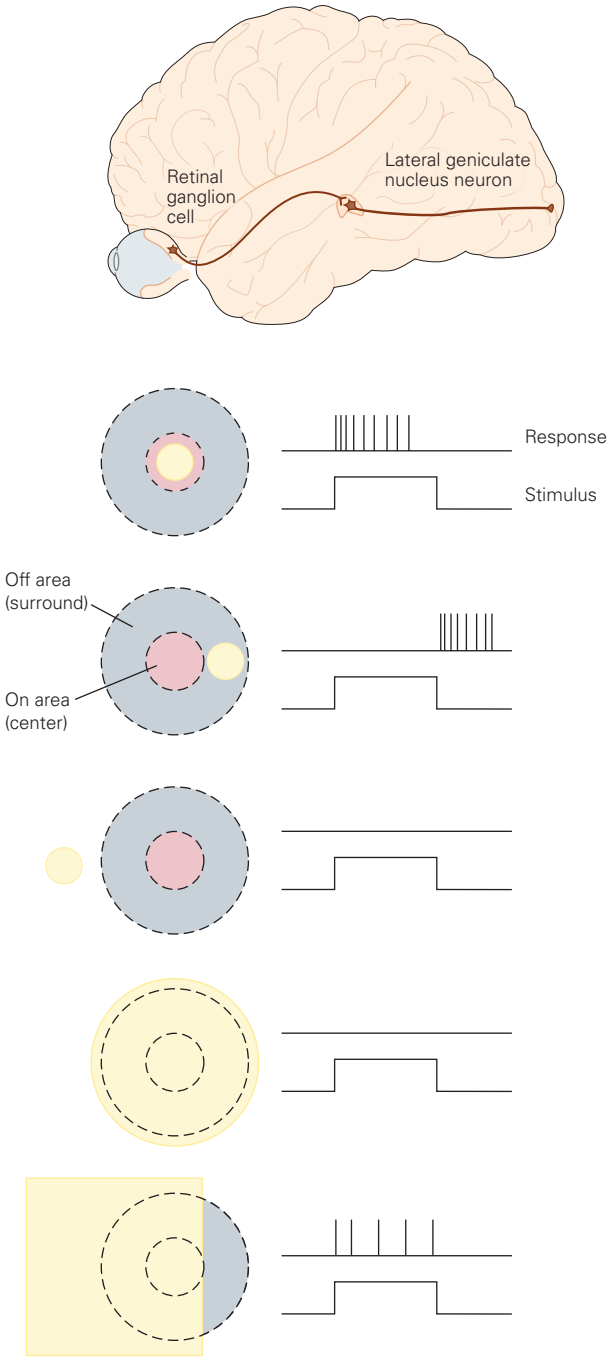


Figure 21–9 Receptive fields of neurons at early relays of visual pathways. A circular symmetric receptive field with mutually antagonistic center and surround is characteristic of retinal ganglion cells and neurons in the lateral geniculate nucleus of the thalamus. The center can respond to the turning on or turning off of a spot of light (**yellow**) depending on whether the receptived field belongs to an "on-center" or "off-center" class, respectively. The surround has the opposite response. Outside the surround, there is no response to light, thus defining the receptive field boundary. The response is weak when light covers both the center and surround, so these neurons respond optimally to contrast (a light–dark boundary) in the visual field.

while studying what visual stimuli provoked activity in neurons in the primary visual cortex. While showing an anesthetized animal slides containing a variety of images, they recorded extracellularly from individual neurons in the visual cortex. As they switched from one slide to another, they found a neuron that produced a brisk train of action potentials. The cell was responding not to the image on the slide but to the edge of the slide as it was moved into position.

The Visual Cortex Is Organized Into Columns of Specialized Neurons

The dominant feature of the functional organization of the primary visual cortex is the visuotopic organization of its cells: the visual field is systematically represented across the surface of the cortex (Figure 21–11A).

In addition, cells in the primary visual cortex with similar functional properties are located close together in columns that extend from the surface of the cortex to the white matter. The columns are concerned with the functional properties that are analyzed in any given cortical area and thus reflect the functional role of that area in vision. The properties that are developed in the primary visual cortex include orientation specificity and the integration of inputs from the two eyes, which is measured as the relative strength of input from each eye, or ocular dominance.

