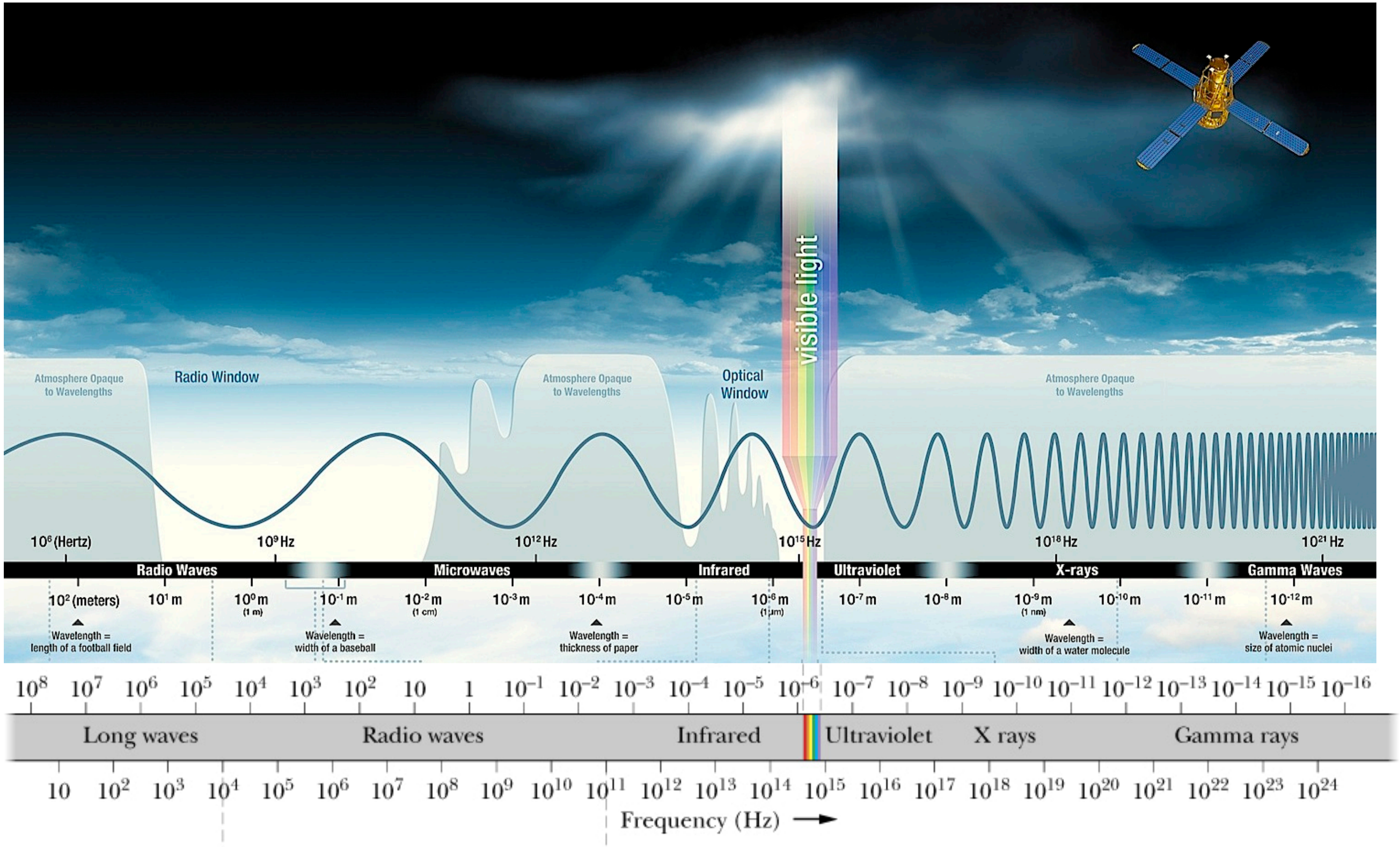
Vision

Kanizsa triangle

The electromagnetic spectrum

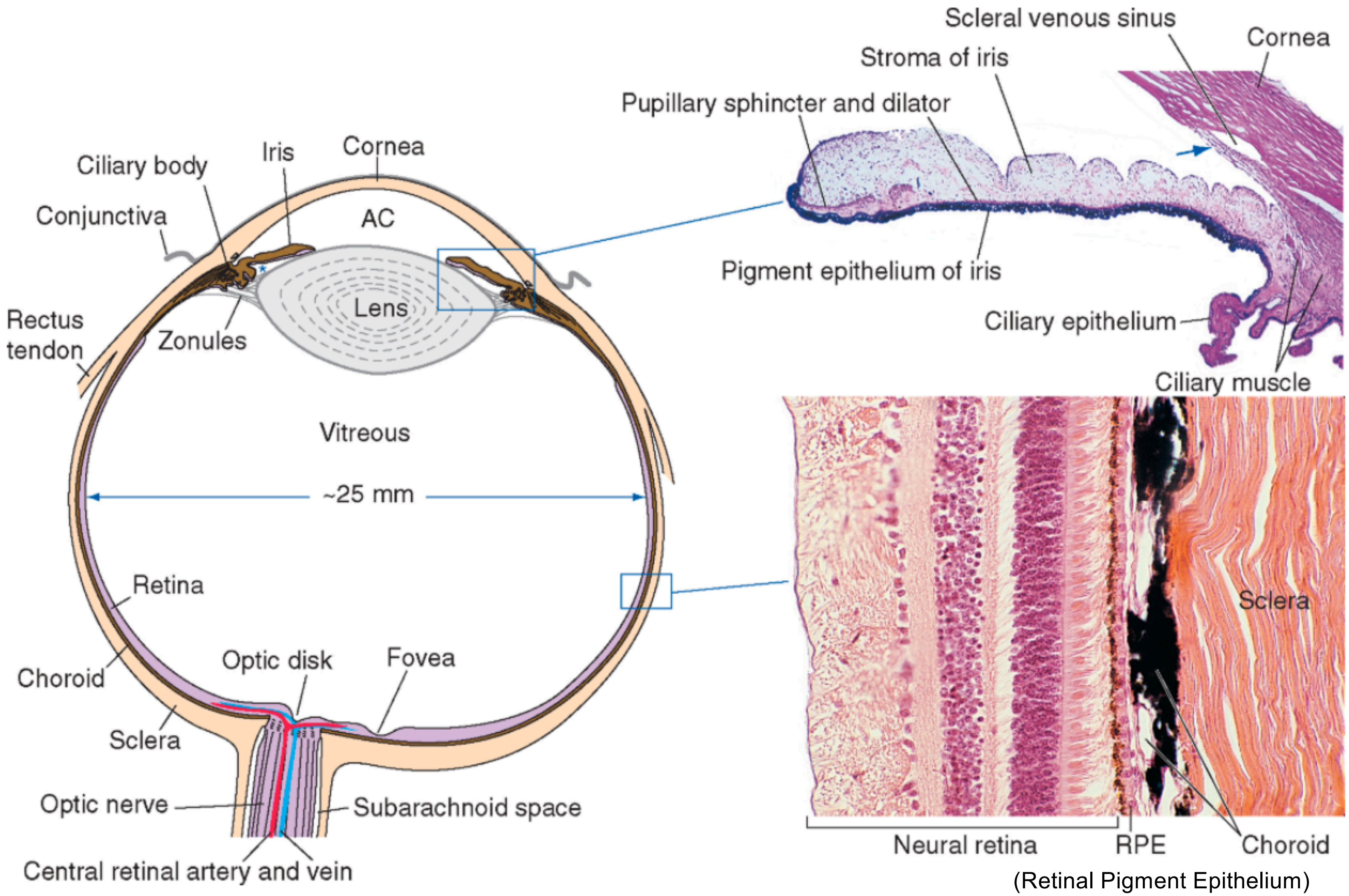


Low energy waves. Too weak to affect molecules. Absorbed by atmospheric water vapor.

Medium energy waves. Absorbed by pigments in plants and animals. On a 10 000 km scale, visible light range would be just 8 mm.

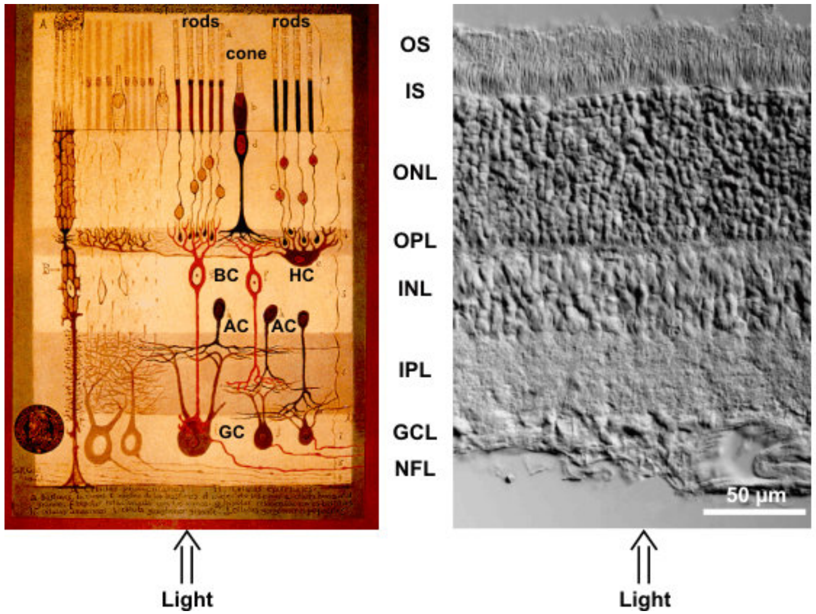
High energy waves. Break molecular bonds. Absorbed by atmospheric ozone.

The eye



The eye is designed to focus the visual image on the retina. The cornea (the transparent front part of the eye) and lens together form the equivalent of the camera lens. They focus light from different distances on the retina where photoreceptors are located.

The mistake of evolution?



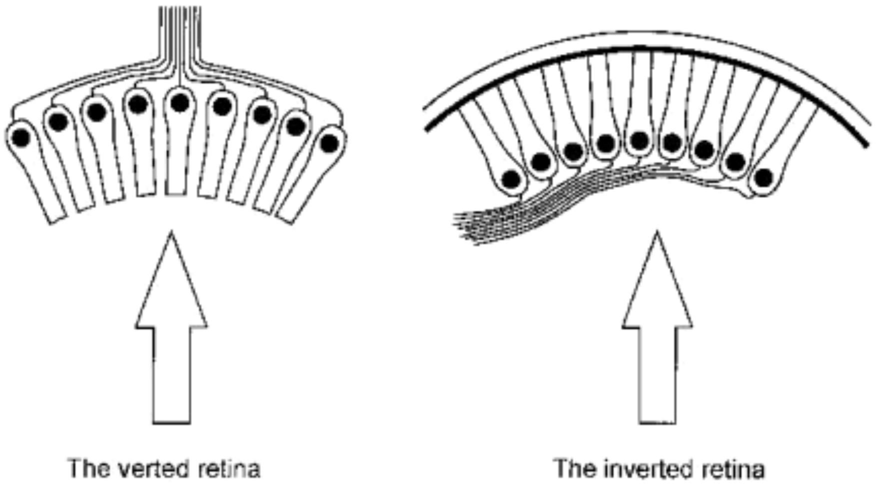
Left: schematic diagram of the retina by Santiago Ramon y Cajal (~1900). Right: section of rat's retina.

Hypotheses:

- protection against the damaging effects of light
- sustaining the photoreceptors by the retinal pigment epithelium (recycling and metabolising their products)

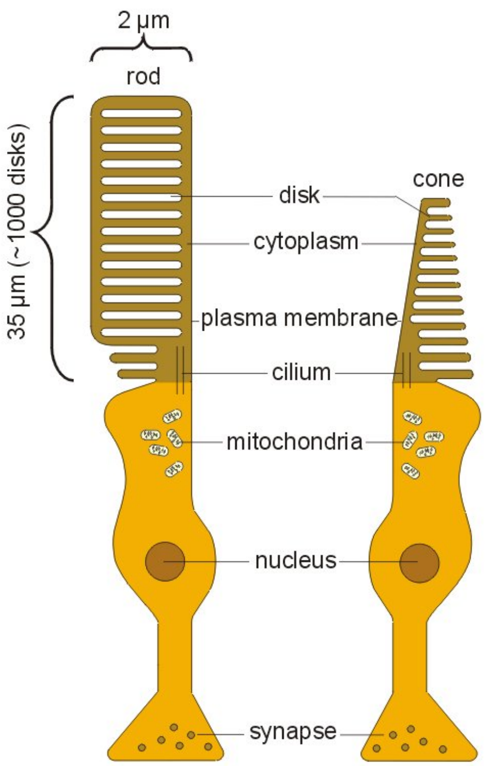
Side effect:

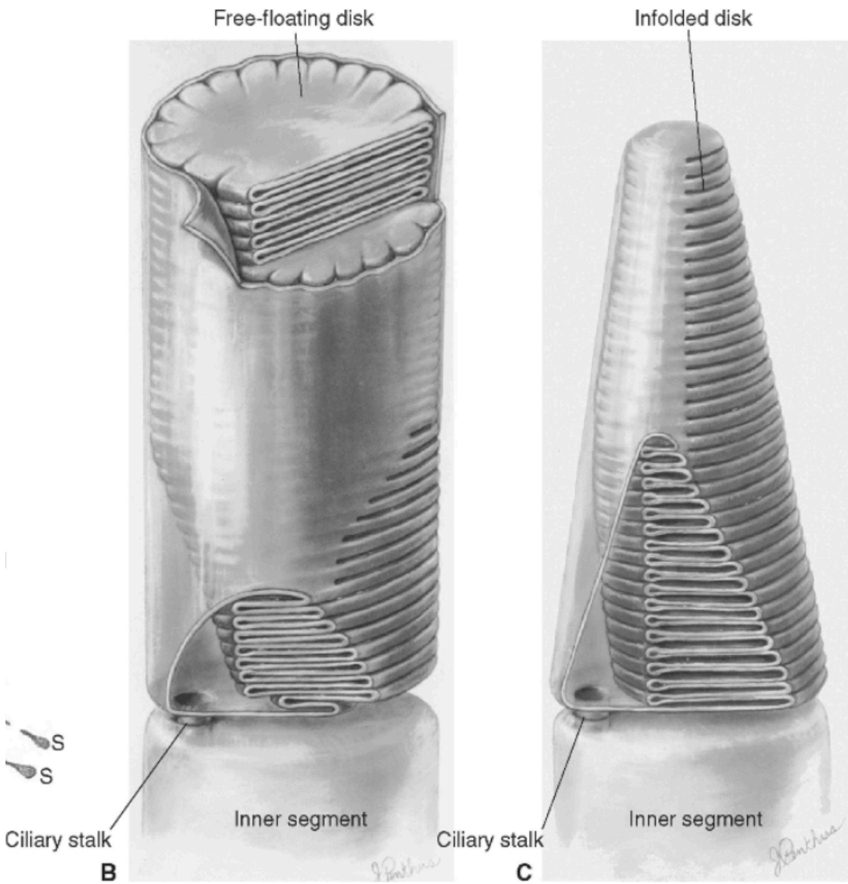
- blind spot



In vertebrates retina the light must pass through several inner layers of nerve cells and their processes before it reaches the photoreceptors. It is typical of vertebrates but rare among invertebrates.

Photoreceptors – rods and cones





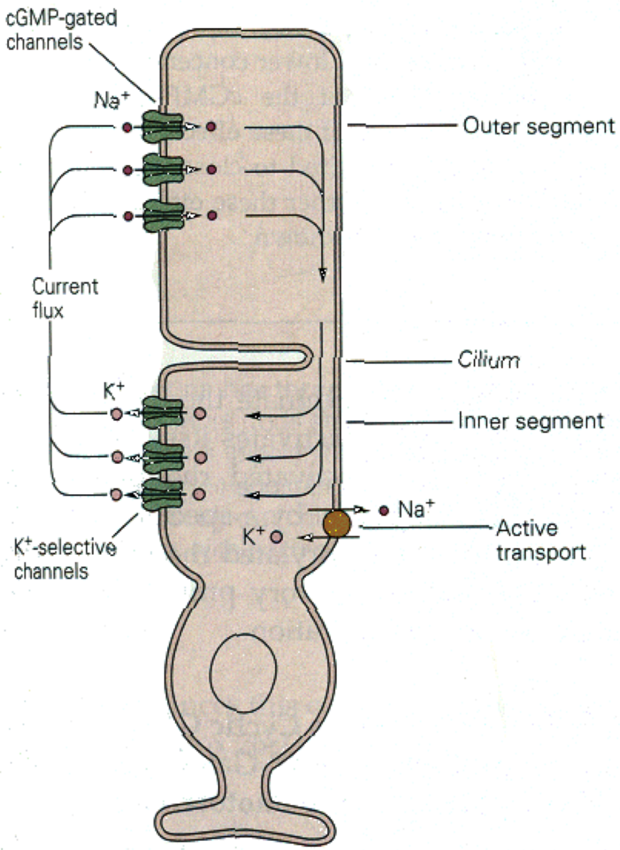
The human retina contains two types of photoreceptors, rods and cones. Cones are responsible for day vision. Rods mediate night vision.

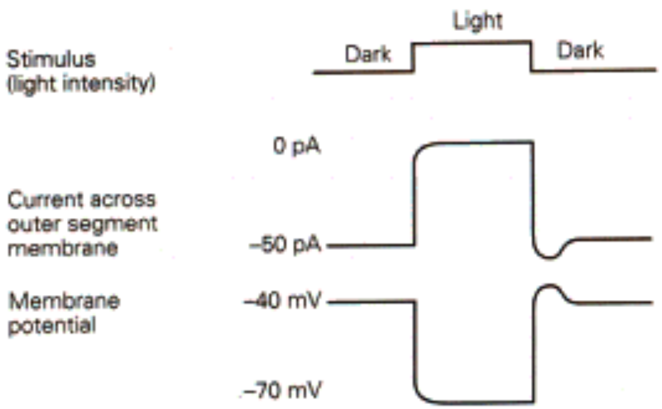
- Rods are 1000 times more sensitive to light than cones

-95% are rods, 5% are cones

Each outer segment of rods and cones is filled with hundreds of flattened membrane disks. They contain visual pigment, which is called **rhodopsin** in rods. It absorbs photons (light) causing response of the cell.

