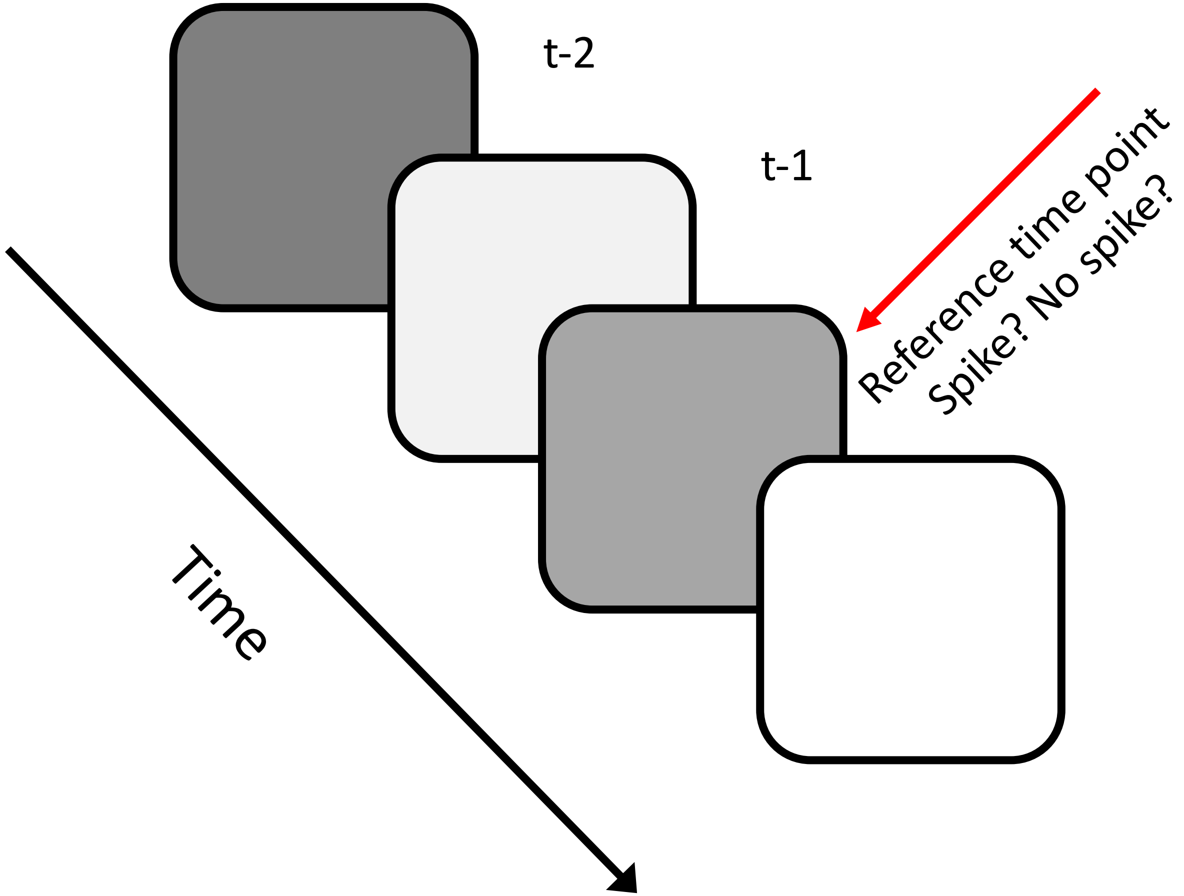

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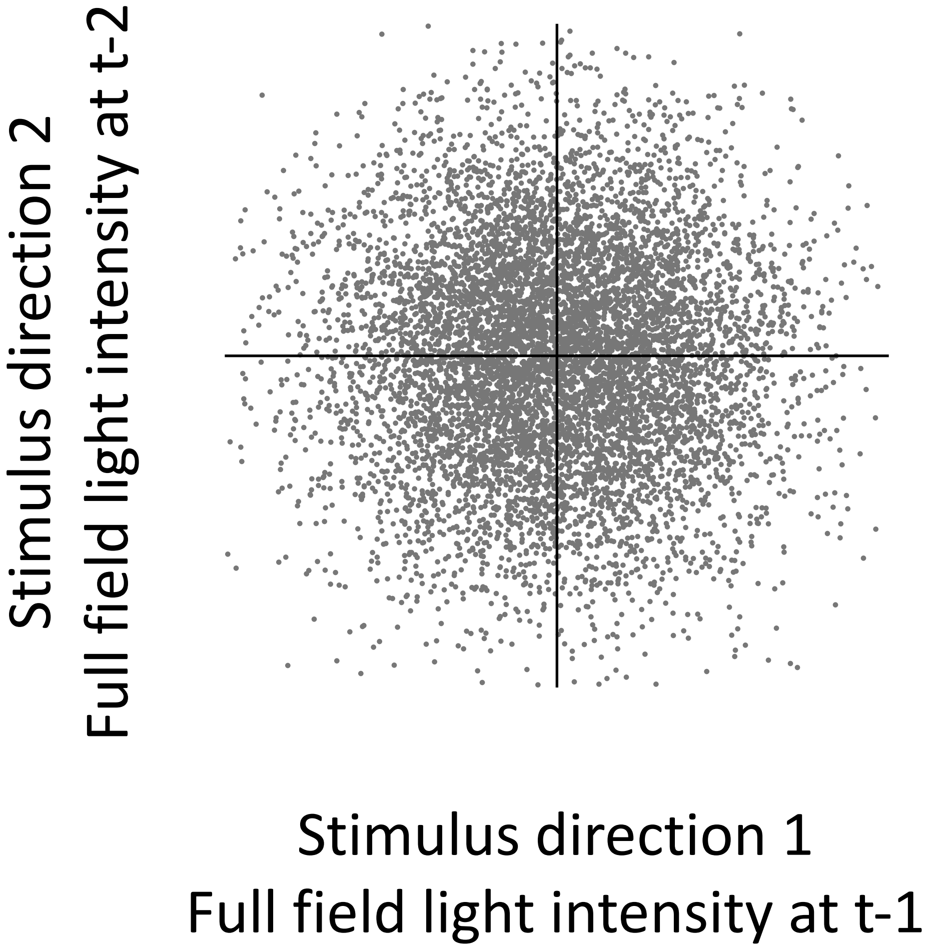

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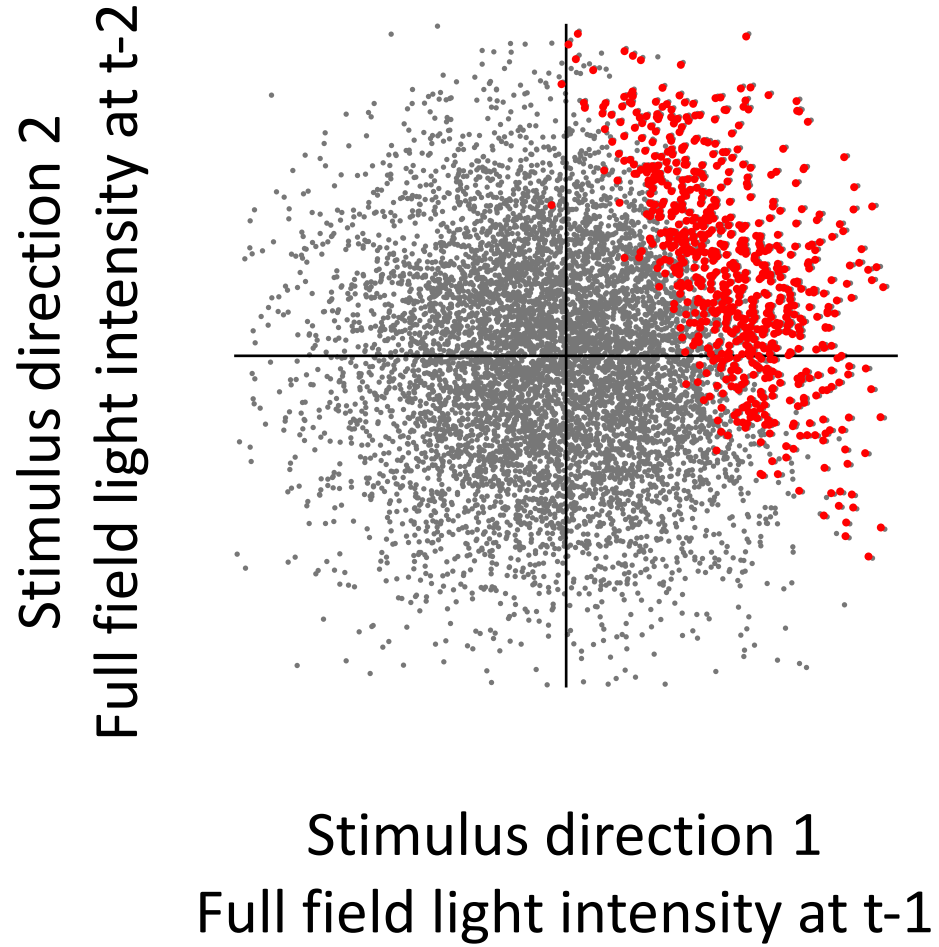

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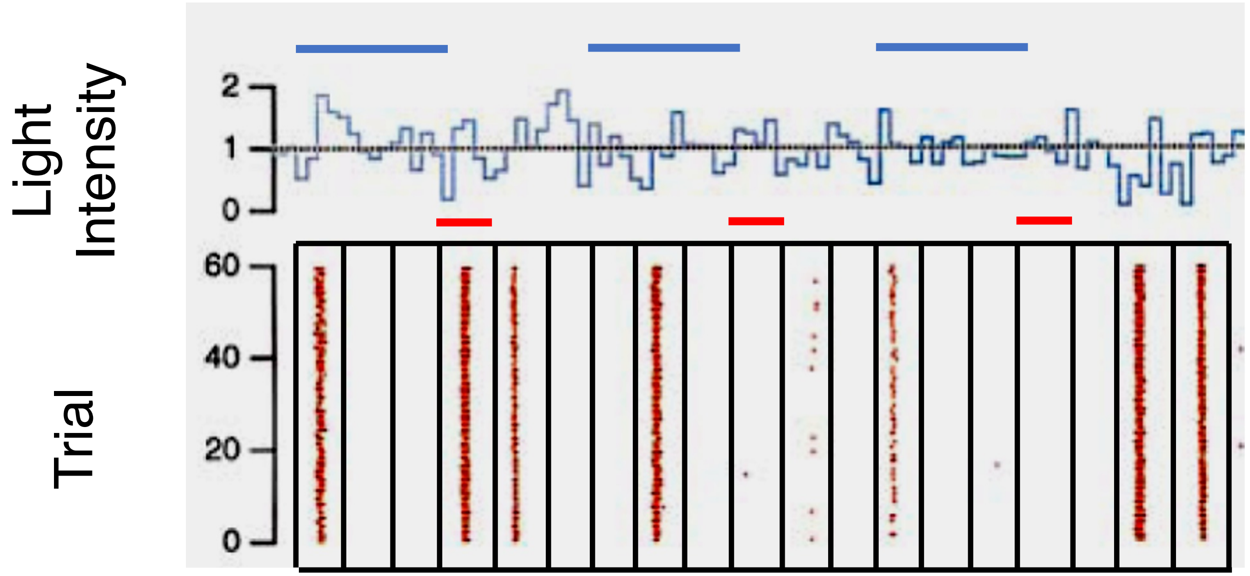

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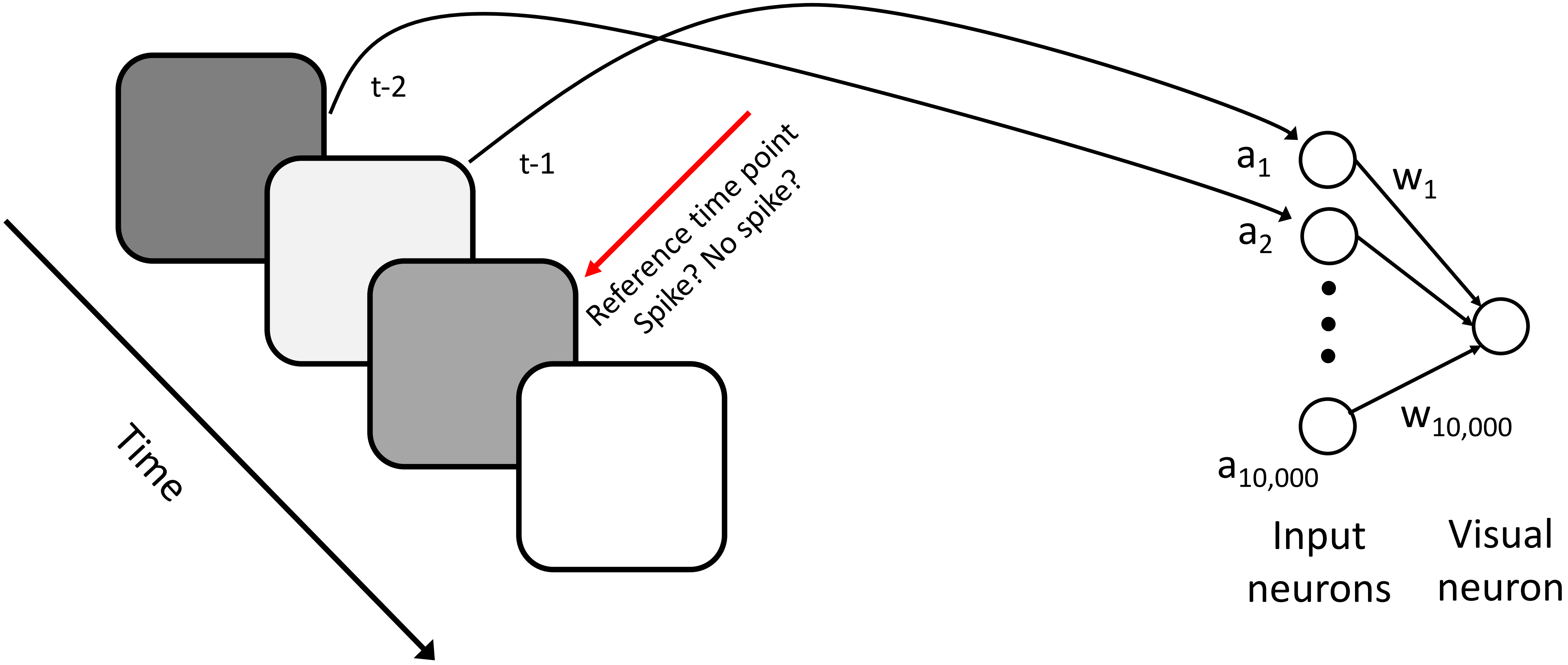

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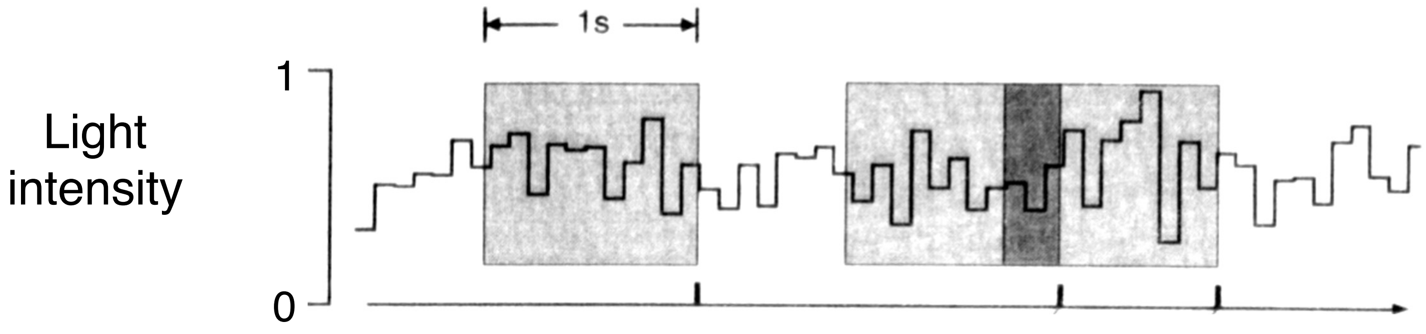

