The Visual System

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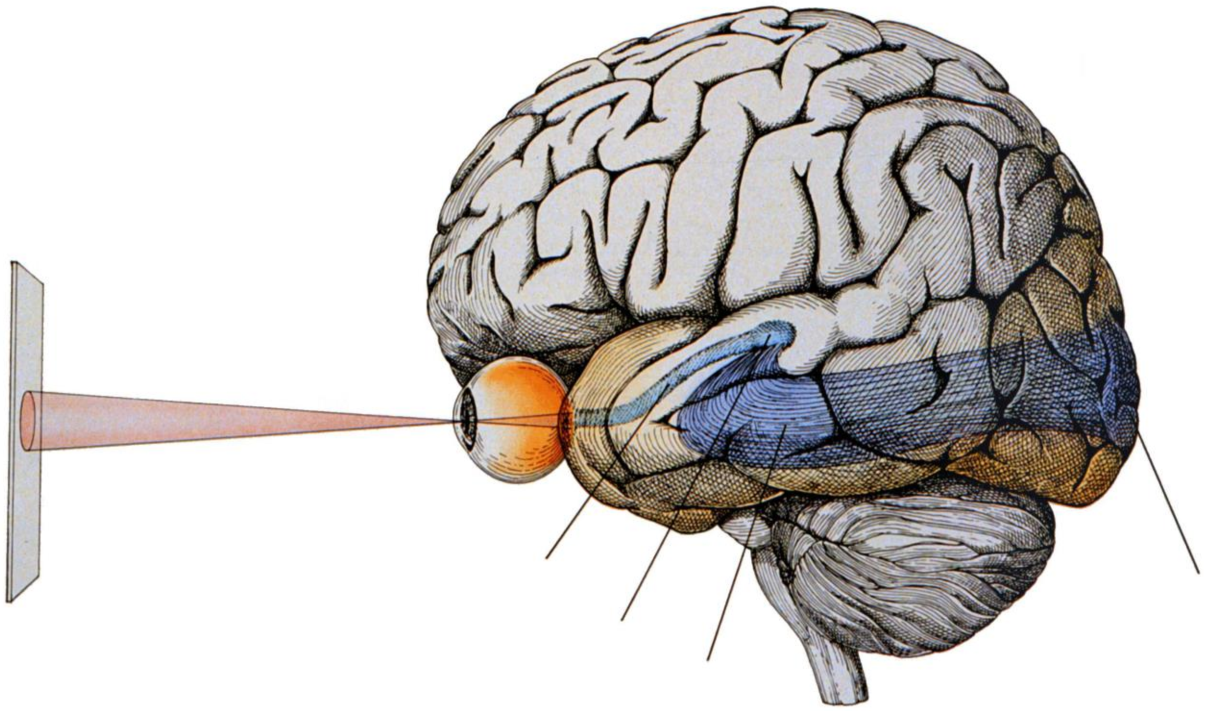
Computational Neuroscience (Lecture 7, 2024/2025)

Outline of Lecture

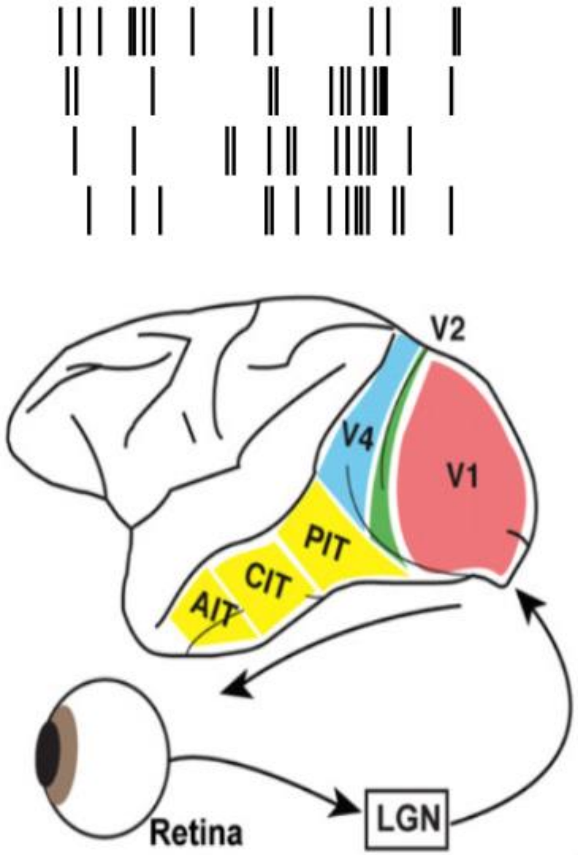
- Overview of the visual system
- Receptive fields in retina, LGN, and V1
- Orientation tuning in visual cortex



The Visual System

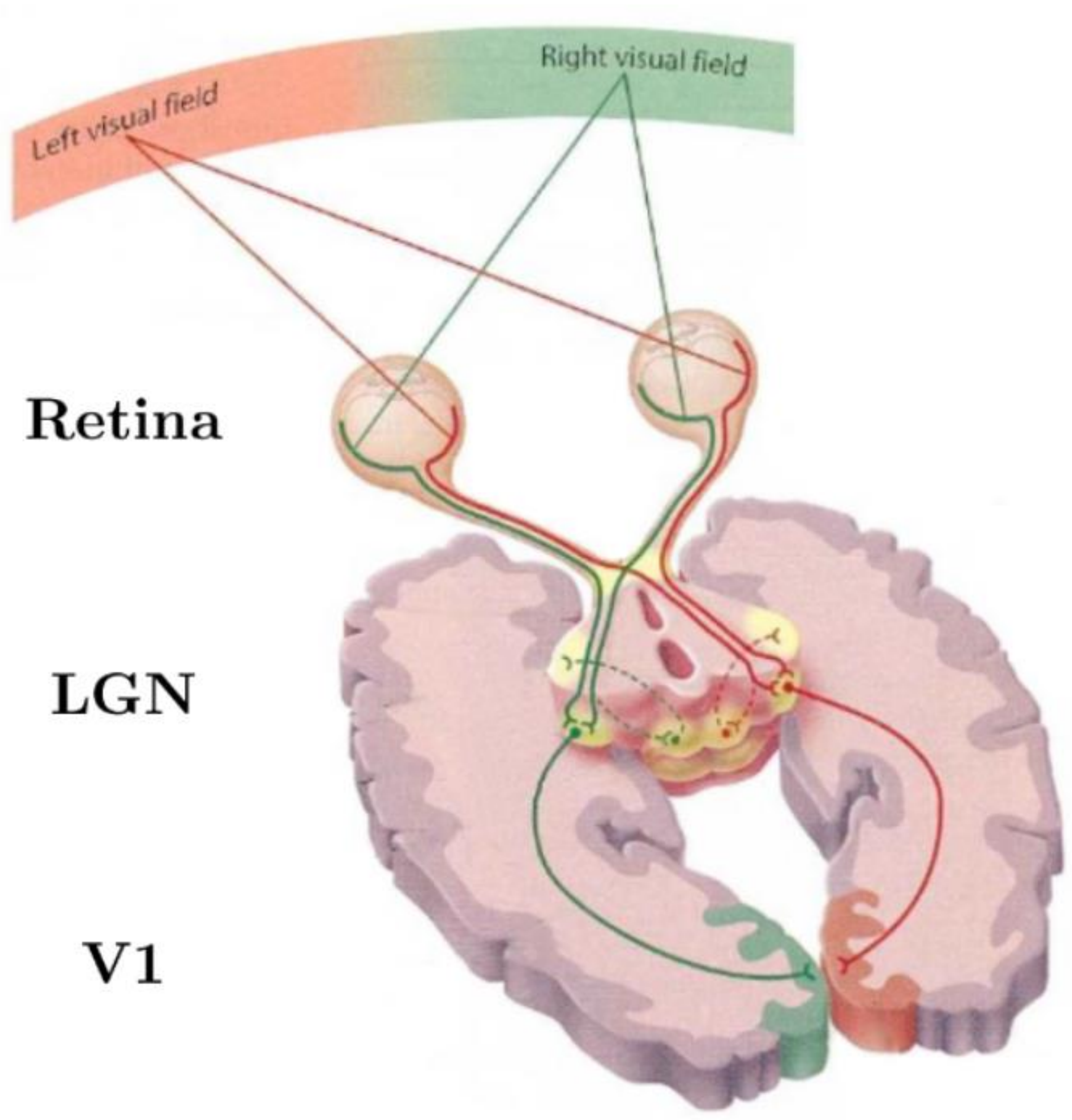
The brain is a machine which transforms sensory input into motor output…
First the brain must extract meaningful features from the sensory input.

Sensory input

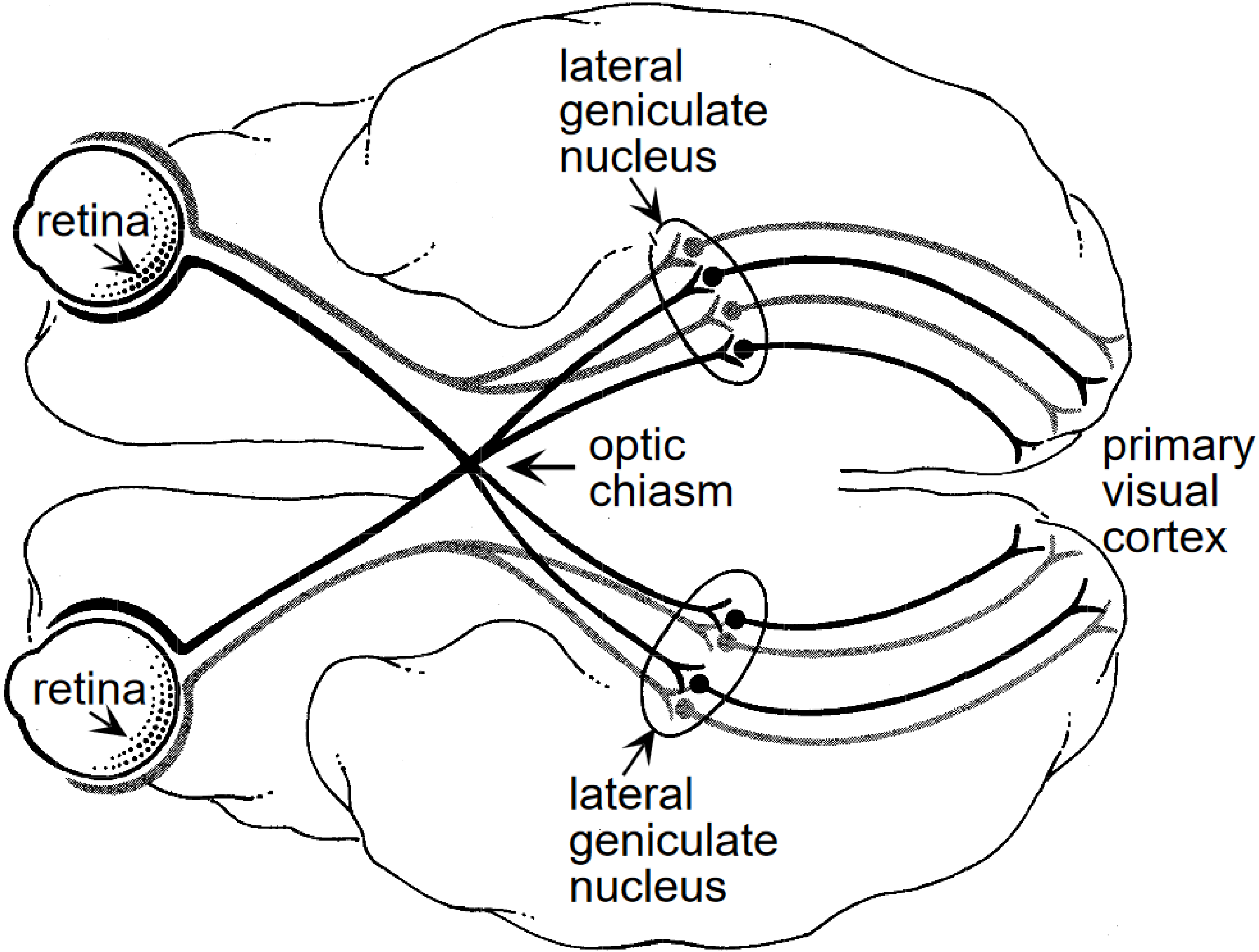


Motor output

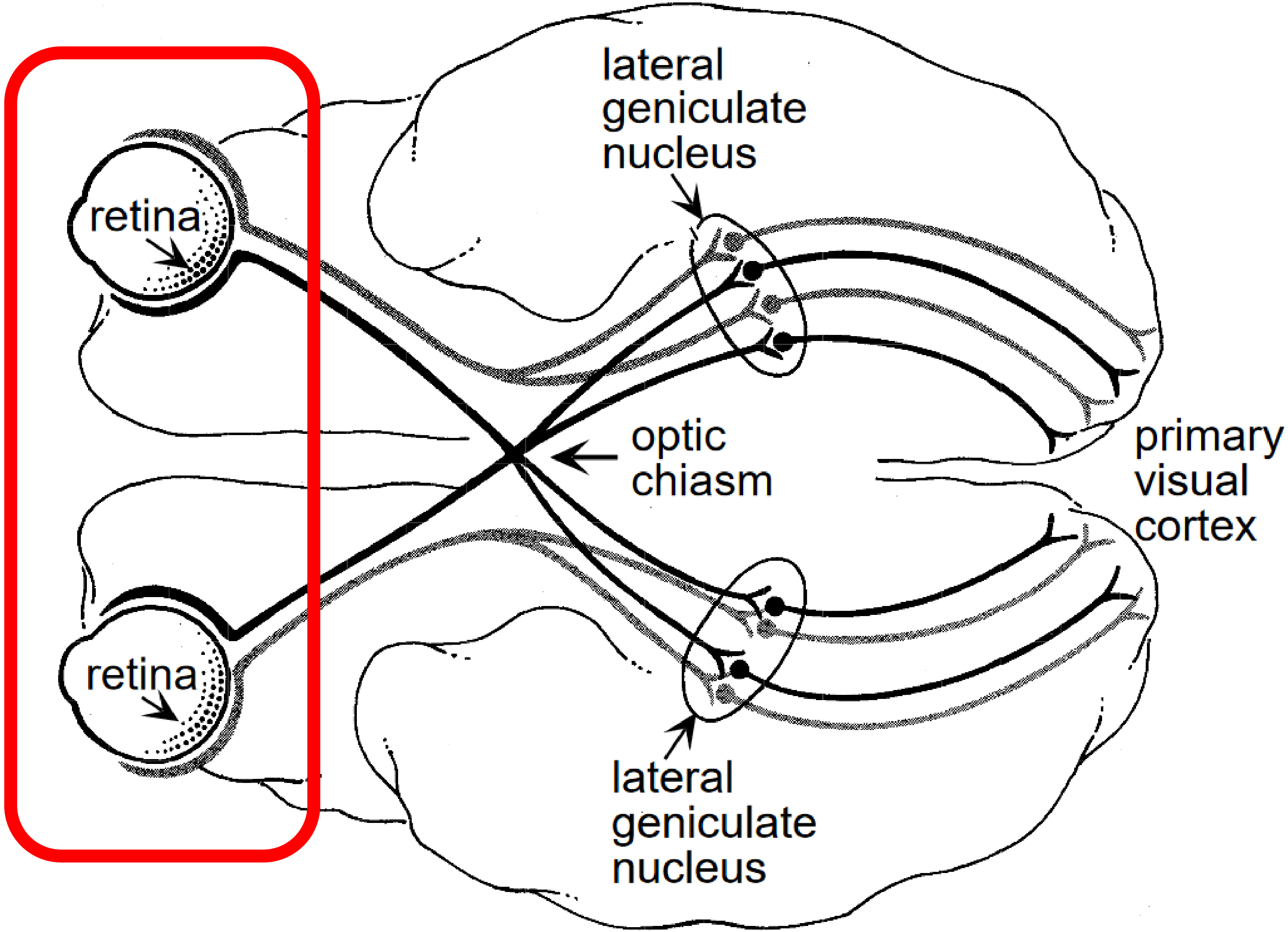
The Early Visual System (Retina, Thalamus, and V1)



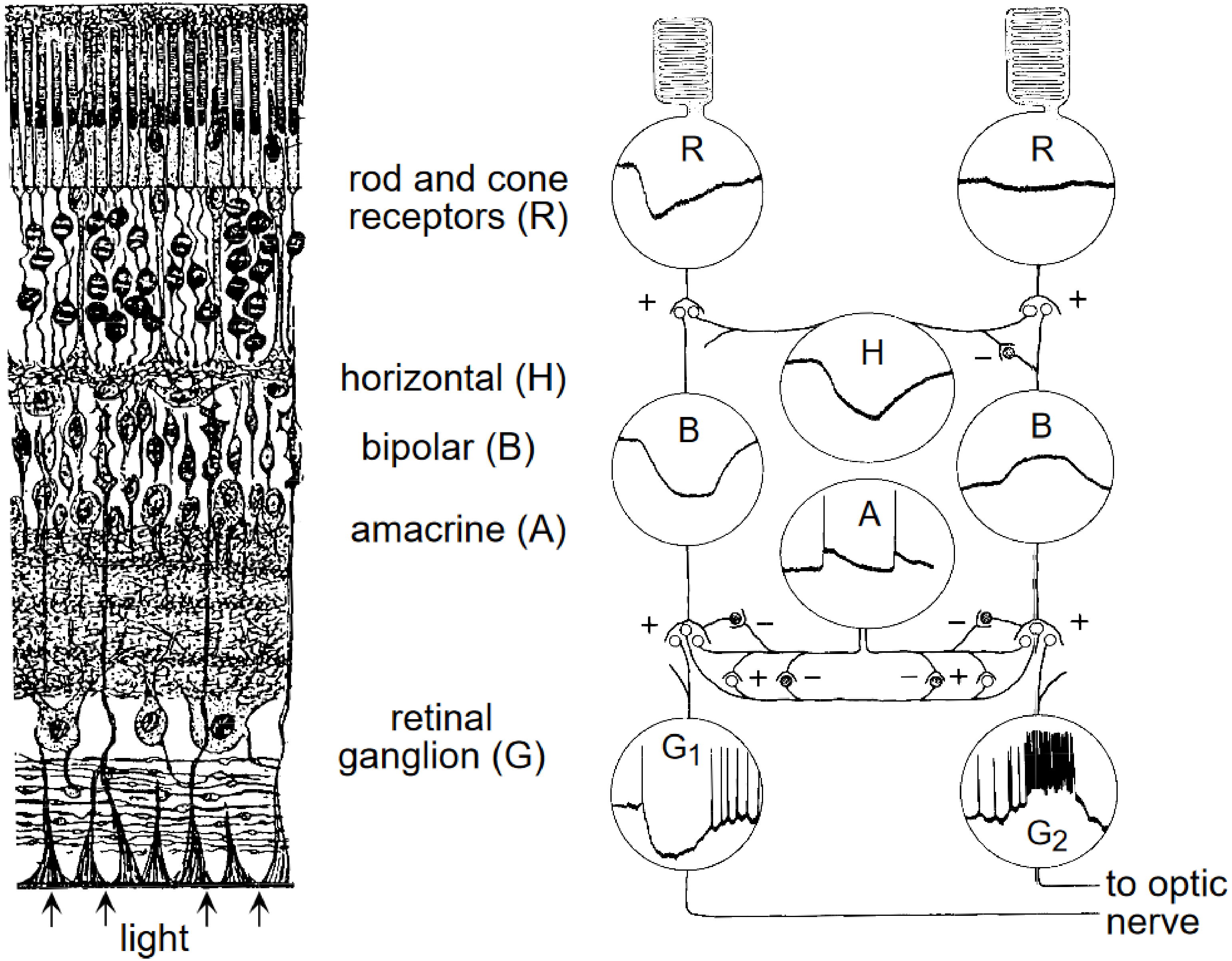
The Early Visual System (Retina, Thalamus, and V1)