The dark current

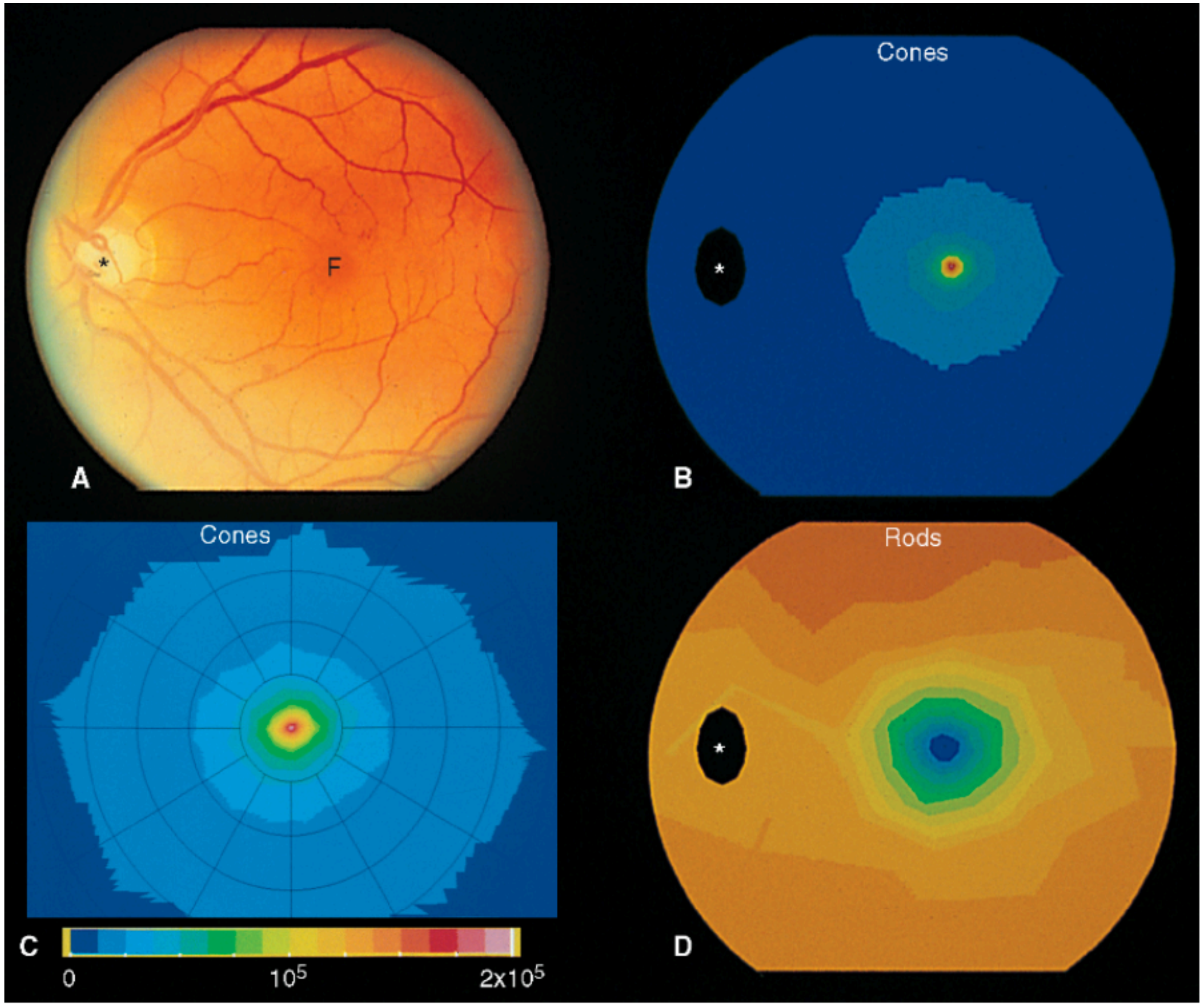




In darkness two currents flow in a photoreceptor. An inward Na+ current flows through cGMP-gated channels, while an outward K+ current flows through nongated K+-selective channels. The outward current carried by the K+ channels tends to hyperpolarize the photoreceptor. The inward current tends to depolarize the photoreceptor. As a result, in darkness the photoreceptor's membrane potential is around -40 mV. The photoreceptor is able to maintain steady intracellular concentrations of Na+ and K+ in the face of these large fluxes because its inner segment has a high density of Na+-K+ pumps, which pump out Na+ and pump in K+ .

In darkness the cytoplasmic concentration of cGMP is high, thus maintaining the cGMP-gated channels in an open state and allowing a steady inward current, called the dark current. When light reduces the level of cGMP, thus closing cGMP-gated channels, the inward current that flows through these channels is reduced and the cell becomes hyperpolarized to around -70 mV.

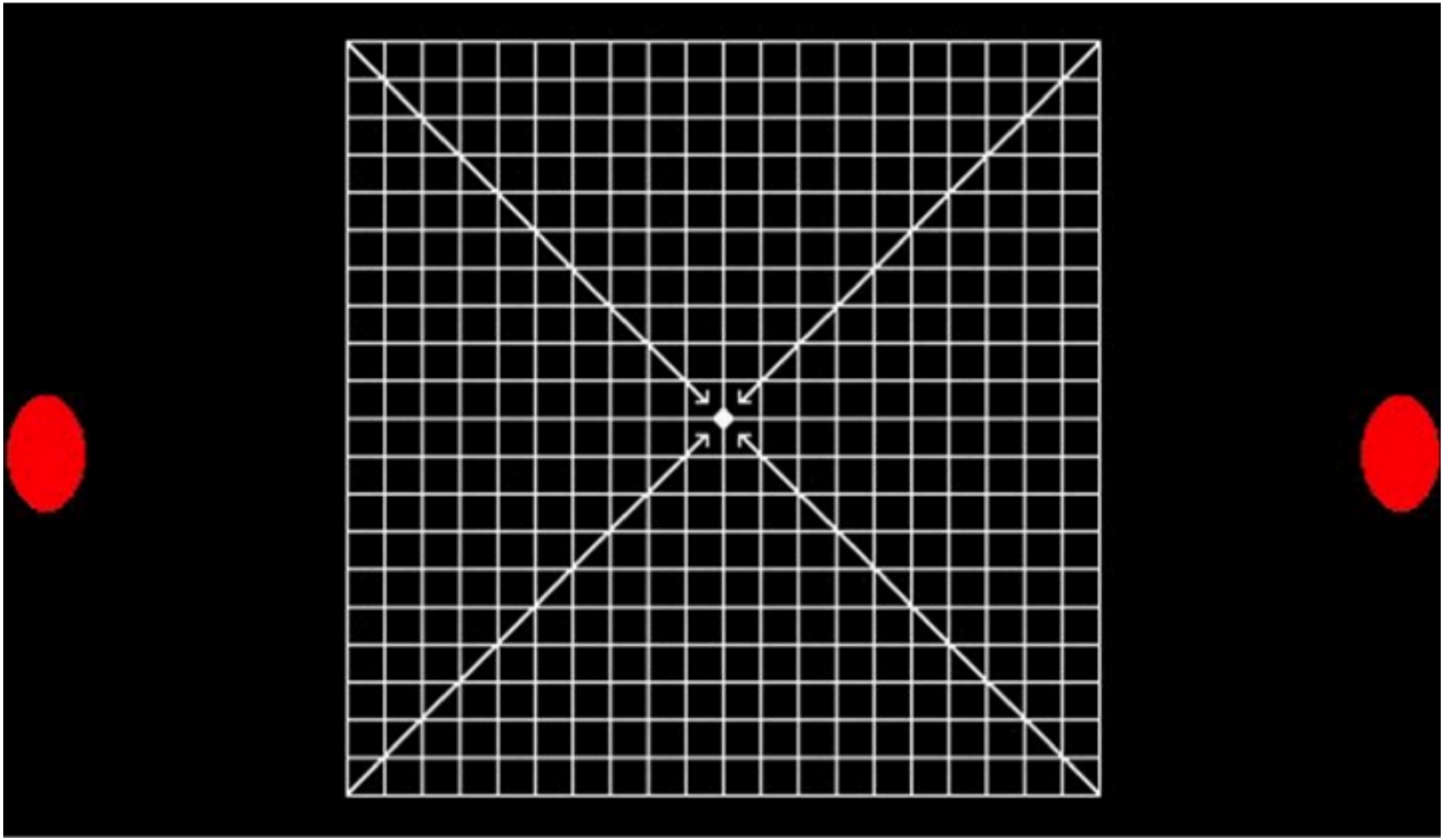
Rods and cones distribution



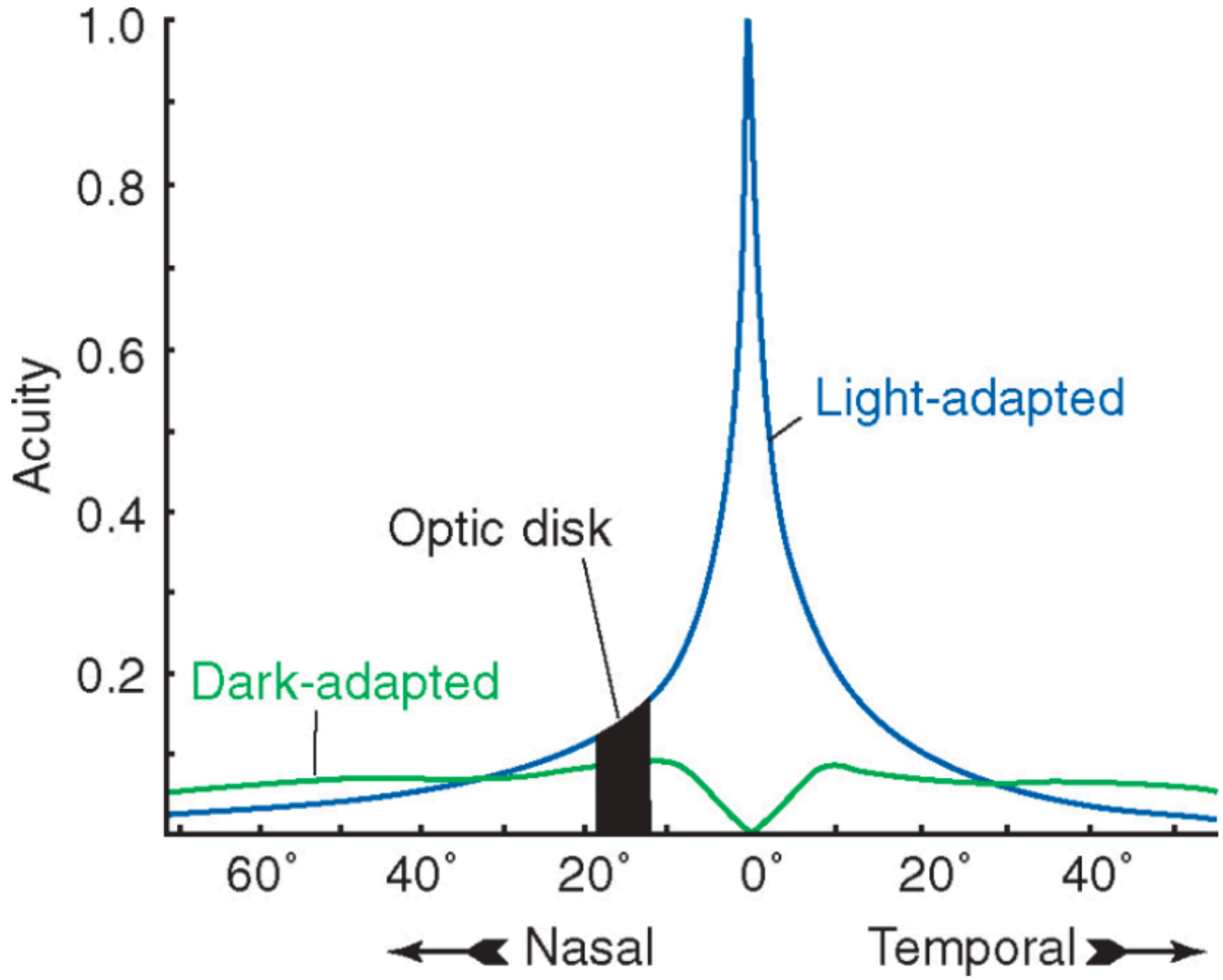
Differential distribution of rods and cones in the human retina. A. View of the retina. Arteries and veins emerge from the optic disk (*). Distributions of cones (B) and rods (D). Cones are distributed mainly in the fovea, rods are distributed in periphery. There is absence of photoreceptors in the optic disk (*). The scale at C shows the number of cells per mm^2.

Find your blind spot!

Stare at the center of X and move head closer until one red spot disappears



Rods and cones vision



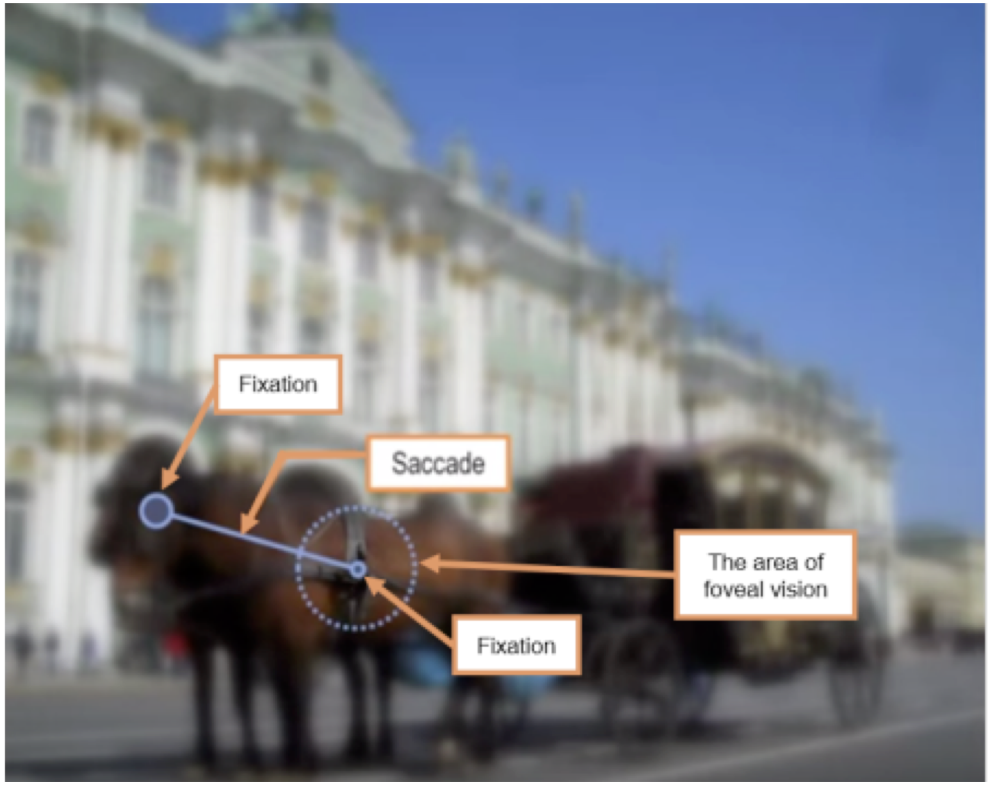
Cones are mostly found within the fovea, providing a clear, color image of the environment in that region. In dim light, information is registered by rods, providing us with blurred, grey scale image.

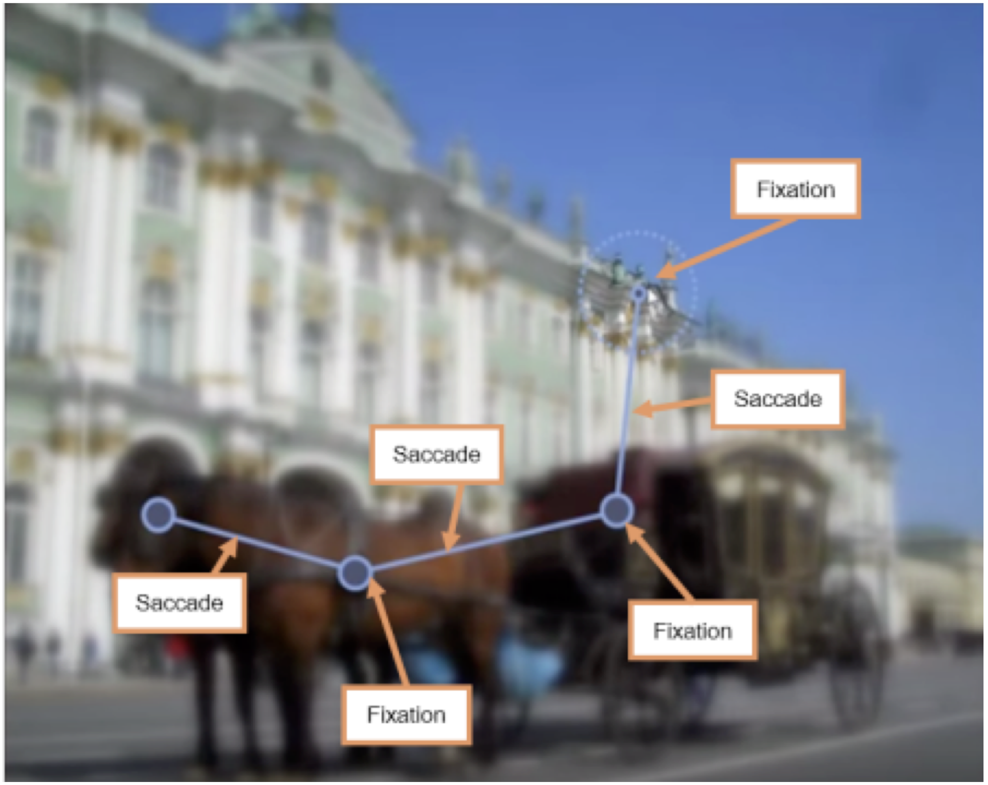
Vision through fovea

The area that is in focus and in full color represents the part of the visual field that is covered by the fovea (about 1–2 visual degrees).

Saccades

We see the world by means of a series of saccadic jumps from one area to another, interspersed with fixations. Saccades bring images to fall onto the fovea. Fixations last 200-300 ms (or longer). During saccadic movement brain blocks visual processing so we don’t see motion of our eyes or gap in perception.

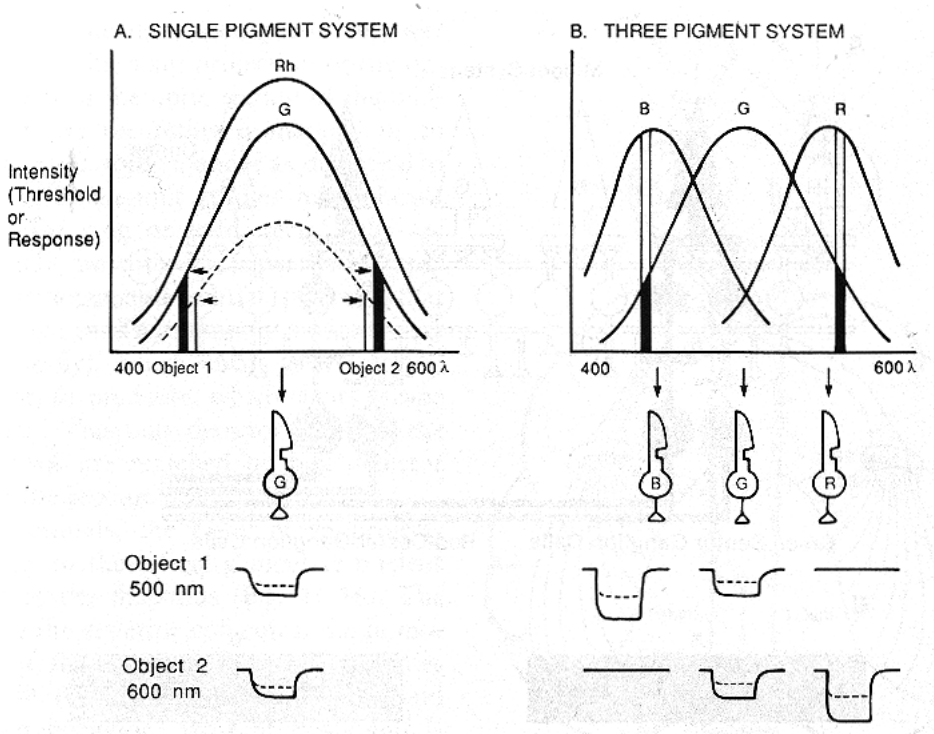




Our eyes move constantly around (100 000 times a day), locating interesting parts of the scene and building up a mental, three-dimensional 'map' corresponding to the scene.
Birds have two foveas in each eye, hence the jerky head movements.