Spikes, MIT press Rieke et al. (1997)

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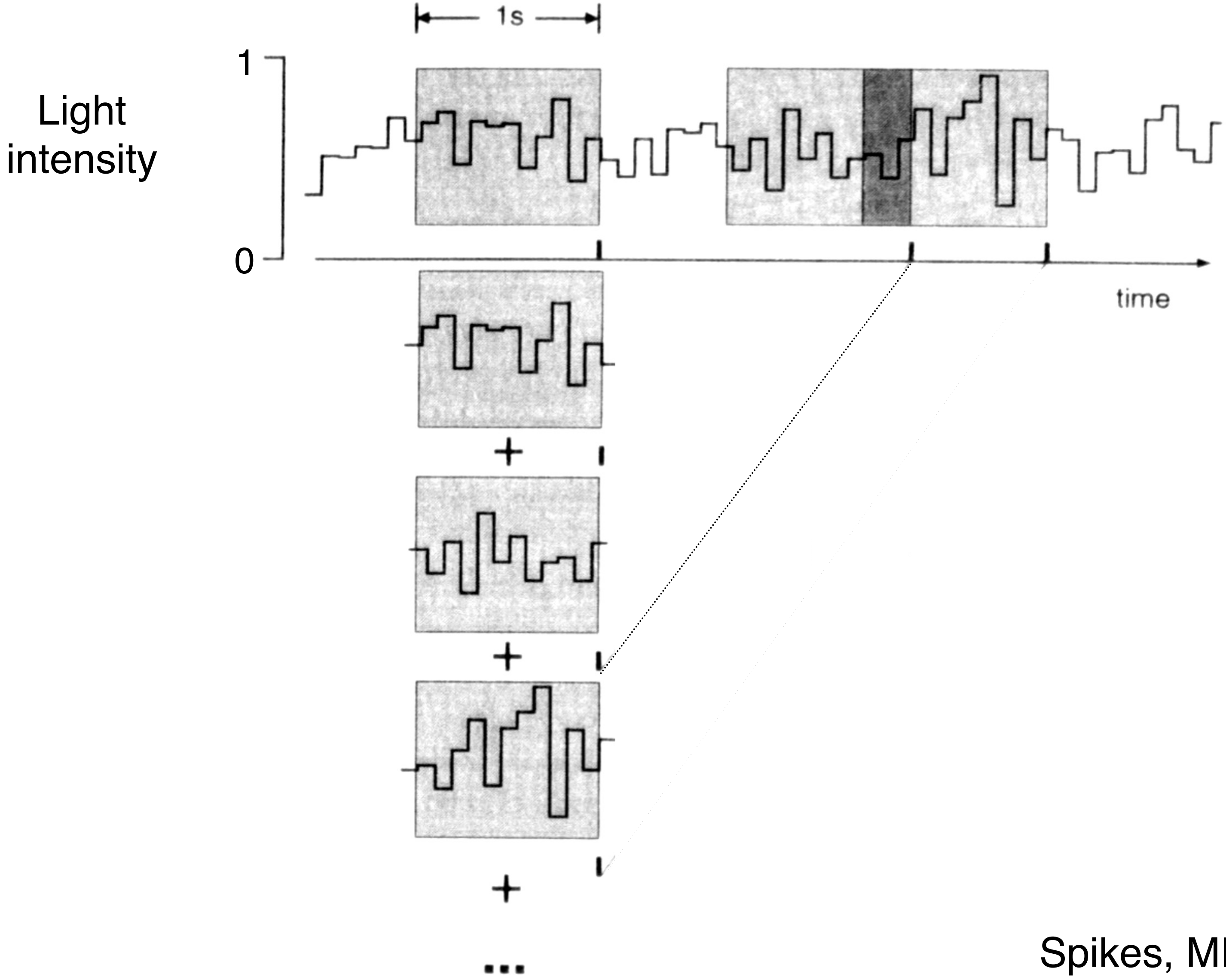

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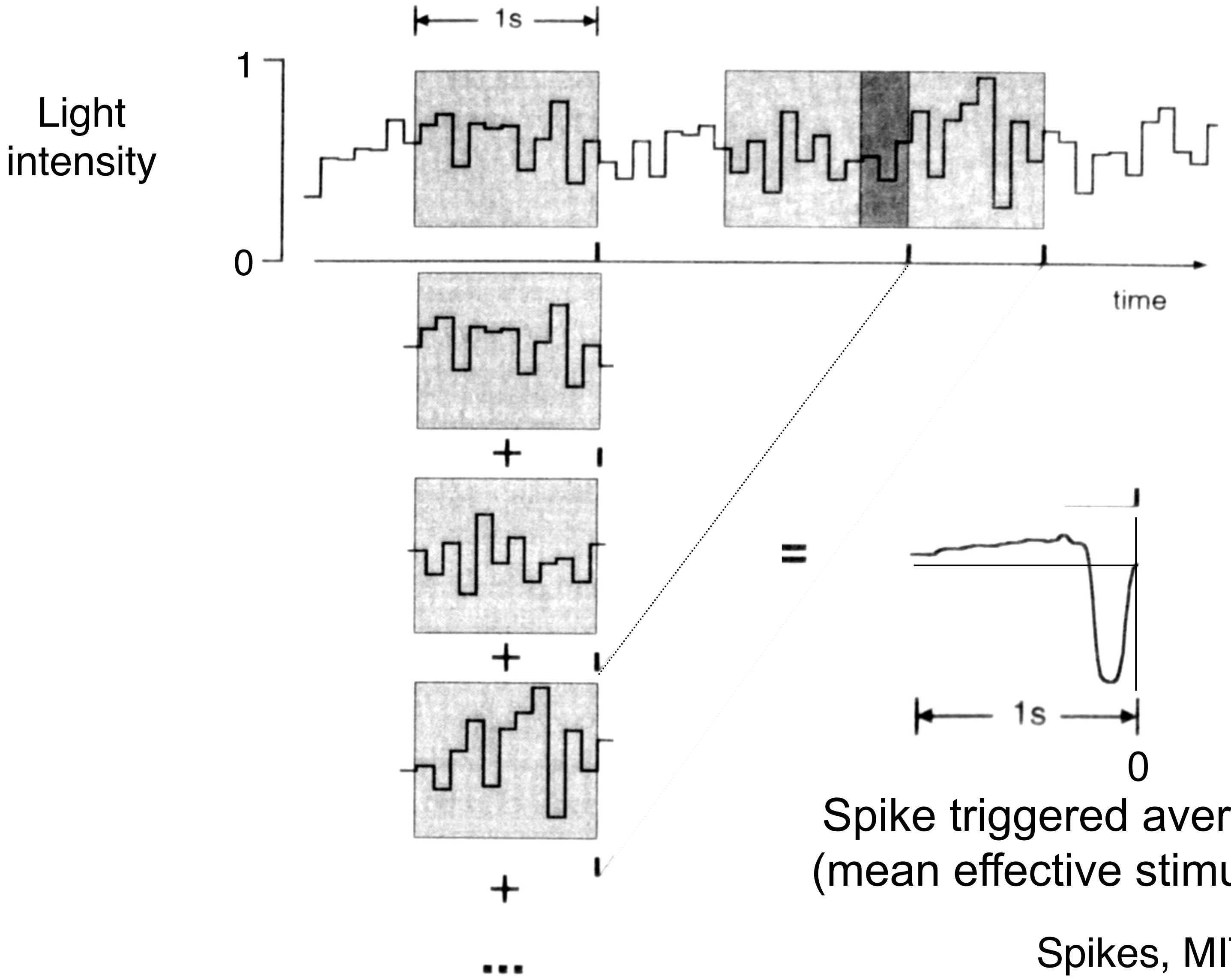

Spike triggered average (mean effective stimulus)

Spikes, MIT press Rieke et al. (1997)

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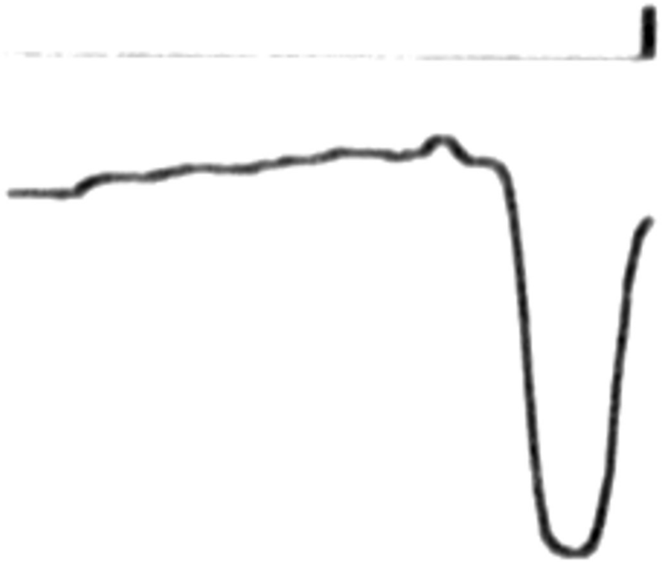

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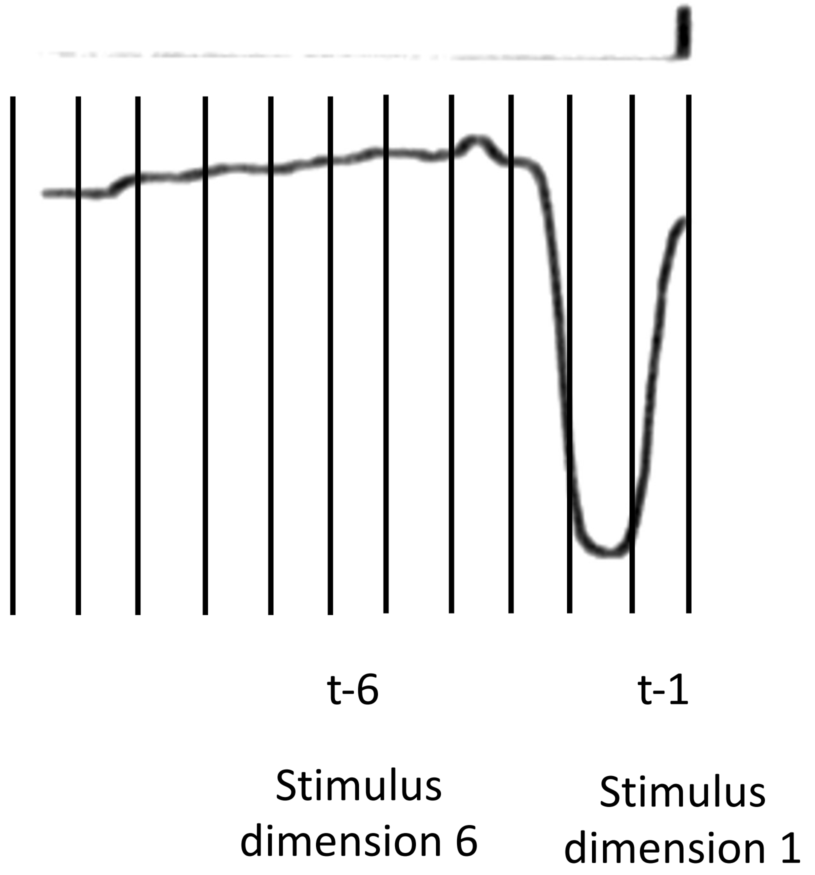

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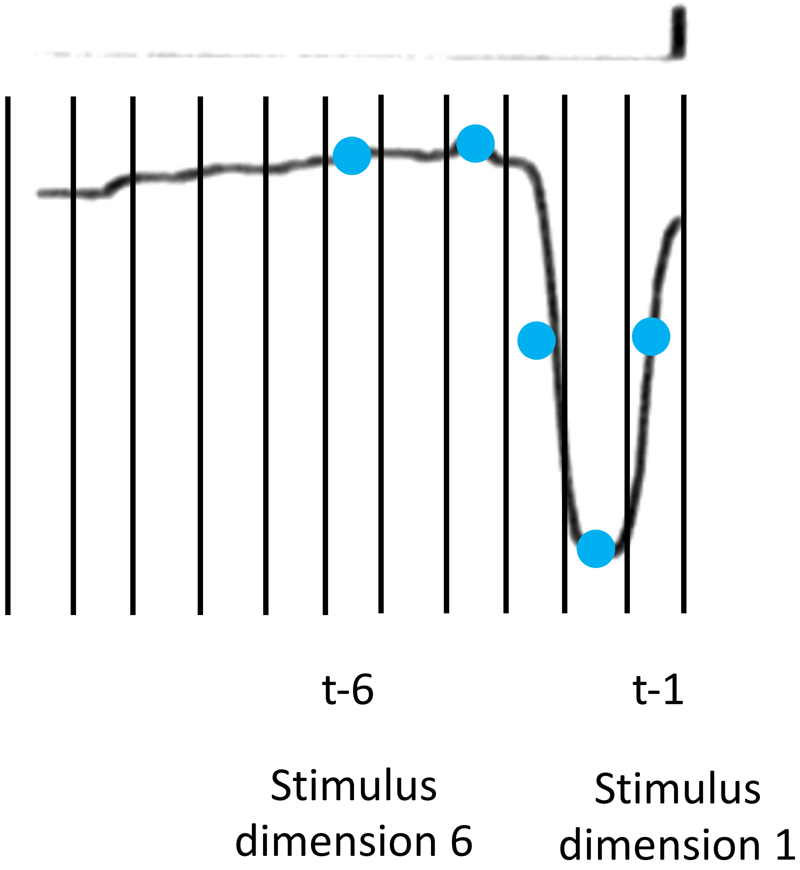