Ocular-dominance columns reflect the segregation of thalamocortical inputs arriving from different layers of the LGN. Alternating layers of this nucleus receive input from retinal ganglion cells located in either the ipsilateral or contralateral retina (Figure 21–12). This segregation is maintained in the inputs from the LGN to the primary visual cortex, producing the alternating left-eye and right-eye ocular dominance bands (Figure 21–11B).

Cells with similar orientation preferences are also grouped into columns. Across the cortical surface, there is a regular clockwise and counterclockwise cycling of orientation preference, with the full 180° cycle repeating every 750 µm (Figure 21–11C). Likewise, the left- and right-eye dominance columns alternate with a periodicity of 750 to 1,000 µm. One full cycle of orientation columns, or a full pair of left- and right-eye dominance columns, is called a *hypercolumn*. The orientation and ocular dominance columns at each point on the cortical surface are locally roughly orthogonal to each other. Thus, a cortical patch one hypercolumn in extent contains all possible combinations of orientation preference and left- and right-eye dominance.

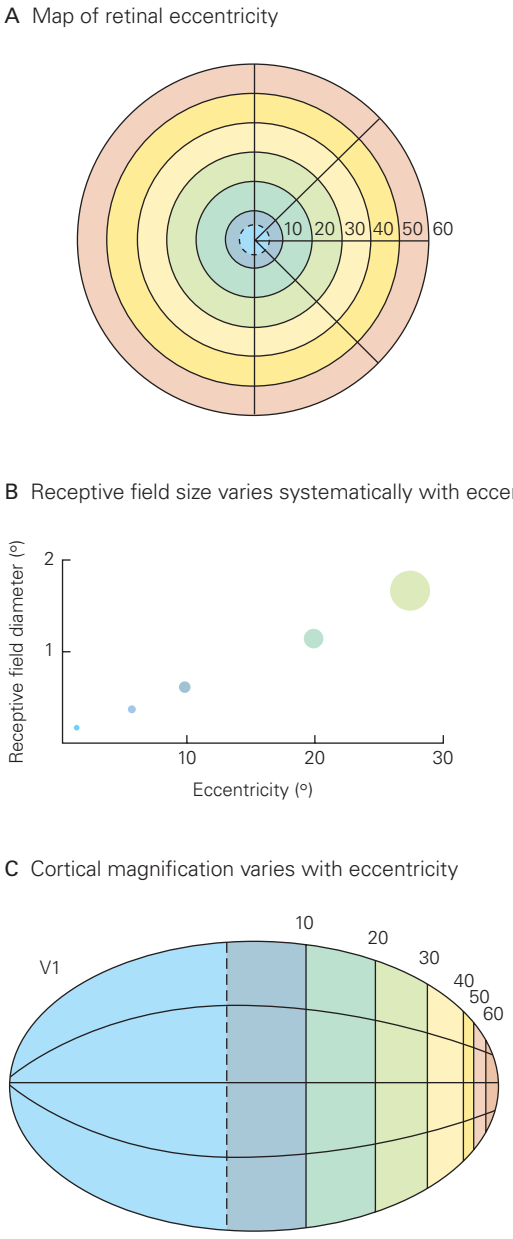


Figure 21–10 **Receptive field size, eccentricity, retinotopic organization, and magnification factor.** The color code refers to position in visual space or on the retina.

A. The distance of a receptive field from the fovea is referred to as the eccentricity of the receptive field.

B. Receptive field size varies with distance from the fovea. The smallest fields lie in the center of gaze, the fovea, where the visual resolution is highest; fields become progressively larger with distance from the fovea.

C. The amount of cortical area dedicated to inputs from within each degree of visual space, known as the magnification factor, also varies with eccentricity. The central part of the visual field commands the largest area of cortex. For example, in area V1, more area is dedicated to the central 10° of visual space than to all the rest. The map of V1 shows the cortical sheet unfolded.

Both types of columns were first mapped by recording the responses of neurons at closely spaced electrode penetrations in the cortex. The ocular-dominance columns were also identified by making lesions or tracer injections in individual layers of the LGN. More recently, a technique known as optical imaging has enabled researchers to visualize a surface representation of the orientation and ocular dominance columns in living animals. Developed for studies of cortical organization by Amiram Grinvald, this technique visualizes changes in surface reflectance associated with the metabolic requirements of active groups of neurons, known as intrinsic-signal optical imaging, or changes in fluorescence of voltage-sensitive dyes. Intrinsic-signal imaging depends on activity-associated changes in local blood flow and alterations in the oxidative state of hemoglobin and other intrinsic chromophores. These techniques are also now being complemented with imaging at cellular resolution using genetically encoded markers of neural activity.

