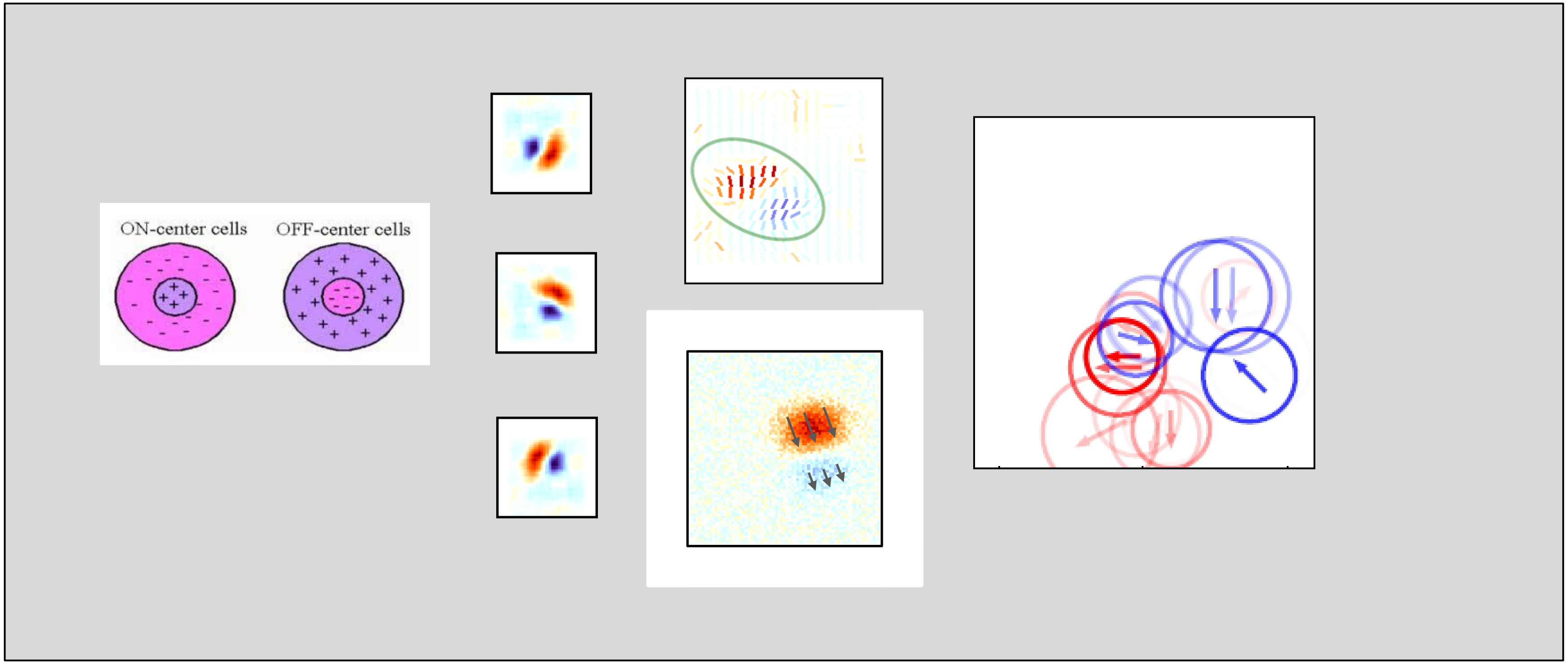
Visual Receptive Fields



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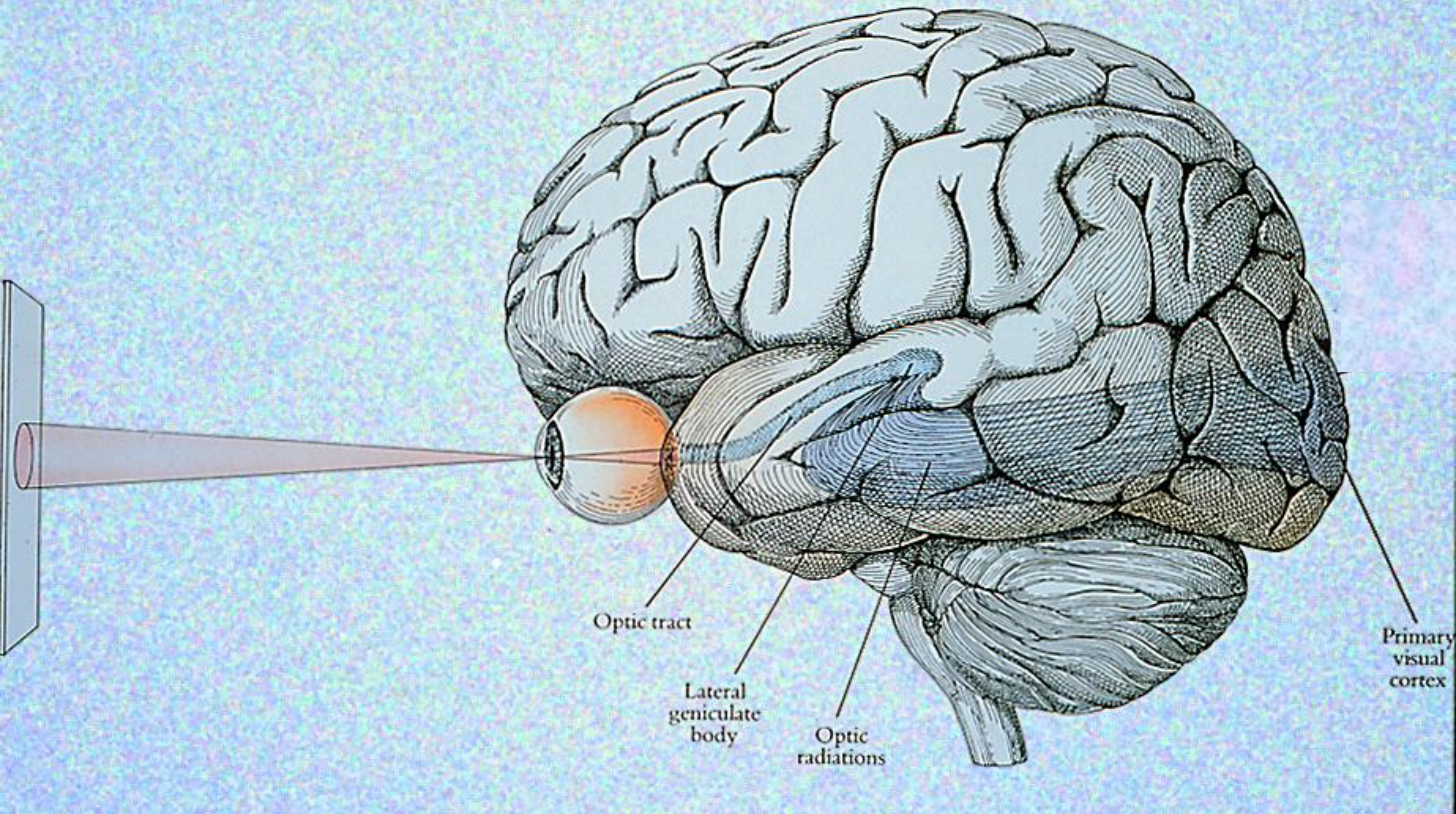
Outline

Introduction to linear systems

Refinement of linear model and applications

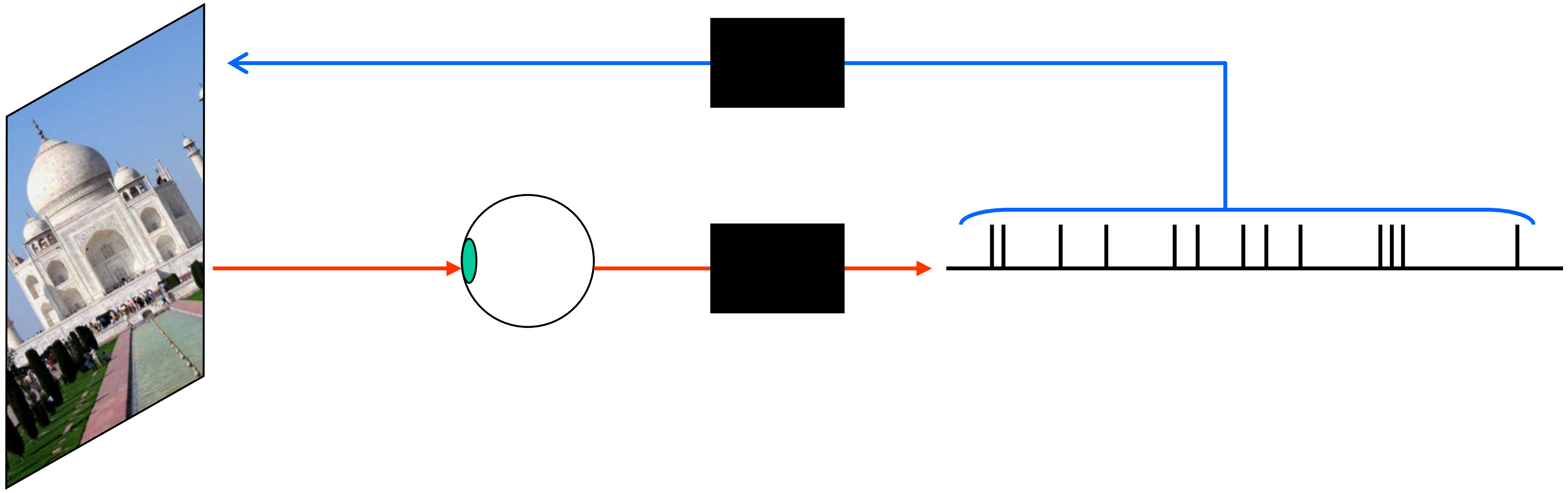
Central Visual Pathways

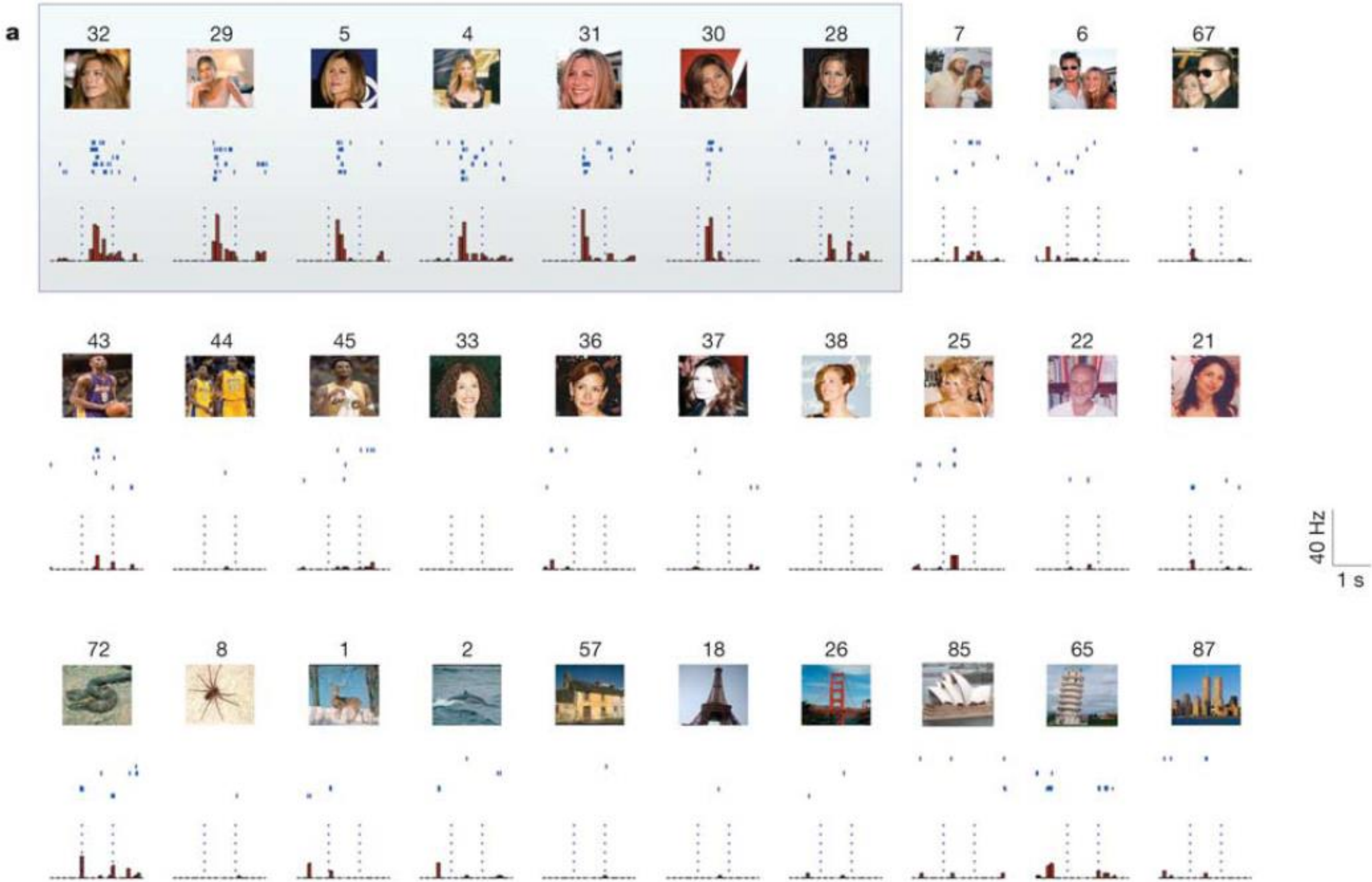


Action Potentials and Spike Trains

Two types of questions for modellers:

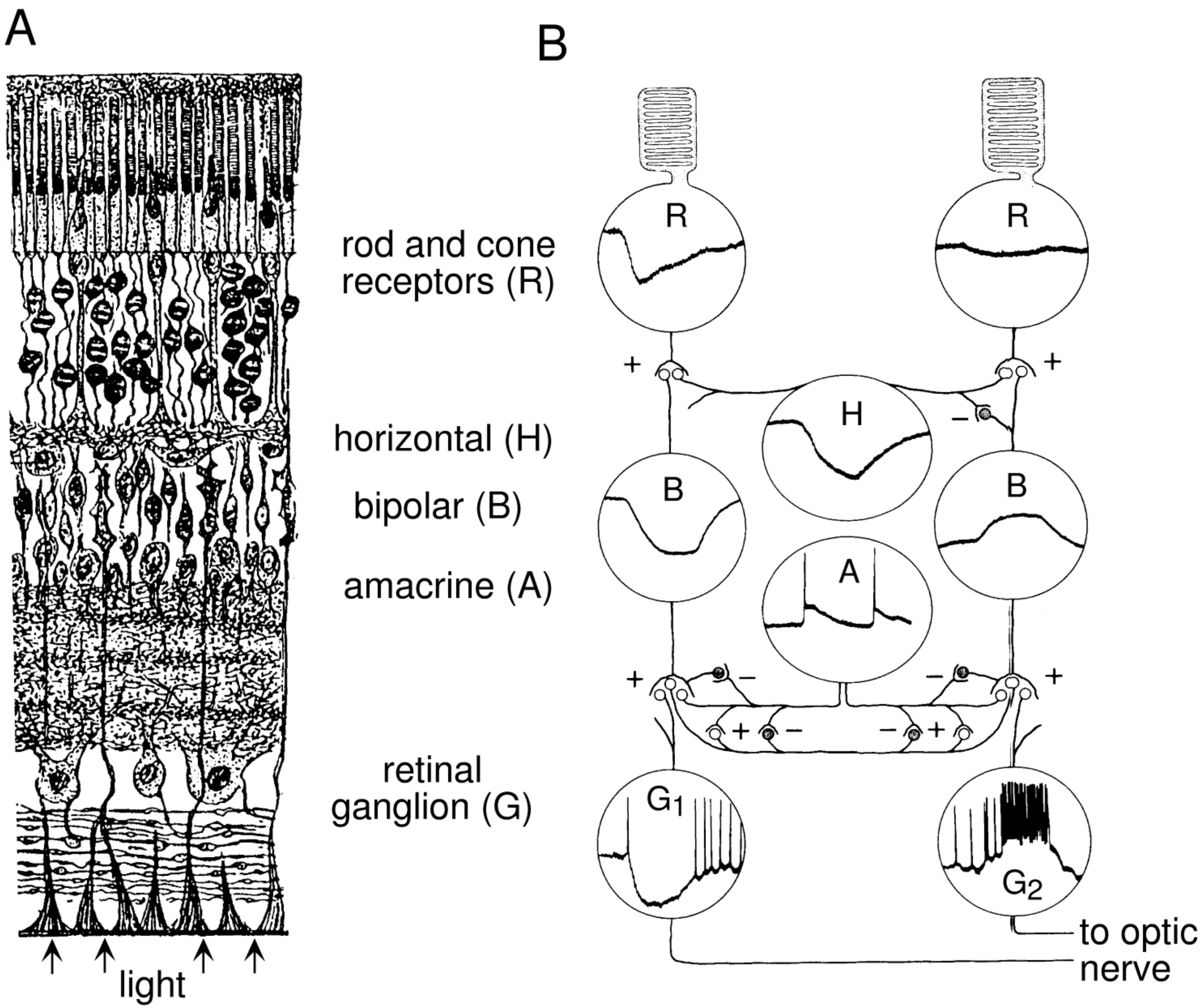
- **Encoding**: If I know the stimulus can I predict the spike train?
- **Decoding**: If I know the spike train, can I figure out what the stimulus was?