Color vision

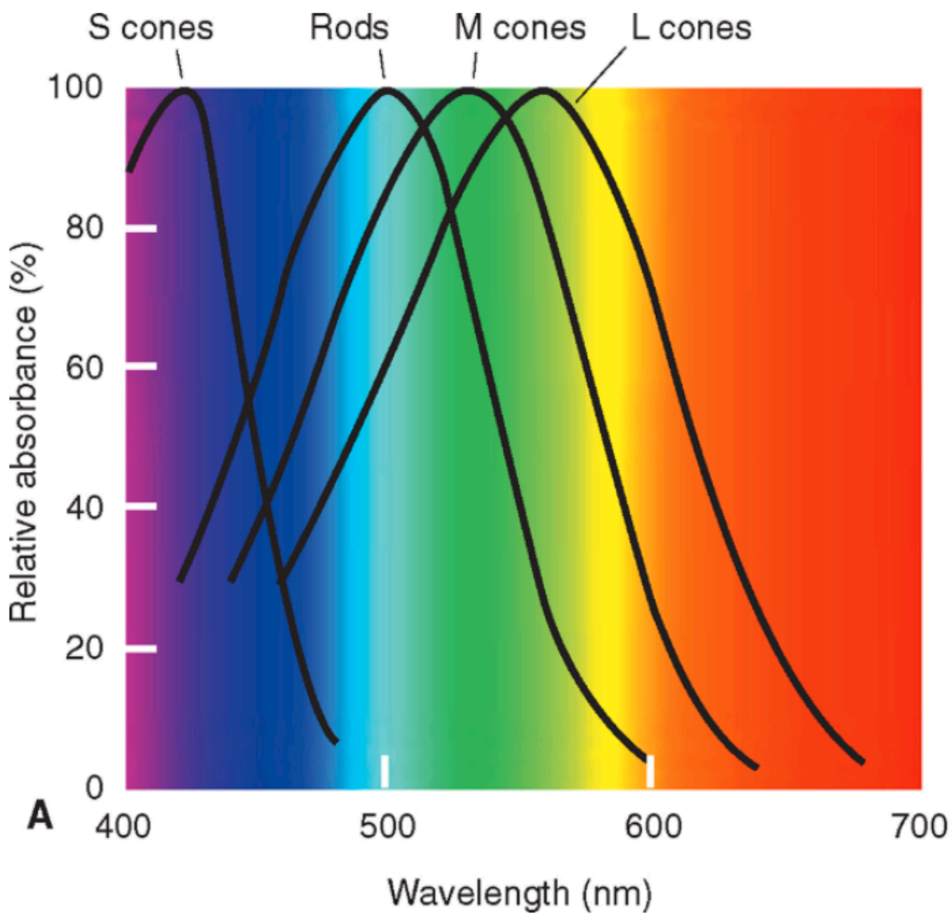
Perception of color begins with specialized retinal (cones) cells containing pigments with different sensitivities to different wavelengths of light.



A. A single pigment gives a receptor different sensitivities to different wavelengths, but the receptor cannot distinguish between wavelenghts at two sides of the curves that produce equal responses. Moreover, it cannot distinguish color from brightness.

B. A three-pigment system can distinghuish wavelength independently of intensity. The pigments must have overlapping spectra. Each object stimulates the receptors to different degrees, so that the color code for each object is unique and is maintained at different luminosities.

Sensitivities of cones and rods



Spectral sensitivities of the three classes of cones and the rods. The different classes of photoreceptors are sensitive to overlapping ranges of wavelengths. L cones have maximal sensitivity to yellow-green but are referred to as “red” because they are the most important for distinguishing red color.

Color vision

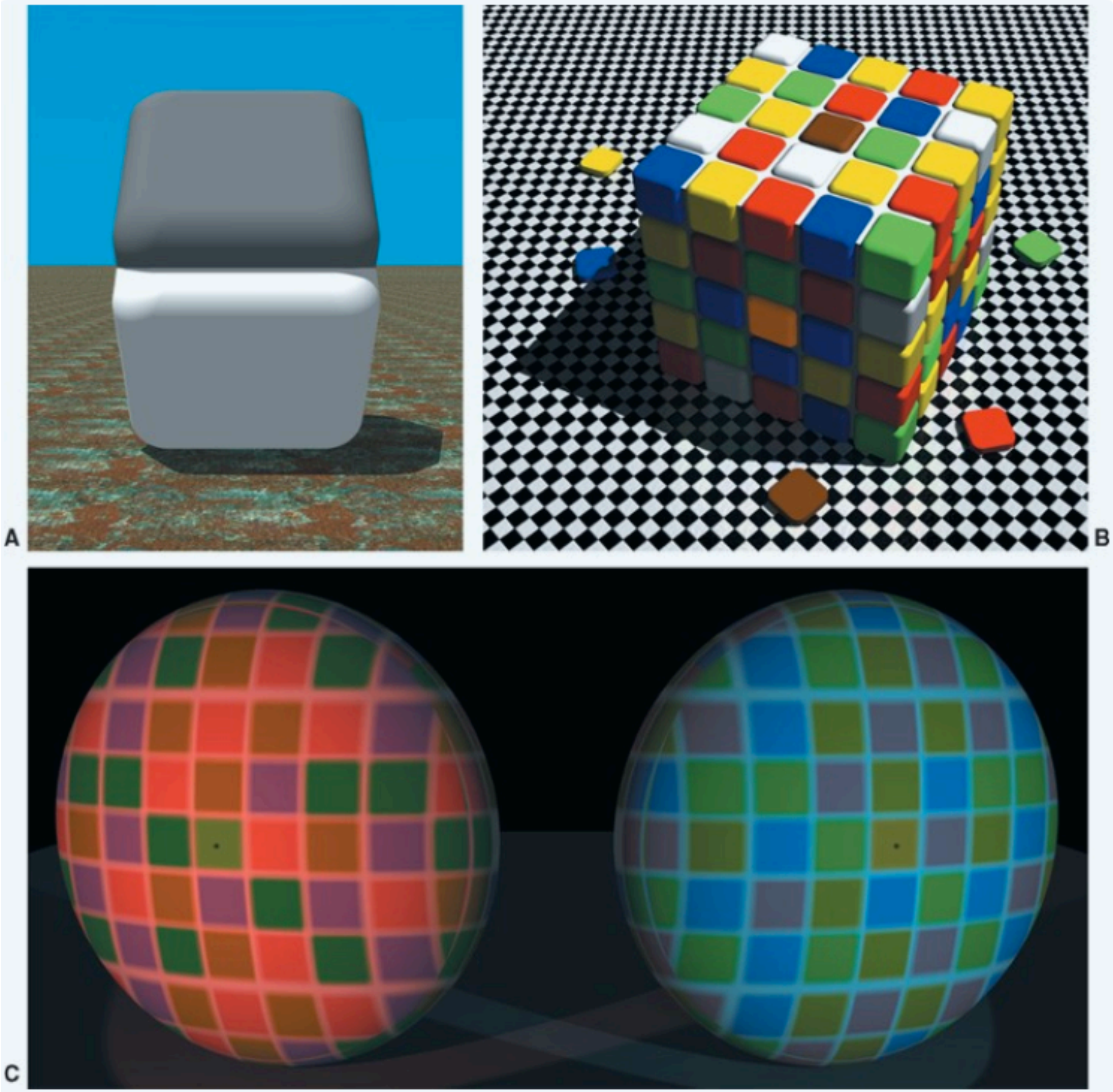
Perception of color depends not only on light wavelengths (chromatic contrast) but also on the light energy (luminance)

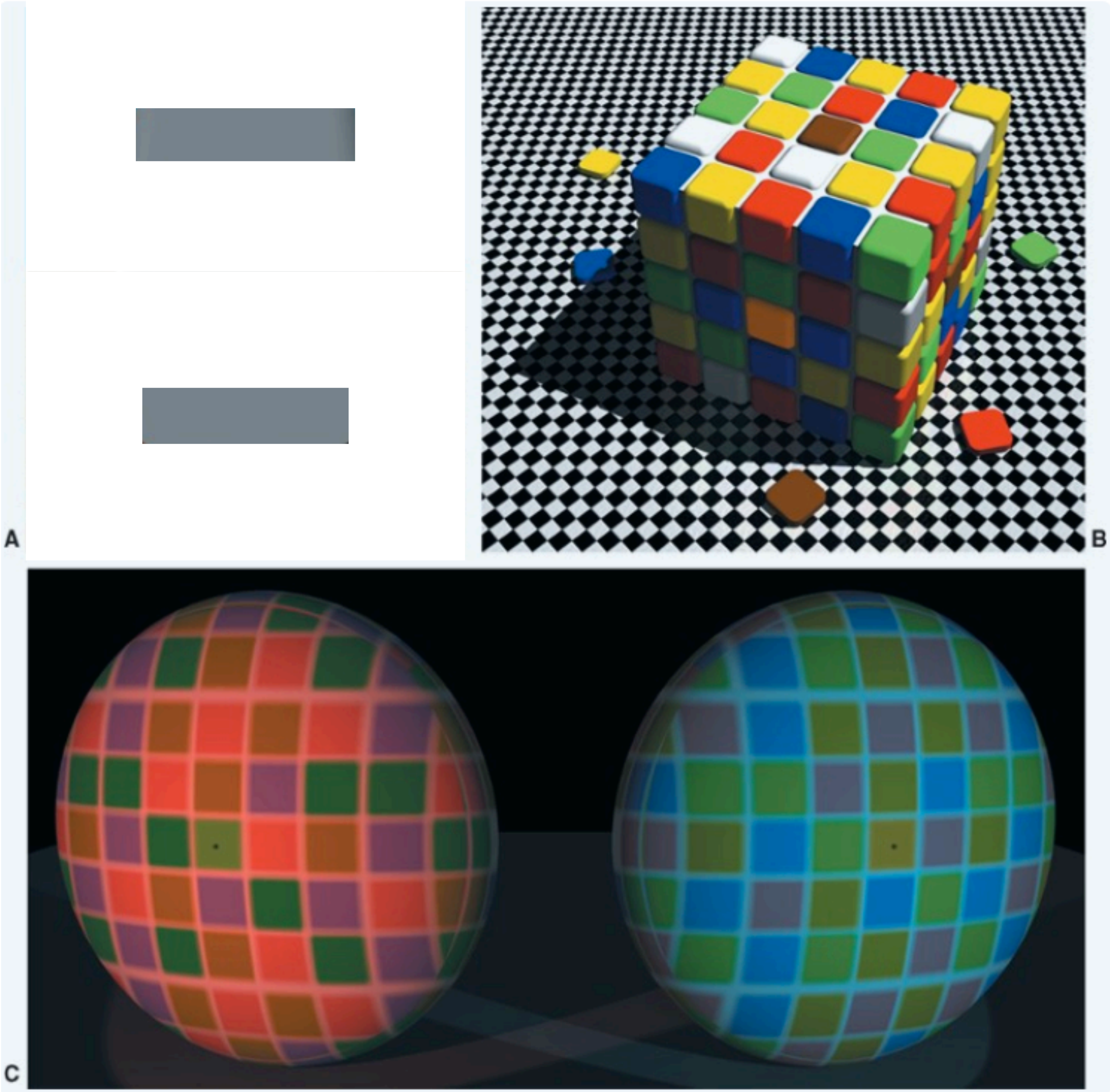
Segment of a painting by Jan van Eyck (1434). Left, the luminace information has been removed, rendering an image based soley on the chromatic contrasts. Right, the chromatic contrast has been removed, rendering an achormatic black-and-white image of the same scene. Center, the fusion of the two different forms of contrast produces color vision.

Color constancy

Colors look the same under widely different viewing conditions

Despite the varying shades of orange, yellow and green in each picture, we perceive fruits on the three bowls to be the same. The visual system determines the approximate composition of the illuminating light and removes it in order to give ‘true colors’. This is performed by neurons in the primary visual cortex, which compute local ratios of cone activity.


A
B
C


A
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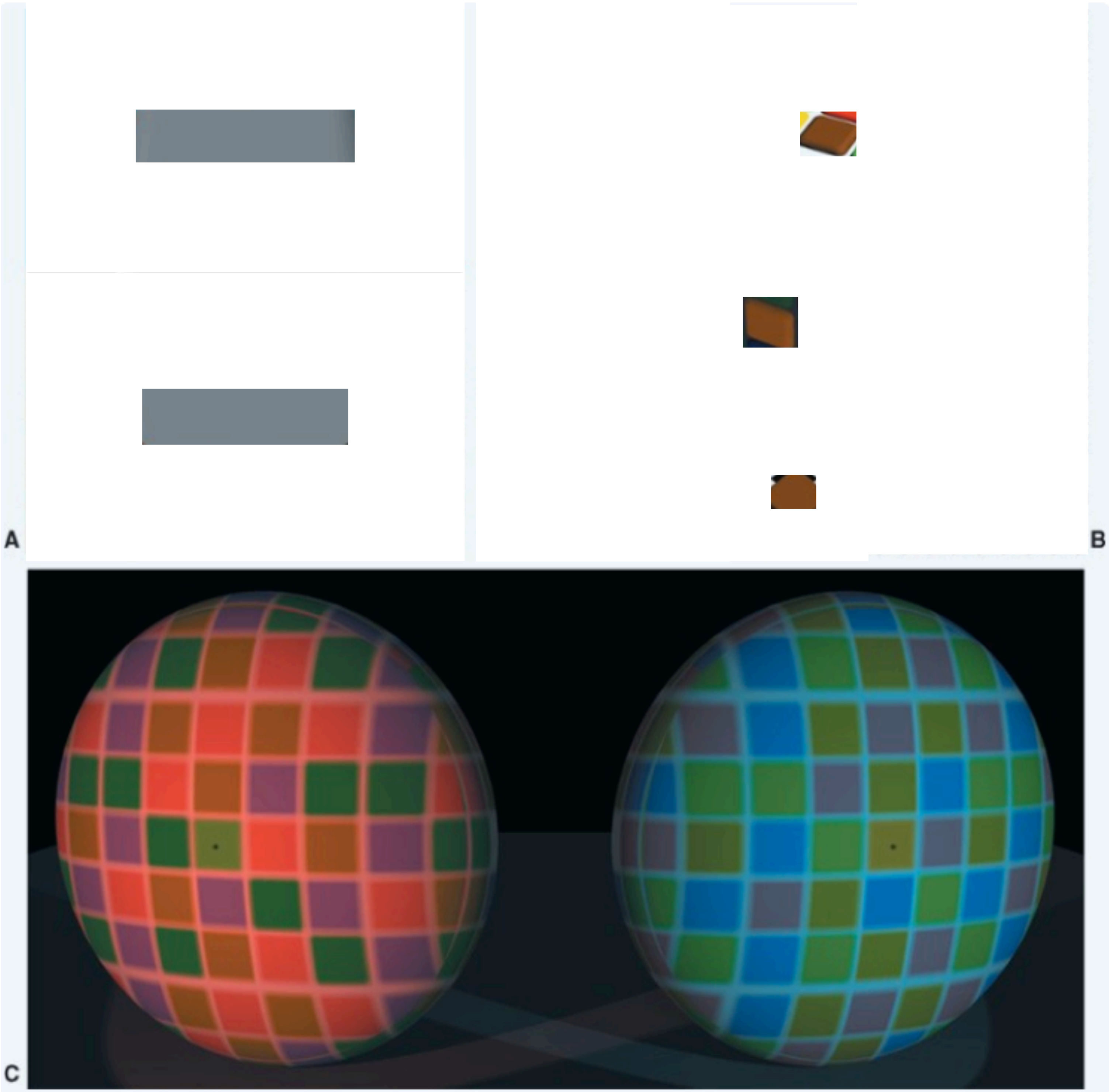
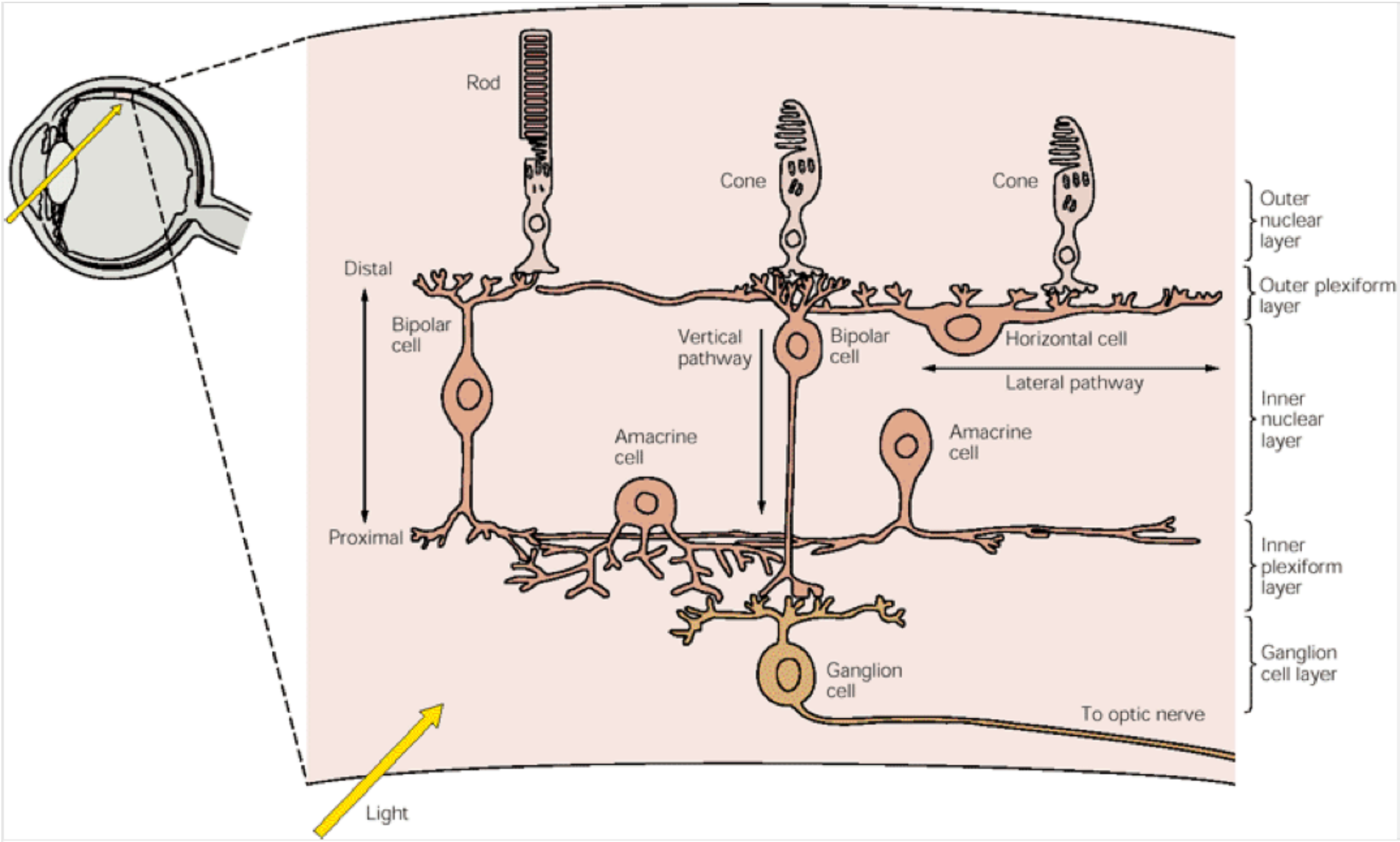

