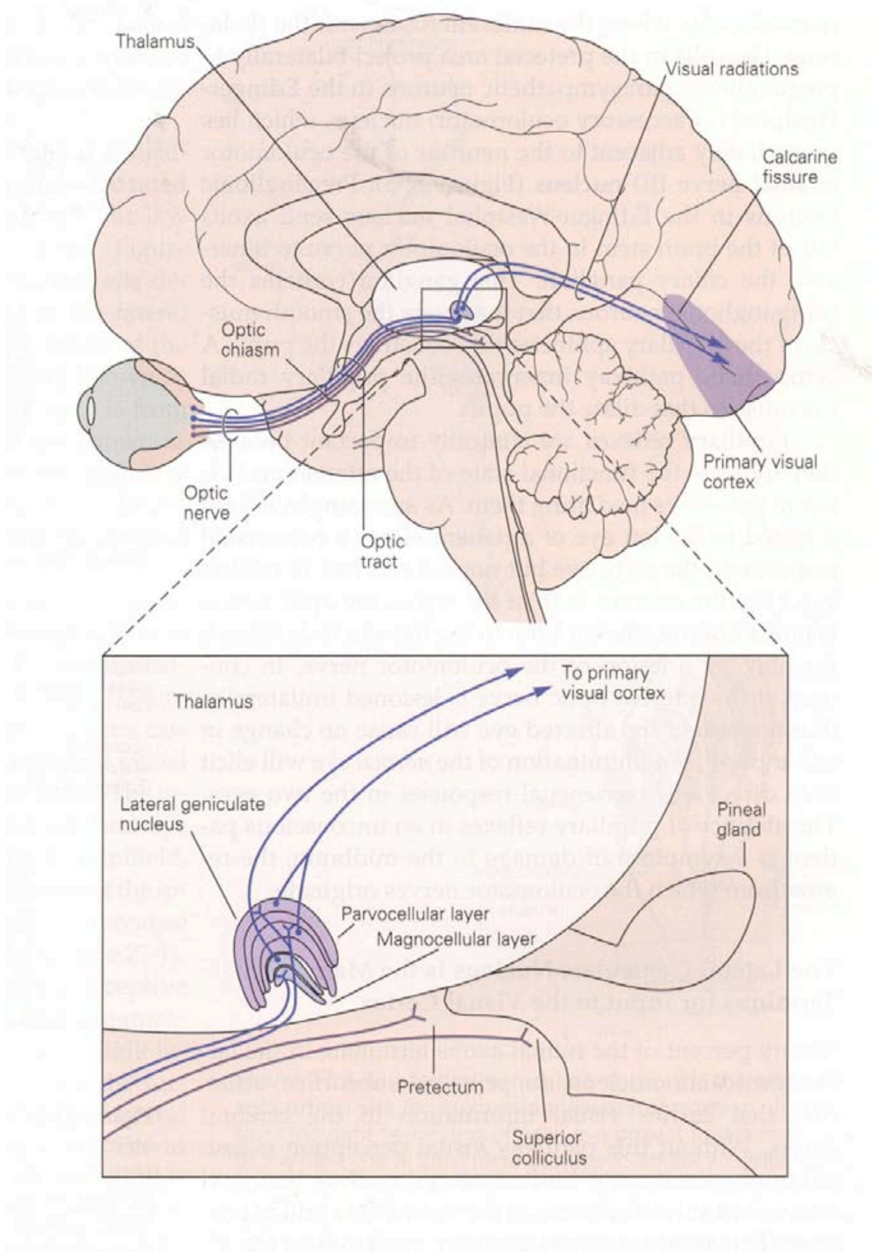
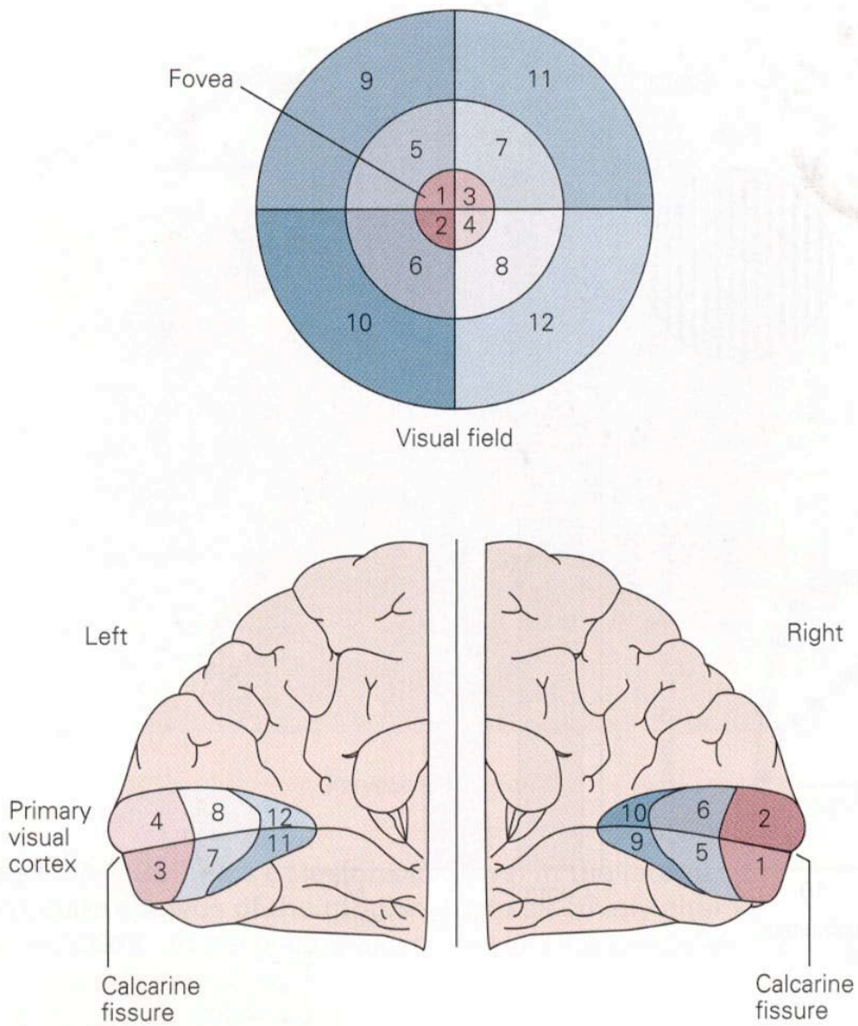
Bi150 (2004)

Vision II: Primary Visual Cortex

10/27/04



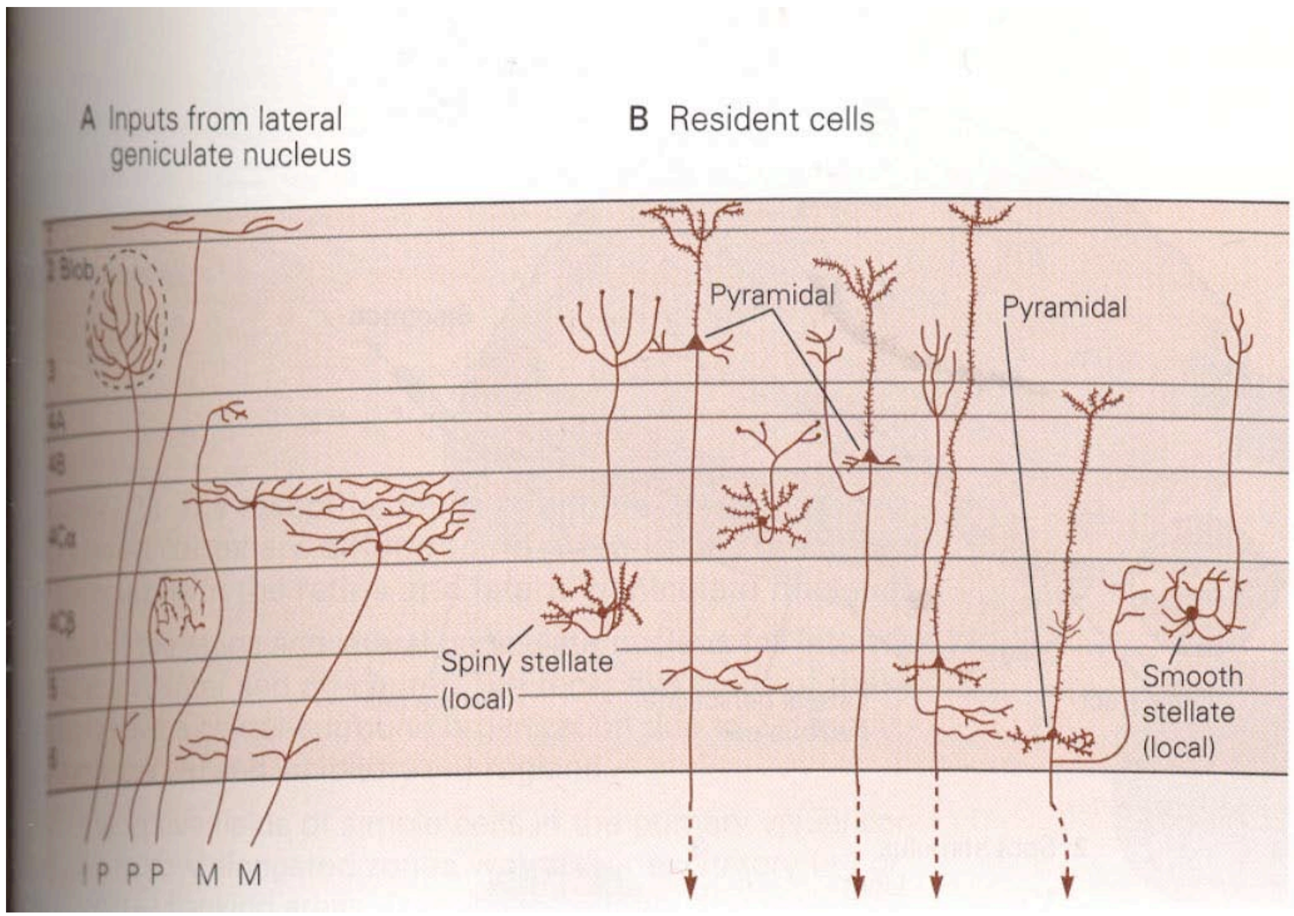
Anatomy of the visual pathways



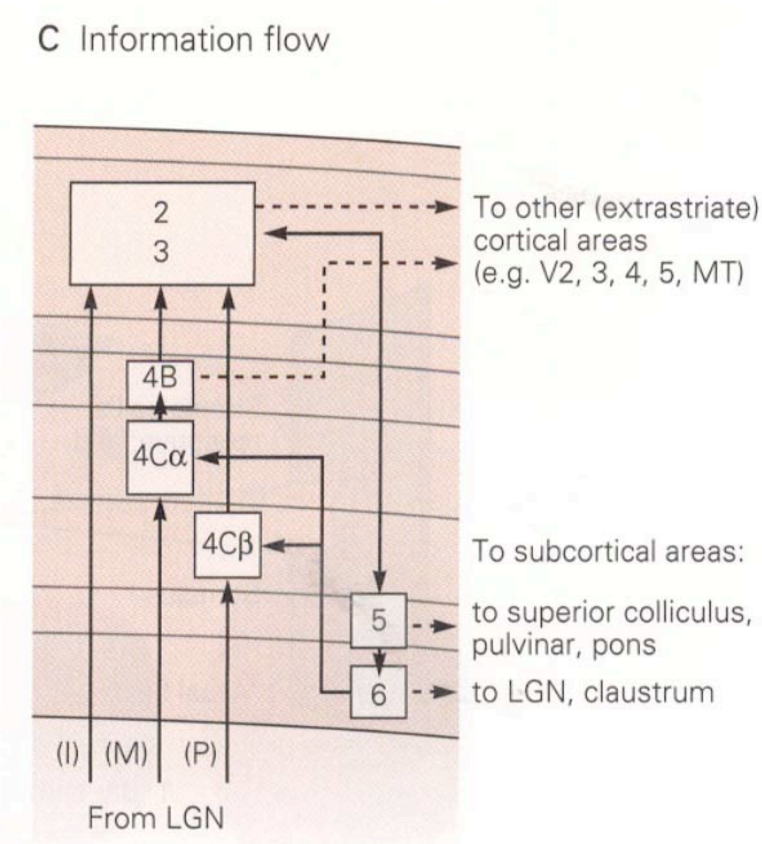
Expansion of the representation of the foveal region in cortex.

