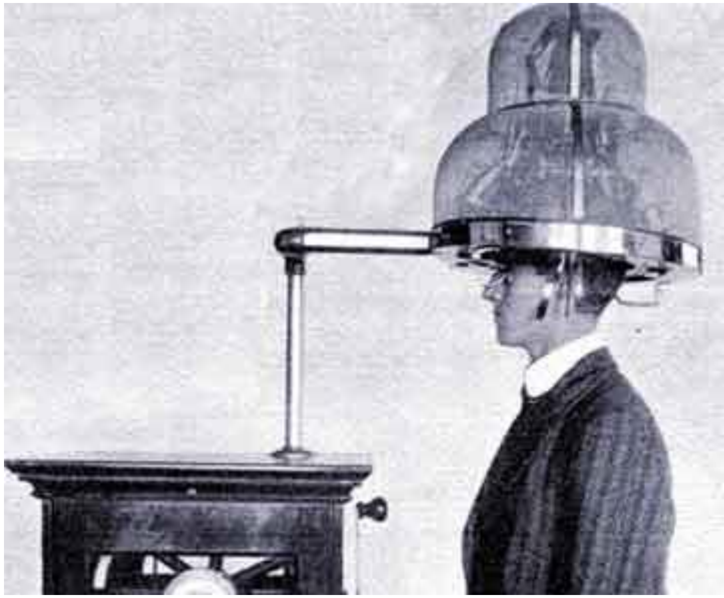
Week 3: Visual Receptive Fields



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Montreal Neurological Institute
McGill University

Outline

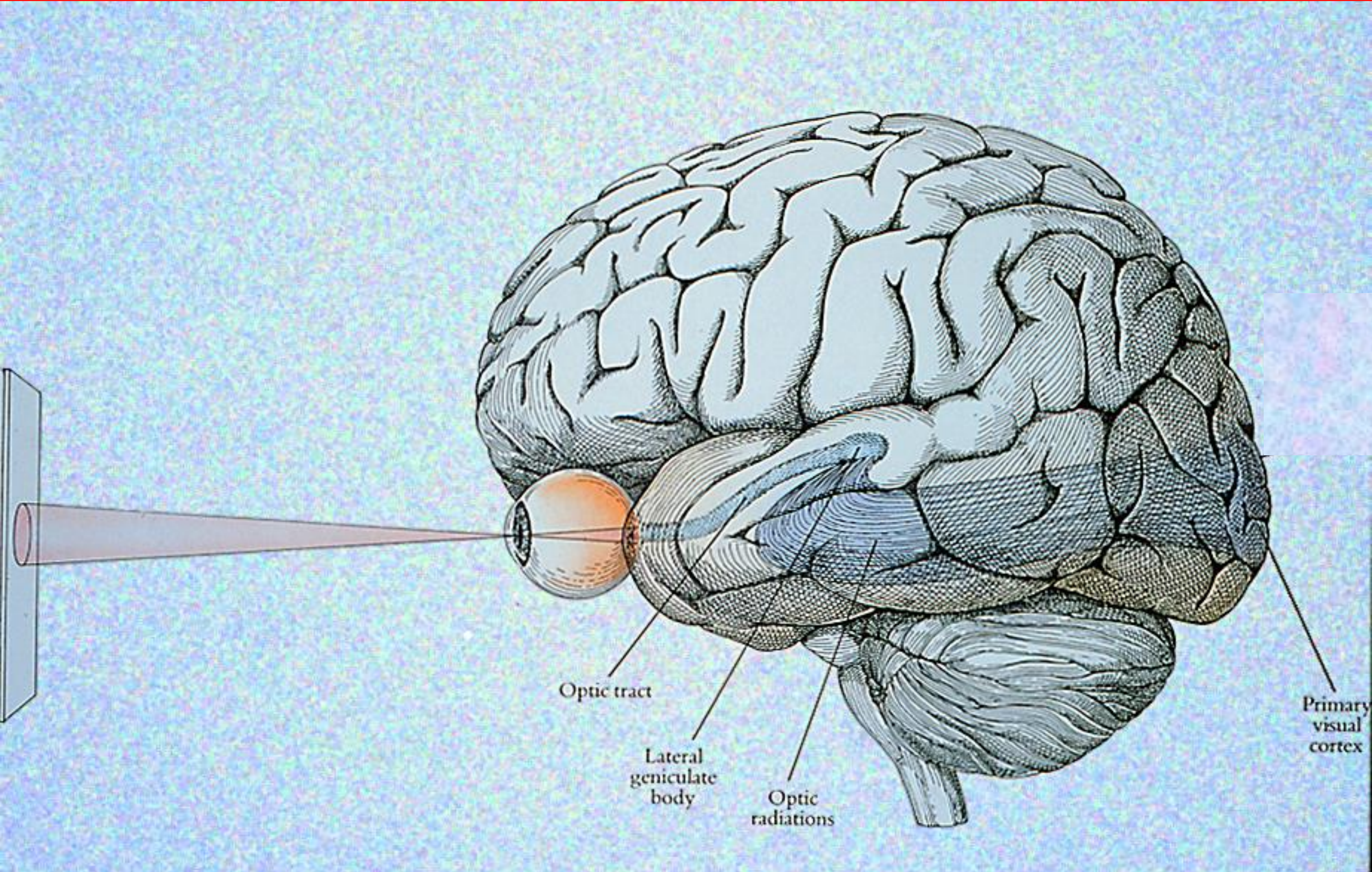
Brief overview of the visual system

Introduction to linear systems with mathematical detour

Refinement of linear model and applications

Encoding

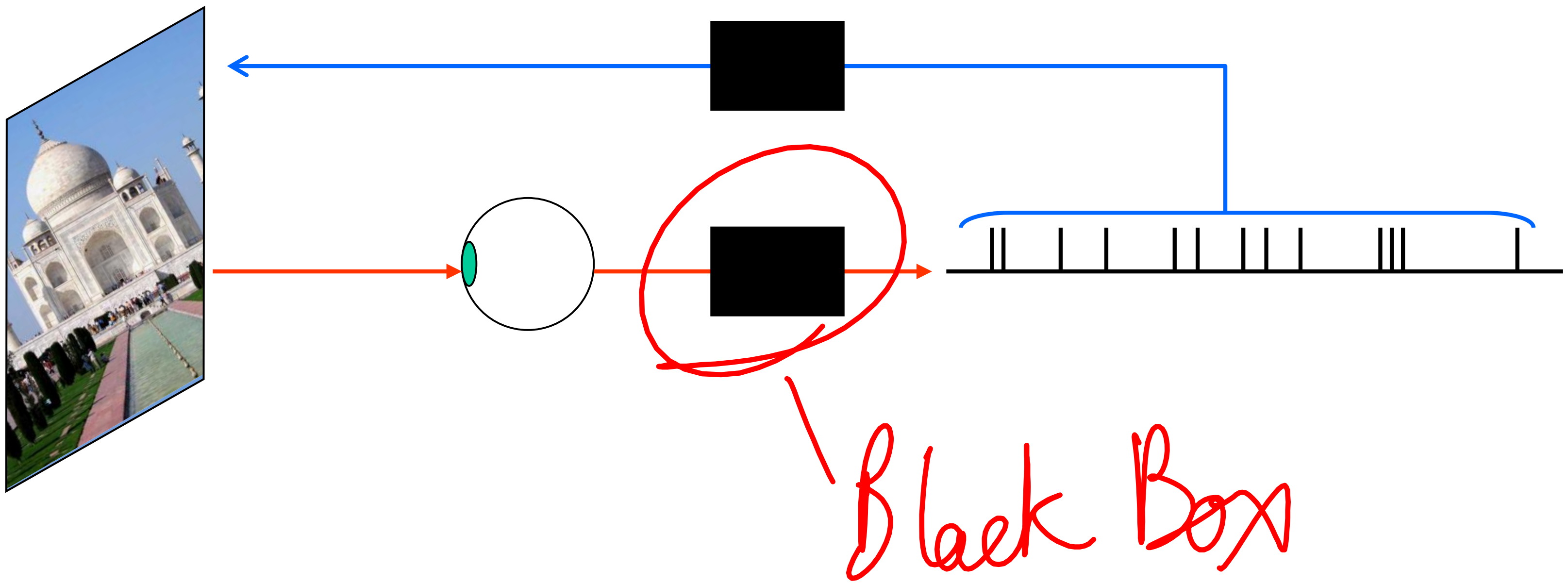
Central Visual Pathways



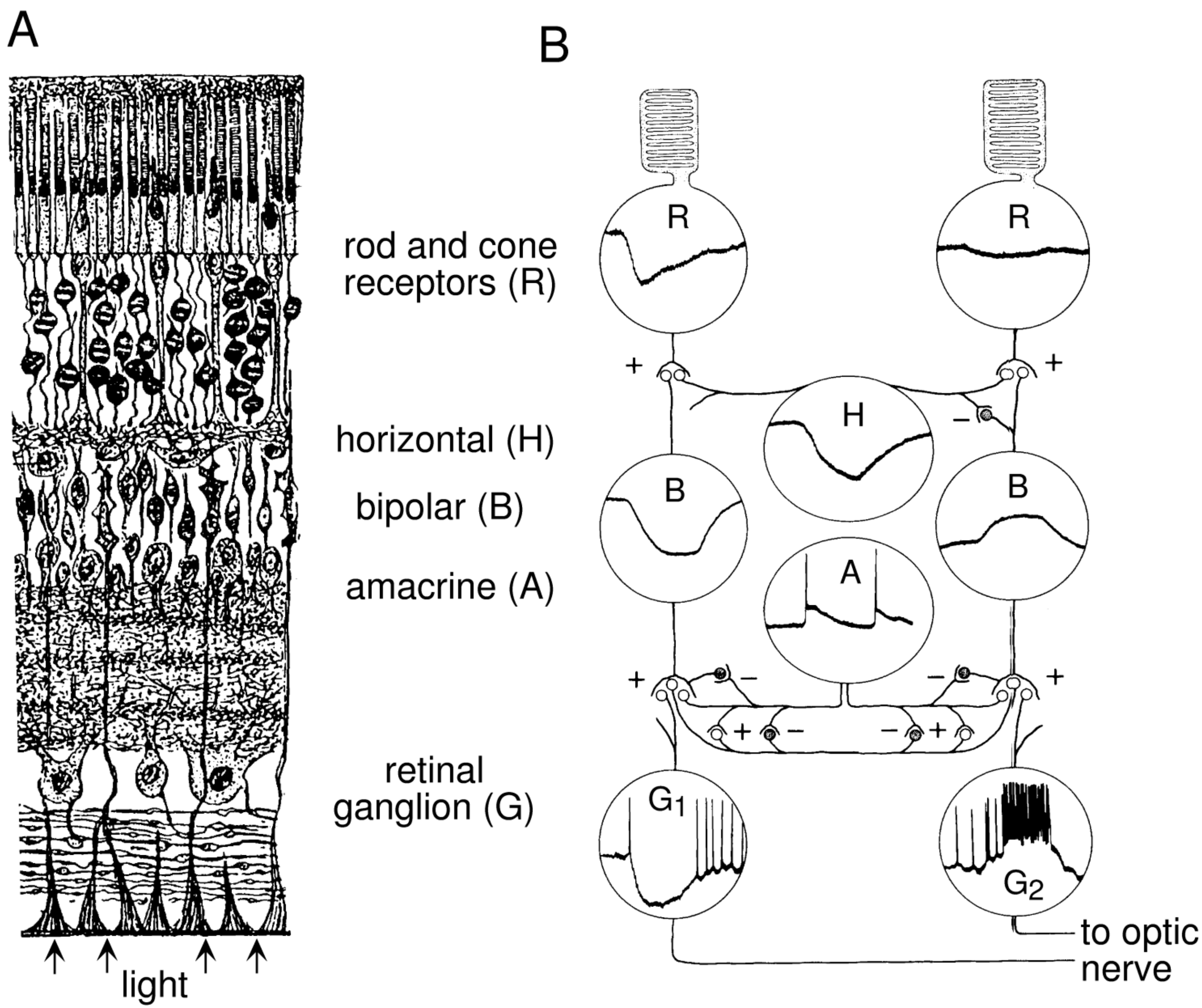
Action Potentials and Spike Trains

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?



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

The Retina

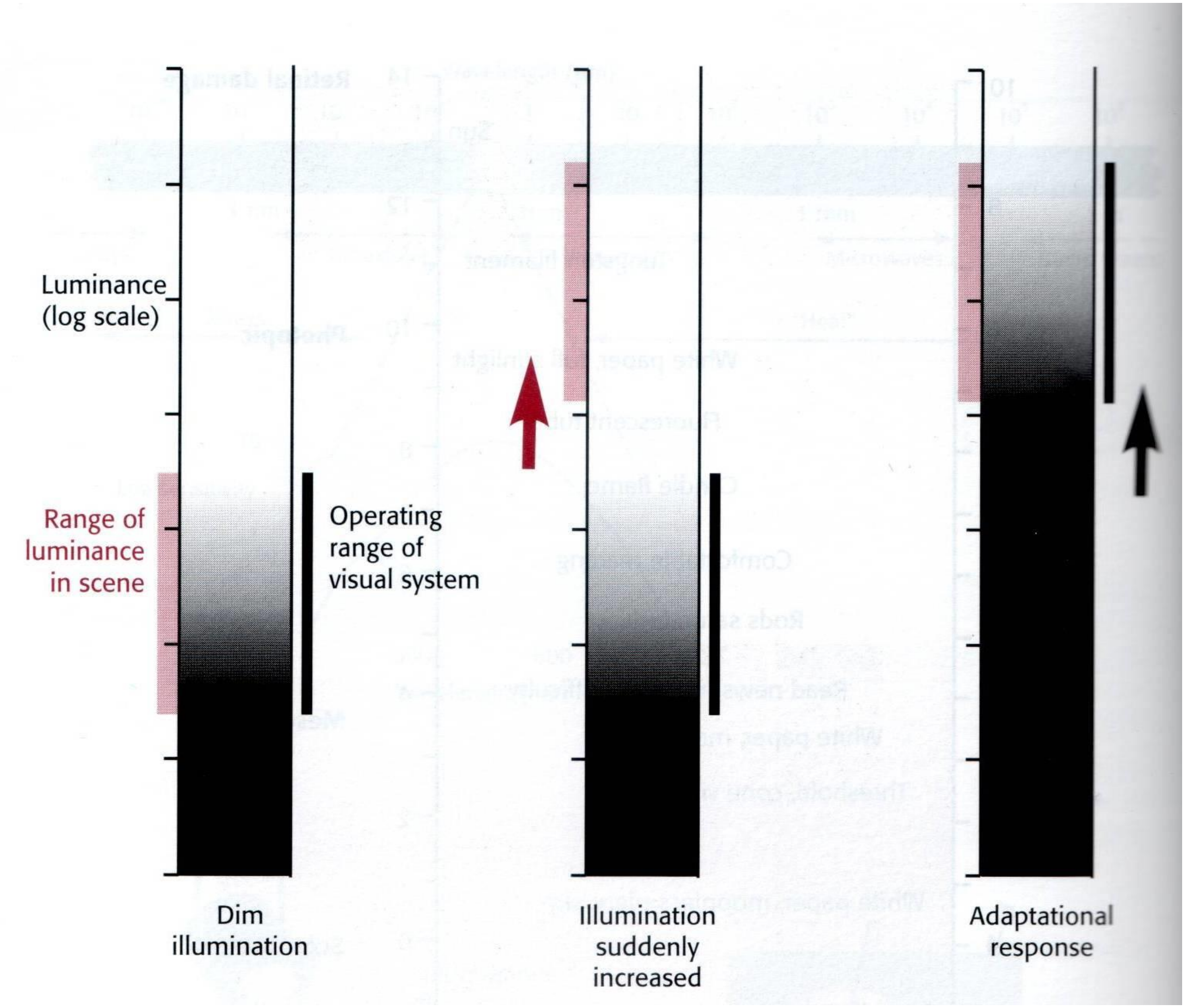
The retinal circuit is complicated, but it receives no feedback from the brain. One of its primary functions is to **adapt** to the statistics of the visual input. For example, vision is largely insensitive to the mean luminance in the input. The cortex operates largely on differences in luminance, so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

Relative info

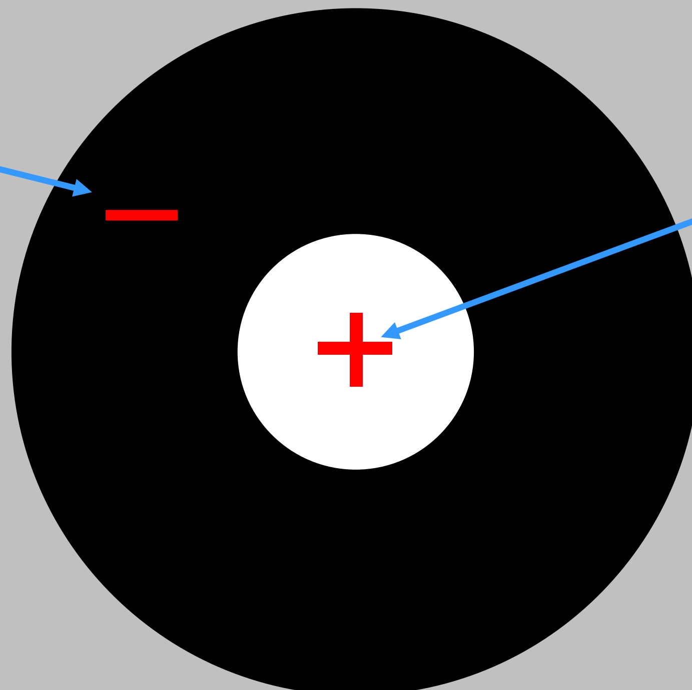
The Retina



Carpenter, Fig 7.4

Receptive fields of retinal ganglion cells

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

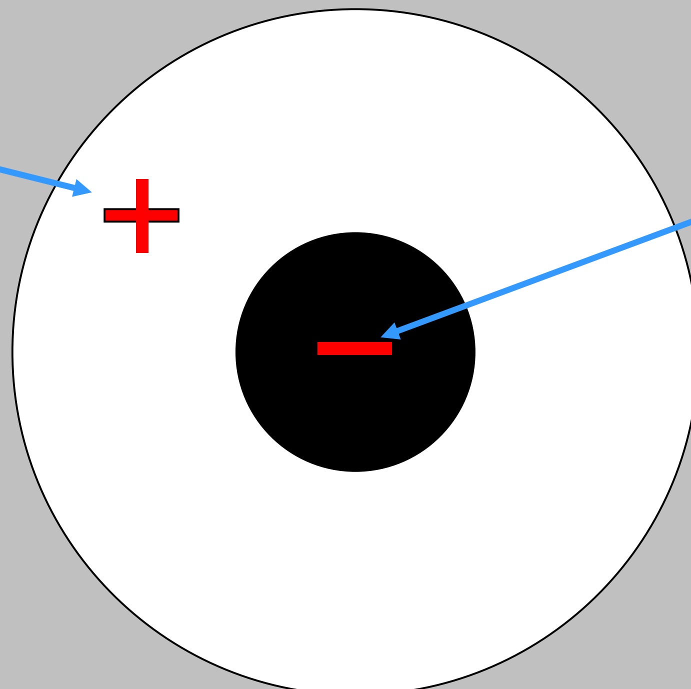


On-center: The neuron responds to a small spot of light, *if it is brighter than the background.*

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.