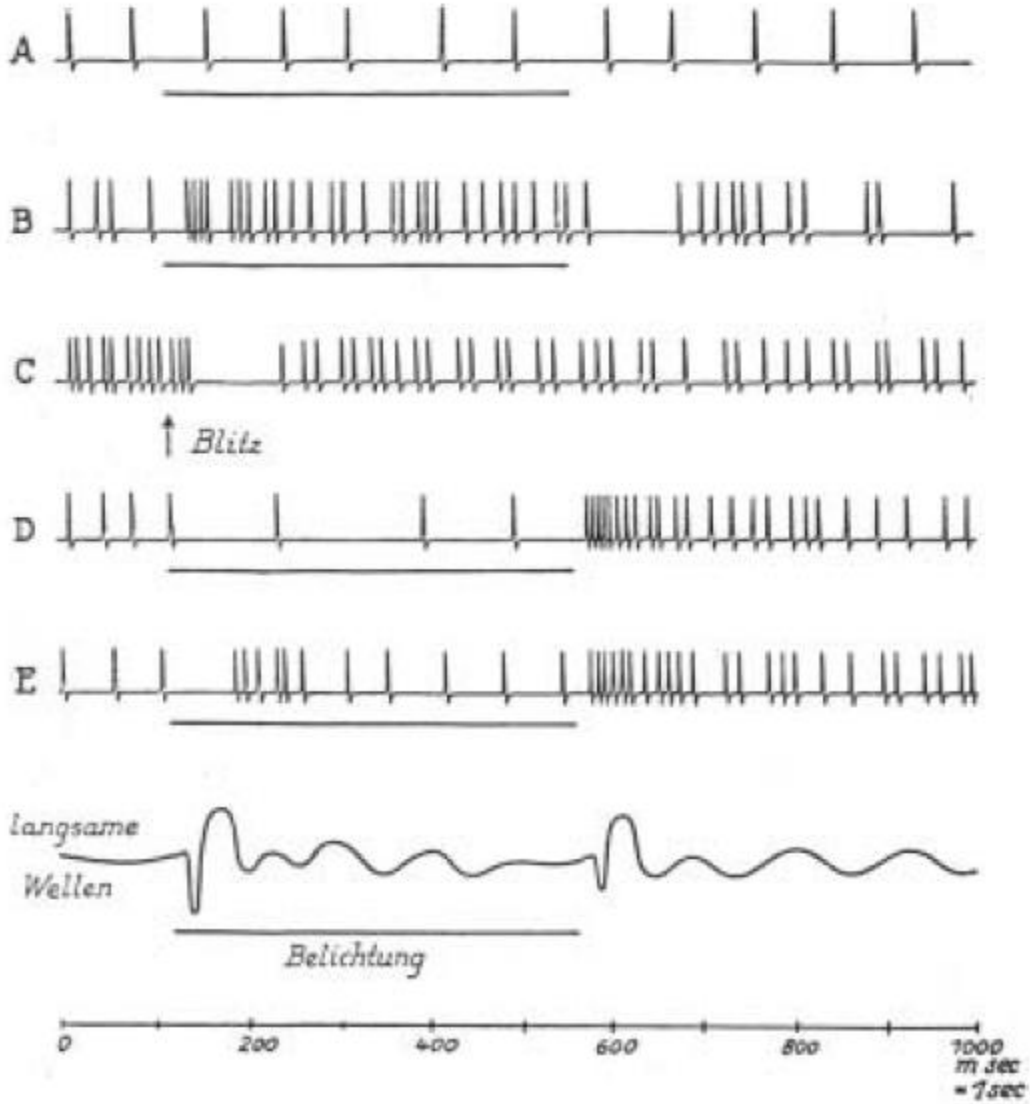
Quiroga et al., Nature, 2005

The Retina



A
B
rod and cone
receptors (R)
horizontal (H)
bipolar (B)
amacrine (A)
retinal
ganglion (G)
light
R
R
H
B
B
A
G_1
G_2
to optic
nerve

Extracellular microelectrode for recording neuronal action potentials



Baumgartner and Jung, 1955

The Retina

The retinal circuit is complicated, but it receives no feedback from the brain. One of its primary functions is to **adapt** to the statistics of the visual input. For example, vision is largely insensitive to the mean luminance in the input. The cortex operates largely on differences in luminance, so that we typically represent the output of the retina by:

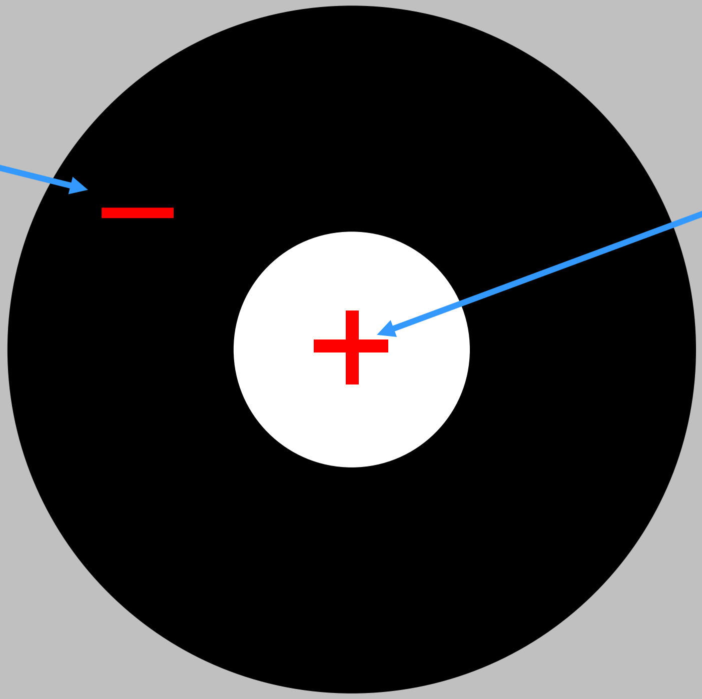
$$s(x, y, t) = I(x, y, t) - \overline{I(x, y, t)}$$

where the average is taken over large extents of space and time.

As a result, the retina is not sensitive to light *per se*, but to patterns of light.

Receptive fields of retinal ganglion cells

Off-surround: The neuron responds to a small spot of light, *if it is darker than the background.*

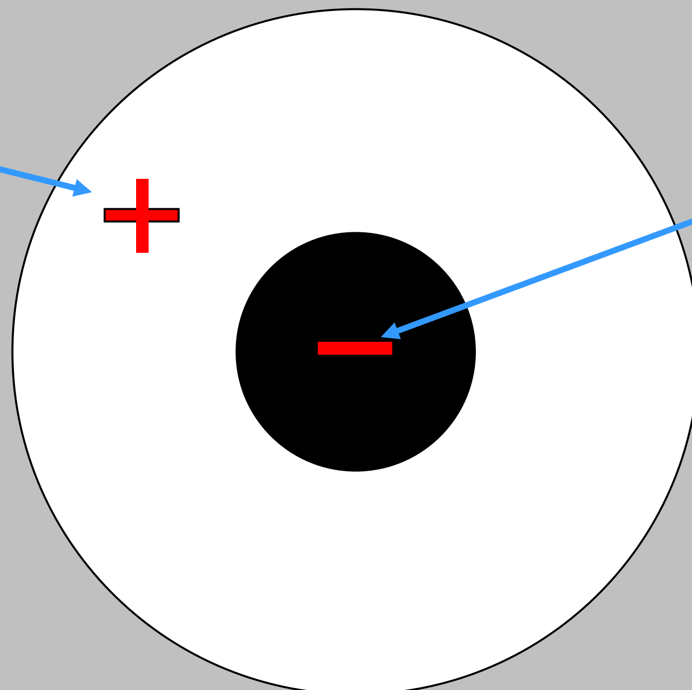


On-center: The neuron responds to a small spot of light, *if it is brighter than the background.*

This is the receptive field of an **on-center, off-surround** retinal ganglion cell.

Receptive fields of retinal ganglion cells

On-surround: The neuron responds to a small spot of light, *if it is lighter than the background.*



Off-center: The neuron responds to a small spot of light, *if it is darker than the background.*

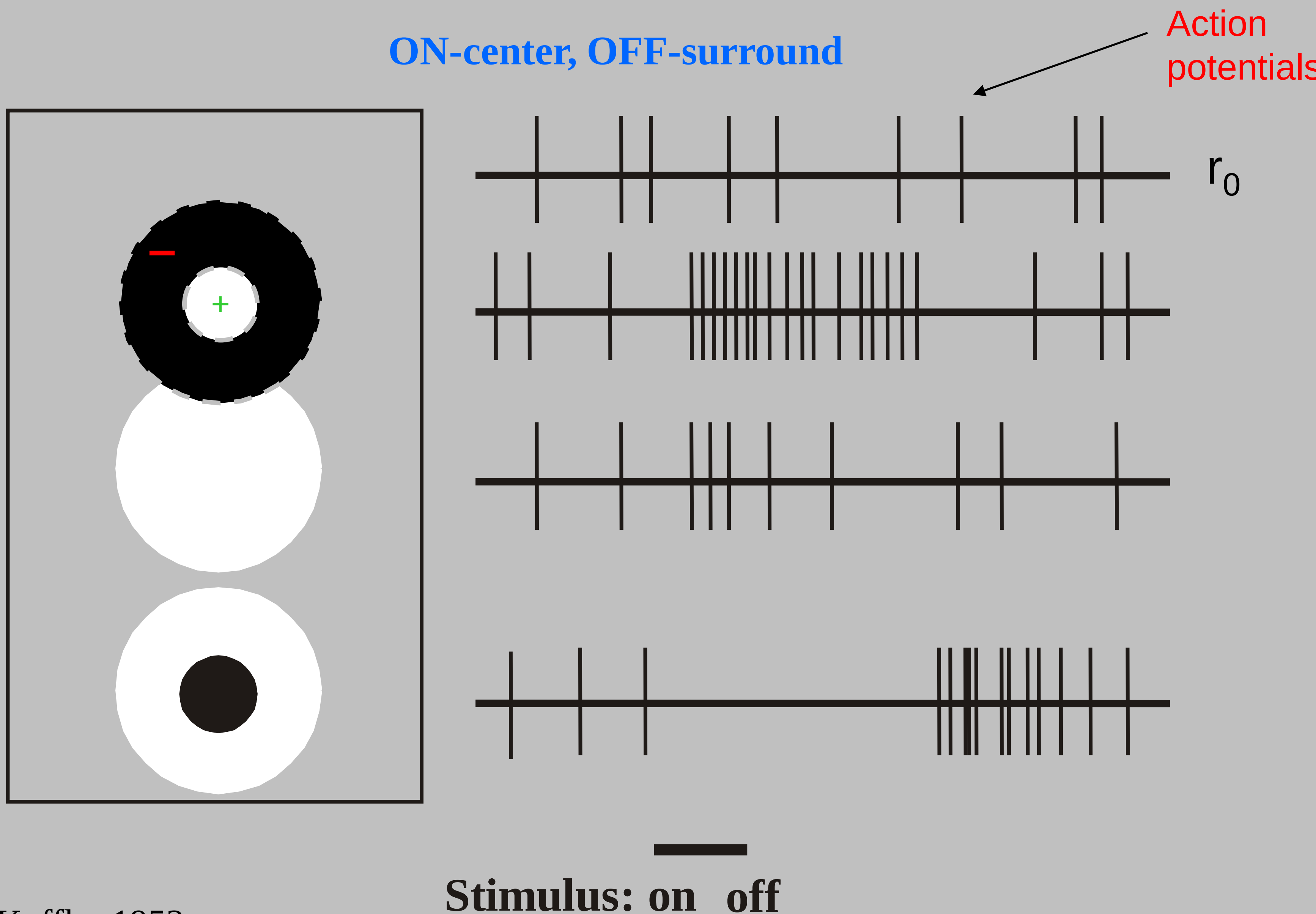
This is the receptive field of an **off-center, on-surround** retinal ganglion cell.

Wiesel Hubel

Hubel/Wiesel movie #1

Retinal Ganglion Cells are the output of the retina

ON-center, OFF-surround

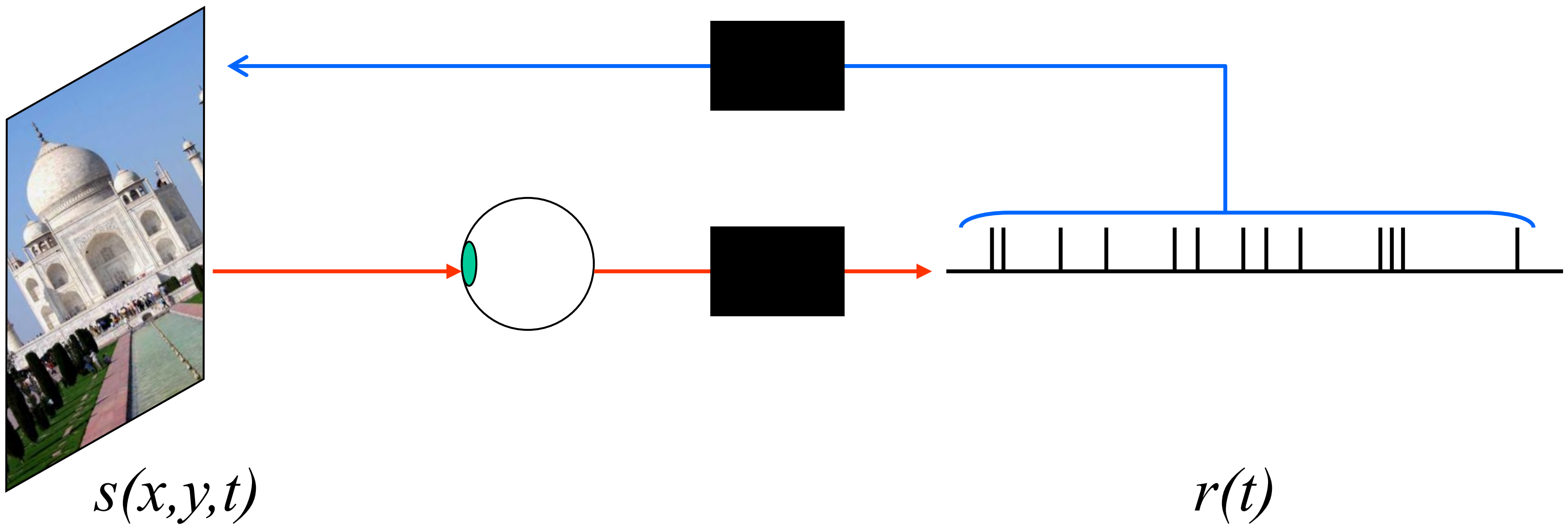


Kuffler 1953

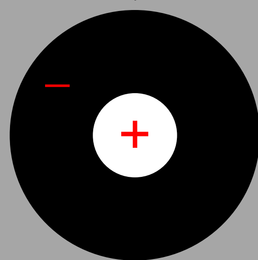
Action Potentials and Spike Trains

Two types of questions for modellers:

- **Encoding**: If I know the stimulus can I predict the spike train?
- **Decoding**: If I know the spike train, can I figure out what the stimulus was?