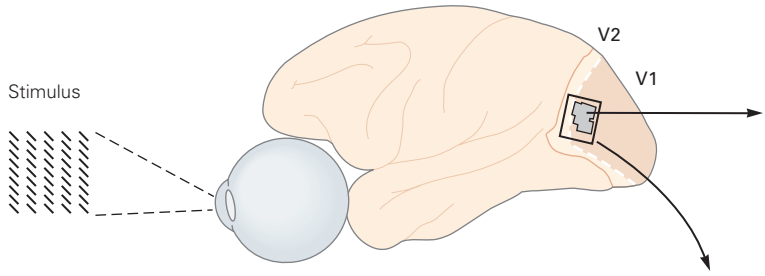
An experimenter can visualize the distribution of cells with left or right ocular dominance, for example, by subtracting the image obtained while stimulating one eye from that acquired while stimulating the other. When viewed in a plane tangential to the cortical surface, the ocular dominance columns appear as alternating left- and right-eye stripes, each approximately 750 µm in width (Figure 21–11B).

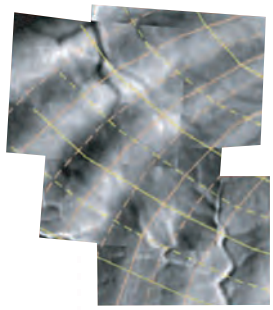
The cycles of orientation columns form various structures, from parallel stripes to pinwheels. Sharp jumps in orientation preference occur at the pinwheel centers and "fractures" in the orientation map (Figure 21–11C).

Embedded within the orientation and ocular-dominance columns are clusters of neurons that have poor orientation selectivity but strong color preferences. These units of specialization, located within the superficial layers, were revealed by a histochemical label for the enzyme cytochrome oxidase, which is distributed in a regular patchy pattern of blobs and interblobs. In the primary visual cortex, these blobs are a few hundred micrometers in diameter and 750 µm apart (Figure 21–11D). The blobs correspond to clusters of color-selective neurons. Because they are rich in cells with color selectivity and poor in cells with orientation selectivity, the blobs are specialized to provide information about surfaces rather than edges.

In area V2, thick and thin dark stripes separated by pale stripes are evident with cytochrome oxidase labeling (Figure 21–11D). The thick stripes contain neurons selective for direction of movement and for binocular disparity as well as cells that are responsive to illusory contours and global disparity cues. The thin stripes hold cells specialized for color. The pale stripes contain orientation-selective neurons.

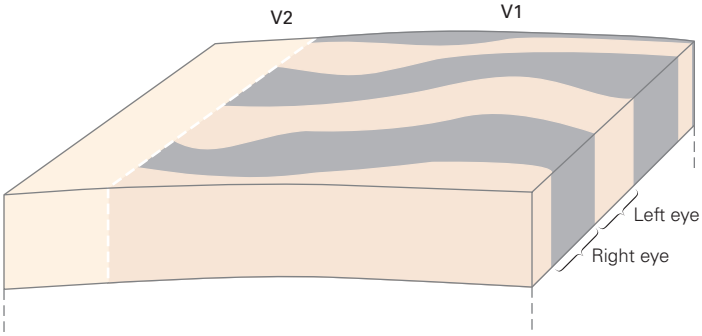
A Visuotopic map

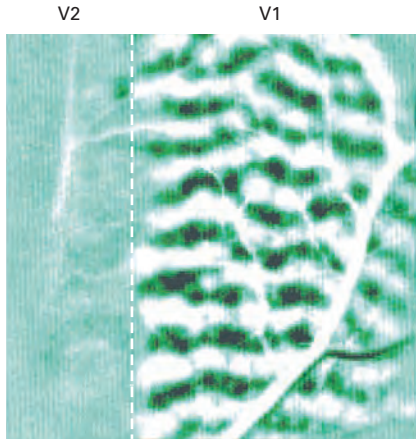




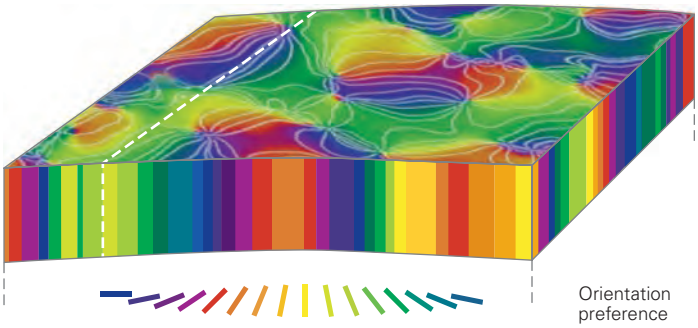
Pattern of excitation in response to striped stimulus