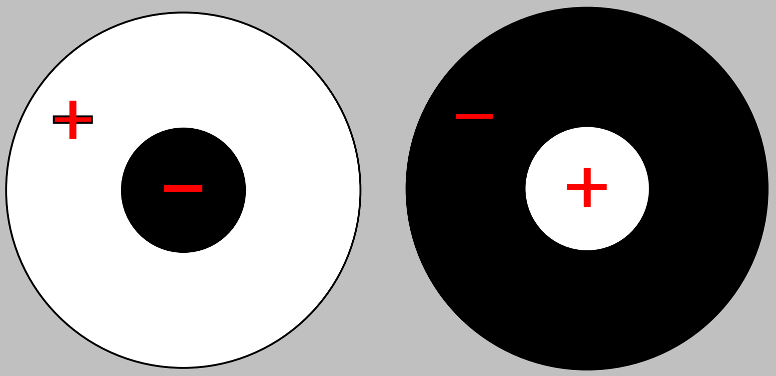
Retinal Ganglion Cells are the output of the retina

The response of a retinal ganglion cell depends (to a first approximation) on the degree of match between the stimulus and the receptive field. Ignoring time for the moment, the response is simply:

Across space

$$R = r_0 + \iint dxdy[s(x,y)\,RF(x,y)]$$

Stimulus



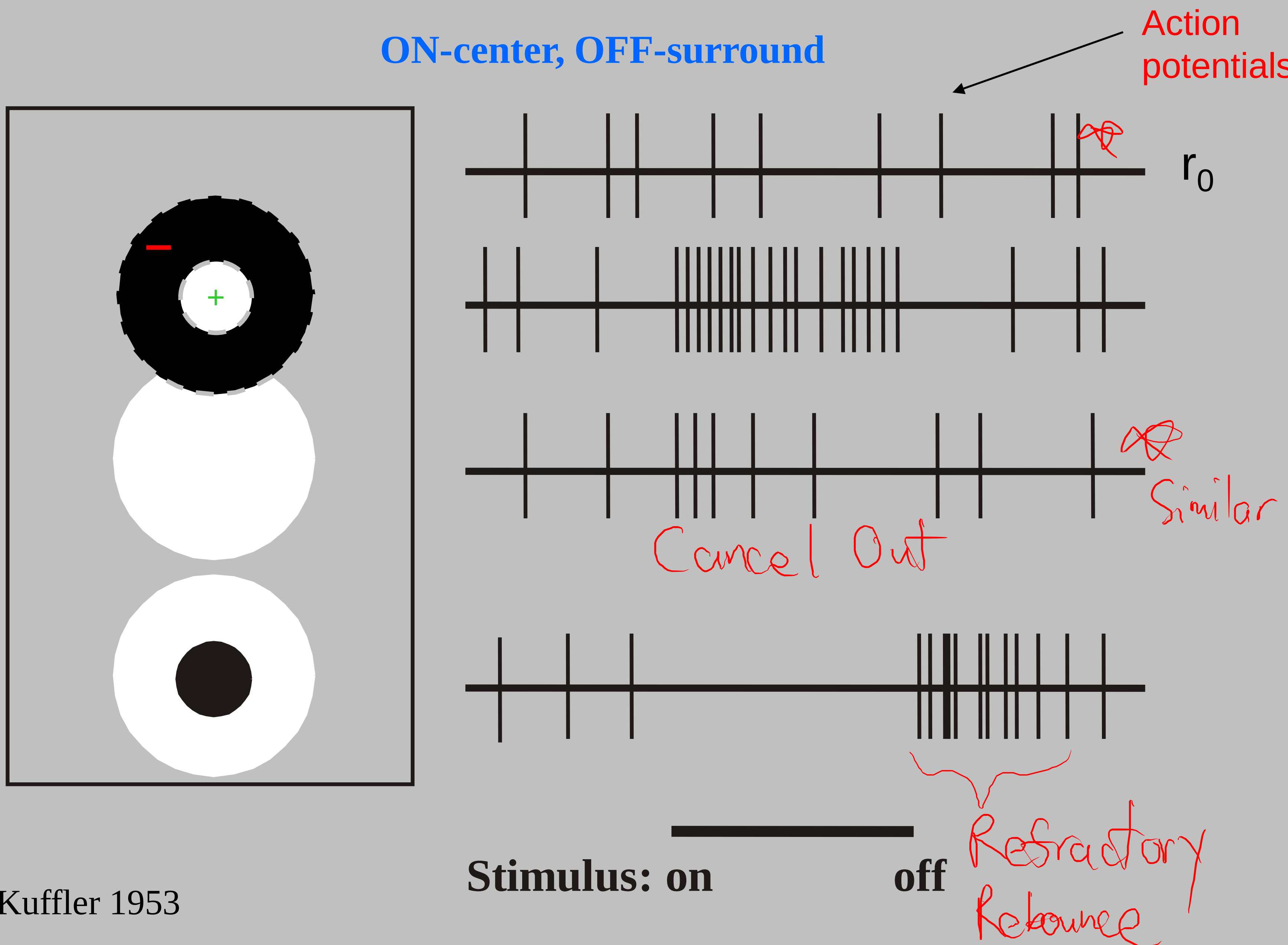
where r_0 is the baseline firing rate.

These cells are (mostly) **linear**. The response to a small spot of light is related to the receptive field and the luminance at that point. And the output of the cell is the sum of the responses at each point in the receptive field.

The output of the neuron describes the **correlation** between the stimulus and the receptive field.

Retinal Ganglion Cells are the output of the retina

ON-center, OFF-surround



Kuffler 1953

Retinal Ganglion Cells are the output of the retina

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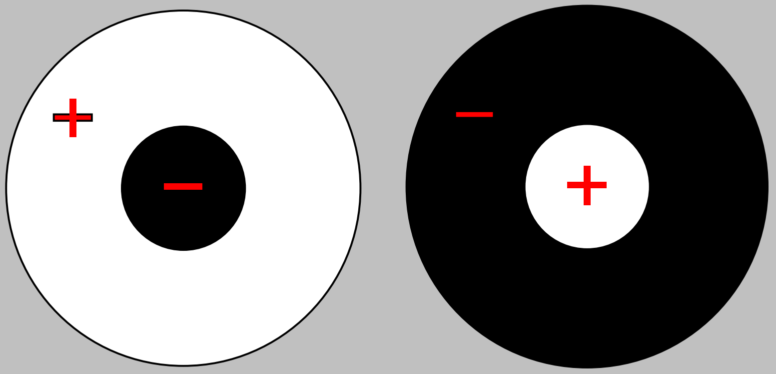

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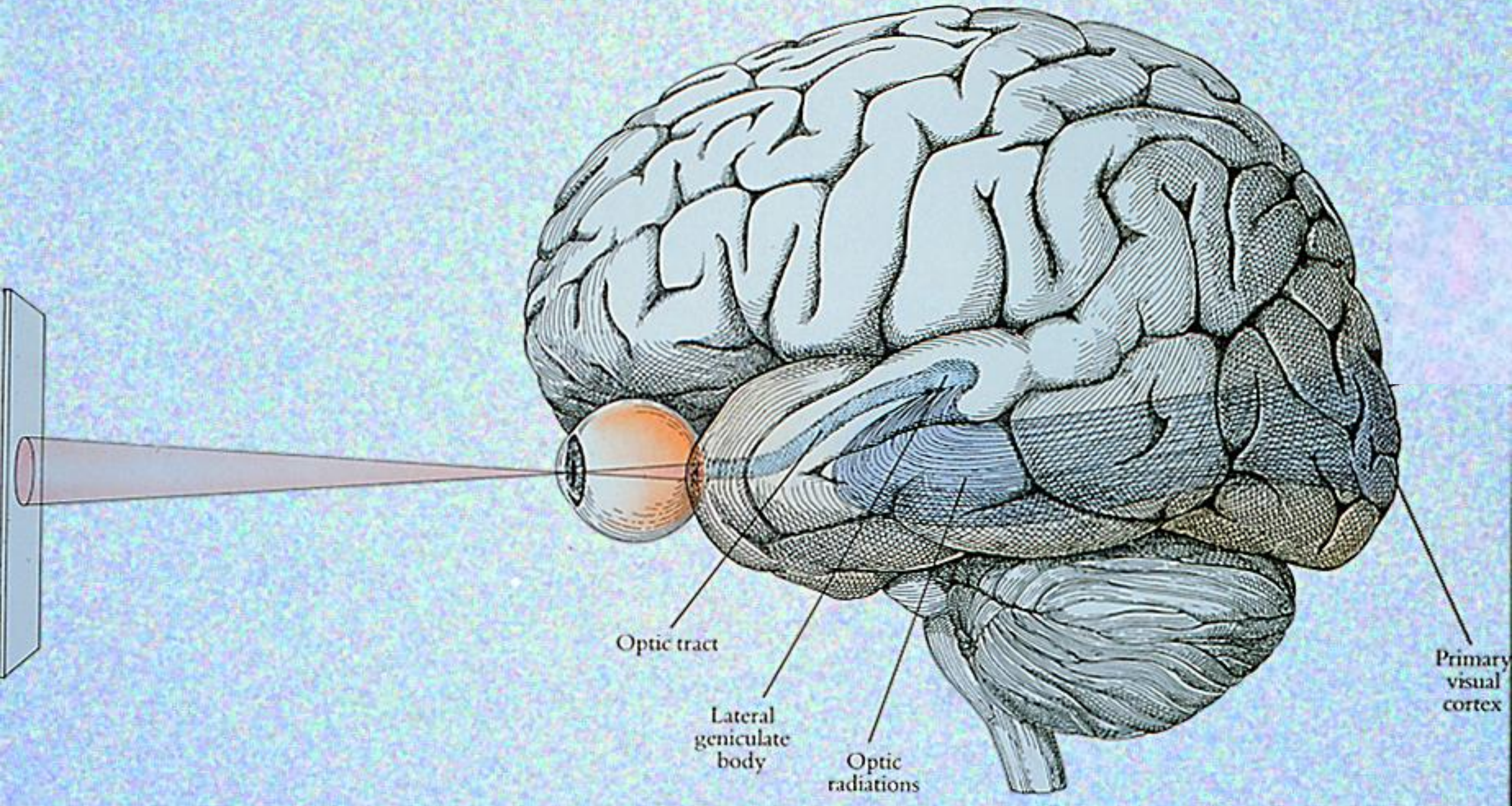
Central Visual Pathways



