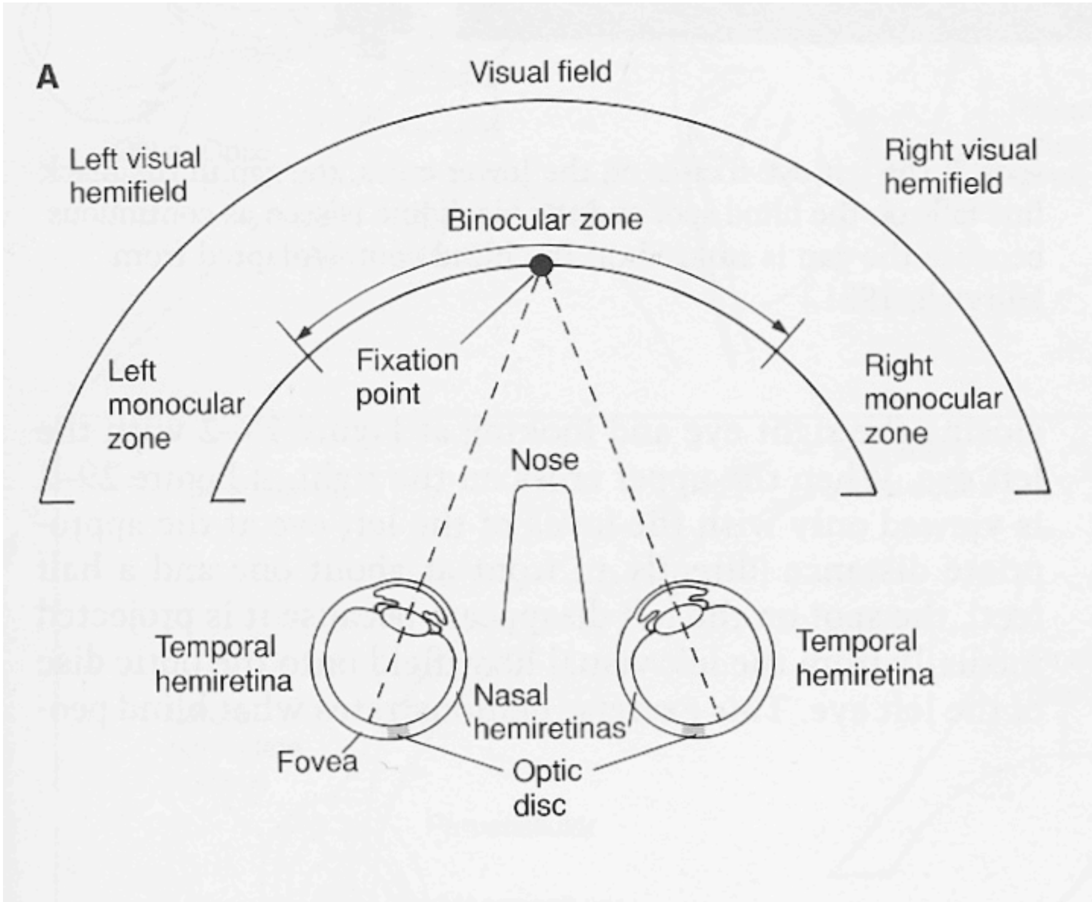
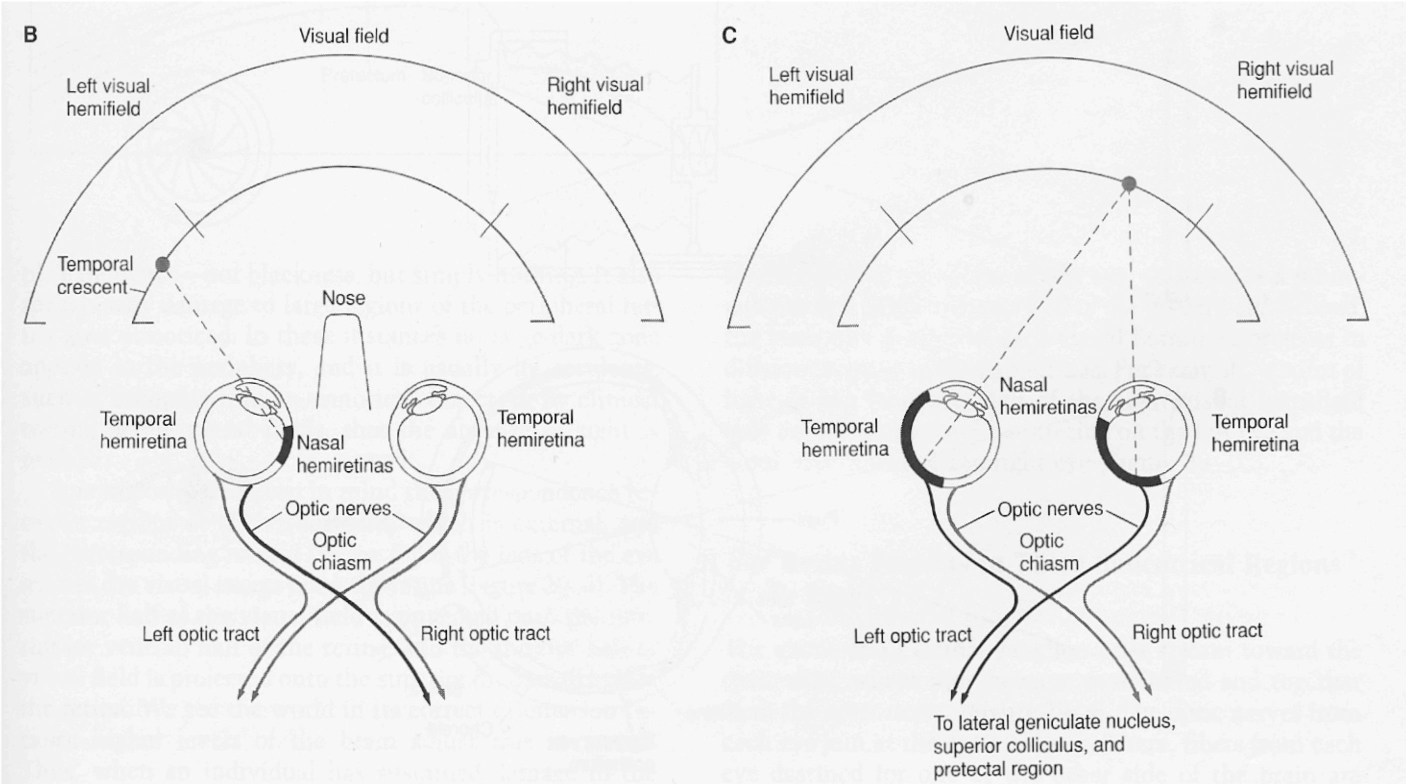
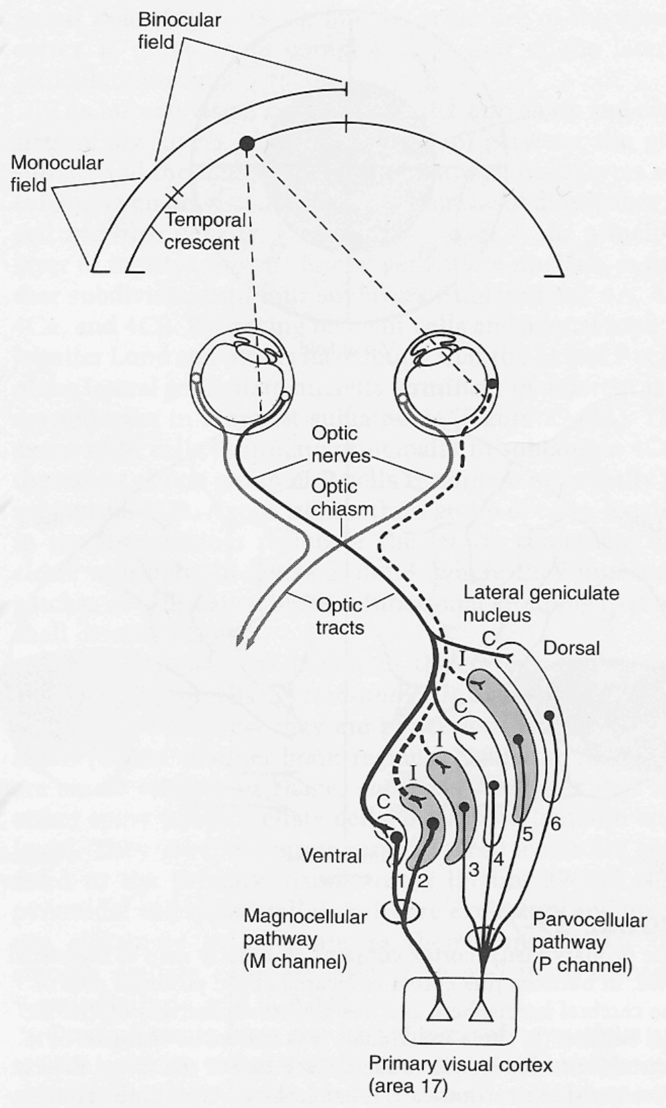
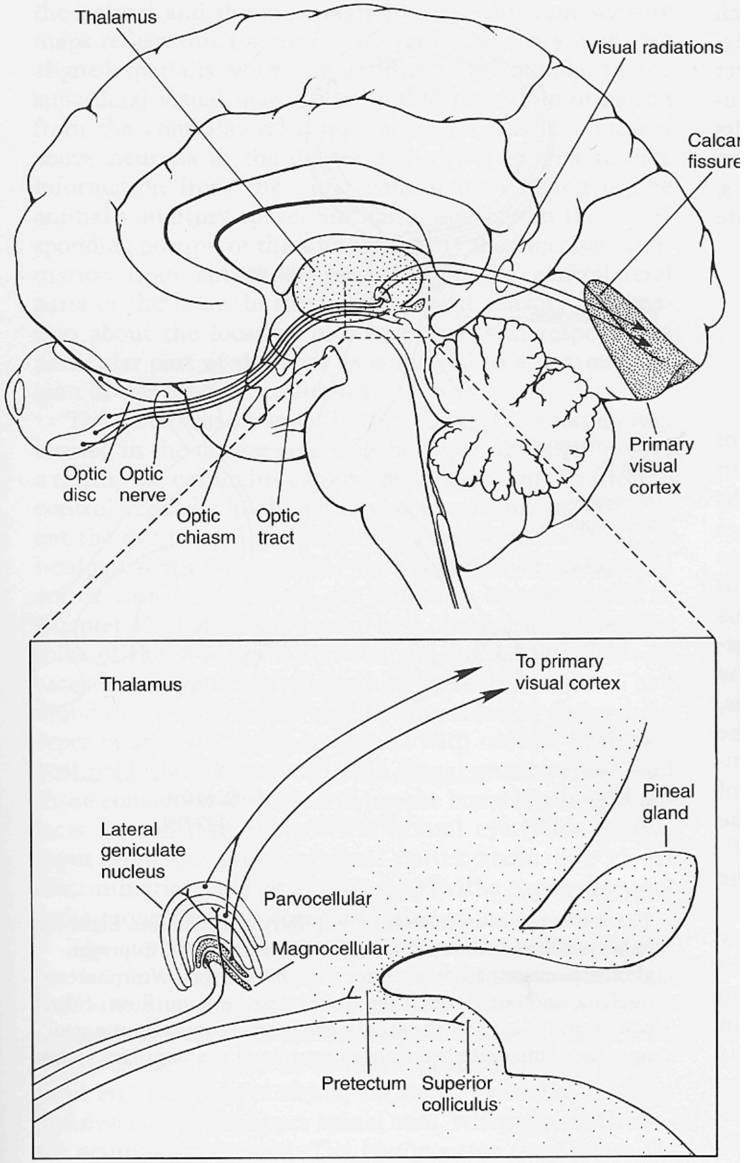
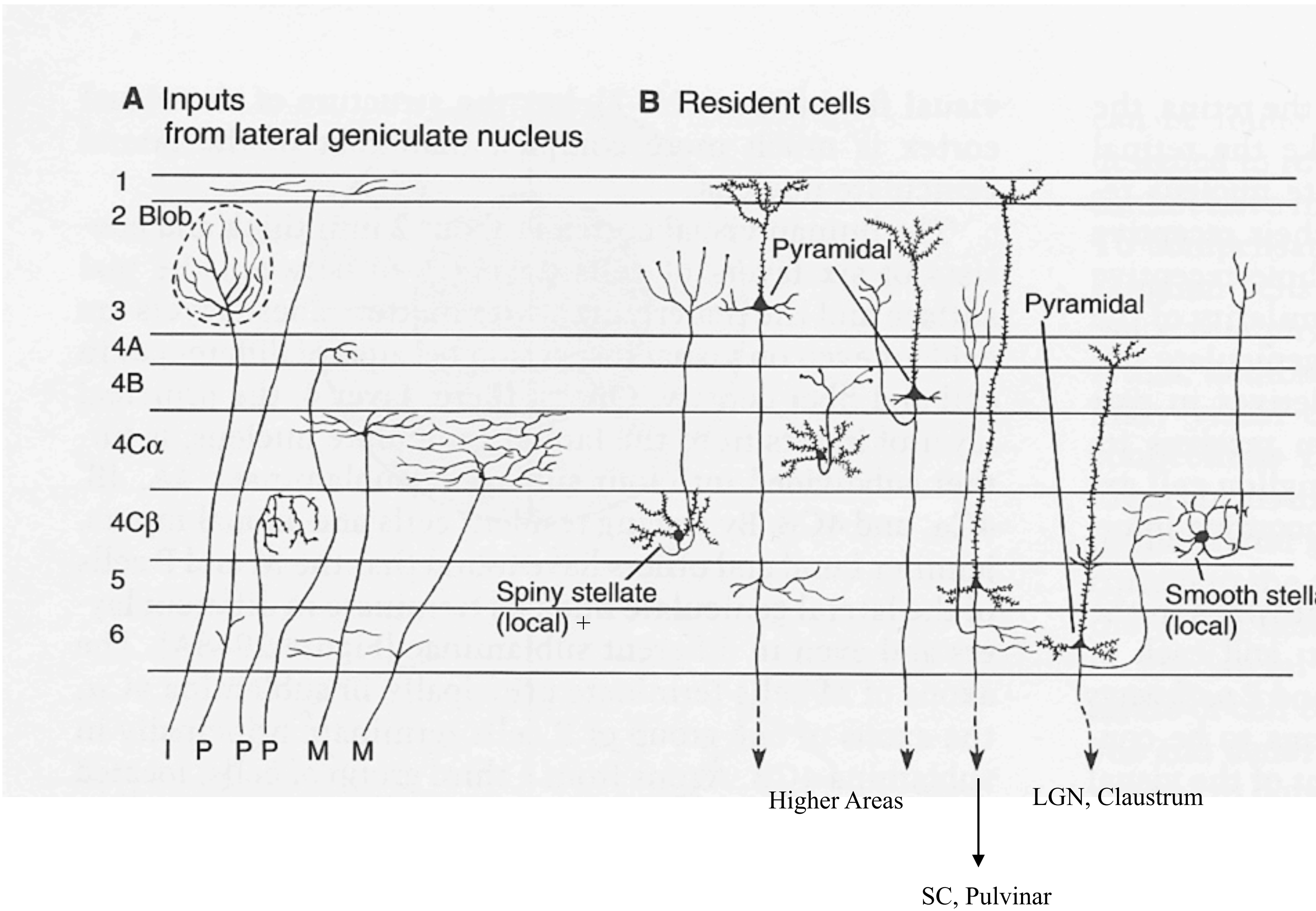