Receptive field as spatial filter



0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

0 0 0 0 0 0 0 -1 -1 -1 0 0 0 0 0 0 0 0

0 0 0 0 0 0 -1 -1 -1 -1 -1 0 0 0 0 0 0

0 0 0 0 -1 -1 -1 -1 -1 -1 -1 -1 0 0 0 0

0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0

0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0

0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0

0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0

0 0 0 0 0 0 -1 -1 -1 -1 -1 -1 0 0 0 0 0

0 0 0 0 0 0 0 -1 -1 -1 -1 0 0 0 0 0 0 0 0

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

Let's call this *h(x,y)*. The neuron responds when the stimulus matches its receptive field. Or more precisely, the neuron computes the degree of ***correlation*** between the stimulus and the receptive field.

Correlation

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 0 0 0 0 0 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 0 0 0 0 0 0
0 0 0 0 -1 -1 -1 -1 -1 -1 -1 -1 0 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 -1 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 -1 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

$$c = \sum_i s_i h_i$$

Normalization

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 0 0 0 0 0 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 0 0 0 0 0 0
0 0 0 0 -1 -1 -1 -1 -1 -1 -1 -1 0 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 -1 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 -1 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

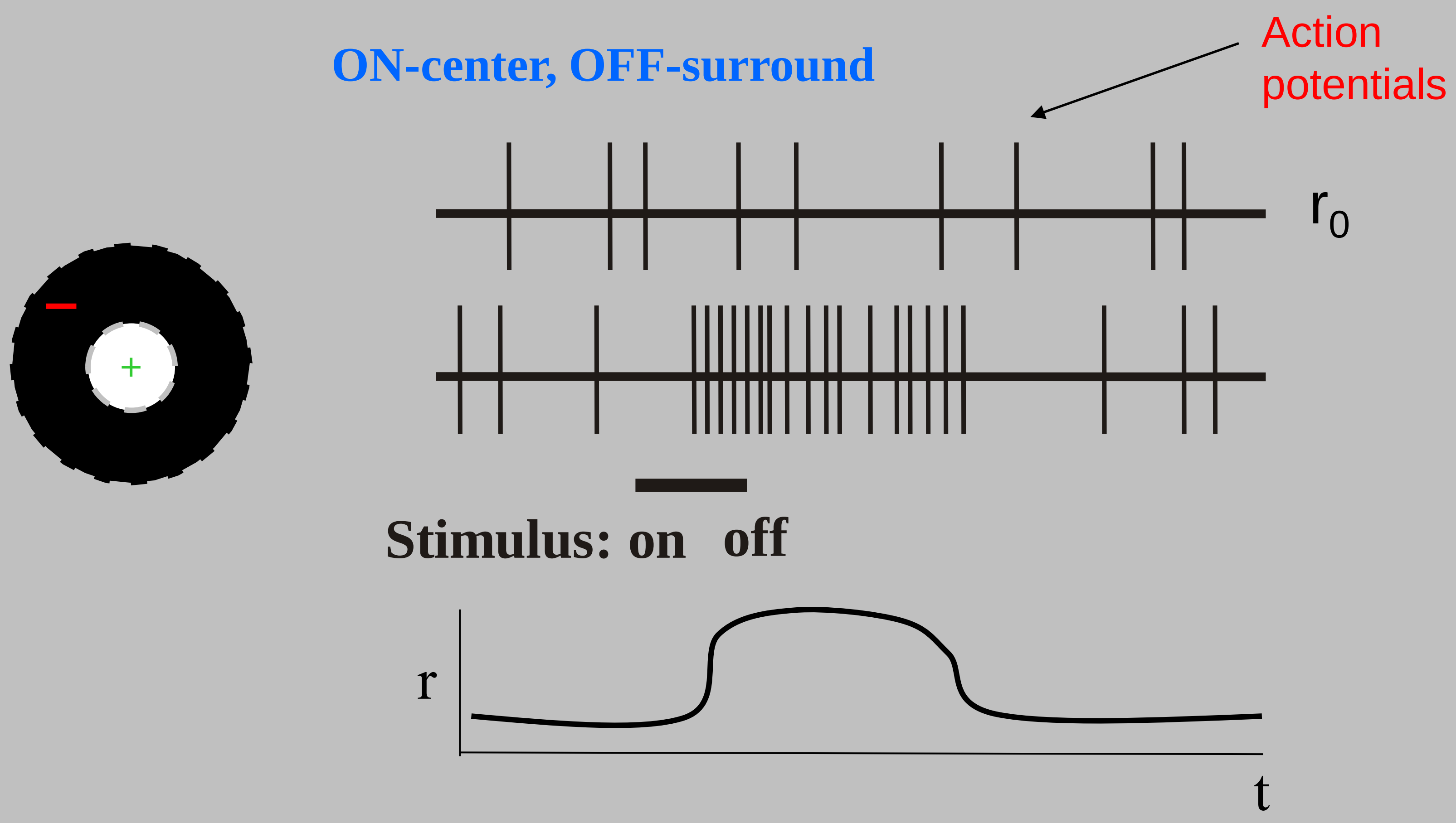
$$c = \sum_i s_i h_i$$

(raw correlation)

$$\hat{c} = \frac{\sum_i s_i h_i}{\|s\|\|h\|}$$

(normalized correlation)

Receptive field as temporal filter



Notice that the response is delayed and that it lasts longer than the stimulus, which is very brief. We call this the ***impulse response***.

Receptive fields in space and time

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

0 0 0 0 0 0 0 -1 -1 -1 0 0 0 0 0 0 0 0

0 0 0 0 0 0 -1 -1 -1 -1 -1 0 0 0 0 0 0

0 0 0 0 -1 -1 -1 -1 -1 -1 -1 -1 0 0 0 0

0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0

0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0

0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0

0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0

0 0 0 0 0 0 -1 -1 -1 -1 -1 -1 0 0 0 0 0

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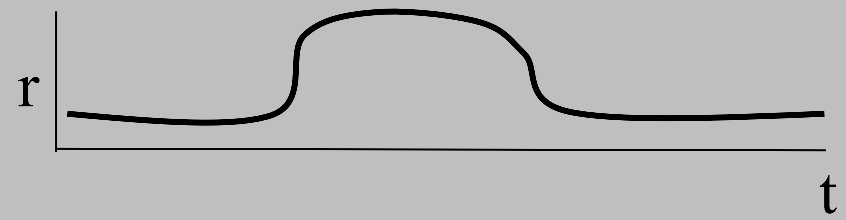
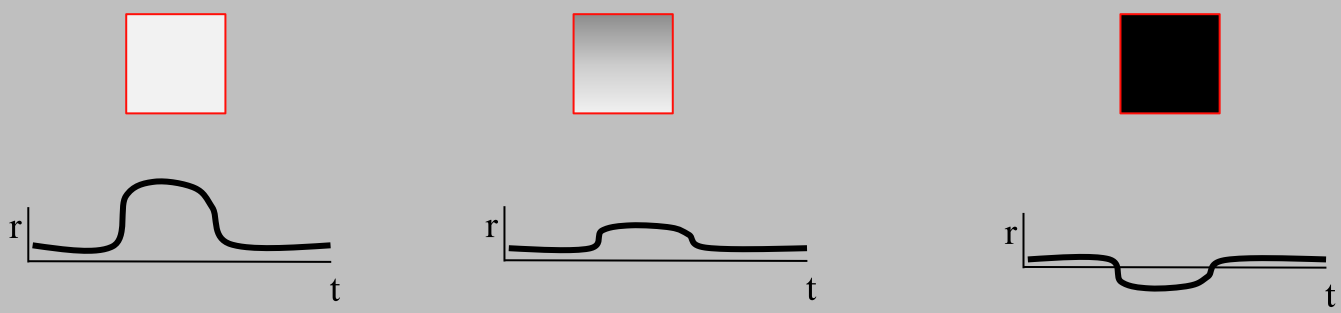
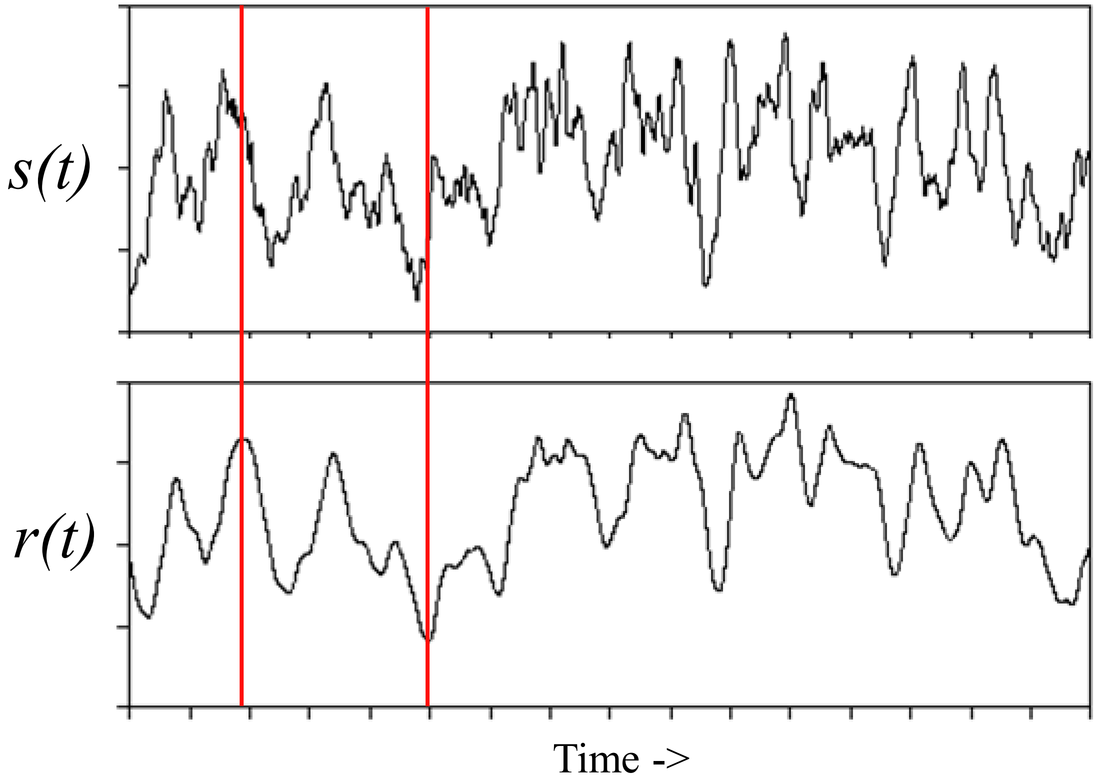


So the receptive field is really two things: A spatial filter and an impulse response. For simplicity, we treat these as *separable*, meaning that we can study the spatial and temporal parts independently. A separable model has the form h(x,y)*h(t).



We’ll consider the temporal part first…



Again notice:

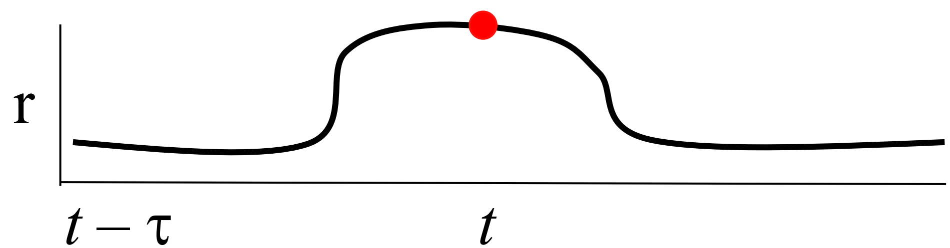
1. The neuron (obviously) responds to stimuli that occurred in the past (i.e. there is a delay).
2. The neural response changes more slowly than the stimulus. This is due to the sluggish impulse response we saw before.

Linear systems

The output of a linear system, for any input, is given by **convolution**:

$$r(t) = \sum_{\tau} s(t-\tau)h(\tau)$$

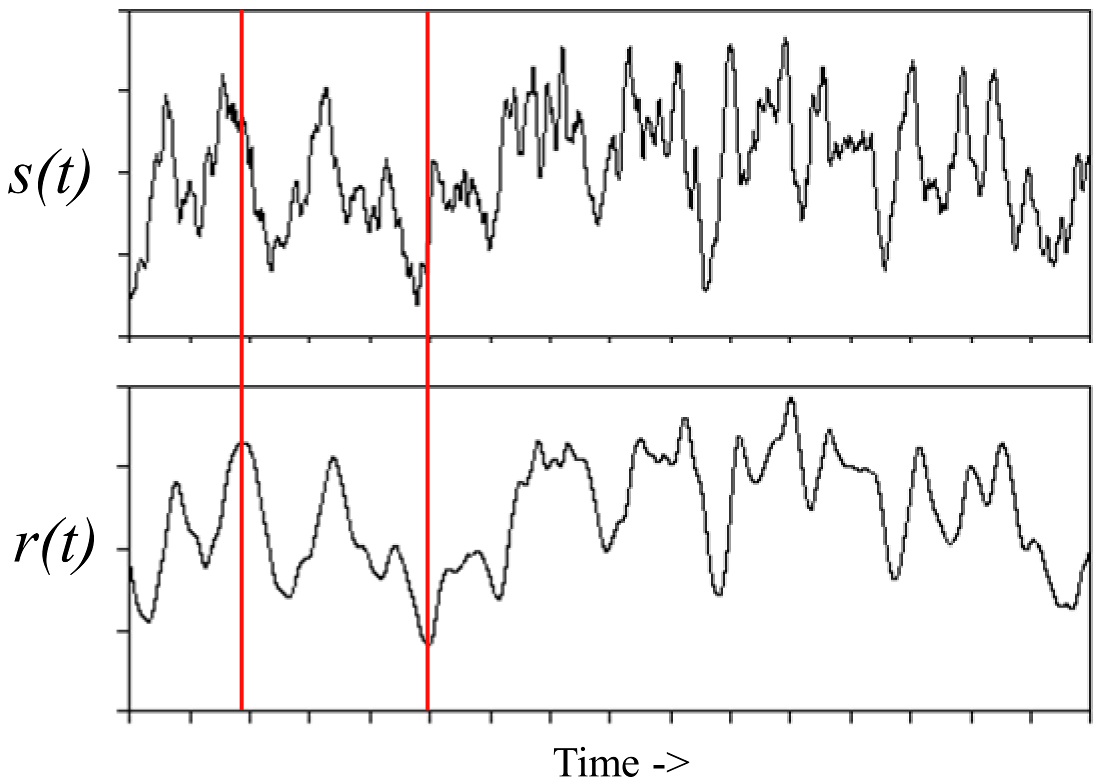
This is a very useful operation. Intuitively, imagine that at time *t*, the stimulus had a certain intensity τ time steps in the past. That caused the impulse response to happen:



So now at time *t*, we observe the response to this stimulus (red dot). But we are also observing all the other responses to all the other stimuli that occurred at different values of τ. The neuron just adds them up (hence the summation over τ), and that is the total response we observe at time *t*.