LGN receptive fields are similar to those of retinal ganglion cells

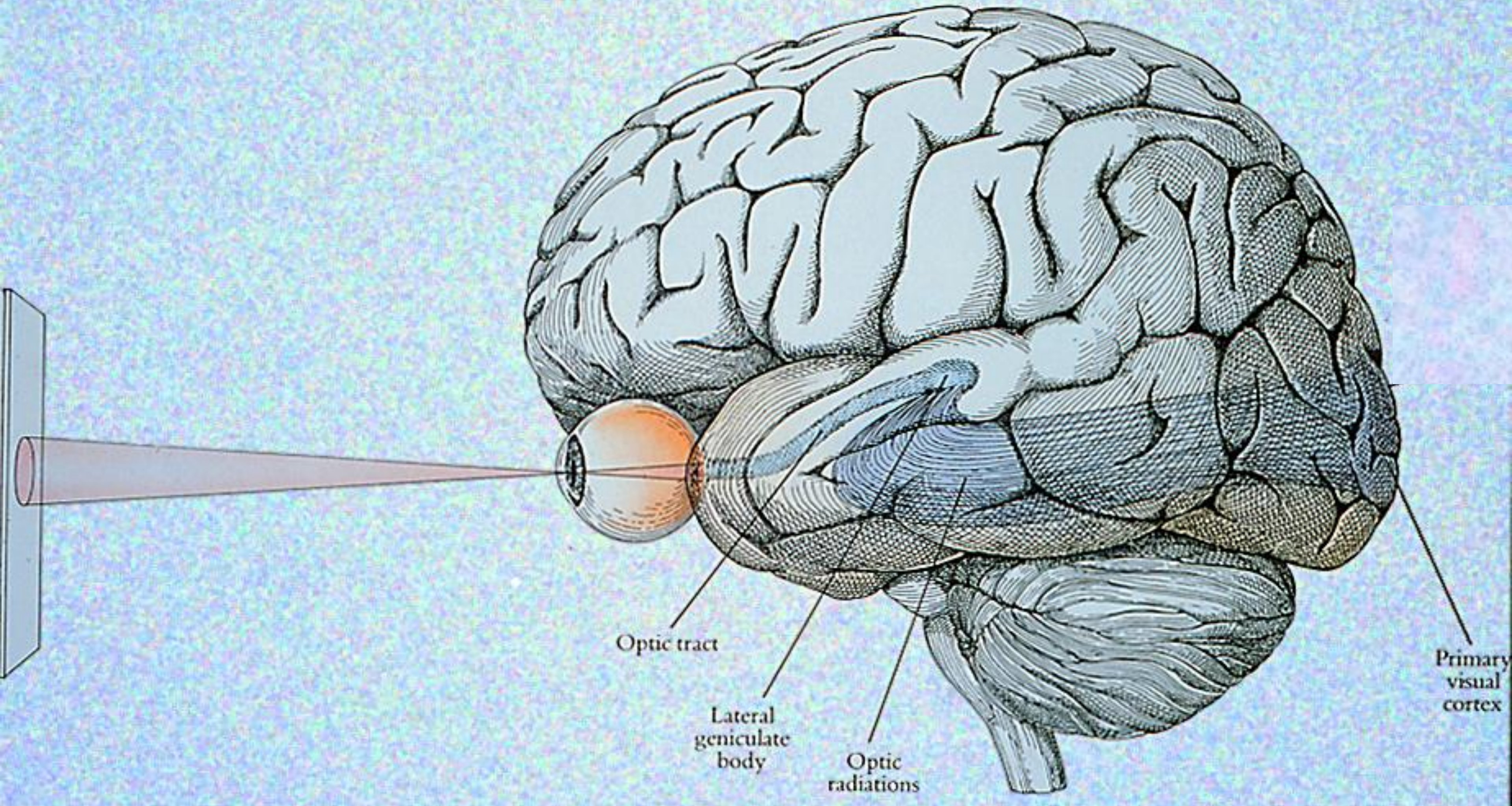
↑ Retina

LGN

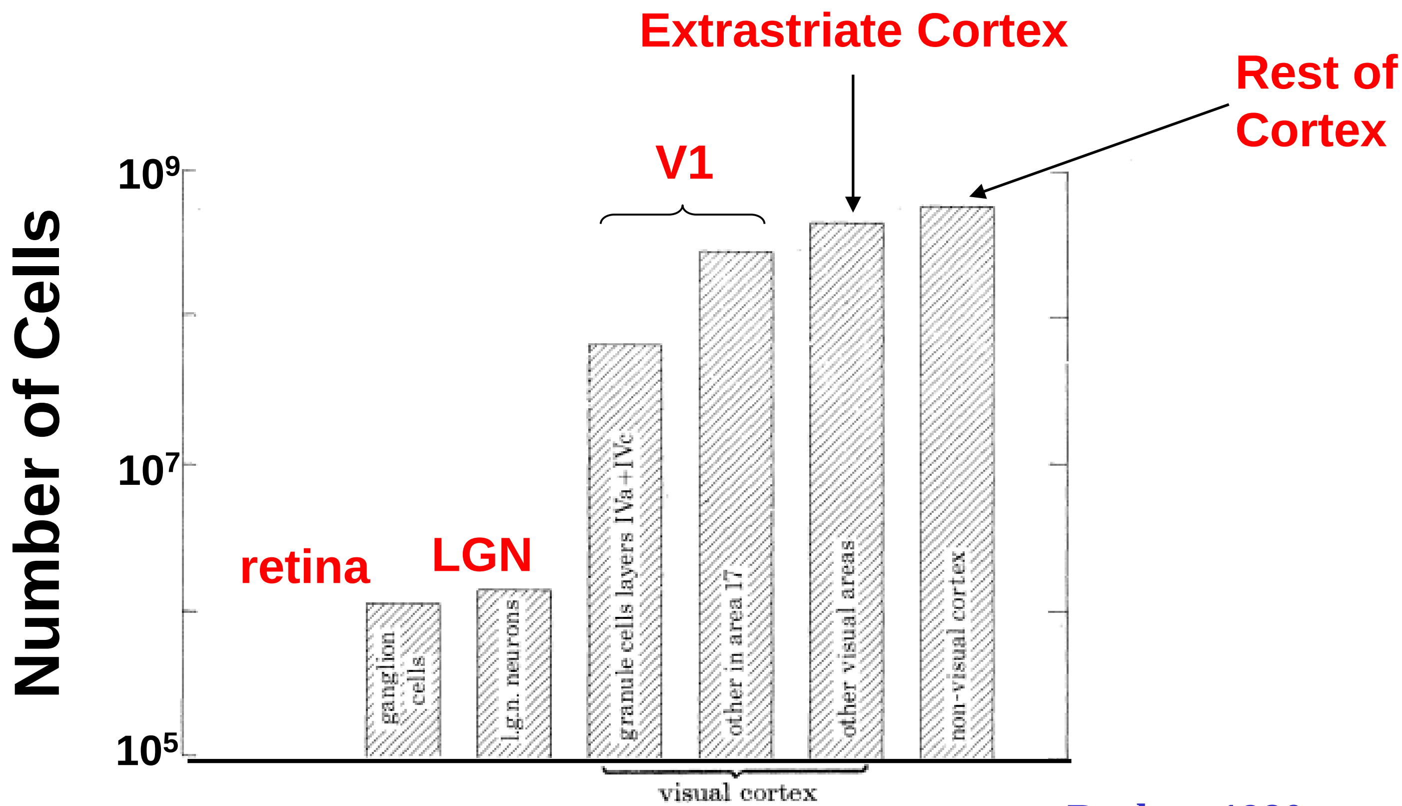
Wiesel Hubel

Hubel/Wiesel movie #1

Central Visual Pathways



Neurons in the Visual Pathway

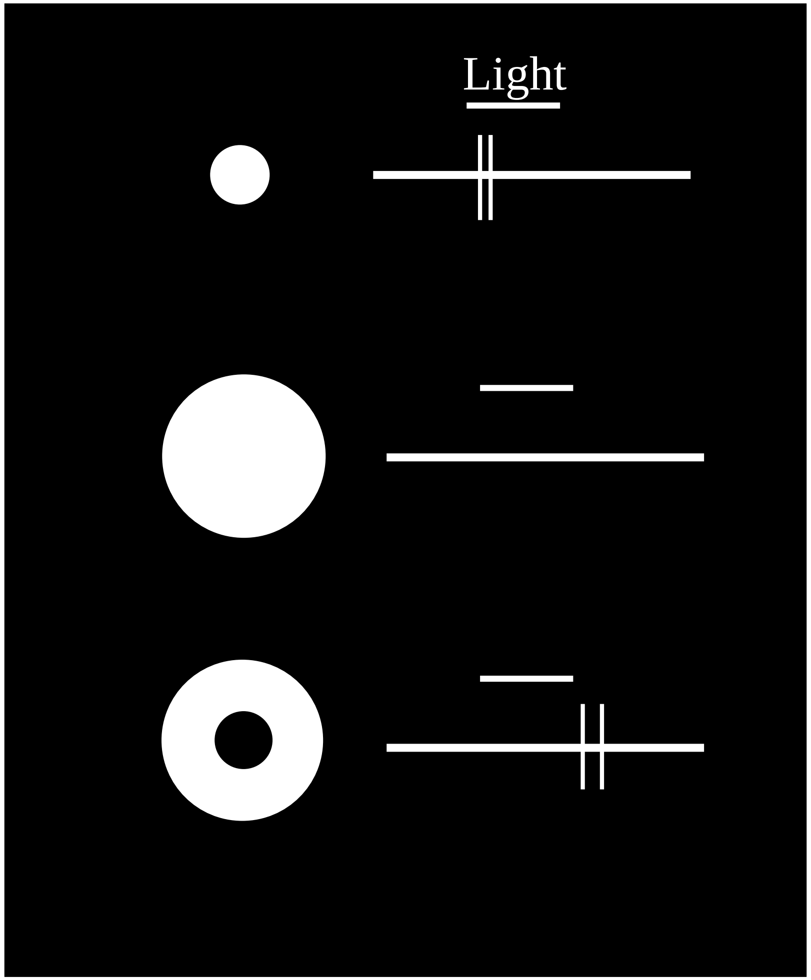


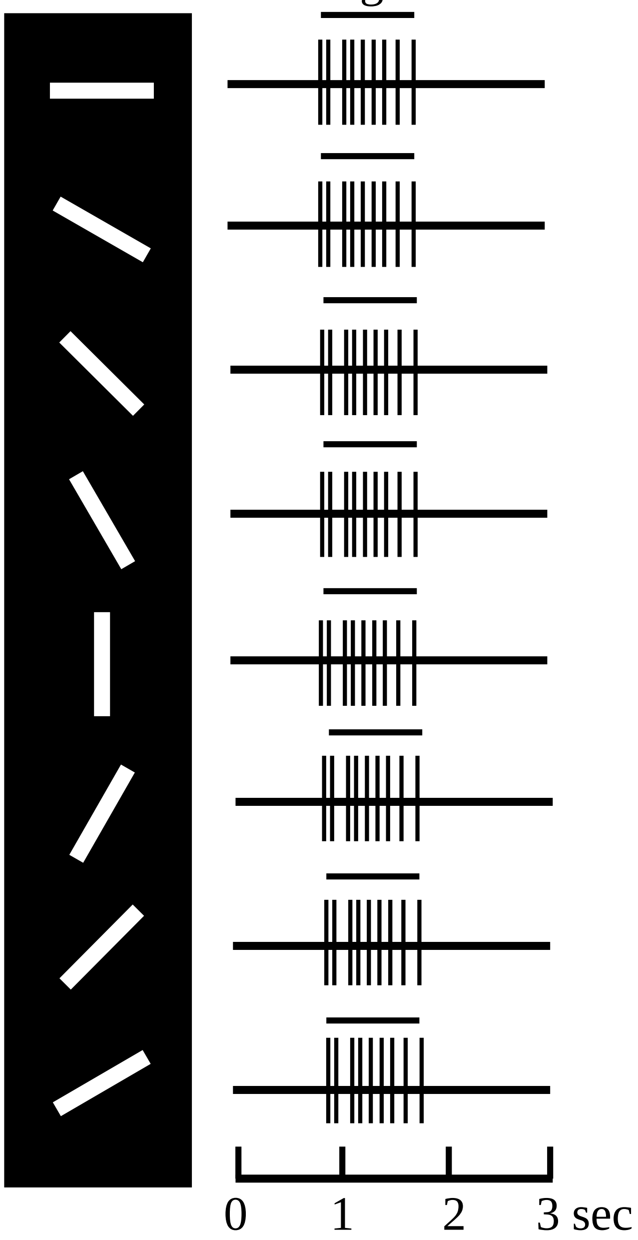
Barlow, 1980

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

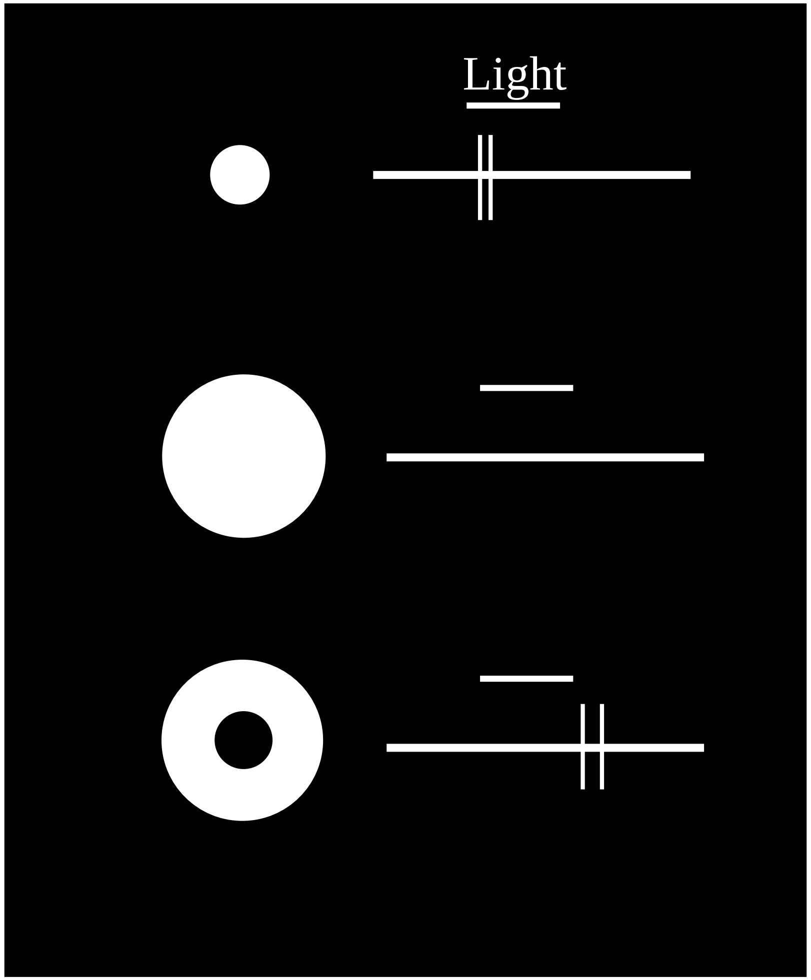
Not Selective



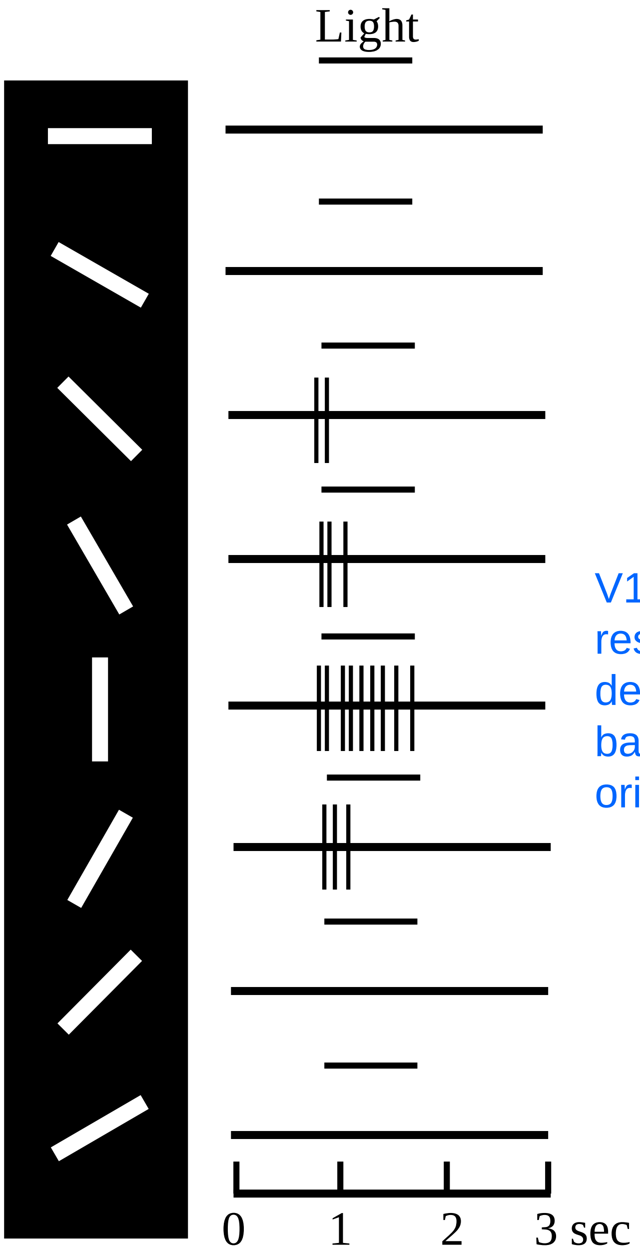


LGN responses do not depend on the orientation of a bar.

Neuronal responses in V1

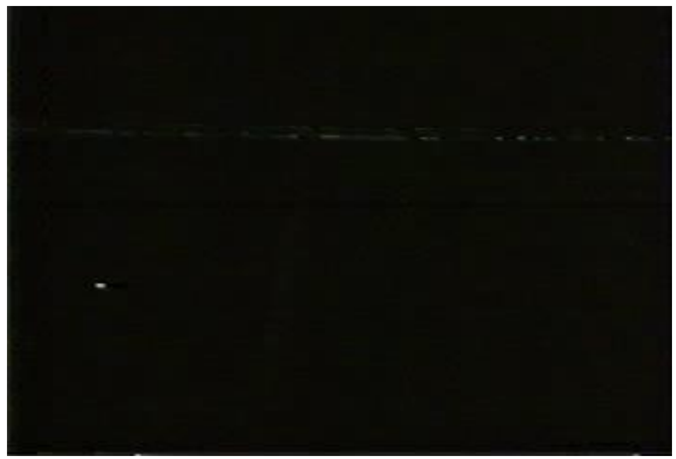


When probed with a small spot, a V1 cell behaves somewhat like an LGN cell.