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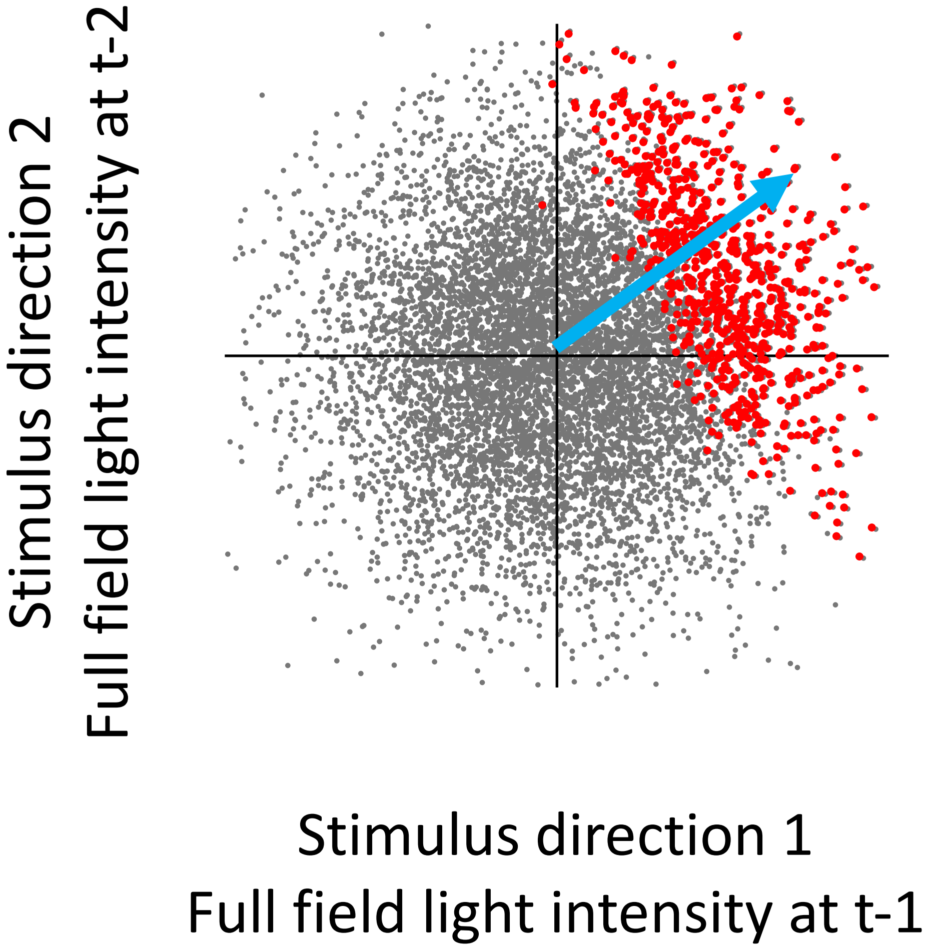
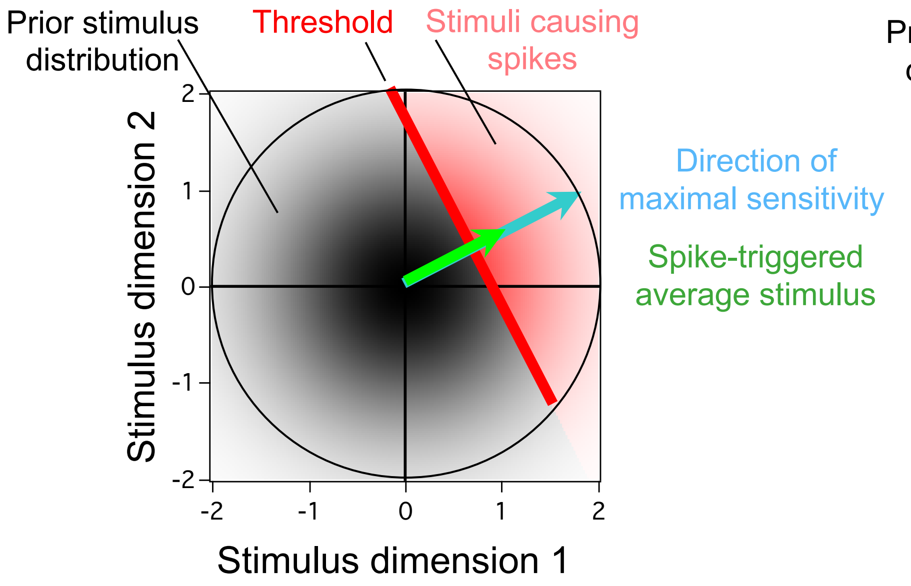
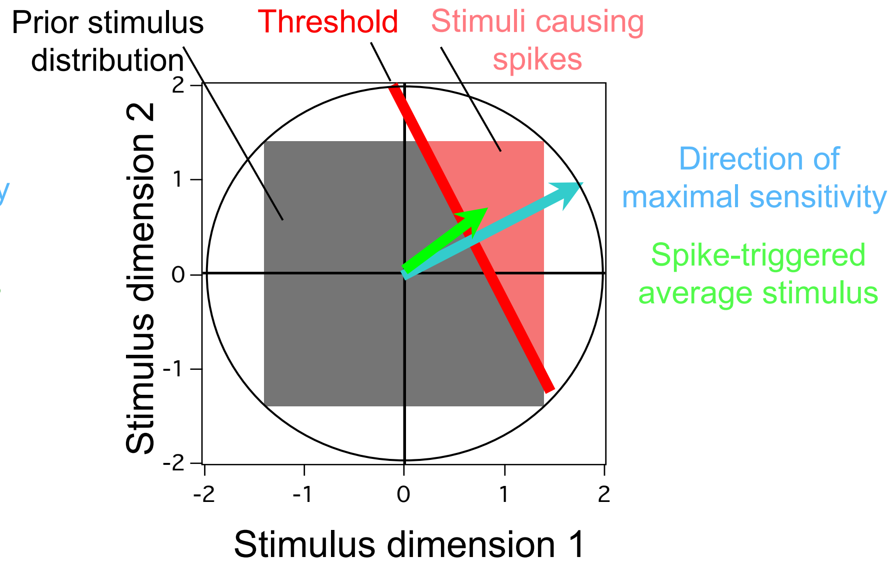


Receptive field
by Spike triggered averaging

Spikes, MIT press Rieke et al. (1997)

Reverse correlation will work (under assumptions)



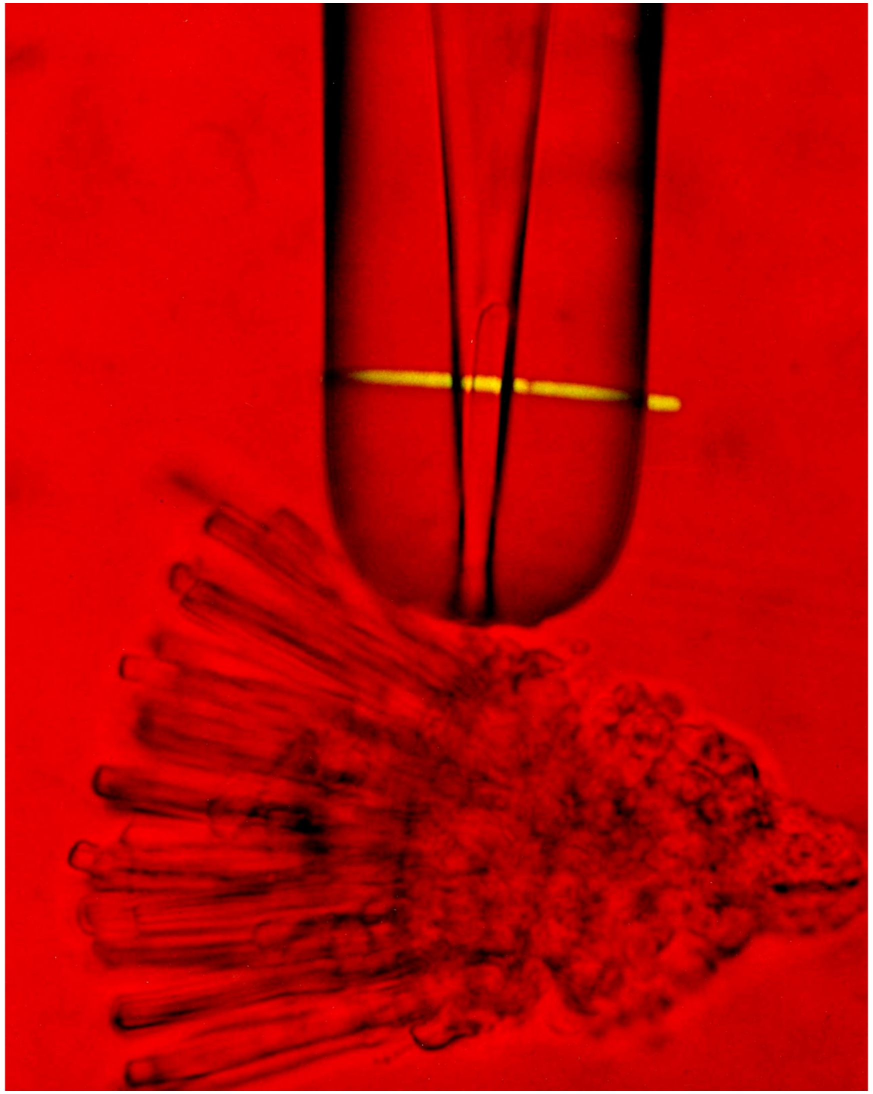


If an input is Gaussian white noise, correlation of the input with the output yields the most effective input

This is true even if there is a distortion of the signal's amplitude such as a threshold or saturation.

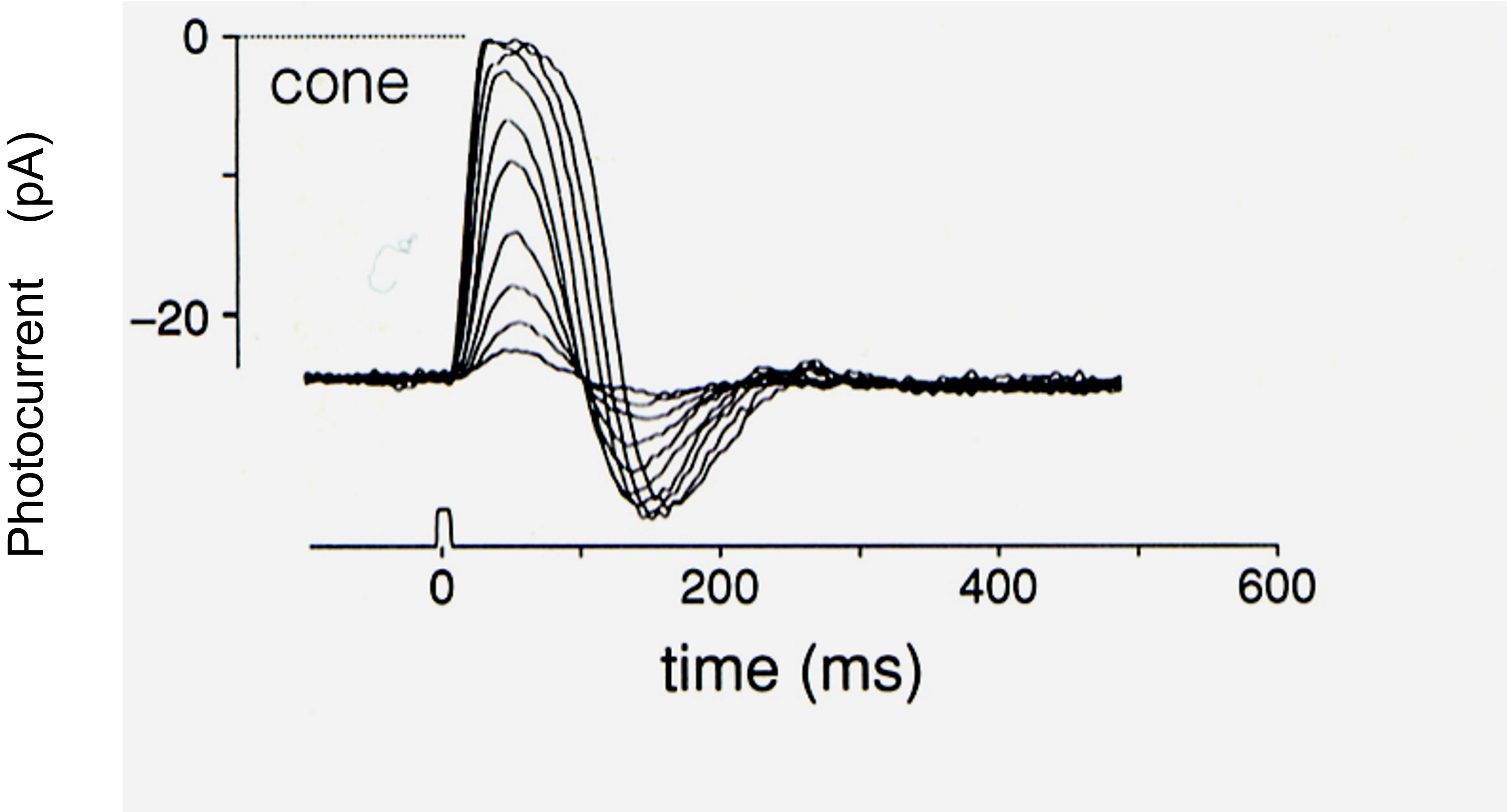
Bussgang (1952)

Opposite direction: will a neuron respond to a stimulus?



Baylor, Lamb and Yau (1979)

Predicting neural responses by impulse response

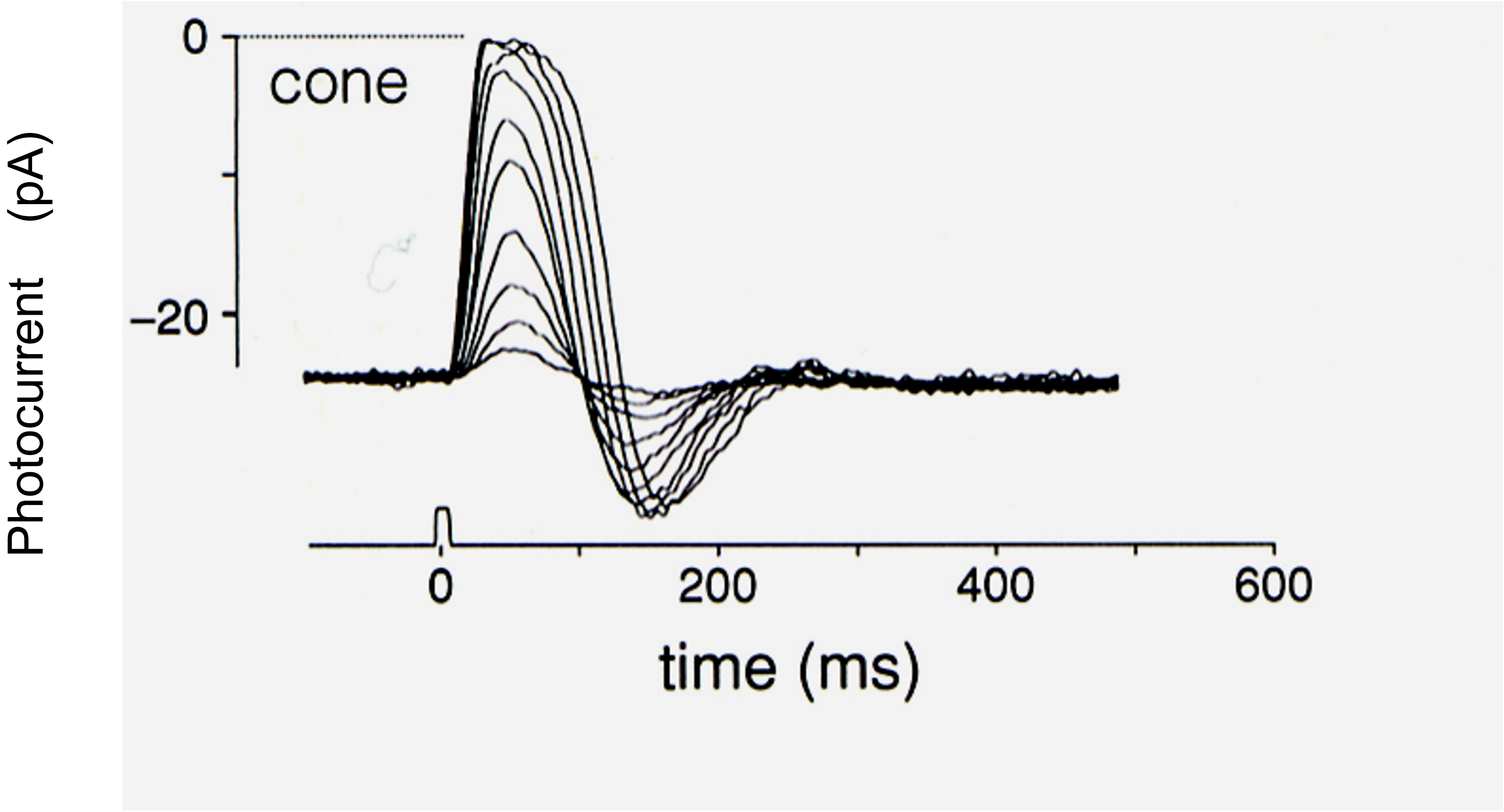


Baylor (1987)

Very important: response of neuron to a brief input lasts a long time

Perceptron model had no notion of time, just respond or not. We need to address time more seriously

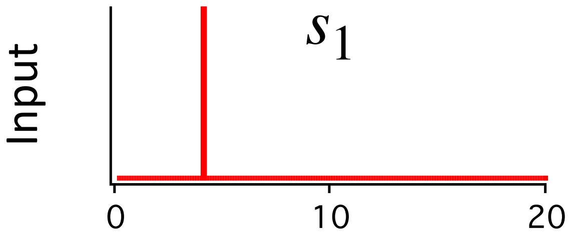
Predicting neural responses by impulse response



Baylor (1987)

Response approximately scales by two when input is multiplied by two. System is approximately linear!