Question: How do we recover the impulse response *h(τ)*?

Cross-correlation



$$Q(\sigma) = \frac{1}{T}\sum_t s(t-\sigma)r(t)$$

Now let's take our linear model of the neuron:

$$r(t) = \sum_{\tau} s(t-\tau)h(\tau)$$

And plug it into our cross-correlation:

$$\mathrm{Q}(\sigma) = \frac{1}{T}\sum_{t} s(t-\sigma)r(t)$$

This yields:

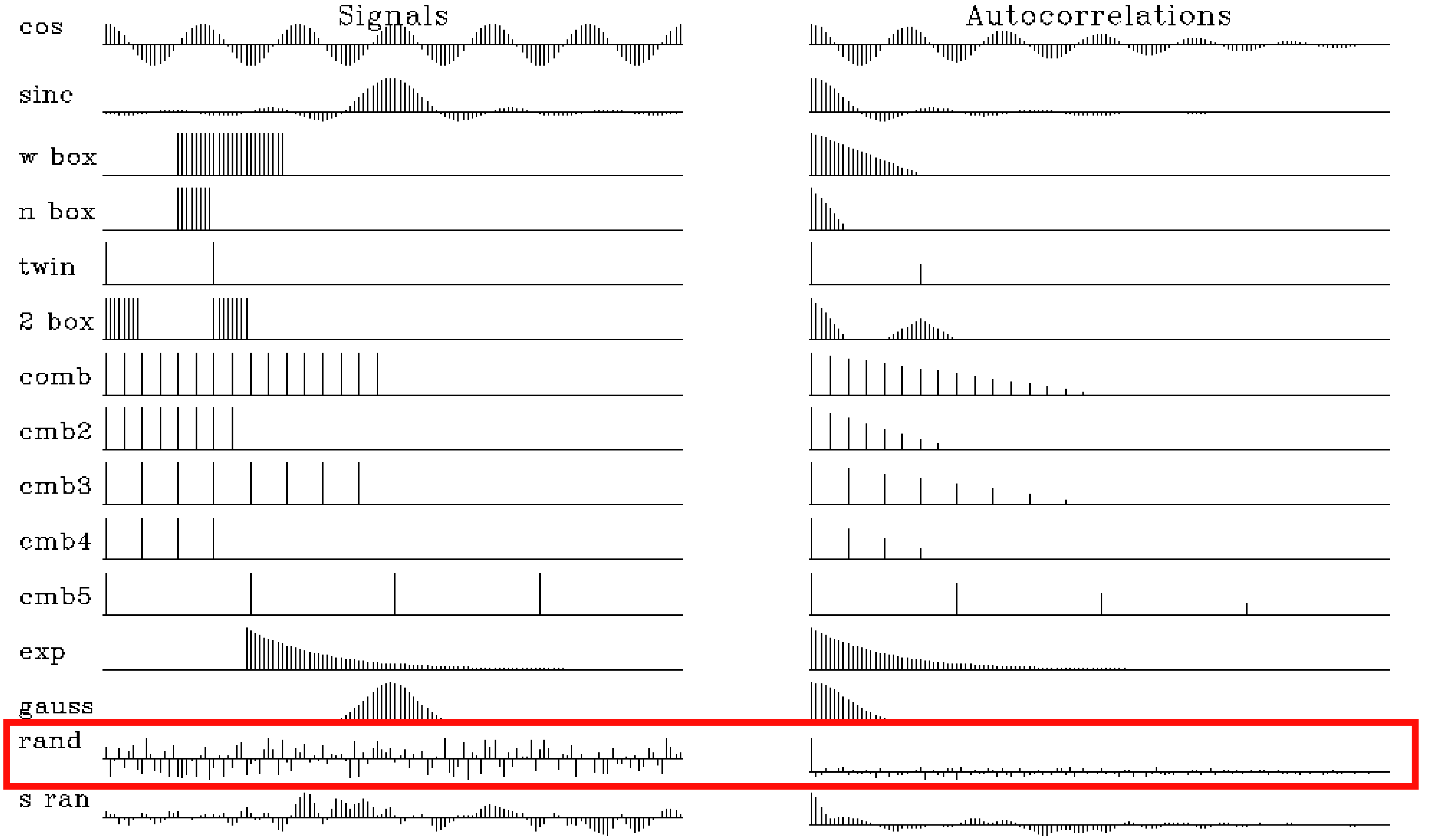
$$\mathrm{Q}(\sigma) = h(\tau)\boxed{\sum_{t} s(t-\sigma)s(t-\tau)}$$

Autocorrelation

Autocorrelation is the cross-correlation of a function with itself:

$$A(\mu) = \sum_{t} s(t)s(t-\mu)$$

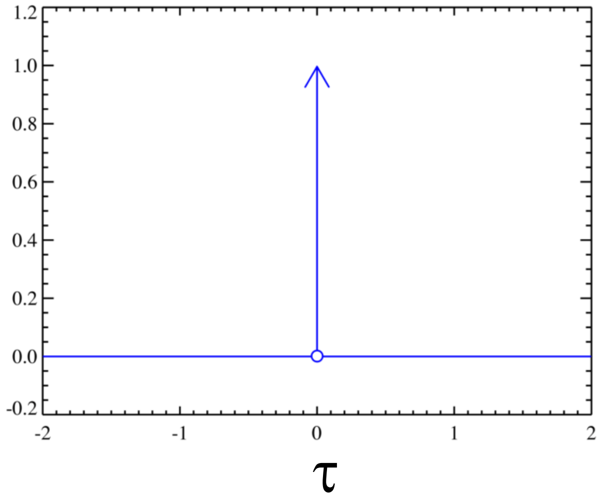
Autocorrelation



Dirac Delta Function

The Delta function takes a constant value at τ = 0 and is 0 everywhere else:

$$\delta(\tau) = \begin{cases} c, & \tau = 0 \\ 0, & \tau \neq 0 \end{cases}$$



The autocorrelation of a random sequence is a delta function.

Now let's take our linear model of the neuron:

$$r(t) = \sum_\tau s(t-\tau)h(\tau)$$

And plug it into our cross-correlation:

$$\mathrm{Q}(\sigma) = \frac{1}{T}\sum_t s(t-\sigma)r(t)$$

This yields:

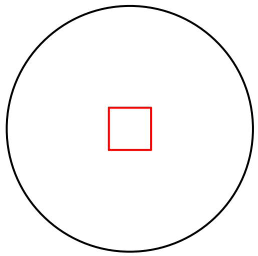
$$\mathrm{Q}(\sigma) = h(\tau)\boxed{\sum_t s(t-\sigma)s(t-\tau)}$$

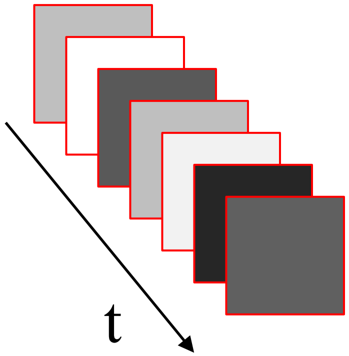
If s is a random function, the autocorrelation is zero, except when $\sigma = \tau$, so in this case we have:

$$\mathrm{Q}(\sigma) \propto h(\tau)$$

Surprising result: If you want to understand visual receptive fields, probe them with random stimuli.

In practice, one can estimate the receptive field position crudely and then probe it more precisely at a spot:





According to the assumptions we have made (linearity, separability), this will be sufficient to recover the temporal impulse response.

Summary and conclusions

We can model receptive fields by assuming that the spatial and temporal responses are separable and linear.

In that case, we can study them by using stimuli that are **random**.

If the stimulus is random, then the temporal response is just the (normalized) cross-correlation between the input and the output.

From there, the spatial part is easy…

Linear systems

The output of a linear system, for any input, is given by **convolution**:

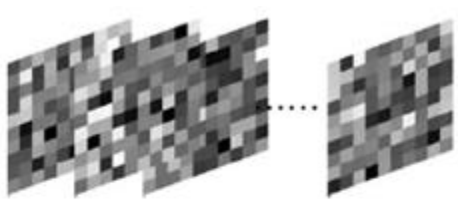
$$r(t) = \sum_\tau s(t-\tau)h(\tau)$$

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 0 0 0 0 0 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 0 0 0 0 0 0
0 0 0 0 -1 -1 -1 -1 -1 -1 -1 -1 0 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 -1 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 -1 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

From the linearity assumption, we can treat the receptive field as a collection of points, each of which elicits a temporal impulse response when stimulated:

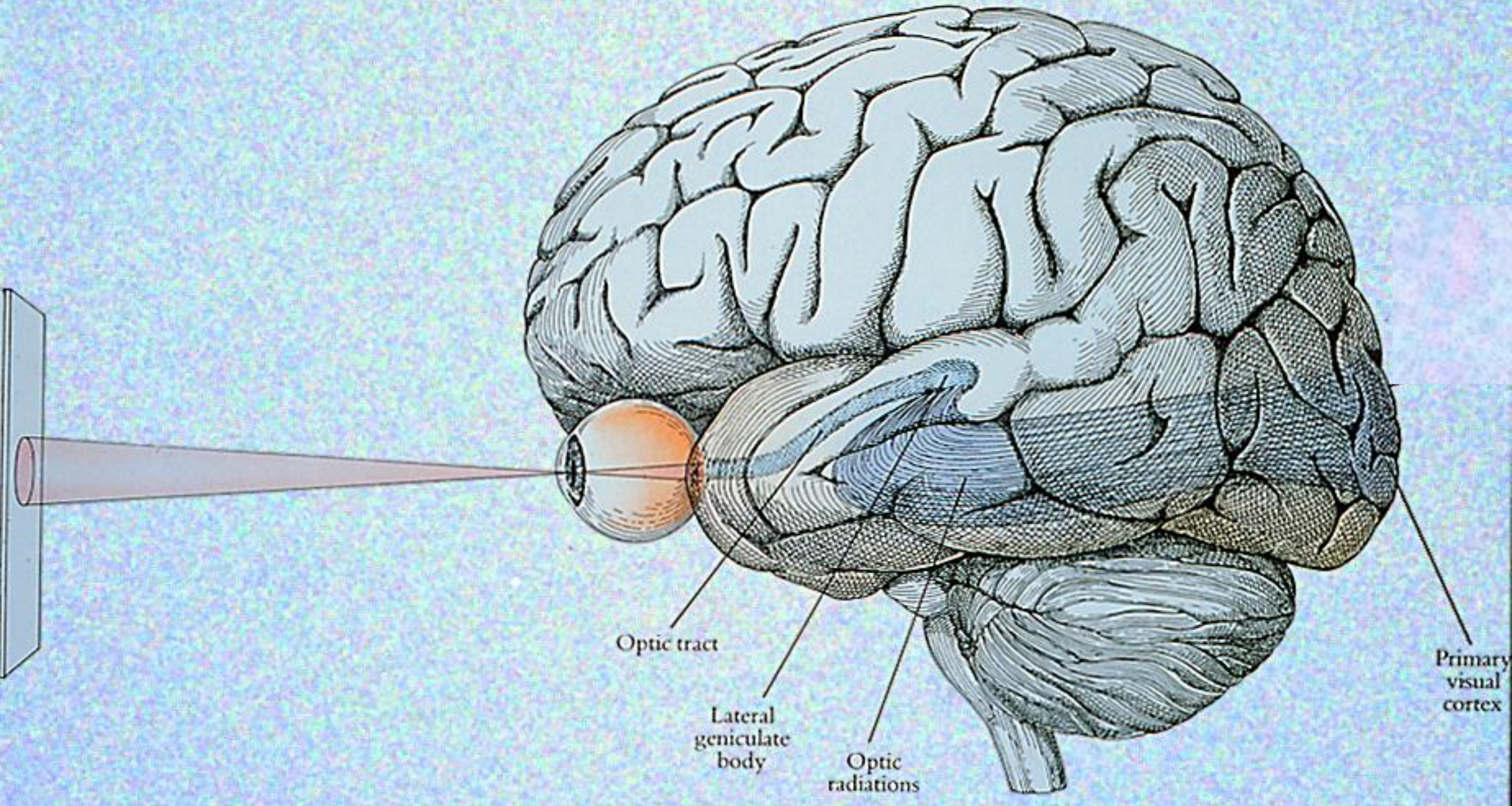
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 0 0 0 0 0 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 0 0 0 0 0 0
0 0 0 0 -1 -1 -1 -1 -1 -1 -1 -1 0 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 +1 +1 +1 +1 -1 -1 0 0 0
0 0 0 0 -1 -1 -1 +1 +1 -1 -1 -1 0 0 0
0 0 0 0 0 0 -1 -1 -1 -1 -1 -1 0 0 0 0 0
0 0 0 0 0 0 0 -1 -1 -1 -1 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

Because they are independent, we can stimulate all the points at once:

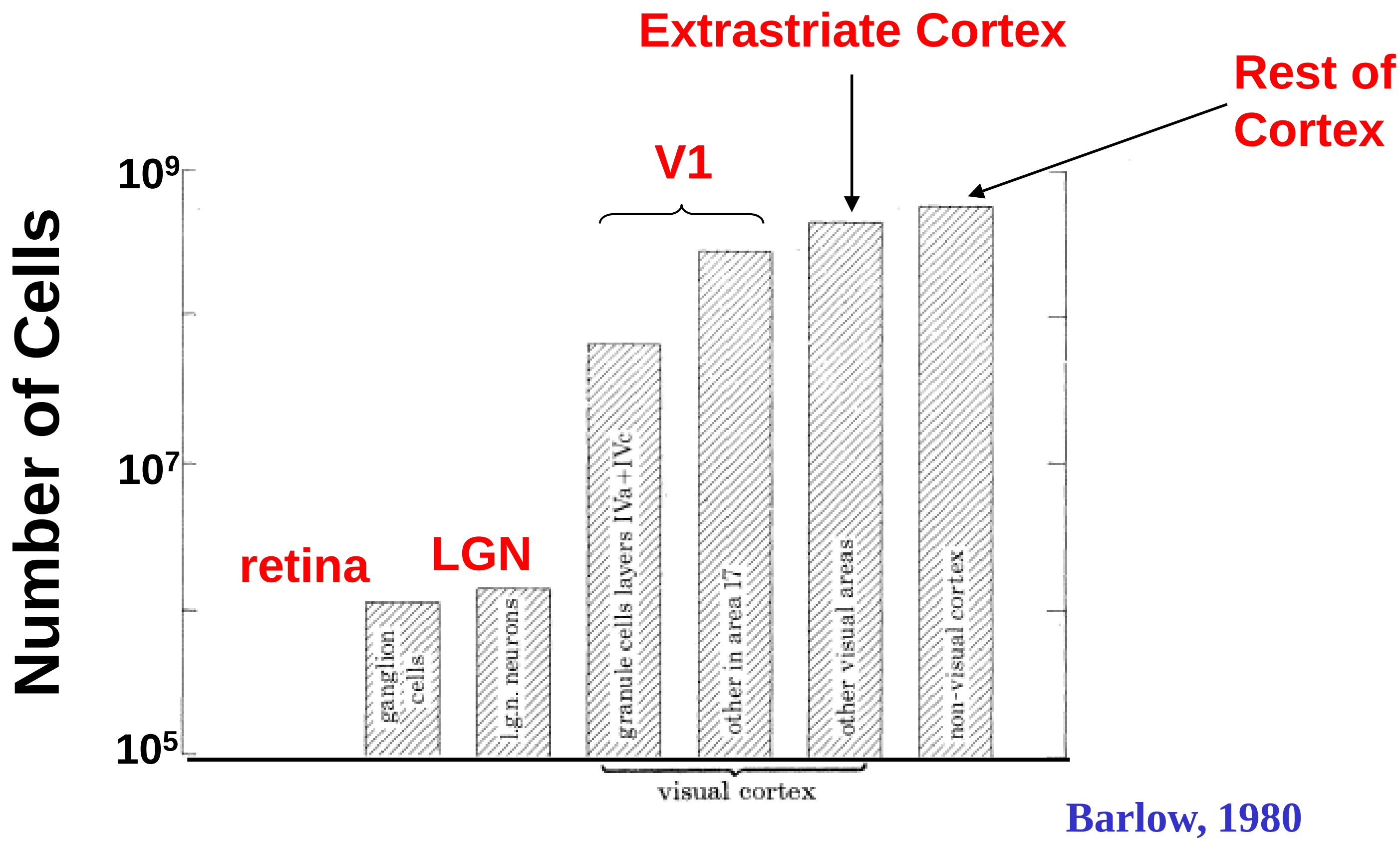


If the stimuli are all random and uncorrelated with each other, we can still recover the spatial and temporal receptive field using cross-correlation. More on this later..