A
Visual field
Left visual hemifield
Right visual hemifield
Binocular zone
Fixation point
Left monocular zone
Right monocular zone
Nose
Temporal hemiretina
Nasal hemiretinas
Temporal hemiretina
Fovea
Optic disc



B
Visual field
Left visual hemifield
Right visual hemifield
Temporal crescent
Nose
Temporal hemiretina
Nasal hemiretinas
Temporal hemiretina
Optic nerves
Optic chiasm
Left optic tract
Right optic tract
C
Visual field
Left visual hemifield
Right visual hemifield
Nasal hemiretinas
Temporal hemiretina
Temporal hemiretina
Optic nerves
Optic chiasm
Left optic tract
Right optic tract
To lateral geniculate nucleus, superior colliculus, and pretectal region


Binocular field
Monocular field
Temporal crescent
Optic nerves
Optic chiasm
Optic tracts
Lateral geniculate nucleus
C
I
Dorsal
Ventral
1
2
3
4
5
6
Magnocellular pathway (M channel)
Parvocellular pathway (P channel)
Primary visual cortex (area 17)


Thalamus
Visual radiations
Calcar
fissure
Primary
visual
cortex
Optic
disc
Optic
nerve
Optic
chiasm
Optic
tract
To primary
visual cortex
Thalamus
Pineal
gland
Lateral
geniculate
nucleus
Parvocellular
Magnocellular
Pretectum
Superior
colliculus