V1 responses depend on bar orientation

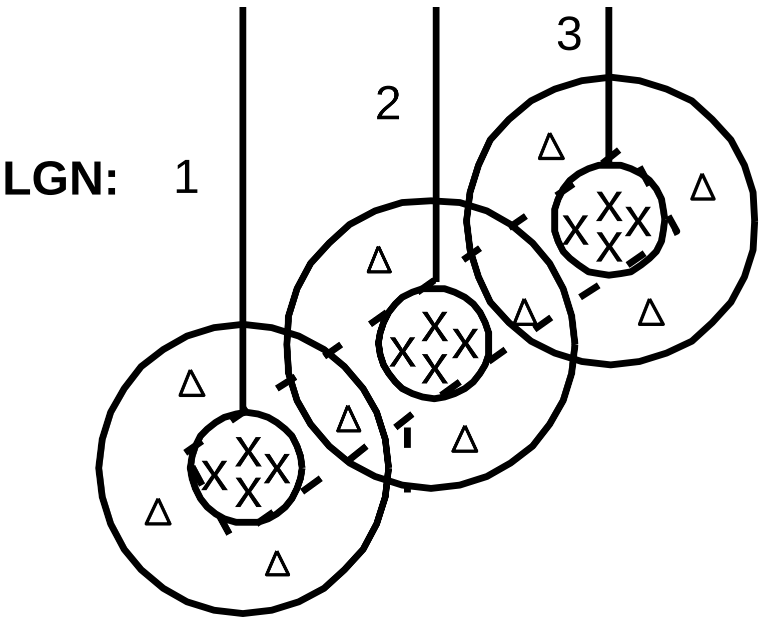
Orientation selectivity is found in V1



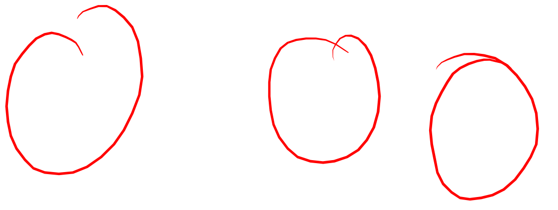
Wiesel Hubel

Hubel/Wiesel movie #2

A Simple Cell Model



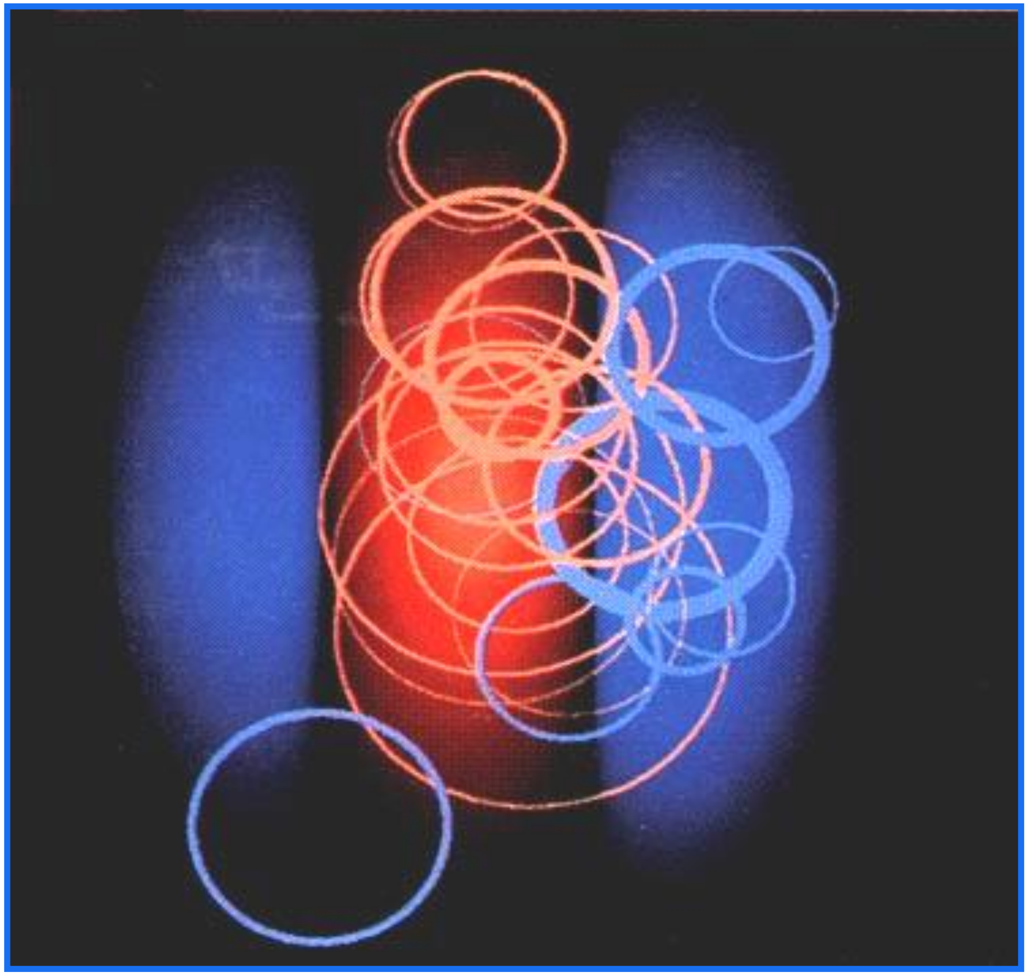
Sum UP



V1

Hubel & Wiesel 1962

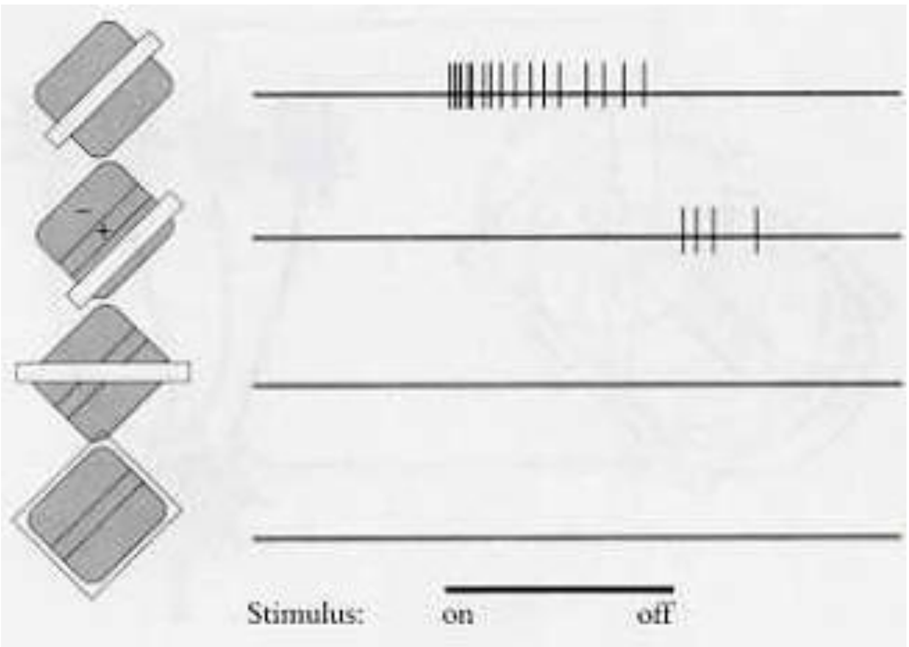
A Simple Cell Model Confirmed



Alonso & Reid, 1995

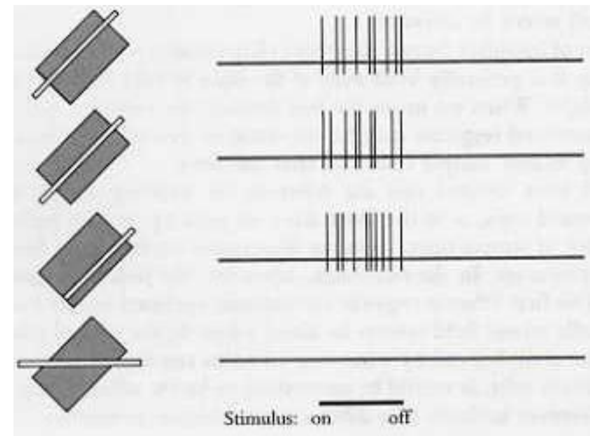
Two kinds of orientation-selective cells in visual cortex

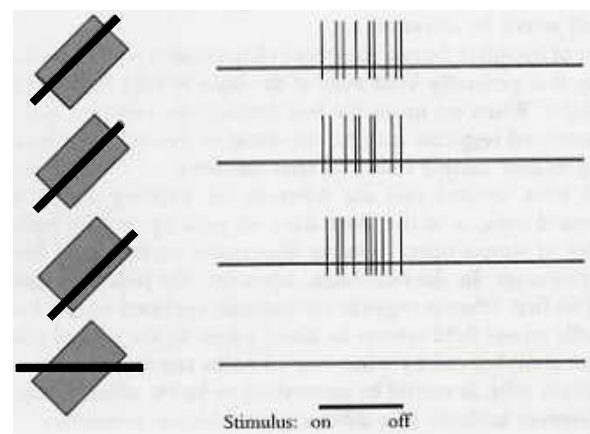
Simple Cell



Hubel and Wiesel

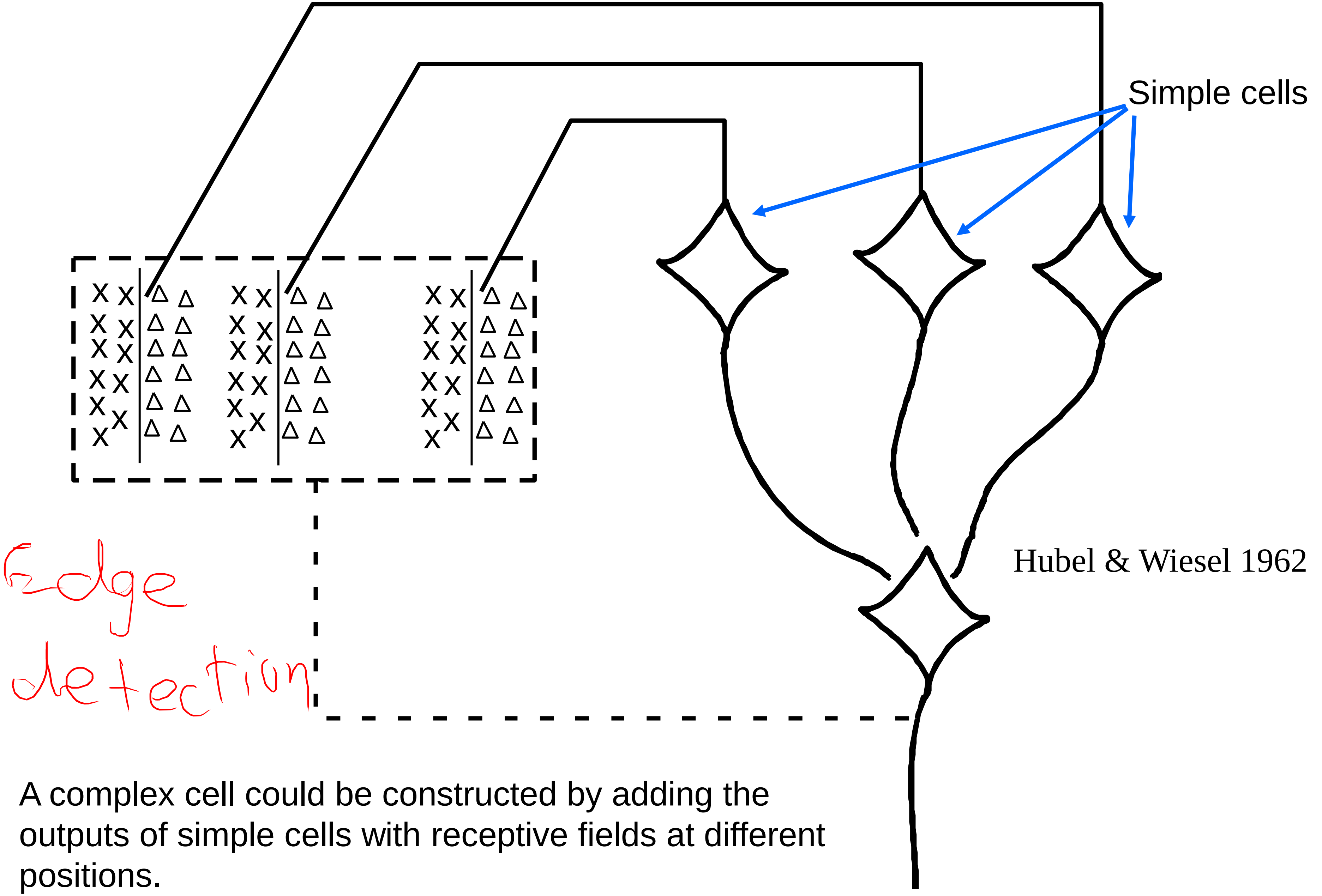
Complex Cell





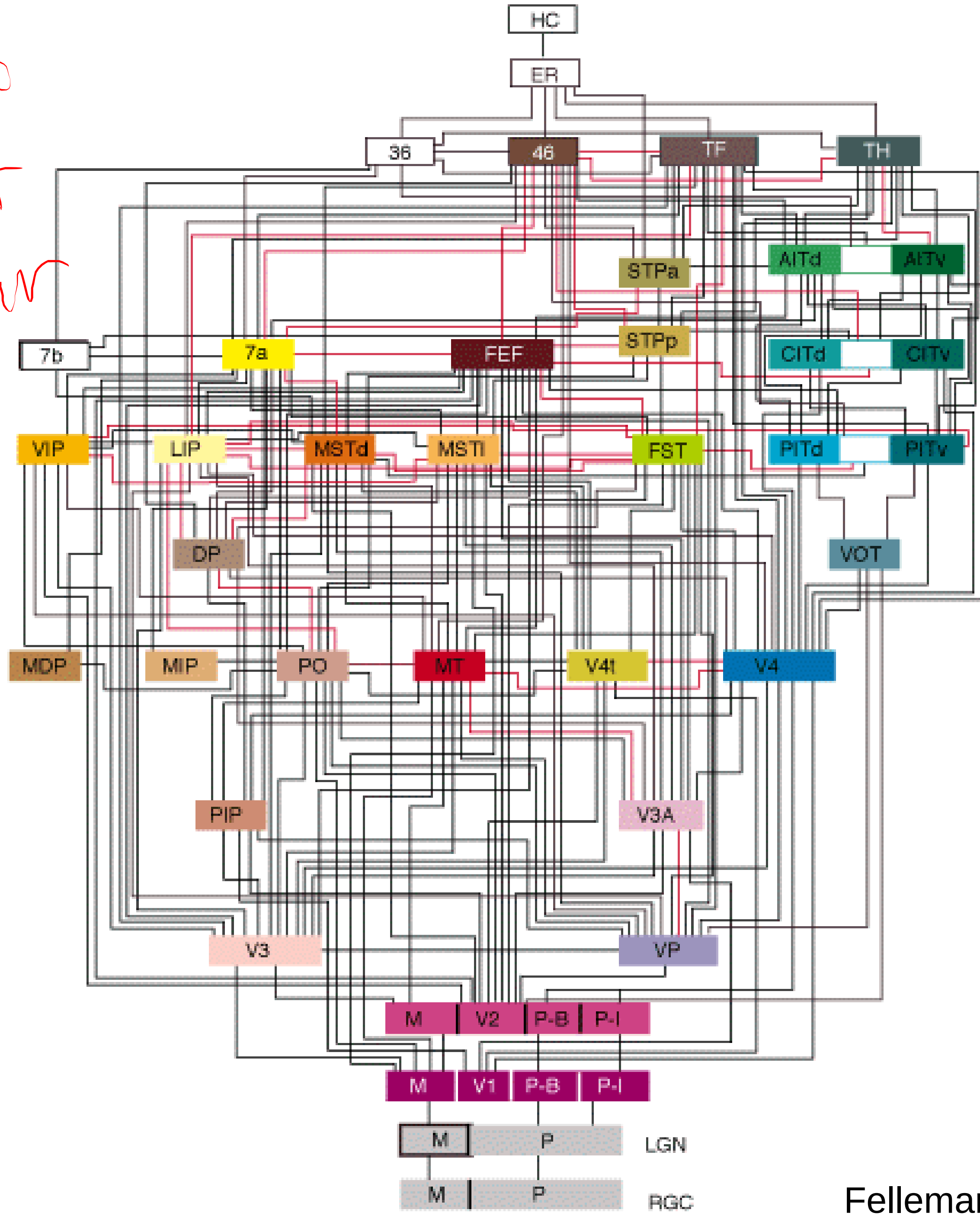
Unlike simple cells, complex cells have no discernable subregions, and they respond equally well to light or dark bars on a gray background.

A Complex Cell Model



A complex cell could be constructed by adding the outputs of simple cells with receptive fields at different positions.

Complex
Abstract
Non-linear



Felleman and Van Essen, 1991


805 ms
75
50
25
albert [0]
art [1]
baby1 [2]
bogart [3]
brando1 [4]
clinton [5]
cole [6]
75
50
25
elvis [7]
jetson [8]
newman [9]
oj [10]
oj_neg [11]
reagan [12]
sting [13]

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Action Potentials and Spike Trains

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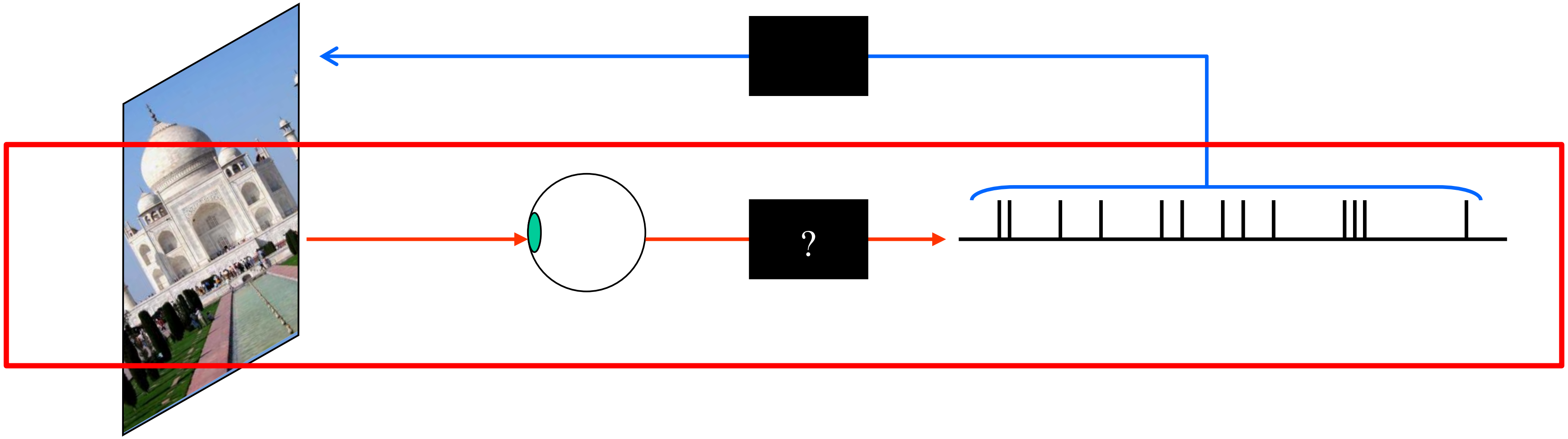
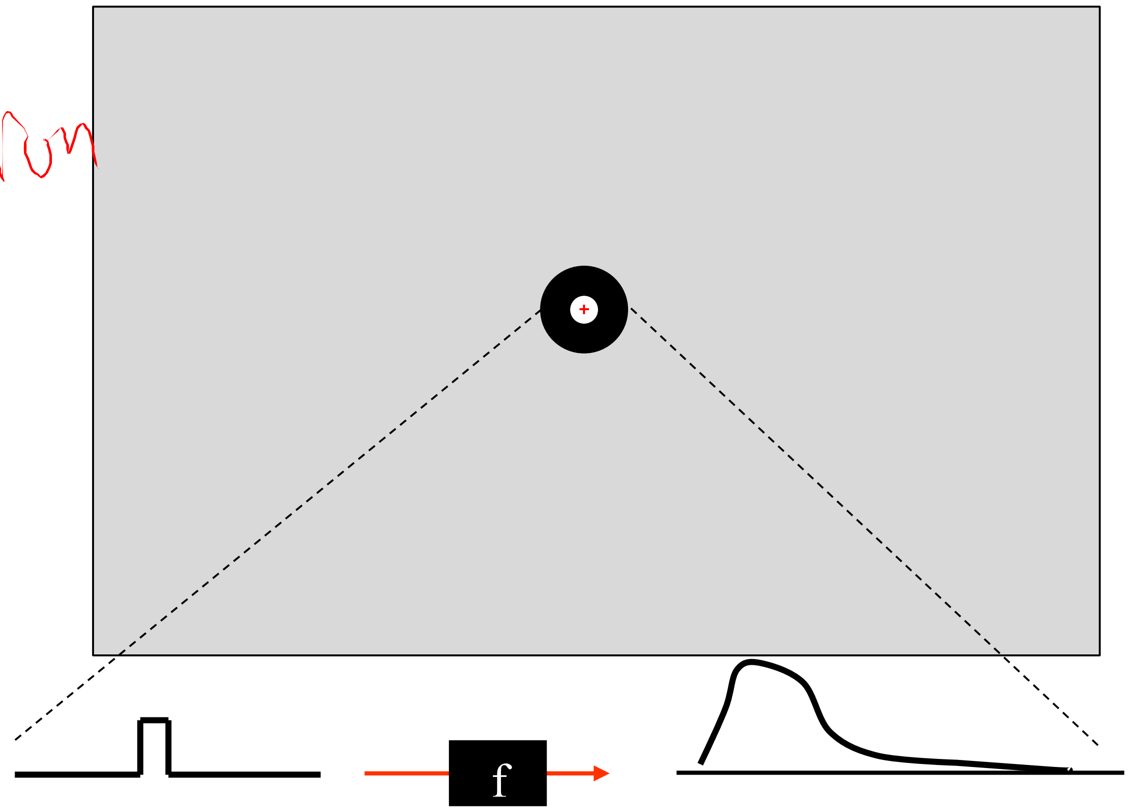


Building encoding models

Hubel and Wiesel were building crude encoding models. Consider the receptive field of an LGN neuron:

Linear
correlation
Limited in
space



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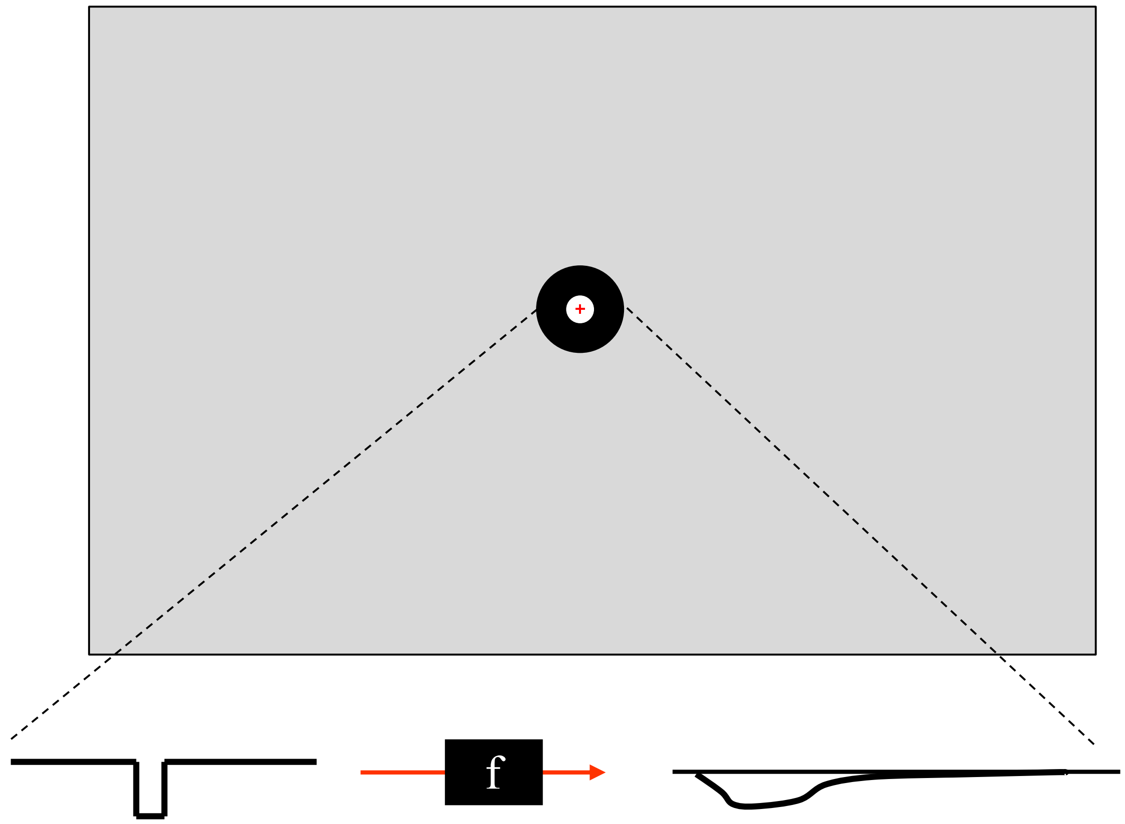

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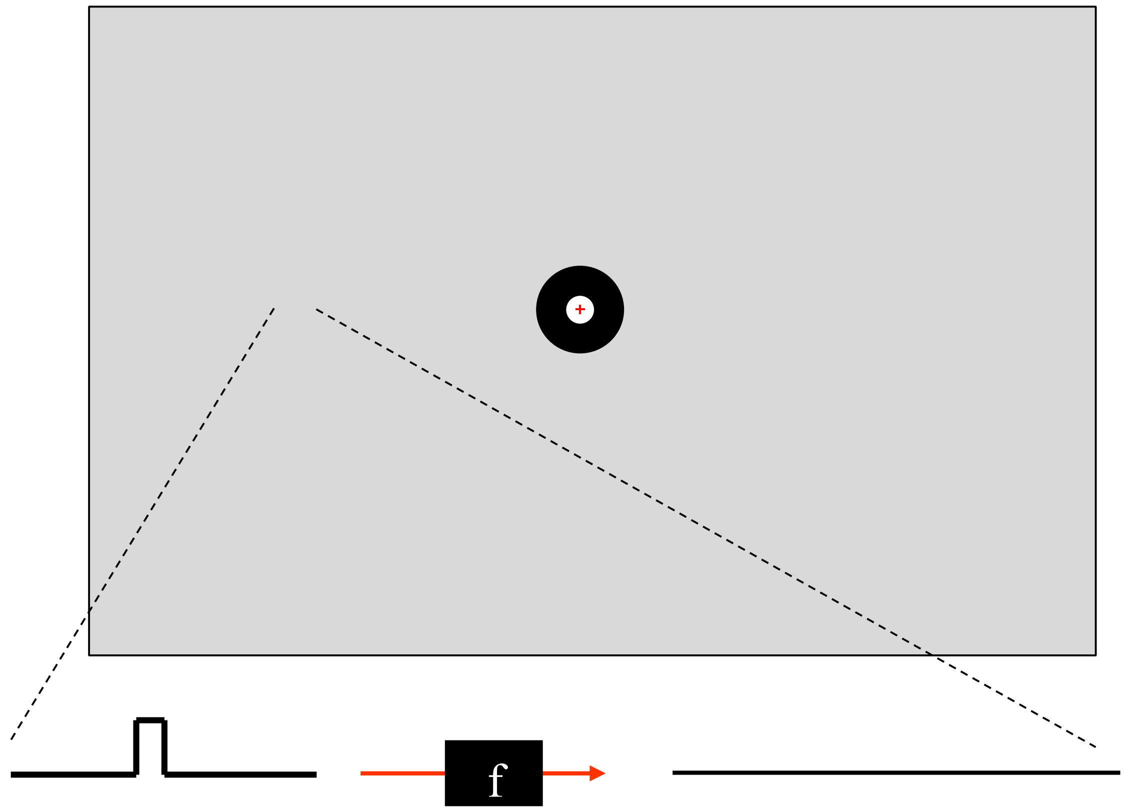


Building encoding models

Hubel and Wiesel were building crude encoding models.

A spot of light placed in the center of an LGN receptive field elicited a response some time later. So we can say that the input and the output were **correlated**, with some delay. Mathematically, we can detect input-output relationships with the **cross-correlation function**.

Cross-Correlation

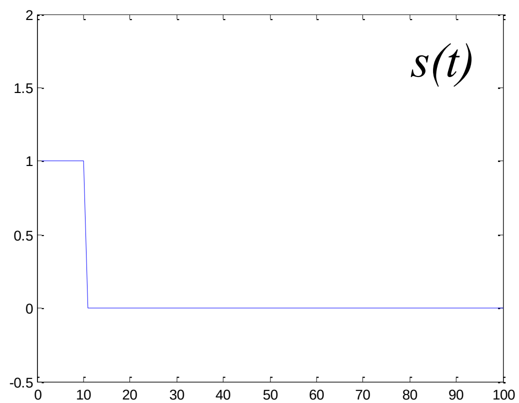
Cross-correlation is a way of looking for a consistent effect of the input *s* on the output *r*. The cross-correlation is a function of the delay τ:

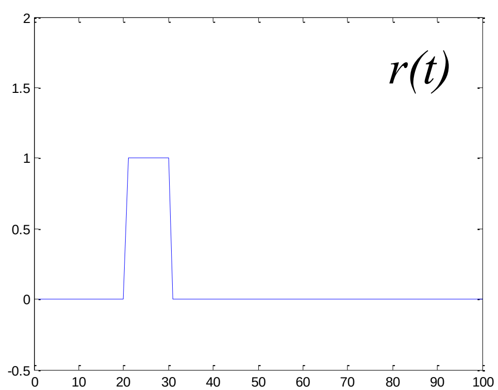
Strength of Relation

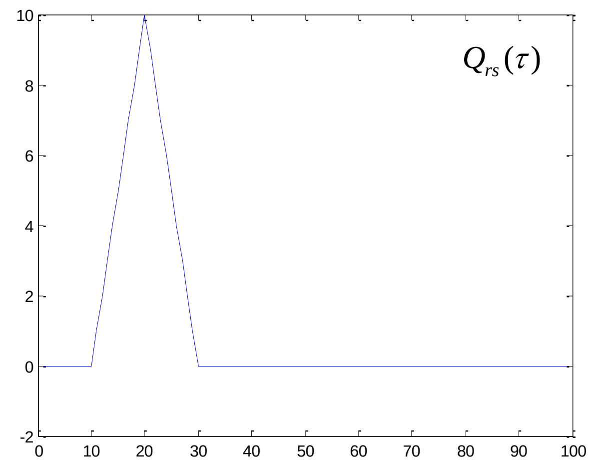
$$Q_{rs}(\tau) = \frac{1}{T}\int_0^T r(t)s(t+\tau)dt$$

Integrate through time

What does s do to r with delay τ



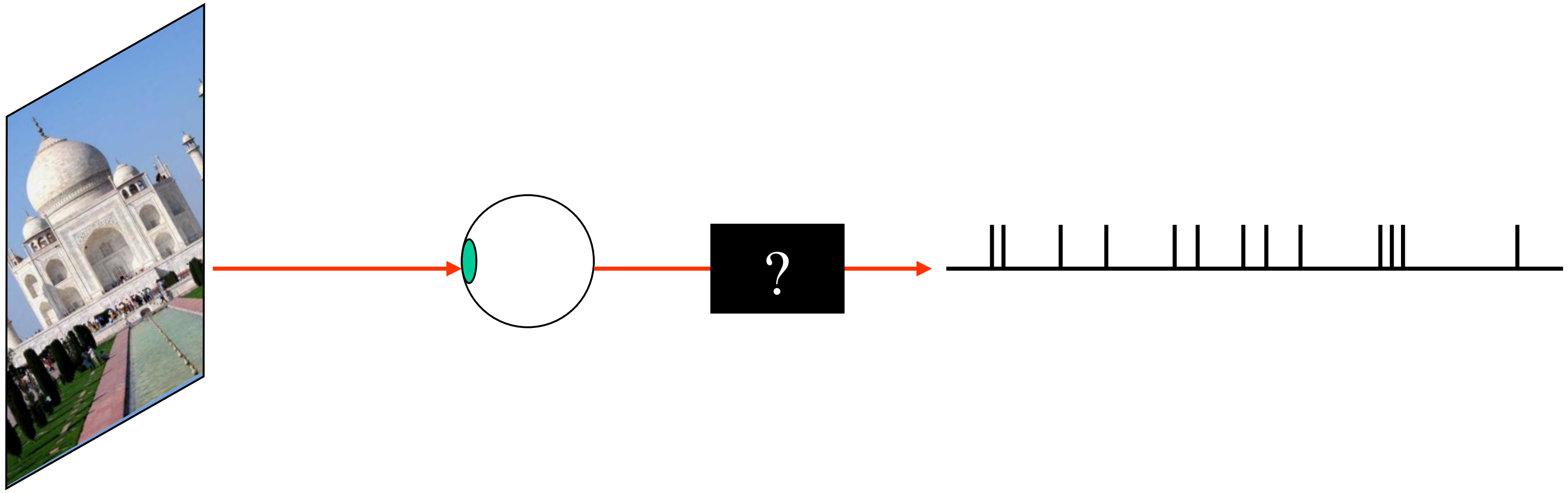




τ

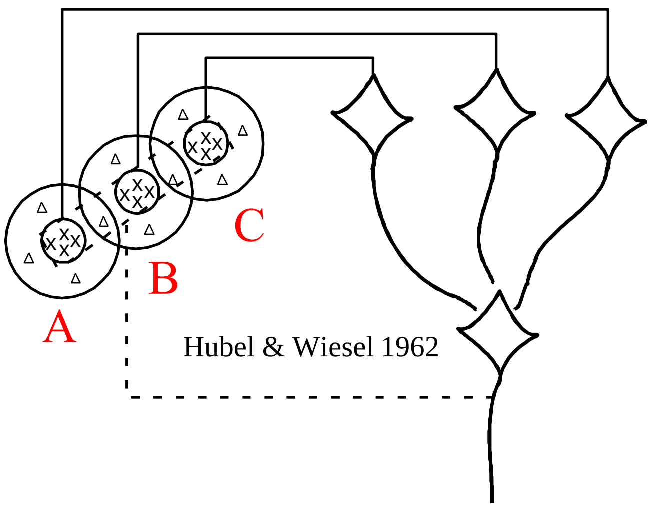
Action Potentials and Spike Trains

Encoding: If I know the stimulus can I predict the spike train?



Answer: Maybe, but we know more than that. We know how neurons work…

How neurons work



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. In a linear system, the response to each individual input is independent of the responses to the other inputs.

So if we assume linear integration, we can profitably study the response of the neuron to individual inputs.

Linear systems have the following two properties:

Superposition: $f(A + B + C) = f(A) + f(B) + f(C)$
Scaling: $f(kA) = kf(A)$

Summation
Linear (Sum is parts added up)
independent

Can study parts independently

Linear systems $\propto$

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

$$L(t) = \int_0^{\infty} f(\tau) s(t-\tau) d\tau$$

Output

Black box

Stimulus

Here L is the output, s is the stimulus, f is the system (the receptive field), and τ is a delay. **How do we find *f*?**

Answer: Cross-correlation.

Cross-Correlation

If we assume that our visual system is linear, then its output is:

Convolution

$$L(t) = \int_0^\infty f(\tau) s(t-\tau) d\tau$$

The cross-correlation between the input and output is:

$$\int_0^\infty L(t) s(t-\sigma) dt =$$

Cross-correlation

Autocorrelation

$$\boxed{\int_0^\infty L(t) s(t-\sigma) dt} = \int_0^\infty f(\tau) \boxed{\left[\int_0^\infty s(t-\sigma) s(t-\tau) dt \right]} d\tau$$

Autocorrelation

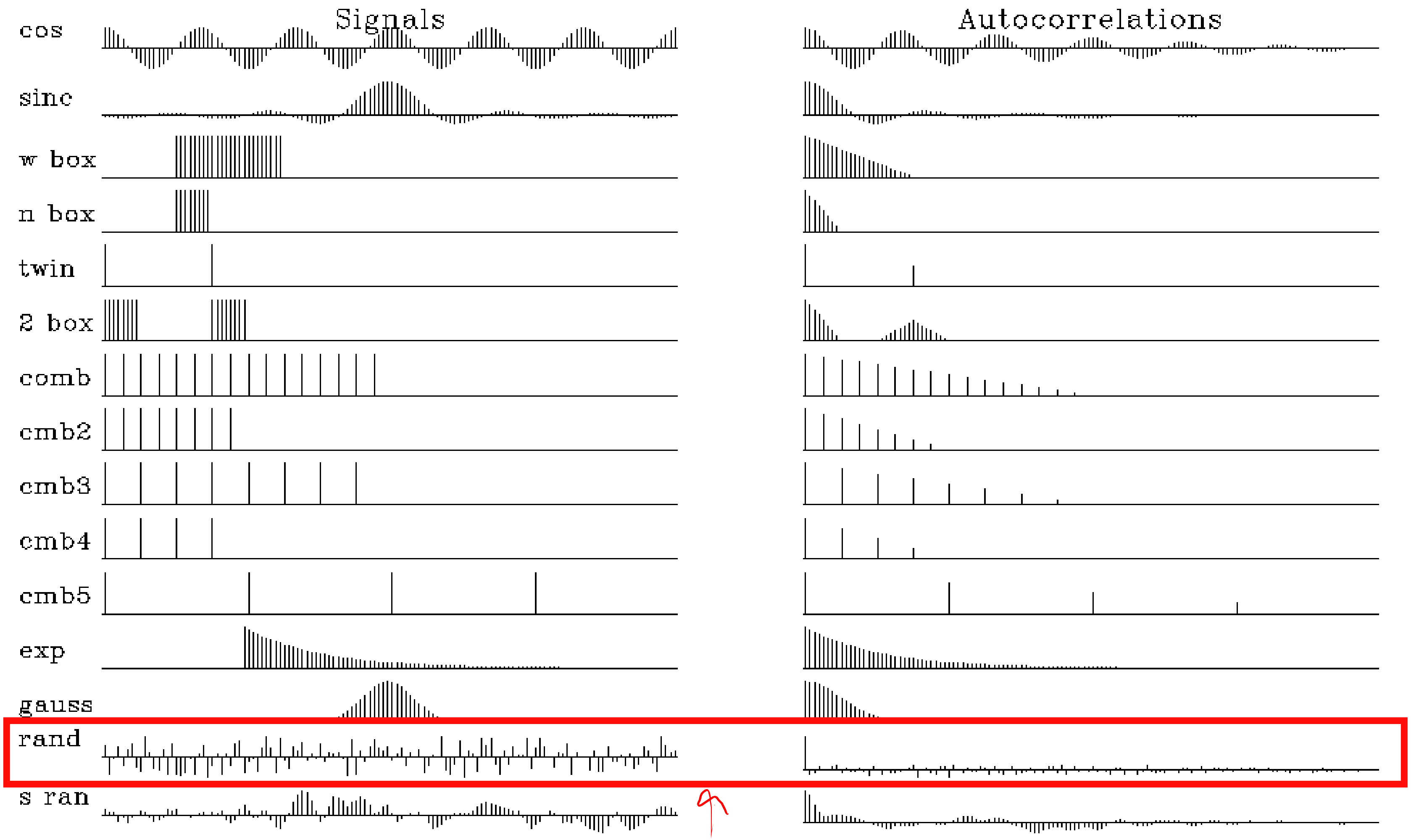
The autocorrelation Q_{SS} of a stimulus s is the stimulus correlated with itself:

$$Q_{SS}(\tau) = \frac{1}{T}\int_0^T dt s(t) s(t+\tau)$$

Autocorrelation functions will always have a peak at $\tau = 0$, since a function is always correlated with itself. Most functions will have additional peaks, particularly if the function is periodic.

Decomposition

Autocorrelation

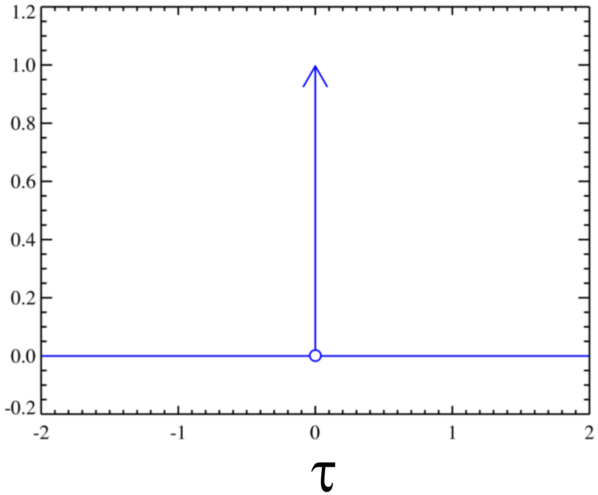


Autocorrelation is flat

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.