Central Visual Pathways

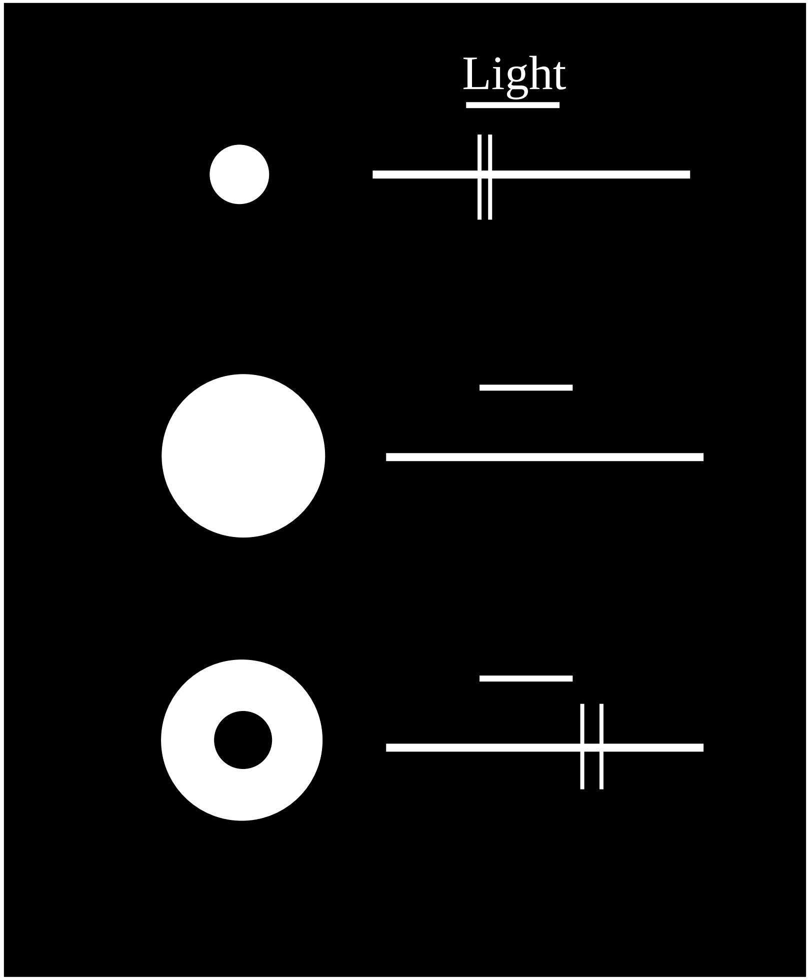


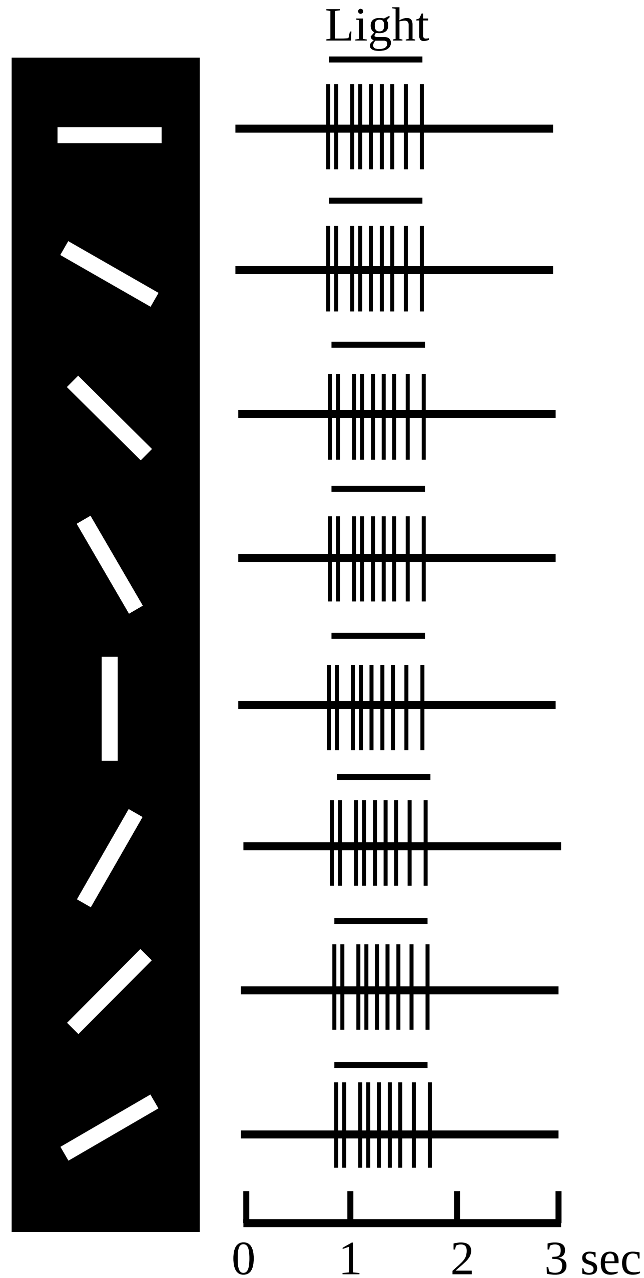
Neurons in the Visual Pathway



The number of neurons increases by a factor of ~200 from the retina/LGN to the visual cortex.
About 50% of all cortical neurons are involved in vision.

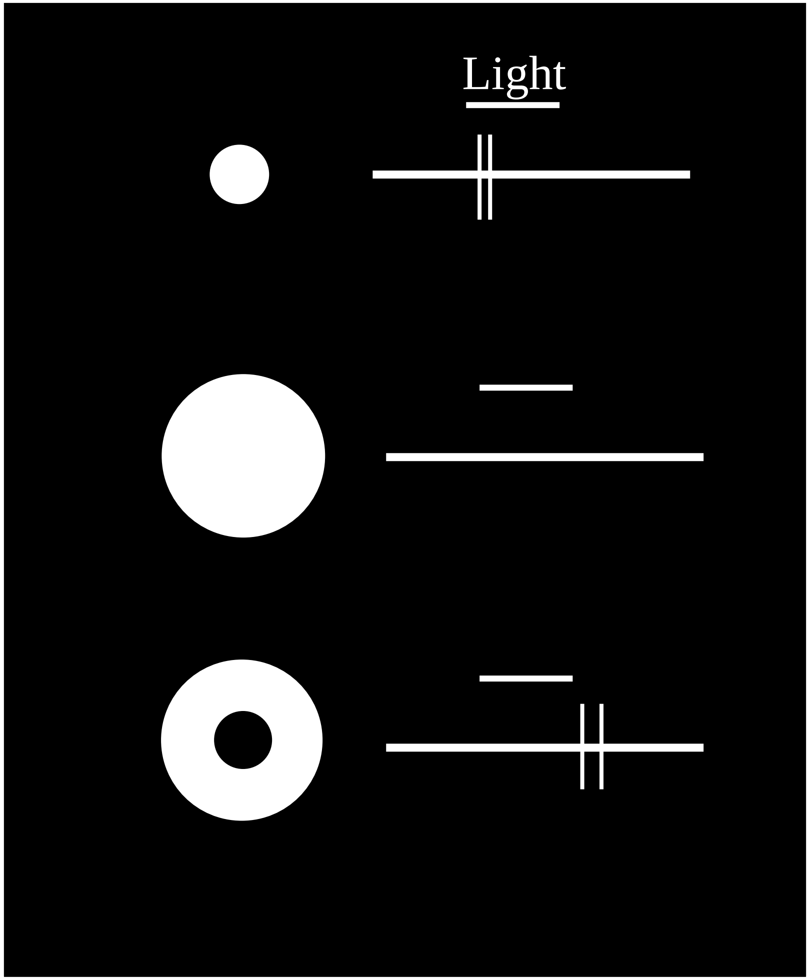
Neuronal responses in the LGN



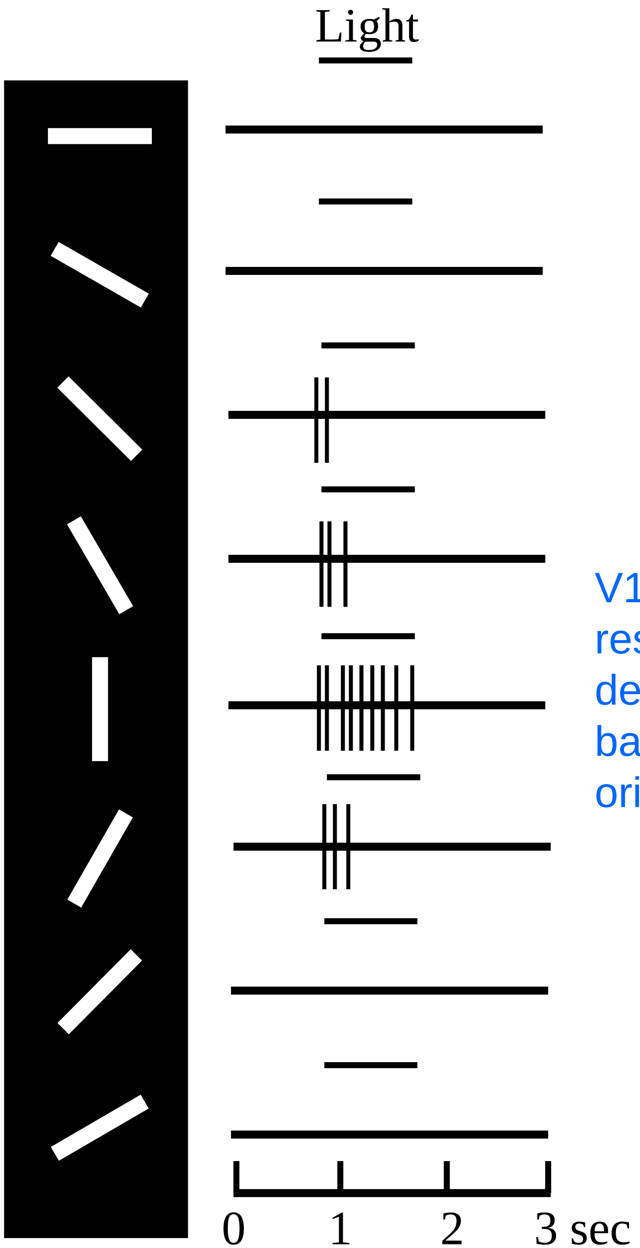


LGN responses do not depend on the orientation of a bar.

Neuronal responses in V1

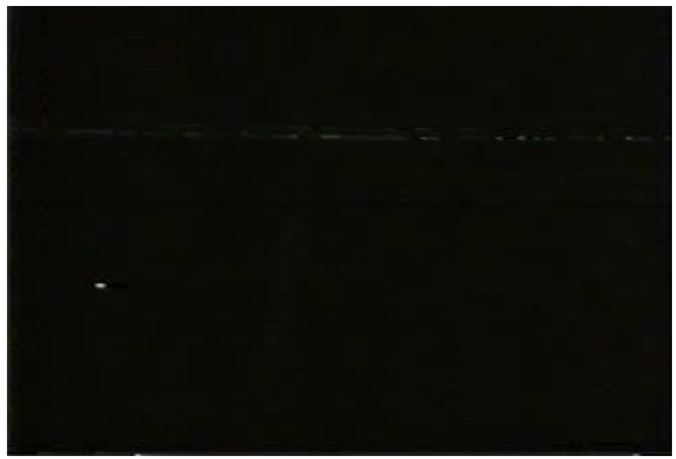


When probed with a small spot, a V1 cell behaves somewhat like an LGN cell.



V1 responses depend on bar orientation

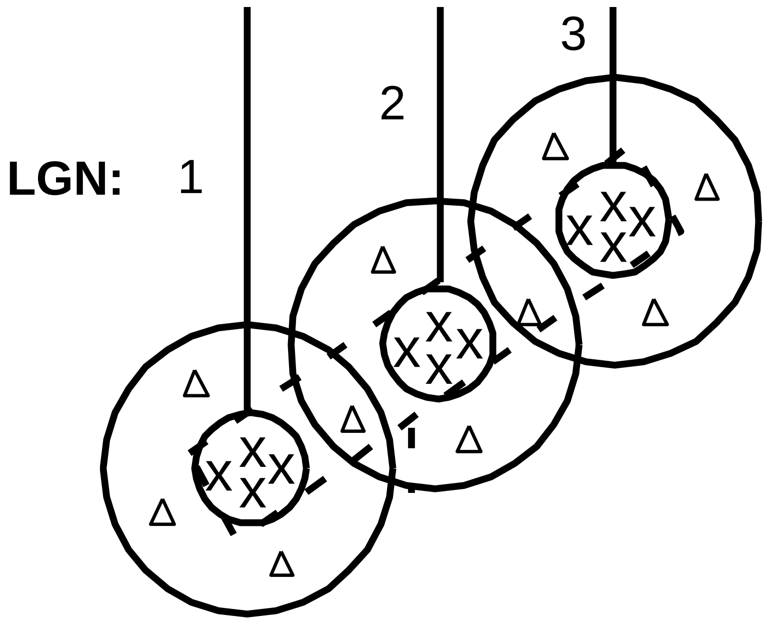
Orientation selectivity in V1 simple cells