The magic of linear systems



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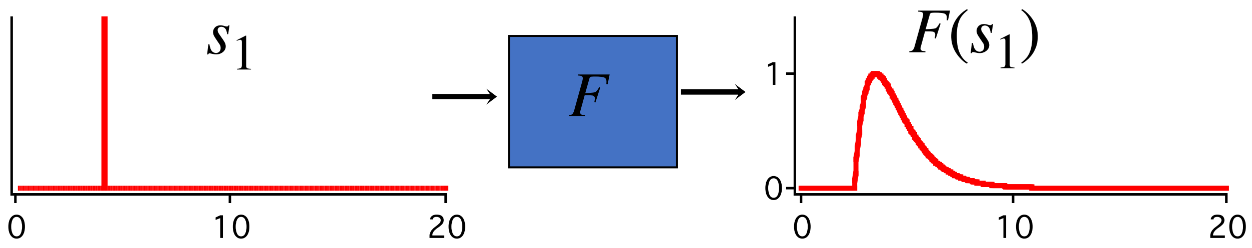

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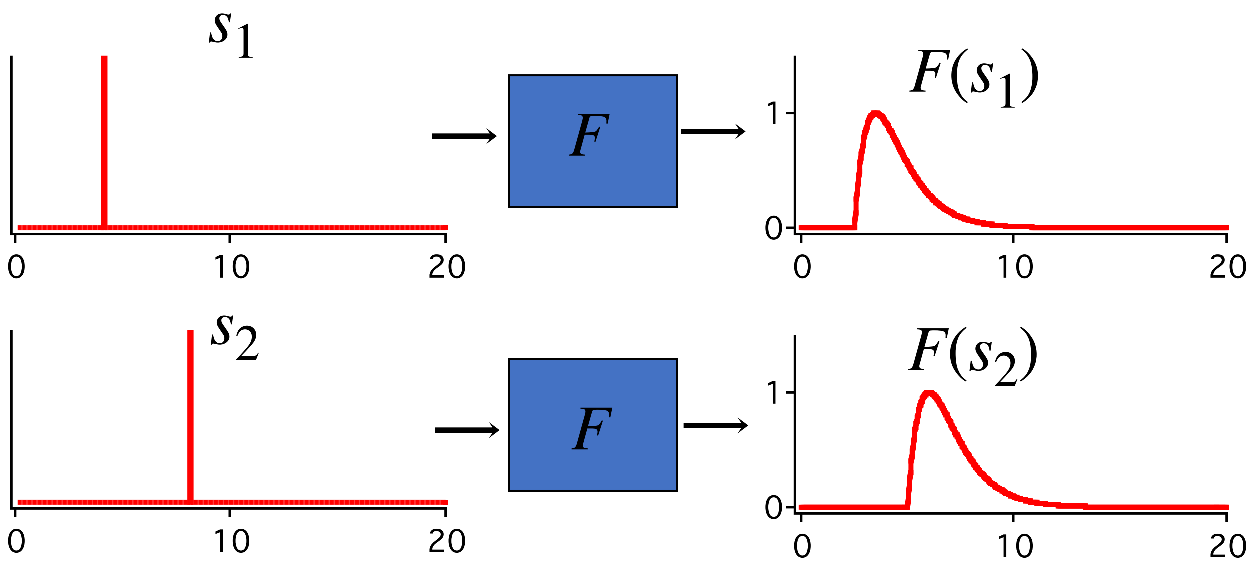
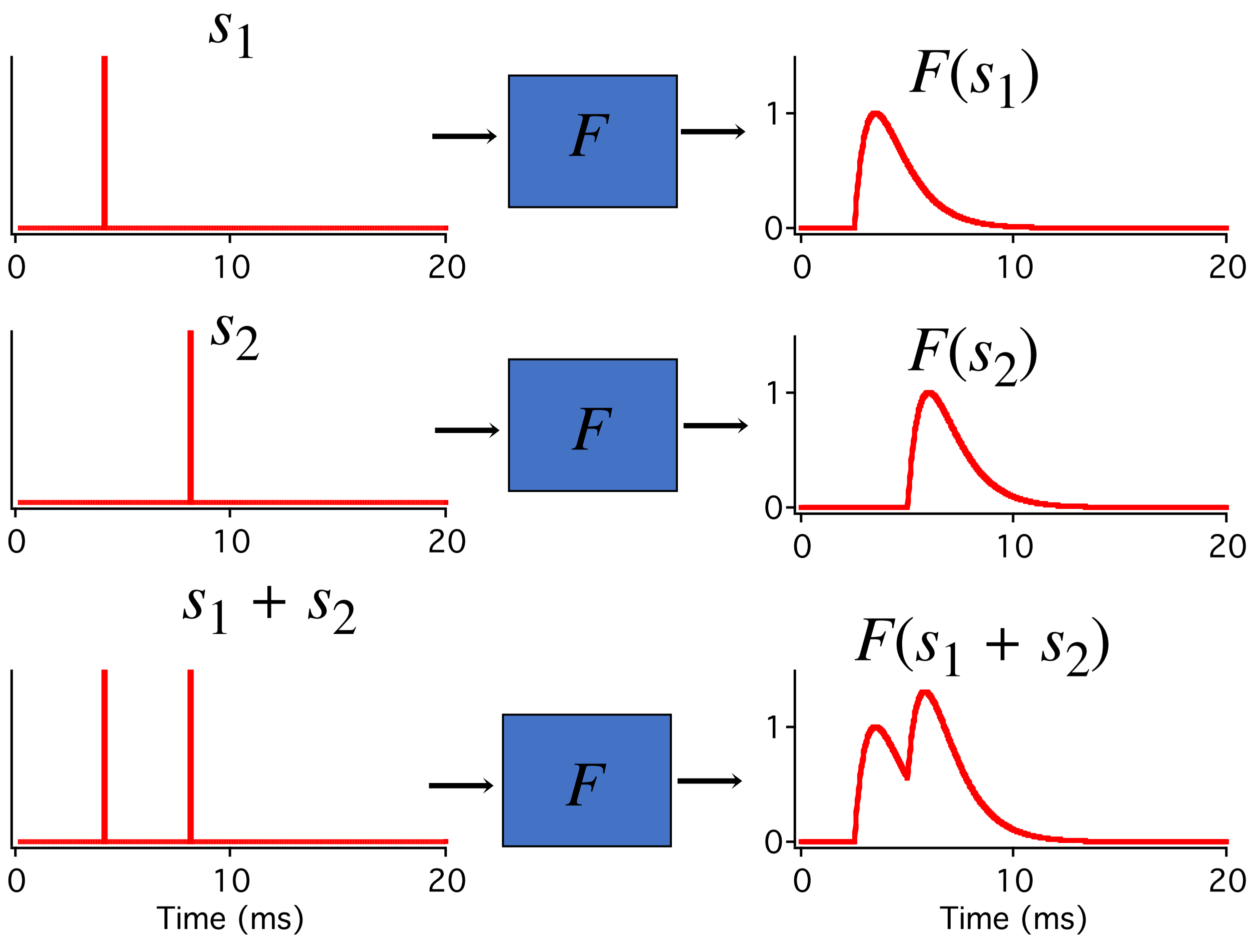


The Superposition Principle

When two inputs are presented to a linear system, their effects sum.
The response to an input that is a sum of two inputs is the sum of the responses to the individual inputs

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

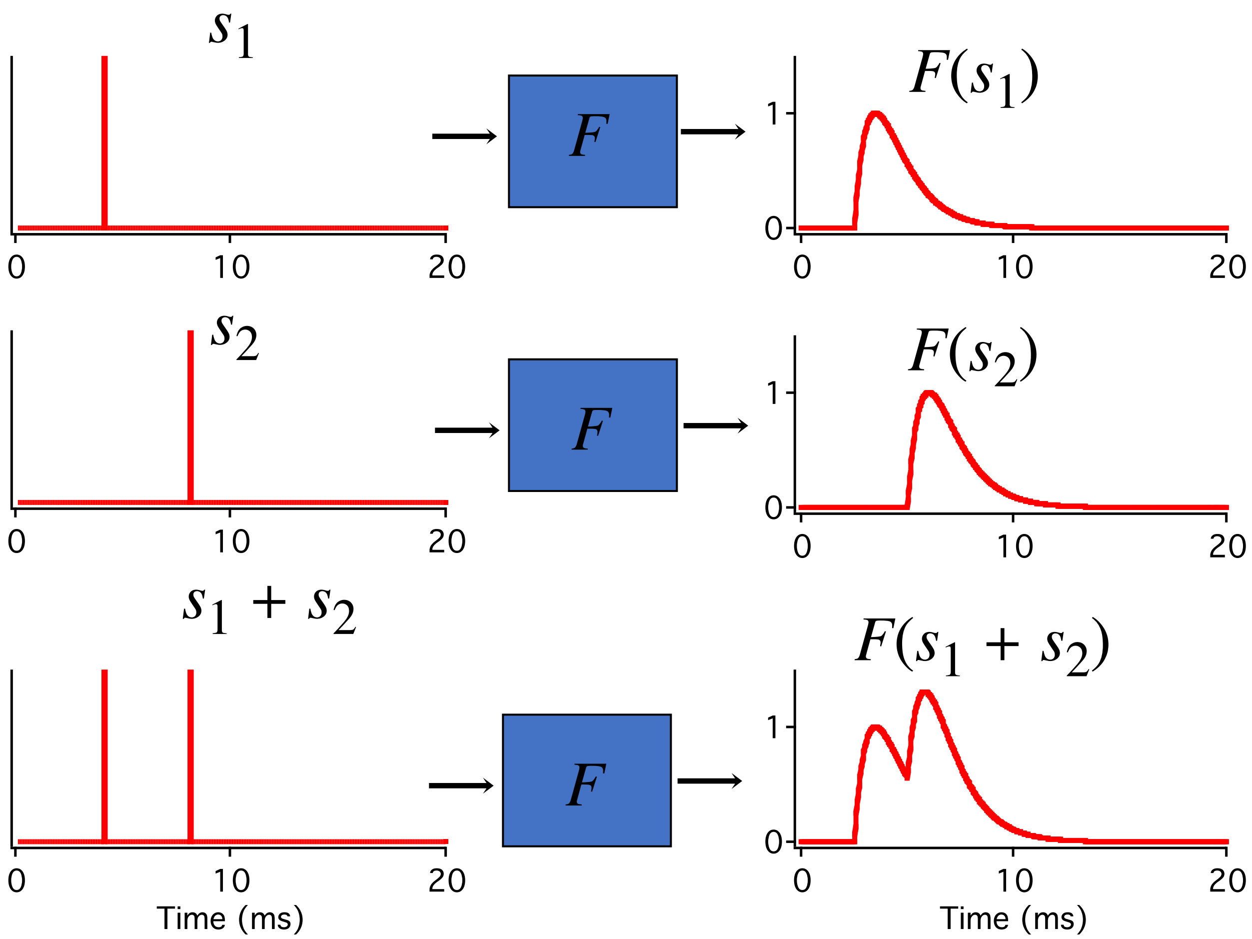
The magic of linear systems



Time invariance principle

The response to an input is the same whether it is presented at one time point or another

The magic of linear systems

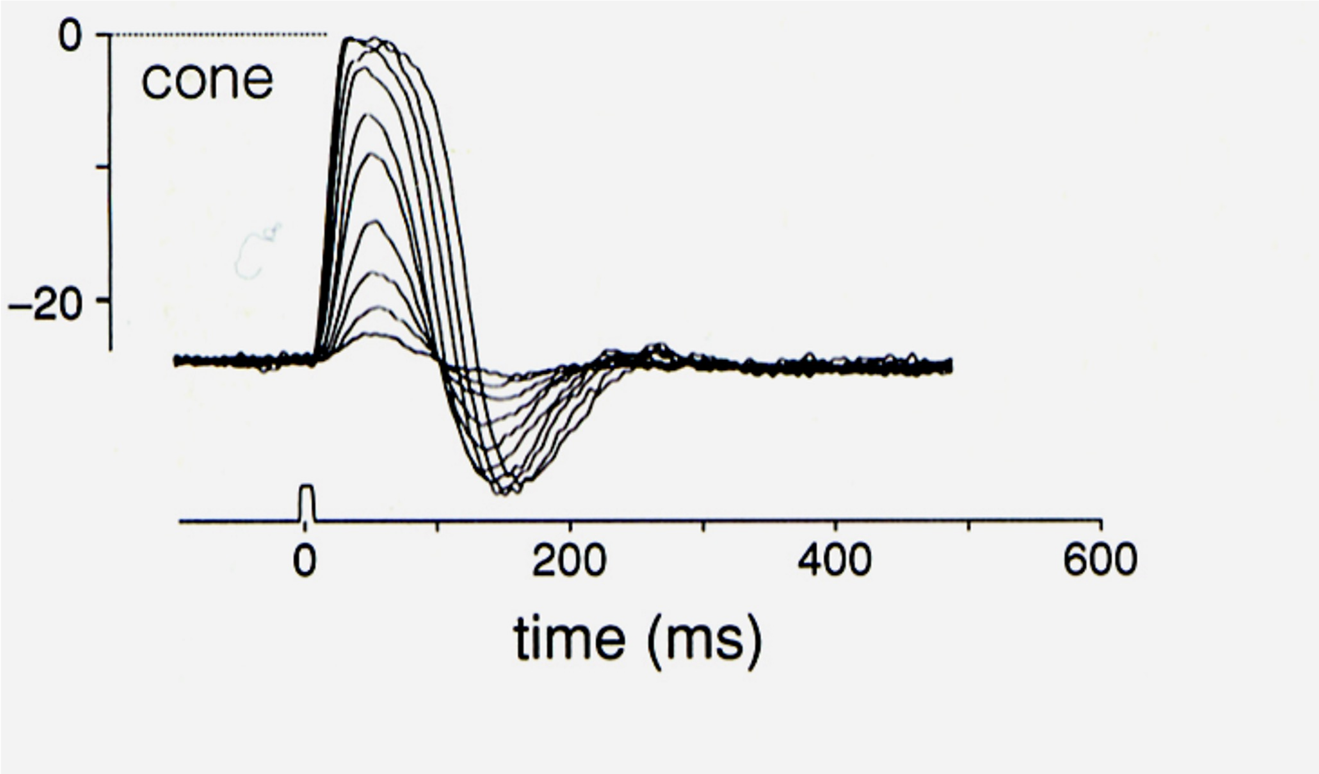


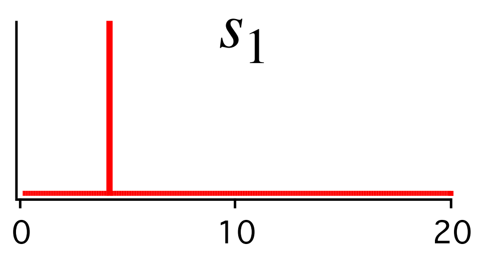
Superposition + Time invariance = predictability by impulse response