A Inputs
from lateral geniculate nucleus
B Resident cells
1
2 Blob
3
4A
4B
4Cα
4Cβ
5
6
I P P P M M
Pyramidal
Pyramidal
Spiny stellate
(local) +
Smooth stella
(local)
Higher Areas
LGN, Claustrum
SC, Pulvinar

C Local information flow and outputs

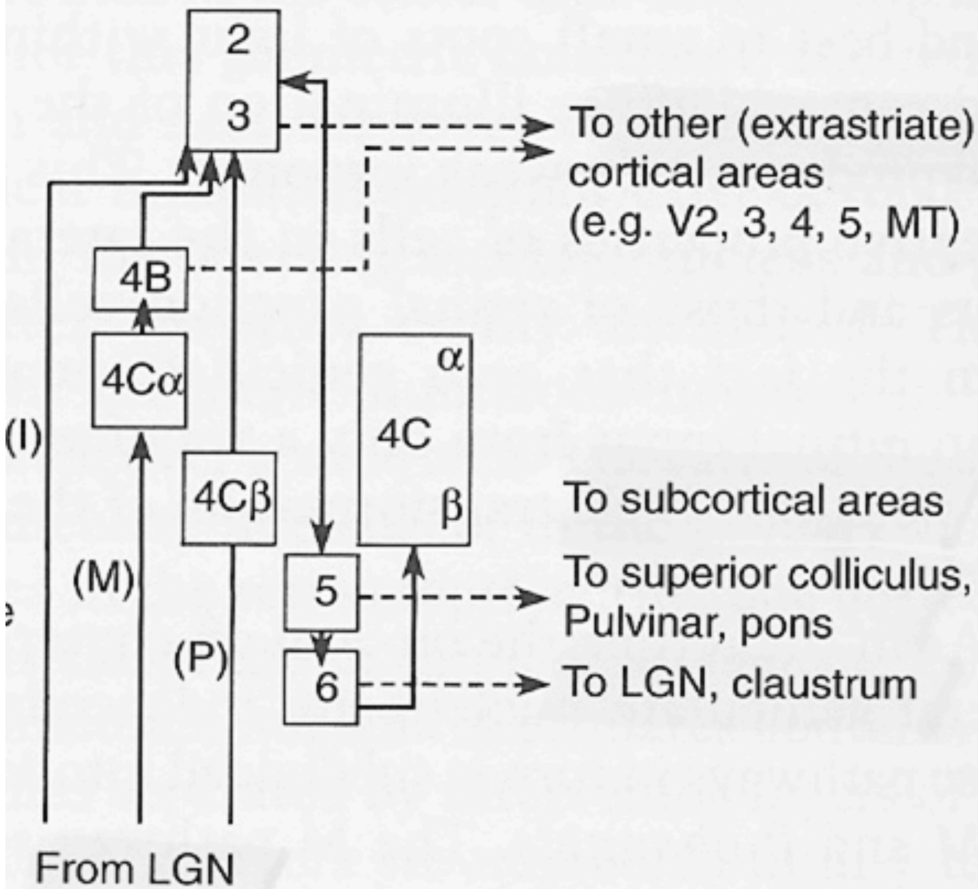
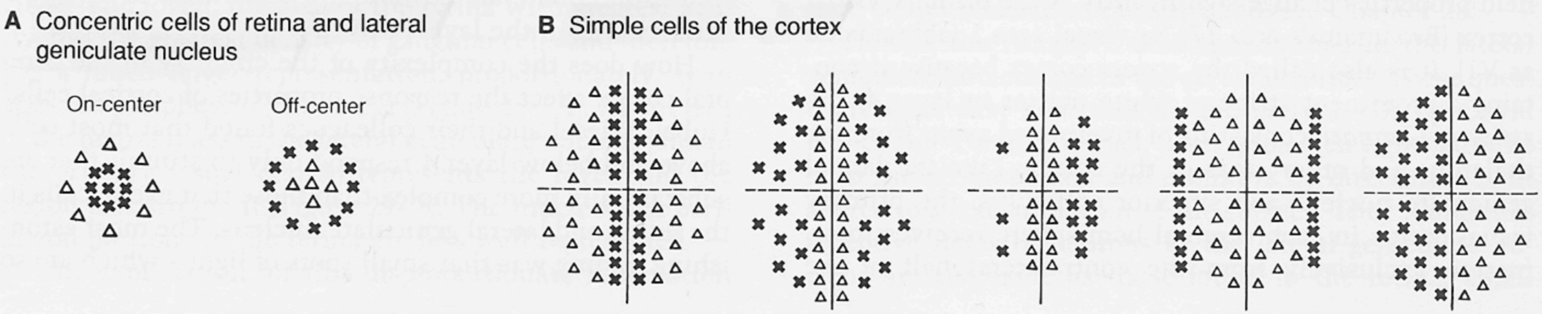


FIGURE 29–9
Comparison of the receptive fields of neurons in the retina and lateral geniculate nucleus with those of simple cells in the primary visual cortex. (Adapted from Hubel and Wiesel, 1962.)

A. Cells of the retina and lateral geniculate nucleus fall into two classes: on-center and off-center (×, excitatory; Δ, inhibitory).

B. Neurons of the primary visual cortex also fall into two major classes, simple and complex, but each of these classes has several subclasses. Several different types of simple cells, all with rectangular receptive fields, are illustrated here. Despite the variety, all simple cells are characterized by three features: (1) specific retinal position, (2) discrete excitatory and inhibitory zones, and (3) a specific axis of orientation. For simplicity, only receptive fields with a vertical axis of orientation (from 12 to 6 o'clock) are shown in this figure. In fact, all axes of orientation—vertical, horizontal, and various obliques—in each region of the retina are represented in the primary visual cortex.