Wiesel Hubel

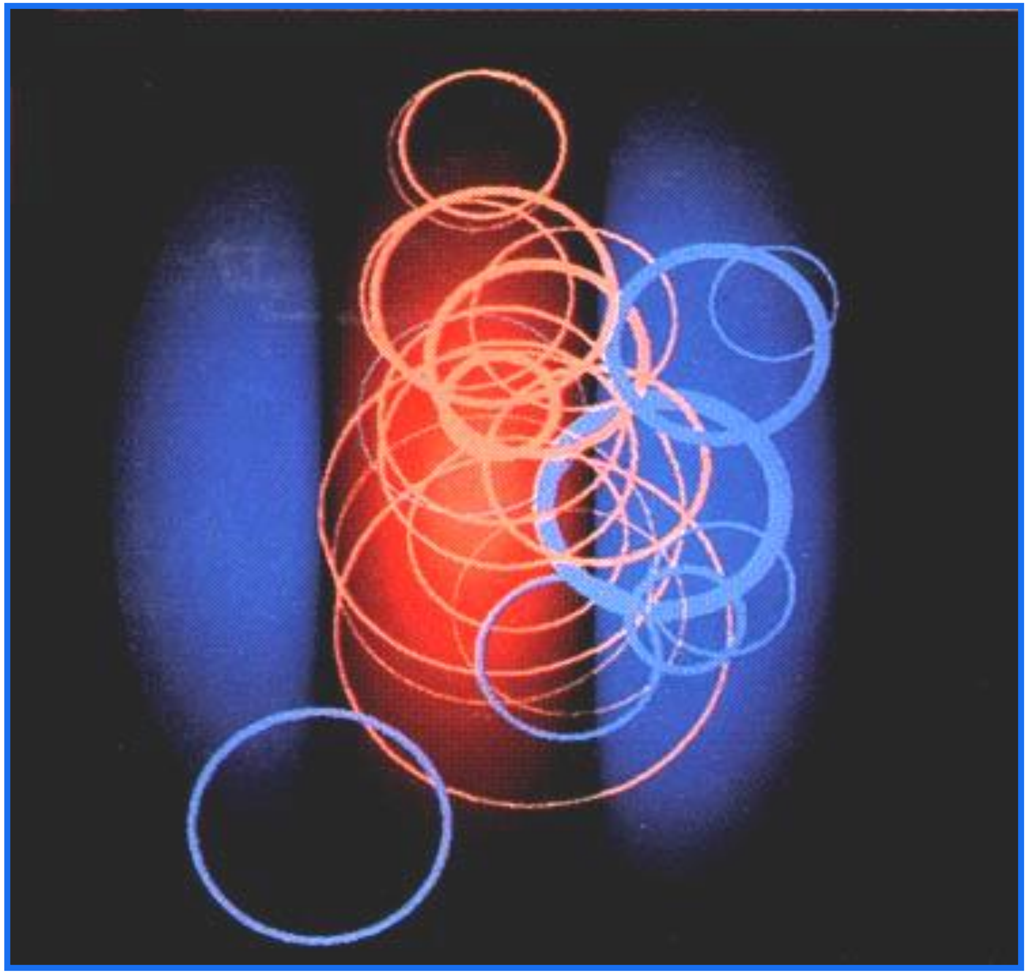
Hubel/Wiesel movie #2

A Simple Cell Model



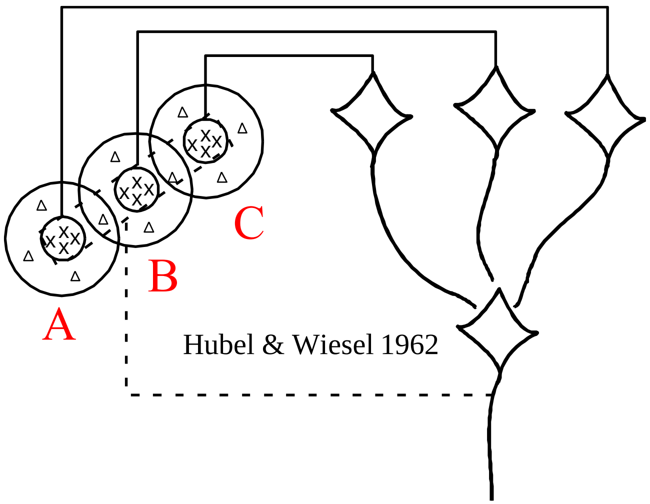
Hubel & Wiesel 1962

A Simple Cell Model Confirmed



Alonso & Reid, 1995

Linear systems



Neurons integrate inputs from other neurons and generate a response. A key assumption of the H/W model of simple cells is that the inputs are (roughly) linearly related to the stimulus.

So our previous approach should still work. Assume a linear system:

$$r(t) = \sum_{\tau} s(t-\tau)h(\tau)$$

And we should still be able to recover the temporal filter by cross-correlation:

$$Q(\sigma) = \frac{1}{T}\sum_{t} s(t-\sigma)r(t)$$

This leads to a very simple trick for recovering the full space-time receptive field…

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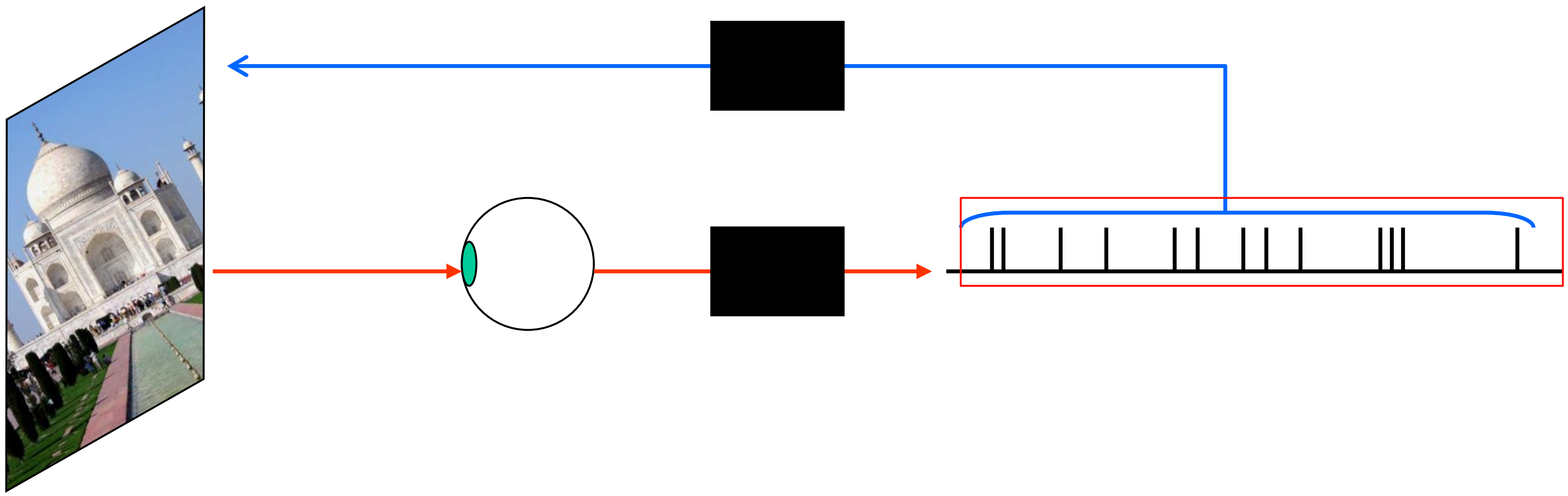
Two types of questions for modellers:

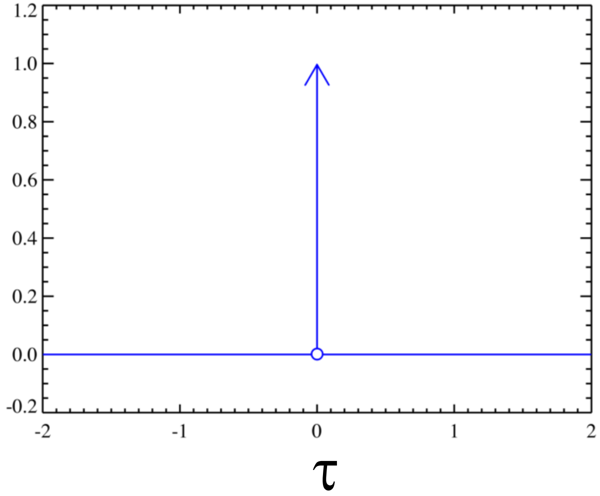
- **Encoding**: If I know the stimulus can I predict the spike train?
- **Decoding**: If I know the spike train, can I figure out what the stimulus was?



Dirac Delta Function

The Delta function takes a constant value at τ = 0 and is 0 everywhere else:

$$\delta(\tau) = \begin{cases} c, & \tau = 0 \\ 0, & \tau \neq 0 \end{cases}$$



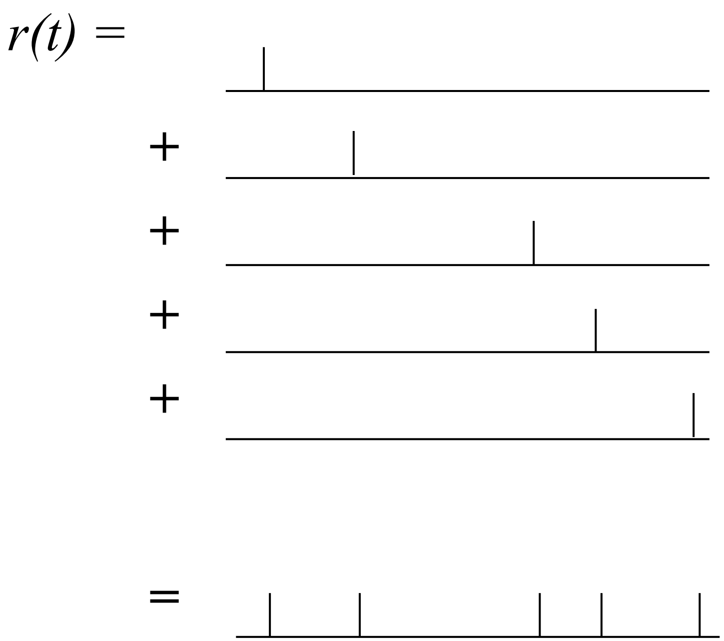
The autocorrelation of a random sequence is a delta function.
(You saw this in Dr. Chacron's lecture.)

Spike-triggered averaging

For spike trains, the neuronal output is (roughly) 1 or 0 at any given moment, so we can write the response *r* as a sum of delta functions:

$$r(t) = \sum_{i=1}^{n} \delta(t - t_i)$$

where t_i is the time of the ith spike. That is,



Spike-triggered averaging

Recall that:

$$\mathrm{Q}(\sigma) = \frac{1}{T}\sum_t s(t-\sigma)r(t)$$

This can be rewritten:

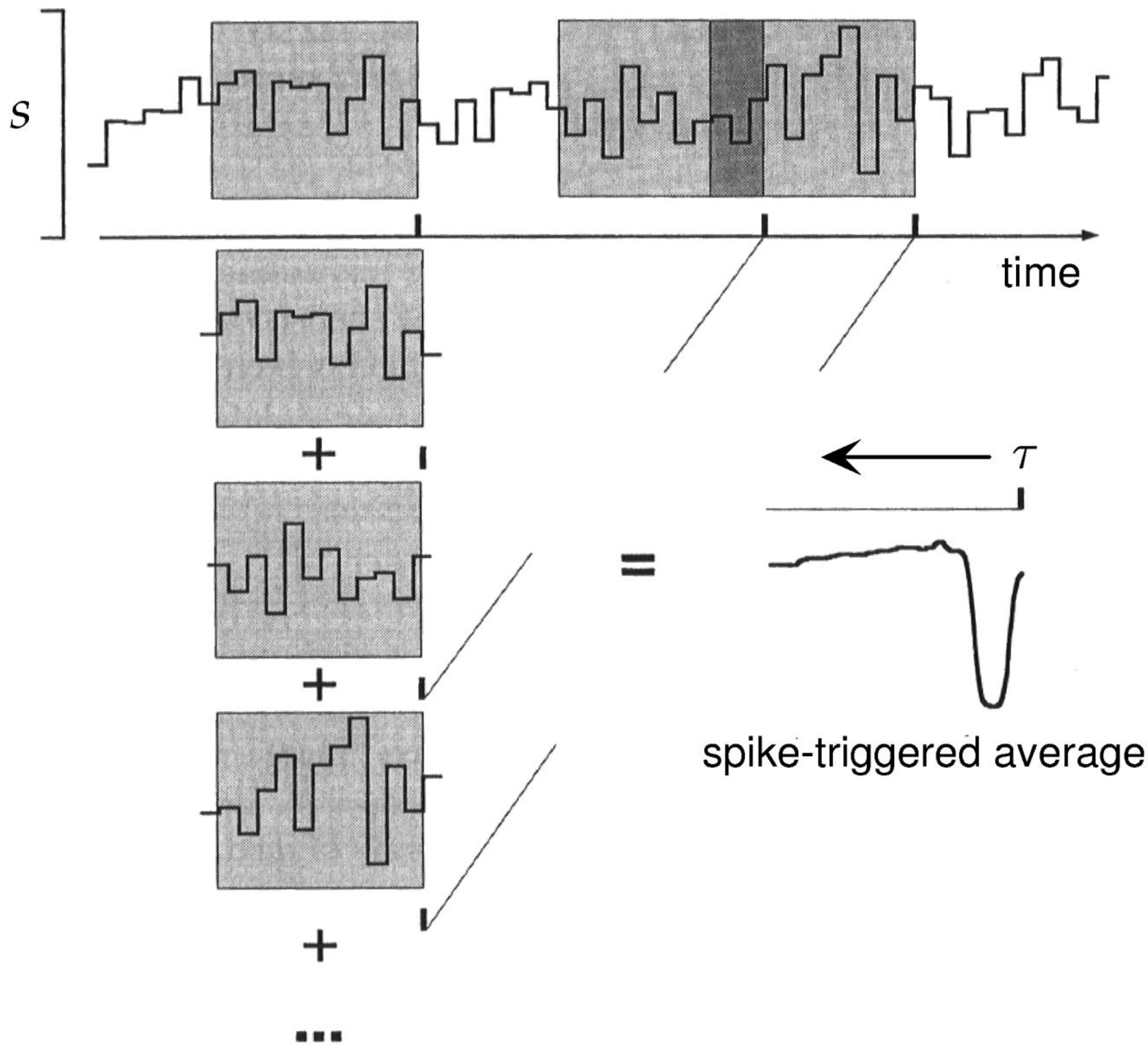
$$\mathrm{Q}(\sigma) = \frac{1}{T}\sum_t s(t-\sigma)\sum_1^n \delta(t-ti)$$

which only has a value when $t = t_i$, so that:

$$Q(\sigma) = \frac{1}{n}\sum_{i=1}^{n} s(t_i - \sigma)$$

In other words, the neuron's temporal response is just the average stimulus that preceded each spike by σ ms. This approach is called *spike-triggered averaging* or *reverse correlation*.