Cortical layering and cell morphologies

- Neocortex is a 6-layered structure.
- Cortical pyramidal cells (excitatory) have apical dendritic trees and descending axonal projections with collaterals.
- There are many classes of local inhibitory interneurons.

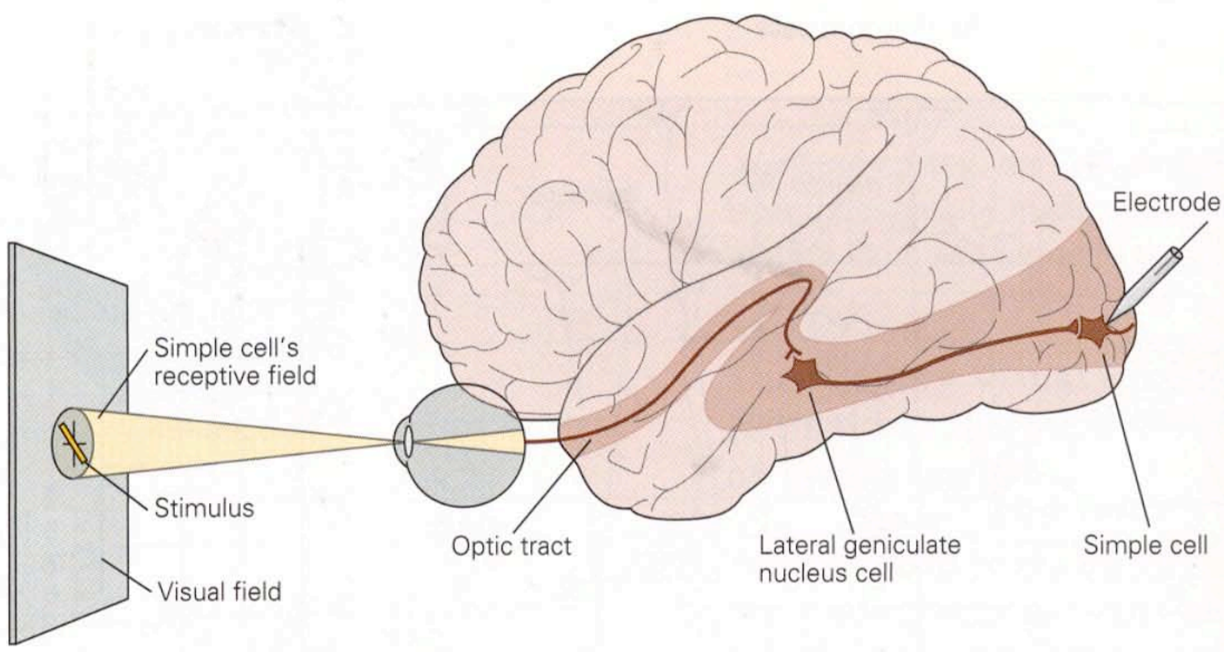


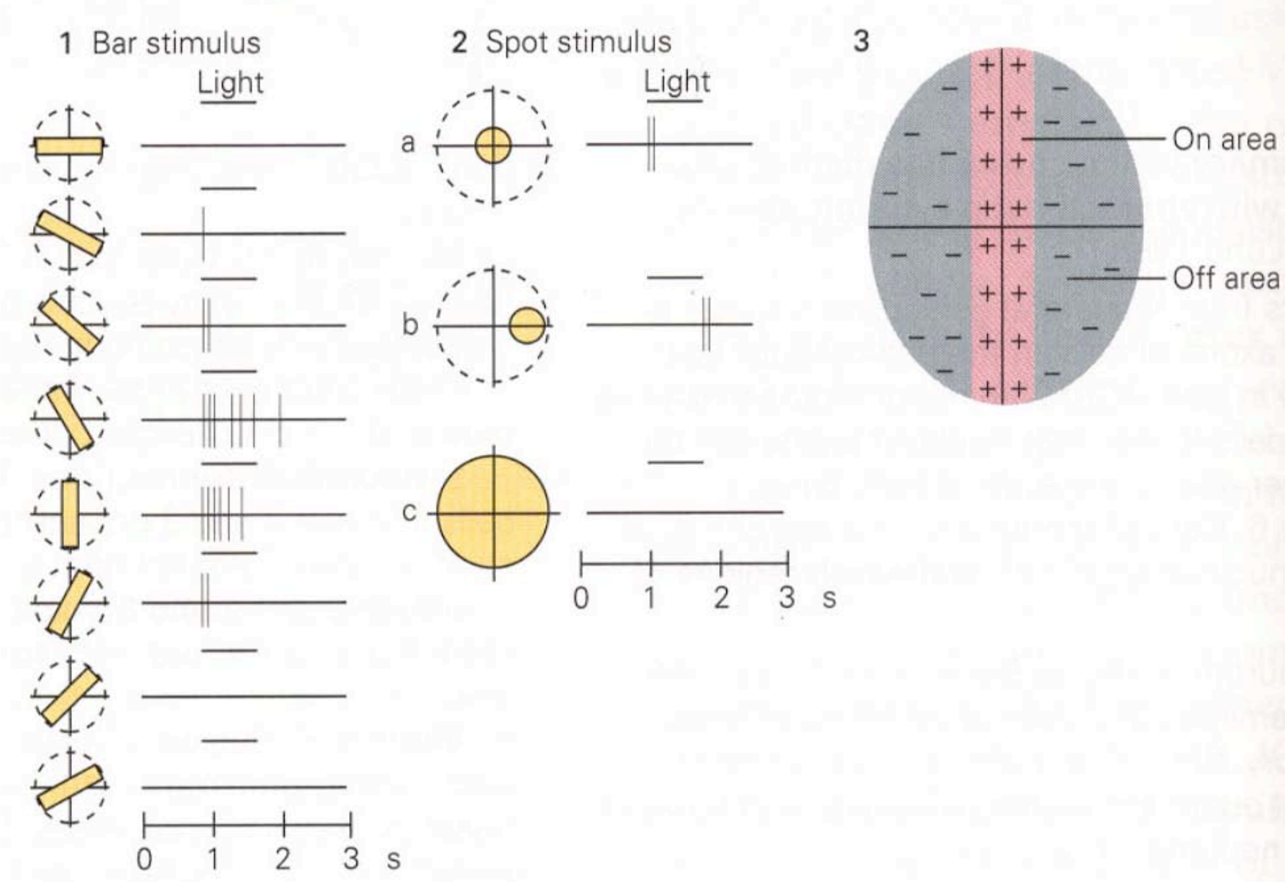
Circuitry in visual cortex



- Sensory areas have expanded layer 4s (input layer).
- LGN axons project to layer 4C,and M and P pathways project to different sublayers.
- Layer 2 and 3 pyramidals project to other cortical areas.
- Layer 5 and 6 neurons project to subcortical areas.
- Layer 6 projects back to LGN.

Setup for extracellular recording of spikes from cells in visual cortex.





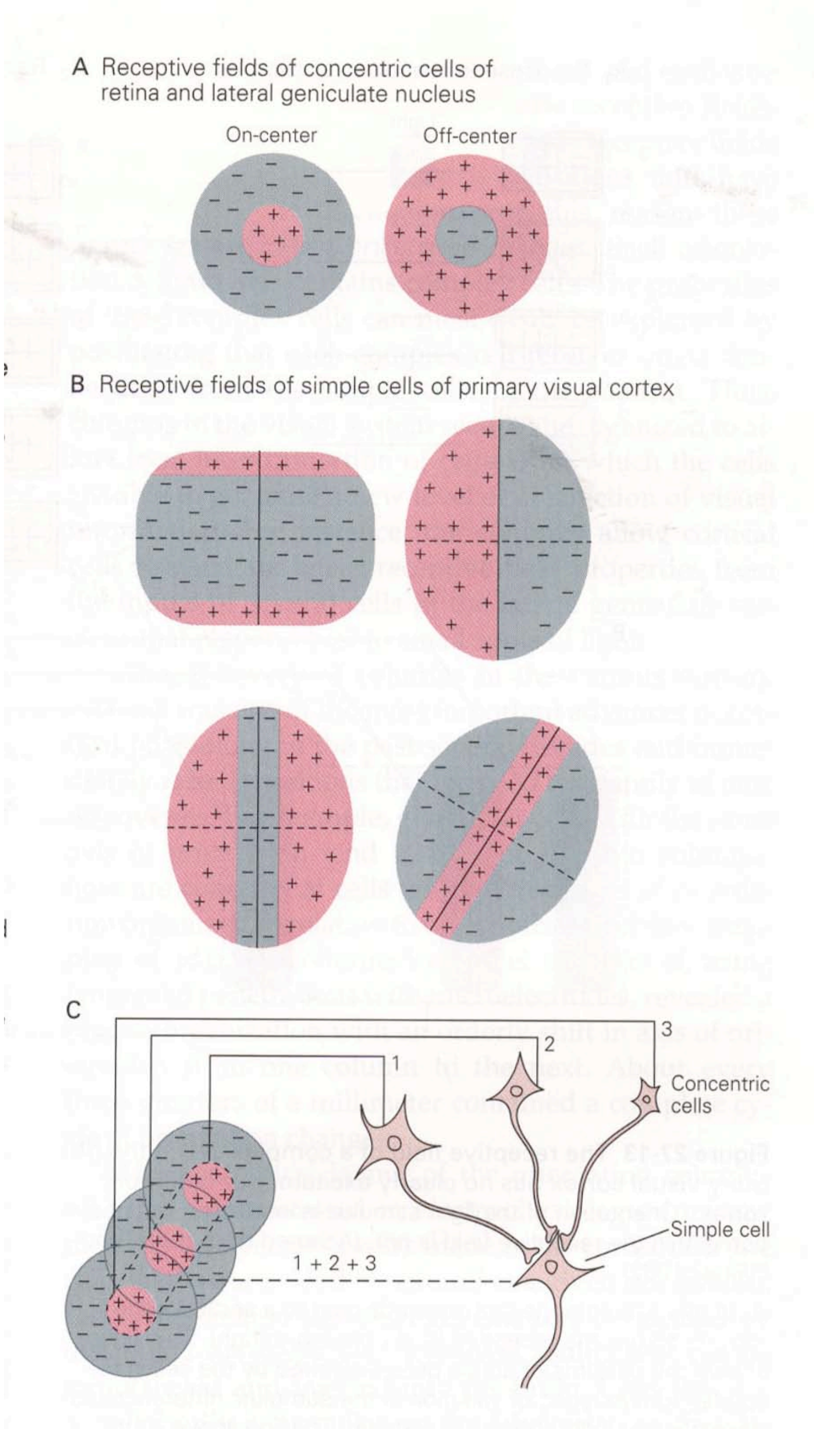
' a simple cell in the primary
d of a cell in the visual system
ty in the cell while spots and
ne visual field at an appropriate
ords shown here are for a sin-
s indicated by a line above
(Adapted from Hubel and

light is strongest if the bar of
:enter of its receptive field.