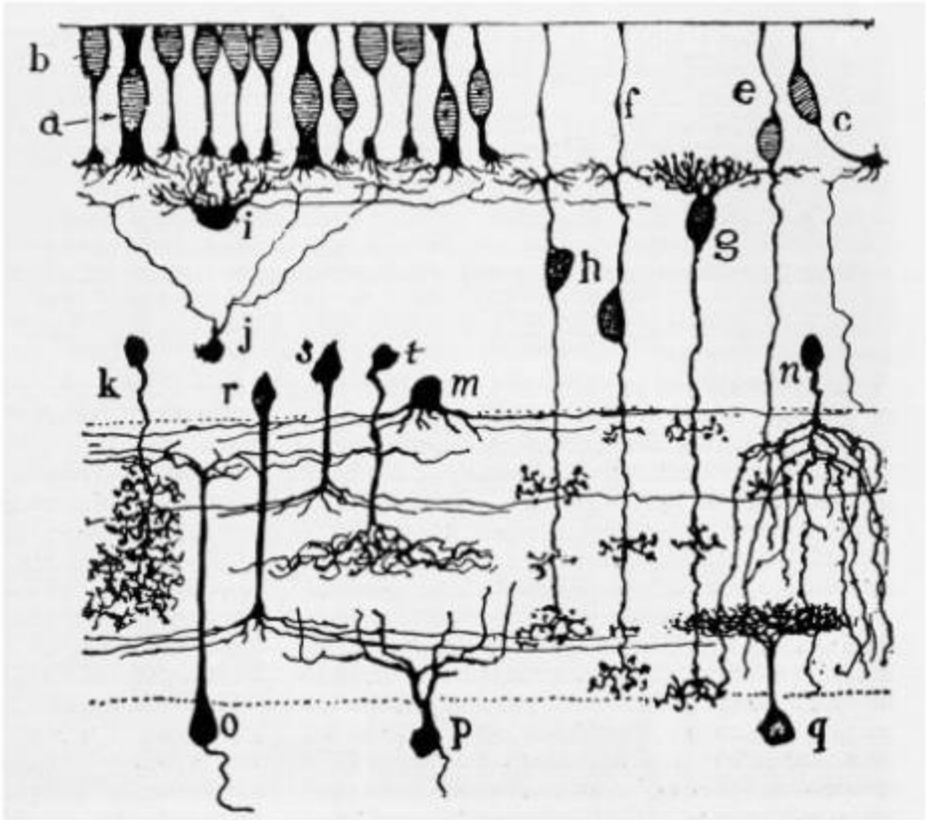
The Early Visual System (Retina, Thalamus, and V1)



The Retina


rod and cone receptors (R)
horizontal (H)
bipolar (B)
amacrine (A)
retinal ganglion (G)
light
R
R
H
B
B
A
G1
G2
+
+
−
+
−
−
+
+
−
−
+
to optic nerve

The Retina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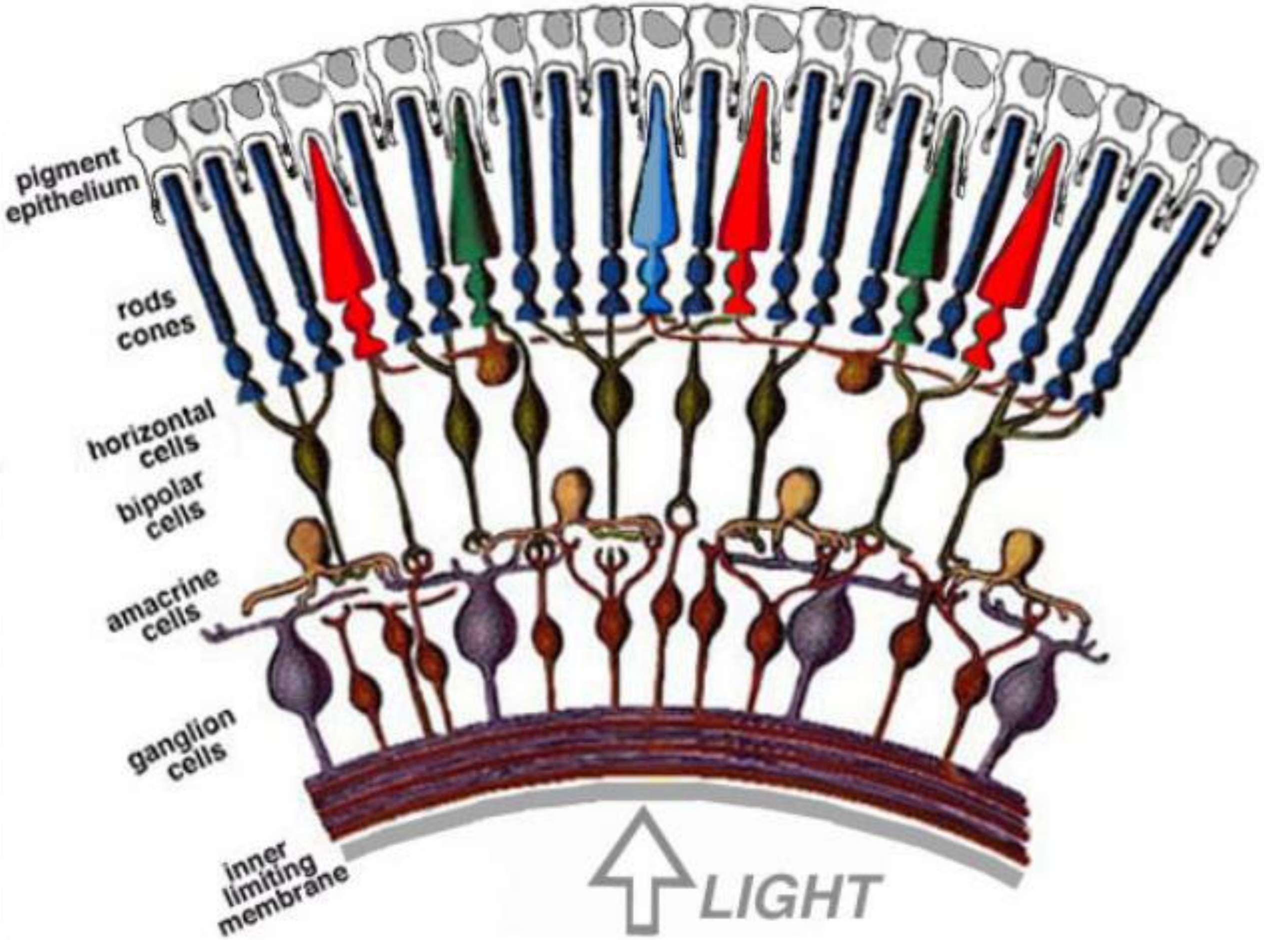
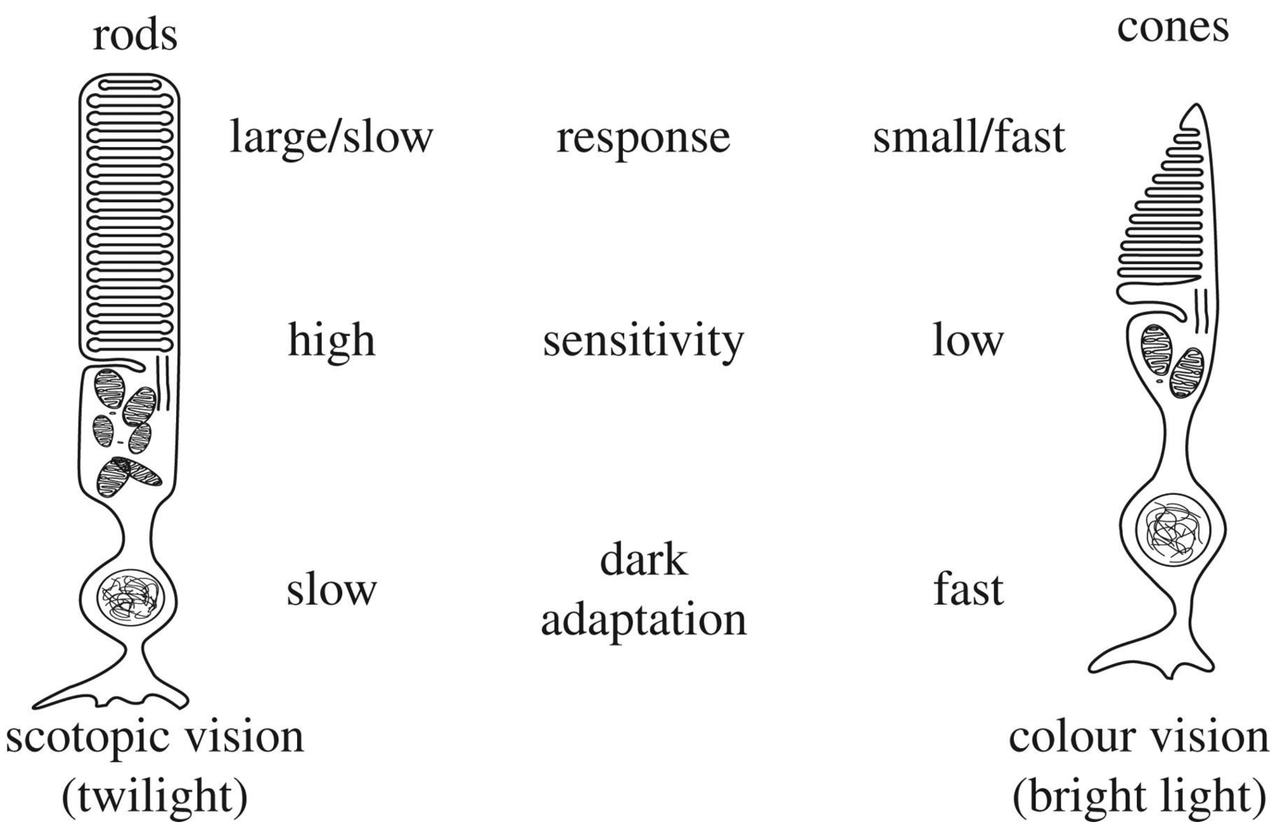
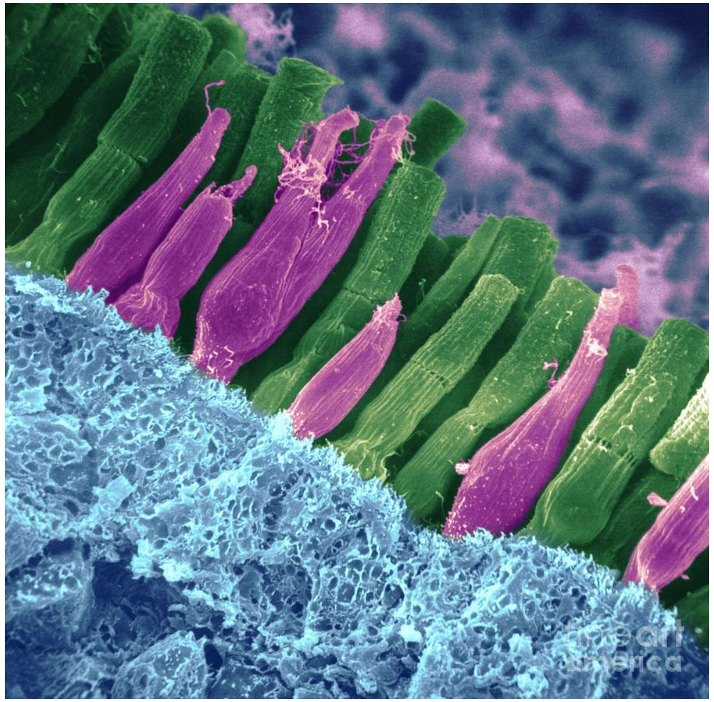

pigment epithelium
rods cones
horizontal cells
bipolar cells
amacrine cells
ganglion cells
inner limiting membrane
LIGHT

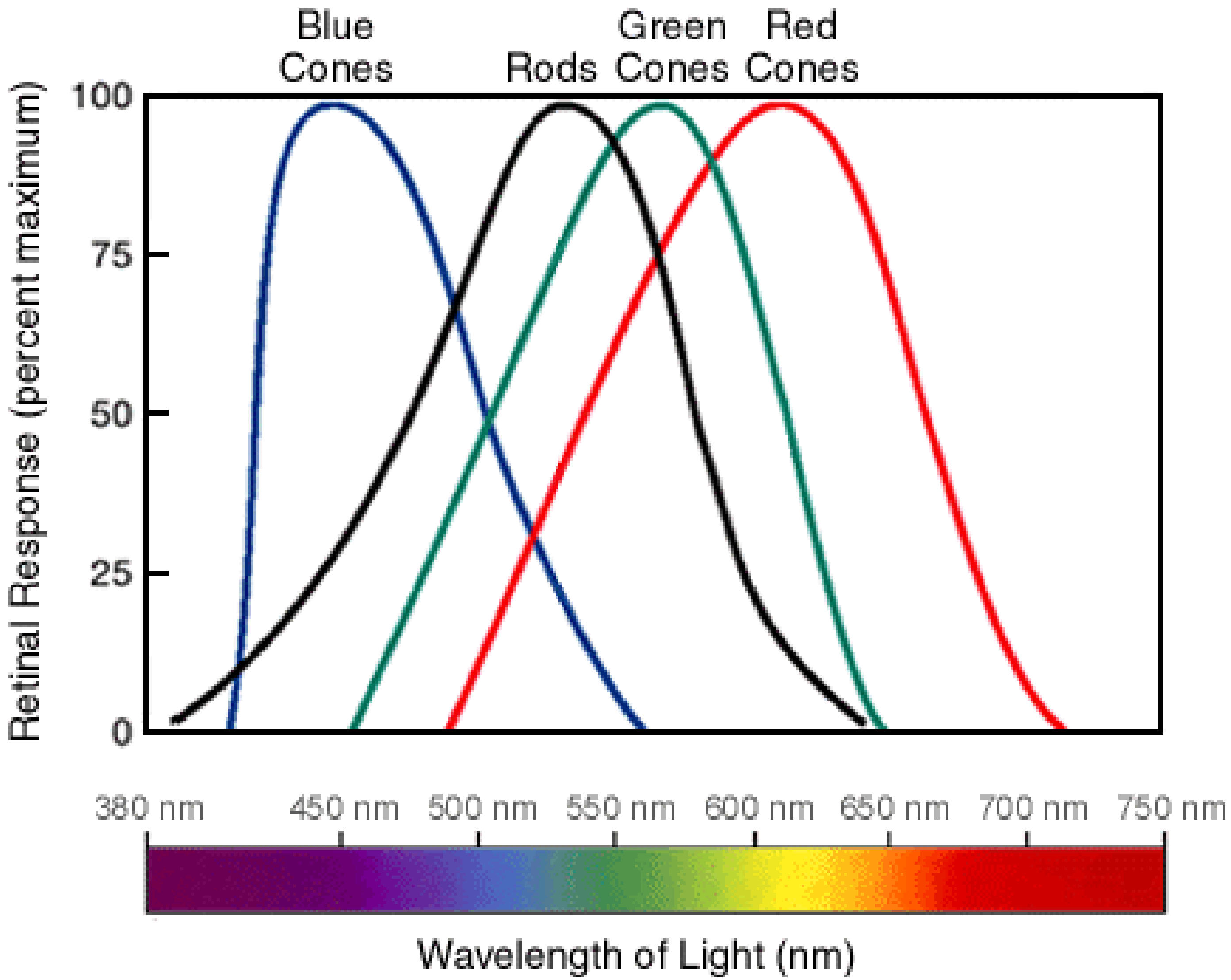
Photoreceptors: Rods and Cones





Rods and cones are photoreceptors.
Rods: seeing in the dark, black and white. Cones: Day vision, colour.

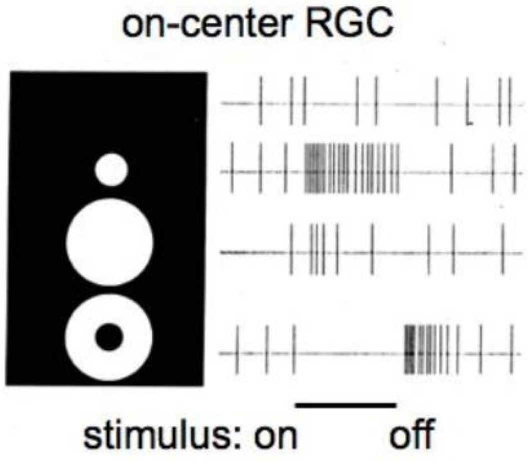
Rods and Cones: Colour Sensitivity



Retinal Ganglion Cells: Centre-Surround Receptive Fields

ON-OFF cell: respond to patch of light in centre + dark in surround

Retinal Ganglion Cell Responses



Note: Cell also responds to change in stimulus over time…

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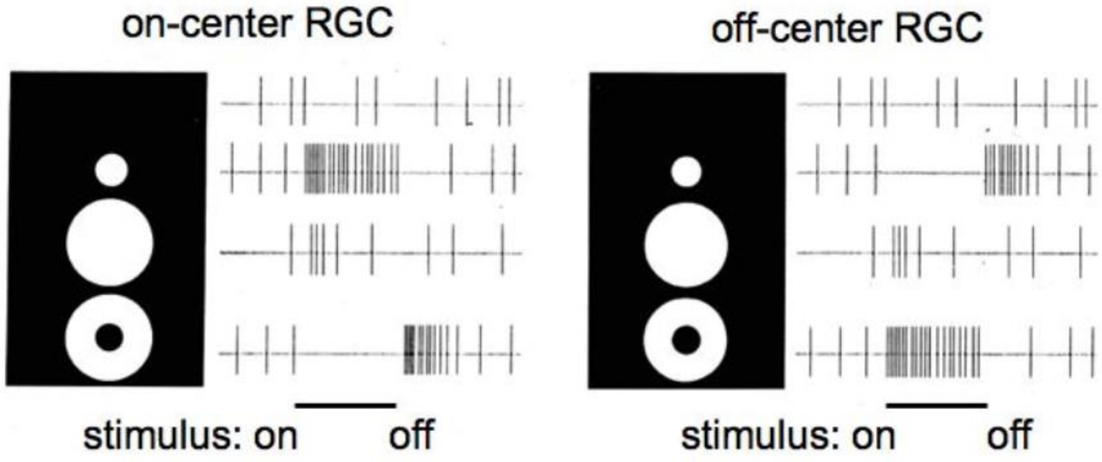