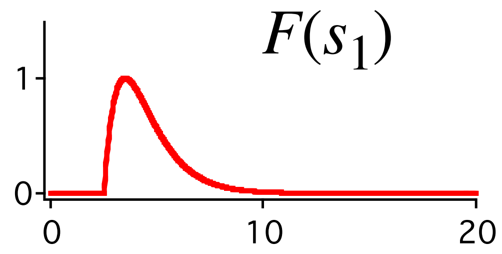
The magic of linear systems

INSERT SHAKA AND ITS DECOMPOSITION

Convolution: dealing with graded, temporally extended responses

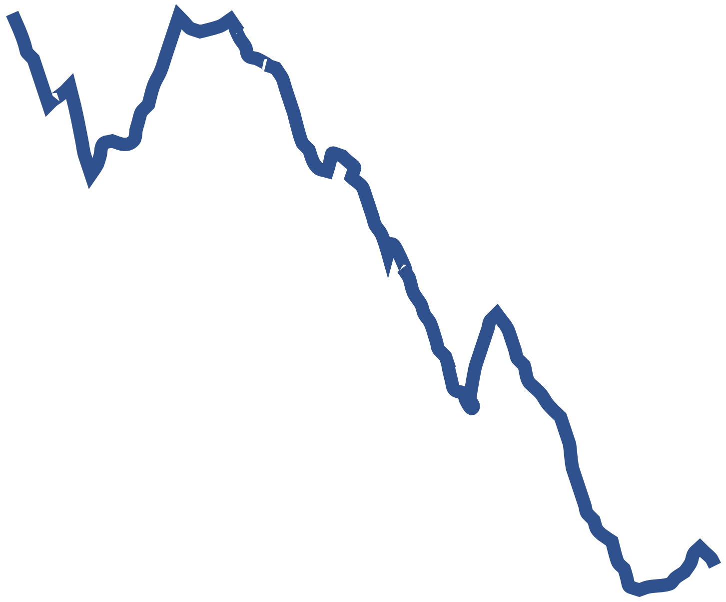






Linear model of neural response by convolution

Complicated input
Whose response
We want to predict



Time

Linear model of neural response by convolution

Treat each time point as a scaled impulse

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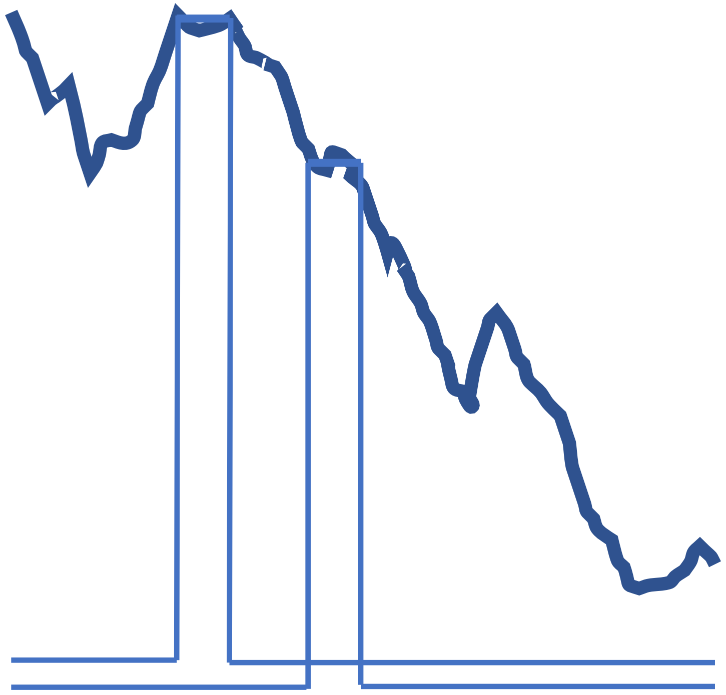

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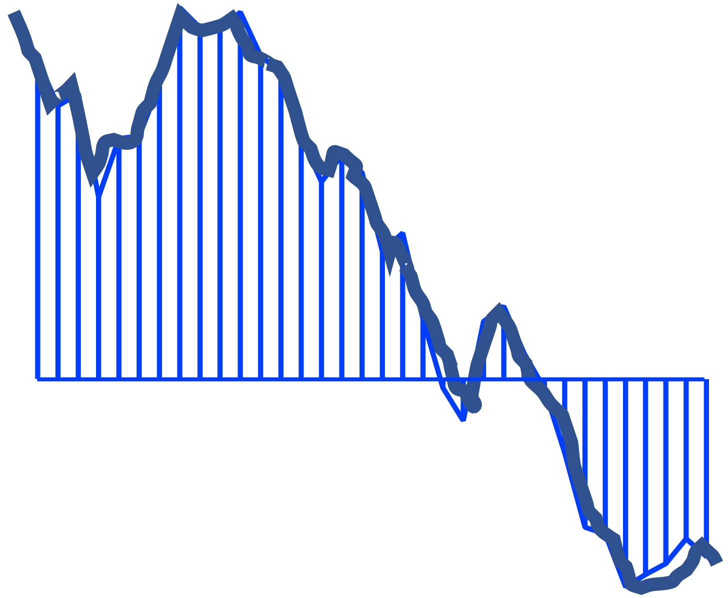

Measure impulse response

Time

Linear model of neural response by convolution

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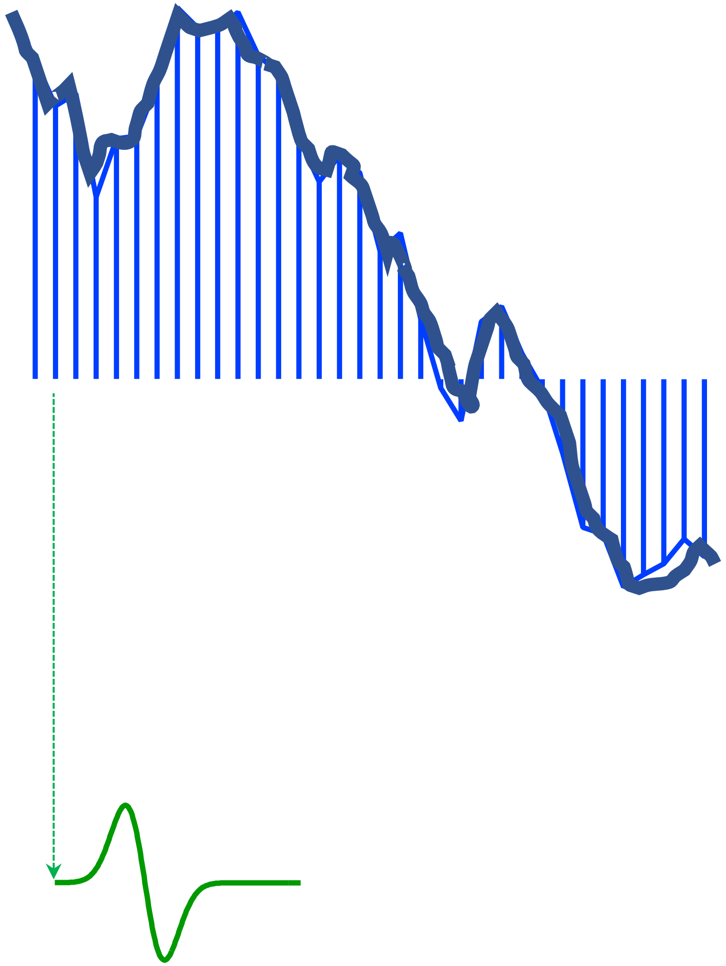

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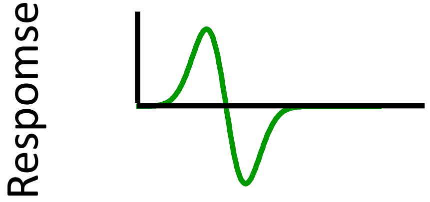

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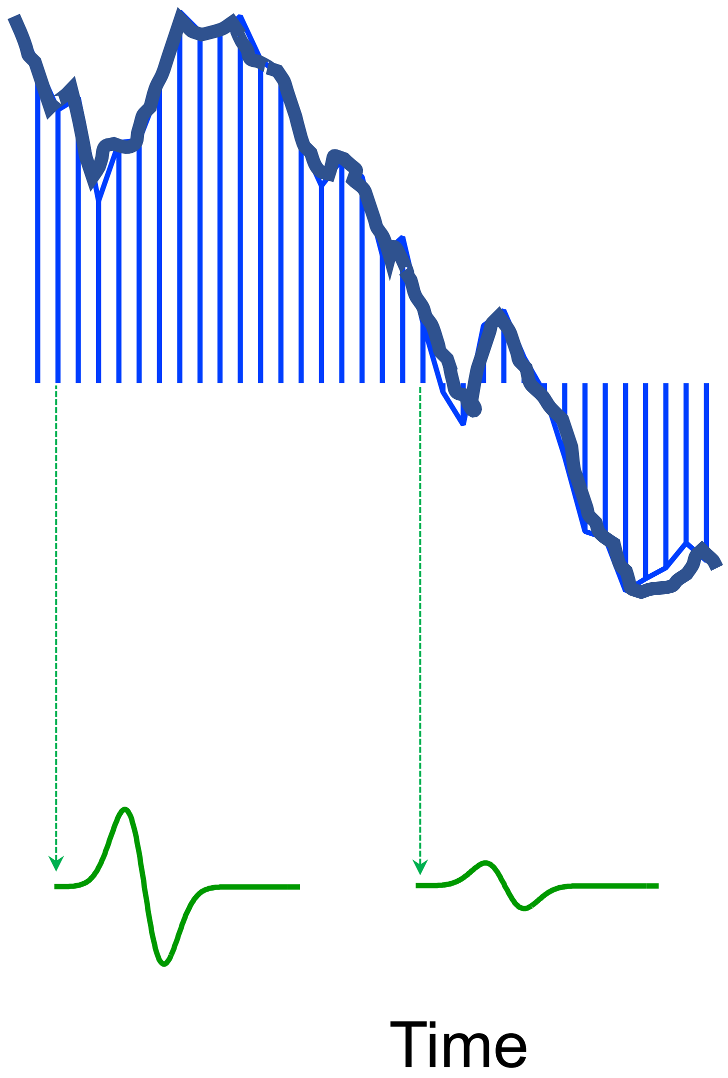

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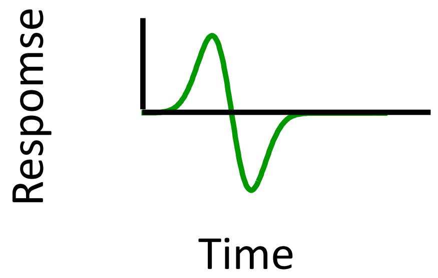

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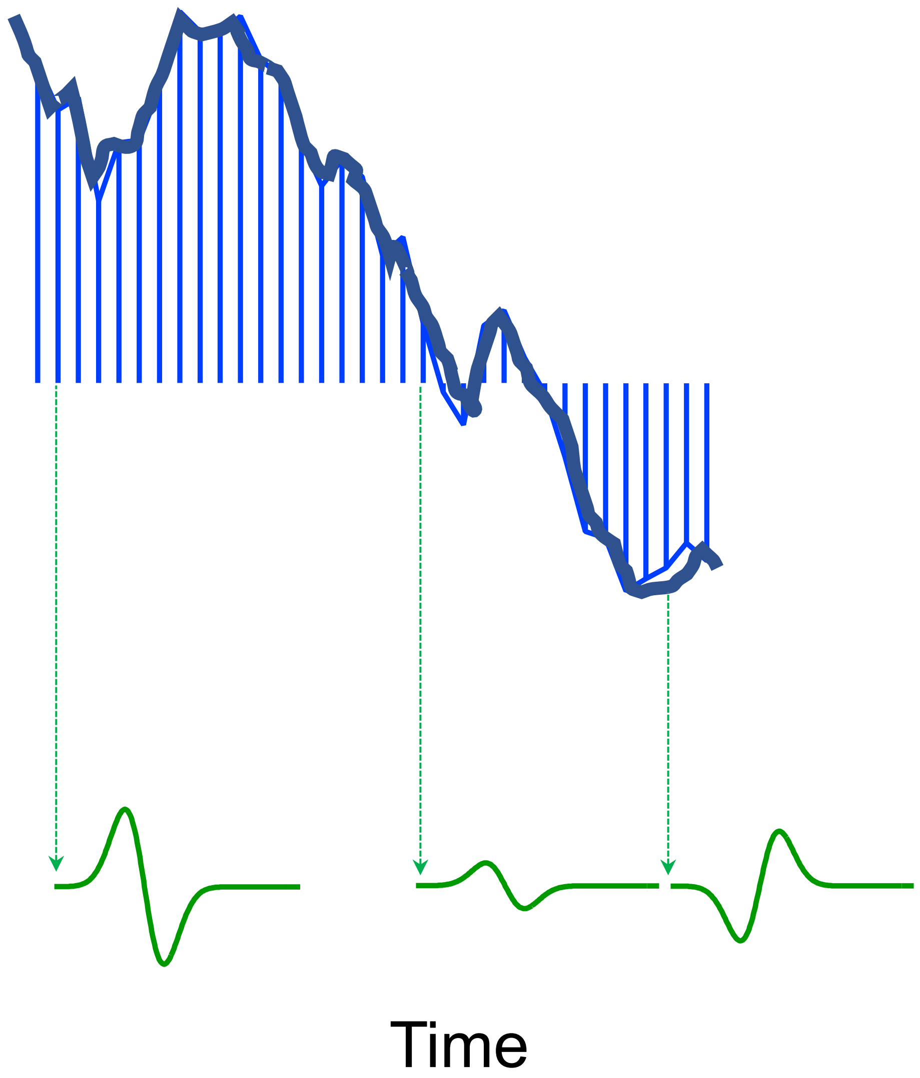
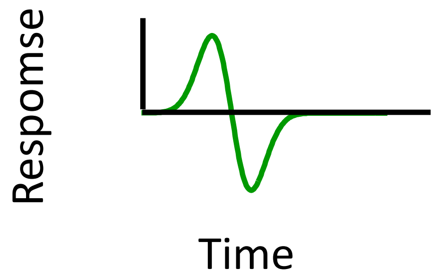


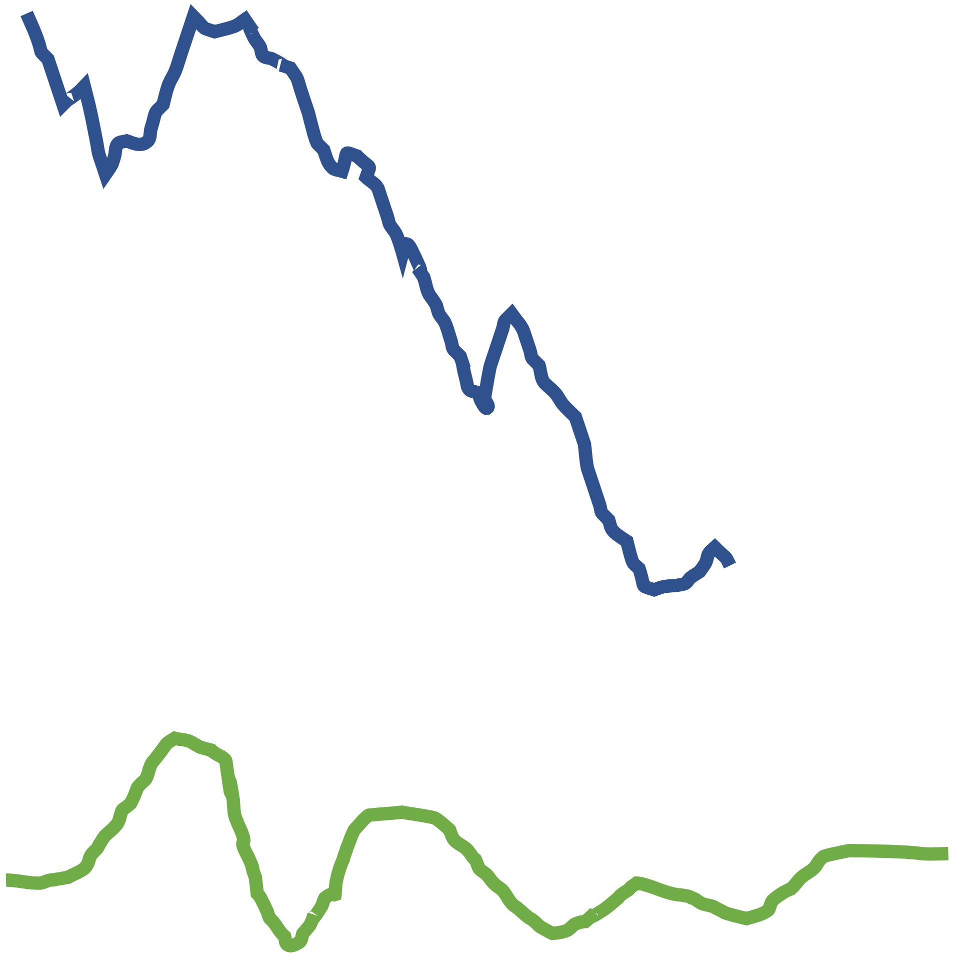
Measure impulse response



Linear model of neural response by convolution

Complicated input
Whose response
We want to predict

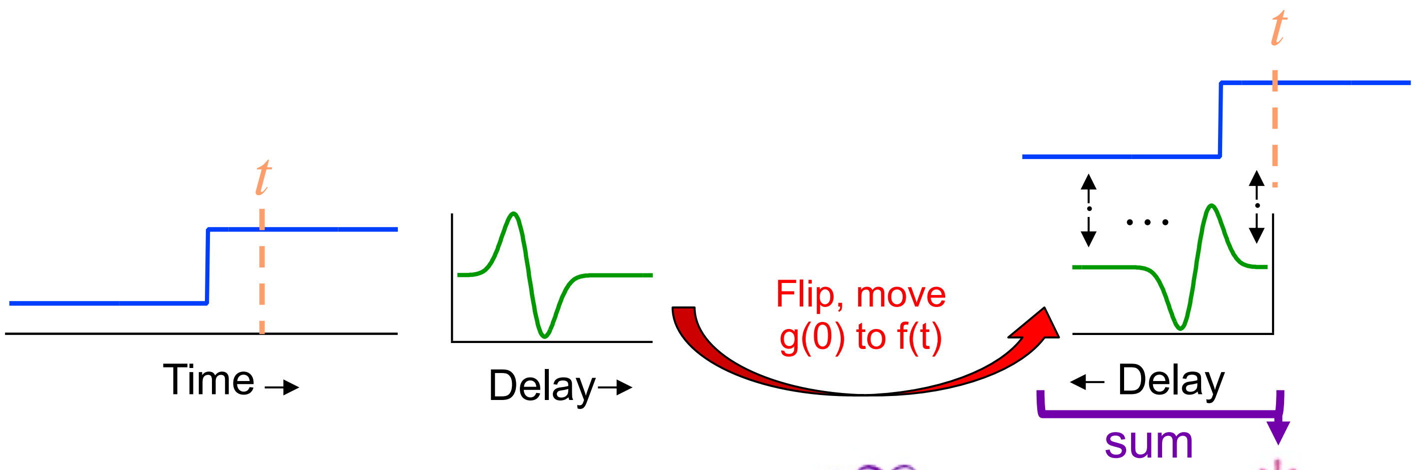
Predicted output



Time

Convolution: white board

Convolution as an integral



$$(f * g)(t) = \int_{-\infty}^{\infty} f(\tau)g(t-\tau)\,d\tau$$

To convolve an input signal with a filter, flip the filter in time, move it to a chosen time, and sum the weighting at each time of the signal by the filter.