Example of Spike-triggered averaging



Linear filtering approach: Application to V1 simple cells

For a one-dimensional input, the output of our linear filter was:

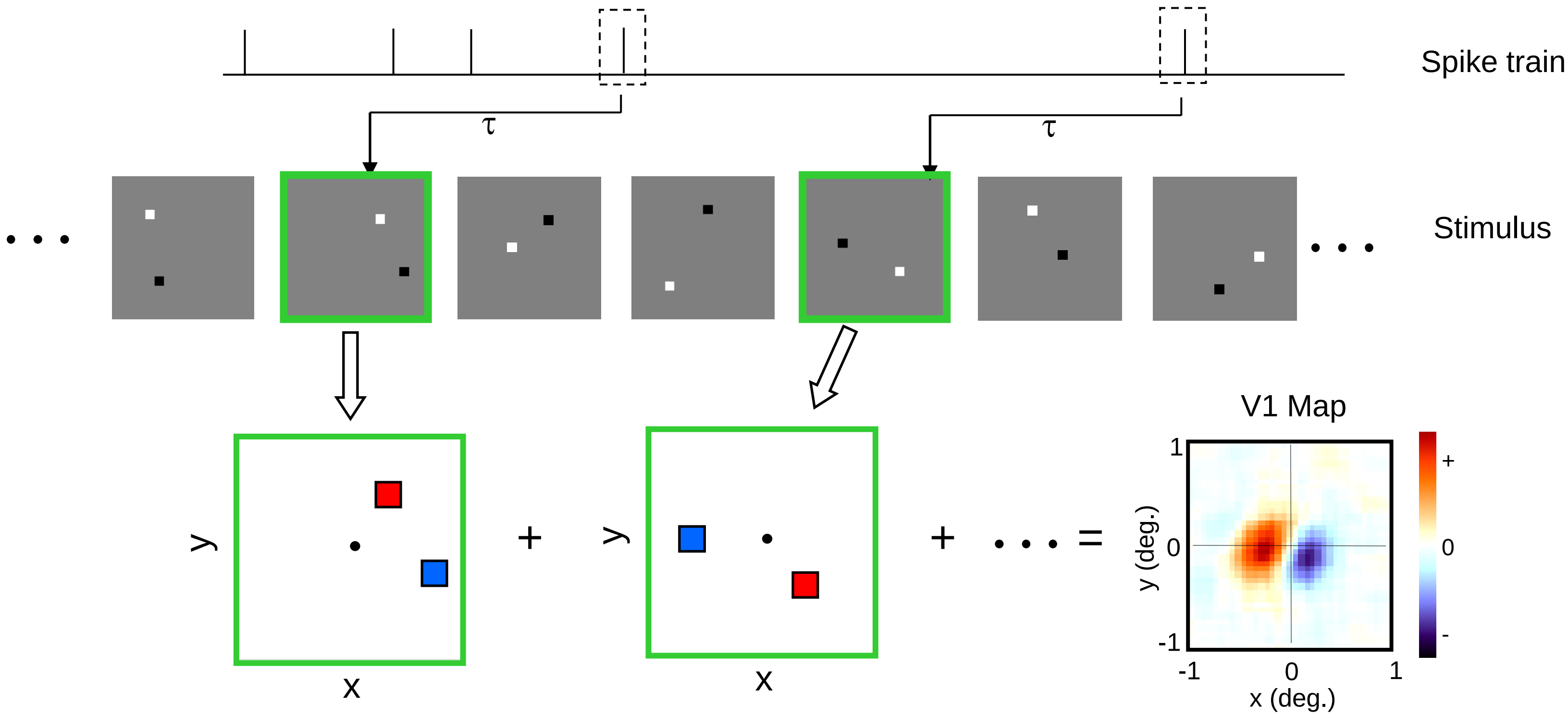
$$r(t) = \sum_{\tau} h(\tau) s(t-\tau)$$

But simple cells respond to (at least) three input dimensions: two for space and one for time. So we need to include them in the equation:

$$r(t) = \sum_{x,y,\tau} s(x,y,t-\tau) h(x,y,\tau)$$

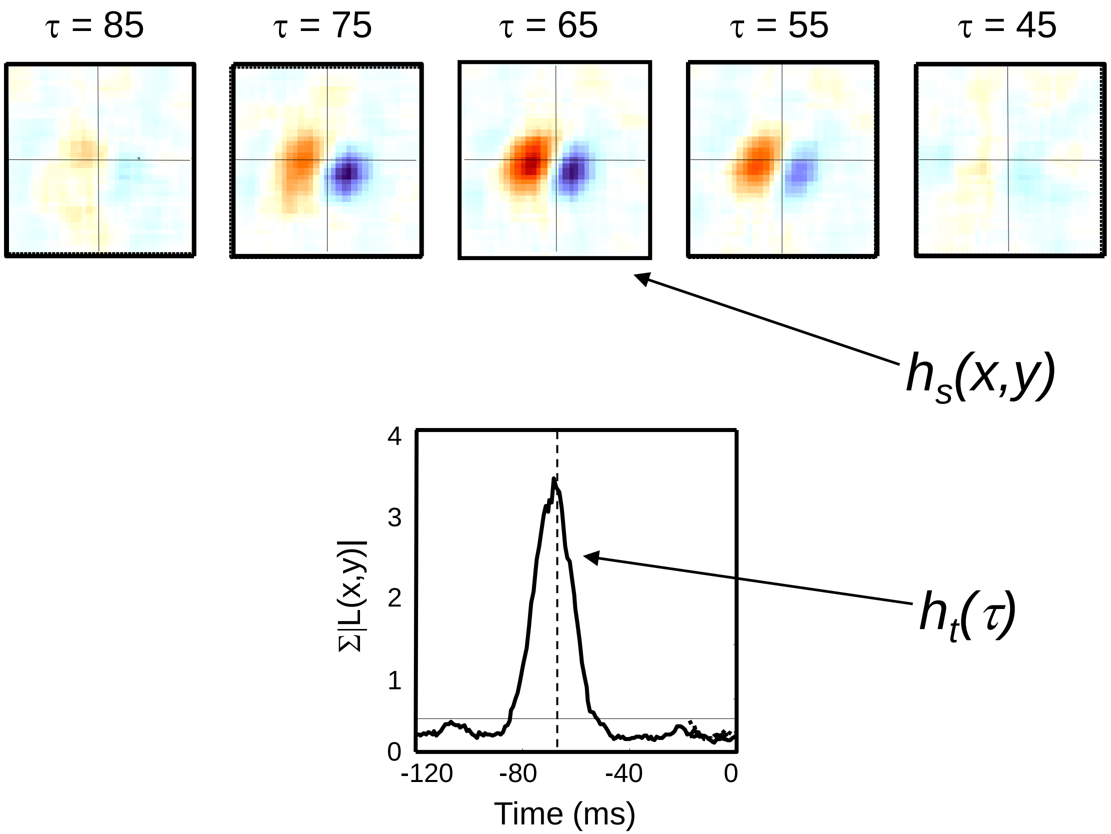
Note that the output depends only on time, so we need to integrate over the spatial dimensions.

Application: V1 simple cell



The **spatial** receptive field at a single value of τ can be measured with spike-triggered averaging.

Application: V1 simple cell



The **temporal** receptive field can be measured by computing the spatial receptive field at different values of τ.

Outline

Introduction to linear systems

Refinement of linear model and applications

Spike-triggered averaging

Assumptions behind spike-triggered averaging:

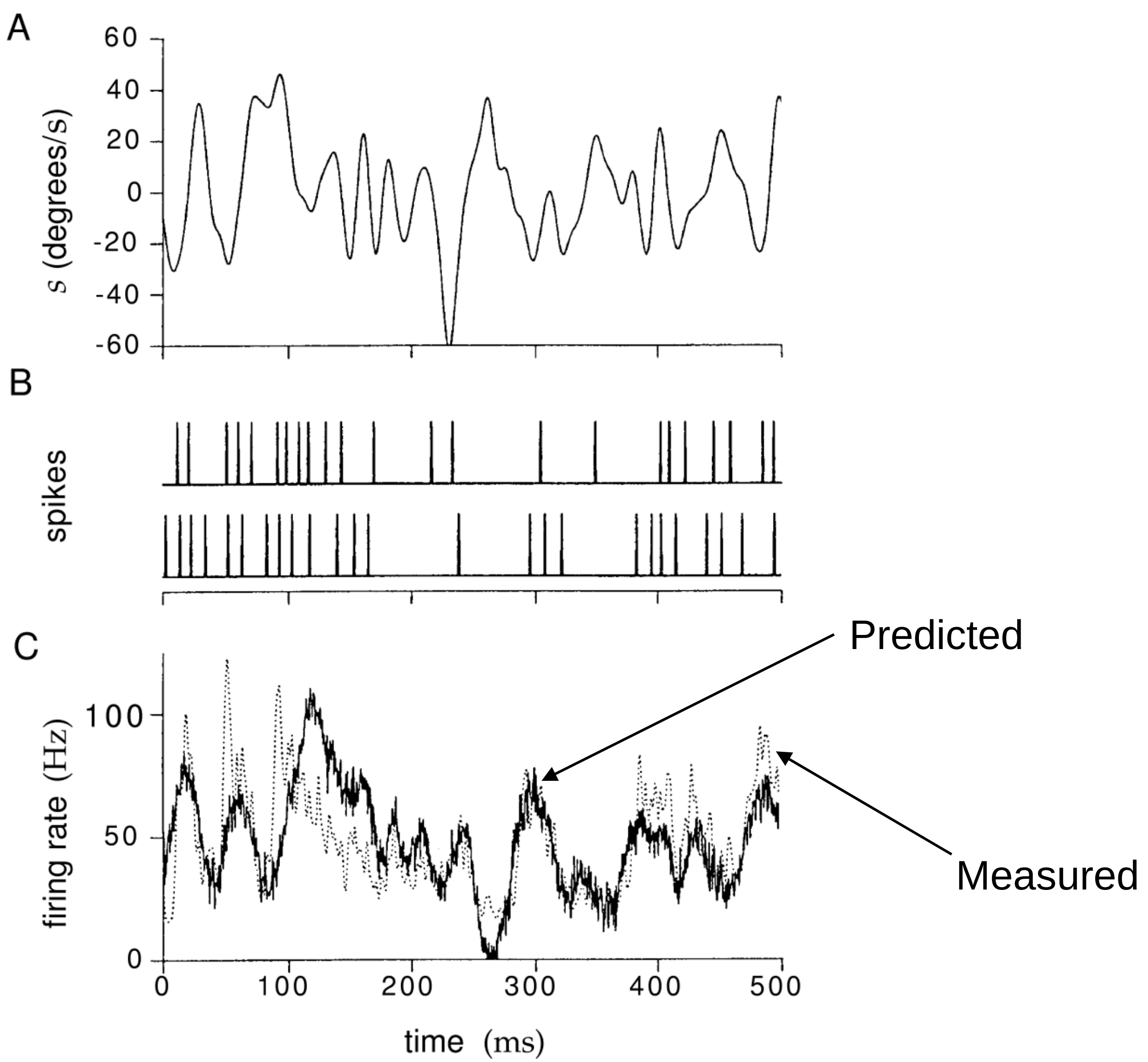
1) Spikes depend on the stimulus, rather than attention, anesthetic levels, other spikes, etc.
2) The stimulus autocorrelation is flat, which usually means that the stimulus is white noise.
3) The cell's response is linear!

Assumption #3 can be tested by plugging our estimate of $h(\tau)$ into:

$$R_{est}(t) = \sum_{\tau} h(\tau)s(t-\tau)$$

If the cell is linear, then we should be able to predict the ***real*** response *R* based on our knowledge of *h* and *s*.

Spike-triggered averaging



Spike-triggered averaging

Spike-triggered averaging (or any linear method) will fail if the neuron:

1) Is affected by something other than the stimulus
2) Has a response that is very nonlinear in its inputs
3) Has a **static nonlinearity** that affects firing rate
   Example: The firing rate cannot be negative.
   Example: The firing rate cannot be infinite.

Static Nonlinearities

Recall the linear response:

$$R_{est}(t) = \sum_{\tau} h(\tau)s(t-\tau)$$

If the cell's response includes a static nonlinearity, we can model it as:

$$m(t) = r0 + F(R_{est}(t))$$

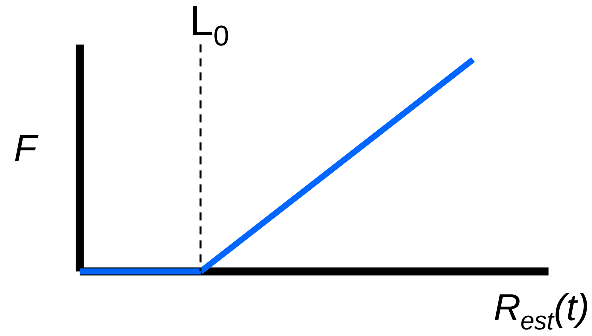
where *F* can in principle be any function. In practice it will have the properties of real neurons: nonnegativity, saturation, and a few others.

Static Nonlinearities

To set a firing **threshold** at L_0:

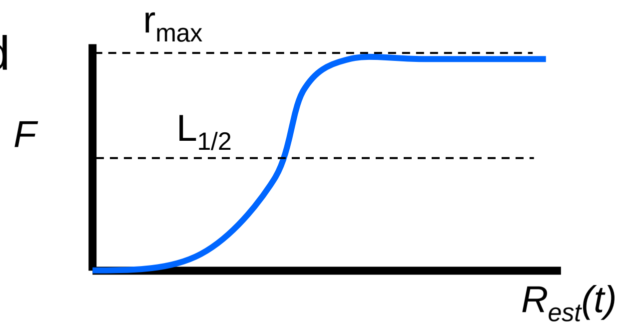
$$F(R_{est}) = G[R_{est} - L_0]_+$$

This function cannot be negative.

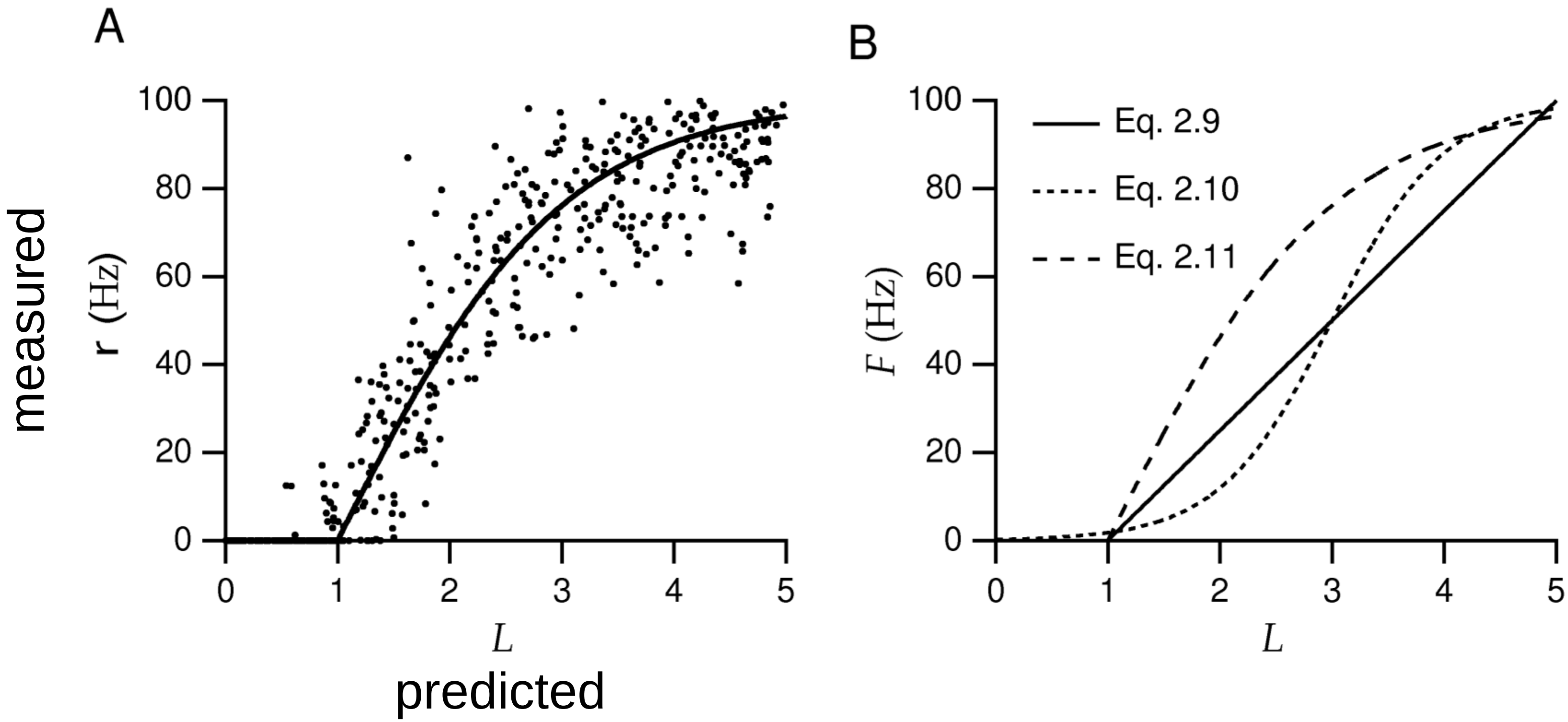


A **sigmoid** function has a threshold, and it saturates for large inputs:

$$F(R_{est}) = \frac{r_{\max}}{1 + \exp(g_1(L_{1/2} - L))}$$



Static Nonlinearities



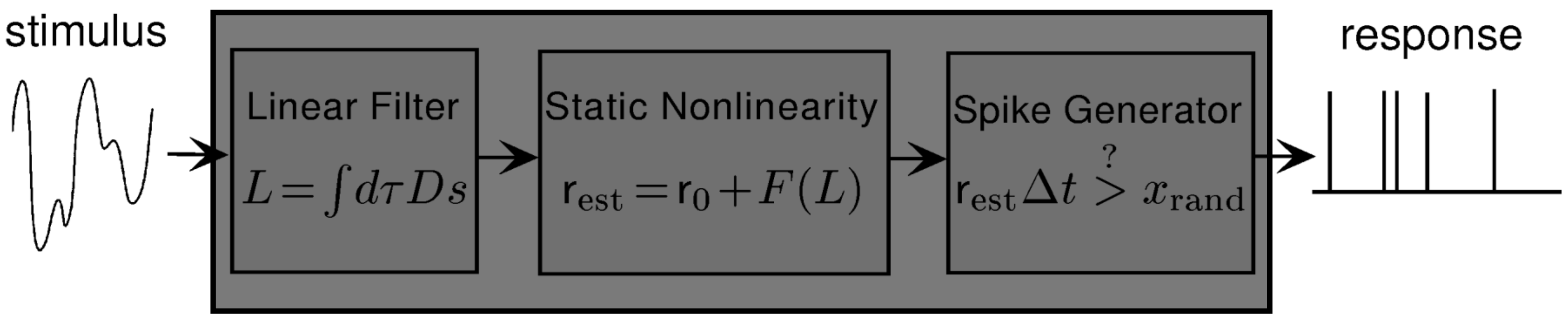
If the linear model were sufficient, the relationship between predicted and measured response would be a straight line. In practice there is usually a nonlinear relationship.