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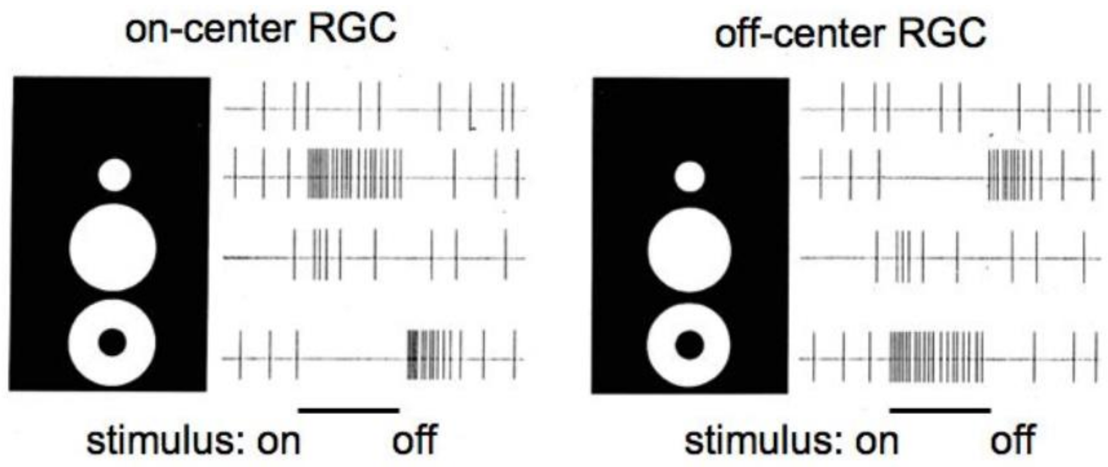
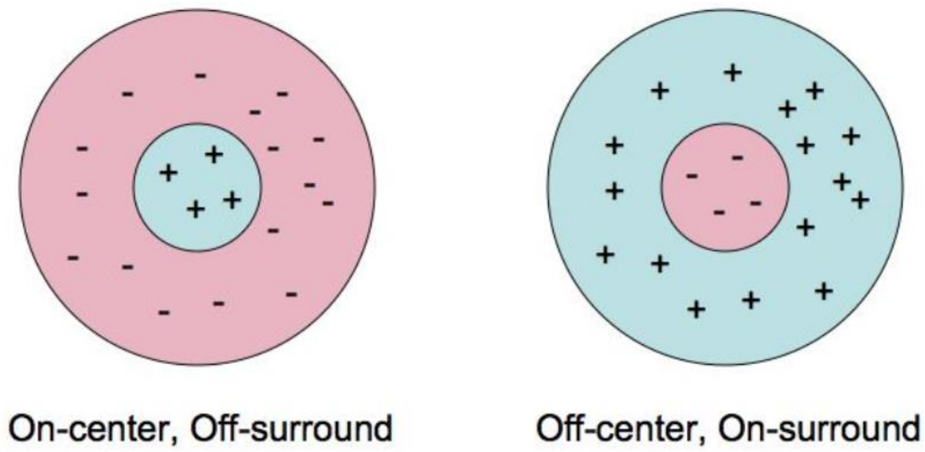


Receptive Fields



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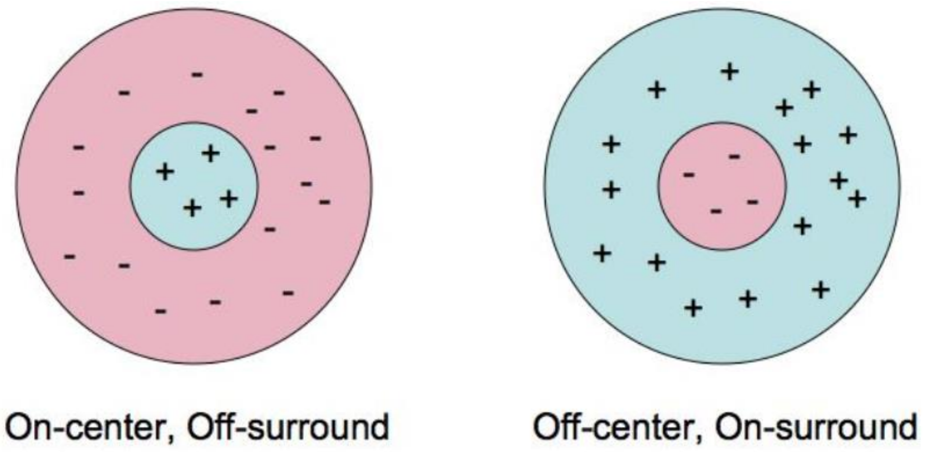
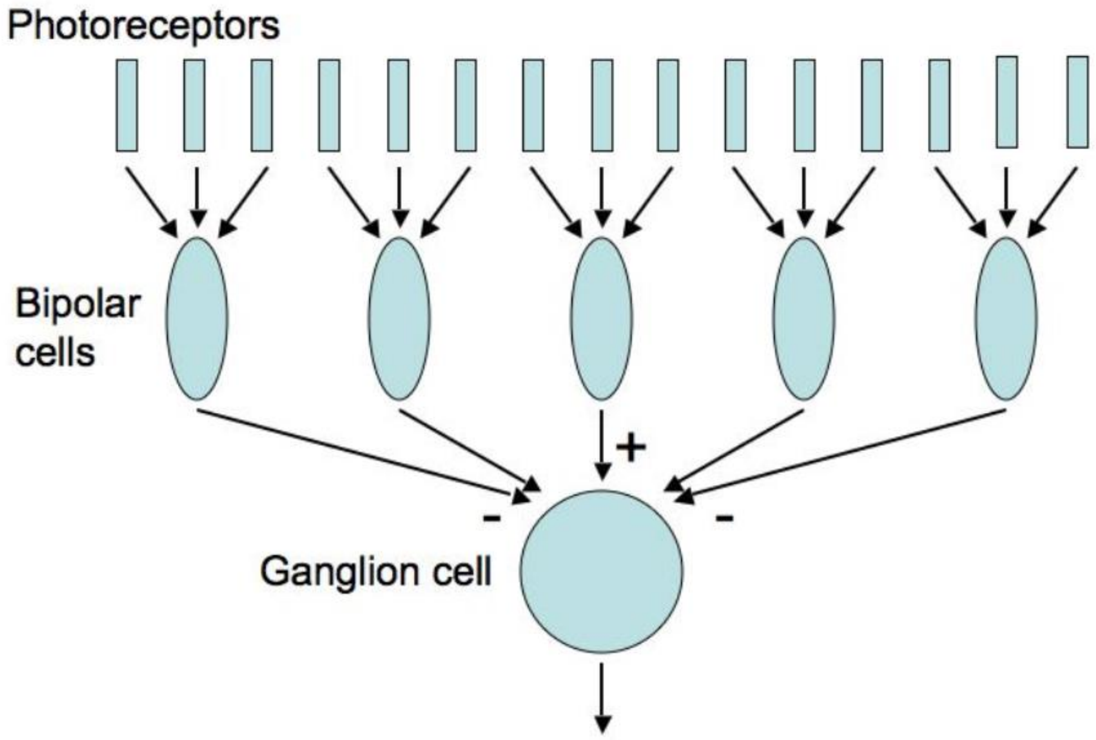


Possible Circuit Mechanism



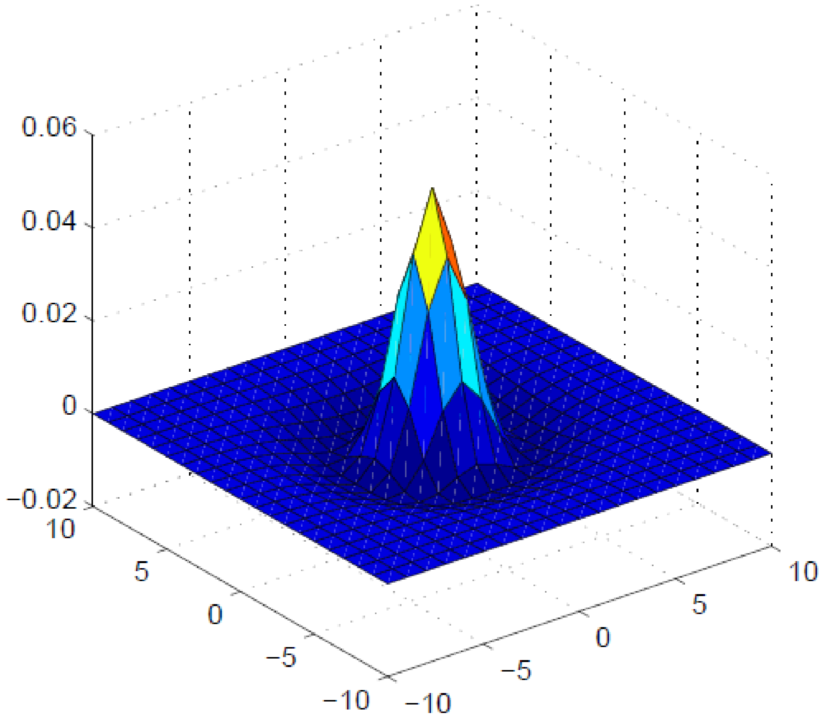
Note: By circuit mechanism we mean the physical explanation of the phenomenon

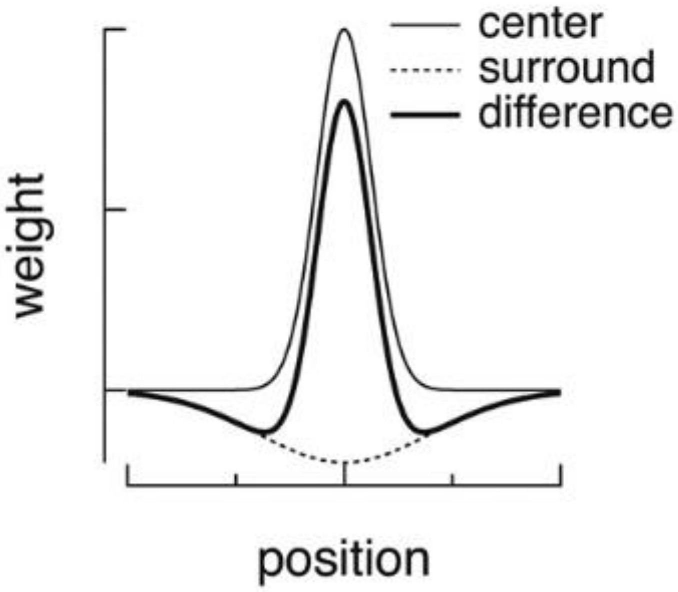
A Receptive Field Model: Difference of Gaussians

A simple model for a centre-surround receptive field *R(x,y)* is:

$$R_{\mathrm{DoG}}(x,y) = \frac{1}{2\pi\sigma_c^2}\exp\left(-\frac{(x-c_x)^2+(y-c_y)^2}{2\sigma_c^2}\right) - \frac{1}{2\pi\sigma_s^2}\exp\left(-\frac{(x-c_x)^2+(y-c_y)^2}{2\sigma_s^2}\right)$$

The coordinates *x, y* specify the location on the visual field (or retina), the *c* parameters specify the centre of the receptive field.





A Receptive Field Model: Difference of Gaussians

If we present an image *I(x,y),* the response of the neuron with receptive field *R(x,y)* is taken as:

$$r = \int\int I(x,y)R(x,y)dxdy$$

where the limits of the integral are the whole image.

For example, *r* could be the firing rate of a retinal ganglion cell, and we could model spike counts *N* with a Poisson distribution *P(N=k) = Poisson(r).*

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Neurons are often better modelled with an additional nonlinearity, but we will ignore that for now:

$$r = f\left(\int\int I(x,y)R(x,y)dxdy\right)$$

Spatial Filtering with a Set of Receptive Fields

If we have many neurons with receptive fields $R_{c_x,c_y}(x,y)$, each centred on a different point in visual space *(cx,cy)*, their joint response to an image *I(x,y)* is:

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But we have (for DoG and other translationally invariant receptive fields):

$$r(c_x,c_y) = \int\int I(x,y) R(c_x - x, c_y - y) dxdy$$

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This is a spatial filter (2D convolution) of the image. We can therefore think of what the retina does in terms of signal processing (as an engineer would). E.g., we can ask questions like:

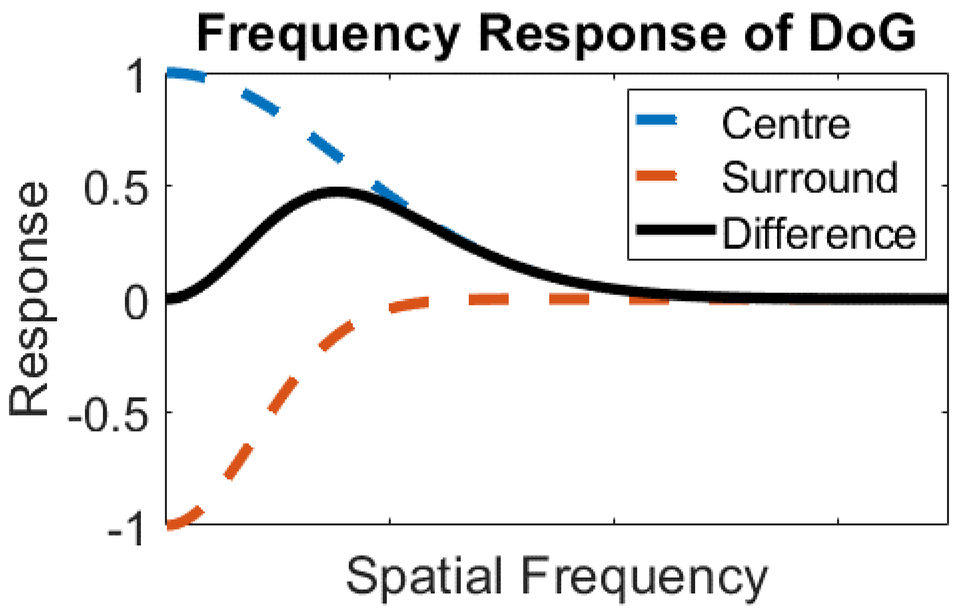
Are centre-surround (DoG) receptive fields good filters for natural images? Why/why not?

Difference of Gaussians are Bandpass Filters

It is often more revealing to work in the frequency domain when analysing filters.

Taking the Fourier transform of the DoG filter gives (in 1D for simplicity):

$$F\left[R_{\mathrm{DoG}}(x)\right](f) = \int_{-\infty}^{\infty} R_{\mathrm{DoG}}(x) e^{-i2\pi f x} dx = e^{-2\pi^2 \sigma_c^2 f^2} - e^{-2\pi^2 \sigma_s^2 f^2}$$



This is a bandpass filter – it emphasises a range of spatial frequencies in the image and suppresses lower and higher frequencies.

Spatial Filtering with Centre-Surround Receptive Fields

Input image (cornea)

“Neural image” (retinal ganglion cells)

Center-surround receptive fields: emphasize edges.

Efficient Coding, Compression, and the Optic Nerve

The retina transforms an image into electrical signals (spikes), which must then be transmitted down the optic nerve and into the brain

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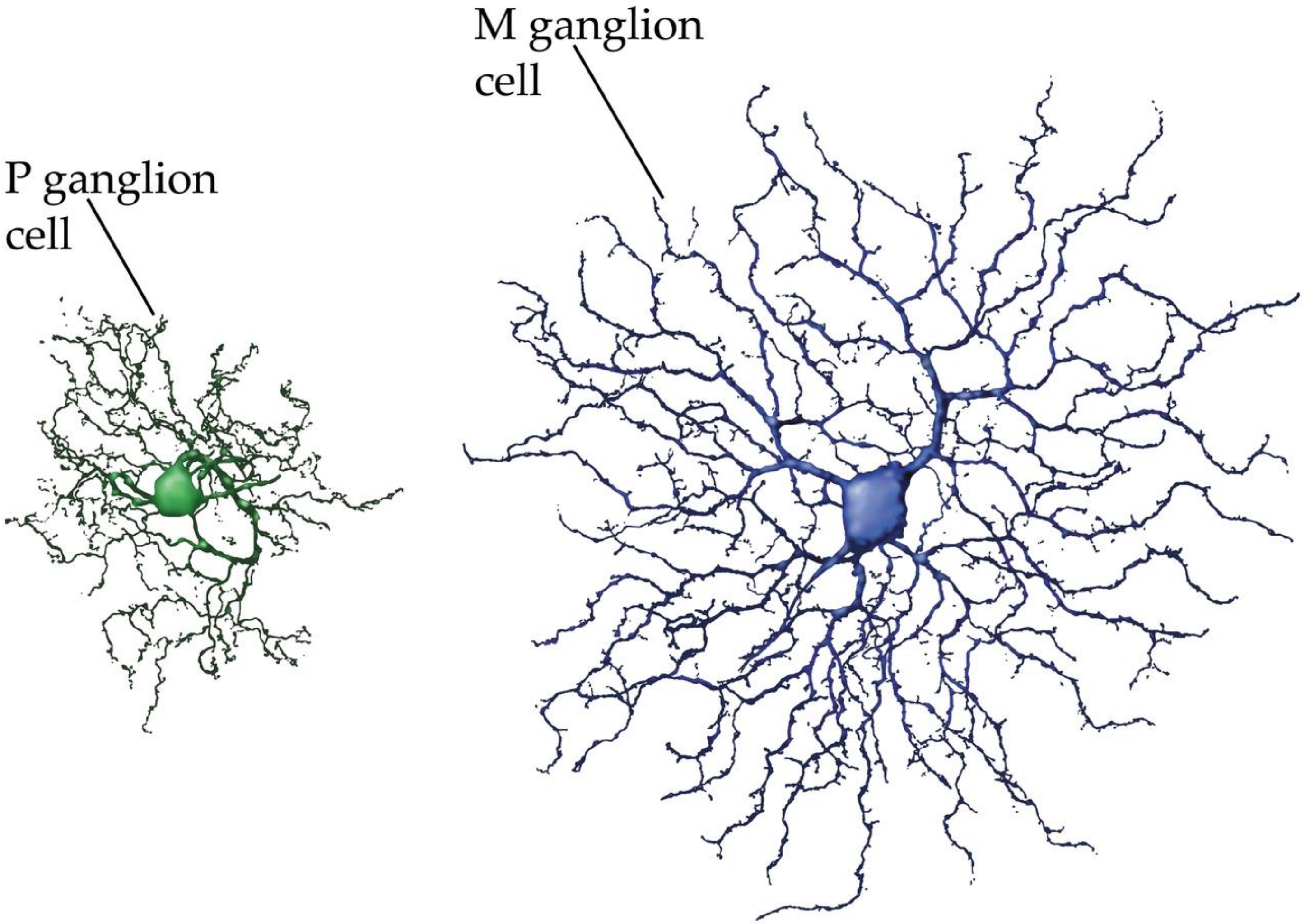
But the pixel representation of natural images is a highly redundant and an inefficient code

Filtering the image with difference of Gaussian receptive fields compresses the image by emphasising edges and ignoring redundant areas of constant luminance