2. Spots of light consistently elicit weak responses or no response. A small spot in the excitatory center of the field its only a weak excitatory response (**a**). A small spot in the hibitory area elicits a weak inhibitory response (**b**). Diffuse produces no response (**c**).

3. By using spots of light, the excitatory or "on" areas (+) inhibitory or "off" areas (–) can be mapped. The map of th sponses reveals an elongated "on" area and a surrounding "off" area, consistent with the optimal response of the ce vertical bar of light.

- Cells in visual cortex have changes in receptive fields; they no longer respond well to spots, but require more complex stimuli.
- Simple cells often respond well to bars.

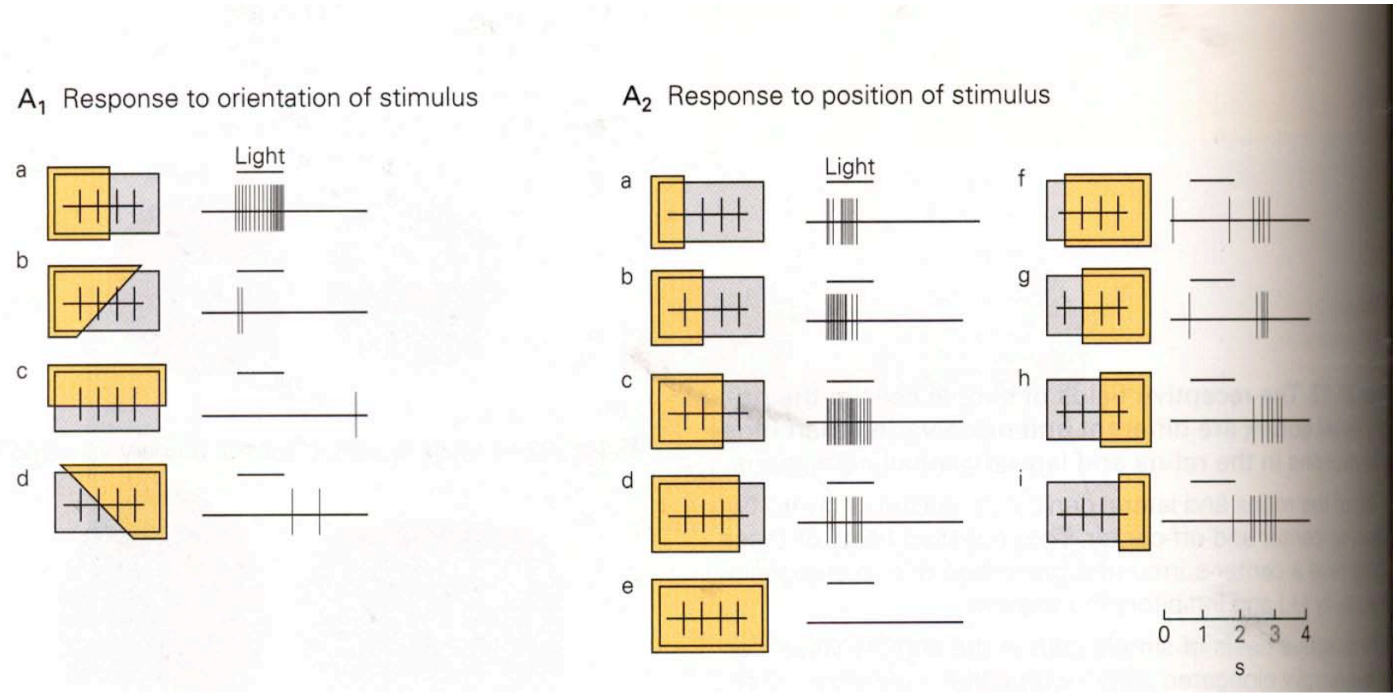


Transformation of receptive field properties between LGN and cortex

- Simple cells can have central areas that are on or off, analogously to LGN cells with on or off centers.
- Simple cell bar receptive fields may be constructed by adding the receptive fields of several LGN cells through their connections to a simple cell.

Complex cells

- Visual cortex has many cells that have on and off areas, but where the position of the border between on and off is not important.
- The orientation of the border, however, is critical.
- In the example here, this cell needs to see light on the left side of its receptive field, with a vertical border separating it from darkness.
- Light on the right generates inhibition followed by a rebound spike train.



B

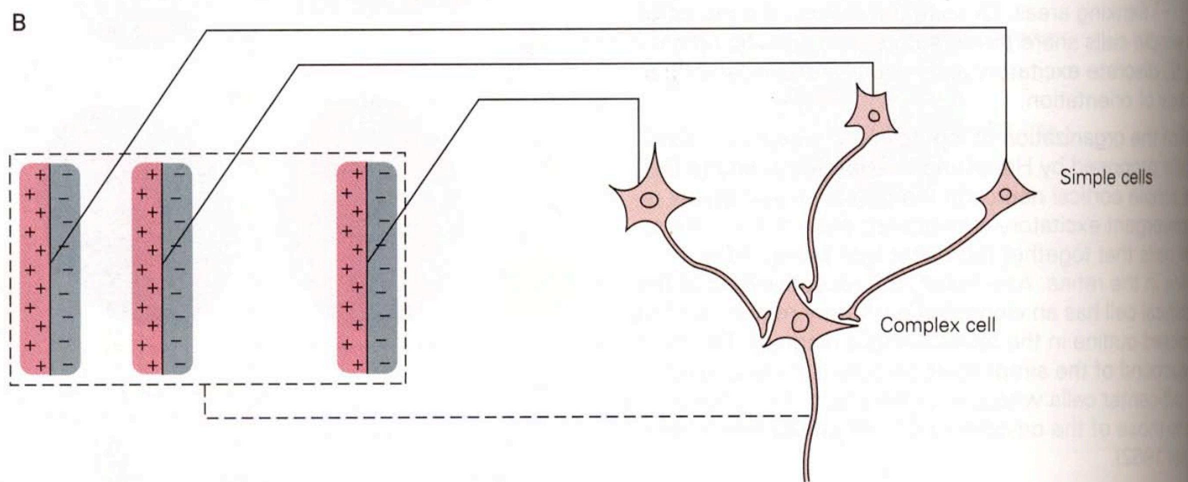


Figure 27-13 The receptive field of a complex cell in the primary visual cortex has no clearly excitatory or inhibitory zones. Orientation of the light stimulus is important, but position within the receptive field is not. (Adapted from Hubel and Wiesel 1962).

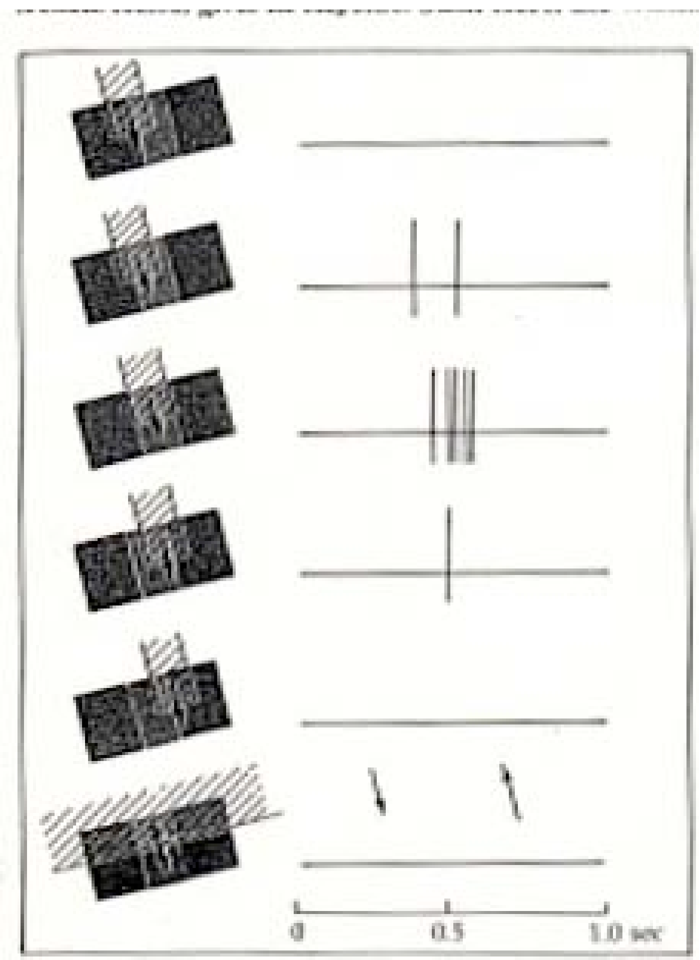
A. In this example the cell responds best to a vertical edge moving across the receptive field from left to right. This figure shows the patterns of action potentials fired by the cell in response to two types of variation in the stimulus: differences in orientation and differences in position. The line above each record indicates the period of illumination. **1.** Different orientations of the light stimulus produce different rates of firing in the cell. A vertical bar of light on the left of the receptive field produces a strong excitatory response **(a)**. Orientations other than vertical are less effective **(b–d)**. **2.** The position of the border of the light within the receptive field affects the type of respo in the cell. If the edge of the light comes from any point on right within the receptive field, the stimulus produces an e tory response **(a–d)**. If the edge comes from the left, the st lus produces an inhibitory response **(f–i)**. Illumination of the tire receptive field produces no response **(e)**.

B. According to Hubel and Wiesel, the receptive fields of c plex cells are determined by the pattern of inputs. Each co plex cell receives convergent excitatory input from several ple cortical cells, each of which has a receptive field with t same organization: a central rectilinear excitation zone (+) flanking inhibitory regions (–). In this way the receptive fi a complex cell is built up from the individual fields of the p naptic cells.