A
B
C

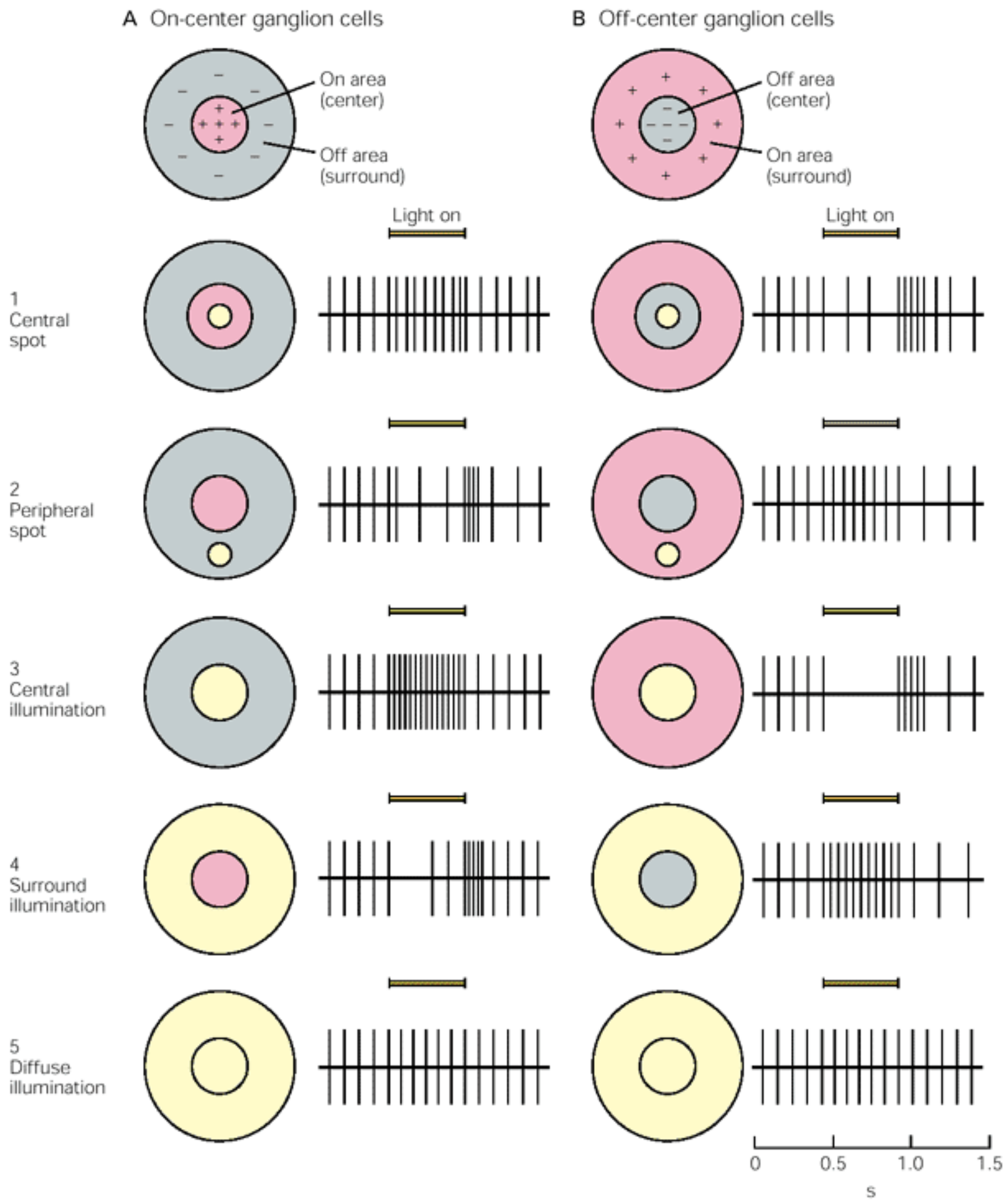

A
B
C

Retinal circuits



The retina has three major functional classes of neurons. Photoreceptors (rods and cones) lie in the outer nuclear layer, interneurons (bipolar, horizontal, and amacrine cells) in the inner nuclear layer, and ganglion cells in the ganglion cell layer. Photoreceptors, bipolar cells, and horizontal cells make synaptic connections with each other in the outer plexiform layer. Information flows vertically from photoreceptors to bipolar cells to ganglion cells, as well as laterally via horizontal cells in the outer plexiform layer and amacrine cells in the inner plexiform layer.

„On” and „Off” ganglion cells



Ganglion cells have circular receptive fields, with specialized center (pink) and surround (gray) regions. On-center cells are excited when stimulated by light in the center and inhibited when stimulated in the surround; off-center cells have the opposite responses.

A. On-center cells respond best when the entire central part of the receptive field is stimulated (3). These cells also respond well, when only a portion of the central field is stimulated by a spot of light (1). Illumination of the surround with a spot of light (2) or ring of light (4) reduces or suppresses the cell firing. Diffuse illumination of the entire receptive field (5) elicits a relatively weak discharge because the center and surround oppose each other's effects.

B. The spontaneous firing of off-center cells is suppressed when the central area of the receptive field is illuminated (1, 3). Light shone onto the surround of the receptive field excites the cell (2, 4).

Conclusion: retinal ganglion cells respond optimally to contrast in their receptive fields.

Ganglion cell types

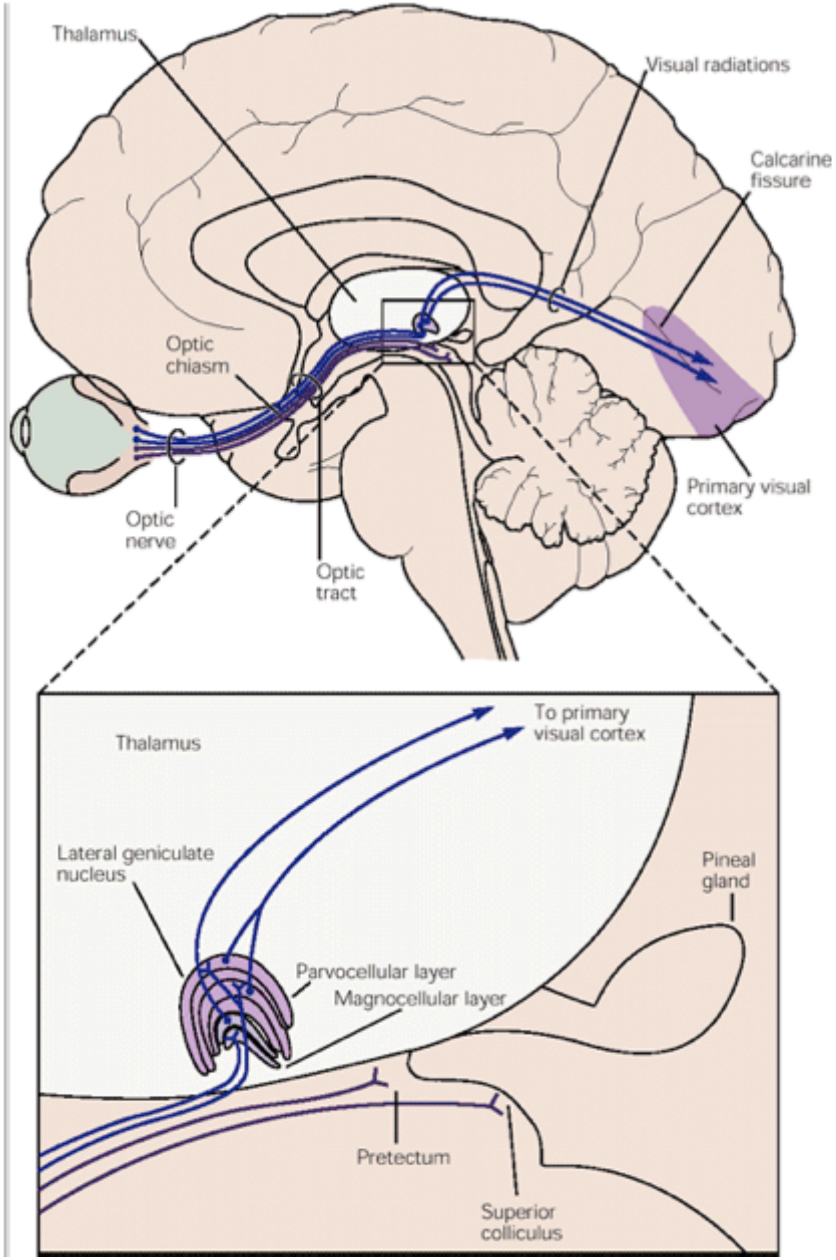
Each region of the retina has several functionally distinct subsets of ganglion cells that convey, in parallel pathways, signals from photoreceptors. Most ganglion cells in the primate retina fall into two functional classes, M (for *magni*, or large) and P (for *parvi*, or small). Each class includes both on-center and off-center cells.

Table 16.2 Summary of different morphological types of retinal ganglion cells and their functional properties, in the cat

	X (P)	Y (M)	W
Morphology			
ganglion cell size	medium (β)	large (α)	varied
number	many; most near fovea	few; most in periphery	few
axons	medium conduction rate	fast conduction rate	varied conduction rate
projection sites	lateral geniculate nucleus	lateral geniculate nucleus and superior colliculus (and medial interlaminar nucleus)	lateral geniculate nucleus and superior colliculus
Function			
spatial summation	linear	nonlinear	mixed
movement sensitivity	+	+ + +	±
directional selectivity	no	no	yes (a few cells)
center–surround antagonism	yes	yes	±
color coded	yes (in primates)	no	?

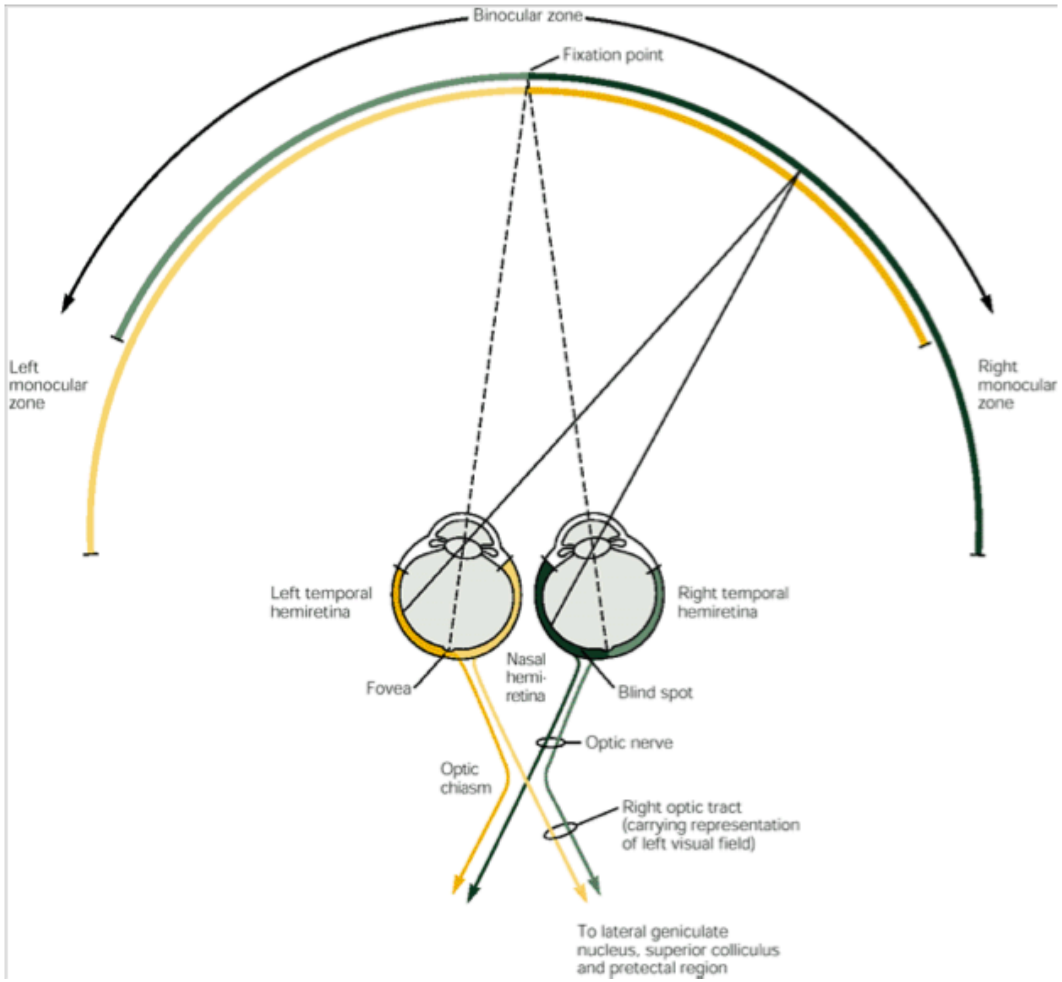
Parallel networks of ganglion cells with different functional properties are the beginning of the segregation of information into parallel processing pathways in the visual system.

Visual pathways



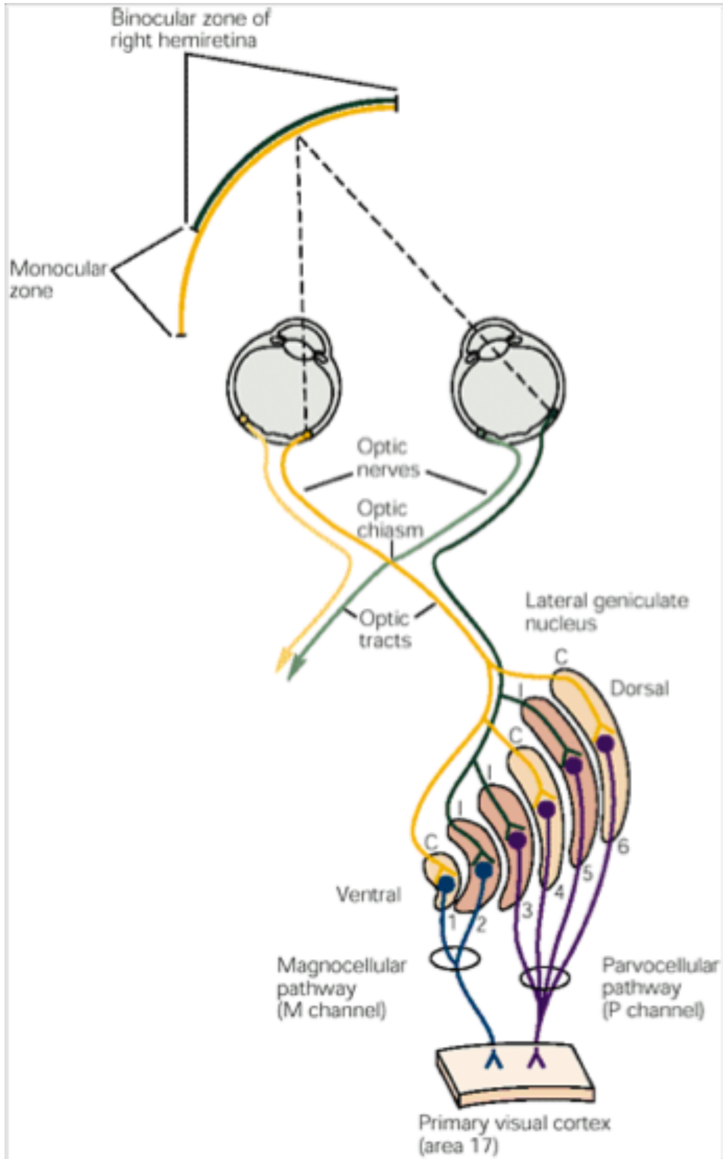
A simplified diagram of the projections from the retina to the visual areas of the thalamus (lateral geniculate nucleus) and midbrain (pretectum and superior colliculus). The retinal projection to the pretectal area is important for pupillary reflexes (change of pupil's diameter in response to light), and the projection to the superior colliculus contributes to visually guided eye movements. The projection to the lateral geniculate nucleus, and from there to the visual cortex, processes visual information for perception. Without this pathway visual perception is lost. The residual vision, possibly mediated by the visual pathway passing through the superior colliculus, has been called blindsight.

Binocular and monocular zones in the visual field



The visual field has both binocular and monocular zones. Light from the binocular zone strikes the retina in both eyes, whereas light from the monocular zone strikes the retina only in the eye on the same side. While each **optic nerve** carries all the visual information from one eye, each **optic tract** carries a complete representation of one half of the binocular zone in the visual field. Fibers from the inner (nasal) hemiretina of each eye cross to the opposite side at the optic chiasm, whereas fibers from the outer (temporal) hemiretina do not cross.