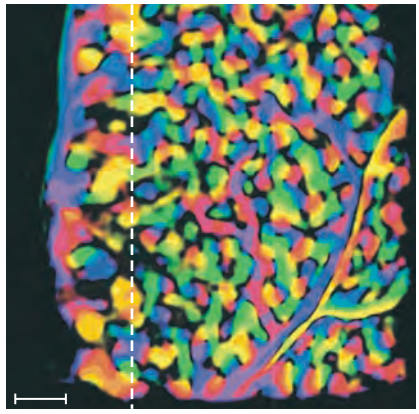
B Ocular dominance columns



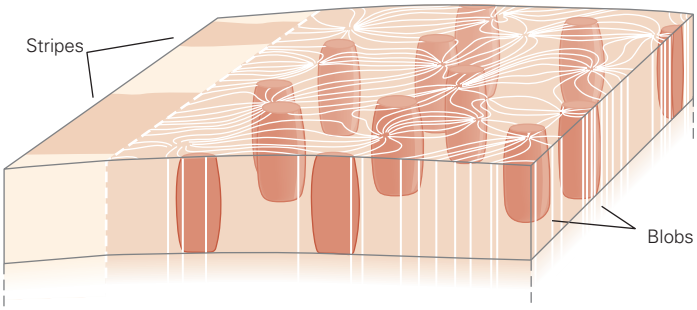


C Orientation columns





D Blobs, interblobs (V1), and stripes (V2)



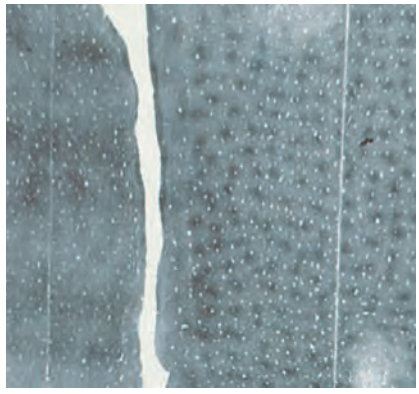


Figure 21–11 (Opposite) **Functional architecture of the primary visual cortex.** (Courtesy of M. Kinoshita and A. Das, reproduced with permission.)

A. The surface of the primary visual cortex is functionally organized as a map of the visual field. The elevations and azimuths of visual space are organized in a regular grid that is distorted because of variation in the magnification factor (see Figure 21–10). The grid is visible here in the dark stripes (visualized with intrinsic-signal optical imaging), which reflect the pattern of neurons that responded to a series of vertical candy stripes. Within this surface map, one finds repeated superimposed cycles of functionally specific columns of cells, as illustrated in **B**, **C**, and **D**.

B. The dark and light stripes represent the surface view of the left and right ocular dominance columns. These stripes intersect the border between areas V1 and V2, the representation of the vertical meridian, at right angles.

C. Some columns contain cells with similar selectivity for the orientation of stimuli. The different colors indicate the orientation preference of the columns. The orientation columns in surface view are best described as pinwheels surrounding singularities of sudden changes in orientation (the center of the pinwheel). The scale bar represents 1 mm. (Surface image of orientation columns on the left courtesy of G. Blasdel, reproduced with permission.)

D. Patterns of blobs in V1 and stripes in V2 represent other modules of functional organization. These patterns are visualized with cytochrome oxidase.