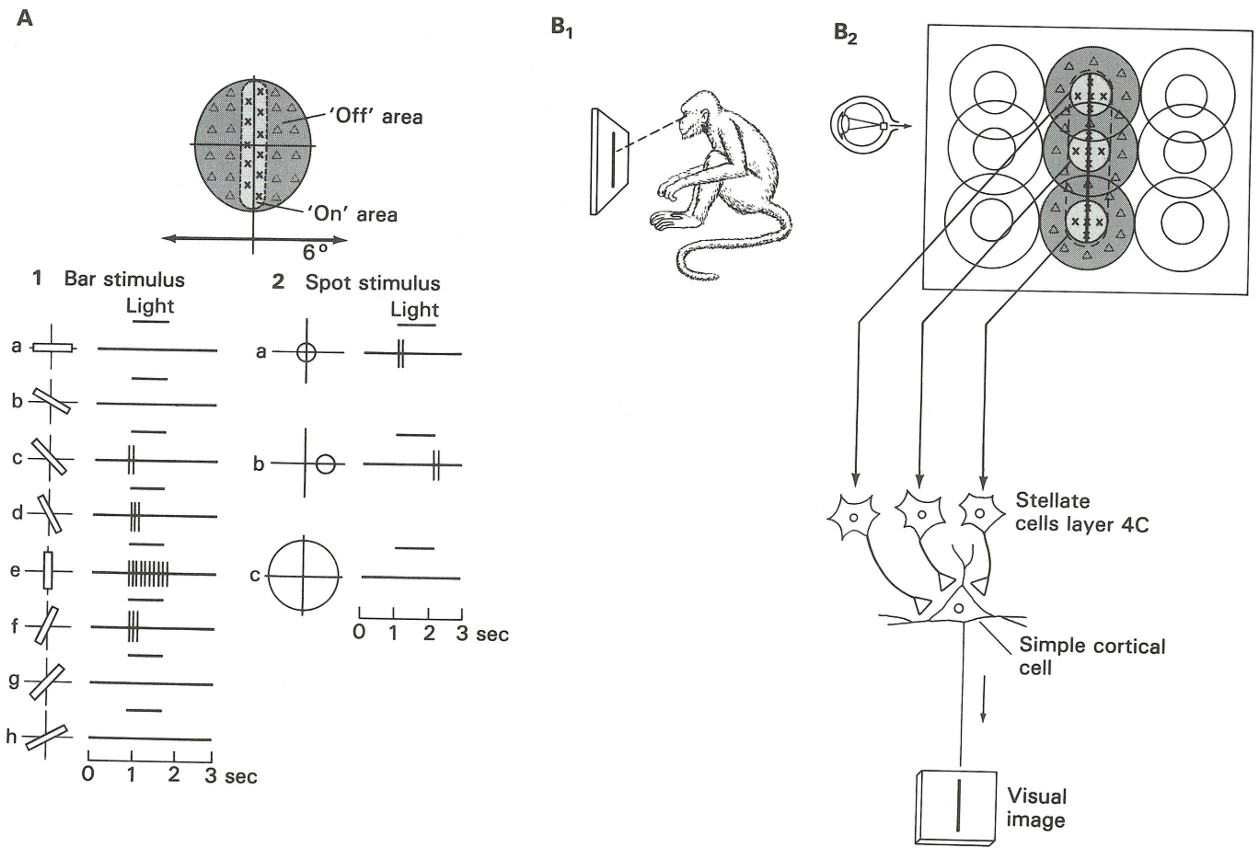
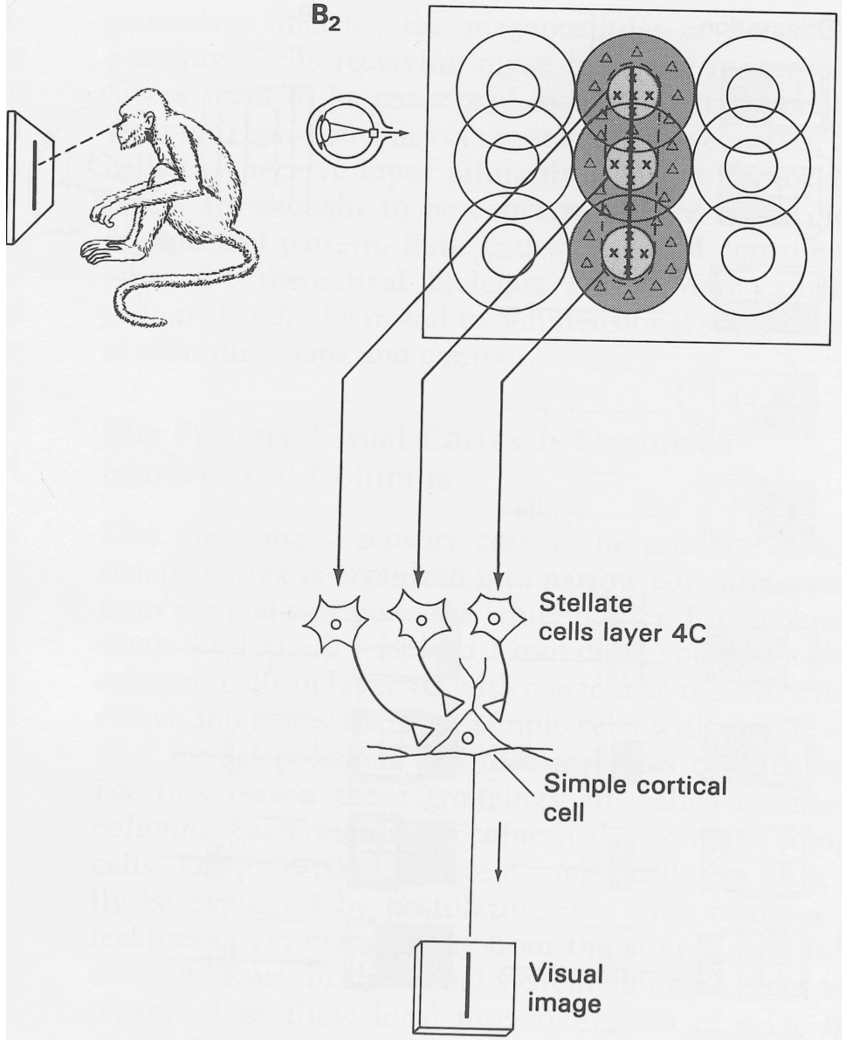


FIGURE 29–10
Receptive field of a simple cell in the primary visual cortex.

A. The receptive field has a narrow rectangular excitatory area (×) in the center flanked by symmetrical inhibitory areas (Δ). The patterns of action potentials fired by the cell in response to two types of stimuli are shown. **1.** The cell's response to a bar of light is strongest if the bar of light (1° × 8°) is vertically oriented in the center of its receptive field. Other orientations (rotated clockwise) are less effective or ineffective. Duration of illumination is indicated by a bar above each record. **2.** Spots of light consistently elicit weak responses or no response. A small spot in the excitatory center of the field **(a)** elicits only a weak excitatory response. A small spot in the inhibitory area **(b)** elicits a weak inhibitory response. Diffuse light **(c)** produces no response. (Adapted from Hubel and Wiesel, 1959.)

B. Model for simple cells. **1.** Arrangement used by Hubel and Wiesel to study simple cells. A monkey faces a target screen on which bars with specific axes of orientation are projected. **2.** The exact process by which the circular receptive fields of geniculate cells are translated to the rectangular fields of simple cells in the visual cortex is not known. According to one idea, illustrated here, a simple cortical neuron in the primary visual cortex receives convergent excitatory connections from three or more stellate cells in layer 4C, each of which have a similar center-surround organization and which together represent light falling along a straight line in the retina. As a result, the receptive field of the simple cortical cell has an elongated excitatory region, indicated by the **dashed outline** in the receptive field diagram. (Adapted from Hubel and Wiesel, 1962.)

B_2



A

B

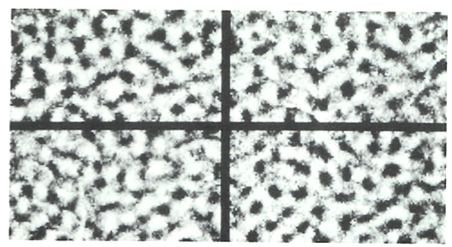
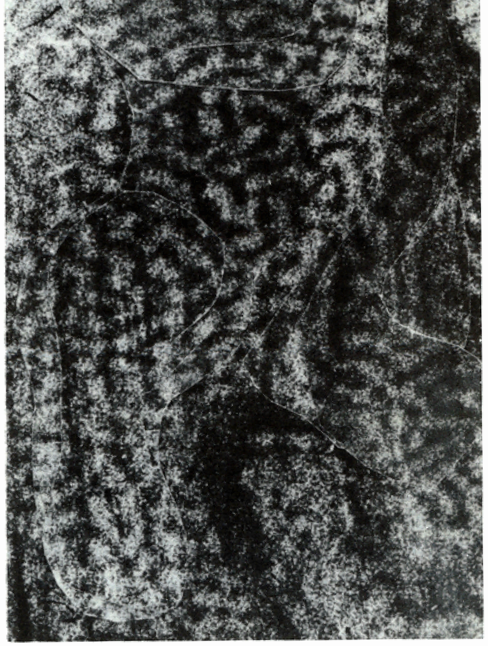


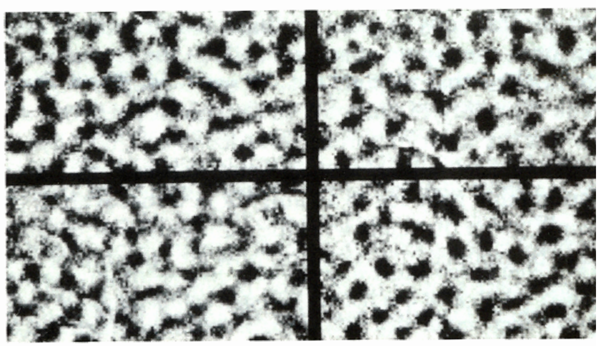
FIGURE 29–12
Orientation columns in the visual cortex.

A. A 2-deoxyglucose visualization of orientation columns in the visual cortex of a monkey binocularly stimulated with vertically oriented lines. Bright areas indicate those neurons responding to the stimulus. The cortex was sectioned tangentially. (From Hubel, Wiesel, and Stryker, 1978.)

B. Images of four different domains in the same cortical area of the primary visual cortex, imaged from the exposed surface of a living monkey brain with a sensitive camera. In each domain the constituent cells had the same axis of orientation. Differences in surface reflectance correspond to differences in the activity of cells. The darker areas correspond to regions of higher activity. Each view represents the pattern of activity occurring during the presentation of gratings having different orientations. (Courtesy of A. Grinvald, C. Gilbert, and R. Frostig.)