Cross-Correlation

Cross-correlation is a way of finding areas of overlap between two signals. If we assume that our visual system is linear, then its output is:

Assignment

$$L(t) = \int_0^\infty f(\tau) s(t-\tau) d\tau$$

The cross-correlation between the input and output is:

$$\int_0^\infty L(t) s(t-\sigma) dt = \int_0^\infty s(t-\sigma) \int_0^\infty f(\tau) s(t-\tau) d\tau dt$$

Cross-correlation

Autocorrelation

$$\boxed{\int_0^\infty L(t) s(t-\sigma) dt} = \int_0^\infty f(\tau) \boxed{\left[\int_0^\infty s(t-\sigma) s(t-\tau) dt\right]} d\tau$$

Autocorrelation of a random stimulus s is 0 unless $\sigma = \tau$.

Cross-Correlation

Cross-correlation

Autocorrelation

$$\boxed{\int_0^\infty L(t)s(t-\sigma)dt} = \int_0^\infty f(\tau)\boxed{\left[\int_0^\infty s(t-\sigma)s(t-\tau)dt\right]}d\tau$$

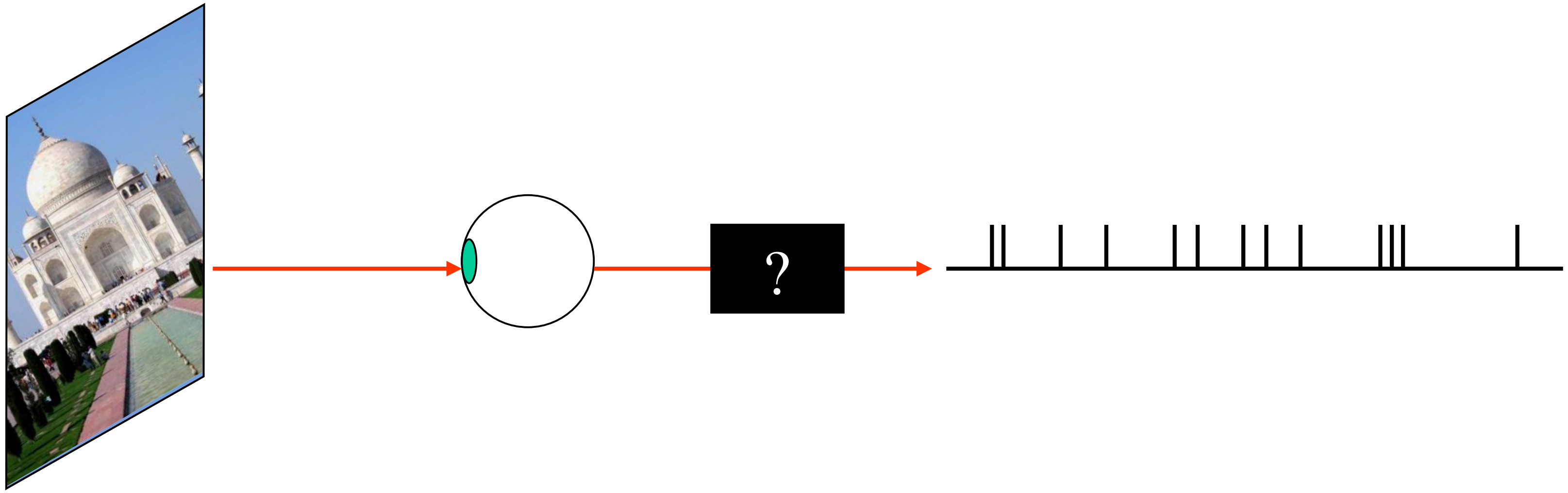
The autocorrelation of a random stimulus s is 0 unless $\sigma = \tau$. So:

$$\int_0^\infty L(t)s(t-\sigma)dt = \int_0^\infty cf(-\sigma)d\tau = cf(-\sigma)$$

Key result: For a random stimulus s, the cross-correlation of the stimulus and response L gives us the receptive field f.

Action Potentials and Spike Trains

Encoding: If I know the stimulus can I predict the spike train?



Answer: Yes, if the neuron is (reasonably) linear. Then we can stimulate it with random noise and compute the cross-correlation between input and output.

This is actually very easy to do…

Spike-triggered averaging

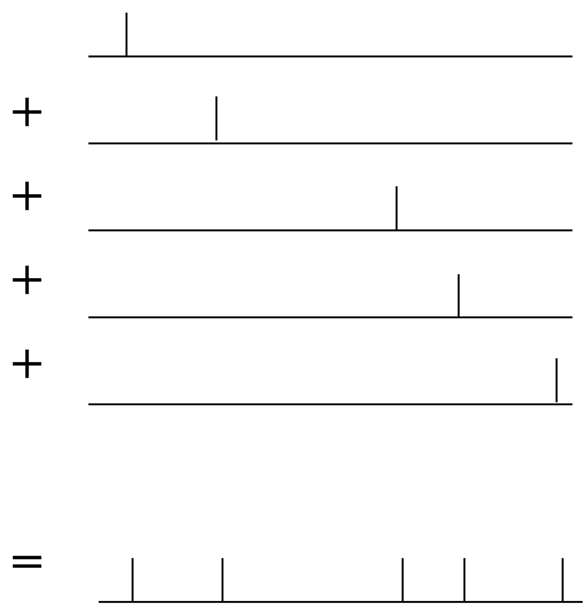
For spike trains, the neuronal output is (roughly) 1 or 0 at any given moment, so we can write the response *r* as a sum of delta functions:

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

← time of spike

where t_i is the time of the i^{th} spike. That is,

$L(t) =$



Sum of delta functions

Spike-triggered averaging

Recall that:

$$Q_{RS}(-\sigma) = \frac{1}{T}\int_0^T \sum_{i=1}^{n} L(t)s(t-\sigma)dt$$

This can be rewritten:

$$Q_{RS}(-\sigma) = \frac{1}{T}\int_0^T \sum_{i=1}^{n} \delta(t-t_i)s(t-\sigma)dt$$

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

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

← Delay

Average stimuli used

In other words, to find the value of *D* at a given value of σ, simply average the stimuli that preceded each spike by σ ms. This approach is called *spike-triggered averaging*.

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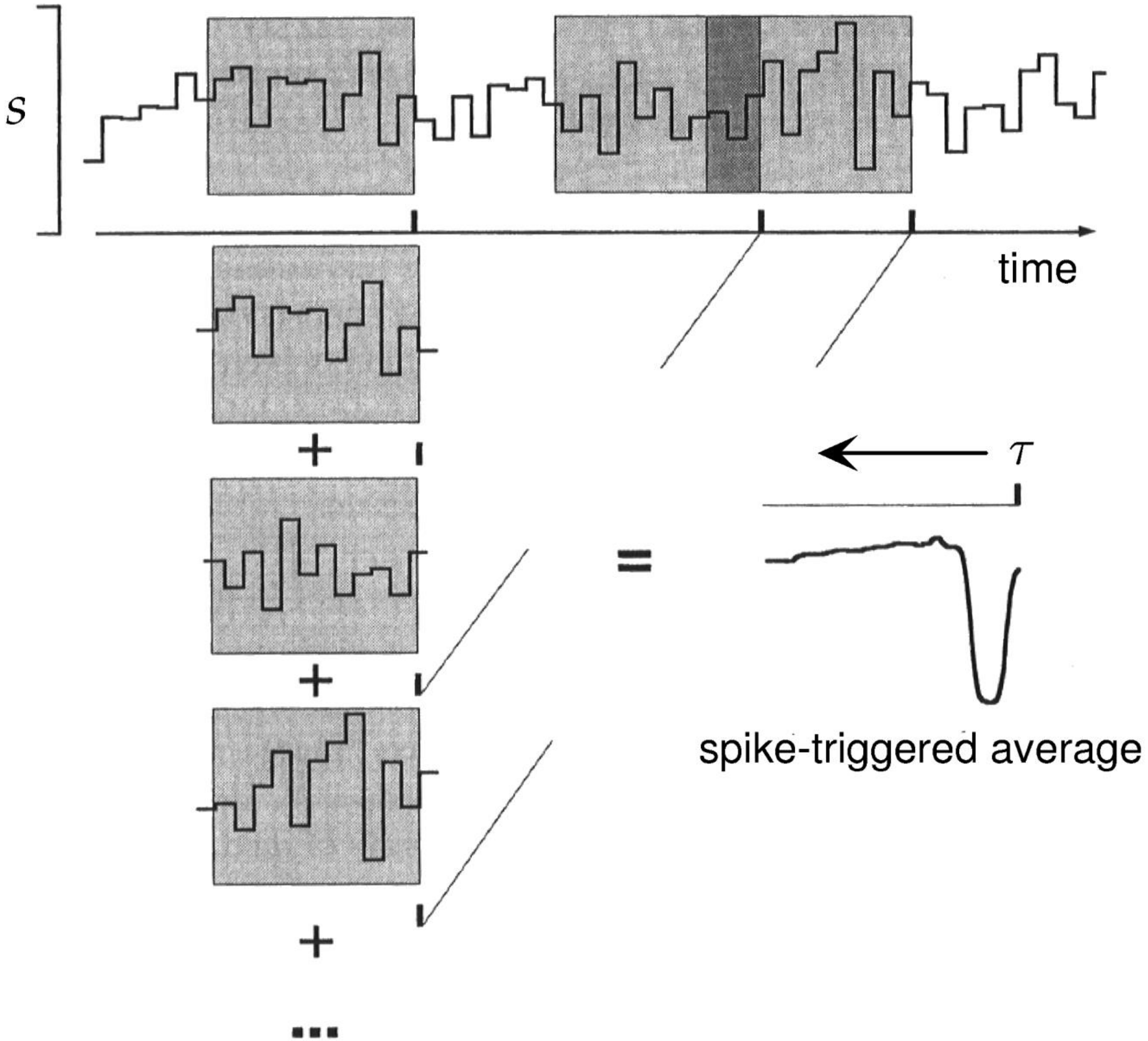


Spike-triggered averaging

Assumptions behind spike-triggered averaging:

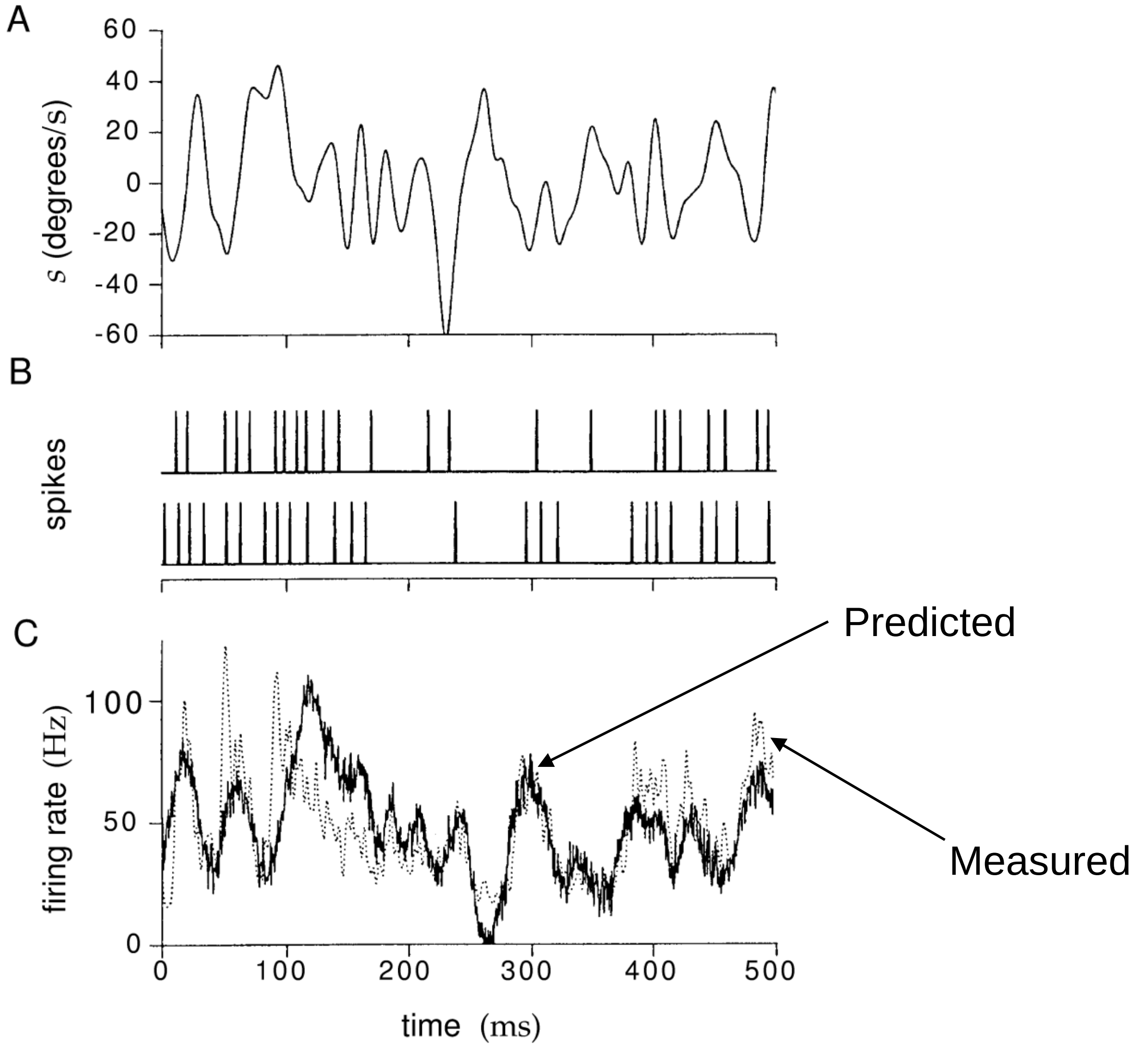
1) Spikes depend on the stimulus, rather than attention, anesthetic levels, other spikes, etc.
2) The stimulus autocorrelation is flat, which usually means that the stimulus is white noise.
3) The cell's response is linear!

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

$$R_{est}(t) = r0 + \int_0^\infty f(\tau)s(t-\tau)d\tau$$

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

Easily checkable

Static Nonlinearities

Recall the linear response:

$$L(t) = \int_0^\infty f(\tau) s(t-\tau) d\tau$$

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

$$r_{est}(t) = r0 + F(L(t))$$

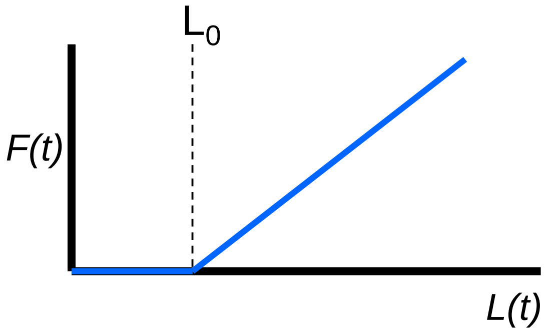
where *F* can in principle be any function. In practice it will have the properties of real neurons: nonnegativity, saturation, and a few others.

Static Nonlinearities

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

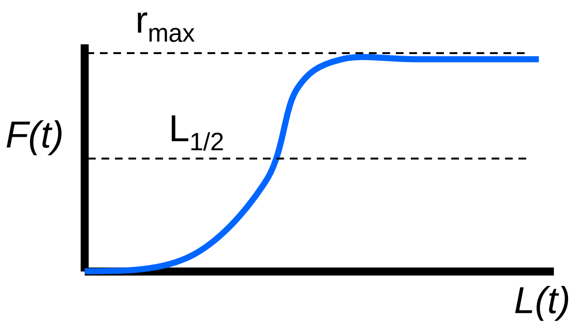
$$F(L) = G[L - L_0]_+$$

This function cannot be negative.