see 'colorized math', betterexplained.com

Convolution as a matrix multiplication

Input Filter Output

Time

$$\begin{bmatrix} s_0 & s_{-1} & s_{-2} & \cdots & s_{-\tau} \\ s_1 & s_0 & s_{-1} & & \\ s_2 & s_1 & s_0 & & \\ \vdots & & & \ddots & \vdots \\ s_T & & & \cdots & s_{T-\tau} \end{bmatrix} \cdot \begin{bmatrix} f_0 \\ f_1 \\ f_2 \\ \vdots \\ f_\tau \end{bmatrix} =$$

Toeplitz matrix

Convolution as a matrix multiplication

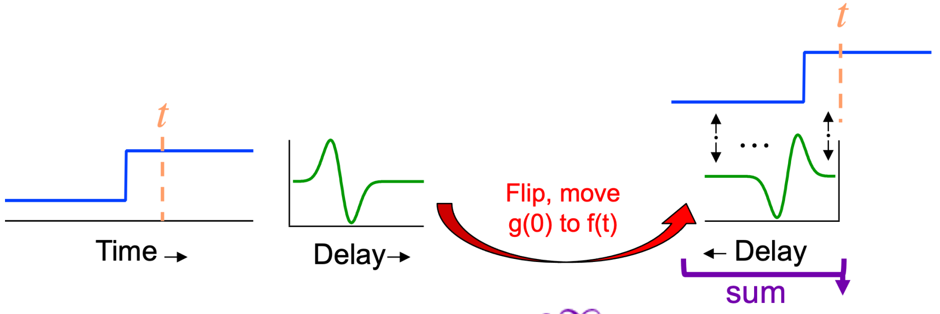
Input | Filter | Output

Time ↓

$$
\begin{bmatrix}
\boxed{s_0 \quad s_{-1} \quad s_{-2} \quad \cdots \quad s_{-\tau}} \\
\boxed{s_1 \quad s_0 \quad s_{-1} \qquad\qquad\qquad} \\
s_2 \quad s_1 \quad s_0 \qquad\qquad\qquad \\
\vdots \qquad\qquad \ddots \quad \vdots \\
s_T \qquad\qquad \cdots \quad s_{T-\tau}
\end{bmatrix}
\cdot
\begin{bmatrix}
f_0 \\ f_1 \\ f_2 \\ \vdots \\ f_\tau
\end{bmatrix}
=
\begin{bmatrix}
\boxed{\sum_{i=0}^{-\tau} s_i f_{-i}} \\
\boxed{\sum_{i=0}^{-\tau} s_{i+1} f_{-i}} \\
\vdots \\
\sum_{i=0}^{-\tau} s_{i+T} f_{-i}
\end{bmatrix}
$$

Time ↓

Toeplitz matrix



$$(f * g)(t) = \int_{-\infty}^{\infty} f(\tau)g(t-\tau)\, d\tau$$

Convolution as a matrix multiplication

Input | Filter | Output

Time

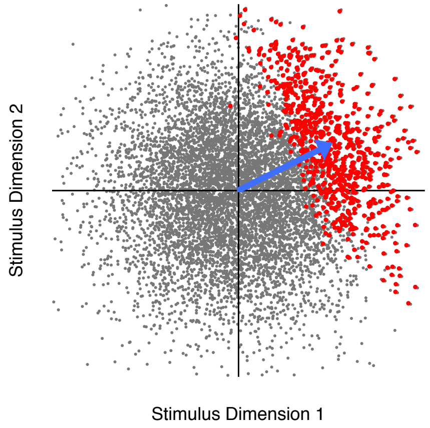
$$\begin{bmatrix} \boxed{s_0 & s_{-1} & s_{-2} & \cdots & s_{-\tau}} \\ s_1 & s_0 & s_{-1} & & \\ s_2 & s_1 & s_0 & & \\ \vdots & & & \ddots & \vdots \\ s_T & & & \cdots & s_{T-\tau} \end{bmatrix} \cdot \begin{bmatrix} f_0 \\ f_1 \\ f_2 \\ \vdots \\ f_\tau \end{bmatrix} = \begin{bmatrix} \boxed{\sum_{i=0}^{-\tau} s_i f_{-i}} \\ \sum_{i=0}^{-\tau} s_{i+1} f_{-i} \\ \vdots \\ \sum_{i=0}^{-\tau} s_{i+T} f_{-i} \end{bmatrix}$$

Time

A second way to think about a convolution – it yields the dot (inner) product of the input and the (time-reversed) filter.

This gives a *geometrical* interpretation to a linear model, because

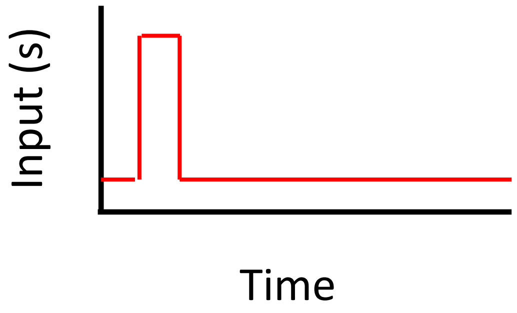
$$\mathbf{a} \cdot \mathbf{b} = \|\mathbf{a}\|\|\mathbf{b}\|\cos\theta$$



The filter is the impulse response function

$$
\begin{array}{ccc}
\text{Input} & \text{Filter} & \text{Output} \\
\begin{bmatrix}
s_0 & s_{-1} & s_{-2} & \cdots & s_{-\tau} \\
s_1 & s_0 & s_{-1} & & \\
s_2 & s_1 & s_0 & & \\
\vdots & & & \ddots & \vdots \\
s_T & & & \cdots & s_{T-\tau}
\end{bmatrix}
\cdot
&
\begin{bmatrix}
f_0 \\ f_1 \\ f_2 \\ \vdots \\ f_\tau
\end{bmatrix}
= &
\end{array}
$$

Impulse in graph format



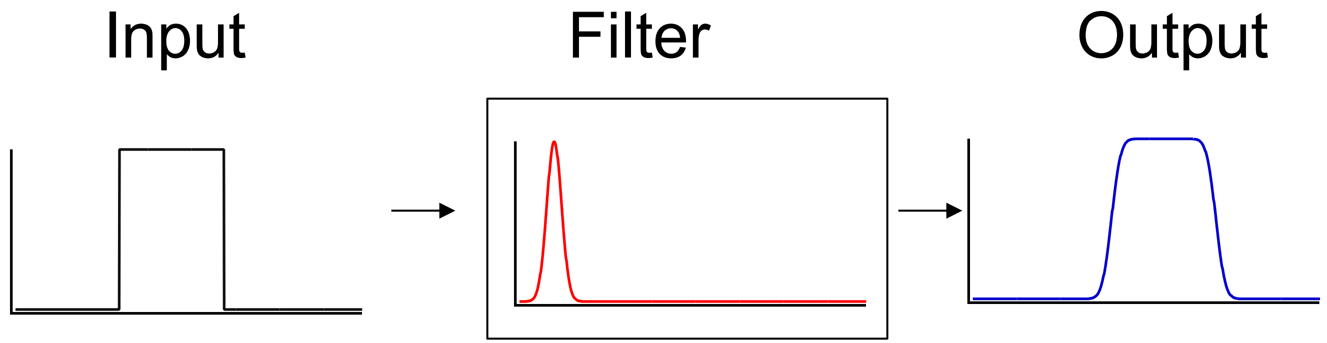
Impulse in vector format

s = [1, 0, 0, 0, 0, 0,….]

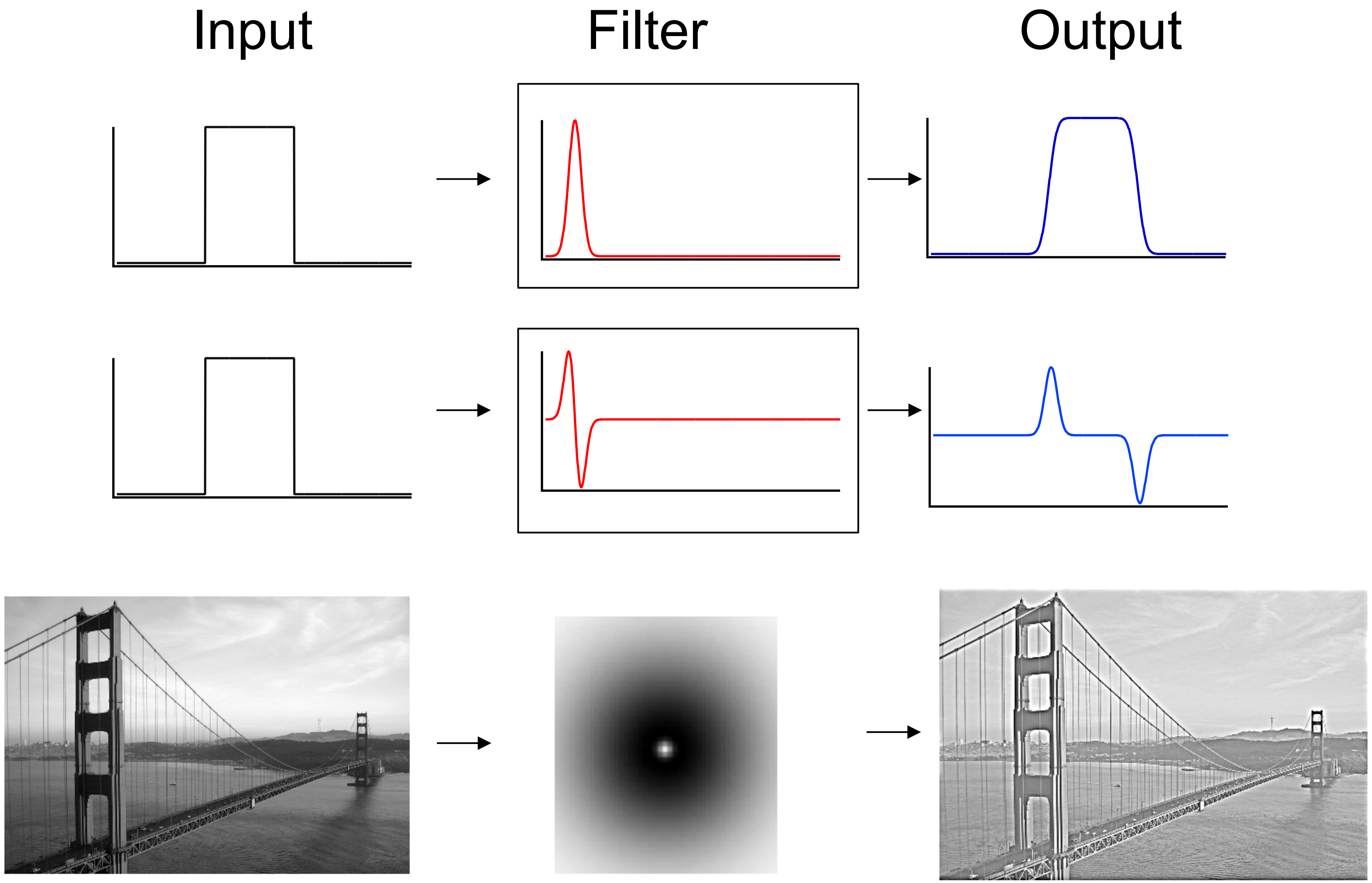
The filter is the impulse response function

$$
\begin{array}{ccc}
\text{Input} & \text{Filter} & \text{Output} \\
\begin{bmatrix} 1 & 0 & 0 & \cdots & 0 \\ 0 & 1 & 0 & & \\ 0 & 0 & 1 & & \vdots \\ \vdots & & & \ddots & \vdots \\ 0 & & & \cdots & 1 \end{bmatrix} \cdot & \begin{bmatrix} f_0 \\ f_1 \\ f_2 \\ \vdots \\ f_\tau \end{bmatrix} = &
\end{array}
$$