B



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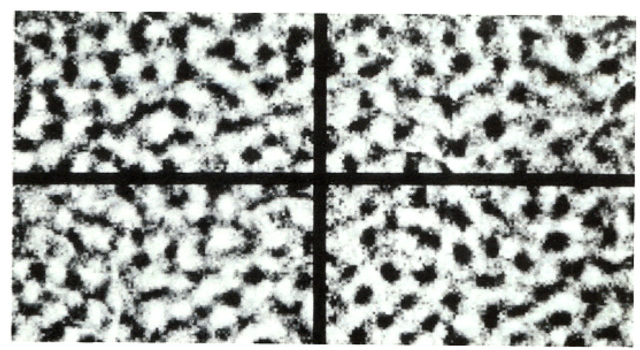
A

B



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vertically oriented lines. Bright areas indicate those neurons

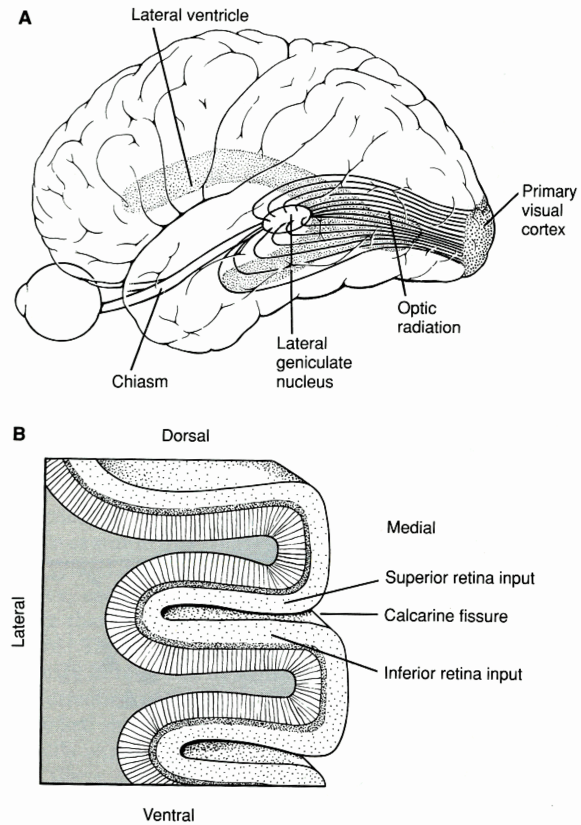


FIGURE 29–17
Projection of the retina and visual fields of the cortex.

A. Course of the fibers in the optic radiation as they sweep around the lateral ventricle to reach the primary visual cortex. Fibers that relay inputs from the inferior retina loop rostrally around the temporal horn of the lateral ventricle, forming Meyer's loop. (Adapted from Brodal, 1981.)

B. A cross section through the primary visual cortex in the occipital lobe. Fibers that relay input from the inferior half of the retina terminate in the inferior bank of the visual cortex; those that relay input from the superior half of the retina terminate in the superior bank.

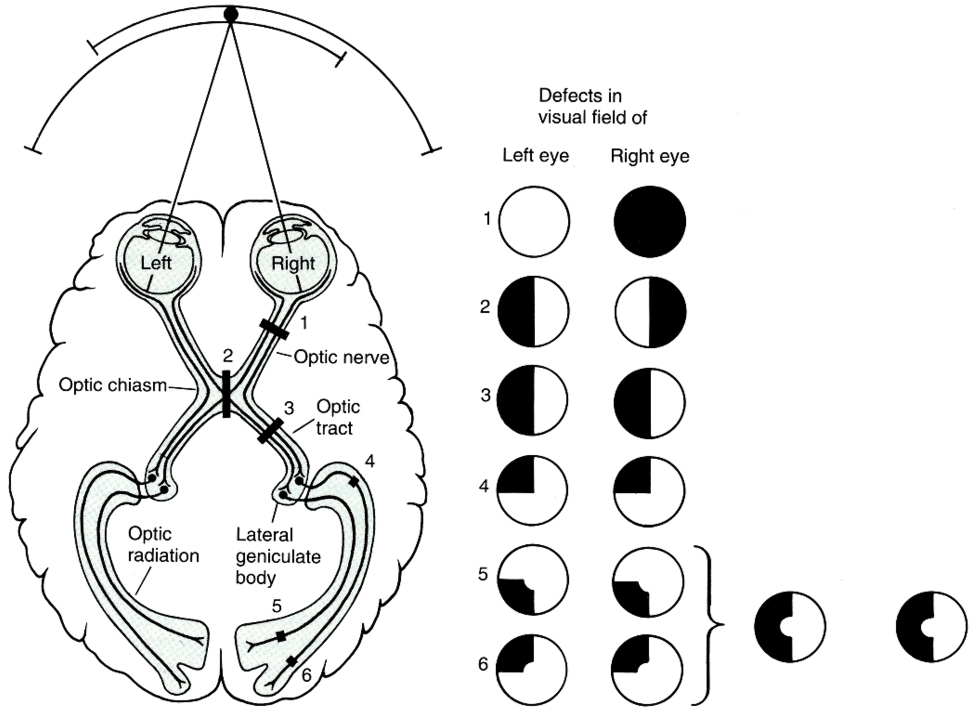


FIGURE 29–18
Visual deficits produced by lesions at various points in the visual pathway. The level of a lesion can be determined by the specific deficit in the visual field. In the diagram of the cortex the **numbers** along the visual pathway indicate the sites of lesions. The visual field deficits that result from lesions at each of these sites are shown in the visual field maps as **dark areas**. Deficits in the visual field of the left eye represent what an individual would see with the right eye closed, not deficits of the left visual hemifield.

1. A lesion of the right optic nerve causes a total loss of vision in the right eye.

2. A lesion of the optic chiasm causes a loss of vision in the temporal halves of both visual fields (bitemporal hemianopsia). Because the chiasm carries crossing fibers from both eyes, this is the only lesion in the visual system that causes a nonhomonymous deficit in vision, a deficit in two *different* parts of the visual field as a consequence of a single lesion.

3. A lesion of the optic tract causes a complete loss of vision in the opposite half of the visual field (contralateral hemianopsia).

4. After leaving the lateral geniculate nucleus the fibers representing both retinas mix in the optic radiation, although this is not indicated in the figure. A lesion of the optic radiation fibers that curve into the temporal lobe (Meyer's loop) causes a loss of vision in the upper quadrant of the opposite half of the visual field of both eyes (upper contralateral quadrantic anopsia).

5–6. Partial lesions of the visual cortex lead to partial field deficits on the opposite side. A lesion in the upper bank of the calcarine sulcus **(5)** causes a partial deficit in the inferior quadrant of the visual field on the opposite side. A lesion in the lower bank of the calcarine sulcus **(6)** causes a partial deficit in the superior quadrant of the visual field of both eyes on the opposite side. A more extensive lesion of the visual cortex, including parts of both banks of the calcarine cortex, would cause a more extensive loss of vision in the contralateral hemifield. The central area of vision, or macular area, is unaffected by cortical lesions (**5 and 6**), probably because the representation of the macula is so extensive that a single lesion is unlikely to destroy the entire representation. The representation of the periphery of the visual field is smaller and hence more easily destroyed by a single lesion.

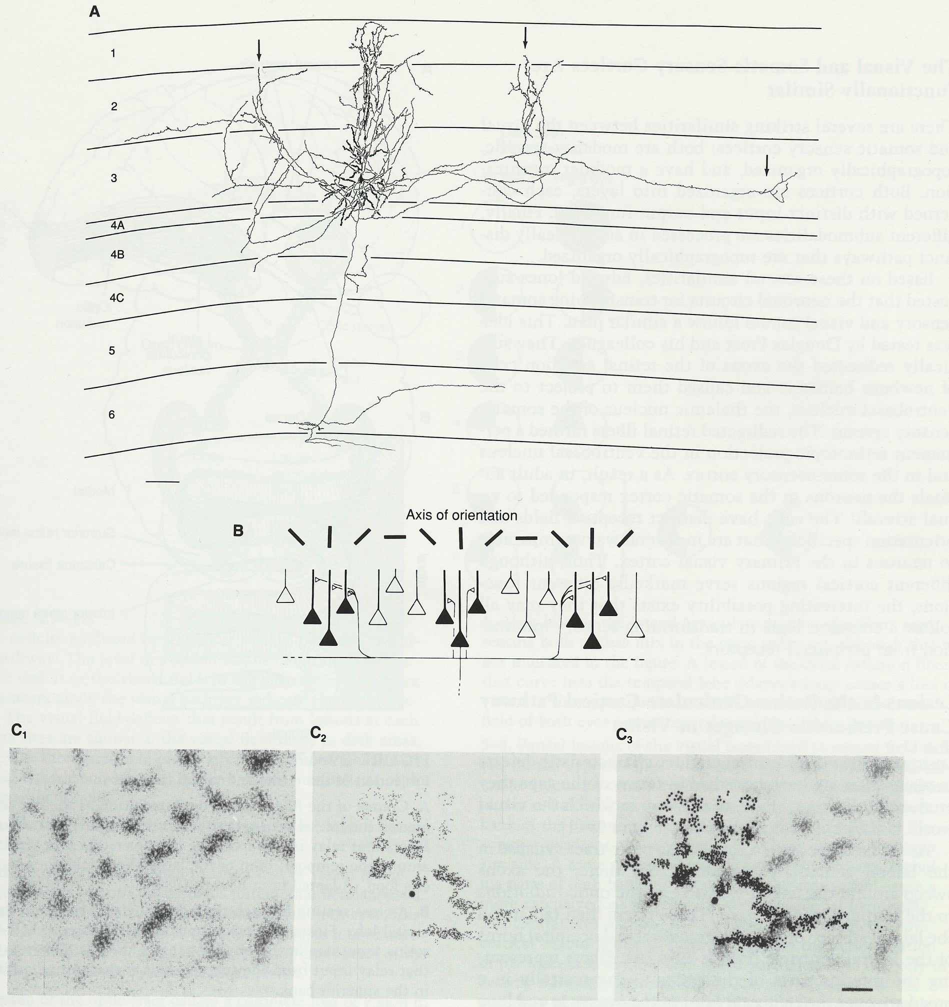
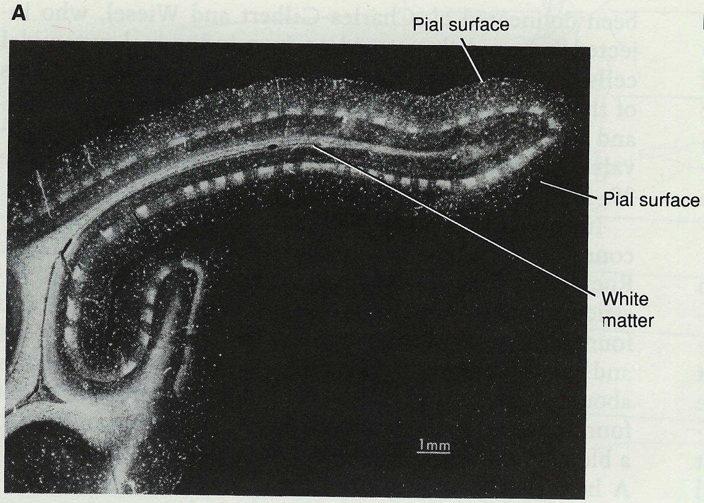