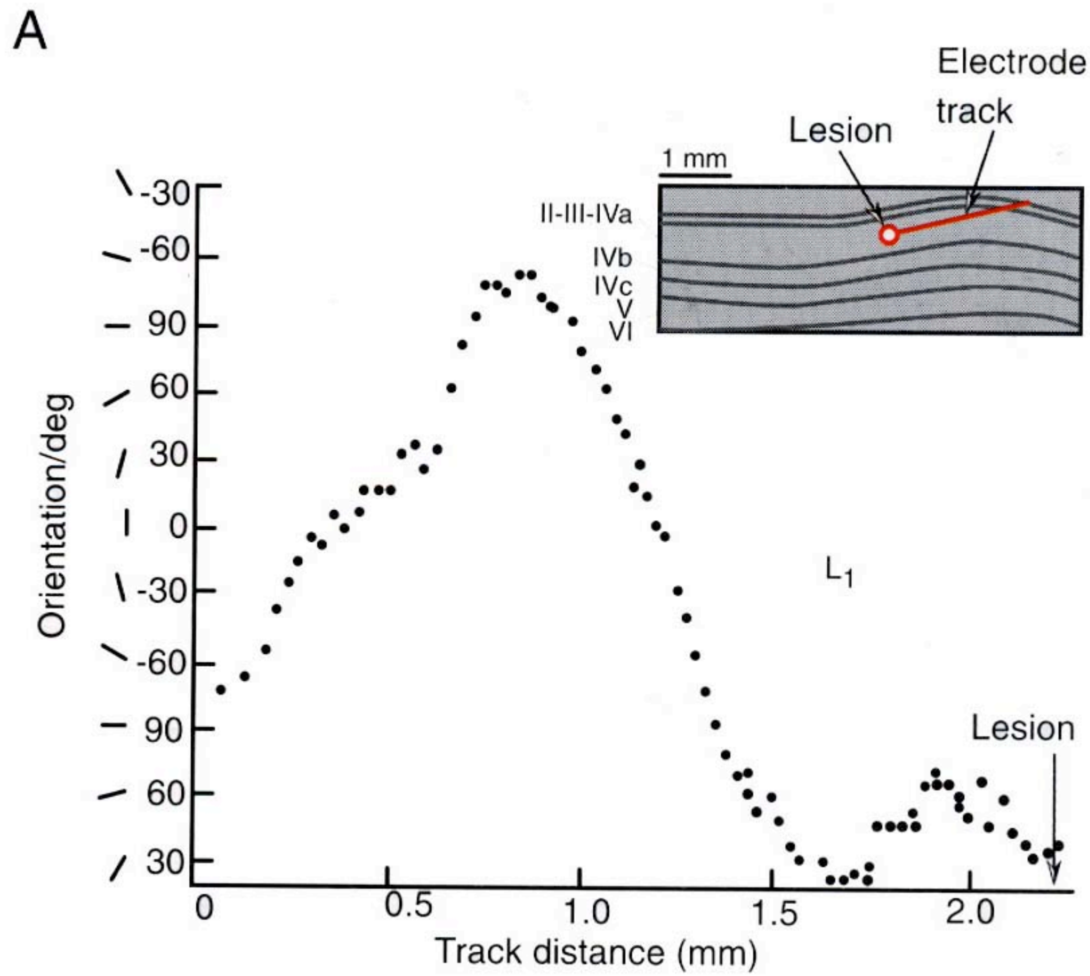
- Complex cell receptive fields might be constructed by adding simple cell fields, in an analogous manner to the construction of simple cell fields from LGN fields.

Some complex cells respond best to moving stimuli

- The cell shown here responds best to a dark bar in the middle of the receptive field, moving downward.
- Shifting the bar into the "off" regions or extending its width reduces or eliminates the response.
- The reduction in efficacy with extension of the bar is called end-stopping.



Orientation columns



- In recording from cortex one can advance the electrode at an oblique angle within a layer.
- When this is done the orientation preference of the recorded cells shifts in an orderly manner.

Arrangement of orientation columns

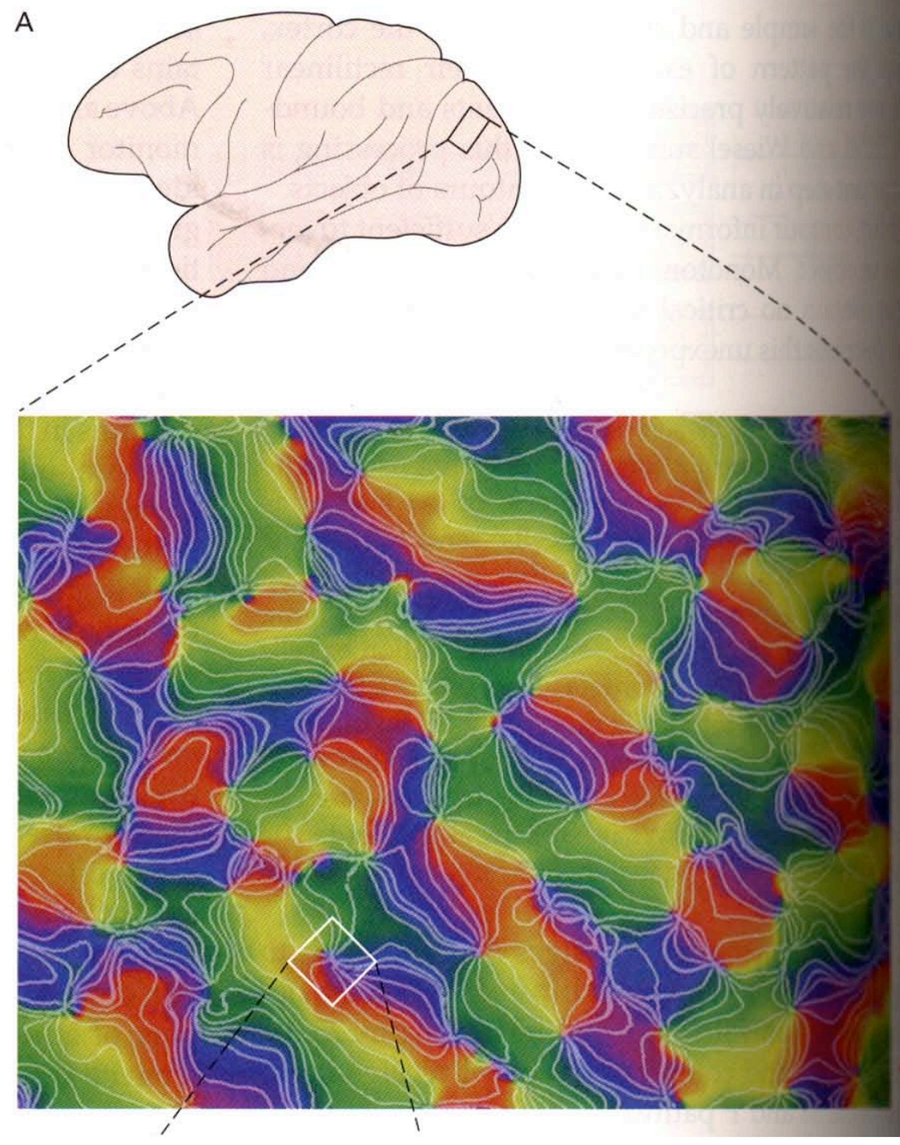
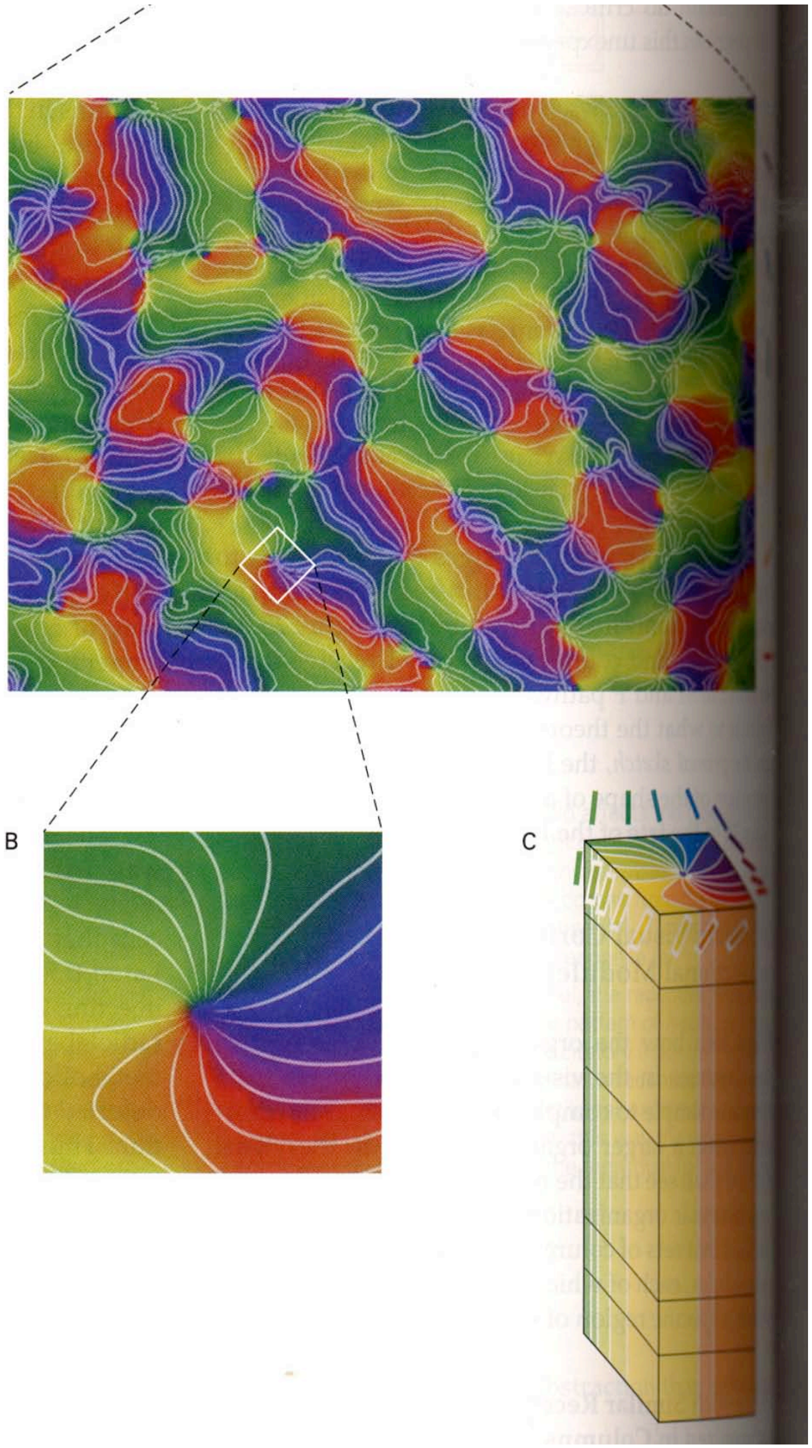


Figure 27-14 Orientation columns in the visual cortex of the monkey. (Courtesy of Gary Blasdel.)

A. Image of a 9 by 12 mm rectangle of cortical surface taken while the monkey viewed contours of different orientations (indicated on the right). This image was obtained through optical imaging and by comparing local changes in reflectance, which indicate activity. Areas that were most active during the presentation of a particular orientation are indicated by the color chosen to represent that orientation (bars on the right). Complementary colors were chosen to represent orthogonal orientations. Hence, red and green indicate maximal activities in response to horizontal and vertical, while blue and yellow indicate greatest activation by left and right oblique.