Magnocellular and parvocellular pathways



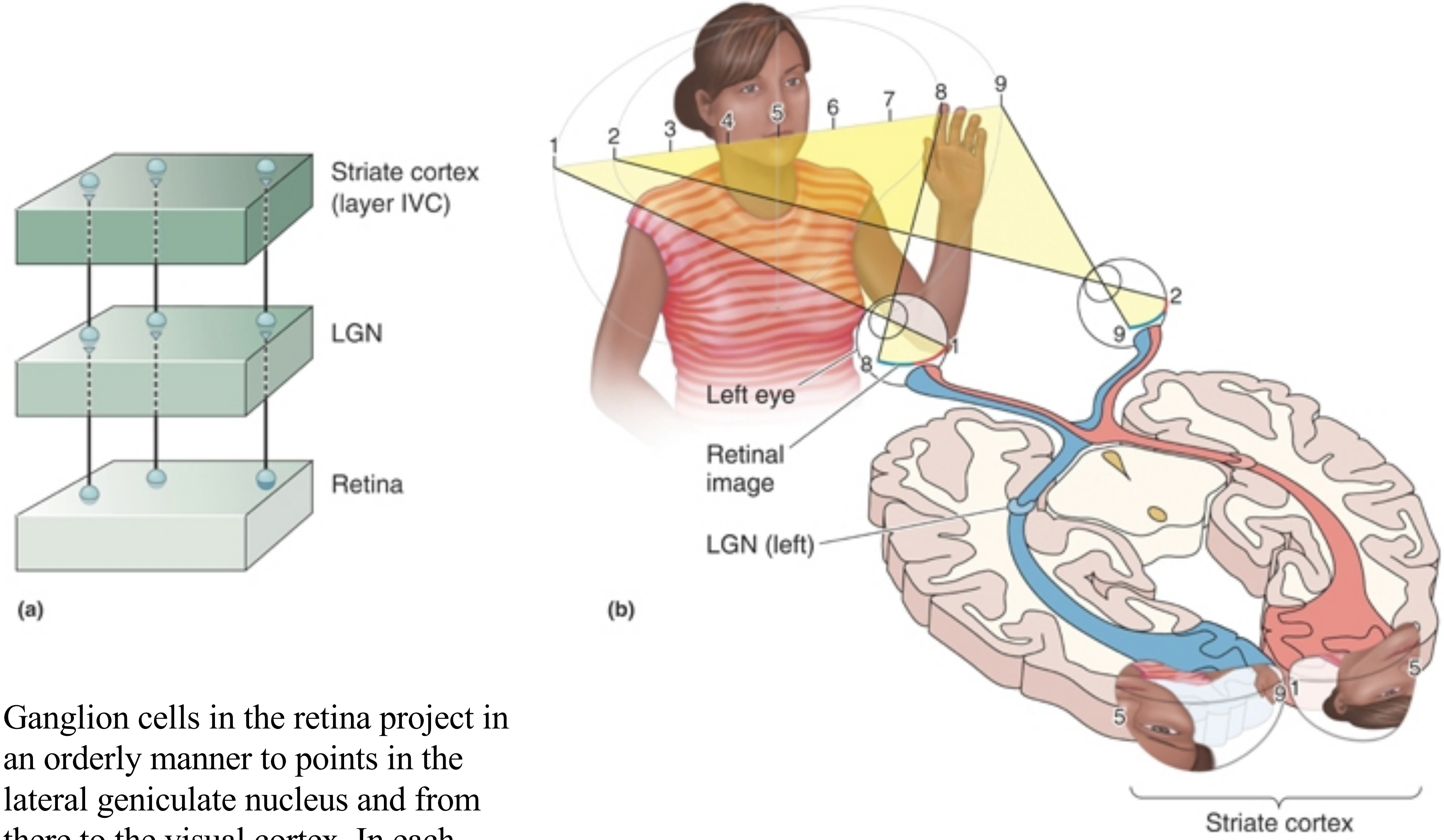
Inputs from the right hemiretina of each eye project to different layers of the right lateral geniculate nucleus to create a complete representation of the left visual hemifield. Similarly, fibers from the left hemiretina of each eye project to the left lateral geniculate nucleus (not shown).

The M ganglion cells of the retina project to the magnocellular layers of the lateral geniculate nucleus and the P ganglion cells project to the parvocellular layers.

Koniocellular neurons (K cells) are present in between the layers. Their role is unclear but they contribute to brightness and colour contrast information in species with colour vision.

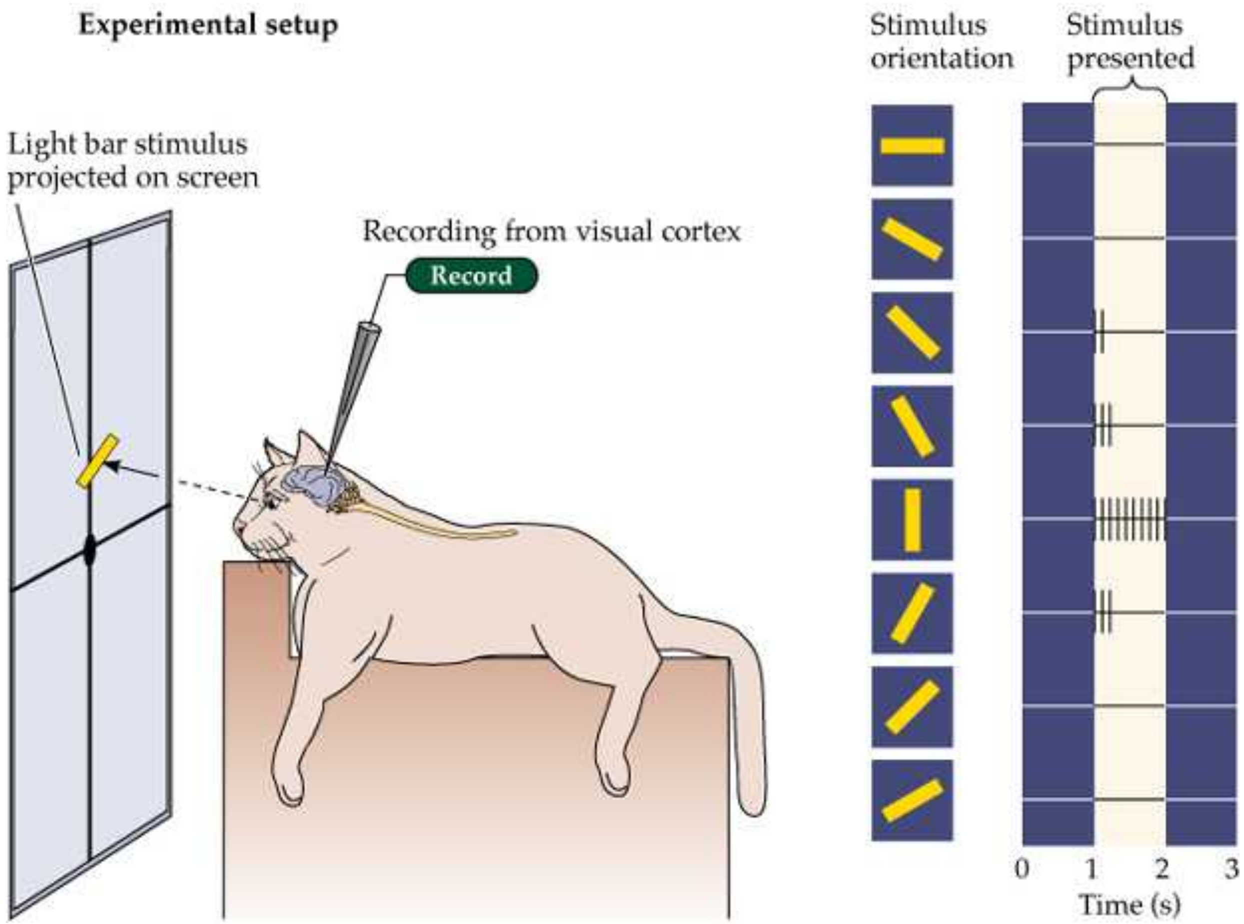
The parvocellular, magnocellular and koniocellular layers in turn project to separate parts of the primary visual cortex. This anatomical segregation leads to parallel pathways, referred to as the M, P and K pathways.

Retinotopic organisation of the visual pathway



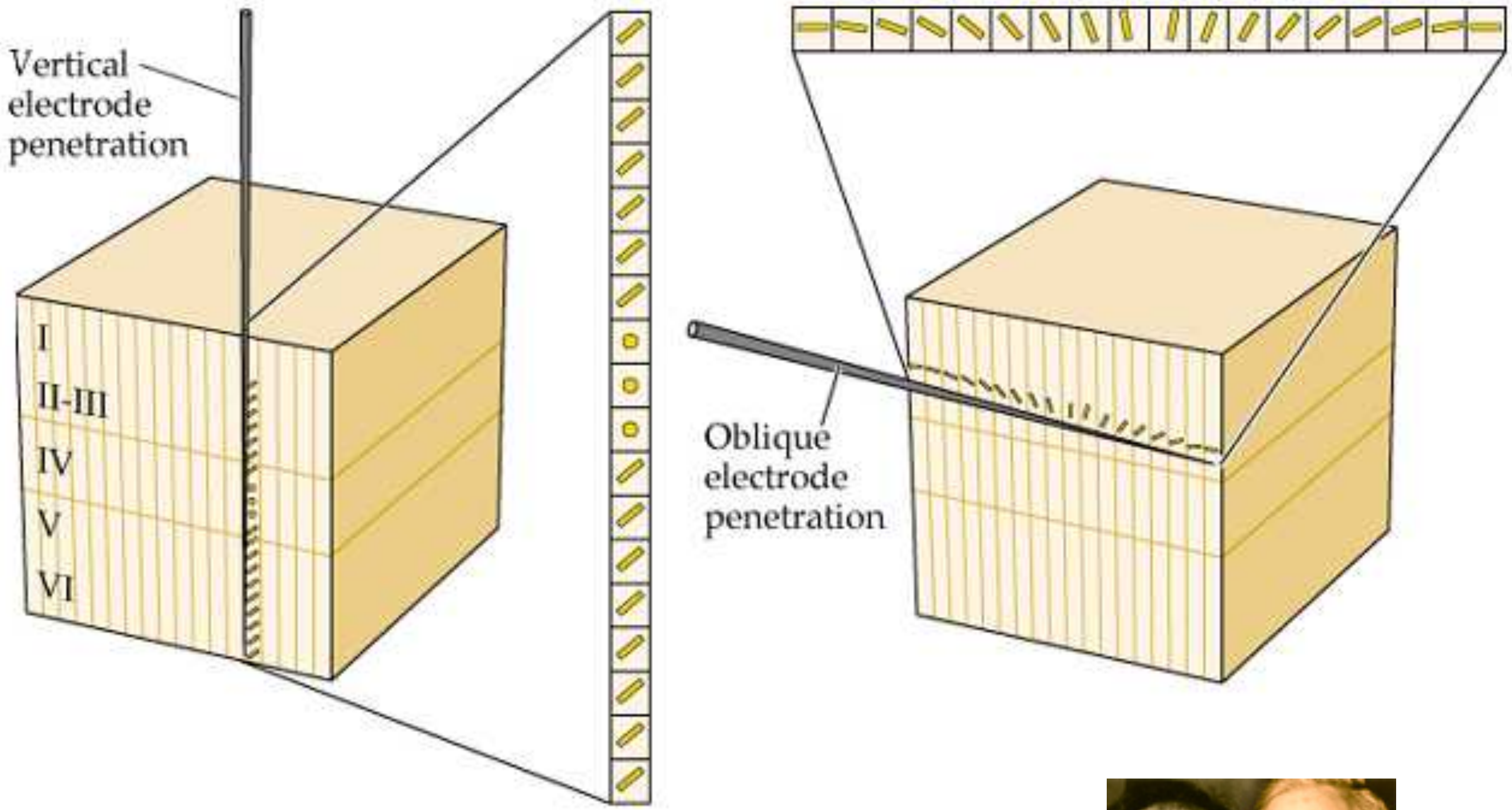
Ganglion cells in the retina project in an orderly manner to points in the lateral geniculate nucleus and from there to the visual cortex. In each lateral geniculate nucleus and in each cortical hemisphere, there is a **retinotopic** representation of the contralateral half of the visual field.

Orientation selectivity in primary visual cortex neurons



Neurons in V1 respond best to a bar of light with a specific orientation, in a particular position in the receptive field. Cells with these properties are called *simple* cells.

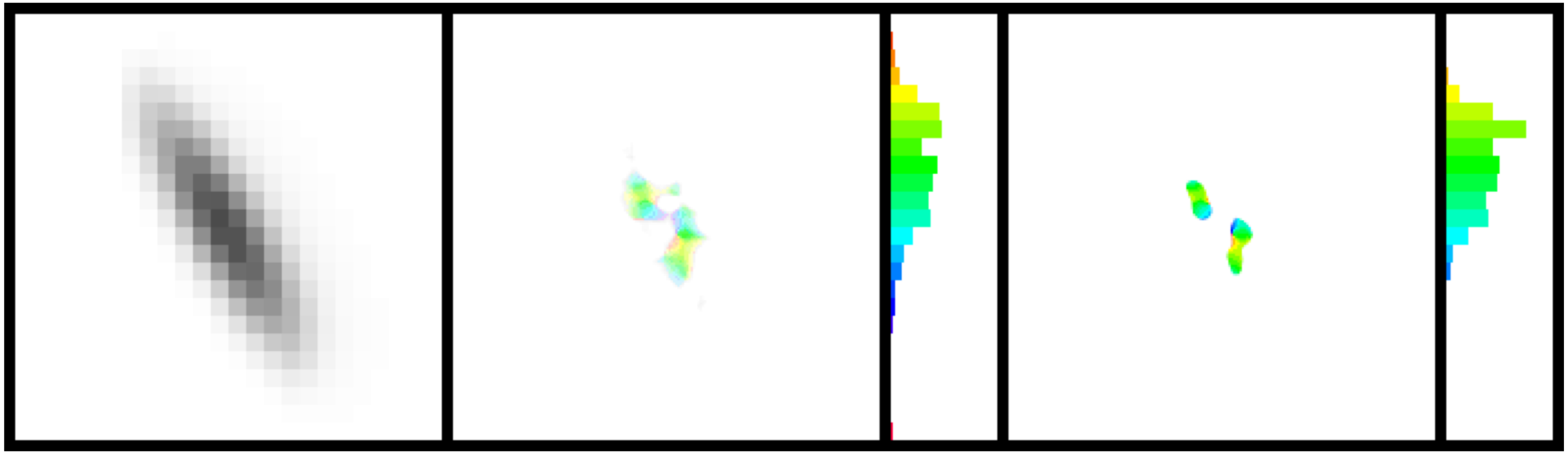
Orientation columns in the visual cortex



The primary visual cortex is organized into narrow columns of cells. Each column is about 30 to 100 μm wide and 2 mm deep. These columns contain simple cells whose receptive fields monitor almost identical retinal positions and respond to identical axes of orientation. These groupings are called *orientation columns.*

Hubel and Wiesel. Nobel Prize in Medicine 1981

Representation and processing orientation in the cortex



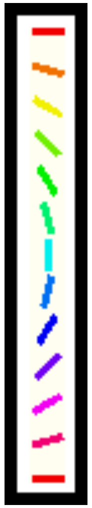
Retinal image

Initial response of the V1 cortex to that image. The orientation map represents a 5 mm x 5mm area of the human (or monkey) cortex

Orientation histogram of the initial response

Settled response of the cortex to that image (after the image has been stable on the retina long enough)

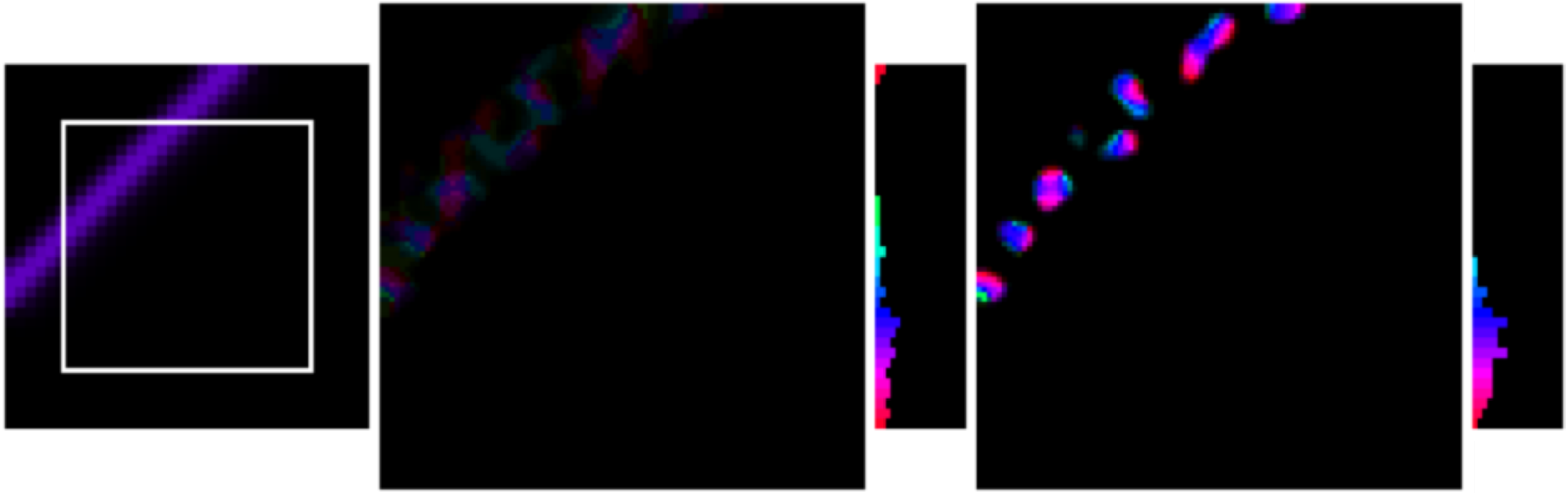
Orientation histogram of the settled response



The color of each neuron represents its orientation preference, using the color key shown below the map.

http://homepages.inf.ed.ac.uk/jbednar/spinning.html

Representation and processing orientation in the cortex



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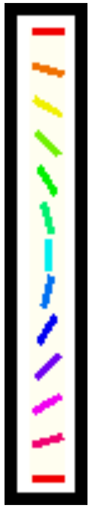
Settled response of the cortex to that image (after the image has been stable on the retina long enough)

Orientation histogram of the settled response



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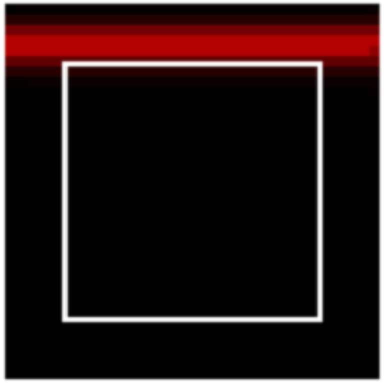
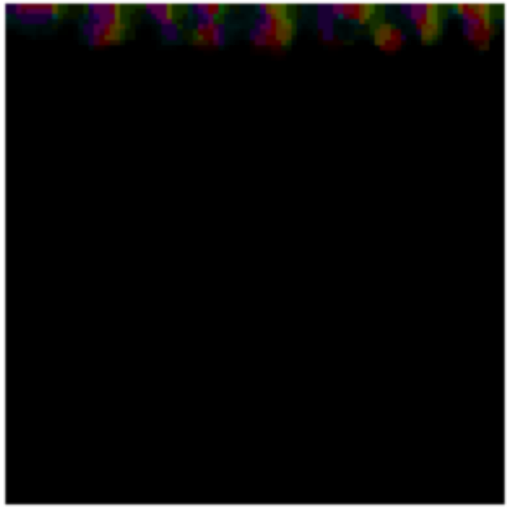
http://homepages.inf.ed.ac.uk/jbednar/sweeping_small.html

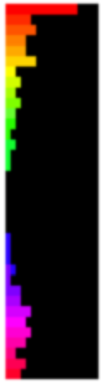
Representation and processing orientation in the cortex



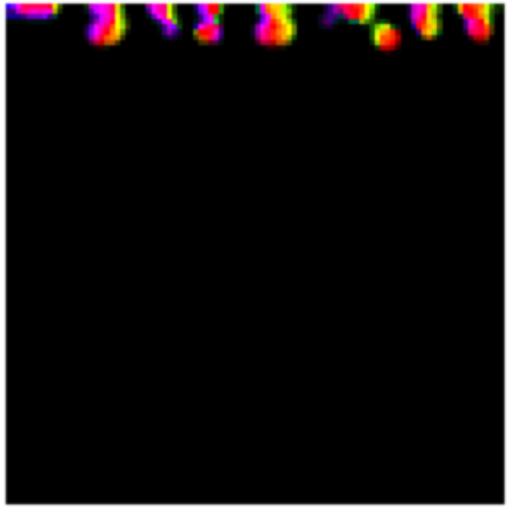
Retinal image



Initial response of the V1 cortex to that image. The orientation map represents a 5 mm x 5mm area of the human (or monkey) cortex

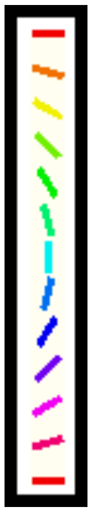


Orientation histogram of the initial response



Settled response of the cortex to that image (after the image has been stable on the retina long enough)

Orientation histogram of the settled response



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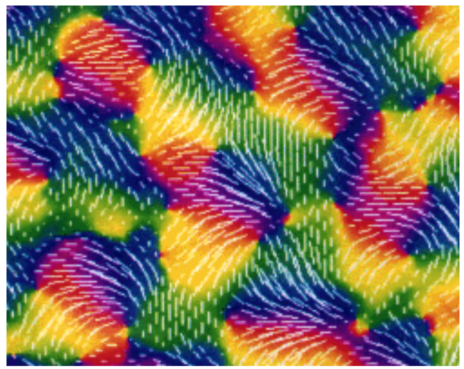


Orientation columns in the visual cortex of the monkey. From Blasdel GG, Salama G. Voltage-sensitive dyes reveal a modular organization in monkey striate cortex. Nature. 1986; 321(6070):579-85.