Two Important Classes of Retinal Ganglion Cell

Not all RGCs are the same, there are different types with different properties…



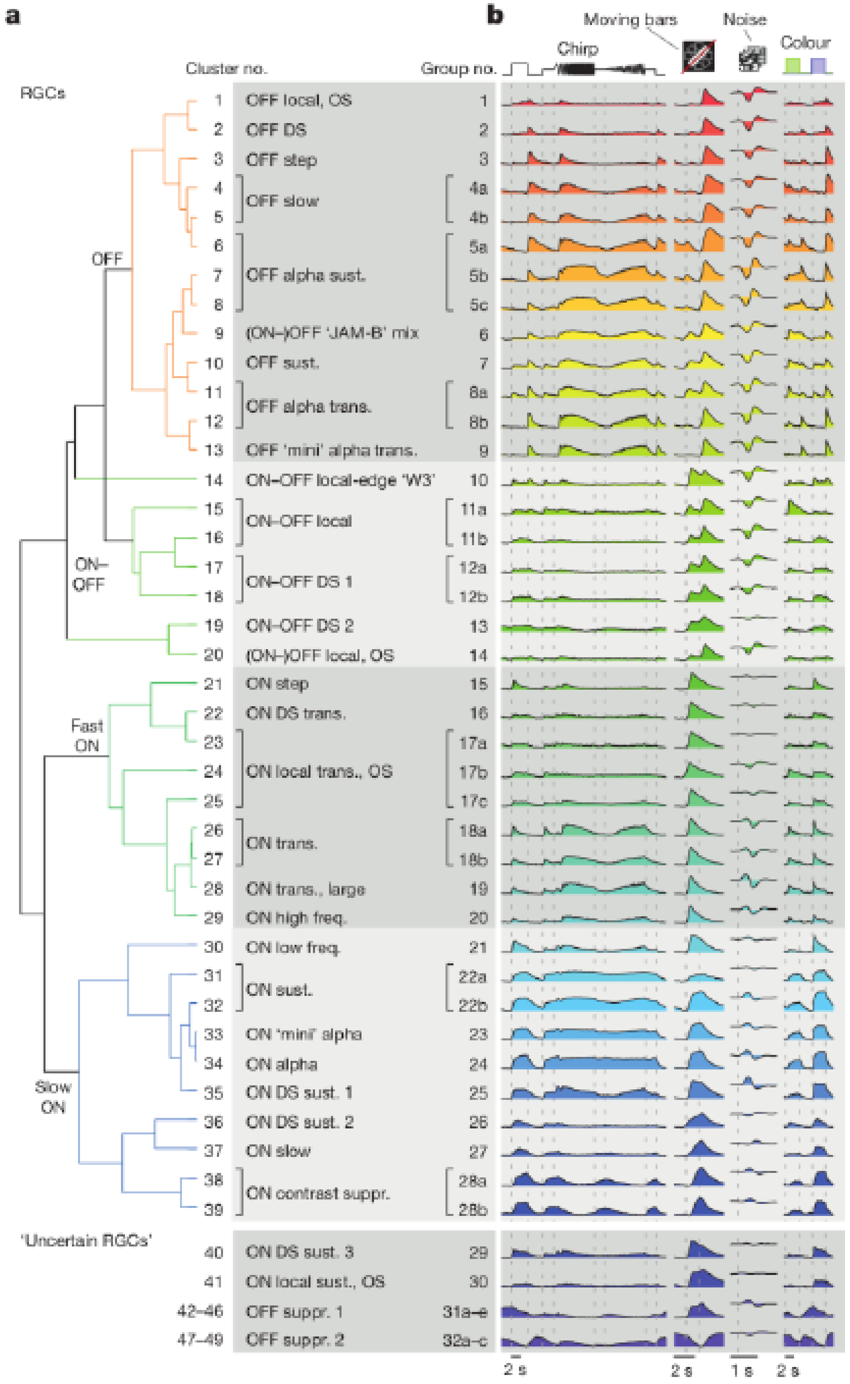
Parvo cells:
e.g. midget cell
Small dendrites
small RFs
sustained responses
Colour sensitive

Magno cells:
e.g. parasol cell
Large dendrites
large RFs
transient responses
Colour insensitive,

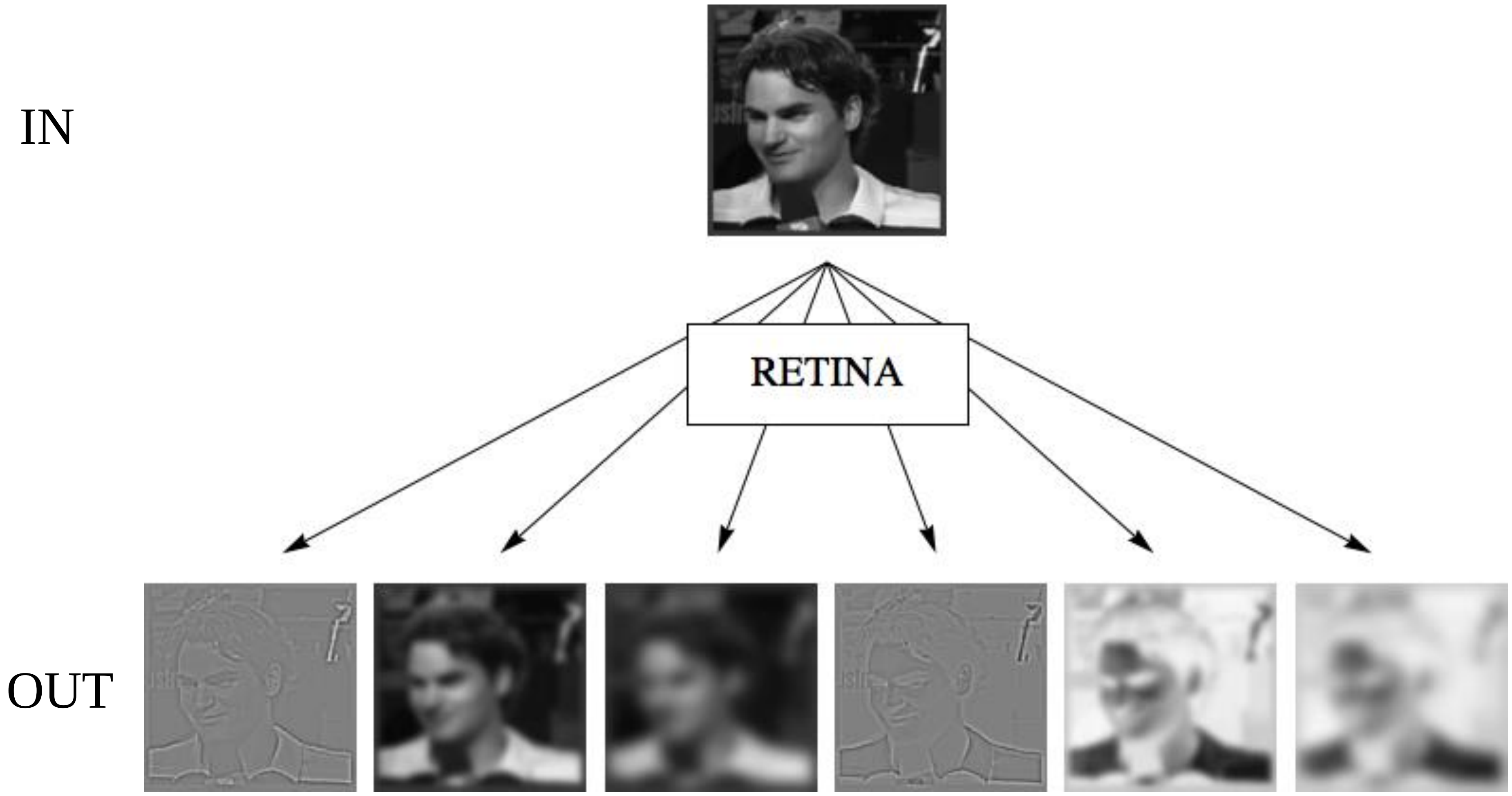
Neural Diversity in the Retina

There are around 50 types of ganglion cell, some colour-sensitive, some not, some have large receptive fields, some small, some motion sensitive, etc.

Thus, multiple parallel streams of information are sent from retina to cortex.



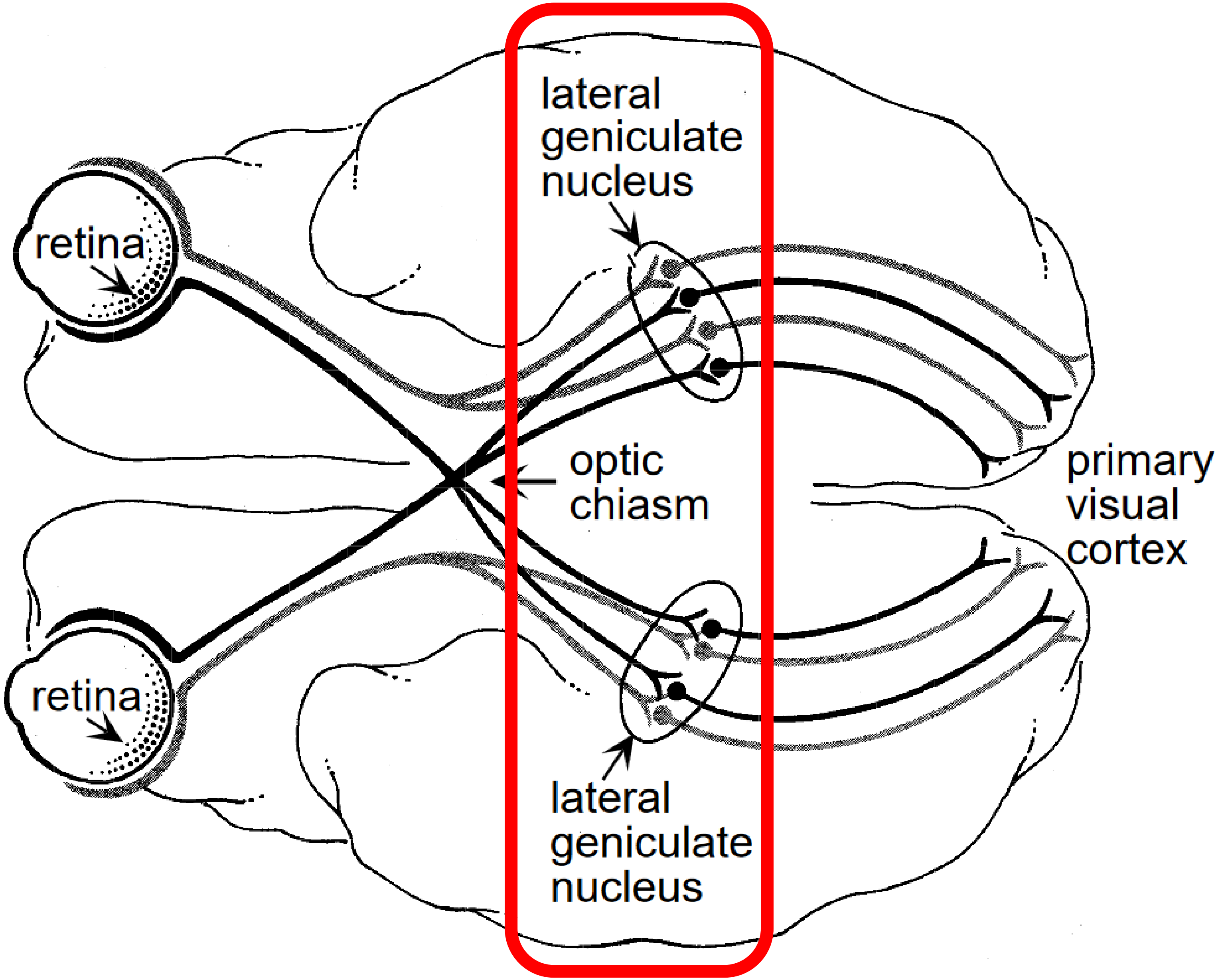
Segregated Streams of Information from Retina to Brain



Summary – the Retina

- The retina transduces photons into patterns of action potentials to send to brain
- The output of retina (retinal ganglion cells) has centre-surround receptive fields
- They act as a bandpass filter, efficiently encoding/compressing images to send to brain
- There are many types of retinal ganglion cell, which send multiple segregated streams of information to brain
- The retina also adapts to efficiently encode image statistics (e.g., day vs night)
- Take home: a lot of computation is performed in the retina, before signals reach the brain!

The Early Visual System (Retina, Thalamus, and V1)



The Thalamus

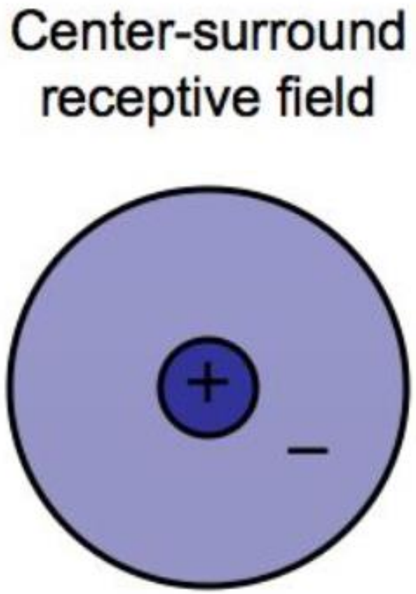
- The thalamus is a structure in the centre of the brain. It receives input from the sensory periphery (eyes, ears, skin, etc.)

- It then sends this information on to specialised cortical areas (visual, auditory, somatosensory, etc.) for further processing

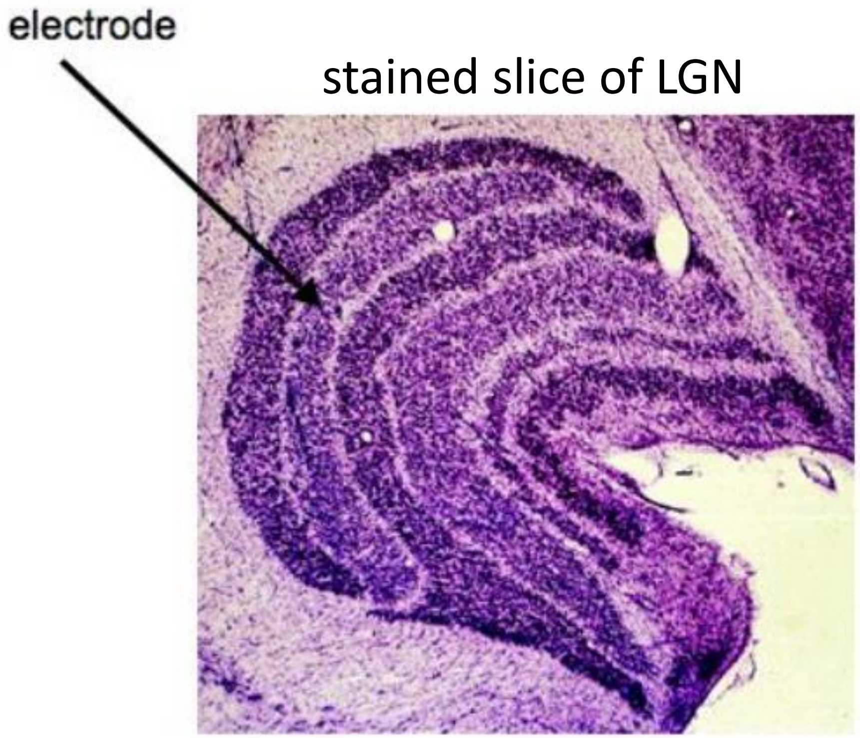
- The visual part of the thalamus is called the lateral geniculate nucleus (LGN), there are also auditory nuclei etc.

The Lateral Geniculate Nucleus (LGN)

- The LGN is in the thalamus, it receives input from the retina and sends this information on to primary visual cortex
- Receptive fields in the LGN are much like those of retinal ganglion cells (ON-OFF, DoG)



stained slice of LGN



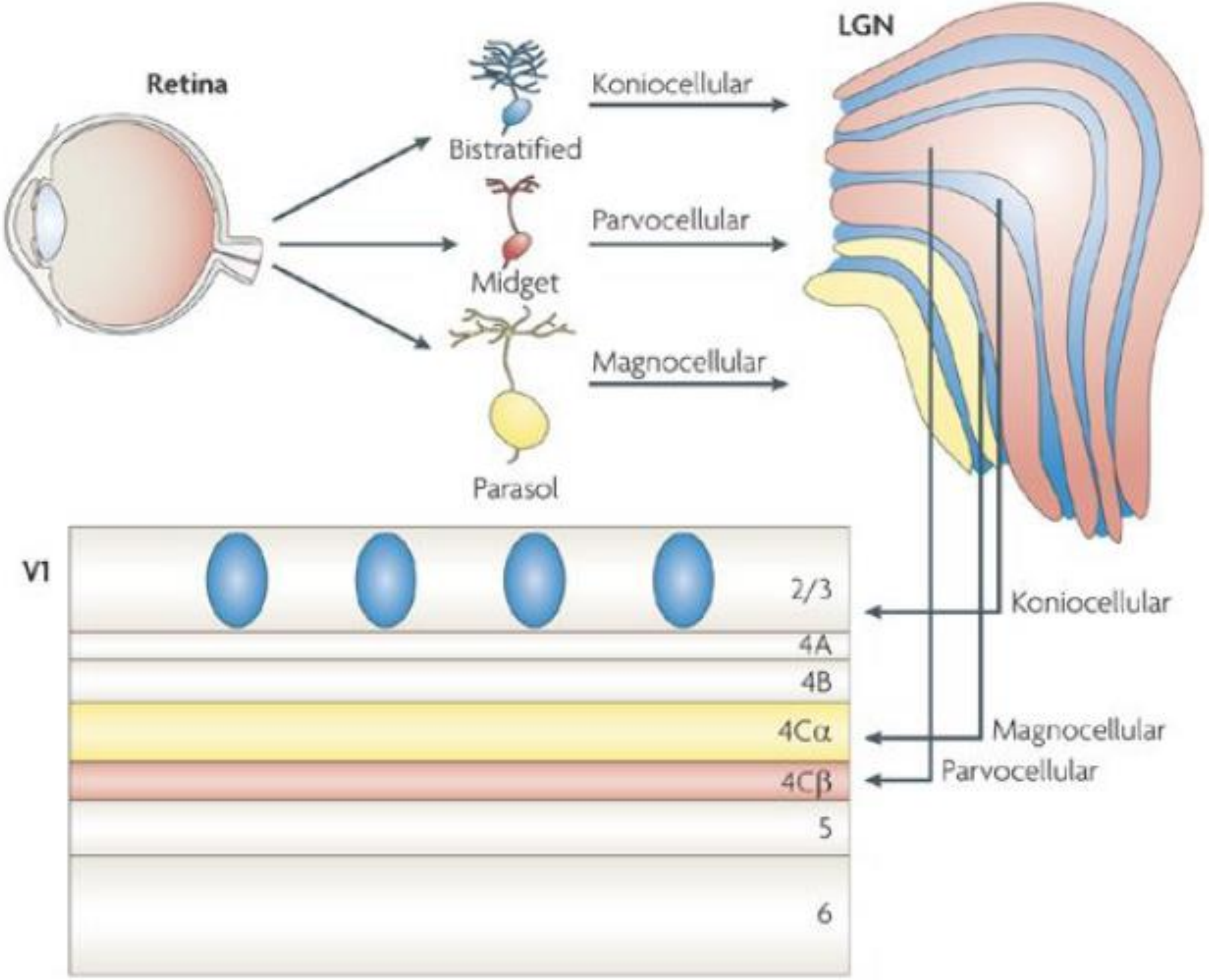
ON cell

Hubel and Wiesel

Recording in LGN

Segregated Streams of Information

- Different retinal cell types project to different parts of LGN
- These then project to different layers of visual cortex