Static Nonlinearities

Static nonlinearities:

1) Depend only on the response at an instant in time.
2) Do not depend directly on the stimulus. This is important because other nonlinearities require a large amount of data to compute.
3) Typically have a threshold and a saturation point

Linear filtering approach: Summary



The neuron's response is modeled as a linear filter that operates on the stimulus, a static nonlinearity that operates on the output of the filter, and a spike generating mechanism that operates on the output of the nonlinearity.

The Weiner/Volterra Approach

Key idea: describe the response of the system in terms of the statistics of the input:

Zeroth-order: **r0**

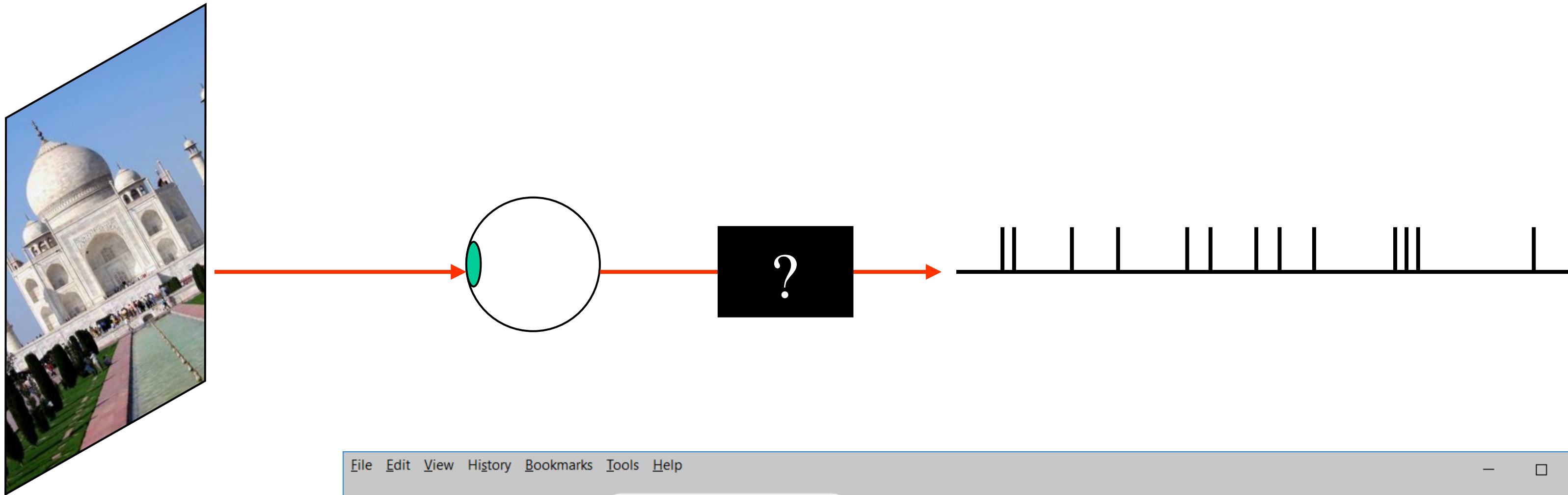
First-order: $$R1_{est}(t) = \int_0^\infty D_1(\tau)s(t-\tau)d\tau$$

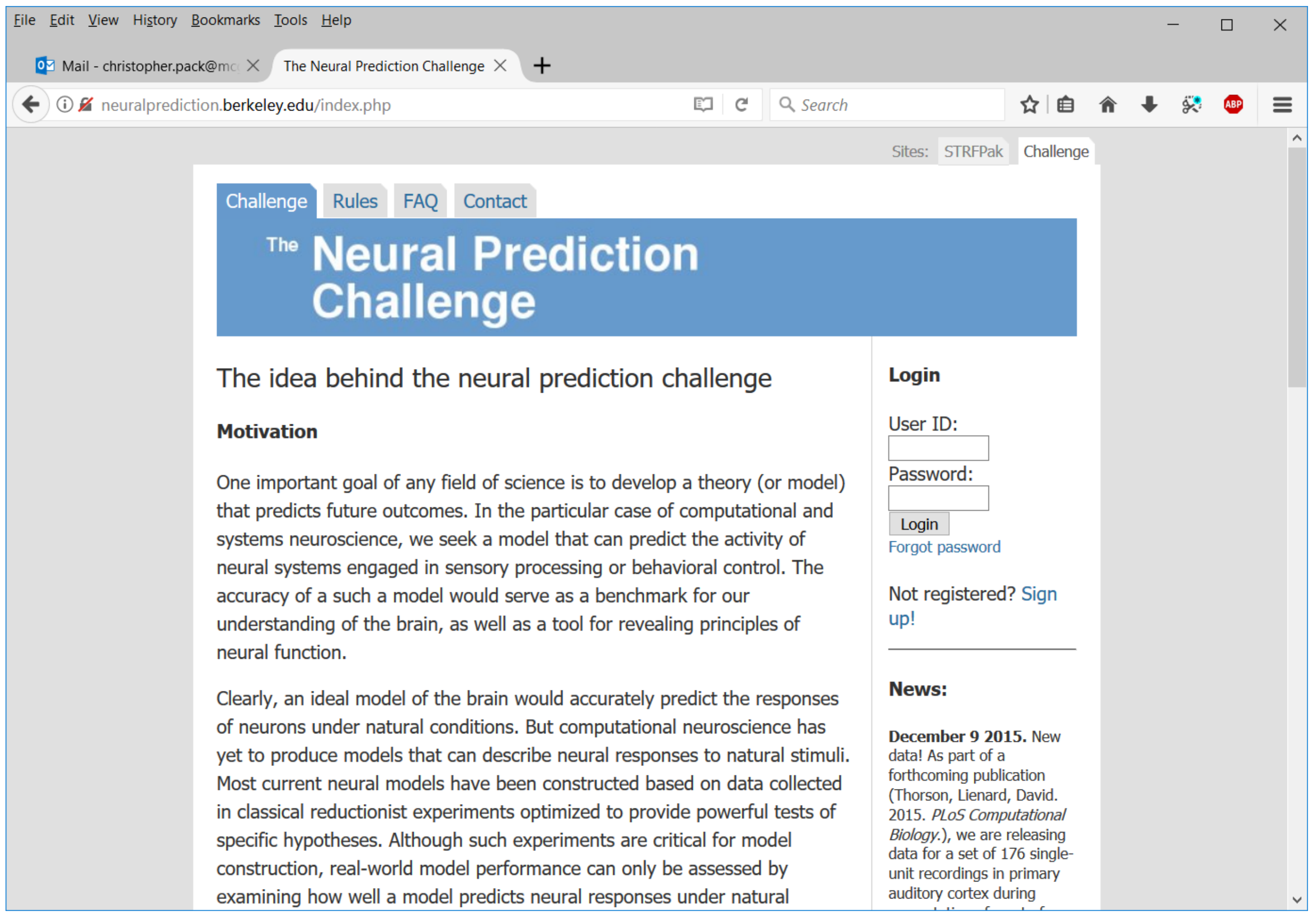
Second-order: $$R2_{est}(t) = \int_0^\infty \int_0^\infty D_2(\tau_1,\tau_2)s(t-\tau_1)s(t-\tau_2)d\tau_1 d\tau_2$$

Complete: $$R_{est}(t) = r0 + \int_0^\infty D_1(\tau)s(t-\tau)d\tau + \int_0^\infty \int_0^\infty D_2(\tau_1,\tau_2)s(t-\tau_1)s(t-\tau_2)d\tau_1 d\tau_2 + \ldots$$

where *s* is the stimulus and D_n is the n^{th} kernel.

If we could find the D_n's, we would know everything about the system!





The Neural Prediction Challenge

The idea behind the neural prediction challenge

Motivation

One important goal of any field of science is to develop a theory (or model) that predicts future outcomes. In the particular case of computational and systems neuroscience, we seek a model that can predict the activity of neural systems engaged in sensory processing or behavioral control. The accuracy of a such a model would serve as a benchmark for our understanding of the brain, as well as a tool for revealing principles of neural function.

Clearly, an ideal model of the brain would accurately predict the responses of neurons under natural conditions. But computational neuroscience has yet to produce models that can describe neural responses to natural stimuli. Most current neural models have been constructed based on data collected in classical reductionist experiments optimized to provide powerful tests of specific hypotheses. Although such experiments are critical for model construction, real-world model performance can only be assessed by examining how well a model predicts neural responses under natural

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News:

December 9 2015. New data! As part of a forthcoming publication (Thorson, Lienard, David. 2015. *PLoS Computational Biology.*), we are releasing data for a set of 176 single-unit recordings in primary auditory cortex during

Summary

Brief overview of the visual system

Visual system is complicated, but some neurons in the primary visual cortex have receptive fields that are somewhat linear.

Introduction to linear systems

The output of a linear system is given by the convolution of its input with a kernel, which for a visual neuron is the receptive field in space and time. The kernel can be recovered by cross-correlating the output and input, provided that the input is random.

Some intuitions

Convolution: The neuron's response at some point in time reflects the sum of the responses to individual stimuli at different time points in the immediate past.

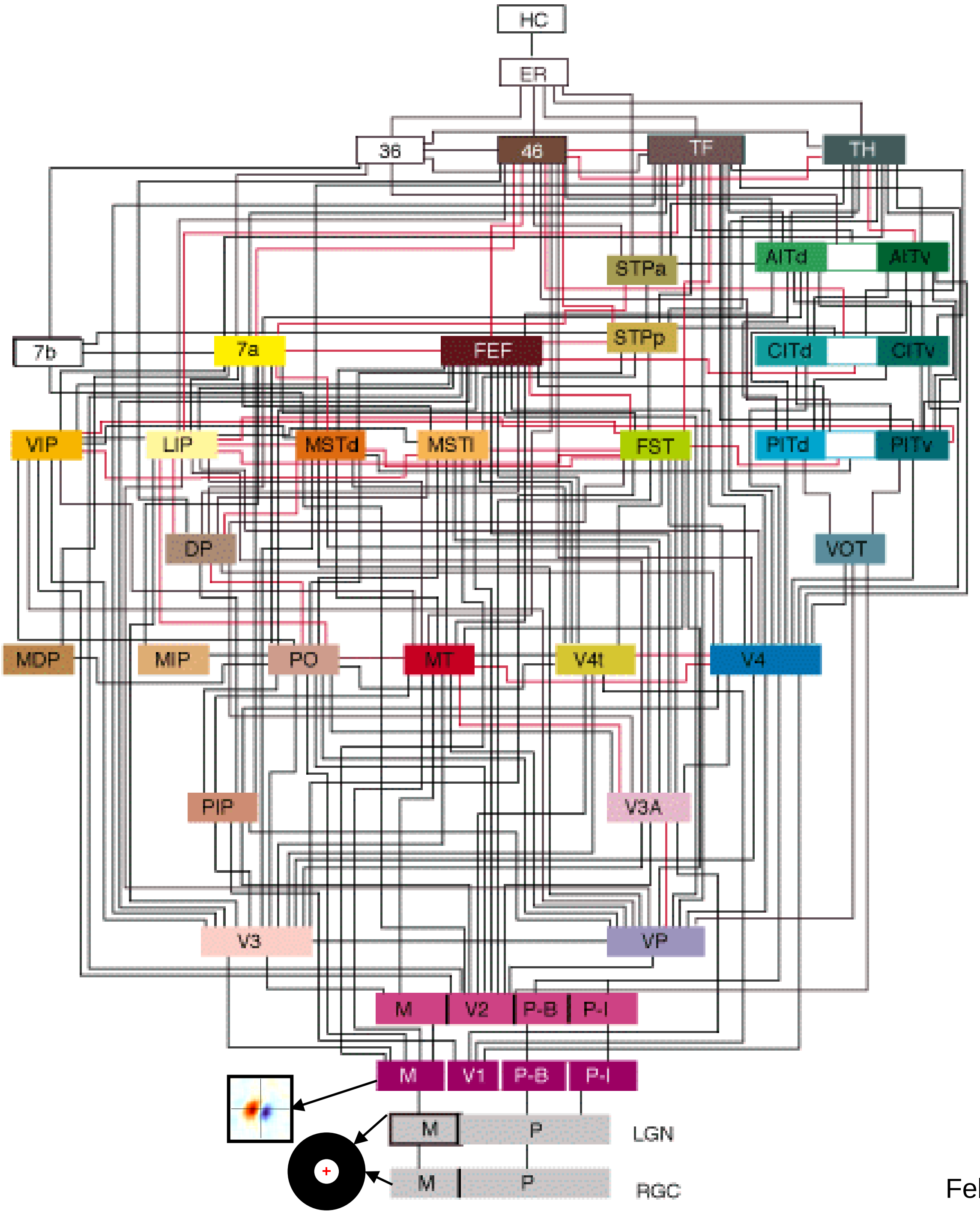
Cross-correlation: When the stimulus value increases, the neuron's response should increase (or decrease for an OFF region) a bit later.

Auto-correlation: The correlation between the stimulus and the response is hard to interpret if there is a correlation between the stimulus and the stimulus.

Spike-triggered averaging: Since the response at each time point is a spike, we can relate it to a snapshot of the stimulus some time earlier.

Refinement of linear model and applications

Linear models fail to capture simple aspects of neuronal responses, such as thresholds and saturation. These can be incorporated as static nonlinearities. Other nonlinear processing requires more complex models.



Felleman and Van Essen, 1991