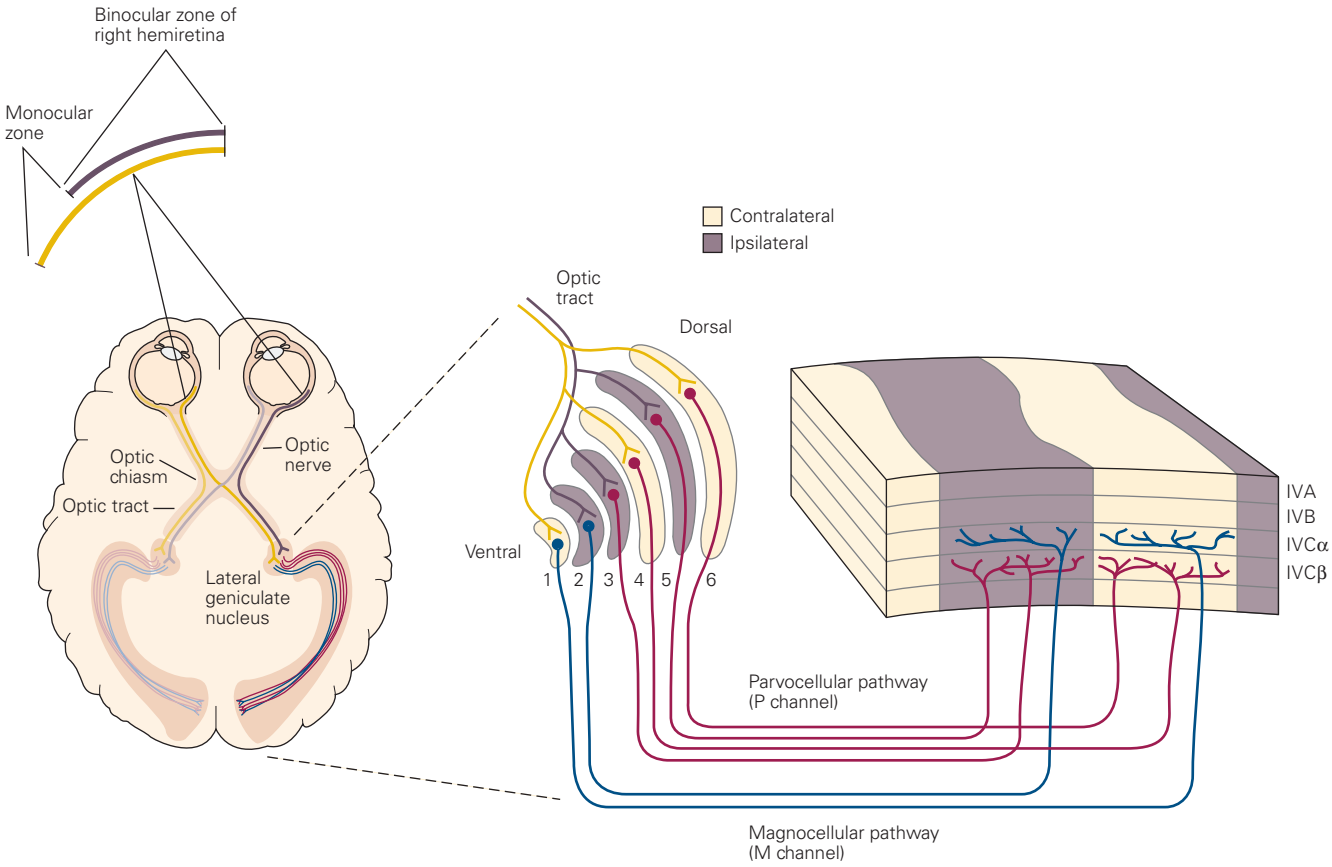


Figure 21–12 **Projections from the lateral geniculate nucleus to the visual cortex.** The lateral geniculate nucleus in each hemisphere receives input from the temporal retina of the ipsilateral eye and the nasal retina of the contralateral eye. The nucleus is a layered structure comprising four parvocellular layers (layers 3 to 6) and two magnocellular layers (layers 1 and 2). Each is paired with an intercalated koniocellular layer. (These layers are represented here by the gaps separating the primary layers. They are unlabeled to avoid clutter. See Figure 21–14.) The inputs from the two eyes terminate in different geniculate layers: The contralateral eye projects to layers 1, 4, and 6, whereas the ipsilateral eye sends input to layers 2, 3, and 5. Neurons from these geniculate layers then project to different layers of cortex. The parvocellular geniculate neurons project to layer IVCβ, the magnocellular ones project to layer IVCα, and the koniocellular ones project to "blobs" in the upper cortical layers (see Figures 21–14 and 21–15). In addition, the afferents from the ipsilateral and contralateral layers of the lateral geniculate nucleus are segregated into alternating ocular-dominance columns.