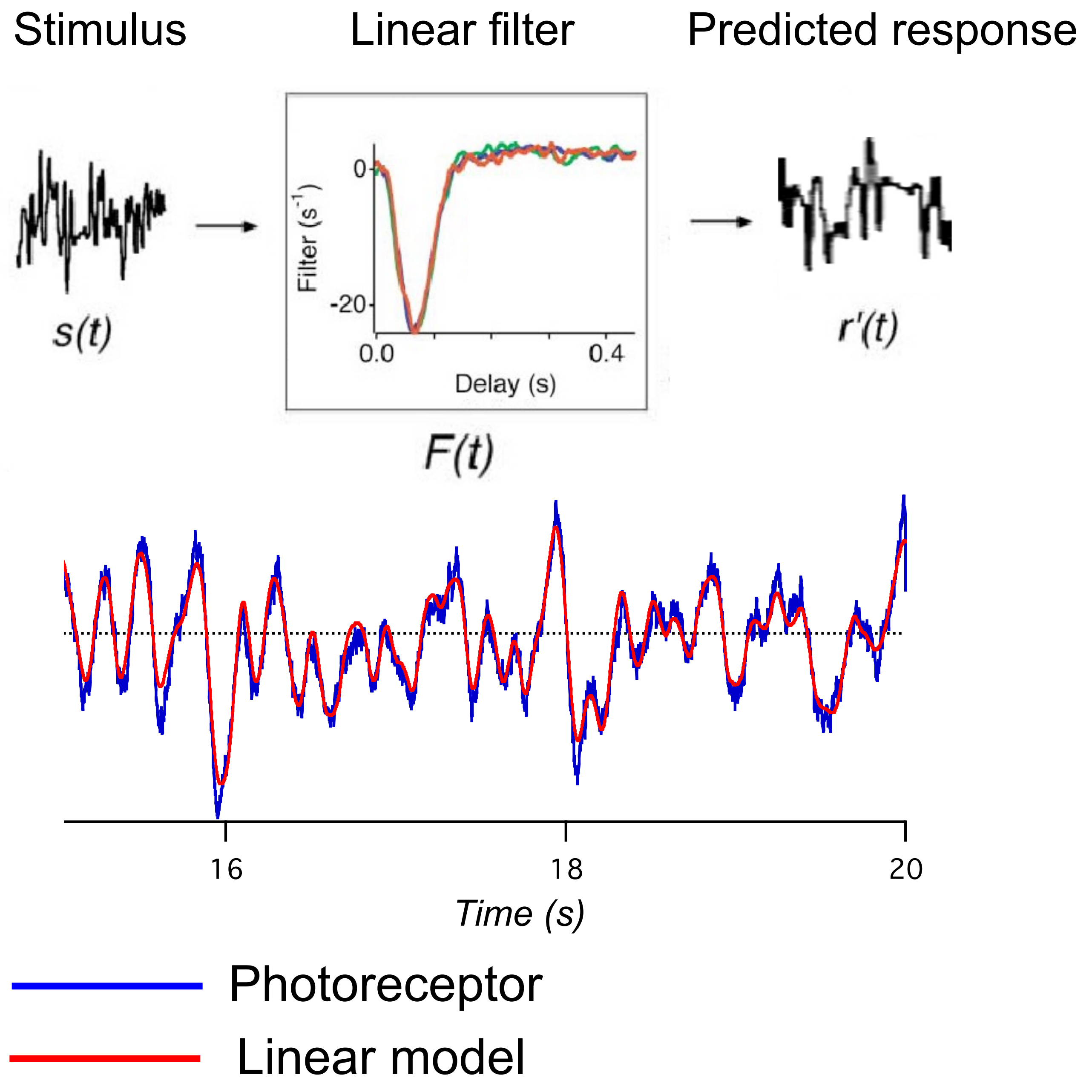
Effects of different filters



Effects of different filters

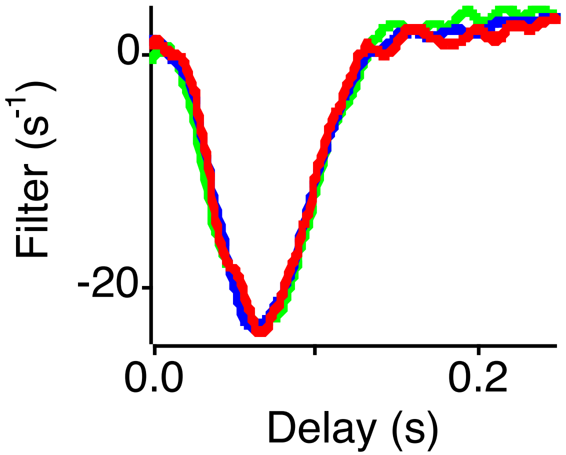


A linear model of the cell's response

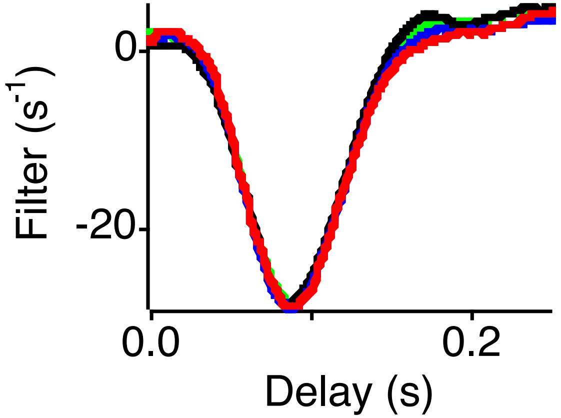


Linear filters in the early visual system

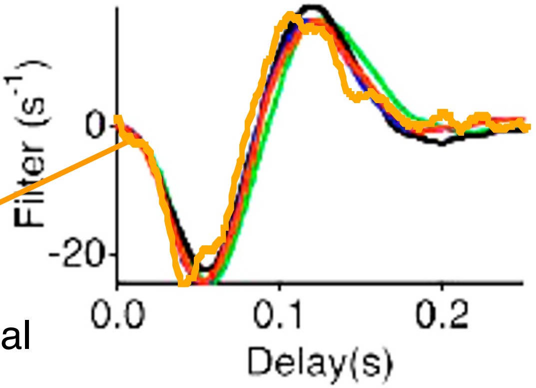
Photoreceptor



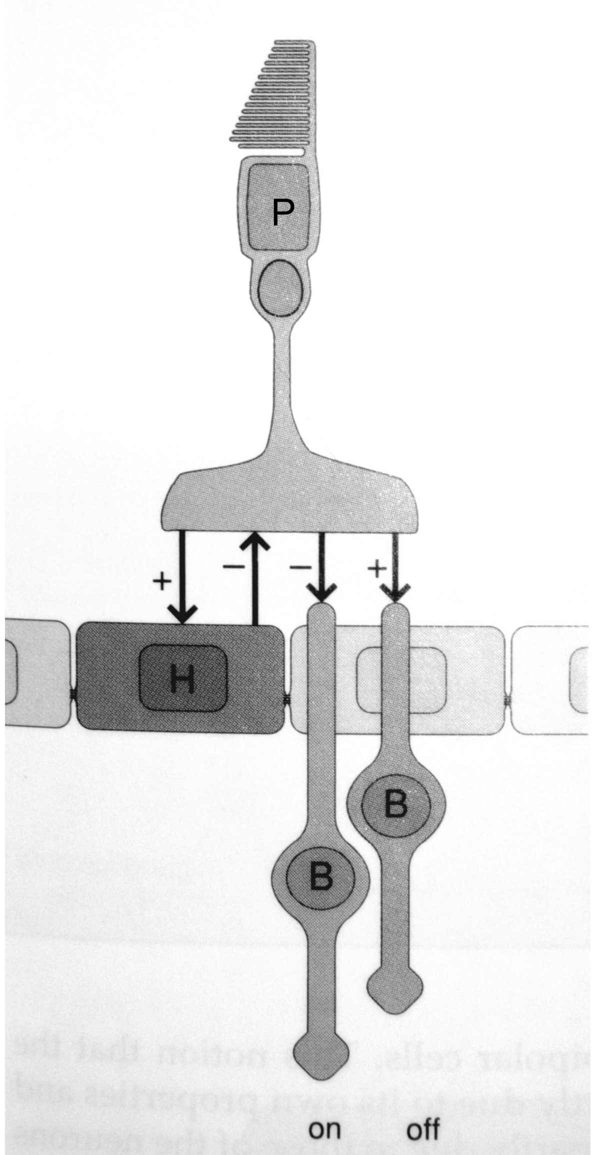
Horizontal cell



Bipolar cell



Weighted sum of Photoreceptor and Horizontal Cell filters

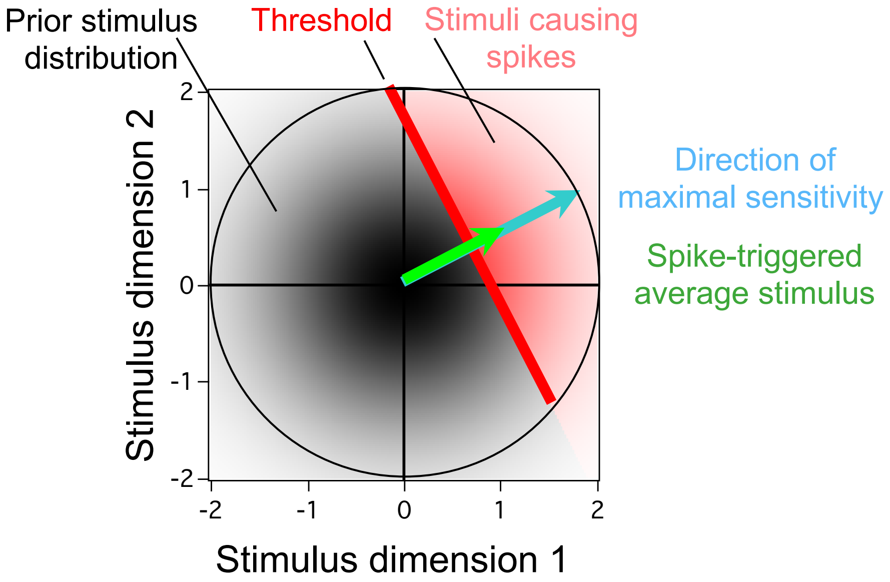


Beyond linear models: are we stuck?

Beyond linear models: are we stuck?

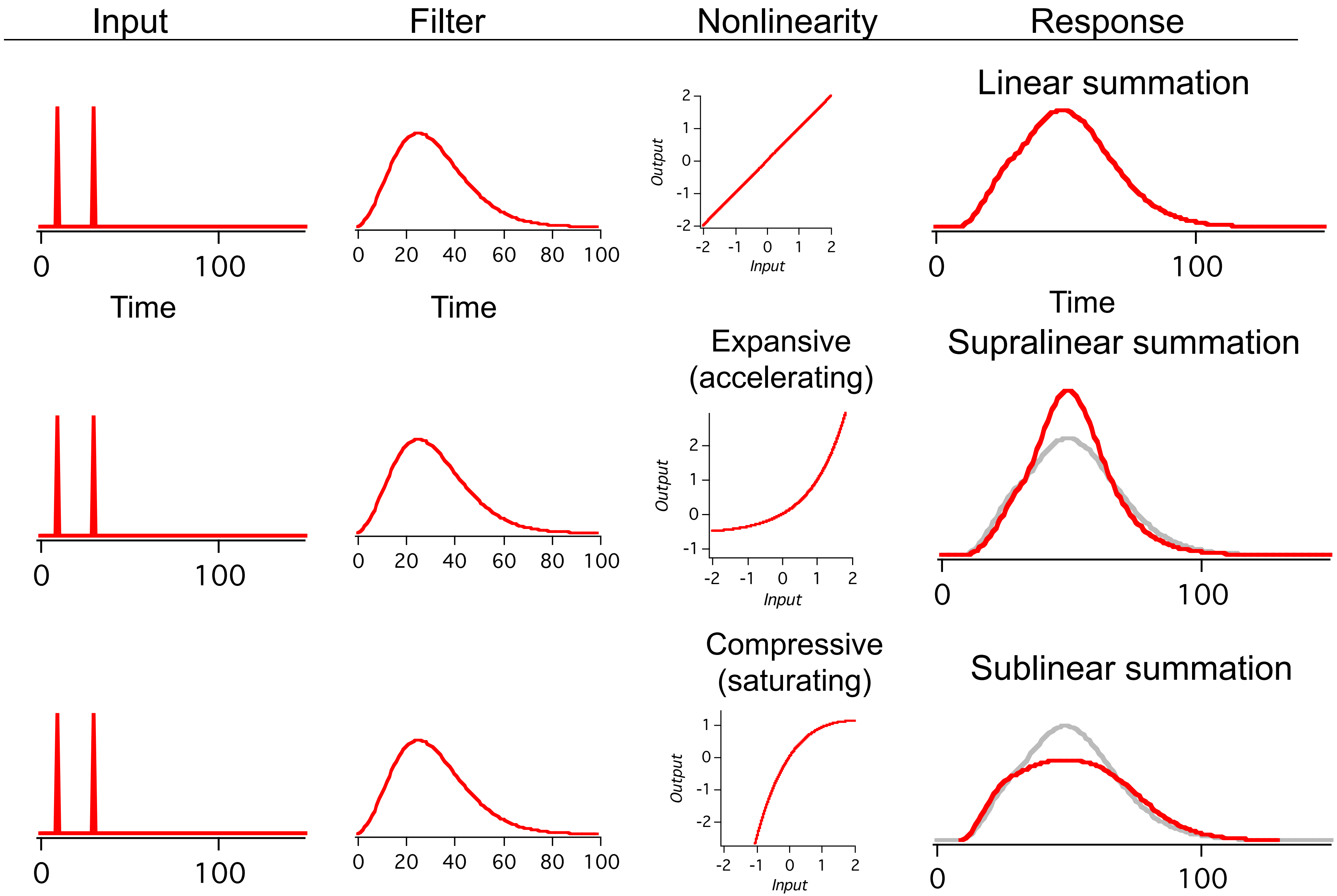
No!

Bussgang's theorem tells us that we can have thresholds and non-linearities and still estimate receptive fields

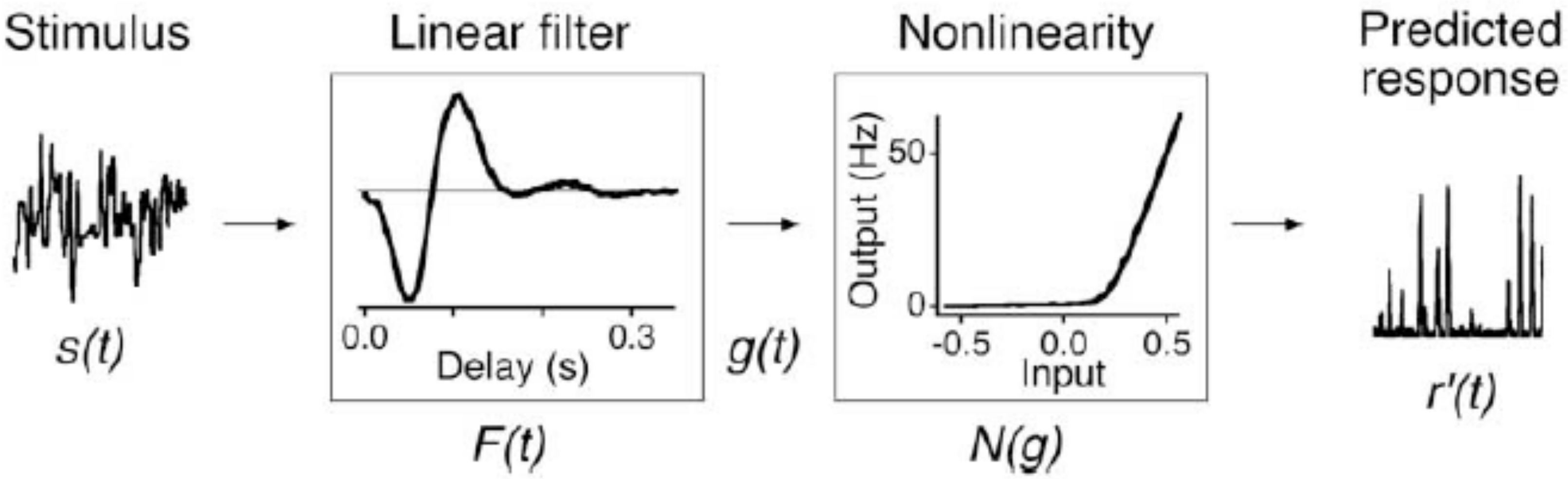


We can estimate receptive field by reverse correlation and then separately estimate non-linearity by regression

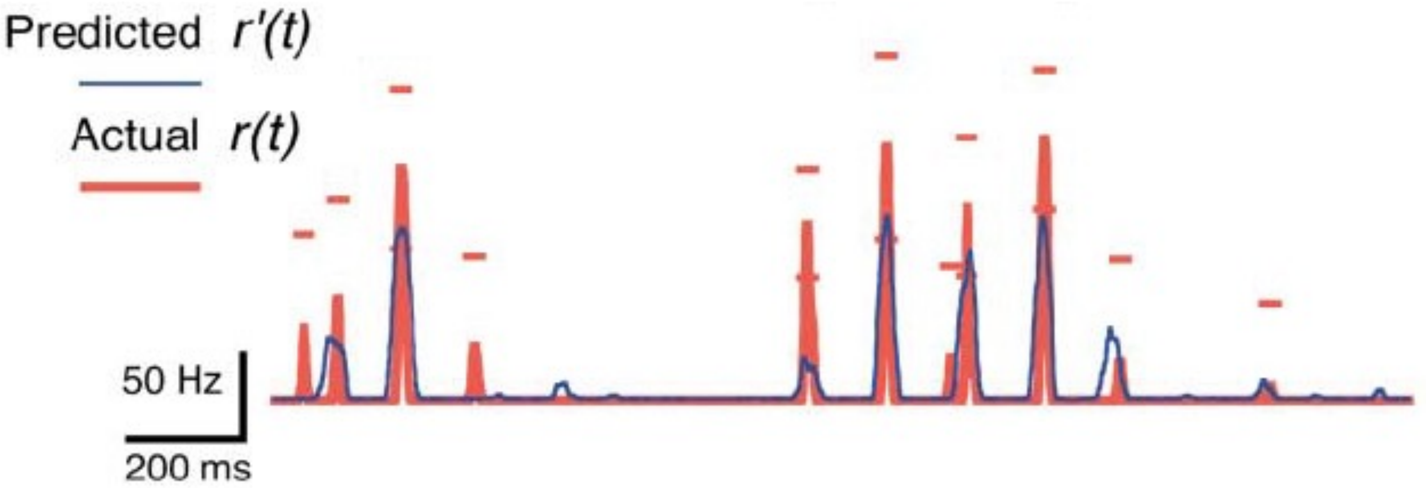
Beyond linear models: linear filter + non-linear transform