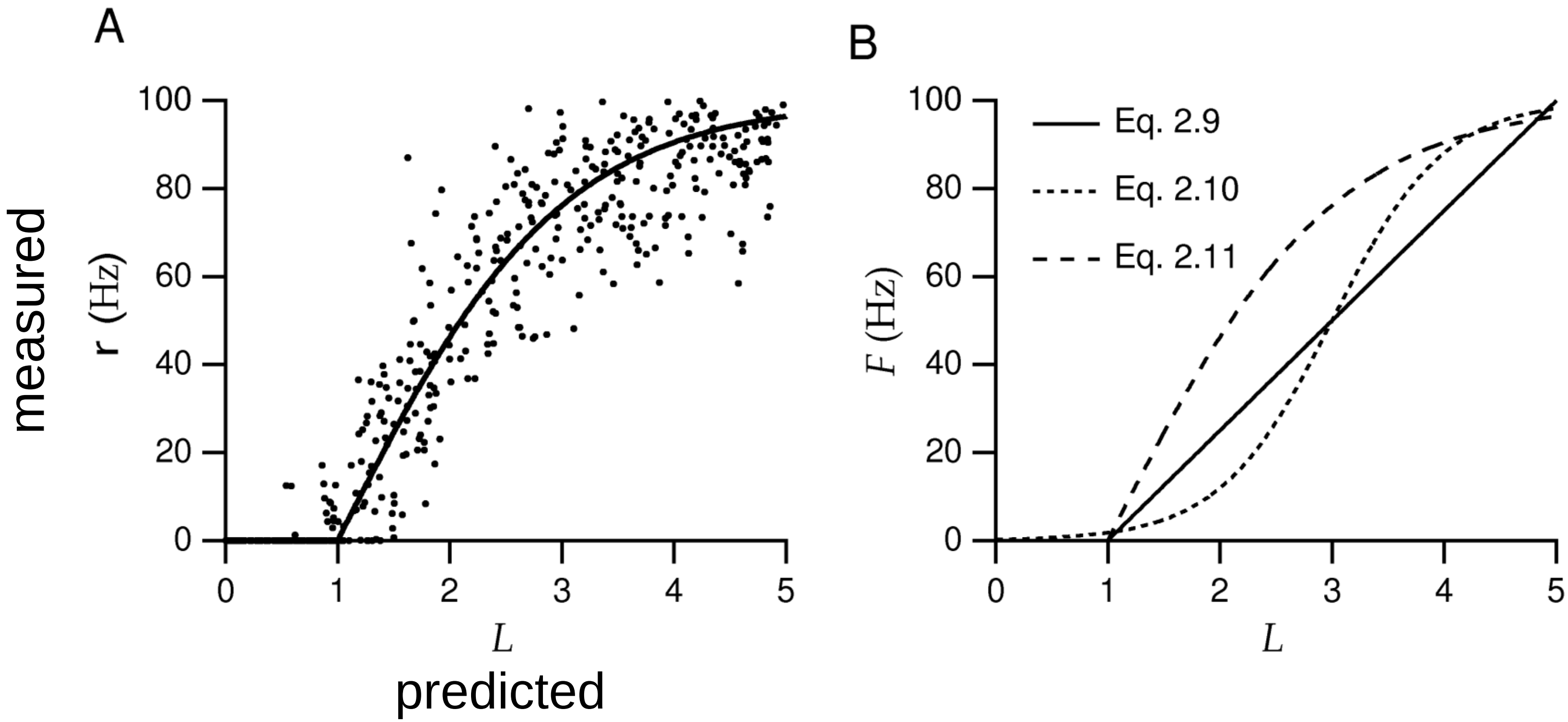


A **sigmoid** function has a threshold, and it saturates for large inputs:

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



Static Nonlinearities



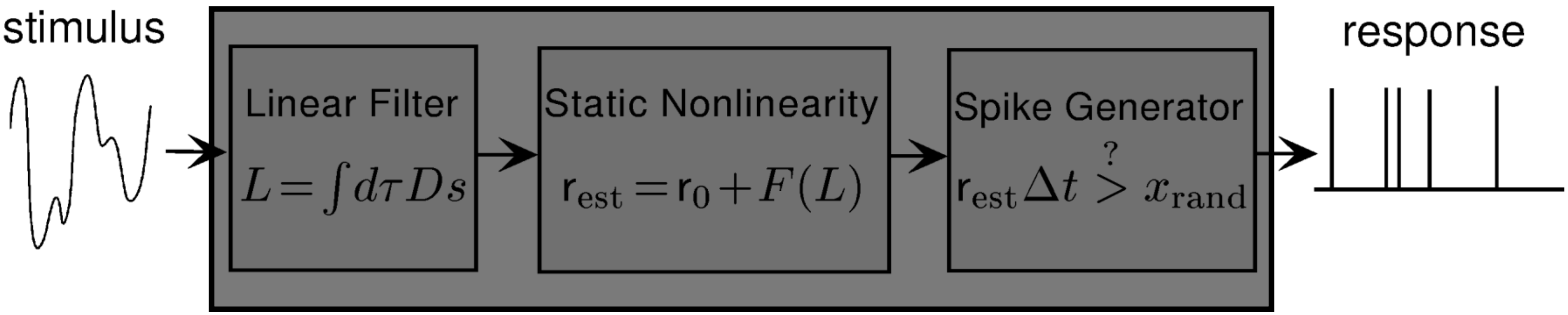
If the linear model were sufficient, the relationship between predicted and measured response would be a straight line. In practice there is usually a nonlinear relationship.

Static Nonlinearities

Static nonlinearities:

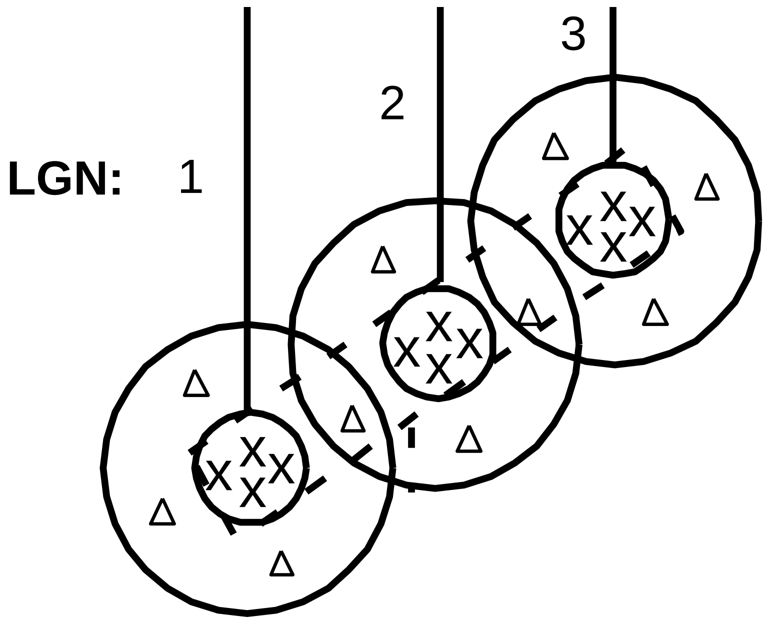
1) Depend only on the response at an instant in time.
2) Do not depend directly on the stimulus. This is important because other nonlinearities require a large amount of data to compute.
3) Typically have a threshold and a saturation point

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.

Linear filtering approach: Application to V1 simple cells



Hubel & Wiesel 1962

Linear filtering approach: Application to V1 simple cells

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

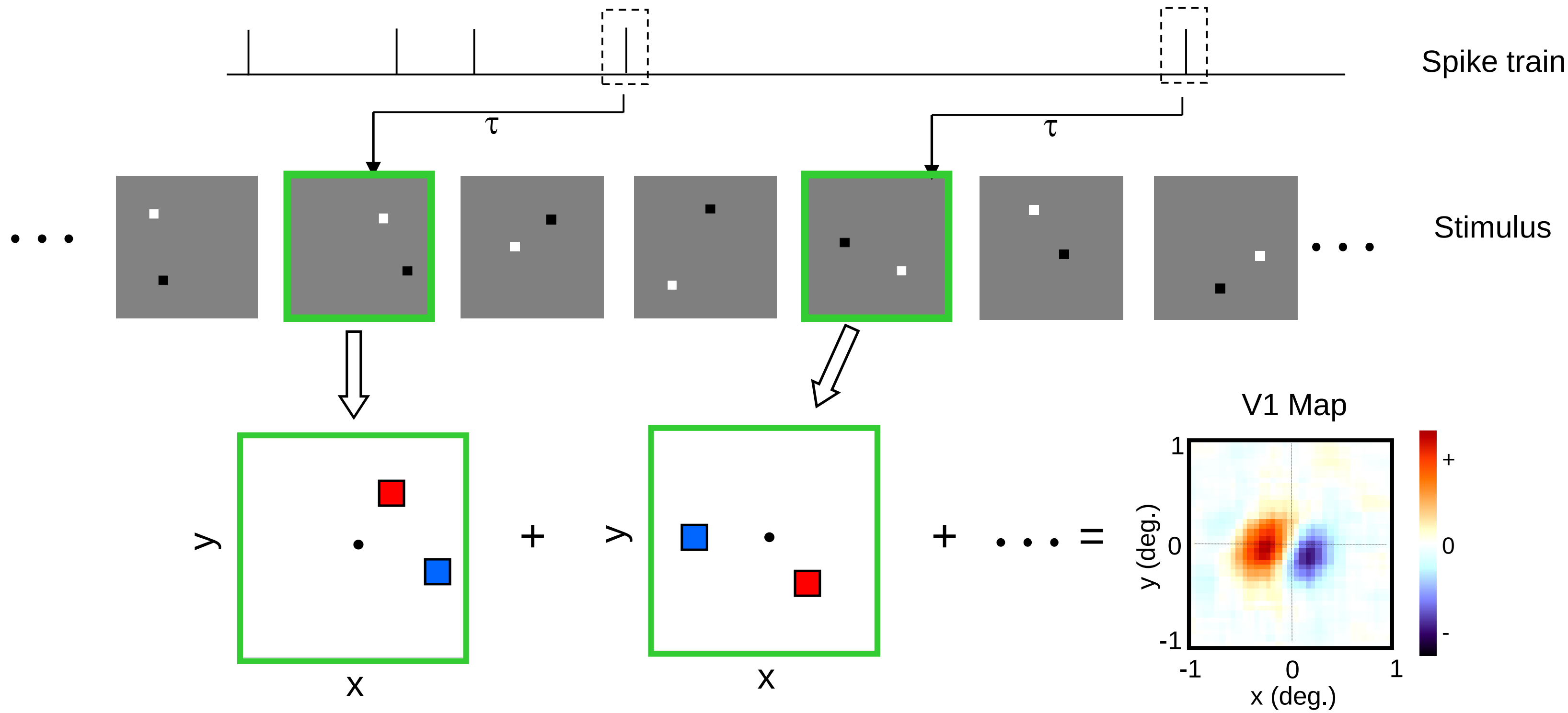
$$L(t) = \int_0^\infty f(\tau)s(t-\tau)d\tau$$

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:

$$L(t) = \int_0^\infty d\tau \int dxdy\, f(x,y,\tau)s(x,y,t-\tau)$$

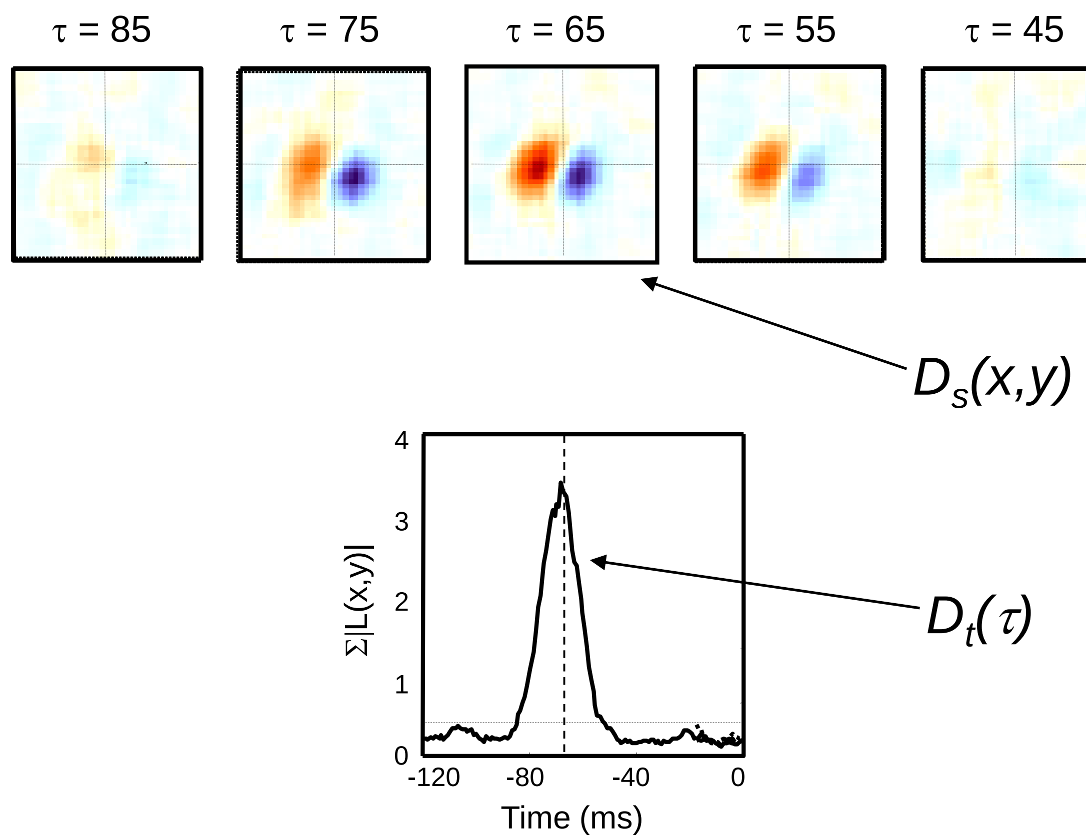
Note that the output depends only on time, so we need to integrate over the spatial dimensions.

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.

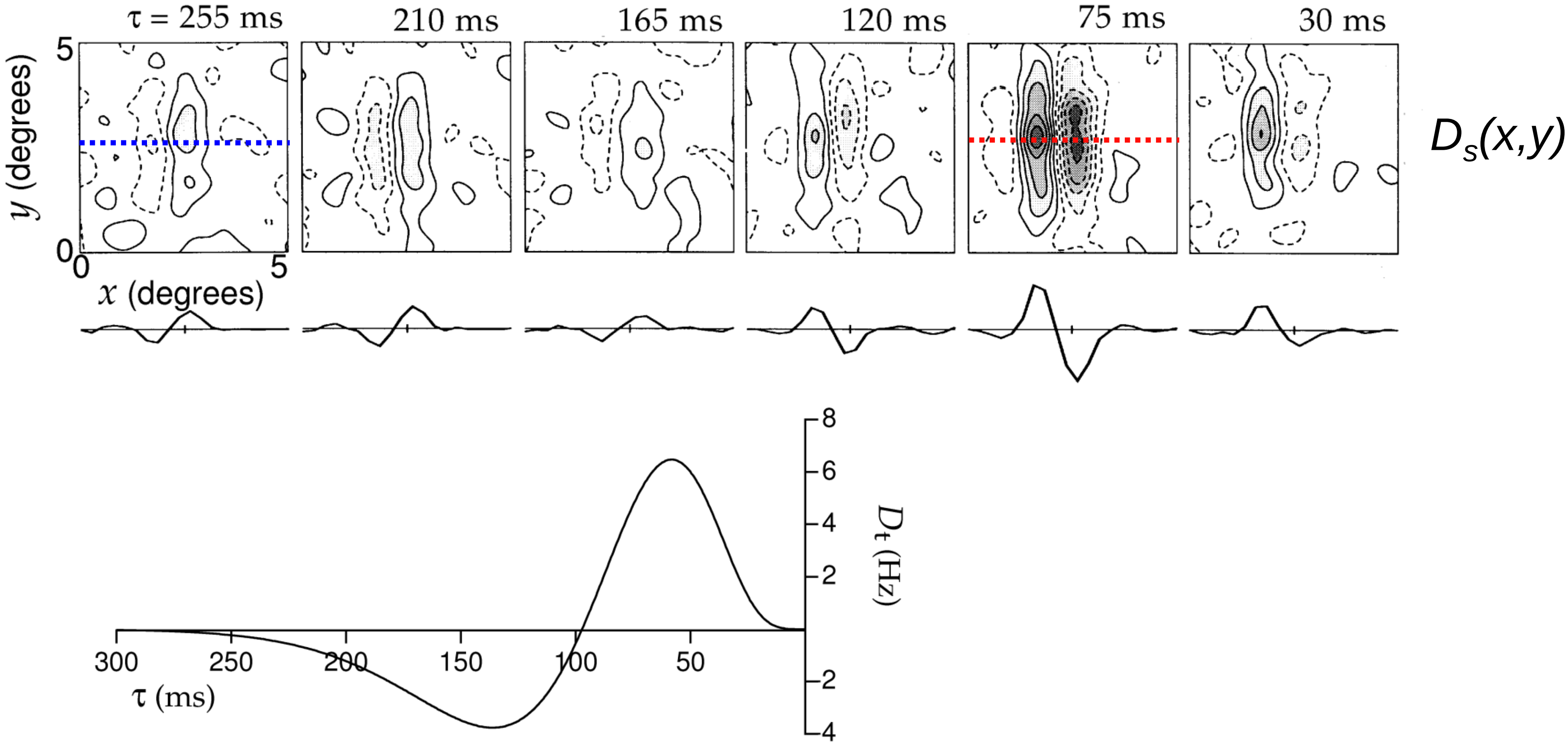
Space-time separability

For most simple cells, the spatial structure of the receptive field does not change over time. Only the amplitude changes. For these cells, we can rewrite the linear filter:

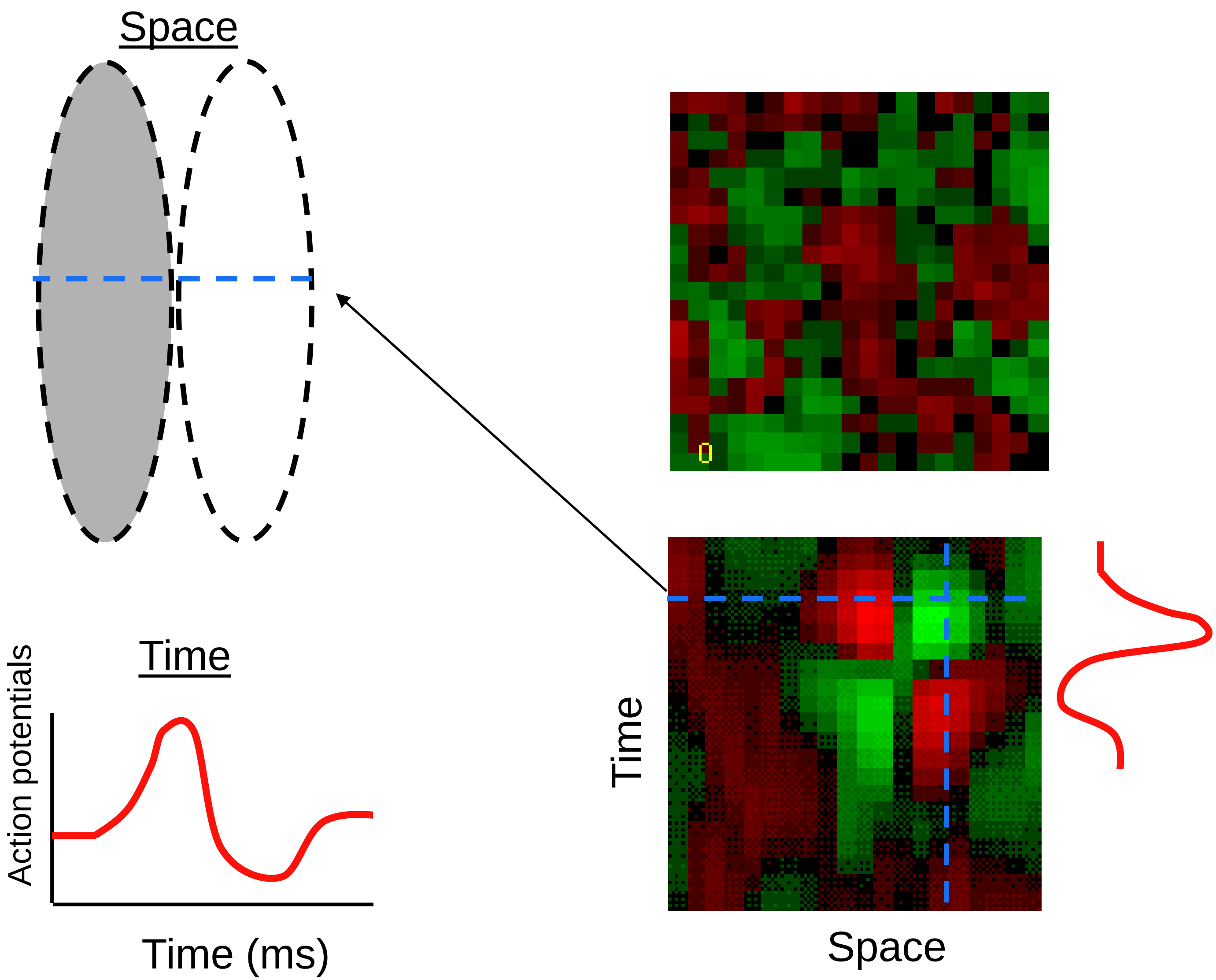
$$f(x, y, \tau) = f_s(x, y)\, f_t(\tau)$$

Such cells are called **space-time separable**, since their responses can be described by separate functions for space and time.