For every visual attribute to be analyzed at each position in the visual field, there must be adequate tiling, or coverage, of neurons with different functional properties. As one moves in any direction across the cortical surface, the progression of the visuotopic location of receptive fields is gradual, whereas the cycling of columns occurs more rapidly. Any given position in the visual field can therefore be analyzed adequately in terms of the orientation of contours, the color and direction of movement of objects, and stereoscopic depth by a single computational module. The small segment of visual cortex that comprises such a module represents all possible values of all the columnar systems (Figure 21–13).

The columnar systems serve as the substrate for two fundamental types of connectivity along the visual pathway. *Serial processing* occurs in the successive connections between cortical areas, connections that run from the back of the brain forward. At the same time, *parallel processing* occurs simultaneously in subsets of fibers that process different submodalities such as form, color, and movement, continuing the neural processing strategy started in the retina.

Many areas of visual cortex reflect this arrangement; for example, functionally specific cells in V1 communicate with cells of the same specificity in V2. These pathways are not absolutely segregated, however, for there is some mixing of information between different visual attributes (Figure 21–14).

Columnar organization confers several advantages. It minimizes the distance required for neurons with similar functional properties to communicate with one another and allows them to share inputs from discrete pathways that convey information about particular sensory attributes. This efficient connectivity economizes on the use of brain volume and maximizes processing speed. The clustering of neurons into functional groups, as in the columns of the cortex, allows the brain to minimize the number of neurons required for analyzing different attributes. If all neurons were tuned for every attribute, the resultant combinatorial explosion would require a prohibitive number of neurons.

Intrinsic Cortical Circuits Transform Neural Information

Each area of the visual cortex transforms information gathered by the eyes and processed at earlier synaptic relays into a signal that represents the visual scene. This transformation is accomplished by local circuits comprising both excitatory and inhibitory neurons.

The principal input to the primary visual cortex comes from three parallel pathways that originate in the parvocellular, magnocellular, and the blue/yellow channels of koniocellular layers of the LGN (see Figure 21–12). Neurons in the parvocellular layers project to cortical layers IVCβ and 6, those in the

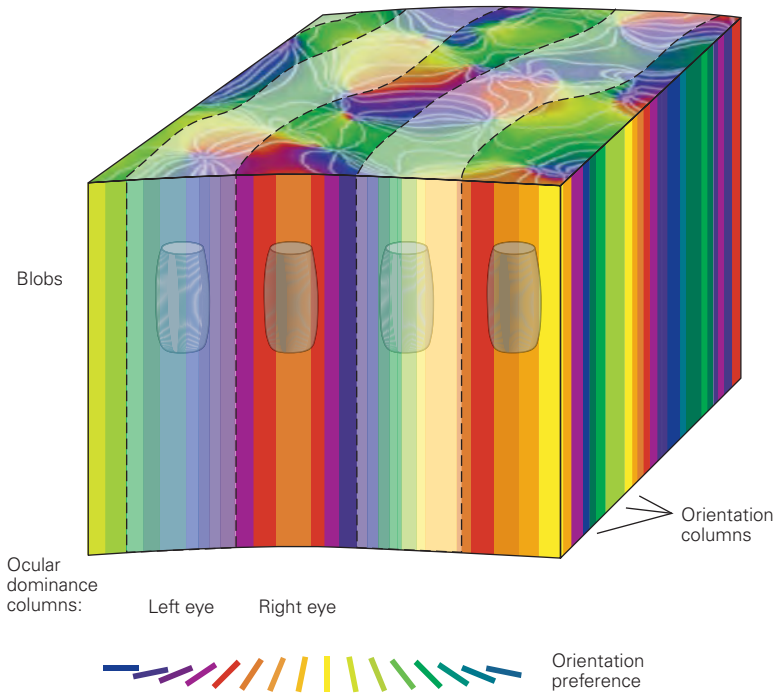


Figure 21–13 A cortical computational module. A chunk of cortical tissue roughly 1 mm square contains an orientation hypercolumn (a full cycle of orientation columns), one cycle of left- and right-eye ocular-dominance columns, and blobs and interblobs. This module would presumably contain all of the functional and anatomical cell types of primary visual cortex, which would be repeated hundreds of times to cover the visual field. (Adapted from Hubel 1988.)