Beyond linear models: linear filter + non-linear transform



Retinal ganglion cell firing rate and LN model

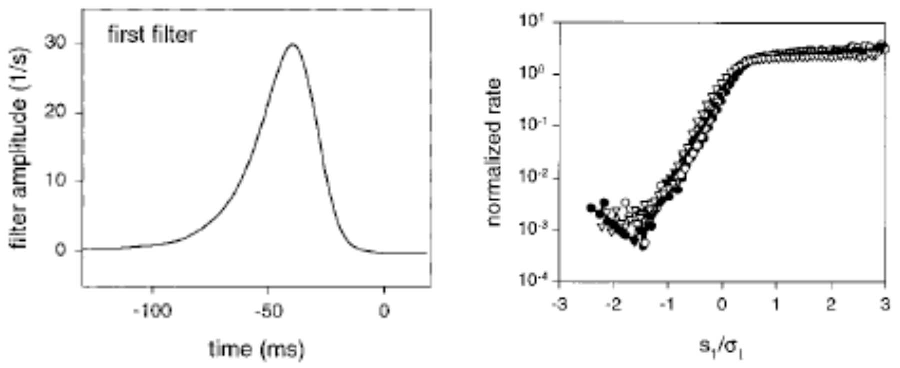


LN models are everywhere

"Filter" Nonlinearity

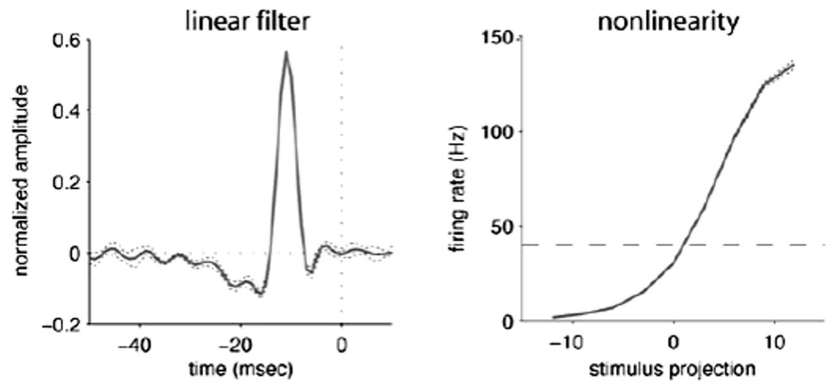
Fly H1 Motion sensitive neuron

Brenner et al., *Neuron* (2000)



Songbird auditory forebrain neuron

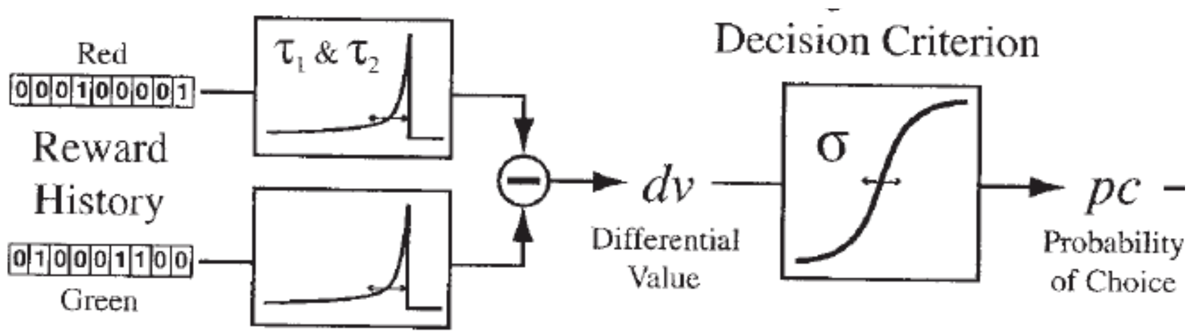
Nagel & Doupe, *Neuron* (2007)



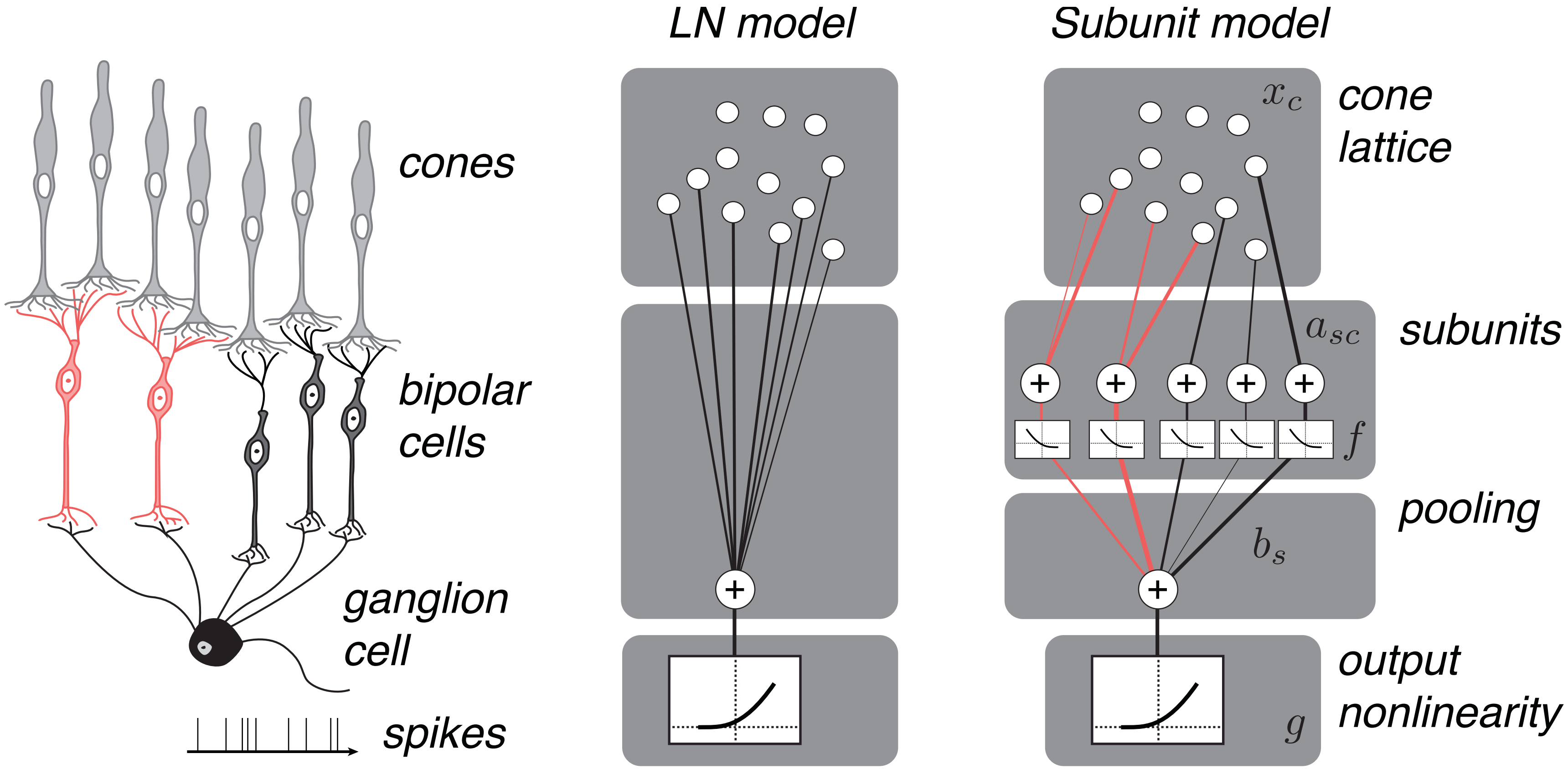
Model of decision making

Corrado, alii et Newsome,

J. Exp. Anal. Behav. (2005)

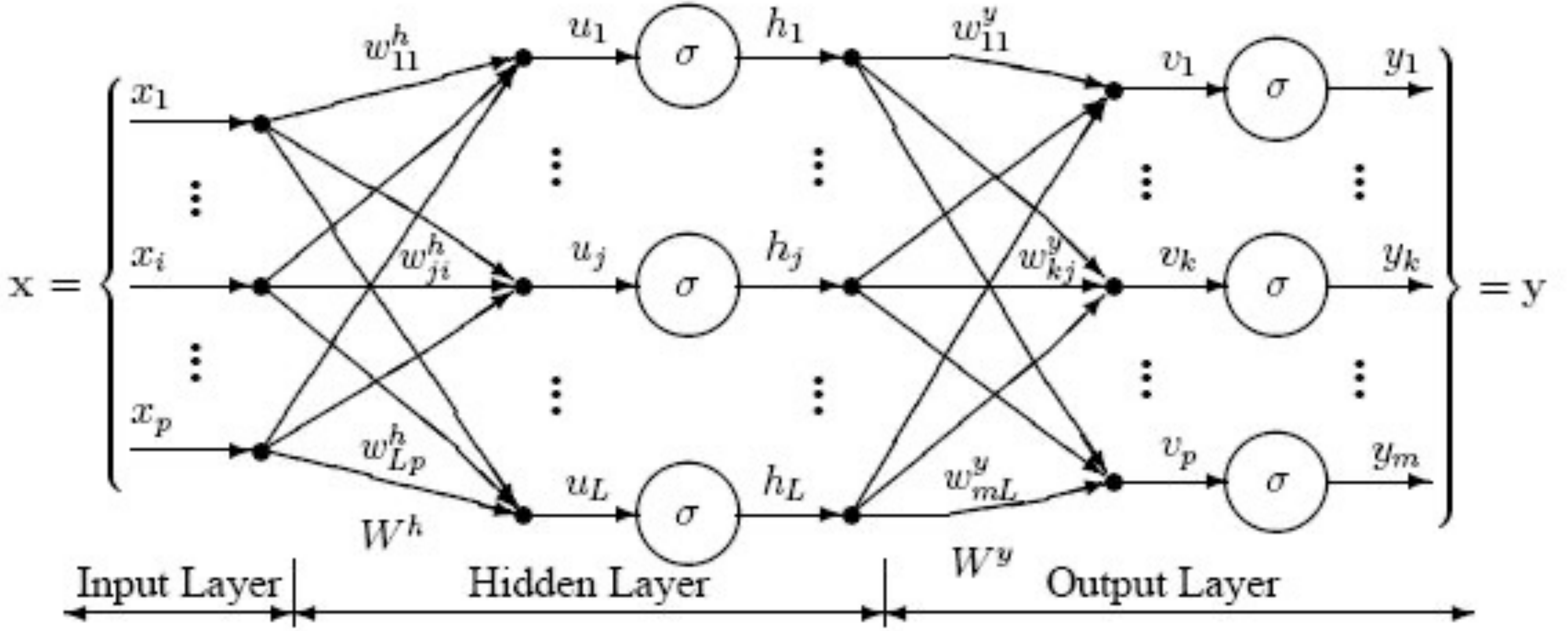


Cascades of LN models in neuroscience

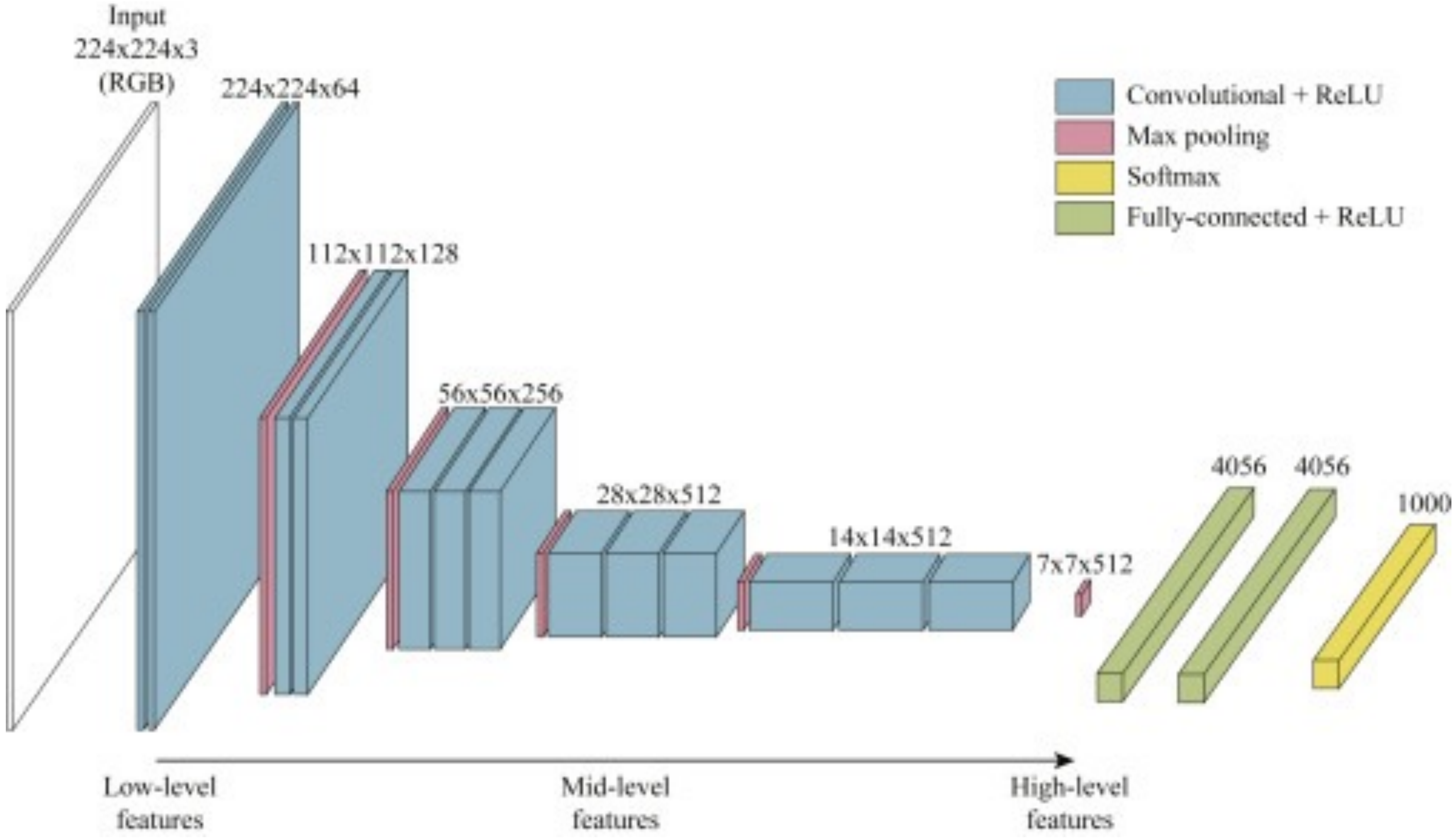


Freeman et al. eLife 2015

Deep neural networks are cascades of LN models



Convolutional neural networks



Summary

We saw how to describe neural responses as a mapping between sensory space and neural activity

We saw how to predict neural responses by extracting a linear filter

Different linear filters represent different processing of stimuli (more on interpreting why a system would use a set of filters next week)

Linear-Nonlinear models are robust models and often the simplest place to start

Cascading nonlinearities can generate complex encoding

Many cellular and circuit mechanisms create these properties, including anatomy, membrane biophysics and synaptic dynamics