FIGURE 29–16
Columnar cell systems with similar function are linked through horizontal connections.

A. A camera lucida reconstruction of a pyramidal cell injected with horseradish peroxidase in layers 2–3 of V1 in a monkey. Several axon collaterals **(arrows)** branch off the descending axon and ramify near the dendritic tree and in three other clusters in layers 2 and 3. The clusters project horizontally and are given off at intervals, extending vertically into several layers. This collateral system is thought to interconnect cells in different cortical columns with similar functional properties. (From McGuire et al., 1990.)

B. The functional specificity of the long-range clustered horizontal connections, as demonstrated by cross-correlation analysis. The axon of one pyramidal cell, in the center of the diagram, synapses on other pyramidal cells in the immediate vicinity as well as pyramidal cells some distance away. The axon makes connections only with cells with the same functional specificity. (Adapted from Ts'o, Gilbert, and Wiesel, 1986.)

C. Combined 2-deoxyglucose and fluorescent-bead labeling within area 17 demonstrate that cells in different columns responding to the stimulus of the same orientation are anatomically linked. **1.** A section of cortex labeled with 2-deoxyglucose shows a pattern of stripes after presentation of a stimulus with a particular orientation. **2.** Microbeads injected into the recording site are taken up by cell bodies through retrograde transport. Reconstruction of the distribution of bead-labeled cells in the same region is visualized in the same section. **3.** Superimposition of 1 and 2. The clusters of bead-labeled cells lie directly over the deoxyglucose-labeled areas, showing that groups of cells in different columns having the same axis of orientation are connected. Scale bar = 1 μm. (From Gilbert and Wiesel, 1989.)



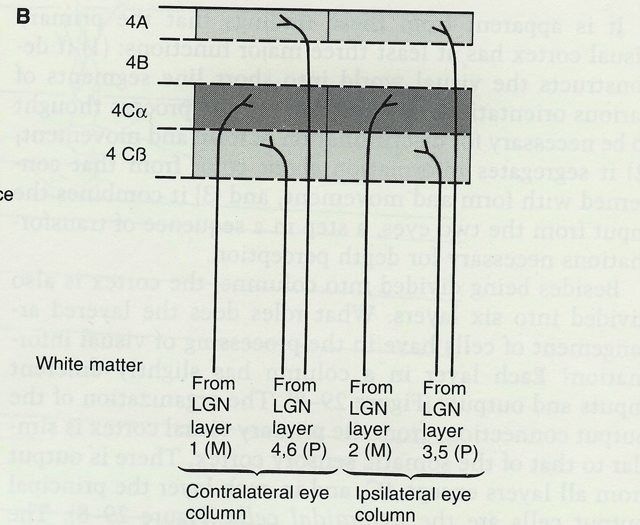


FIGURE 29–14
The ocular dominance columns.

A. This autoradiograph of the primary visual cortex in an adult monkey demonstrates the input from the lateral geniculate nucleus to the cortex. Labeling was achieved by injection of tritiated proline and fucose in the ipsilateral eye 2 weeks before. The label was transported to the lateral geniculate nucleus, then crossed synapses to the geniculocortical relay cells, whose axons terminate in layer 4 of the visual cortex. Areas that receive input from the injected eye are heavily labeled and appear white, and alternate with adjacent unlabeled patches that receive input from the uninjected eye. In all, some 56 columns can be counted in layer 4C. This section cuts through the gray matter of the cortex twice. Beginning at the pial surface (**top** of the figure) the section then goes through the gray matter and reaches layer 4, where the patches of label appear as bright bands. The section goes deeper through the gray matter to the underlying white matter, where labeled axons are evident. The section continues through the gray matter on the opposite side of the gyrus, through another band of columns in layer 4, and then reaches the pial surface. (From Hubel and Wiesel, 1979.)

B. Schematic representation of the projection from each eye through the lateral geniculate nucleus to the ocular dominance columns in subdivisions of layer 4 of the visual cortex. (See Figures 29–6 and 29–8.)

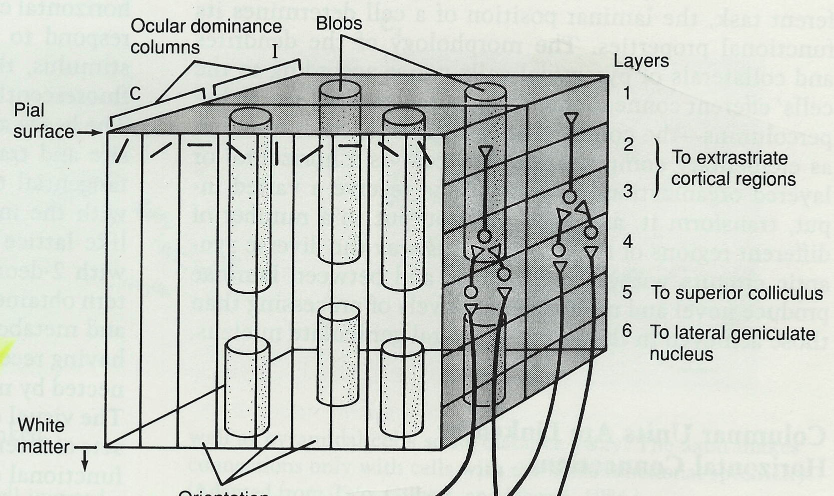


FIGURE 29–15
Small regions of the visual field are analyzed in the primary visual cortex by an array of complex cellular units called *hypercolumns*. A single hypercolumn represents the neural machinery necessary to analyze a discrete region of the visual field. Each contains a complete set of orientation columns, representing 360°, a set of left and right ocular dominance columns, and several blobs, regions of the cortex in which the cells are specific for color.