- Orientation columns can be visualized by optical imaging of activity at the cortical surface.
- Orientation columns come together at ‘pinwheel’ singularities.
- Going around a pinwheel, one traverses an orderly series of orientation preferences.
- There are both right-handed and left-handed pinwheels.

Ocular dominance columns

- Most cells in V1 are binocularly driven, but exhibit a preference for one eye over the other (that is, when the receptive field is stimulated identically in each eye, the cell fires more spikes in response to one eye than to the other).
- Ocular dominance can be visualized by tracing the pattern of connections from one eye to the brain.

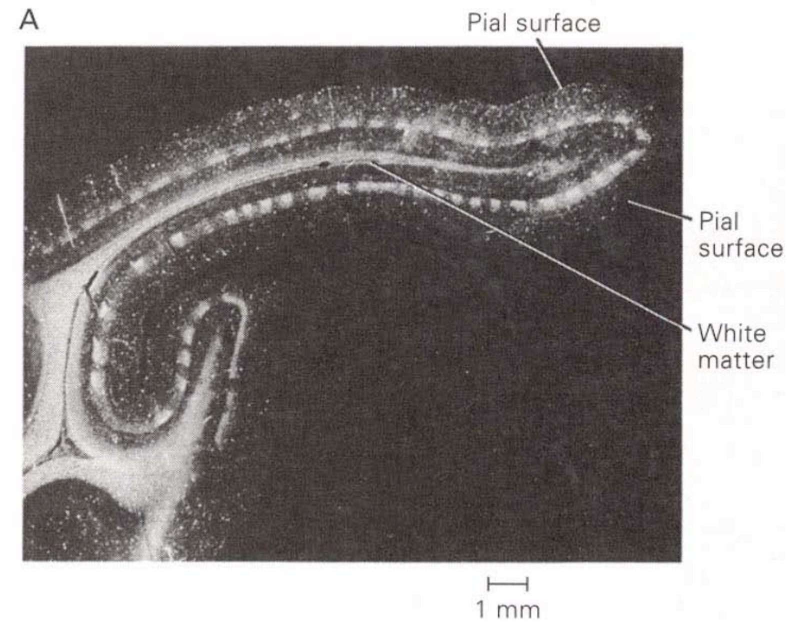
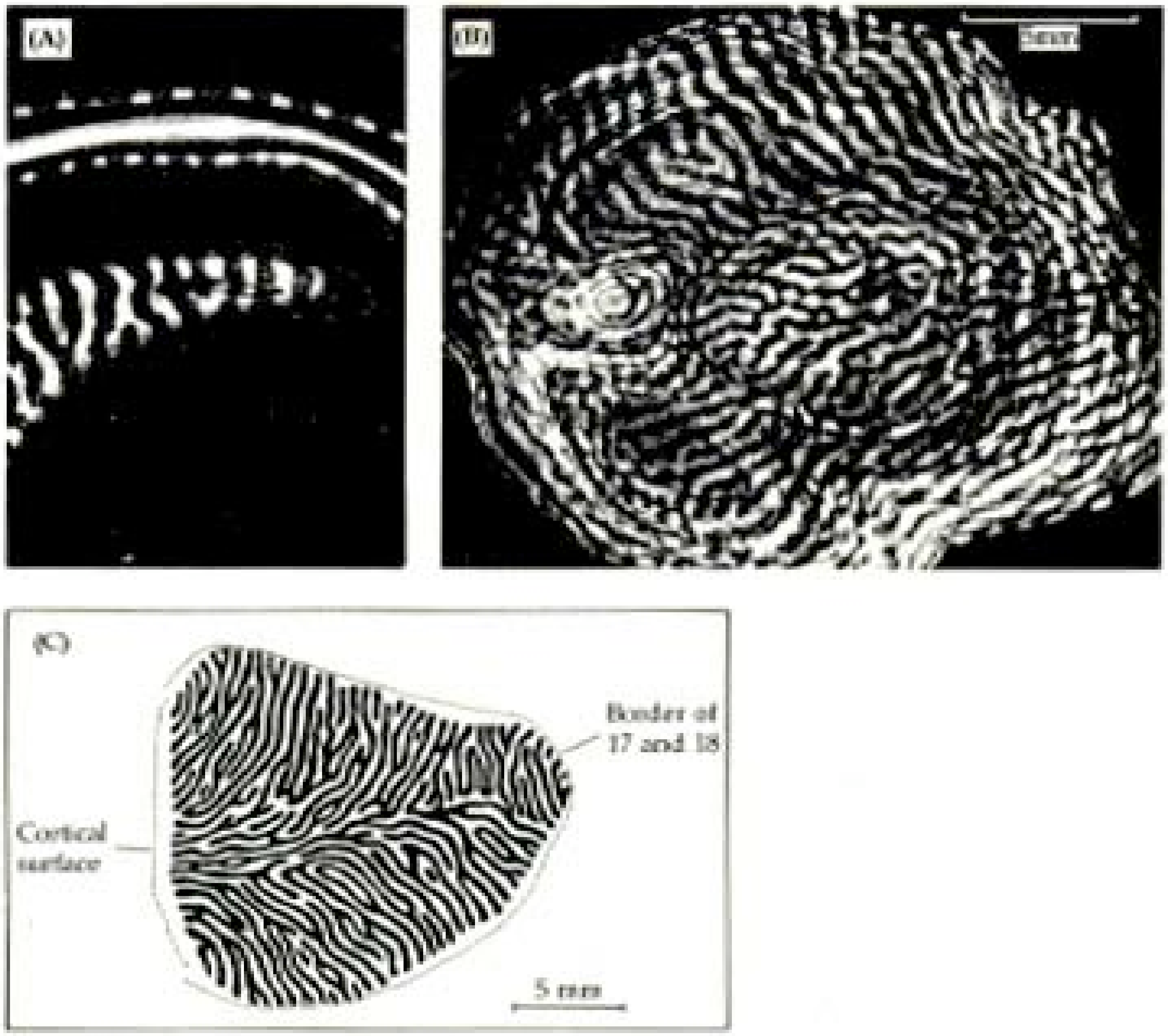
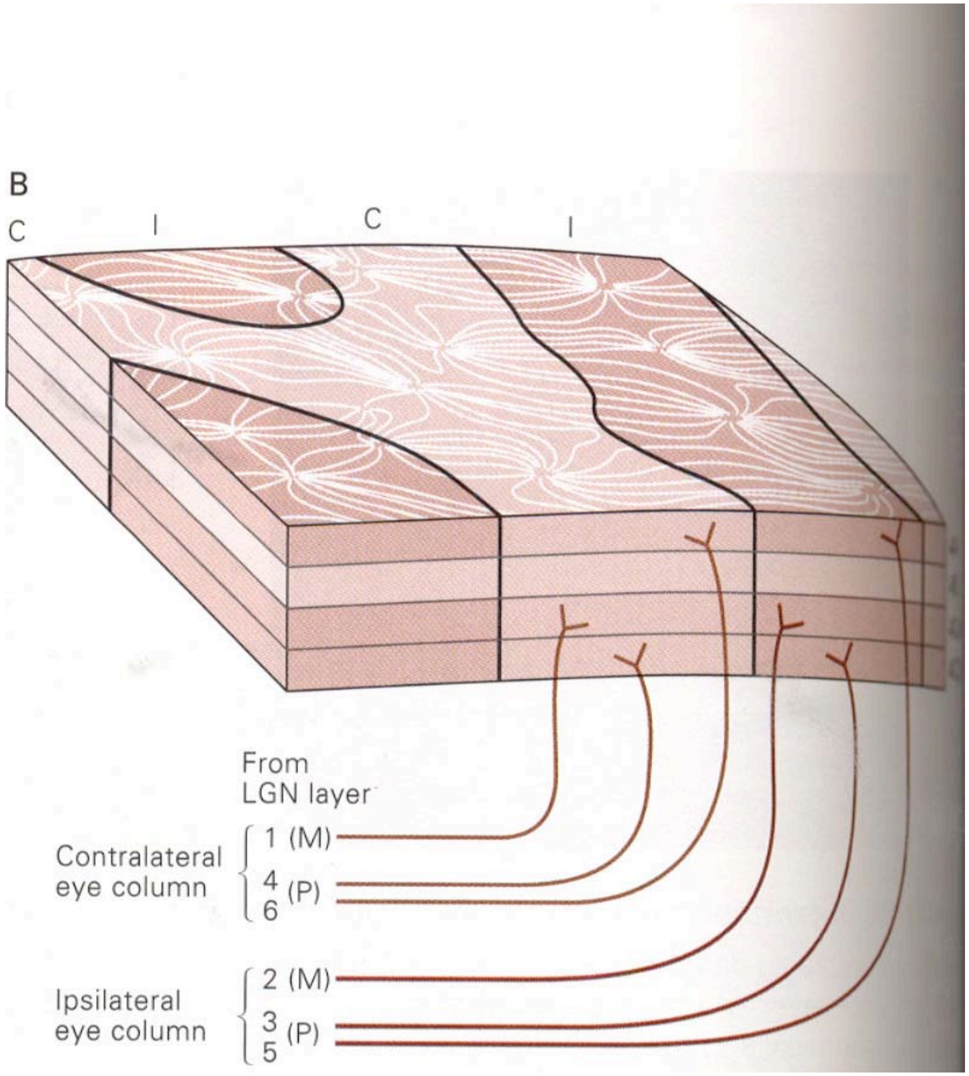


Figure 27-16 The ocular dominance columns.

A. This autoradiograph of the primary visual cortex of an a monkey shows the ocular dominance columns as alternat white and dark (labeled and unlabeled) patches in layer 4 c cortex, below the pial surface. One eye of the monkey wa jected with a cell label, which over the course of 2 weeks transported to the lateral geniculate nucleus and then acro synapses to the geniculocortical relay cells, whose axons nate in layer 4 of the visual cortex. Areas of layer 4 that re input from the injected eye are heavily labeled and appear