Representation and processing orientation in the cortex

Retinal image

Initial response of the V1 cortex to that image. The orientation map represents a 5 mm x 5mm area of the human (or monkey) cortex

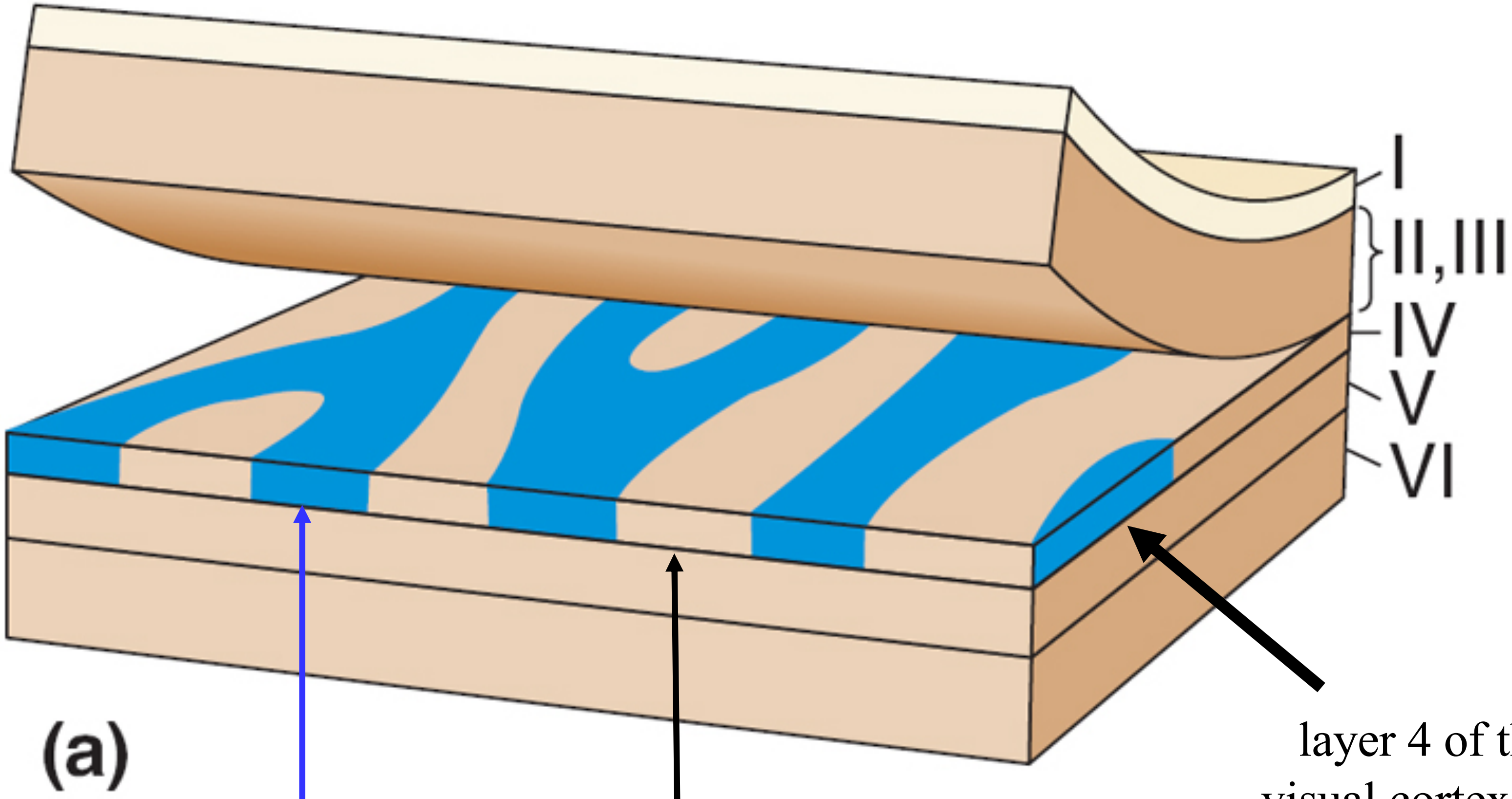
Orientation histogram of the initial response

Settled response of the cortex to that image (after the image has been stable on the retina long enough)

Key showing color assigned to each angle

http://homepages.inf.ed.ac.uk/jbednar/ring_small.html

The ocular dominance columns



layer 4 of the visual cortex, V1

Inputs from the contralateral eye

Inputs from the ipsilateral eye

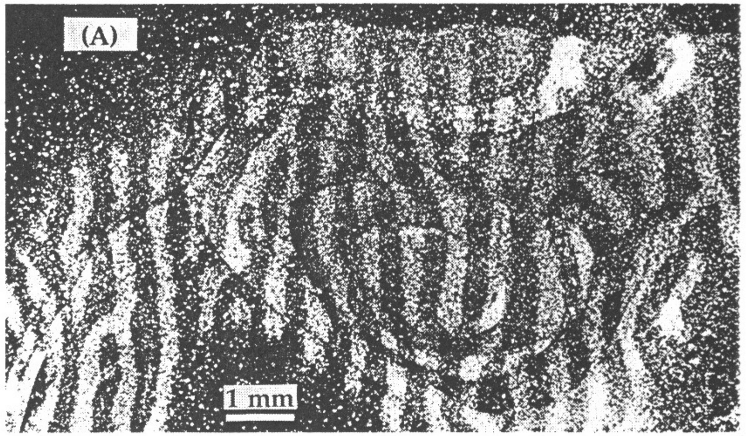
In addition to columns of cells responsive to axis of orientation there is also a system of *ocular dominance* columns receiving separate inputs from each eye. The ocular dominance columns have been visualized using transsynaptic transport of radiolabeled amino acids injected into one eye.

Hubel and Wiesel. Nobel Prize in Medicine 1981

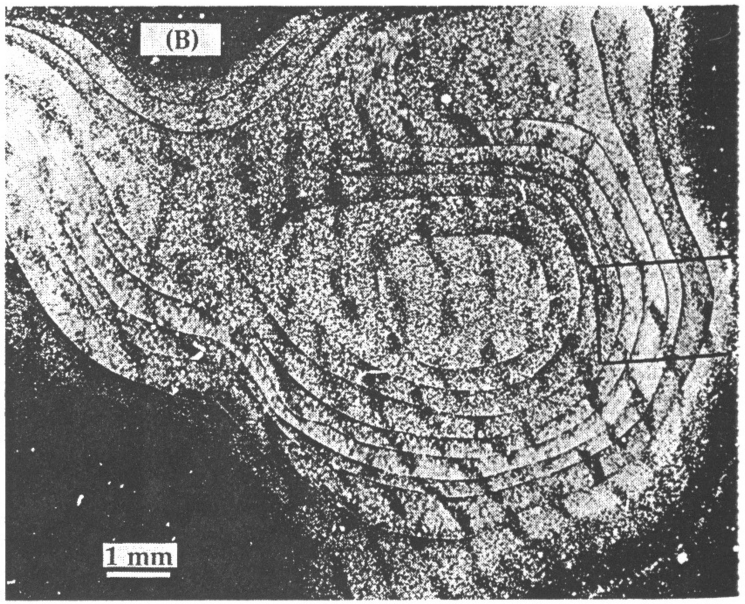
The ocular dominance columns are plastic

Visual deprivation of one eye during a critical period of development reduces the width of the ocular dominance columns for that eye.

Normal

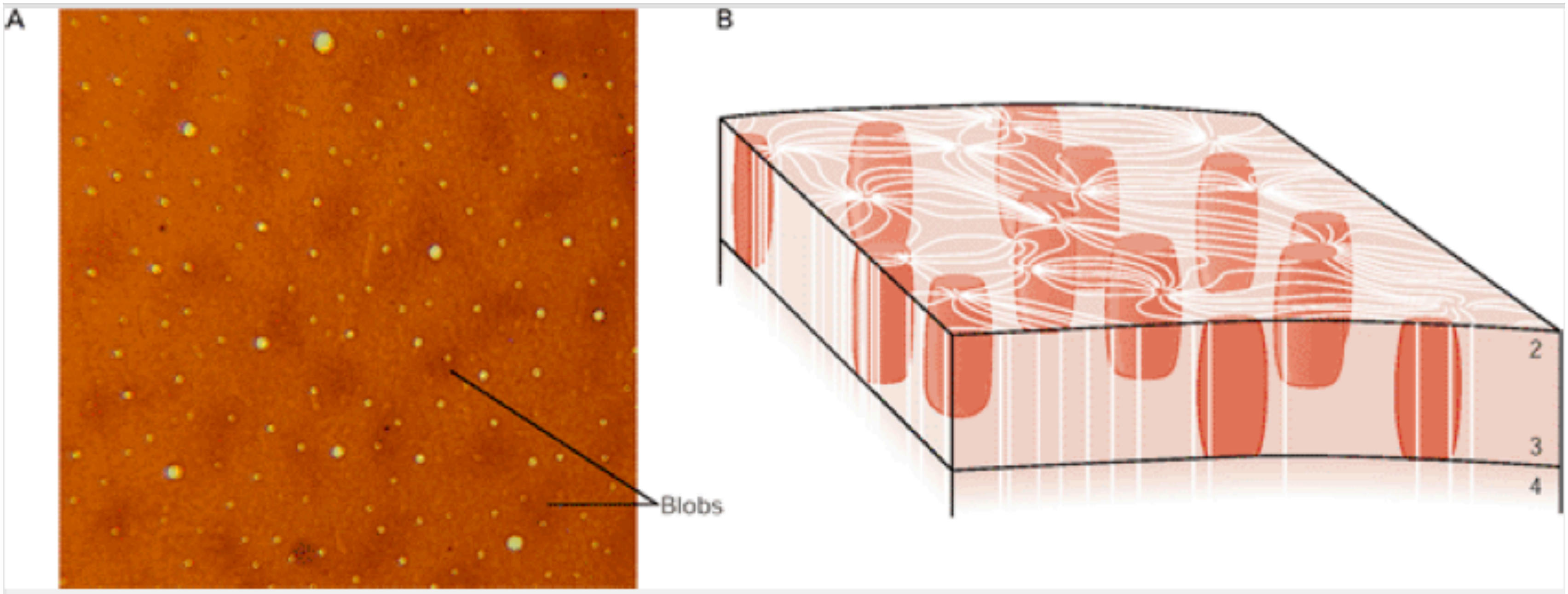


After deprivation of one eye from 2 weeks to 18 months of age. The wider white stripes correspond to inputs from the open eye. The narrower dark stripes correspond to inputs from the closed eye.



Cortical blobs

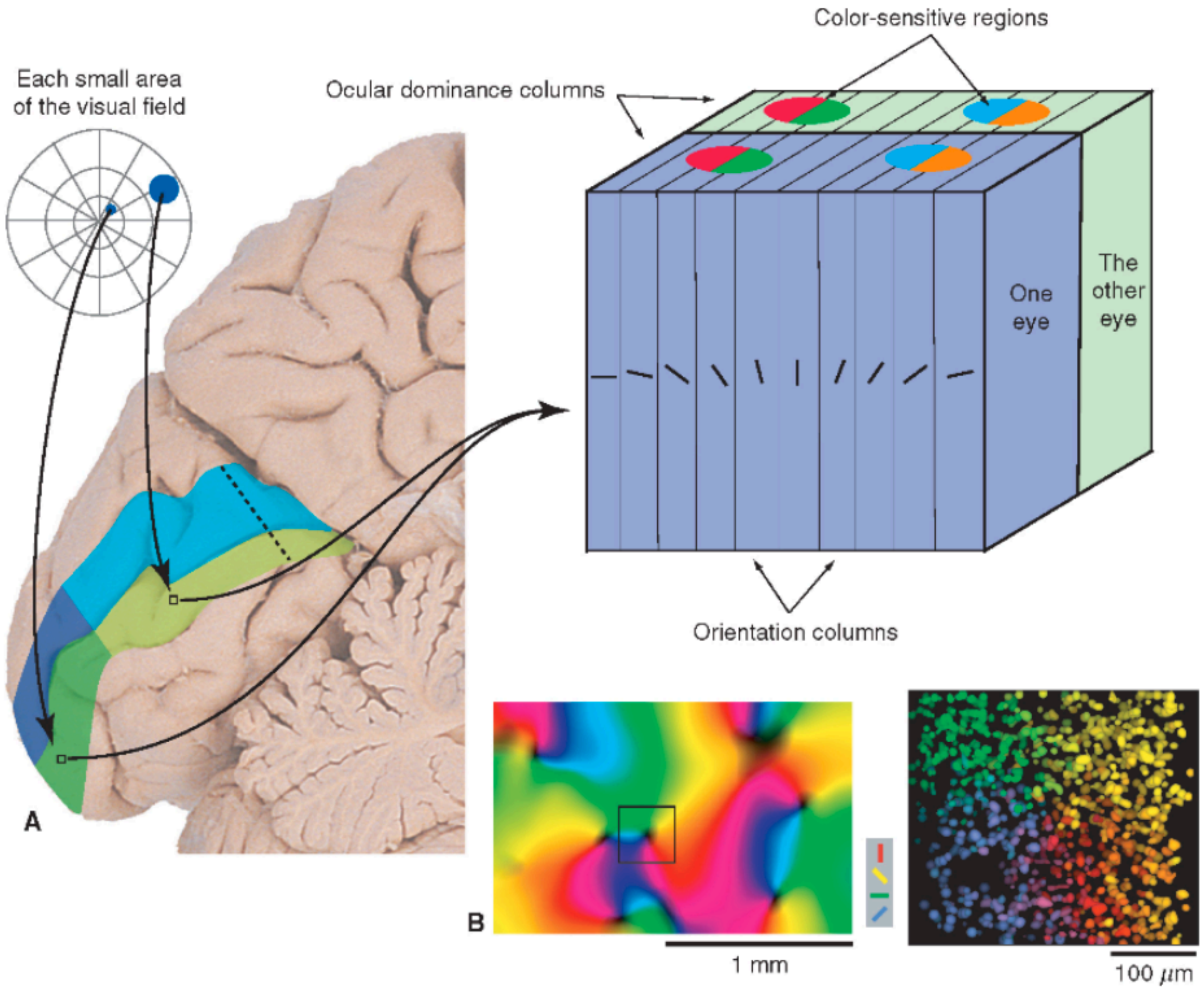
Blobs are sections of the visual cortex containing groups of neurons that are sensitive to color stimuli, and their receptive fields have no specific orientation.



A. Photograph of a single 40μm thick layer of upper cortex where blobs are visible as dark patches.
B. Organization of the blobs in relation to the orientation columns. The blobs are prominent in layers 2 and 3 of V1.

Organization of primary visual cortex.

The primary visual cortex is organized into functional modules. Each module contains one complete set of orientation columns, one set of ocular dominance columns (right and left eye), and several blobs.



Visual cortical areas

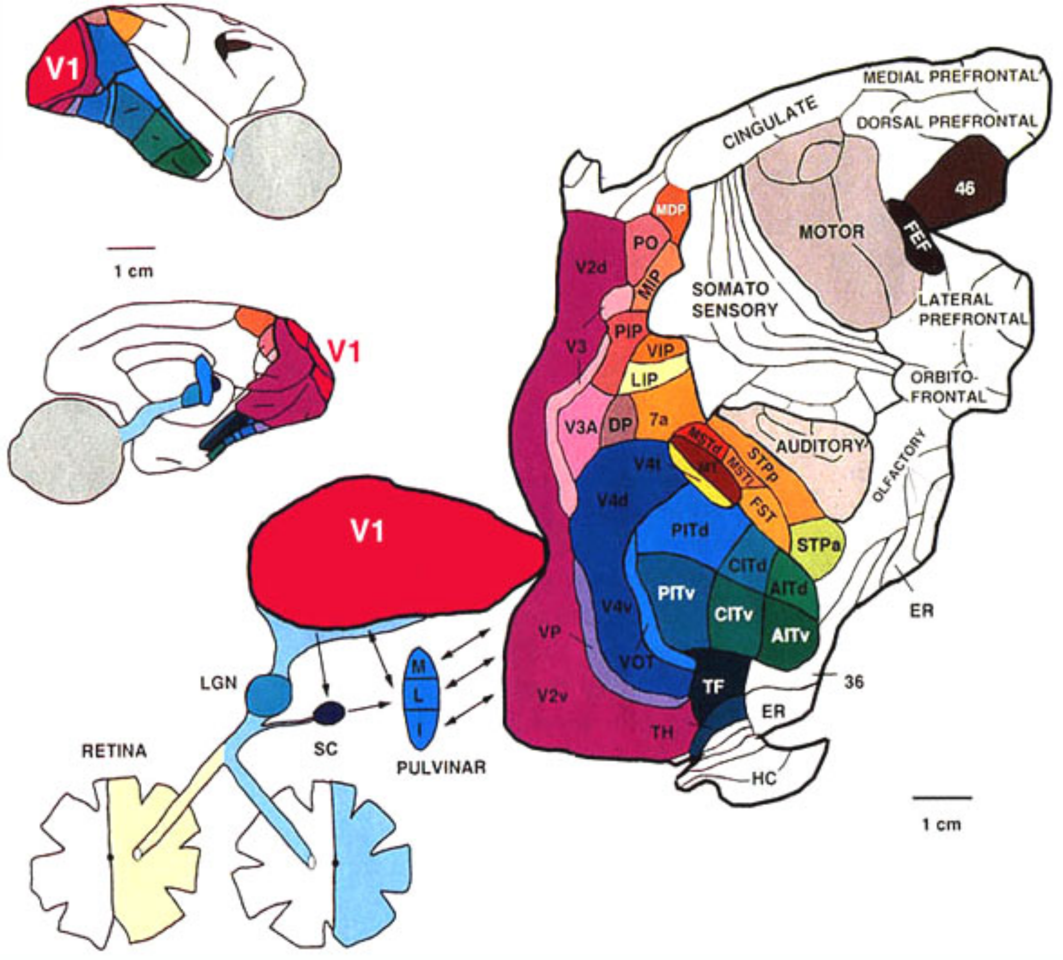


Figure 19. Much of V1 is located in the calcarine sulci and its relationship to other brain areas is best shown by unfolding the brain and showing it flattened open. The visually responsive areas of the macaque monkey are shown in color. From Van Essen et al. (1992).