Segregated Streams of Information

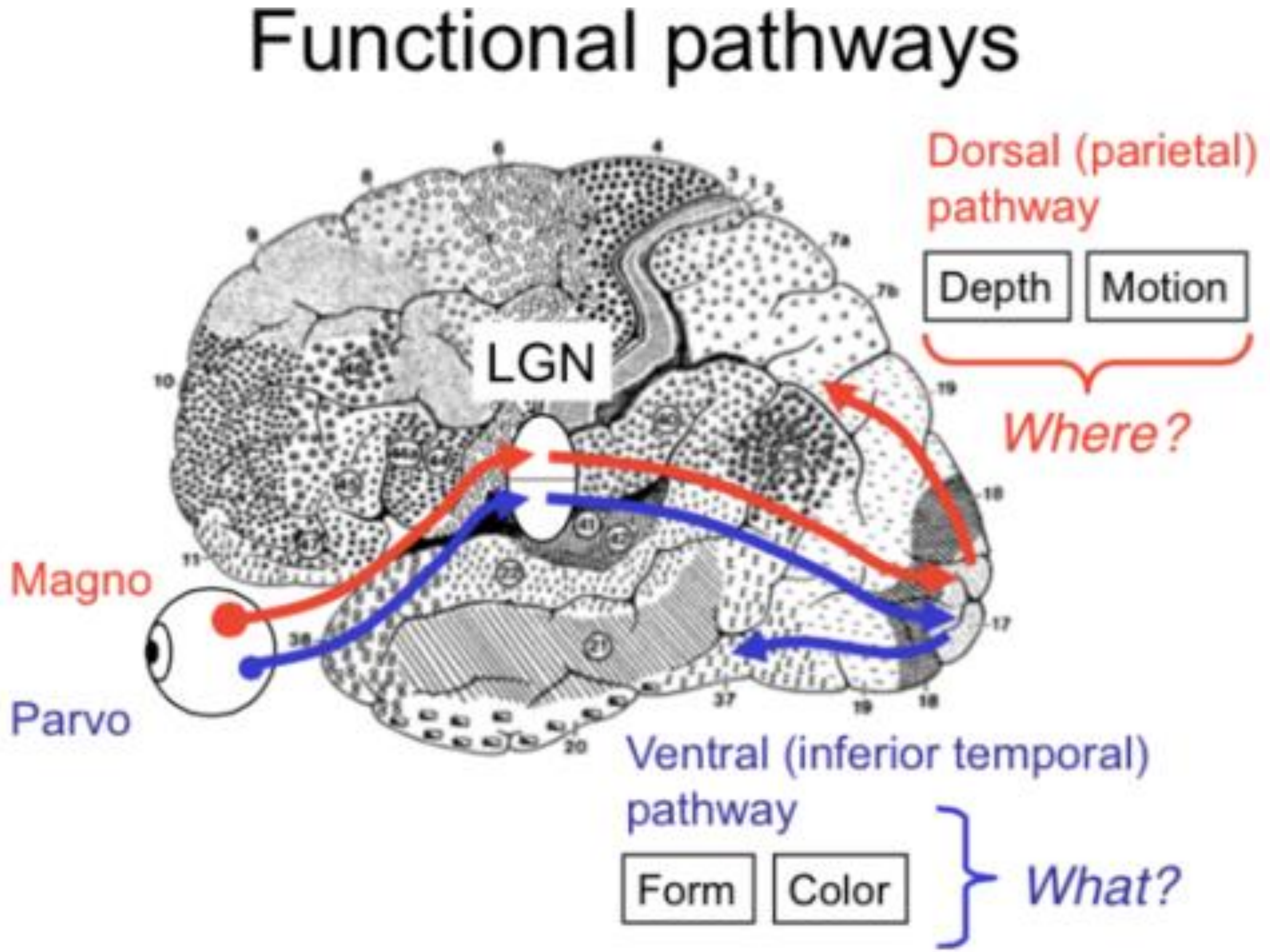
- Even after primary visual cortex, these streams are sent to to different brain areas

- Ventral stream: “what?”

  (e.g., object recognition)

- Dorsal stream: “where?”

  (e.g., motion, depth perception)



The Thalamus – What Does it Do?

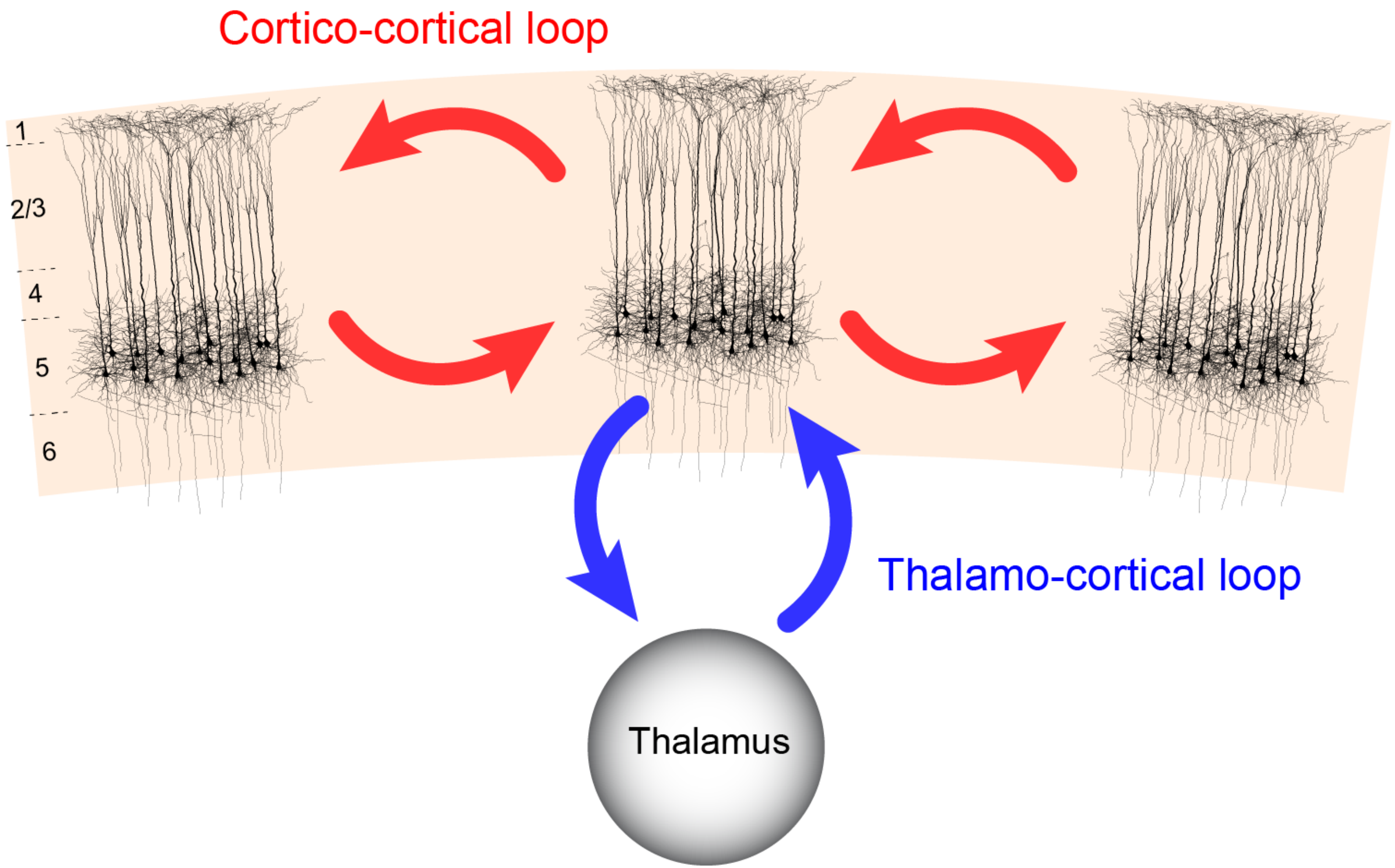
- Why is the thalamus there? Is it simply a relay? Or does it do some processing? Why not wire retina directly to V1?

- Answer is unclear, but:

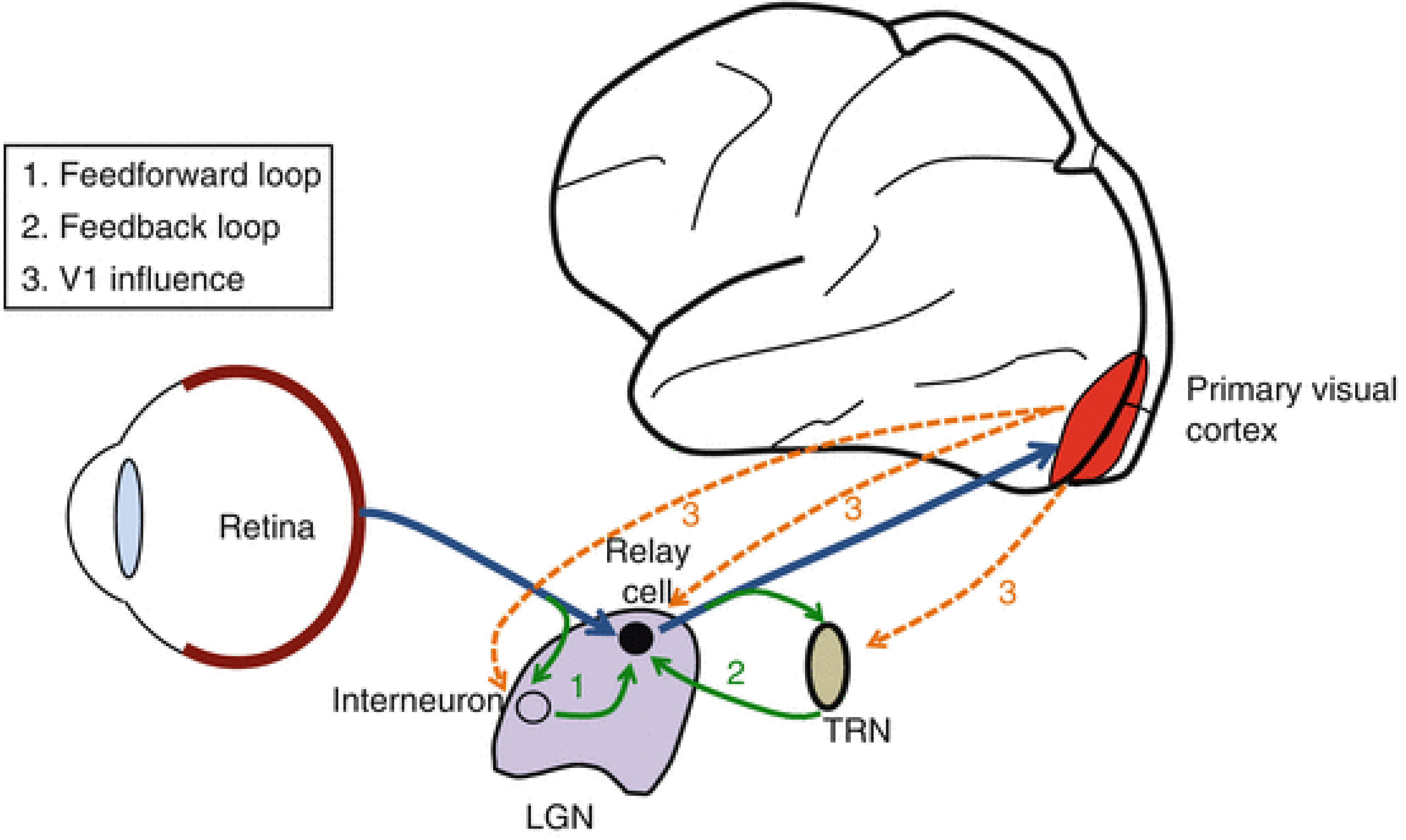
1) Some processing of sensory information does go on in thalamus
2) Feedback from cortex can modulate processing thalamus, potentially sculping sensory processing before information arrives in cortex

- There are many more projections from cortex to thalamus than from thalamus to cortex. The reason for this massive feedback is still mysterious, but theories include attention, prediction, etc.

Thalamo-Cortical Loops



LGN-V1 Loops


1. Feedforward loop
2. Feedback loop
3. V1 influence
Retina
Primary visual
cortex
Relay
cell
Interneuron
LGN
TRN
1
2
3
3
3

Summary: Thalamus (LGN)

- Optic nerve transmits retina to LGN, a part of the thalamus
- LGN then sends information to V1
- LGN receptive fields are similar to retina (ON-OFF)
- Multiple segregated streams of information coming in and going out of LGN
- There are massive recurrent loops between thalamus and cortex (so LGN is not “just a relay”)

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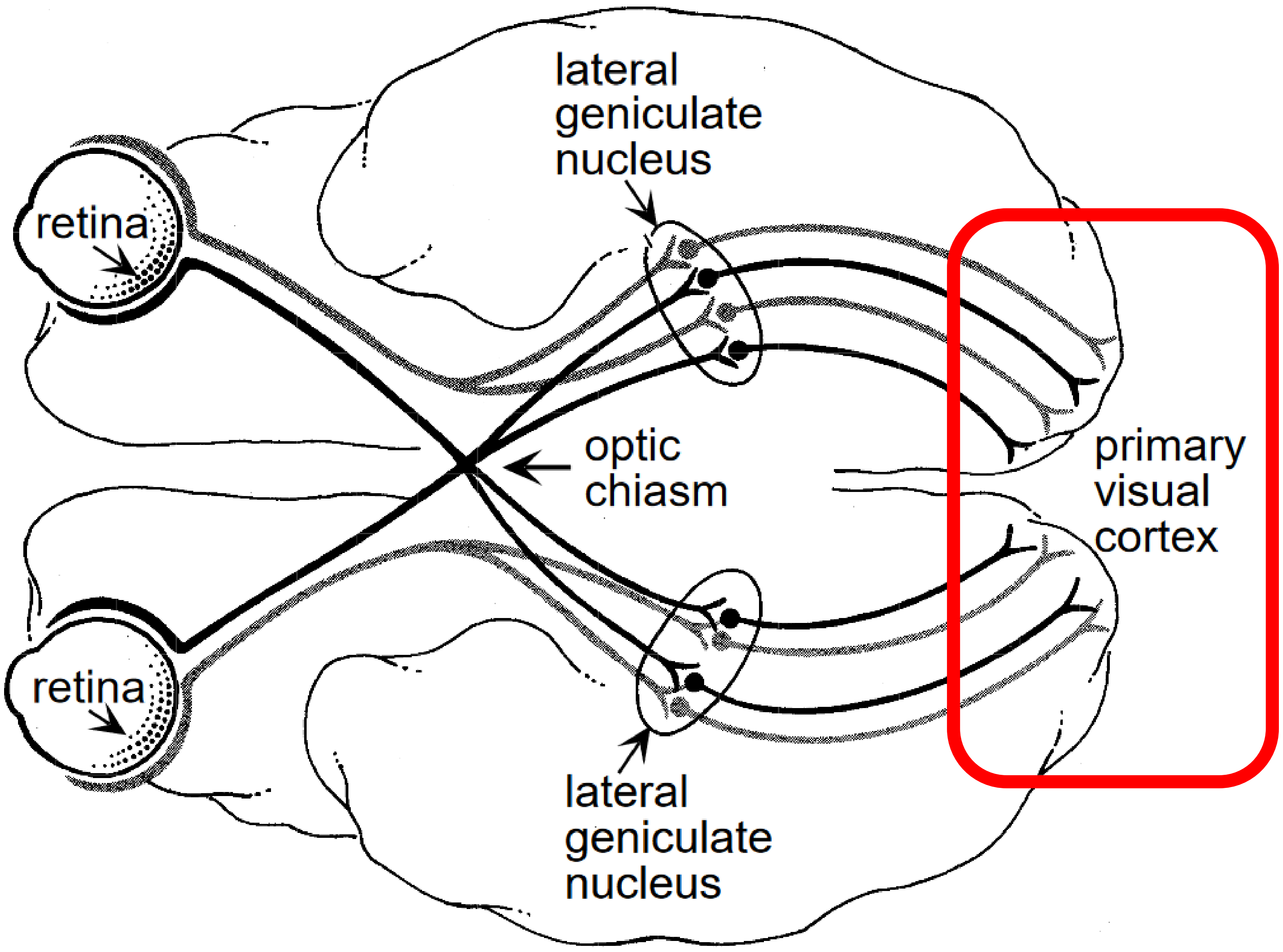


Primary Visual Cortex (V1)

- Primary visual cortex (also called “striate cortex”, V1, and area 17) is the first cortical area in the visual pathway
- It is arguably the first area where “interesting” representations of the visual world begin to emerge
- It is a very well-studied brain area, and has been mapped out in many different species
- It is sometimes considered a kind of “model system” – similar principles to those found in V1 seem to occur in many other brain areas, so hopefully insights from V1 generalise

Retinotopic Maps

- The visual system exhibits retinotopic maps – retinal coordinates are represented across the cortical surface
- Each location on visual cortex responds to a specific part of the retina
- The retinotopic coordinate system in V1 is nonlinearly transformed relative to the retina

Retinal Coordinates

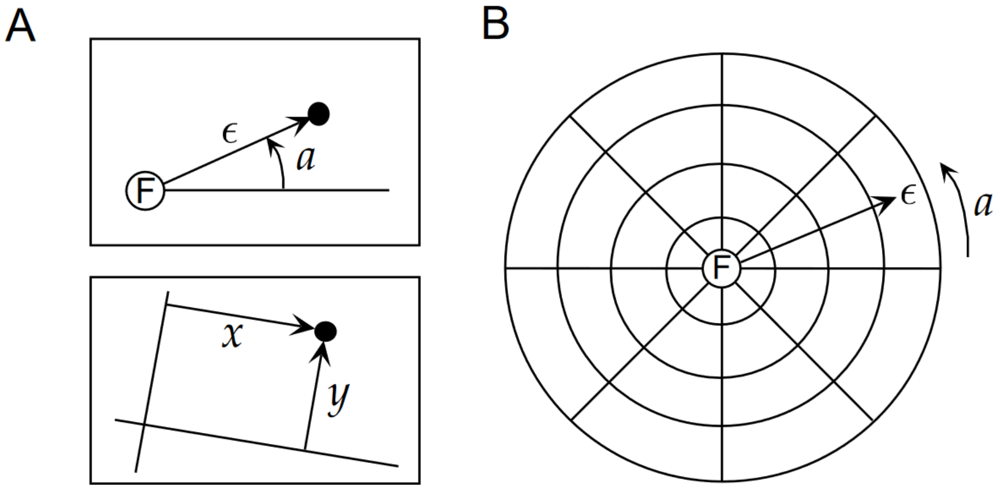


Figure 2.6 (A) Two coordinate systems used to parameterize image location. Each rectangle represents a tangent screen, and the filled circle is the location of a particular image point on the screen. The upper panel shows polar coordinates. The origin of the coordinate system is the fixation point F, the eccentricity ϵ is proportional to the radial distance from the fixation point to the image point, and a is the