(A)
(C)
Border of
17 and 18
Cortical
surface
5 mm

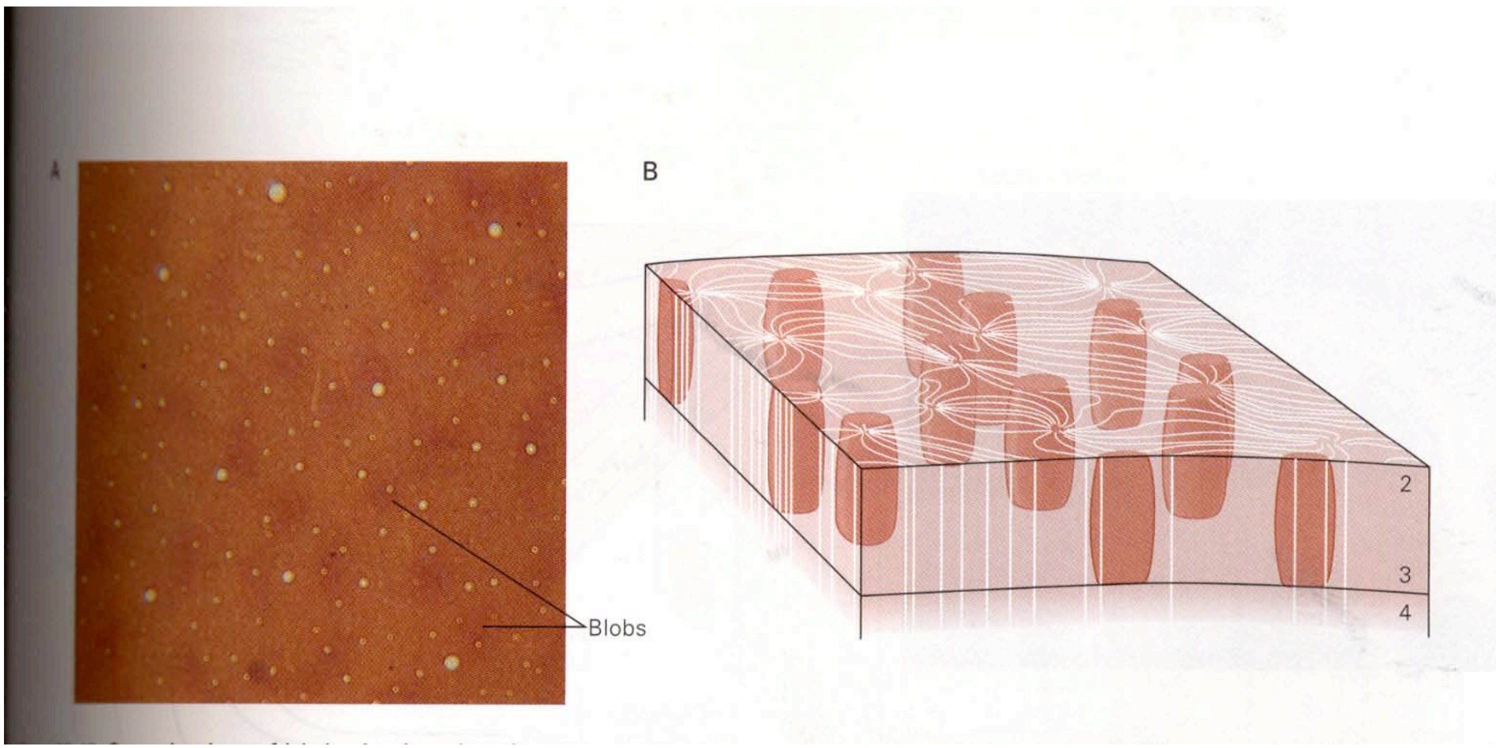
Relationships of ocular dominance and orientation columns

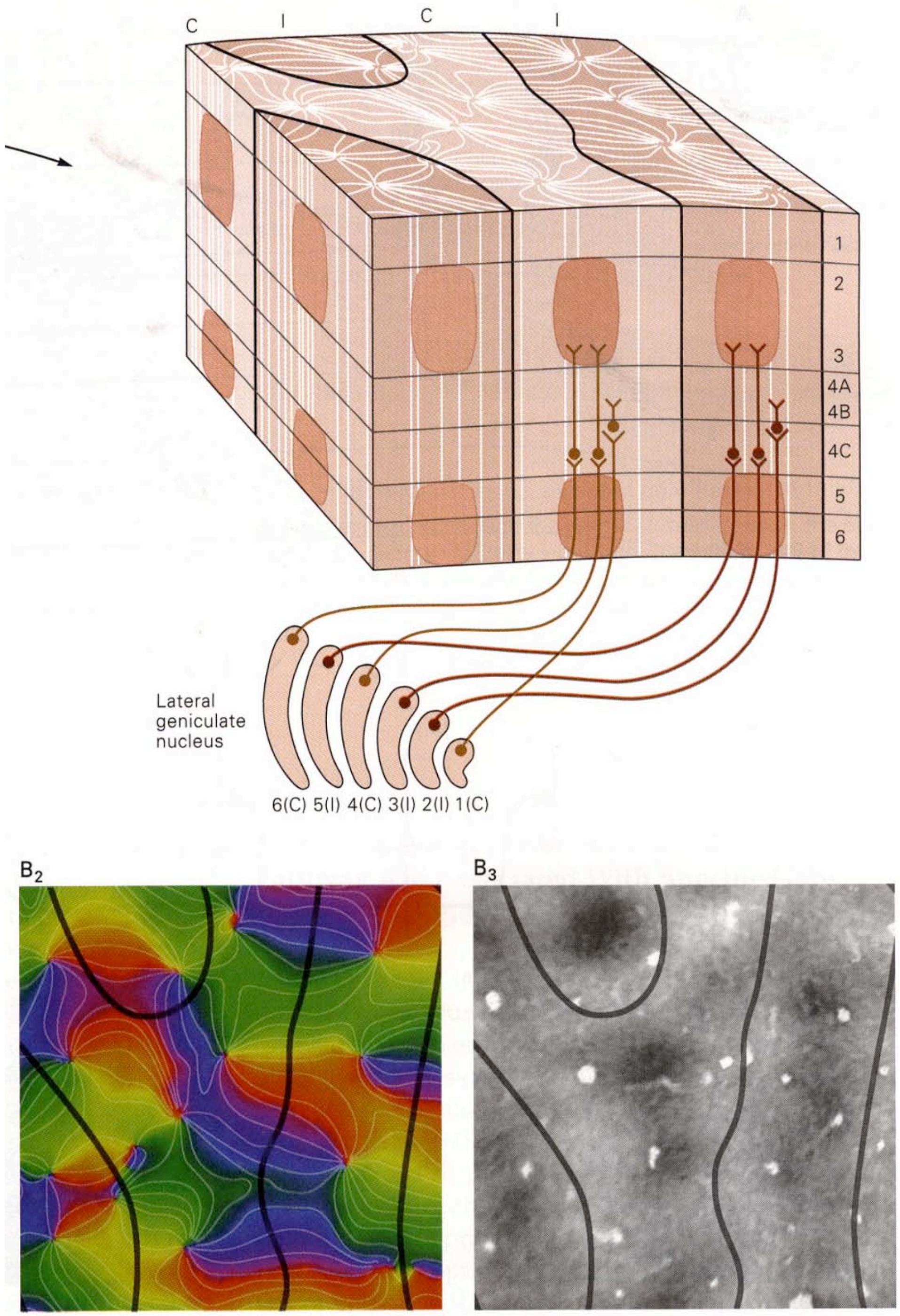


- OD columns include sets of orientation columns arranged around their pinwheels.
- At a given point in cortex, a vertical penetration will record cells that all have the same orientation and eye preferences, but which exhibit many kinds of receptive fields (simple, complex, selective for moving stimuli, etc.)

Blobs

- Imbedded within orientation-selective areas are groups of cells that exhibit little orientation preference.
- These cells are strongly sensitive to color, however, and fire well in response to stimuli of the preferred color.
- They are recognized by cytochrome oxidase staining, which is thought to be a reporter of neural activity.



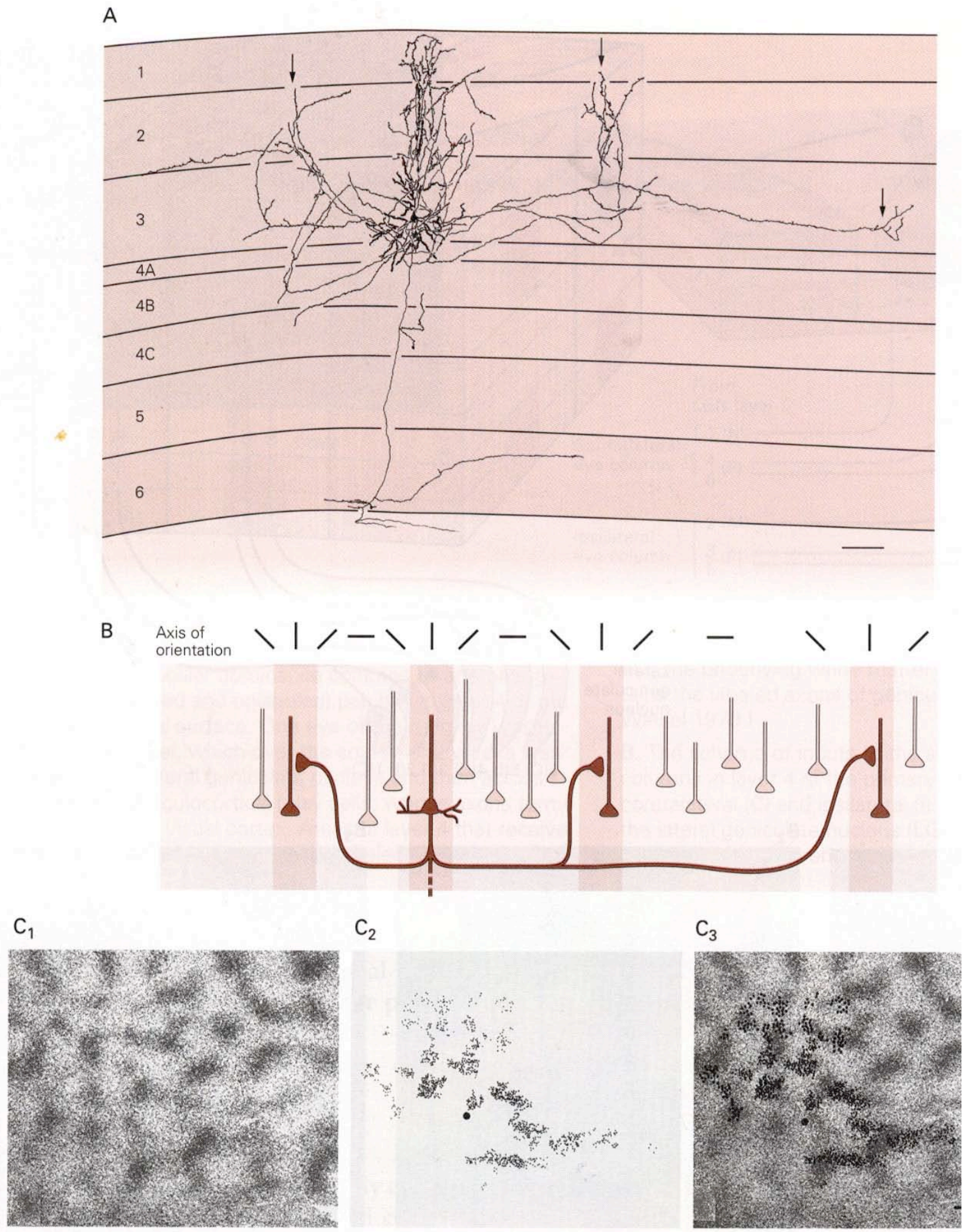


Hypercolumns

- Combining OD columns, orientation columns, and blobs produces the ‘hypercolumn’ structure.
- Each hypercolumn represents a small portion of visual space.
- Within it are ipsi and contra eye regions, and within these a complete set of orientation columns and a blob.
- Simple and complex cells are stacked vertically, as are cells receiving input from M and P layers of the LGN.