Representation of the retina has been found in 32 cortical areas. These areas are functionally specialized and analyze different aspect of visual information (motion, color, depth, faces).

Contribution of the cortical areas in processing of sensory information:

50%   - visual cortex

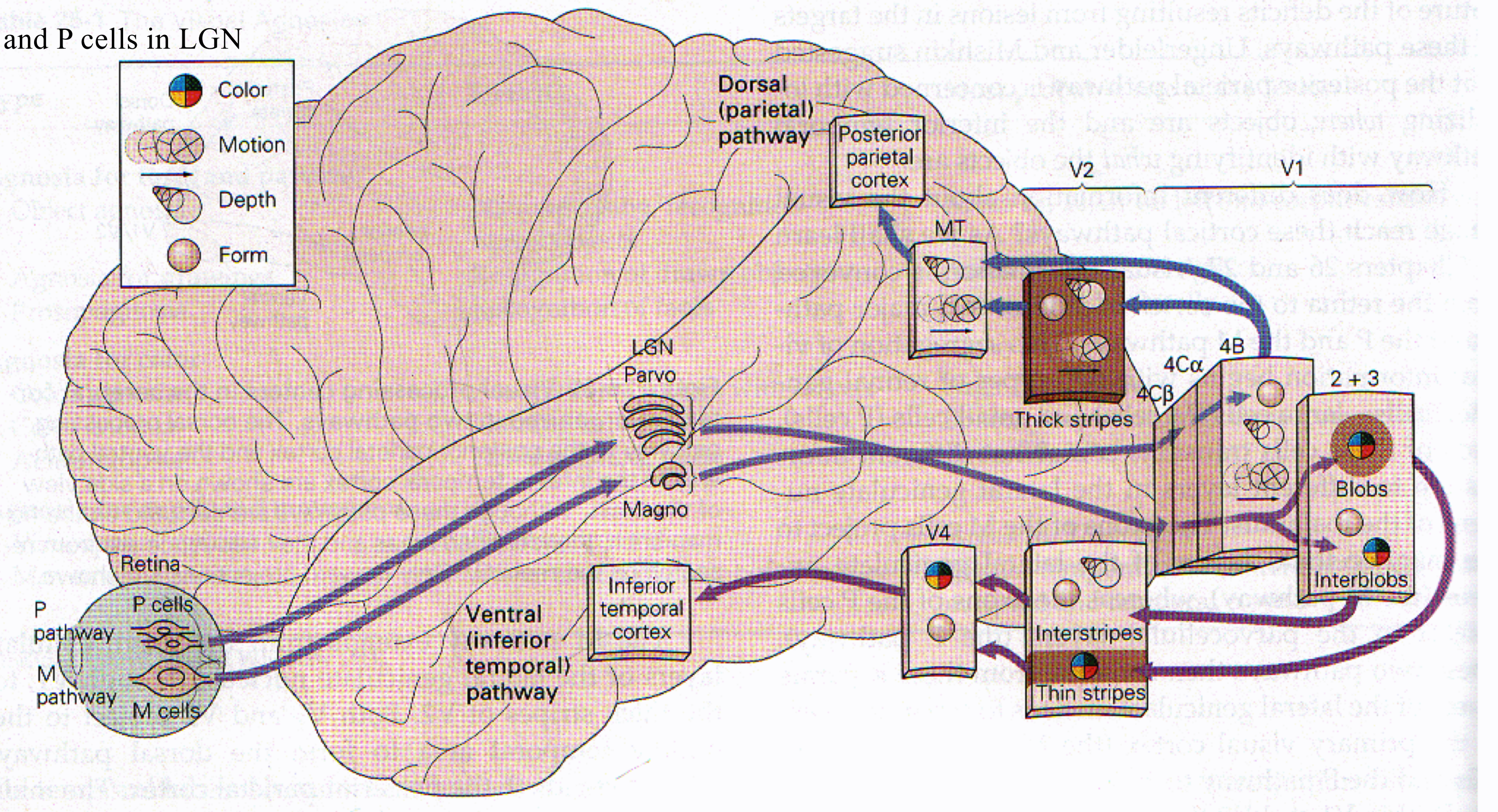
11% - somatosensory cortex

3% - auditory cortex

	Sensitivity	
Stimulus	M (Y)	P (X)
Color contrast	No	Yes
Luminosity contrast	High	Low
Spatial frequency	Low	High
Temporal frequency	High	Low

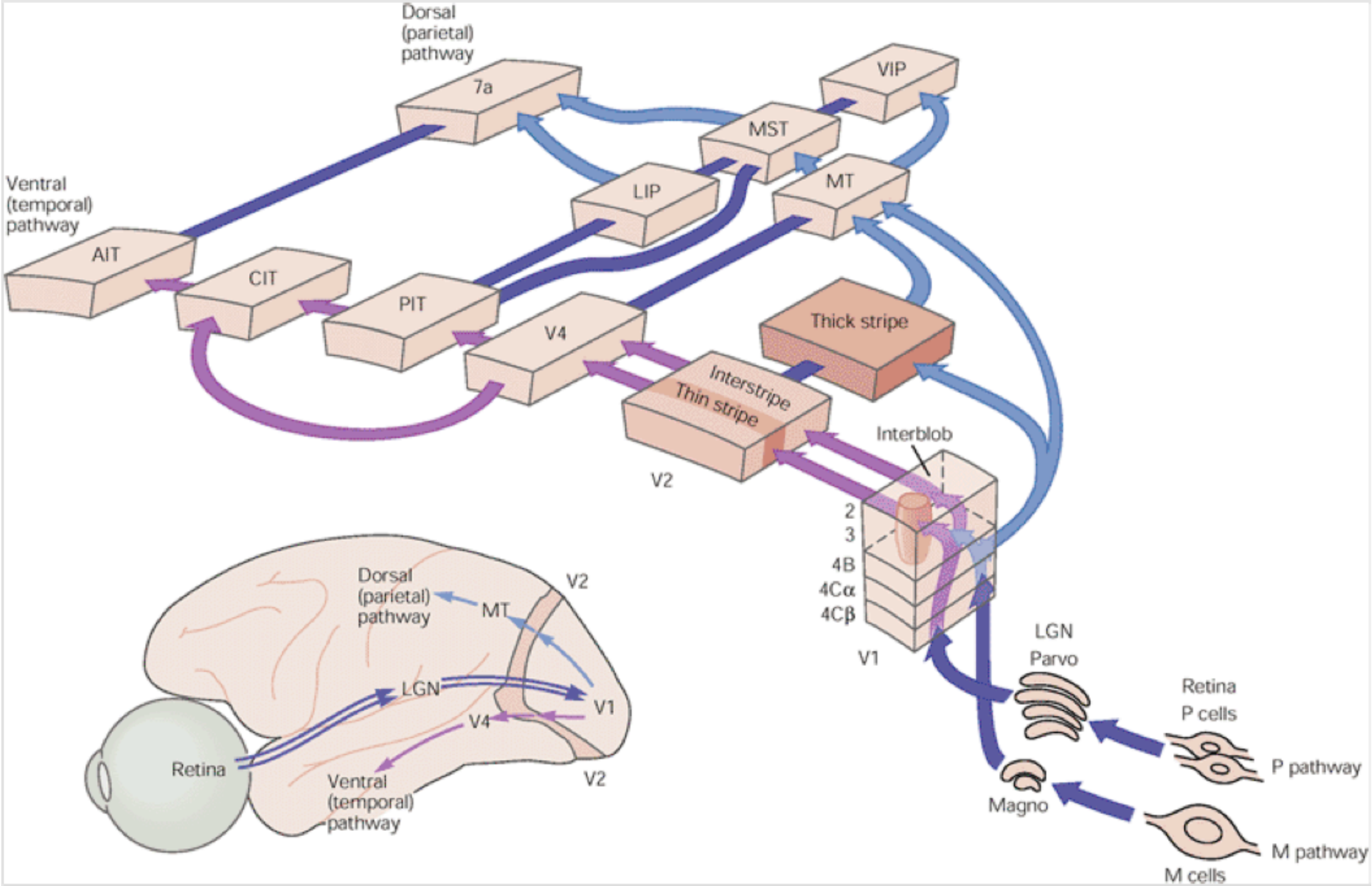
Two visual pathways – 'Where' and 'What'

Tab. Differences between M and P cells in LGN



The visual information is processed by the parallel parvocellular and magnocellular pathways. They remain segregated in the striate cortex (V1) and give rise to two processing pathways in extrastriate cortex. The P pathway (ventral cortical pathway) continues in the inferior temporal cortex, and the M pathway becomes the dorsal pathway. The dorsal pathway is concerned with determining where an object is (motion and depth), whereas the ventral pathway is involved in recognizing what the object is (form and color).

Visual pathways – a more detailed view



Separate pathways to the temporal and parietal cortices course through the extrastriate cortex beginning in V2. Only selected anatomical connections are shown and many cortical areas are omitted. There are cross connections between the two pathways in several cortical areas. The parietal pathway receives input from the M pathway only but the temporal pathway receives input from both the M and P pathways.

Properties of IT neurons

Cells in the certain regions of inferior temporal cortex (IT, V7) are particularly sensitive to faces or complex shapes that resemble facial patterns.

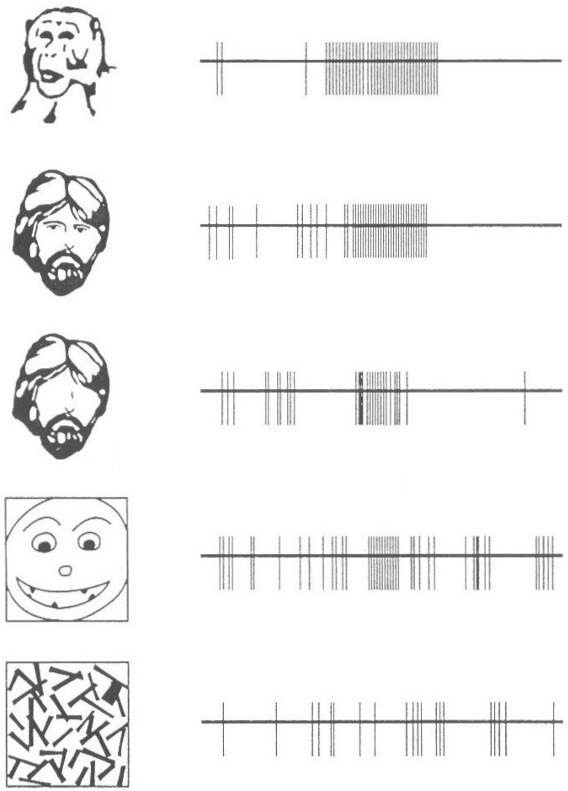


Figure 4.13
Responses of a neuron in a monkey's area IT to various stir uli. This neuron responds best to a full face, as shown by it response to monkey and human faces in the top two record Removing the eyes or presenting a caricature of a face reduces the response. This neuron does not respond to a rai dom arrangement of lines. (From Bruce, Desimone, & Gross, 1981.)

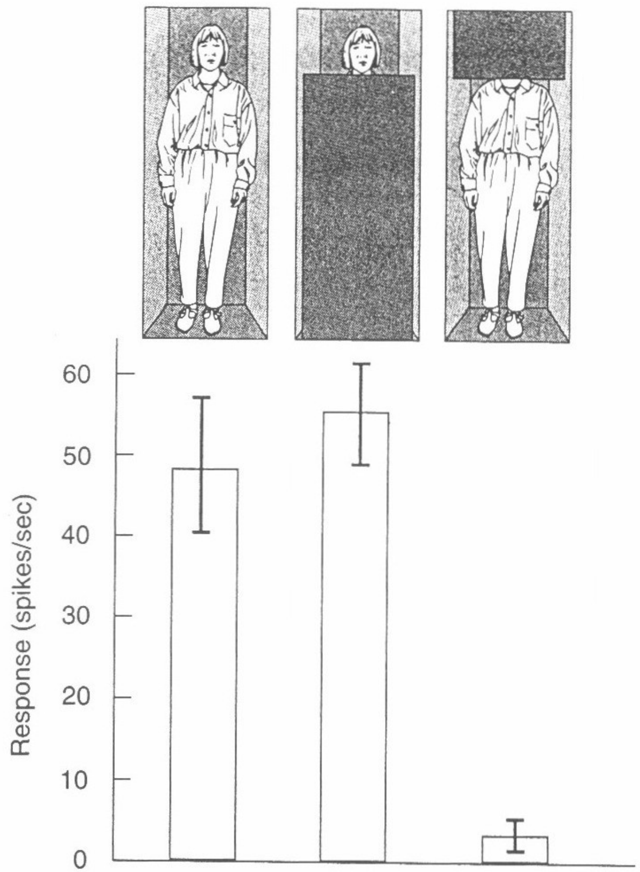
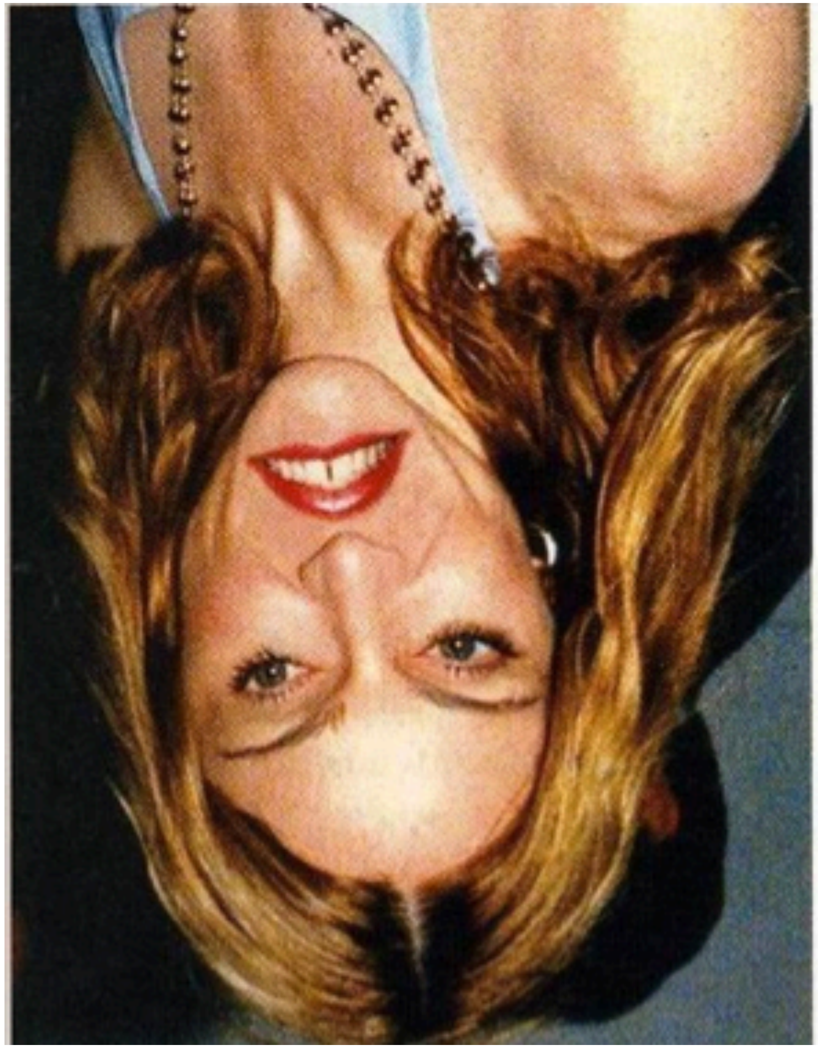
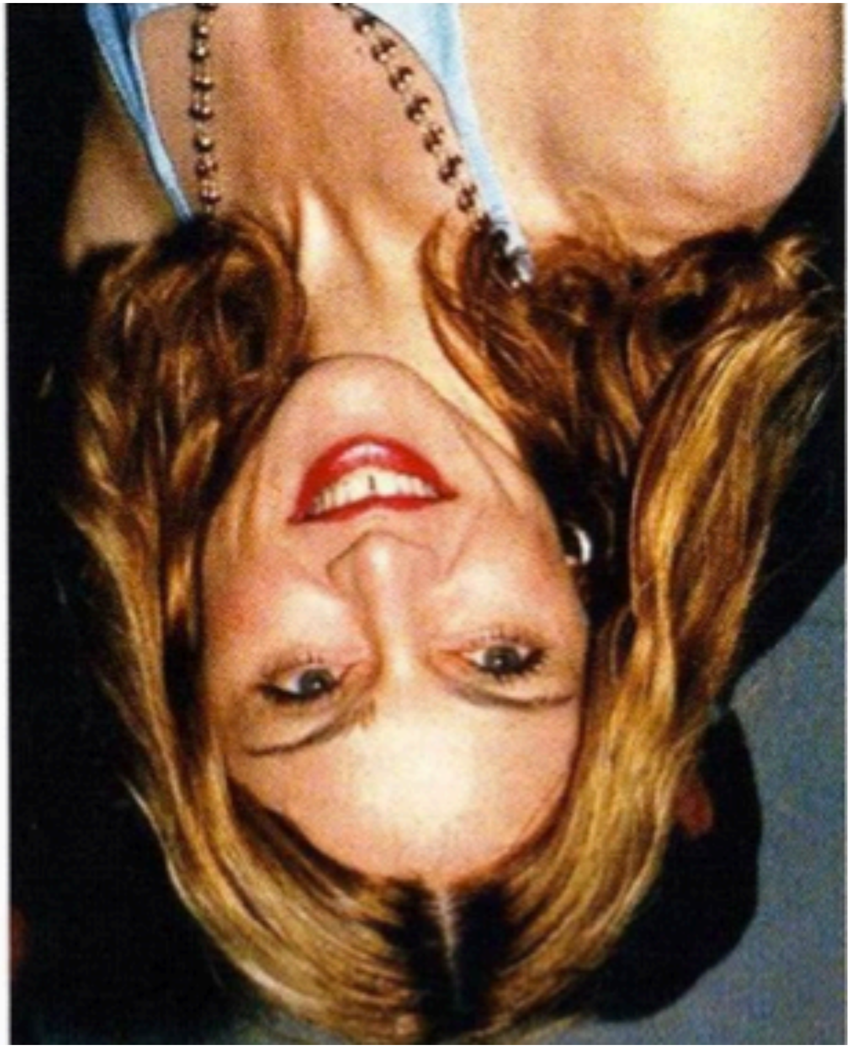


Figure 4.14
Response of a neuron in IT cortex that responds only to a picture of a person's head. Actual stimuli were photographs. (From Wachmuth, Oram, & Perrett, 1994.)

Face recognition

Which of these portraits could express best the emotional feelings of Madonna after MTV declined to show her latest video?