V1 Coordinates

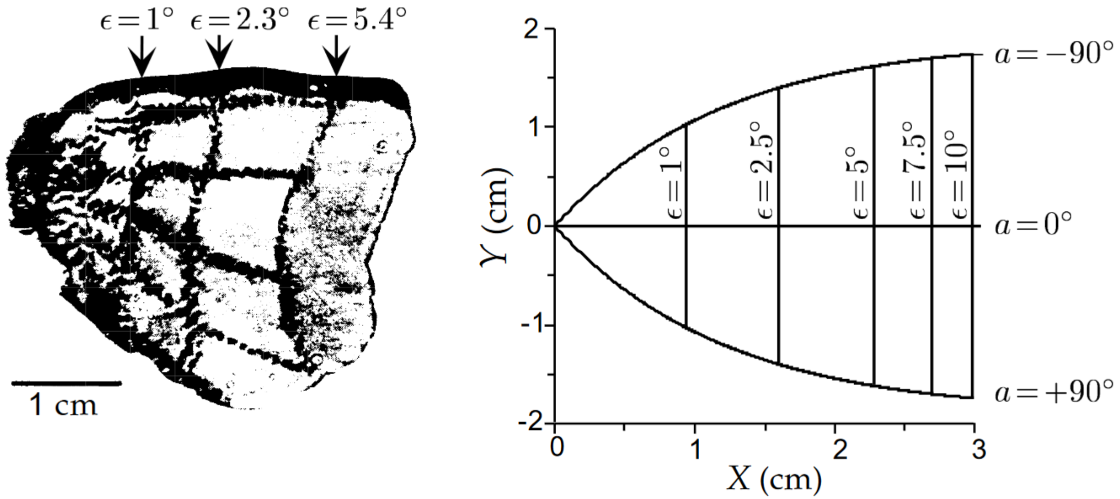
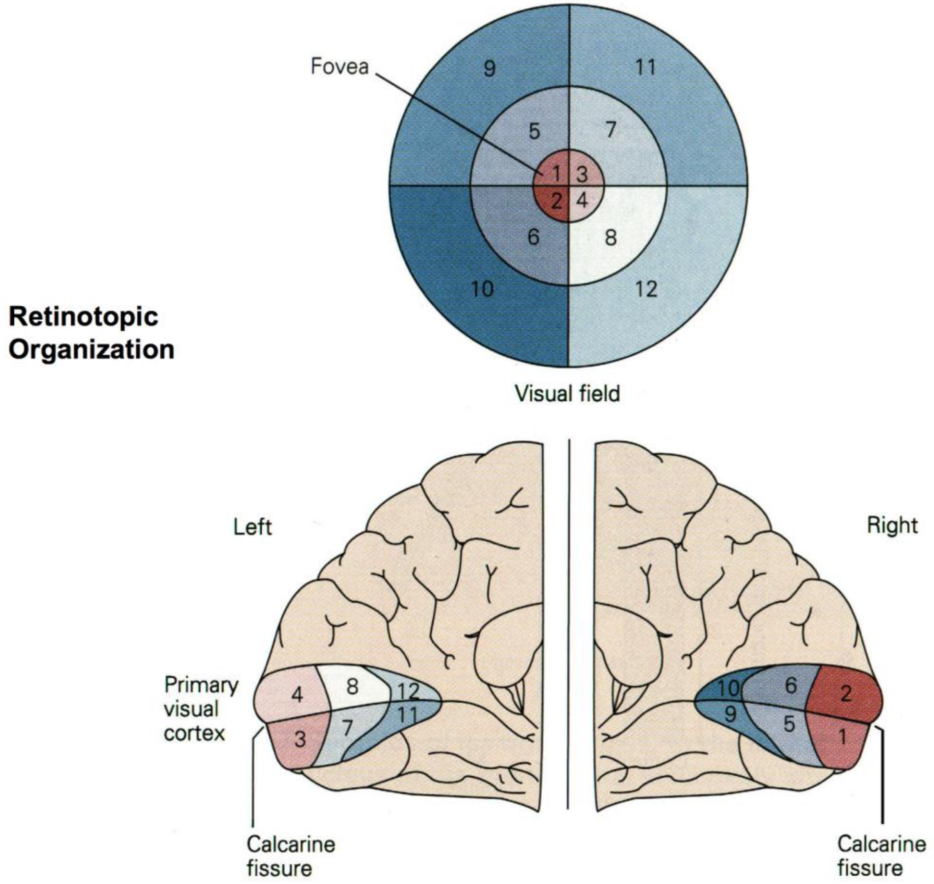
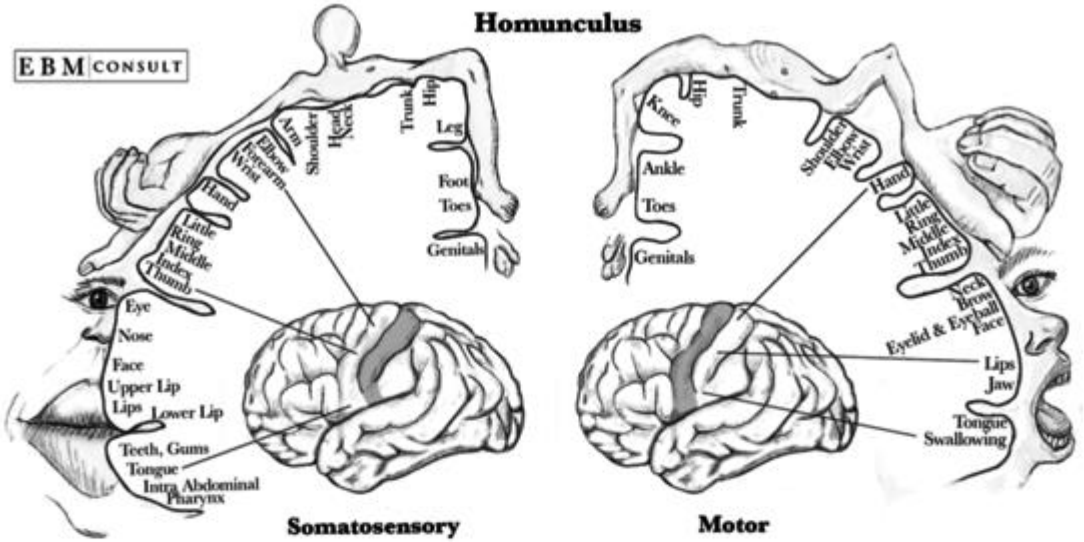


Figure 2.7 (A) An autoradiograph of the posterior region of the primary visual cortex from the left side of a macaque monkey brain. The pattern is a radioactive trace of the activity evoked by an image like that in figure 2.6B. The vertical lines correspond to circles at eccentricities of 1°, 2.3°, and 5.4°, and the horizontal lines (from top to bottom) represent radial lines in the visual image at a values of $-90°$, $-45°$, $0°$, $45°$, and $90°$. Only the part of cortex corresponding to the central region

Topographic Maps

- There are many topographic maps in the brain, in sensory, motor and cognitive domains





Orientation Tuning Curves

- Hubel and Wiesel discovered that many V1 neurons are tuned to the orientation of a bar moving across the visual field
- This was a seminal result and won them the Nobel prize.

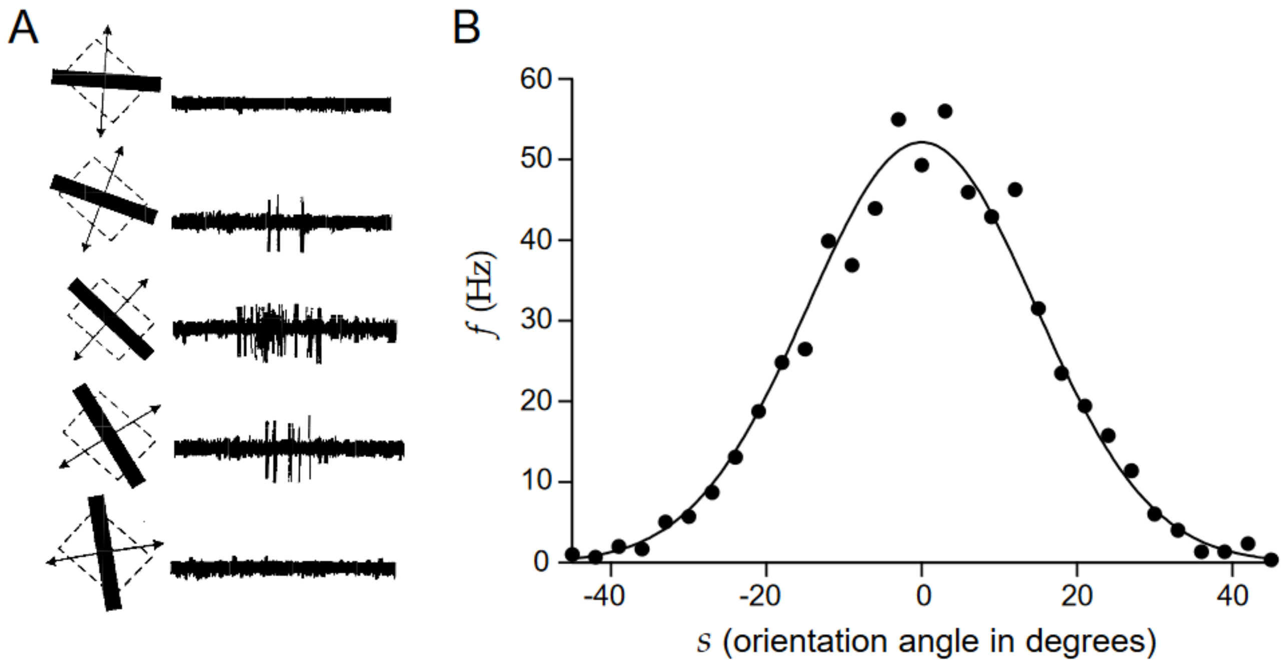


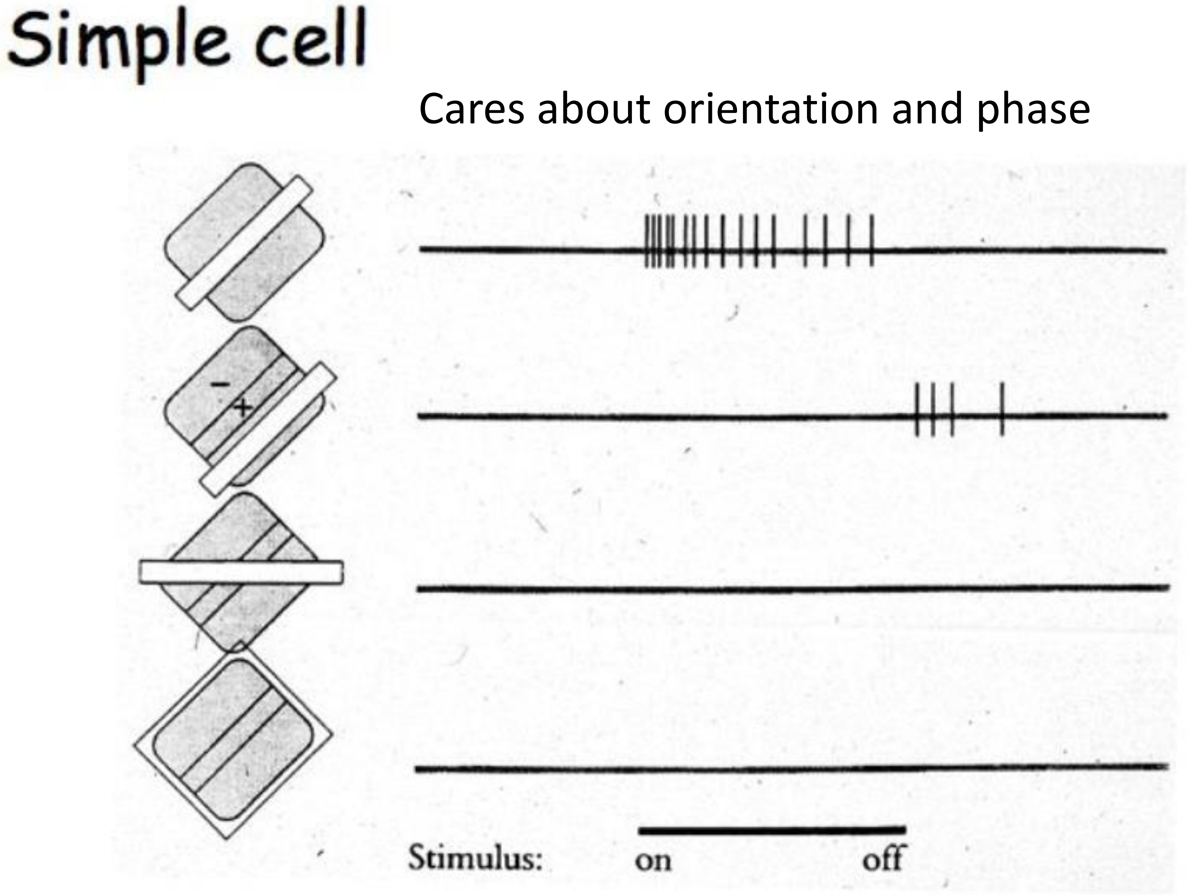
Figure 1.5 (A) Recordings from a neuron in the primary visual cortex of a monkey. A bar of light was moved across the receptive field of the cell at different angles. The diagrams to the left of each trace show the receptive field as a dashed square and the light source as a black bar. The bidirectional motion of the light bar is indicated by the arrows. The angle of the bar indicates the orientation of the light

Simple cell in visual cortex

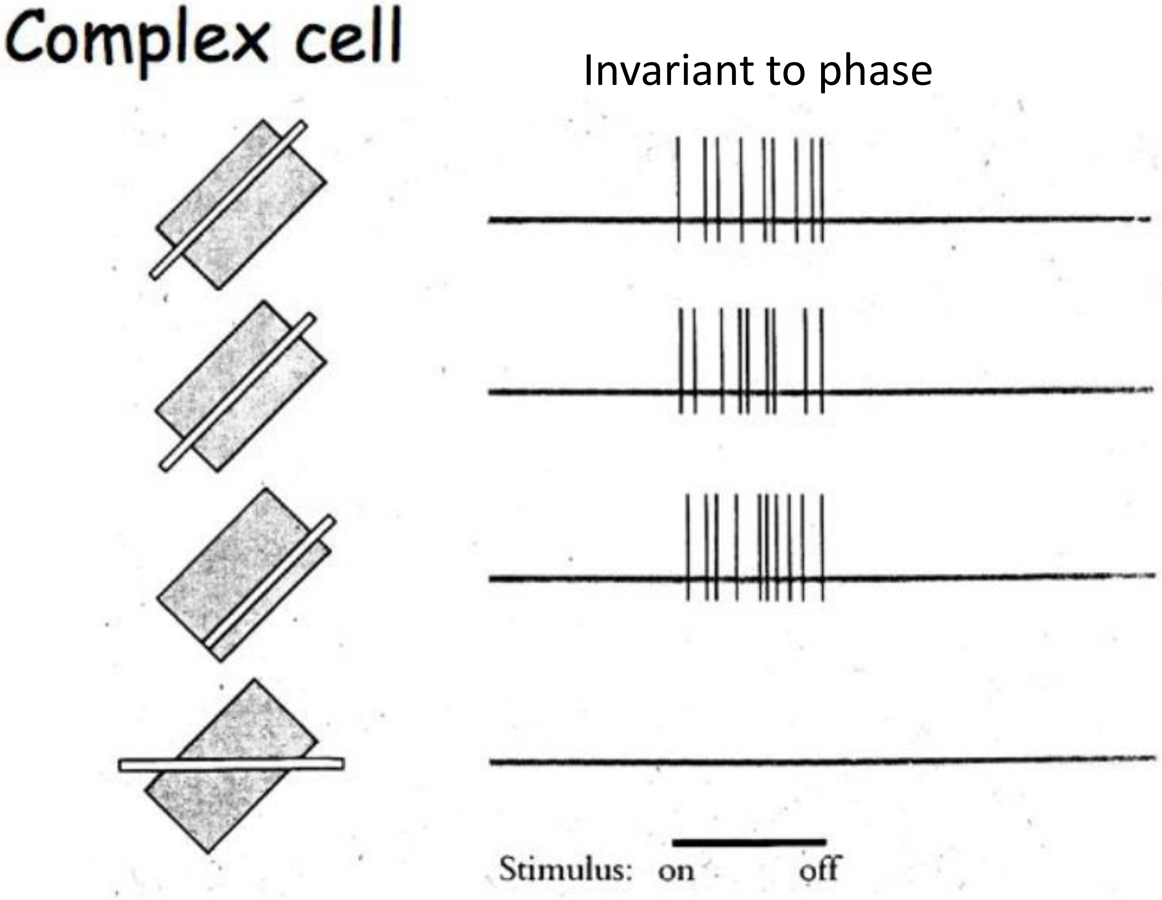
Hubel and Wiesel

Simple and Complex Cells

Cares about orientation and phase



Invariant to phase

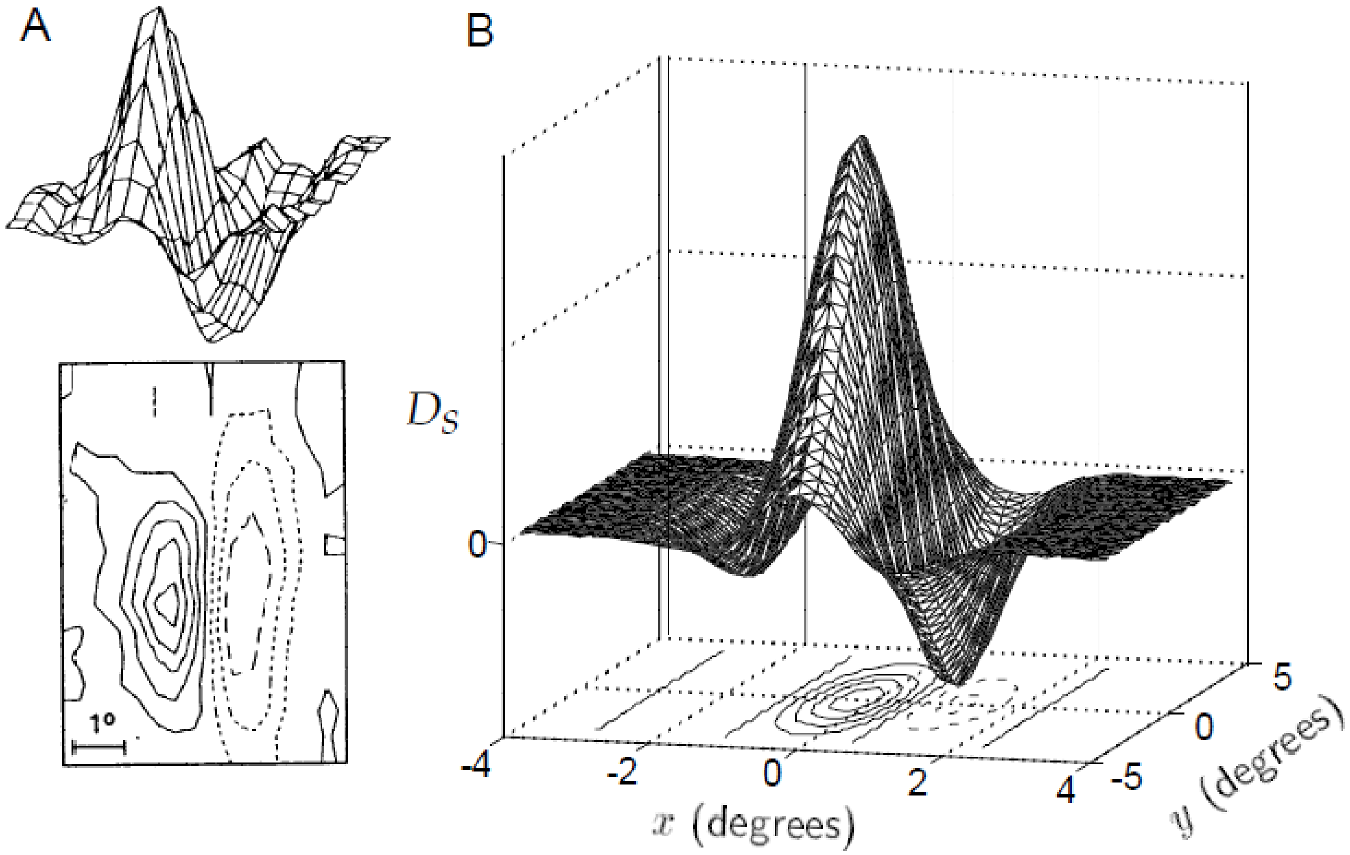


Simple Cells as Gabor Filters

Preferred phase

$$R_{\text{simple}}(x, y) = \exp\left(-\frac{(x - x_c)^2}{2\sigma_x^2} - \frac{(y - y_c)^2}{2\sigma_y^2}\right)\cos(\mathbf{k}\cdot\mathbf{x} - \phi)$$