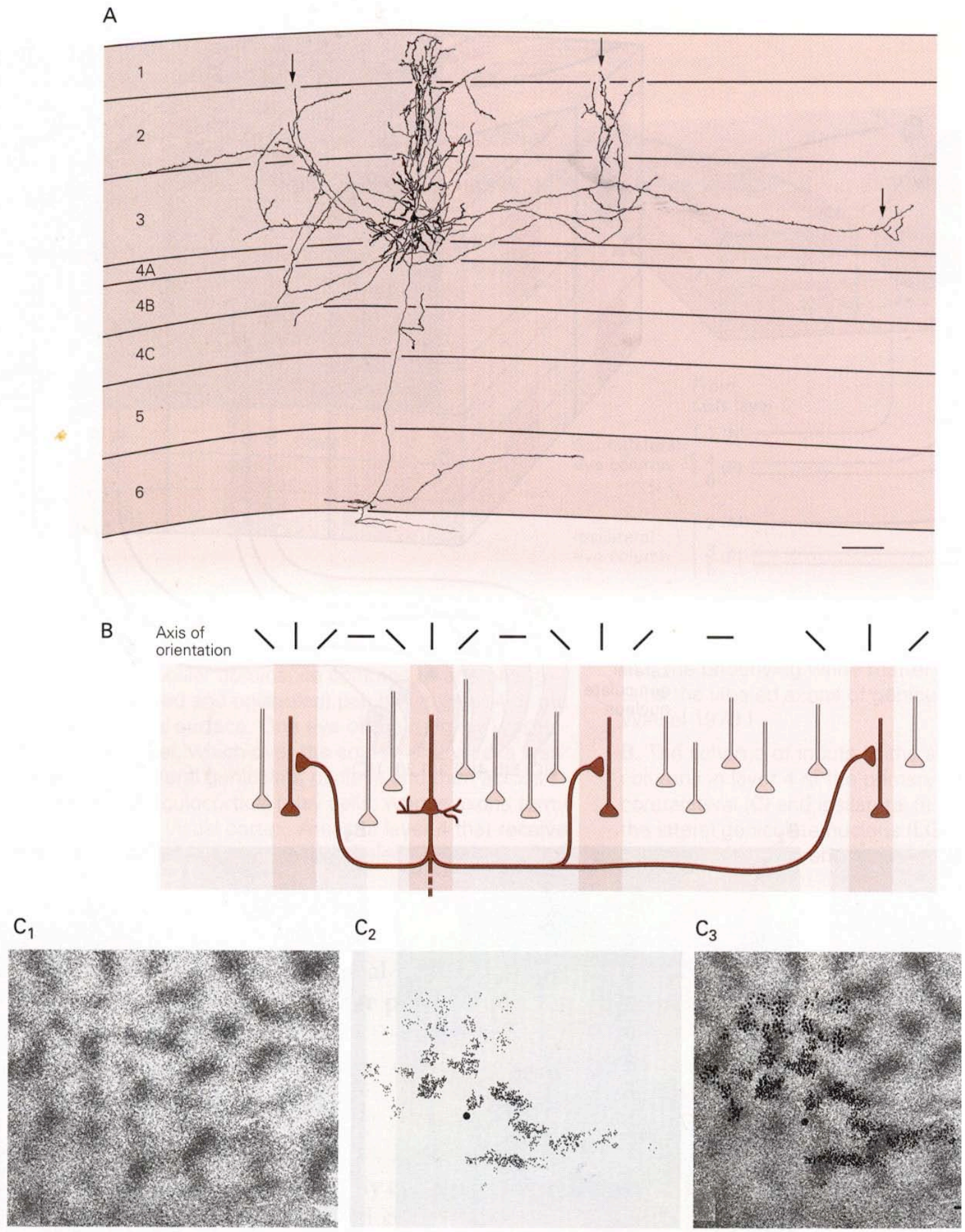
Horizontal connections between hypercolumns

- Each hypercolumn represents an ‘analysis unit’ for a small segment of visual space.
- To preserve the continuity of objects, however, connections must exist that link adjacent parts of the visual field.



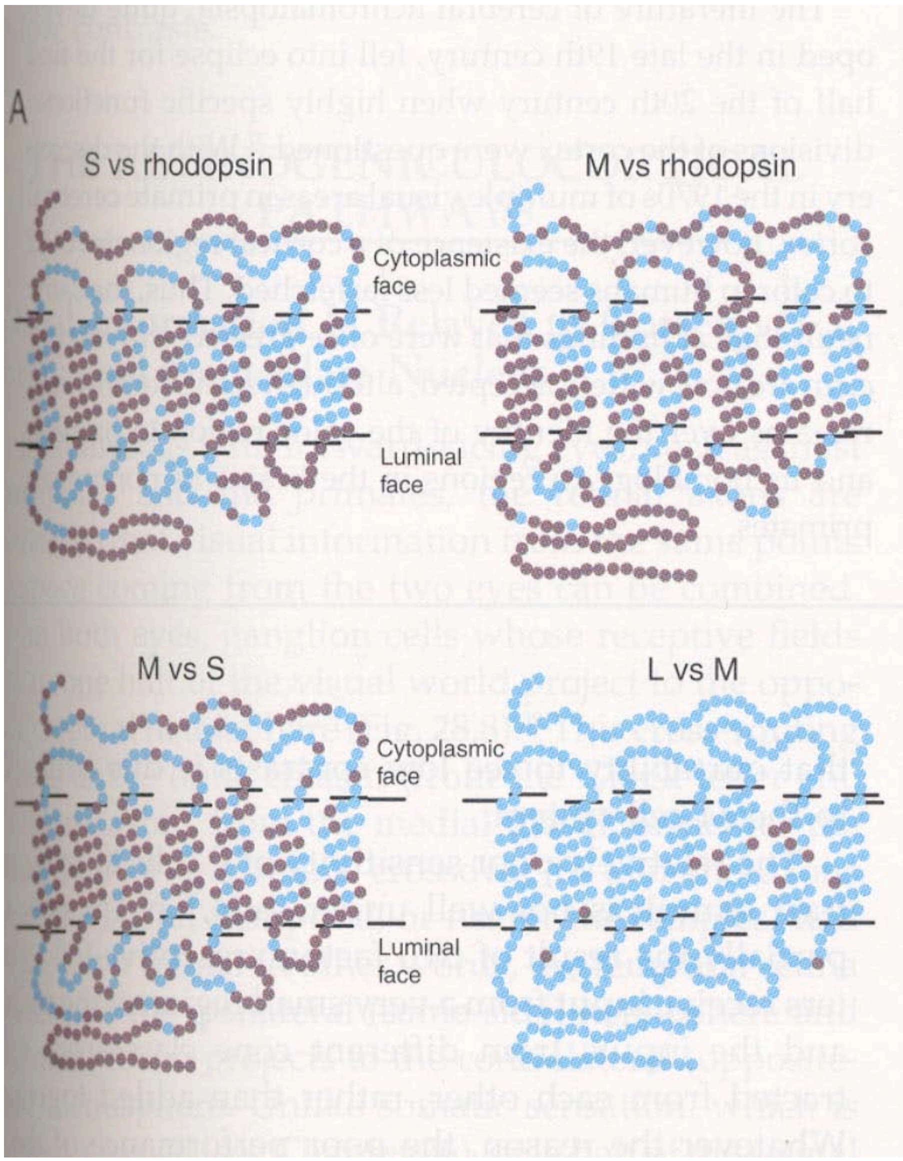
Horizontal connections between hypercolumns II

- Single pyramidal cells have horizontal connections that link domains in adjacent hypercolumns that respond to stimuli with the same orientation.
- This can be visualized by combining axonal tracing with visualization of orientation-specific neural activity.