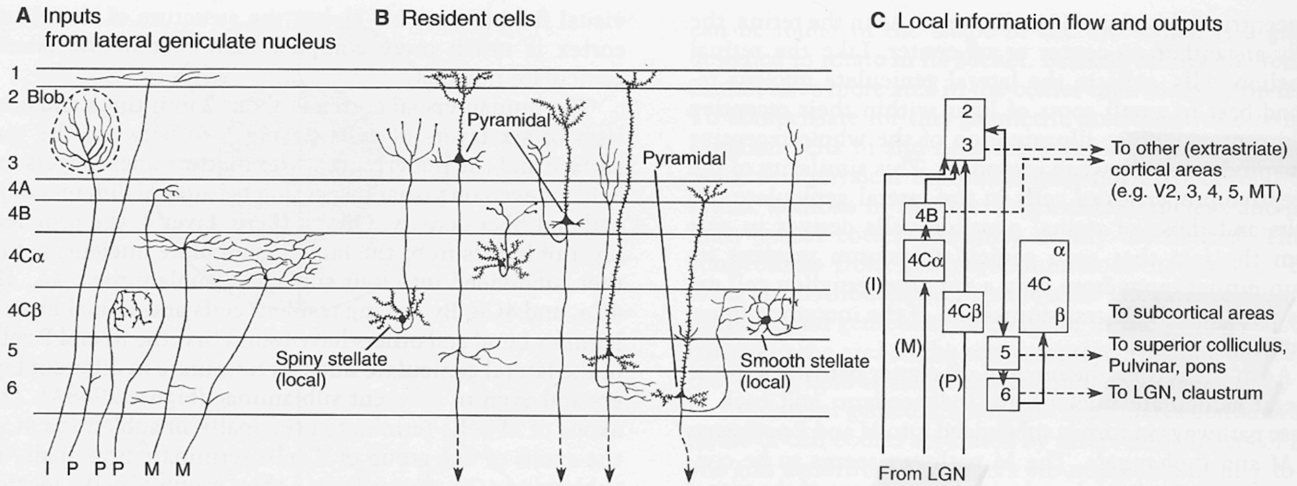


FIGURE 29–8

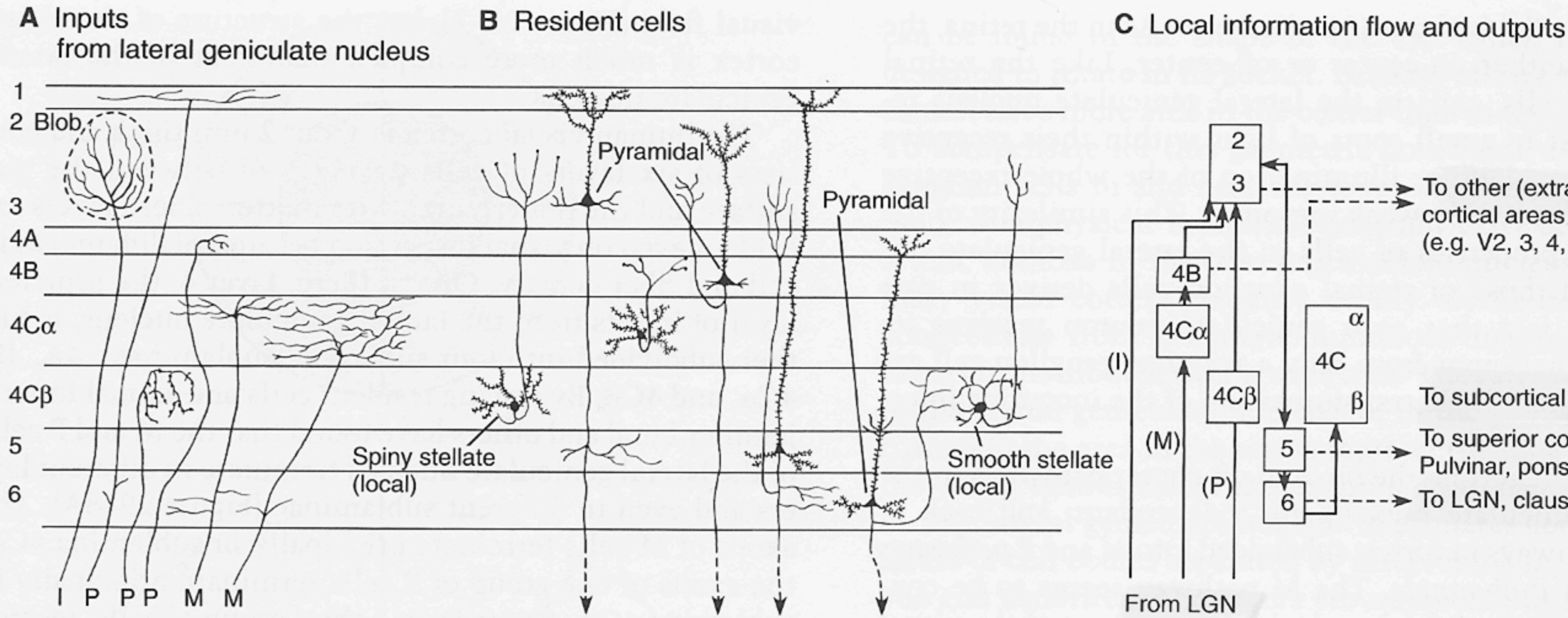
The primary visual cortex has distinct anatomical layers, each with characteristic synaptic connections.

A. Most afferent fibers from the lateral geniculate nucleus terminate in layer 4. Axons of type P cells (in the parvocellular layers) terminate primarily in layer 4Cβ, with minor inputs to 4A and 1, while axons from type M cells (in the magnocellular layer) terminate primarily in layer 4Cα. Collaterals of both types of cells also terminate in layer 6. Cells of the intralaminar regions of the lateral geniculate nucleus terminate in layers 2 and 3.

B. Several types of resident neurons make up the primary visual cortex. Spiny stellate and pyramidal cells, both of which have spiny dendrites, are excitatory. Smooth stellate cells are inhibitory. Pyramidal cells project out of the cortex, whereas both types of stellate cells are local neurons.

C. Afferents from M and P cells in the lateral geniculate nucleus end on spiny stellate cells in layer 4C, and these cells project axons to layer 4B and the upper layers 2 and 3. Cells from the interlaminar zones (**I**) in the lateral geniculate nucleus project directly to layers 2 and 3. From there, pyramidal cells project axon collaterals to layer 5 pyramidal cells, whose axon collaterals project both to layer 6 pyramidal cells as well as back to cells in layers 2 and 3. Axon collaterals of layer 6 pyramidal cells then make a loop back to layer 4C onto smooth stellate cells. Each layer, except for 4C, has different outputs. The cells in layers 2, 3, and 4B project to higher visual cortical areas. Cells in layer 5 project to the superior colliculus, the pons, and the pulvinar. Cells in layer 6 project back to the lateral geniculate nucleus and the claustrum. (Adapted from Lund, 1988.)

END OF V1 LECTURE



A Inputs
from lateral geniculate nucleus
1
2 Blob
3
4A
4B
4Cα
4Cβ
5
6
I P P P M M
B Resident cells
Pyramidal
Pyramidal
Spiny stellate
(local)
Smooth stellate
(local)
C Local information flow and outputs
2
3
4B
4Cα
4Cβ
4C
α
β
5
6
(I)
(M)
(P)
From LGN
To other (extra
cortical areas
(e.g. V2, 3, 4,
To subcortical
To superior co
Pulvinar, pons
To LGN, claus