Face recognition

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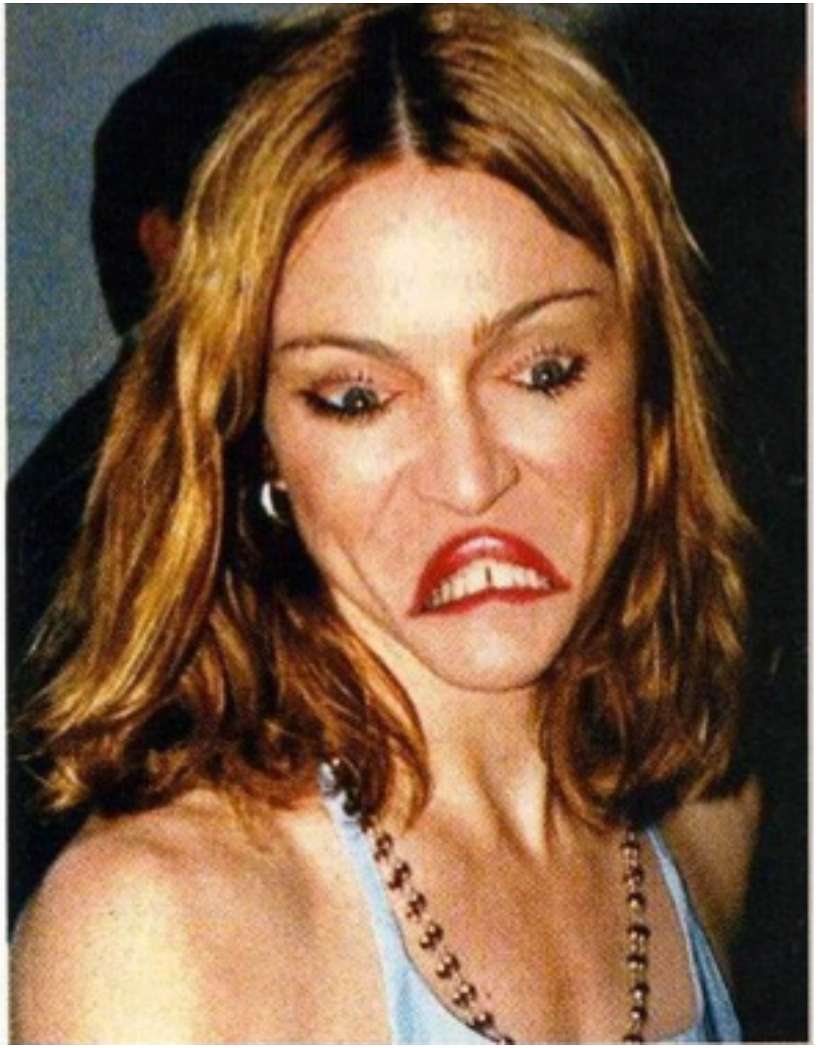
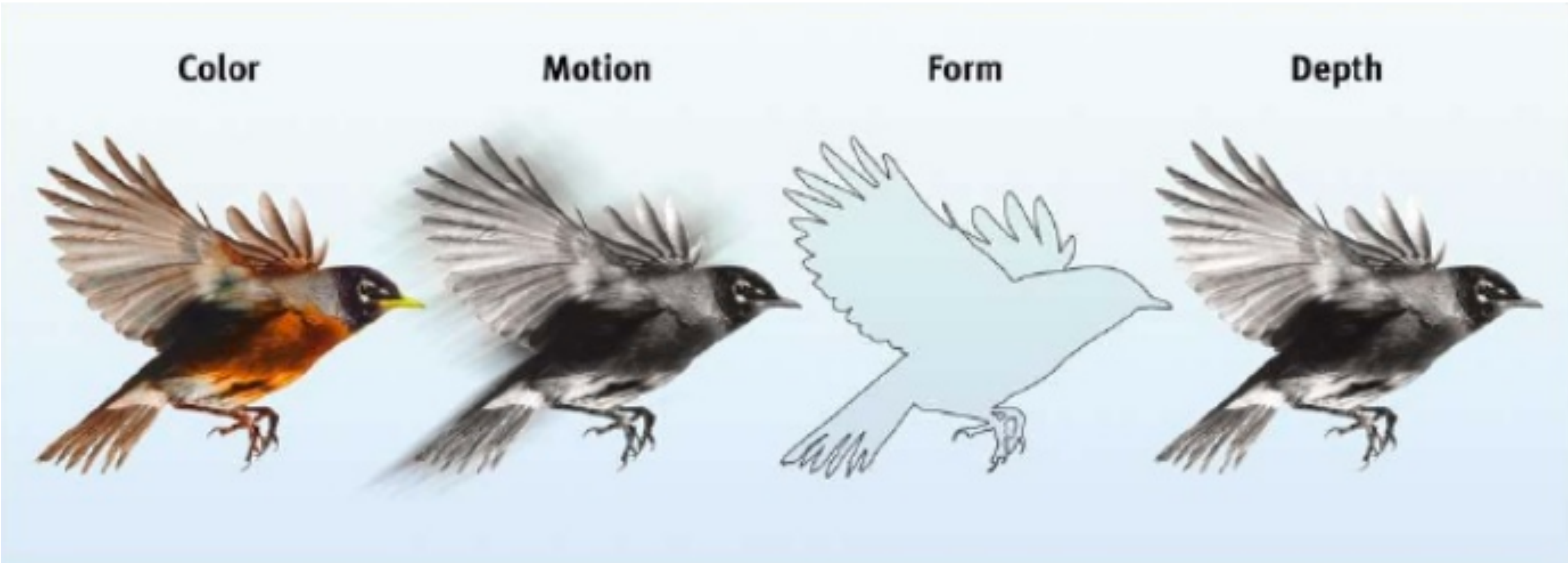


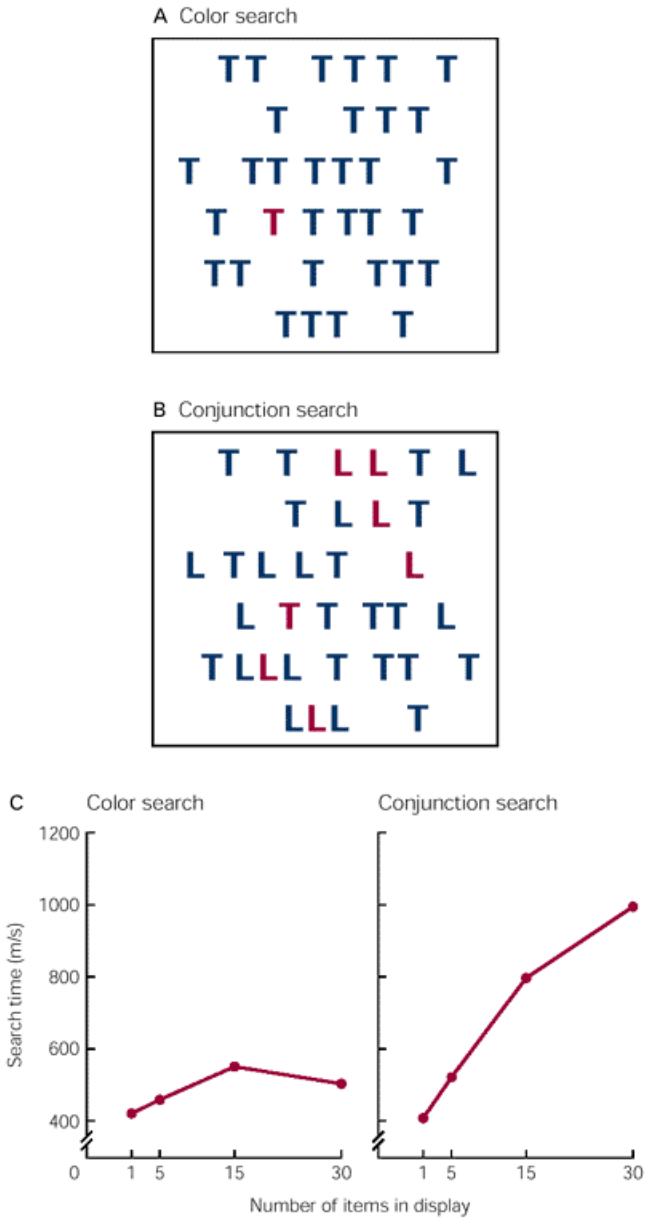
From: P. Zimbardo, R. Gering Psychologie, Pearson Studium

The binding problem

The brain divides visual scene into subdivisions such as color, depth, form and motion. They are processed simultaneously in different brain areas. How they are put back together?



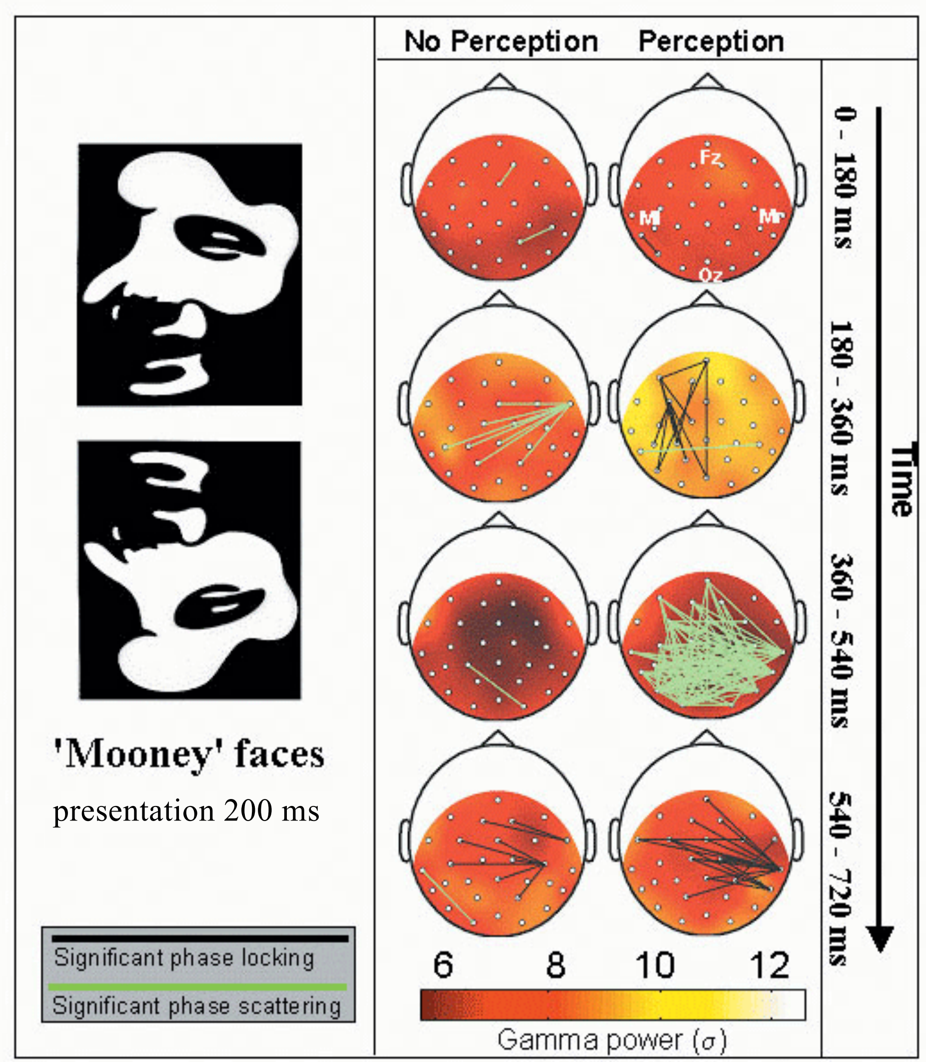
The binding mechanism



There are different hypotheses regarding the binding mechanisms. However, it seems that feature integration require focused *attention* on elements in the visual field.

In **A** the unique stimulus (color) “pops out” – search time is independent on how many items are present in the display (here we are using preattentive scanning)
In **B** the unique item (color and shape) does not pop out. The more items present, the longer the search takes. When we must bind the features we perform serial search and successive shifts of attention.

Gamma band synchrony



Subjects were shown upright and upside-down Mooney figures (high contrast faces), which are easily perceived as faces when presented upright, but usually perceived as meaningless black-and-white forms when upside-down. The subjects' task was a rapid two-choice button response of whether or not they perceived a face at first glance.

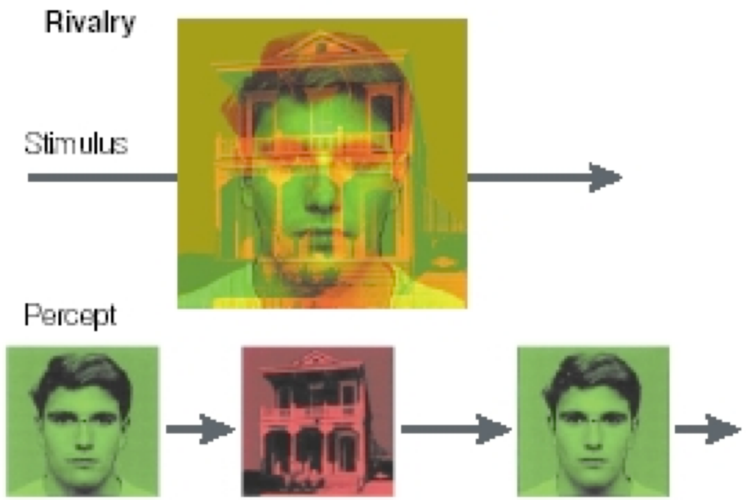
EEG was recorded from electrodes on the scalp surface and the maps show average scalp distribution of gamma activity and phase synchrony. Color-coding indicates gamma power (averaged in a 34-40 Hz frequency range) from a given electrode and during a 180 ms time window, from stimulation onset (0 ms) to motor response (720 ms).

In the condition where the figures were recognized, transient episodes of large-scale synchrony appeared after the presentation of the stimuli, followed by a period of phase scattering and a second period of synchrony during the motor response. Such patterns of synchrony were not present when the pictures were not recognized. Synchrony between electrode pairs is indicated by black and green lines, corresponding to a significant increase or decrease in synchrony, respectively.

Synchrony in the gamma band may represent **binding mechanism**.

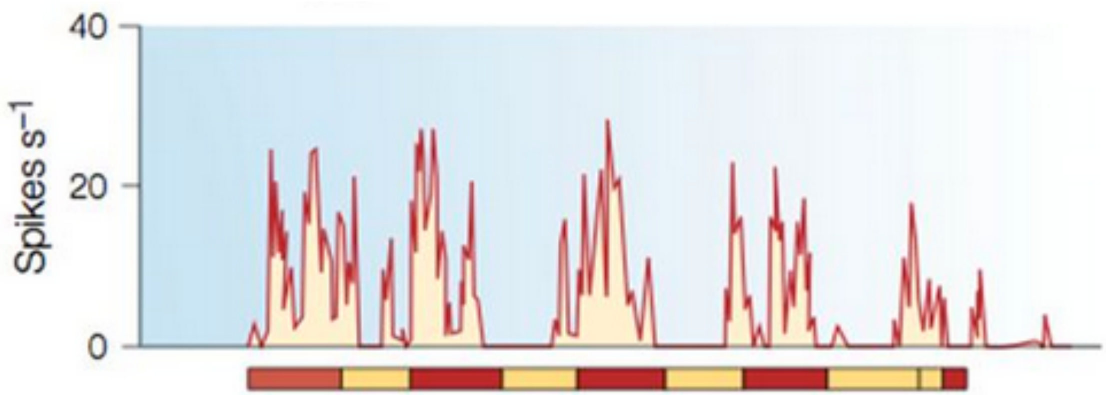
From: Rodriguez E, George N, Lachaux JP, Martinerie J, Renault B, Varela FJ. Perception's shadow: long-distance synchronization in the human brain. Nature 1999.

Neural correlates of awareness are investigated during binocular rivalry and other bistable percepts, by localizing brain areas which are activated in synchrony with the perceptual switching between the two images.



Neural correlates of awareness

- Many brain brain regions are strongly correlated with percept. E.g., neurons in IT cortex:

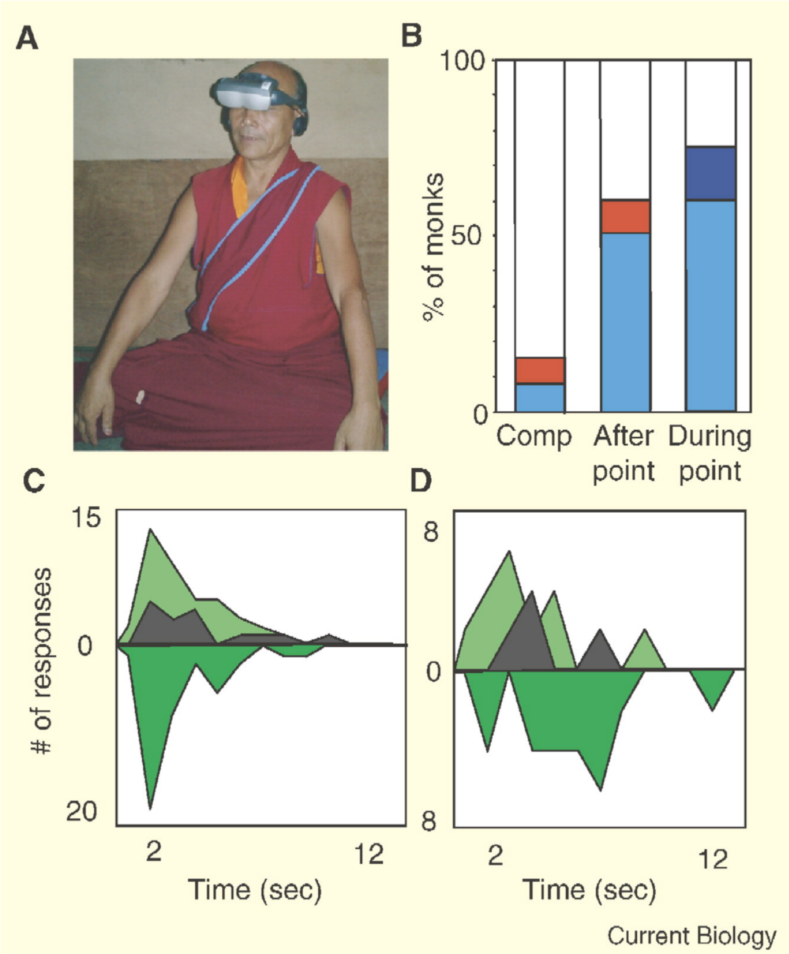


- Consciousness is probably distributed rather than in one locus.

- According to Integrated Information Theory, consciousness corresponds to the capacity of a system to *integrate* information. This capacity is provided by multitude of interactions among various parts of the brain.

Stabilization of perception during binocular rivalry

‚One-point’ meditation but not compassion meditation lead to significant prolongation of perceptual dominance durations during binocular rivalry. The subjects were Tibetan Buddhist monks varying in experience from 5 to 54 years of training.



- Slower switch rate

- Faster switch rate

- Full stabilization

- Horizontal percepts

- Vertical percepts

- Mixed percepts

Three ‘retreatist’ meditators, each with at least 20 years experience in isolated mountain retreats reported complete perceptual stability throughout the entire 5 minute meditation period

(A) Retreatist meditator wearing display goggles. (B) Proportion of monks reporting changes in rivalry switch. (C) Histogram showing time between perceptual switch after no meditation. (D) The same monk showing longer durations after one-point meditation. O.L. Carter et al., Meditation alters perceptual rivalry in Tibetan Buddhist monks. Current Biology, 2005.