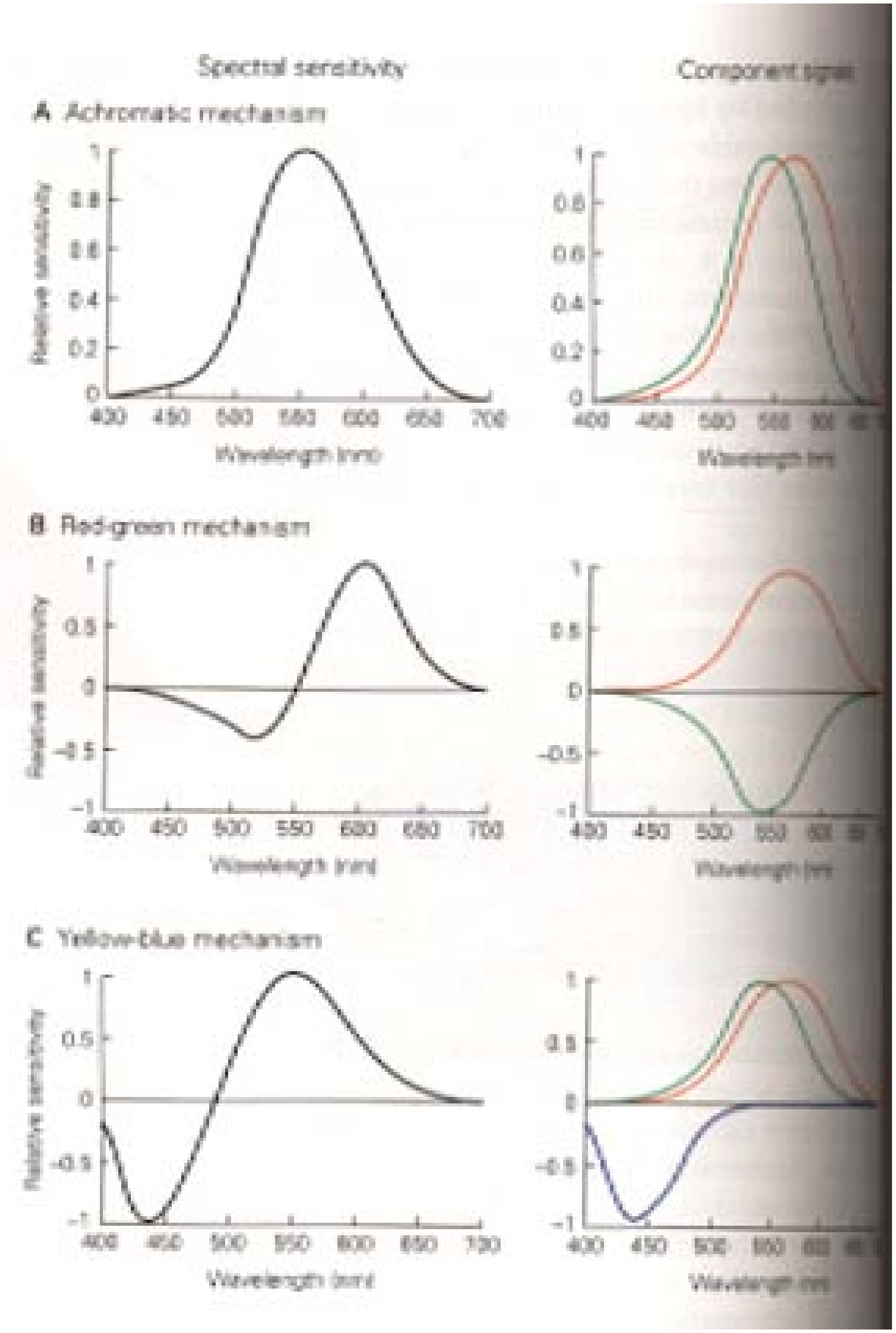


Color vision

Sequences of cone photopigments



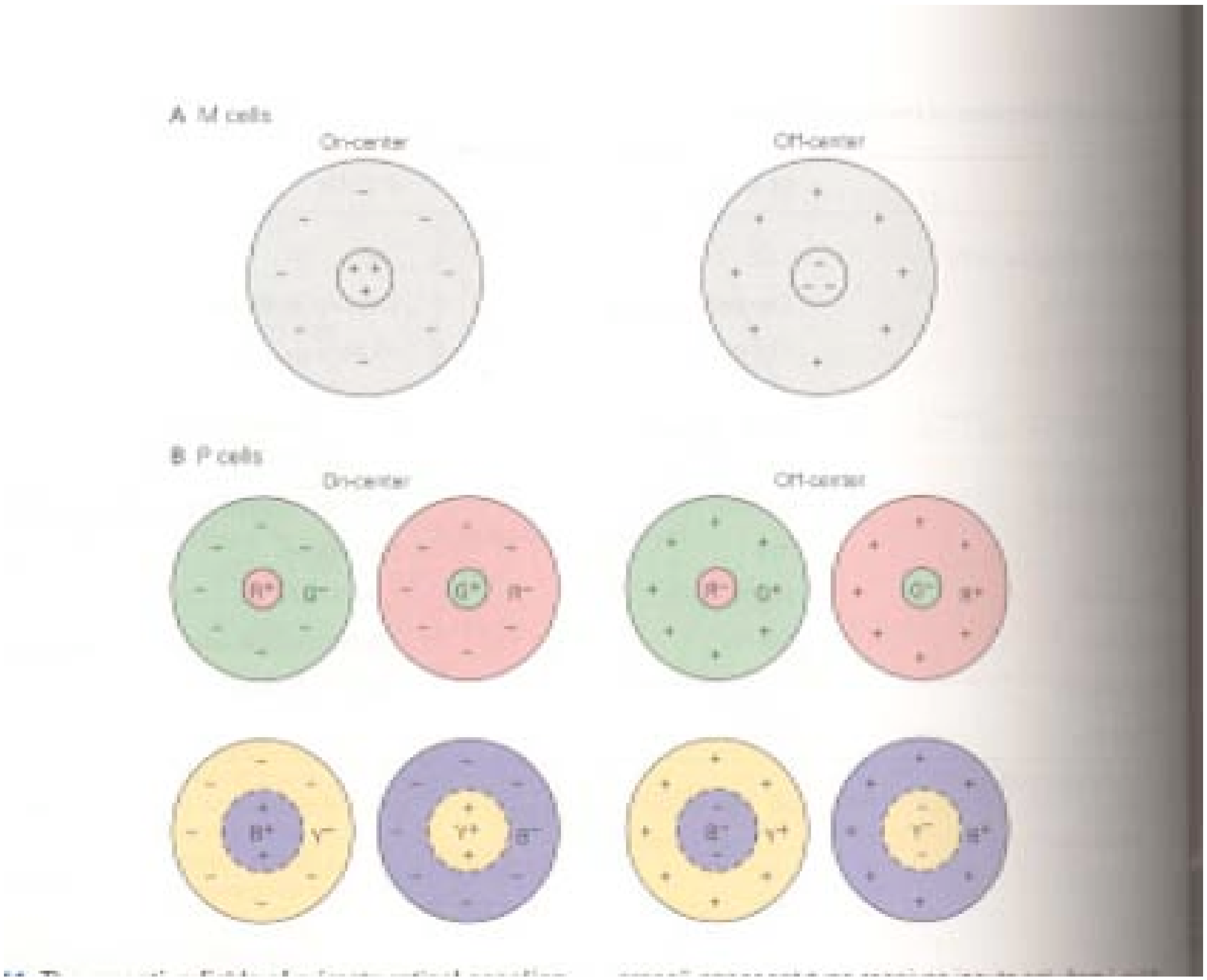
- There are 3 types of cones in the human retina: long-wavelength (red), middle (green), and short (blue). R and G are much more common than B.
- Each cone type has a different photopigment with a retinal chromophore and an opsin protein.
- L and M cone opsins are almost identical in sequence and absorb light at similar wavelengths. S cone opsin differs more, and absorbs maximally at much shorter wavelengths.



Combining cone responses generates color discrimination

- R and G cones are much more numerous than B cones, and many foveal RGCs are connected to both types.
- Adding the R and G responses produces a measure of overall brightness.
- Subtracting R from G gives good color discrimination at >475 nm.
- Subtracting B from (R+G) gives good discrimination at <475 nm.

Color opponency in RGCs



- RGC receptive fields correspond to these calculations.
- M cells can measure brightness; they oppose center (R+G) to surround without regard to cone type.
- Red-green opponent P cells oppose R in center to G in surround, and vice versa; so they measure (R-G).
- Yellow-blue opponent P cells oppose B in center to Y (=R+G) in surround.

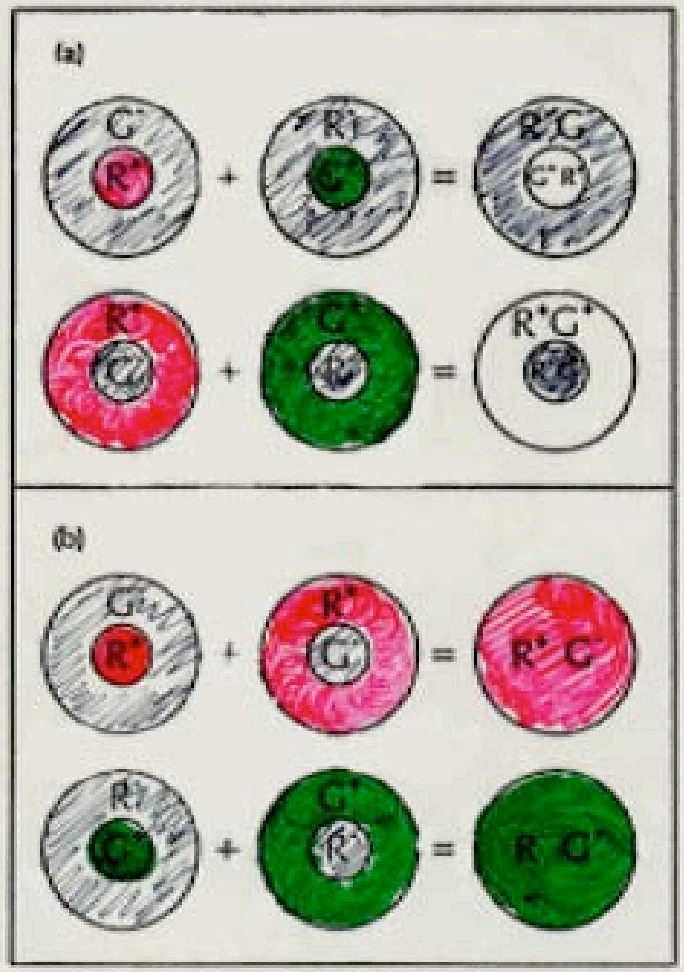


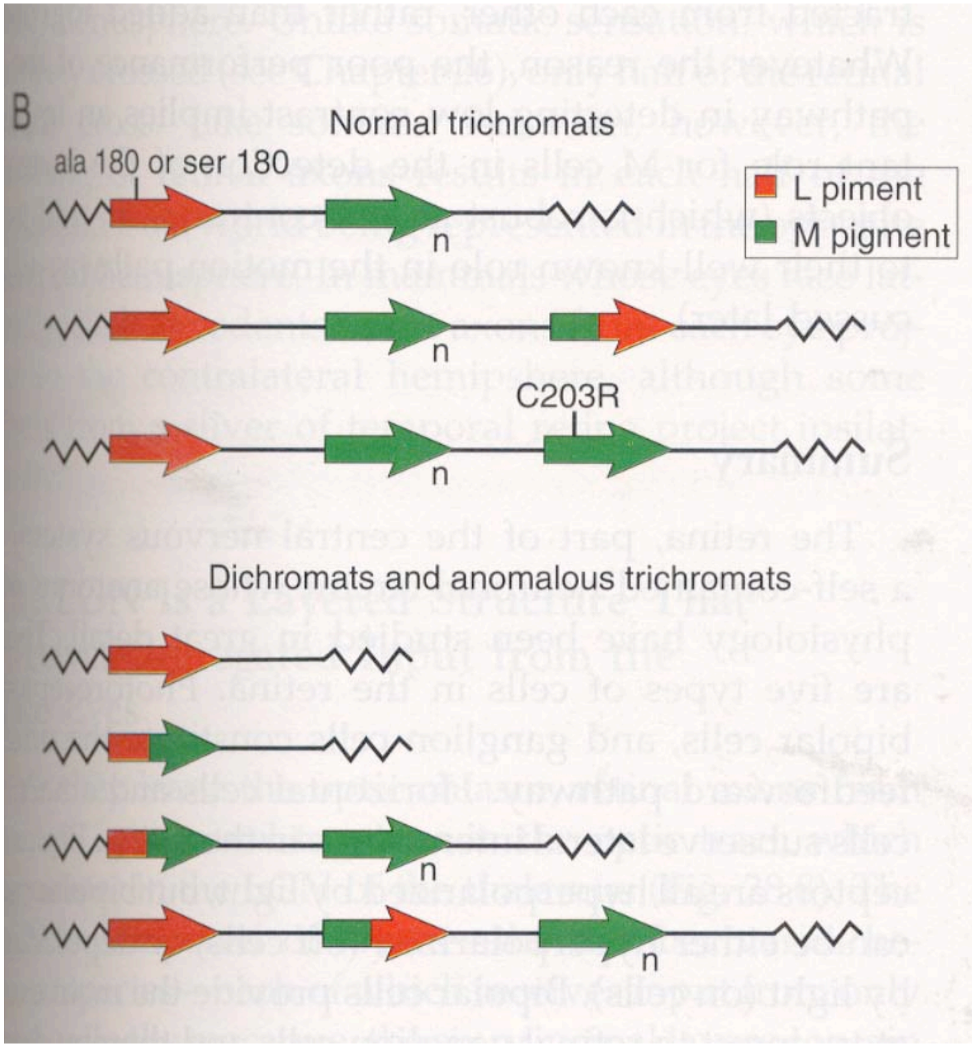
Fig. 3. The Lennie/D'Zmura model for extracting chromatic and luminance signals from Type 1 cells.

>Single-opponent cells cannot distinguish the color signal from The brightness signal, because they are excited both by large colored spots and by small white or yellow spots in the center of their receptive fields.

>Adding the responses of single-opponent LGN cells to create cortical double-opponent cells can distinguish these signals.

>Thus, adding (R+/G-)+(G+/R-)= (G+R+/G-R-), which measures brightness in center vs. surround.

>Adding (R+/G-)+(G-/R+)= R+G-, which measures color across the whole receptive field.



Color-blindness

- The red and green pigment genes are located next to each other on the X.
- Because the genes are so similar, unequal crossing over can take place between them to delete genes and generate hybrid genes.
- Only males exhibit phenotypes, because females have 2 Xs.
- Red-green colorblindness is very common in males. Color-blind people can still distinguish most colors because they retain 2 cone pigments.