Another V1 simple cell

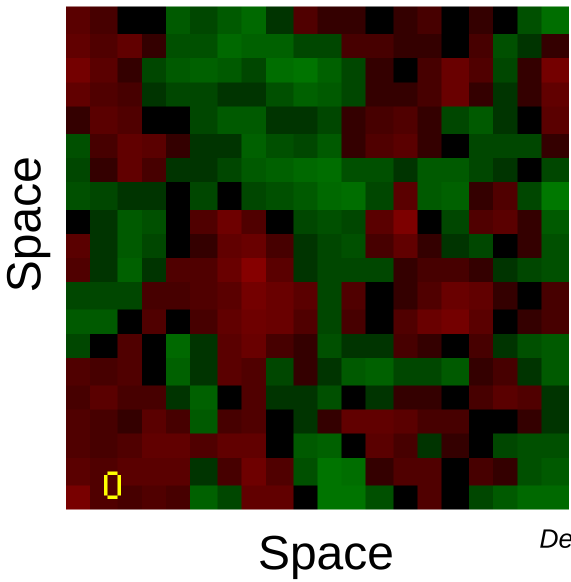


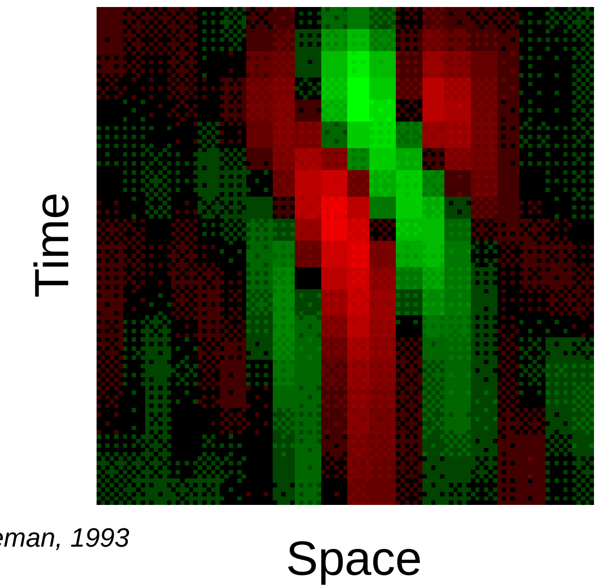
Still another V1 simple cell



DeAngelis, Ohzawa, and Freeman, 1993

Yet another V1 simple cell



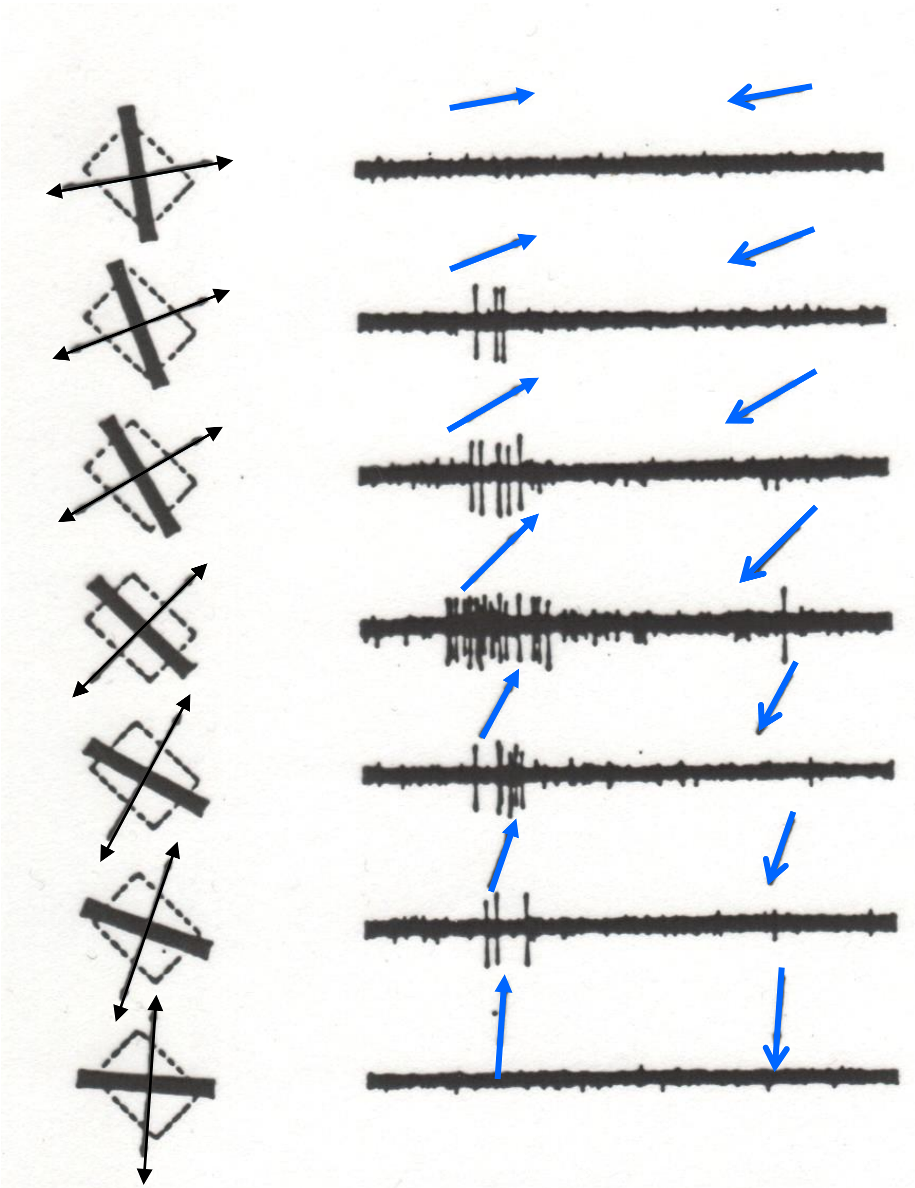


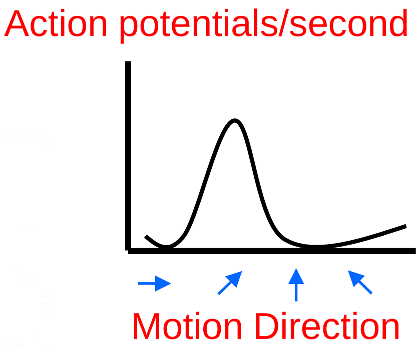
DeAngelis, Ohzawa, and Freeman, 1993

Space-time change
Motion

In some cells the spatial receptive fields change over time. These cells are not space-time separable.

Selectivity for motion direction in visual cortex





Hubel and Wiesel, 1968

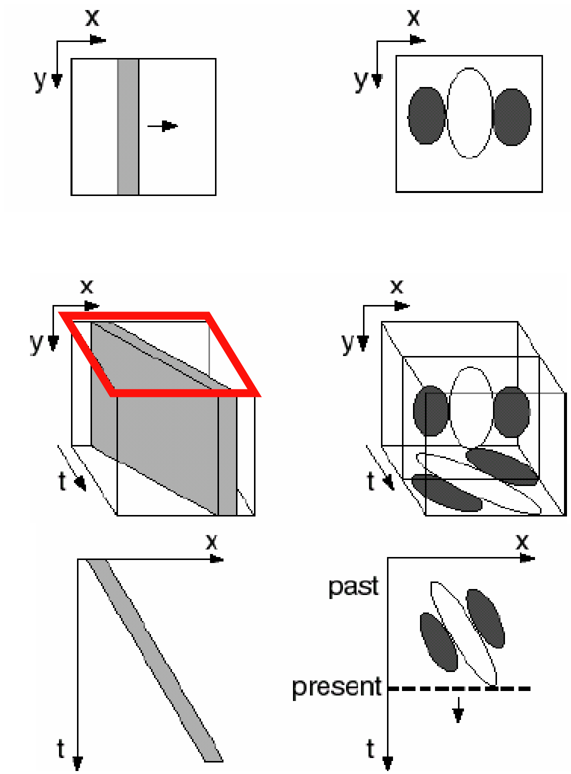
Selectivity for motion direction in visual cortex

[HW Direction selective cell]

Wiesel Hubel

Hubel/Wiesel movie #5

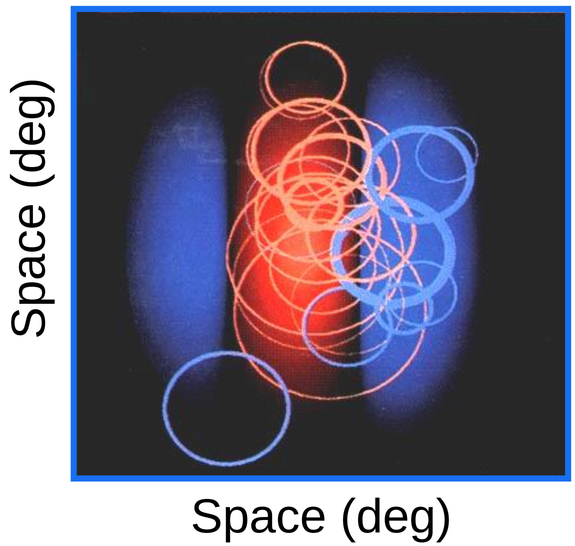
Selectivity for motion direction in visual cortex

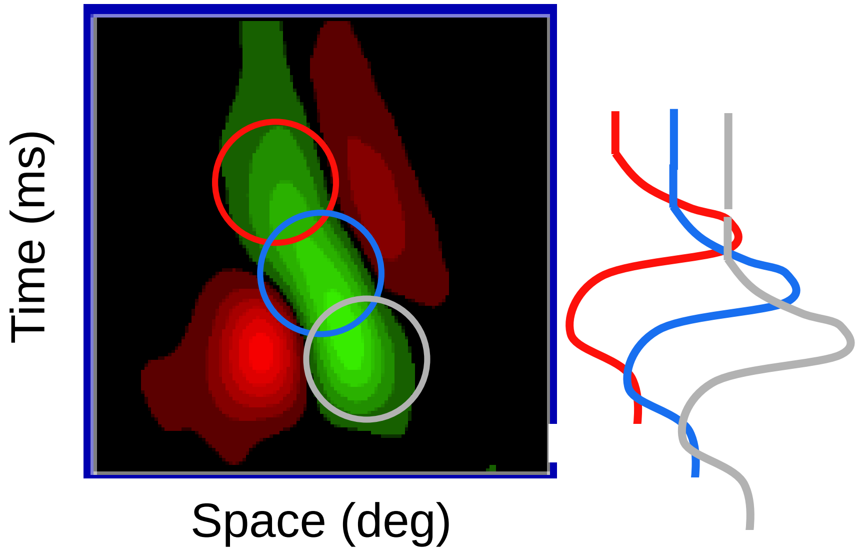


Adelson & Bergen, 1985

Motion can be described by an oriented line in space-time. A neuron can measure velocity by detecting orientation in space-time.

Selectivity for motion direction in visual cortex

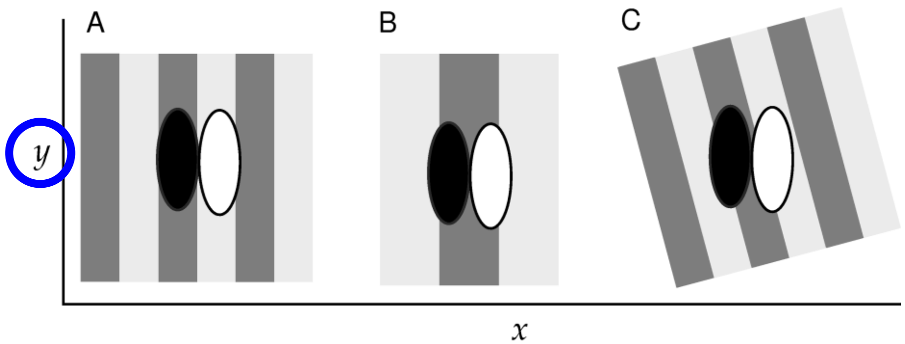




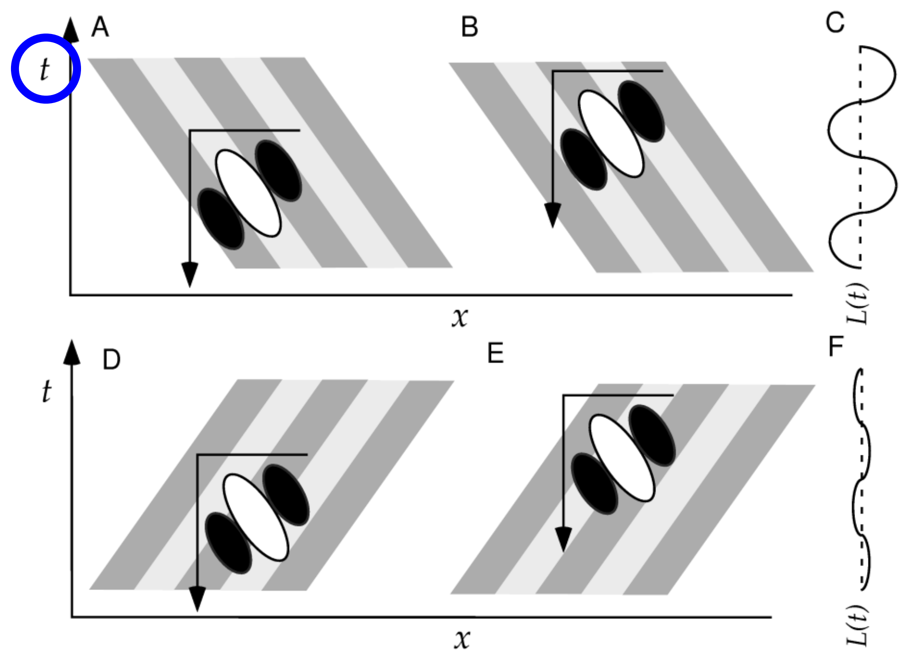
Direction-selective simple cells can be constructed from LGN inputs, just like orientation-selective simple cells.

DeAngelis, Ohzawa, Freeman, 1995

Space-time inseparability



Computation of velocity is formally equivalent to computation of orientation.

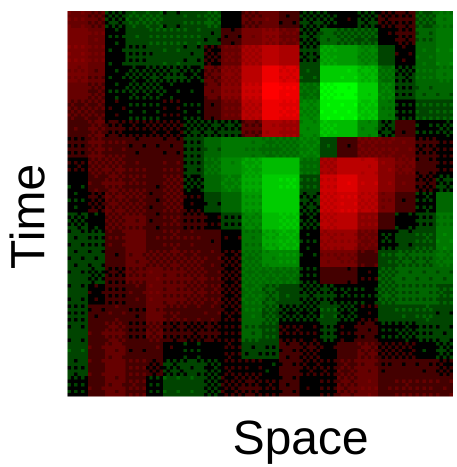


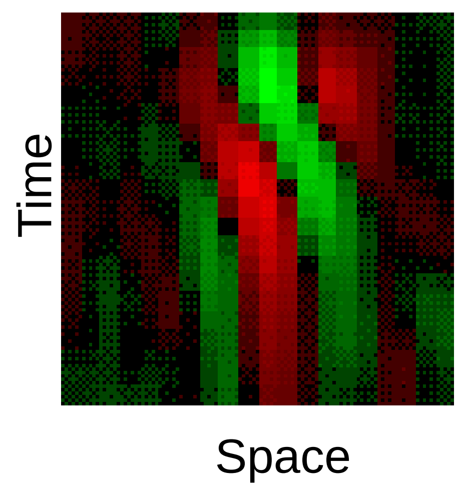
Space-time inseparability

For some simple cells, the spatial structure of the receptive field does changes over time. These cells are generally selective for the velocity of the stimulus. Their linear filter can be written:

$$f(x, y, \tau) = f(x', y)\, f(\tau')$$

where x' and τ' represent rotations of the space-time receptive field. The amount of rotation determines the preferred speed of the neuron.





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: $R1_{est}(t) = \int_0^\infty f_1(\tau)s(t-\tau)d\tau$

Second-order: $R2_{est}(t) = \int_0^\infty \int_0^\infty f_2(\tau_1, \tau_2)s(t-\tau_1)s(t-\tau_2)d\tau_1 d\tau_2$

Complete: $R_{est}(t) = r0 + \int_0^\infty f_1(\tau)s(t-\tau)d\tau + \int_0^\infty \int_0^\infty f_2(\tau_1, \tau_2)s(t-\tau_1)s(t-\tau_2)d\tau_1 d\tau_2 + \ldots$

where *s* is the stimulus and f_n is the nth kernel.

If we could find the f_n's, we would know everything about the nonlinear system.