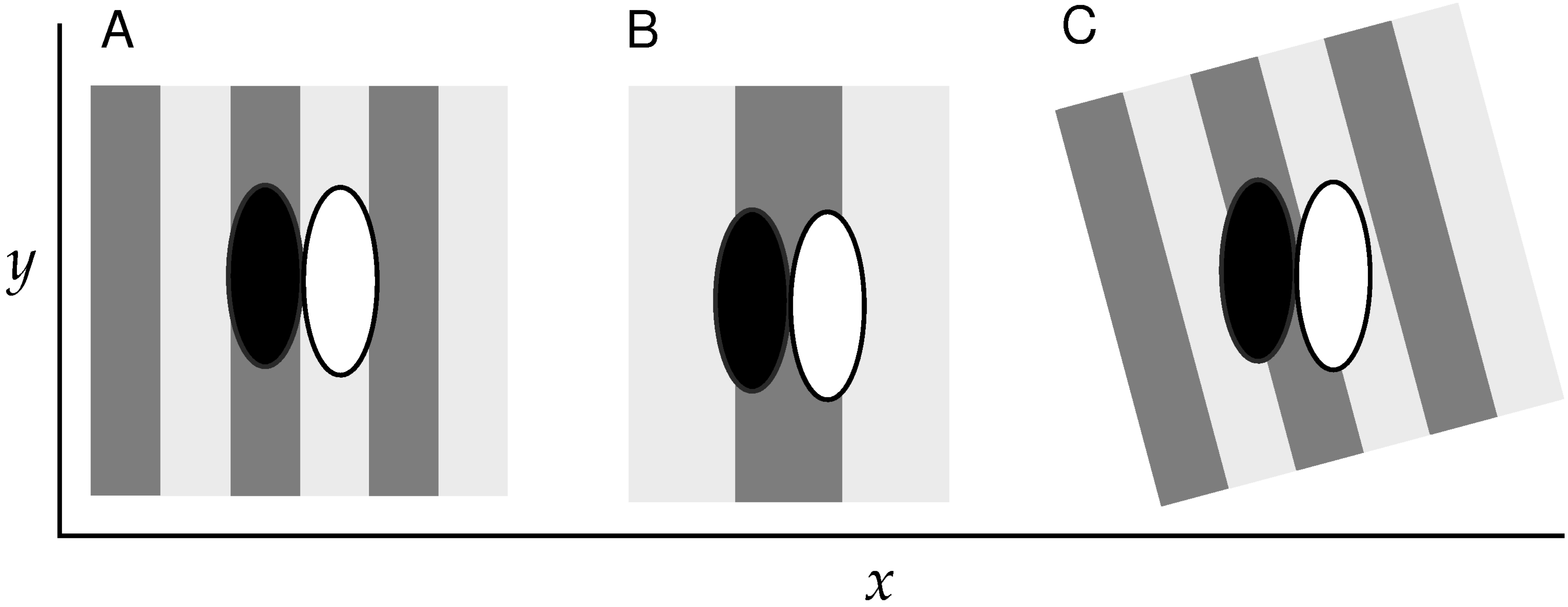
Preferred orientation and spatial frequency



Simple cells are reasonably well described as having Gabor filter receptive fields, i.e. the product of a Gaussian and a sinusoid.

Panel A shows a receptive field from a real neuron estimated via a technique called reverse correlation, B shows a Gabor filter.

Simple Cells as Gabor Filters



The above figure illustrates how tuning to both orientation and phase is explained by Gabor filters

Complex Cells as Nonlinear Combinations of Simple Cells

If we model the response of a simple cell to an image *I(x,y)* as:

$$r_{\text{simple}}(\phi) = \int\int I(x,y) \exp\left(-\frac{(x-c_x)^2}{2\sigma_x^2} - \frac{(y-c_y)^2}{2\sigma_y^2}\right) \cos(\mathbf{k}\cdot\mathbf{x} - \phi) dx dy$$

Complex Cells as Nonlinear Combinations of Simple Cells

If we model the response of a simple cell to an image *I(x,y)* as:

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a simple model for the firing rate of a complex cell is:

$$r_{\text{complex}} = \left[r_{\text{simple}}(\phi)\right]^2 + \left[r_{\text{simple}}(\phi-\pi/2)\right]^2$$

Complex Cells as Nonlinear Combinations of Simple Cells

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a simple model for the firing rate of a complex cell is:

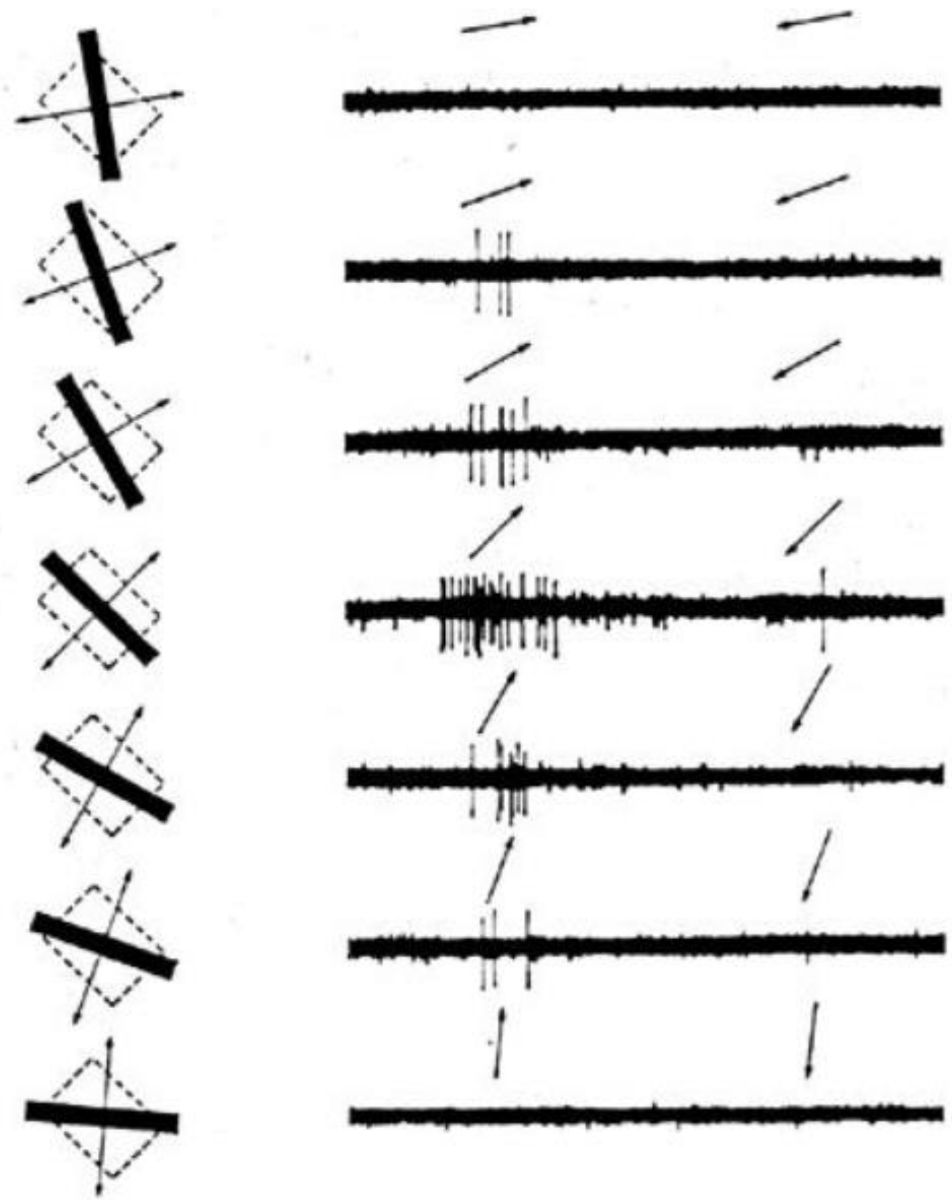
$$r_{\text{complex}} = [r_{\text{simple}}(\phi)]^2 + [r_{\text{simple}}(\phi - \pi/2)]^2$$

This suggests that complex cells may pool responses of simple cells with opposing phases.

Note that this model for complex cells is a nonlinear filter, whereas the model for simple cells is a linear filter.

Direction Selectivity

- V1 neurons can be selective to direction as well as orientation
- This V1 neuron responds to movement north-east but not south-west
- Receptive field models usually involve both temporal and spatial components (see Dayan and Abbott)



What are Gabor Filters For?

- Just as difference of Gaussian RFs act as a bandpass filter and emphasise edges, Gabor filters emphasise oriented edges in an image (edge detection)

- Gabor filters are often used in image processing applications, they help to efficiently encode the image and act as useful basis functions (better than pixel representation)

- Complex cells have greater invariance than simple cells – much of visual processing involves generating increasing levels of invariance to irrelevant features (e.g., invariance to object pose or luminance)

- Similar representations emerge when certain models are trained on natural images (e.g., convolutional neural networks, independent components analysis, etc.) – fundamental structure of natural image statistics which any well-adapted system will exploit

Topographic Maps for Orientation

Orientation preference of neurons varies systematically across the surface of V1

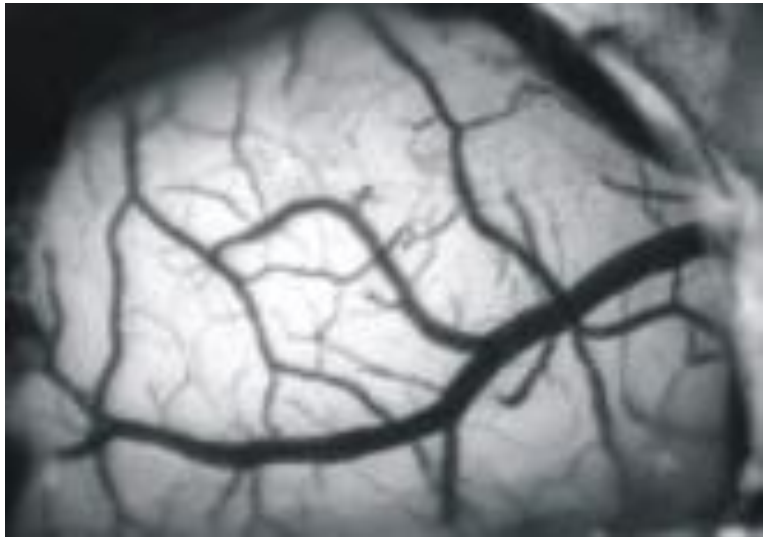
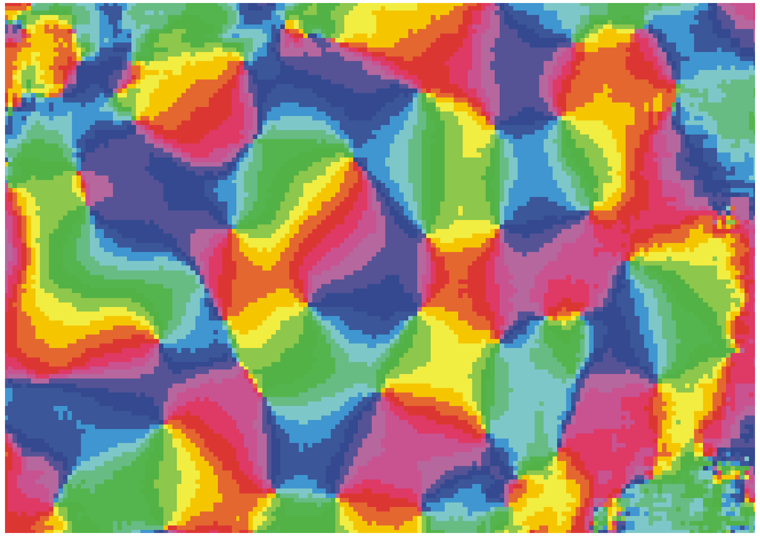
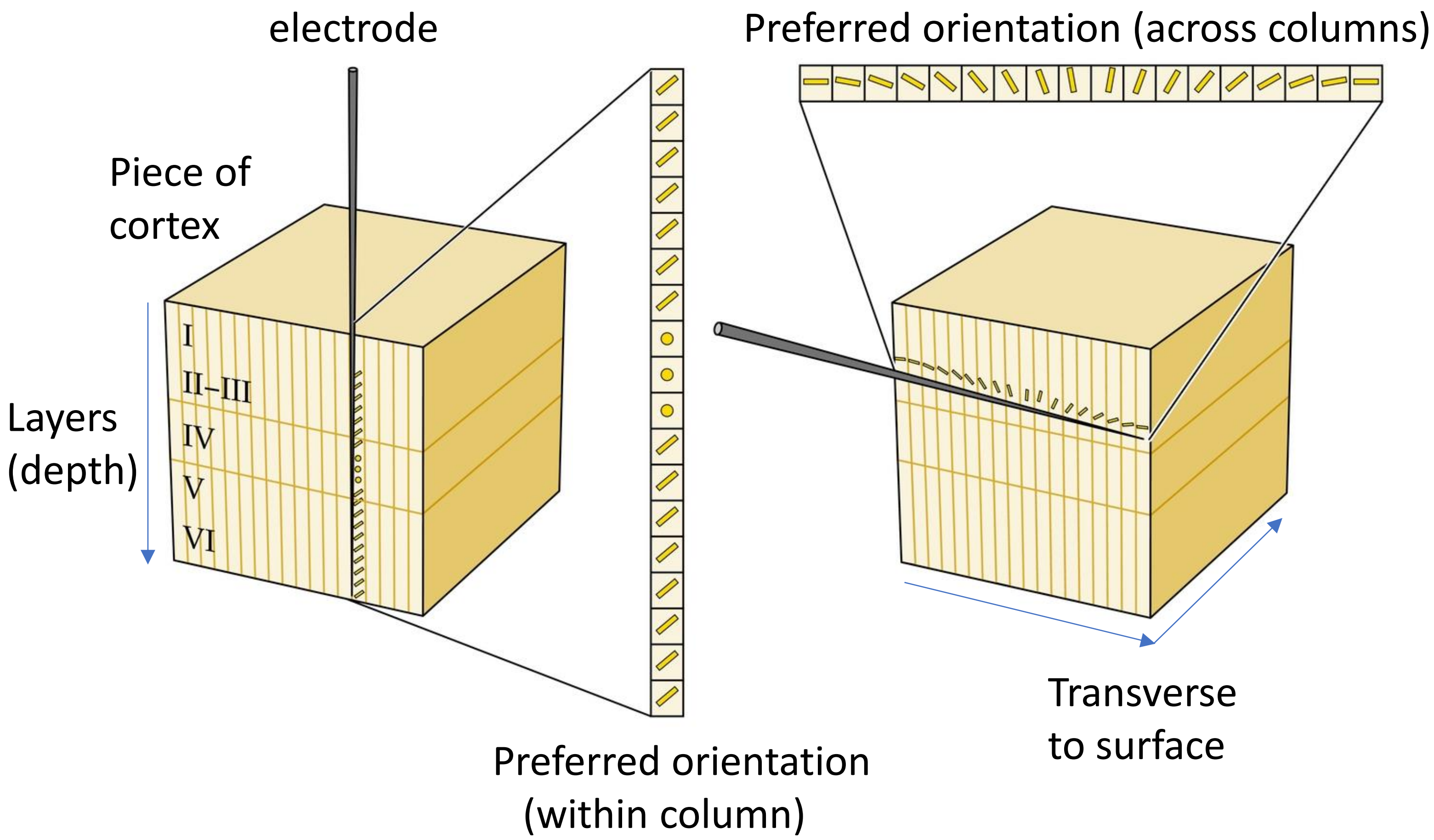


Image of cortical surface (V1)



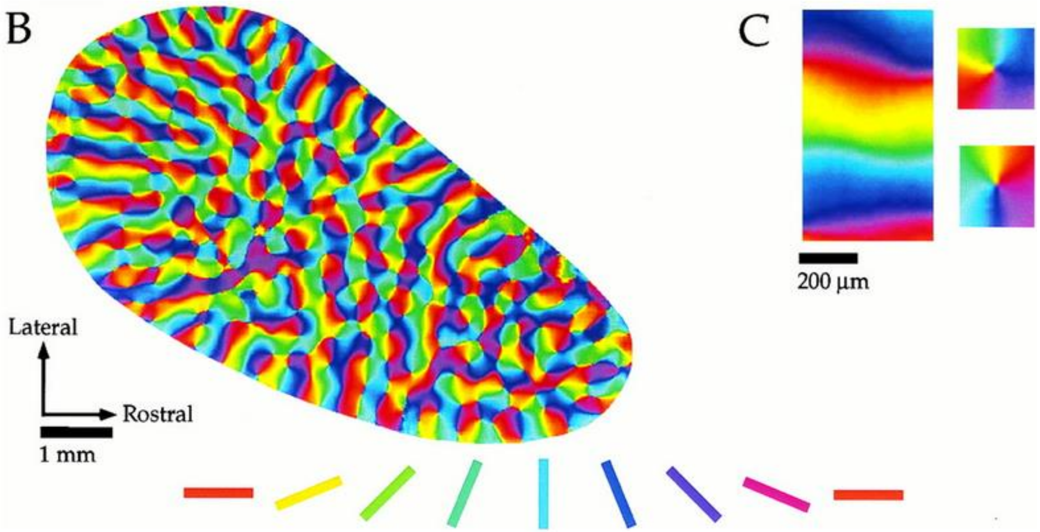
Preferred orientation of neurons
at each point on cortical surface