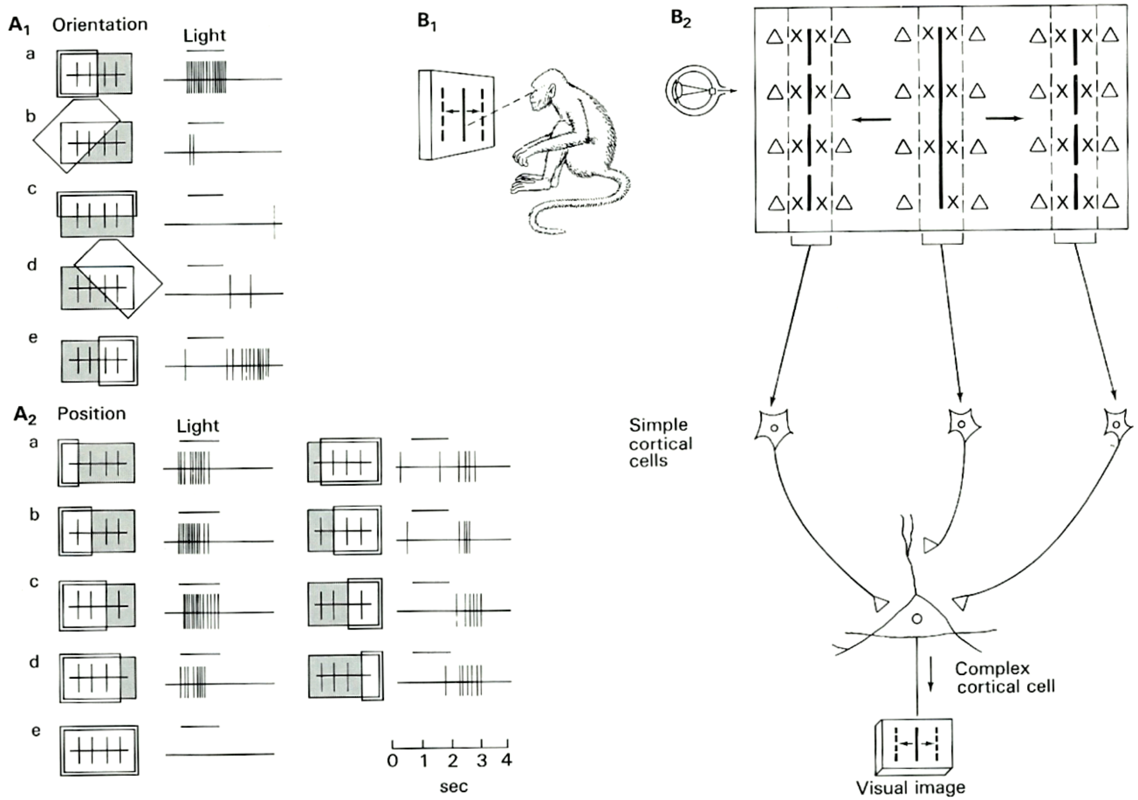


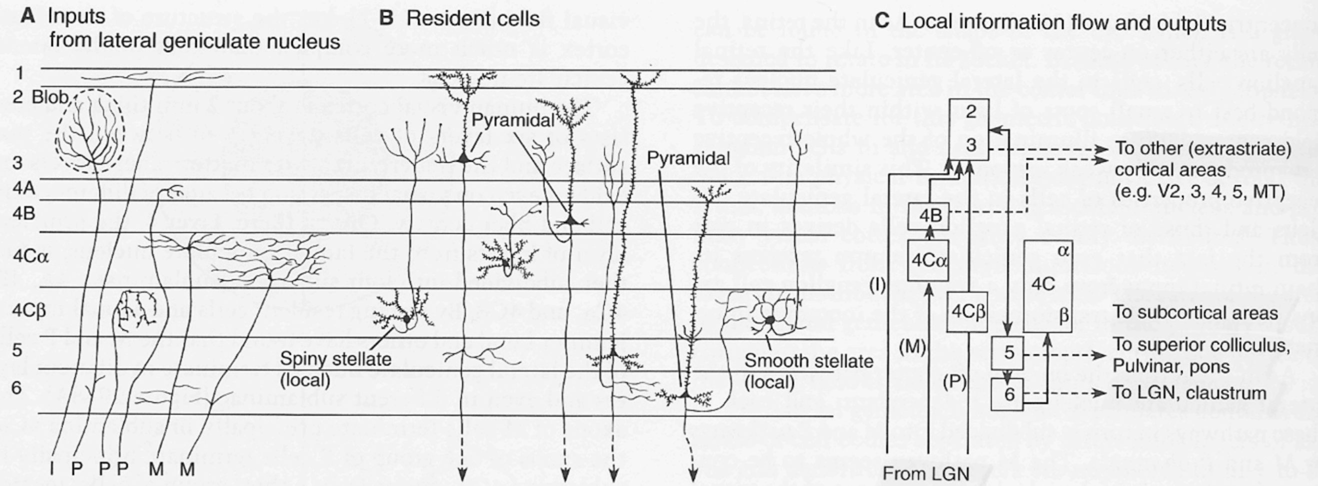
FIGURE 29–11

The receptive field of a complex cell in the primary visual cortex has no clearly distinct 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. **1.** Different orientations of the light stimulus produce different rates of firing in the cell. (The bar above each record indicates duration of illumination.) Light on the left and dark on the right produces a strong excitatory response (**a**). Light on the right produces an inhibitory response (**e**). Orientation other than vertical is less effective. **2.** The position of the border of the light within the field affects the type of response in the cell. If the edge of the light comes from any point on the right within the field, the stimulus produces an excitatory response. If the edge comes from the left, the stimulus produces an inhibitory response (**a–d**). Illumination of the entire receptive field produces no response (**e**).

B. Model for complex cells. **1.** Arrangement used to study complex cells as in Figure 29–10. **2.** According to Hubel and Wiesel, the properties of complex receptive fields may be explained by the pattern of input. A complex cortical neuron with a vertical orientation receives convergent excitatory input from several simple cortical cells, each of which has a vertical axis of orientation, a central excitation zone (×), and two flanking inhibitory regions (Δ), and thus represent light falling along a straight line in the retina. The receptive field of the complex cell is built up from the individual fields of the presynaptic cells.

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. The temporal crescent is not represented in contralateral inputs (see Figure 29–1B). Layers 1 and 2 comprise the magnocellular layers; layers 4 through 6 comprise the parvocellular layers. All of these project to area 17, the primary visual cortex. There are major pathways from the retina through the lateral geniculate nucleus to area 17 of the cortex, which process, in parallel, different aspects of visual information. As we shall learn in the next chapter, three major parallel pathways have been identified: one magnocellular and two parvocellular pathways. The first is concerned primarily with movement and gross features of the stimulus; the second primarily carries information on detail and form; the third is concerned with color.



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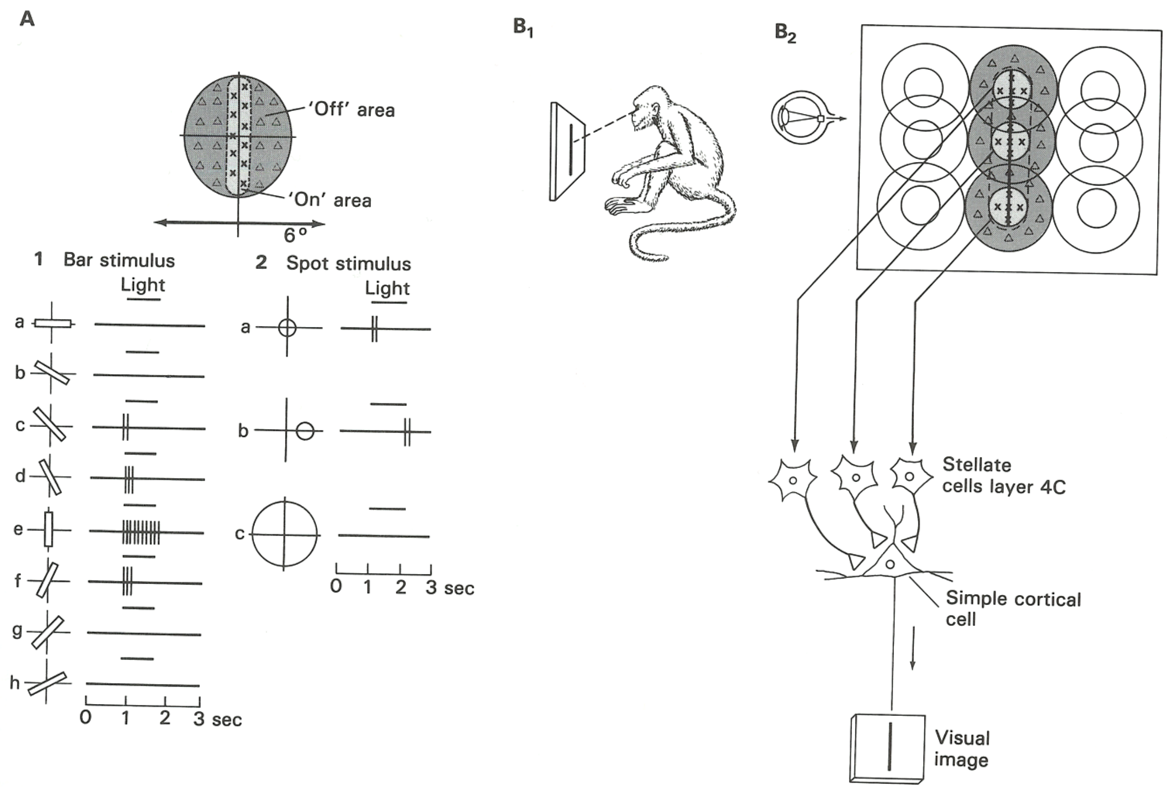

FIGURE 29–10
Receptive field of a simple cell in the primary visual cortex.

A. The receptive field has a narrow rectangular excitatory area (×) in the center flanked by symmetrical inhibitory areas (Δ). The patterns of action potentials fired by the cell in response to two types of stimuli are shown. **1.** The cell's response to a bar of light is strongest if the bar of light (1° × 8°) is vertically oriented in the center of its receptive field. Other orientations (rotated clockwise) are less effective or ineffective. Duration of illumination is indicated by a bar above each record. **2.** Spots of light consistently elicit weak responses or no response. A small spot in the excitatory center of the field **(a)** elicits only a weak excitatory response. A small spot in the inhibitory area **(b)** elicits a weak inhibitory response. Diffuse light **(c)** produces no response. (Adapted from Hubel and Wiesel, 1959.)

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