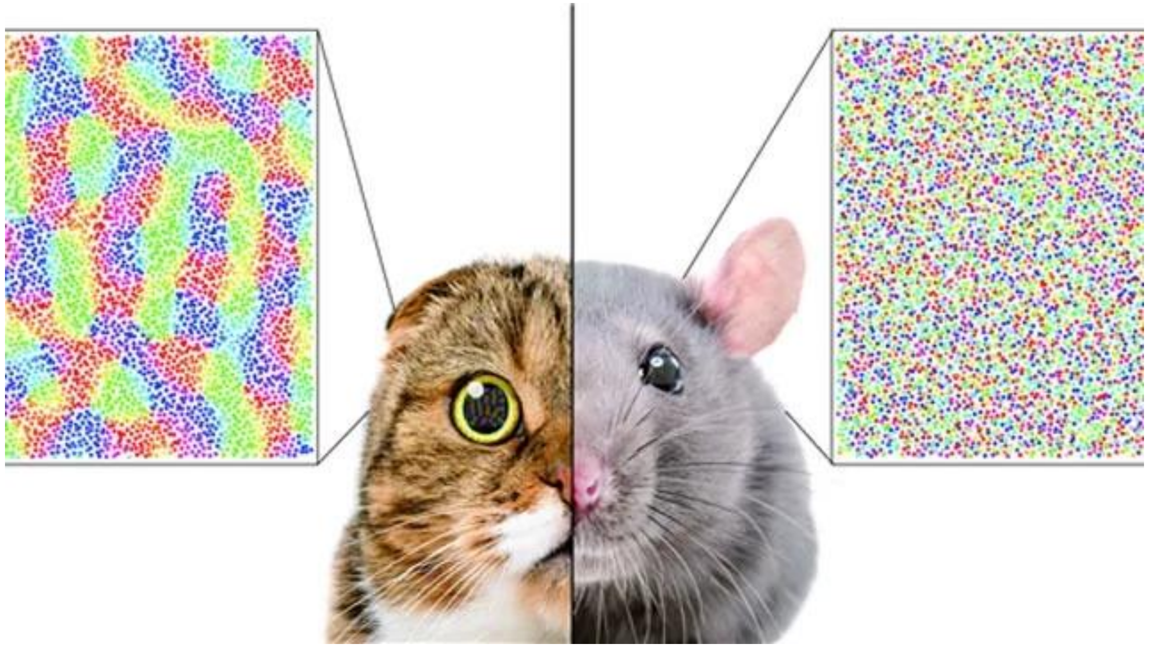
Topographic Maps for Orientation



Topographic Maps for Orientation: Species-Dependence

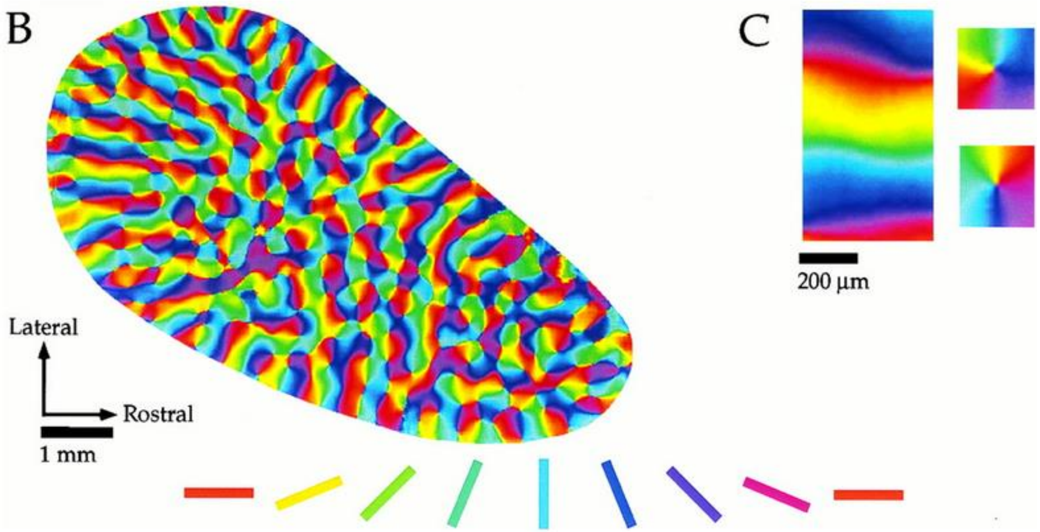
Tree Shrew V1

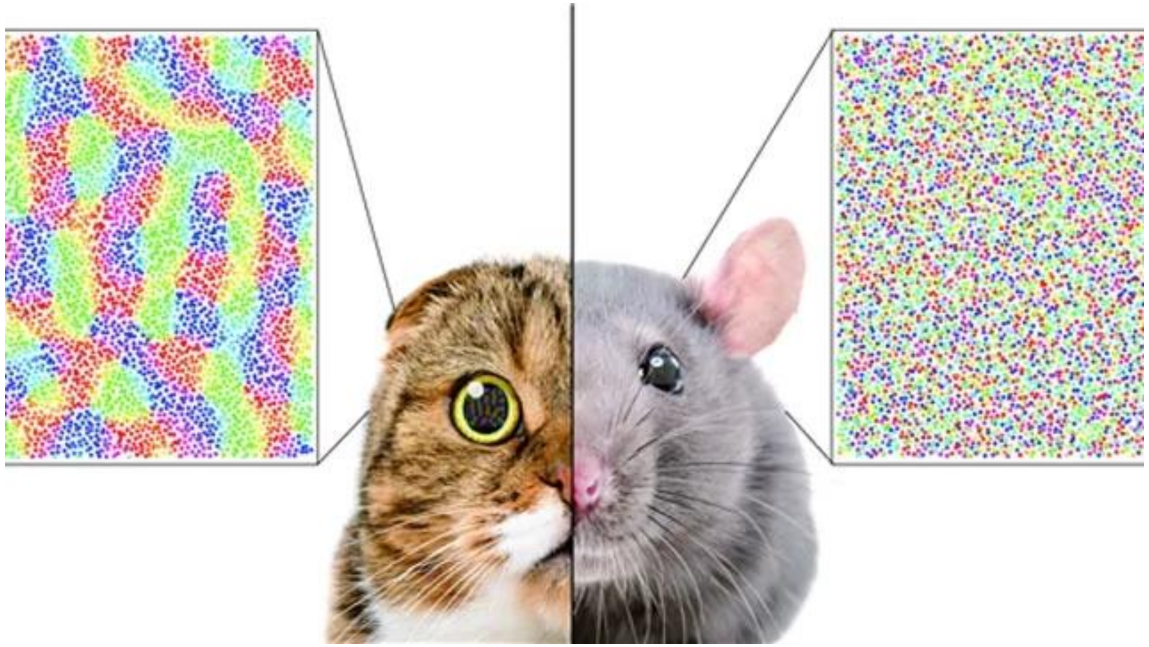


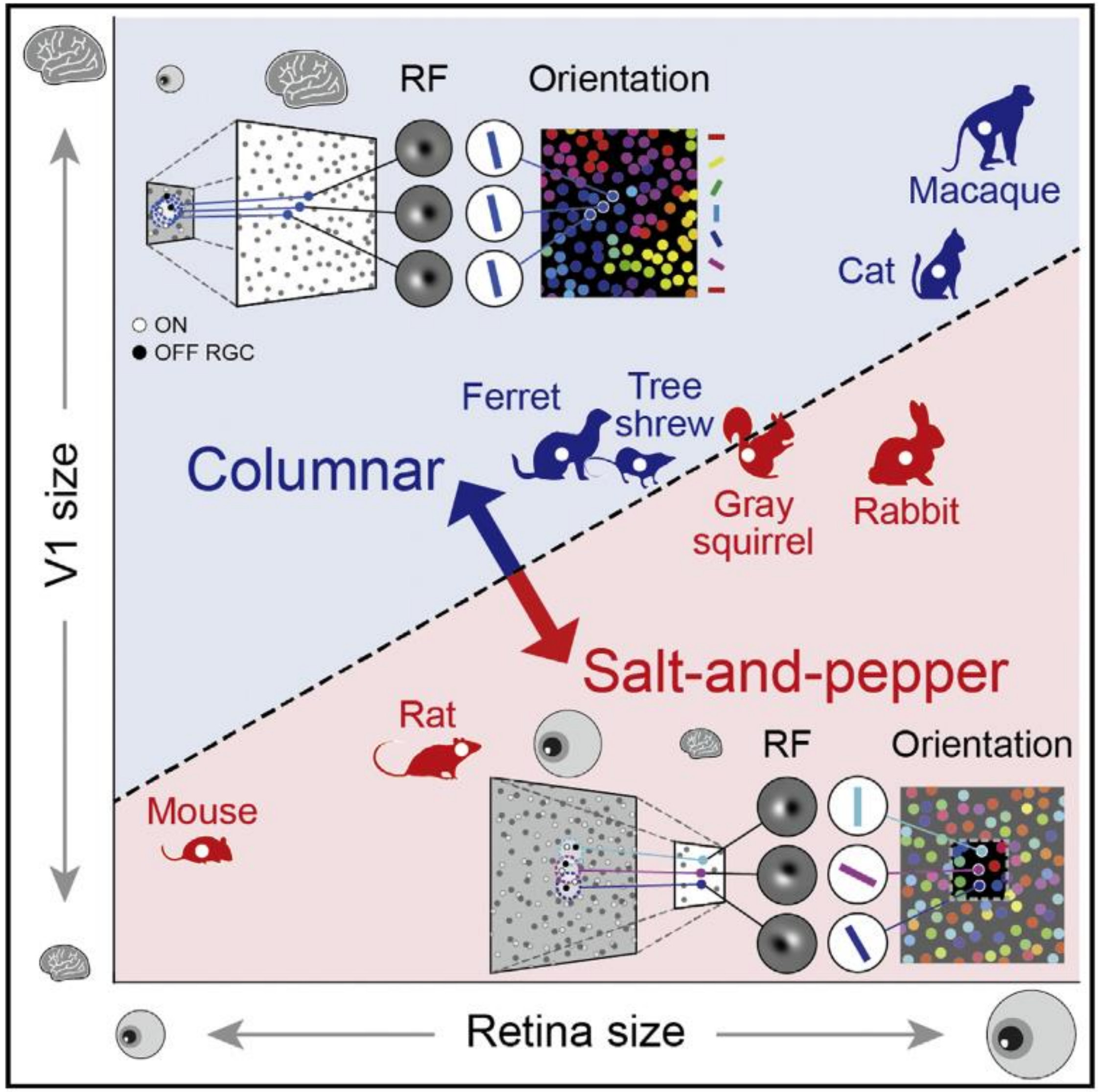


Topographic Maps for Orientation: Species-Dependence

Tree Shrew V1

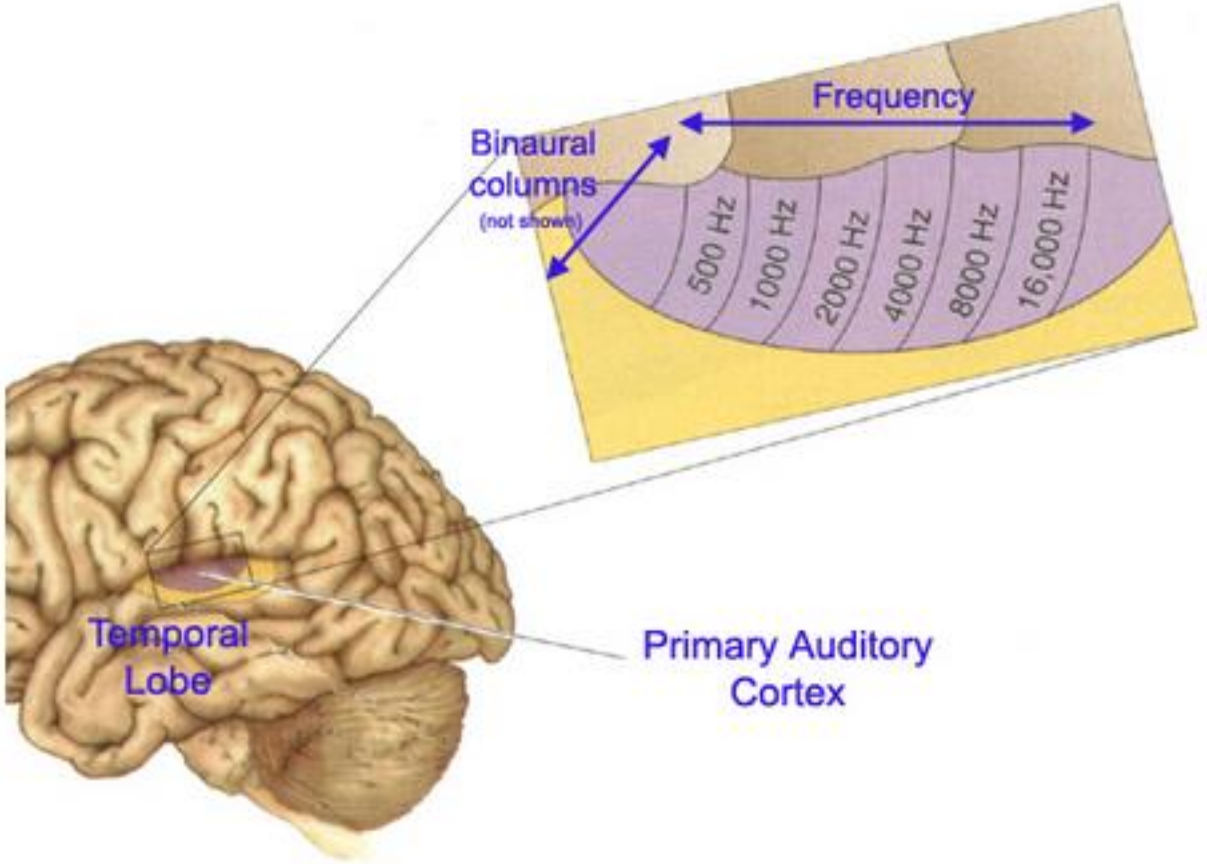




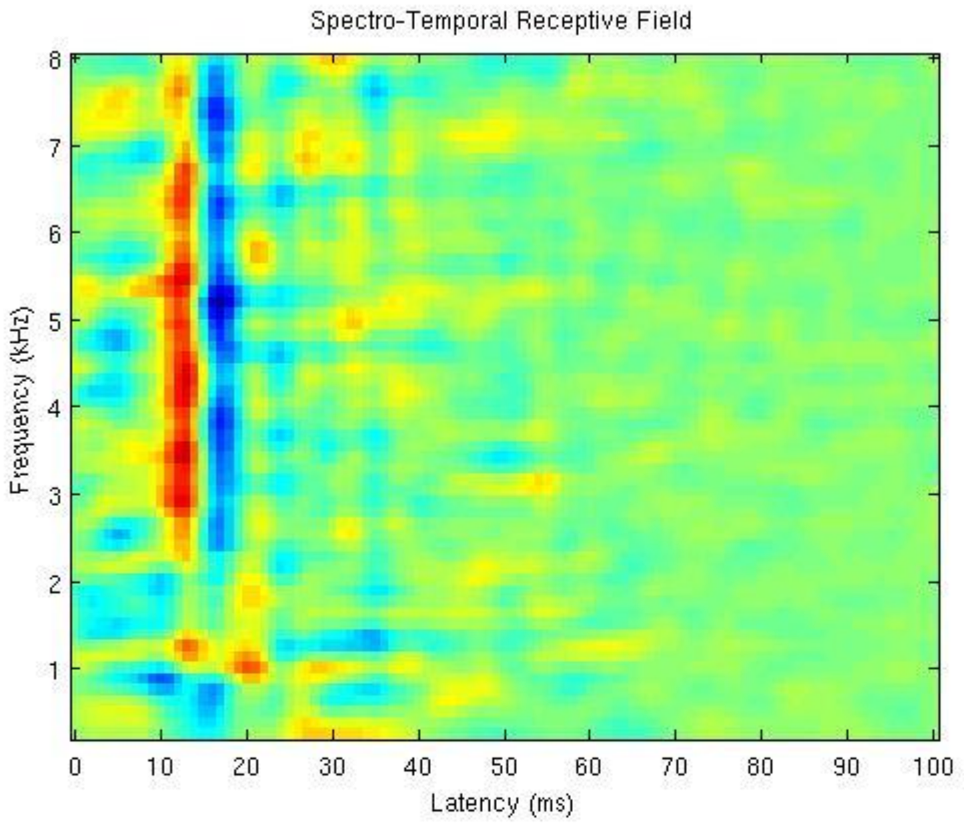


Topographic Maps and Receptive Fields in Auditory Cortex

Auditory cortex has a “tonotopic map” –
preferred frequency shifts across cortical surface

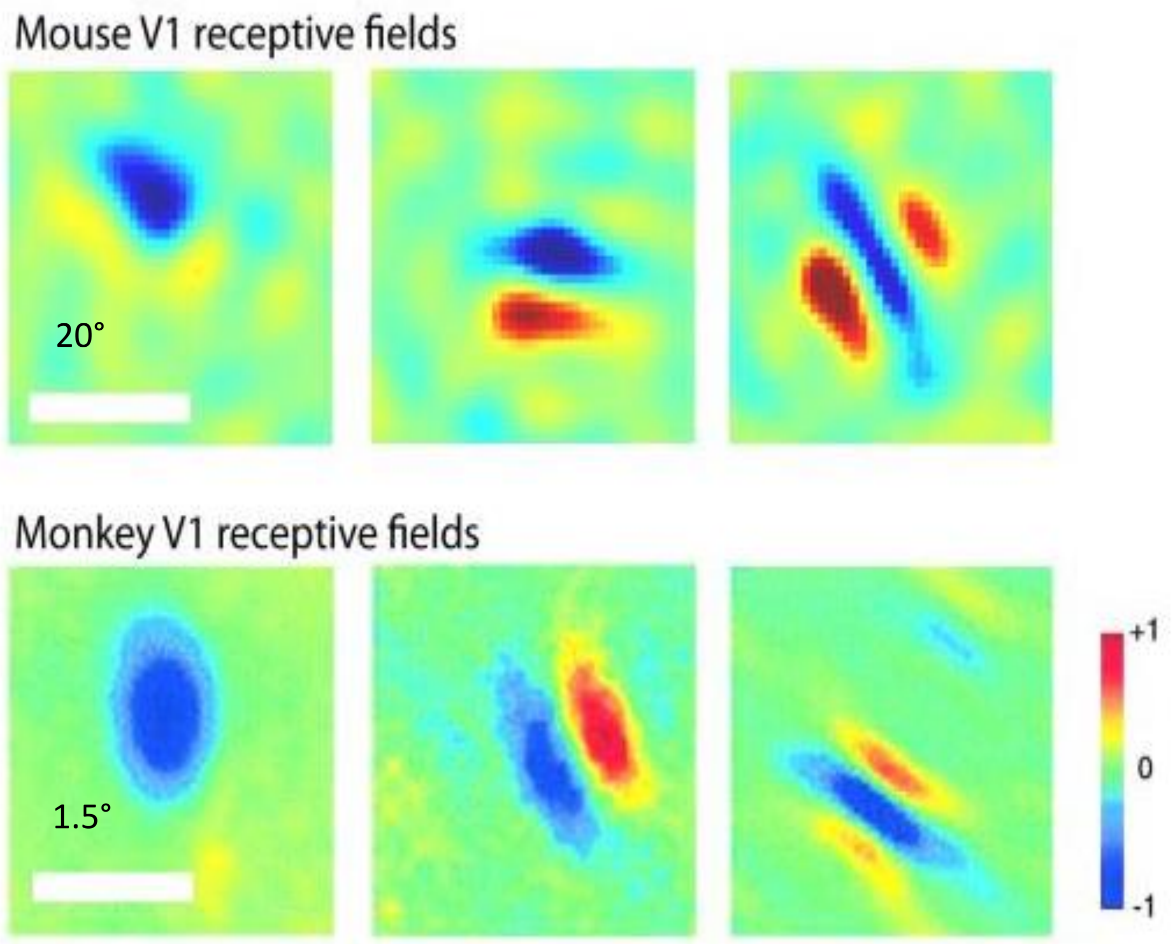


Individual auditory neurons have
“spectro-temporal receptive fields”



Take home: principles from visual system tend to generalise to all other sensory systems
(sometimes even non-sensory systems)

Conservation Across Species



From Niell & Huberman, 2011

Summary – Primary Visual Cortex

- V1 is the first cortical area to process visual input
- V1 cells are tuned to stimulus orientation, and have Gabor filter receptive fields
- V1 has a retinotopic map, and a topographic map for orientation (but not in all species)
- There are simple, complex, and hypercomplex cells, direction and speed tuned cells, etc.
- We didn’t discuss: tuning to temporal/spatial frequency, colour, contrast, etc.

Summary of Lecture

- We discussed the first three stages of visual processing (retina, LGN, and V1)
- Each stage extracts features of the image, performs some processing, and sends to the next stage
- In retina and LGN, we find ON-OFF receptive fields, which emphasise edges
- In V1, we find orientation tuning and Gabor filter receptive fields, which detect oriented edges

Bibliography

- Dayan and Abbott Chapter 2

- Course notes: Chapter 7, 8