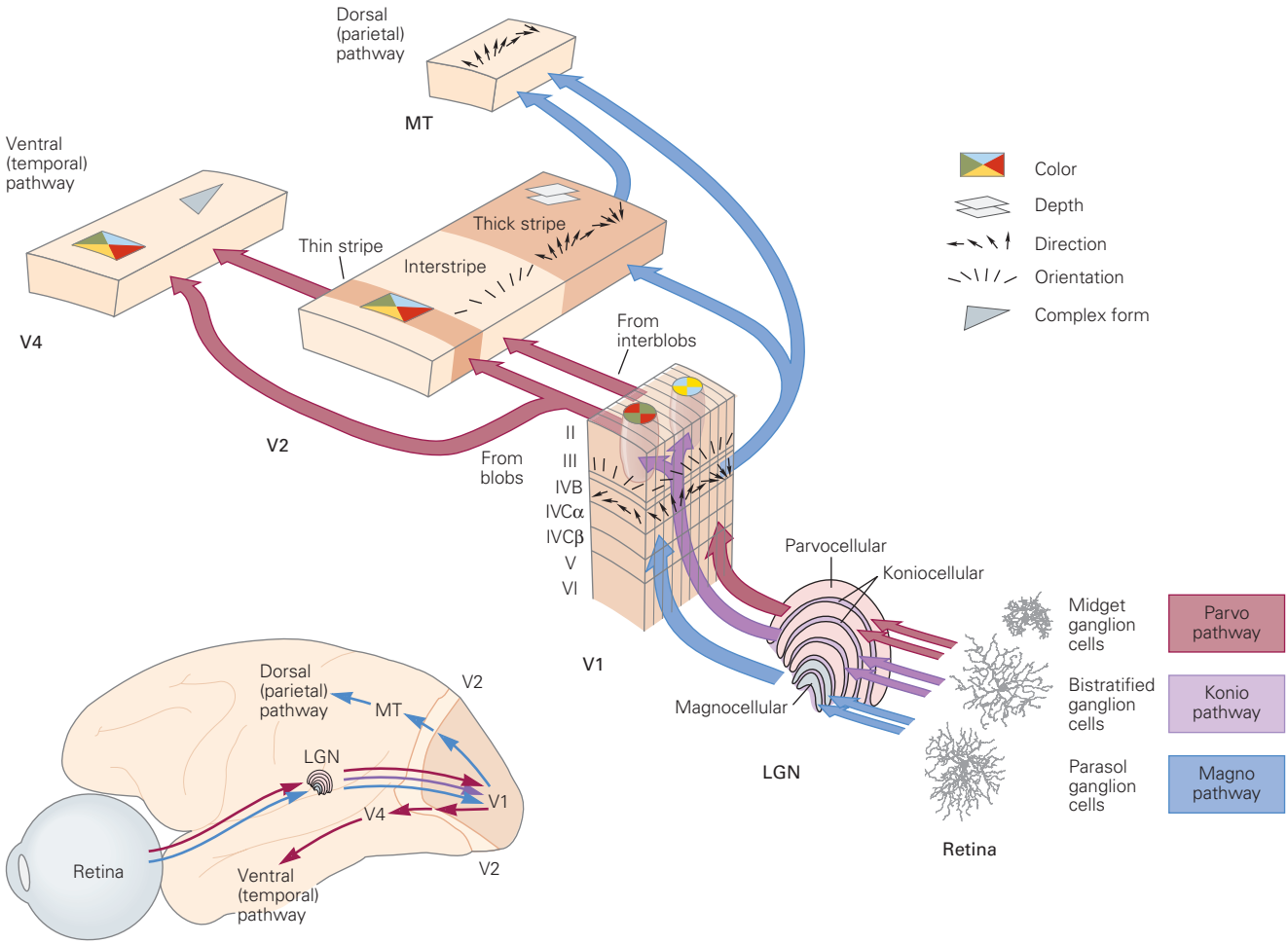


Figure 21–14 Parallel processing in visual pathways. The ventral stream is primarily concerned with object identification, carrying information about form and color. The dorsal pathway is dedicated to visually guided movement, with cells selective for direction of movement. These pathways are not strictly segregated, however, and there is substantial interconnection between them even in the primary visual cortex. (Abbreviations: **LGN**, lateral geniculate nucleus; **MT**, middle temporal area.) (Retinal ganglion cell images courtesy of Dennis Dacey, reproduced with permission.)

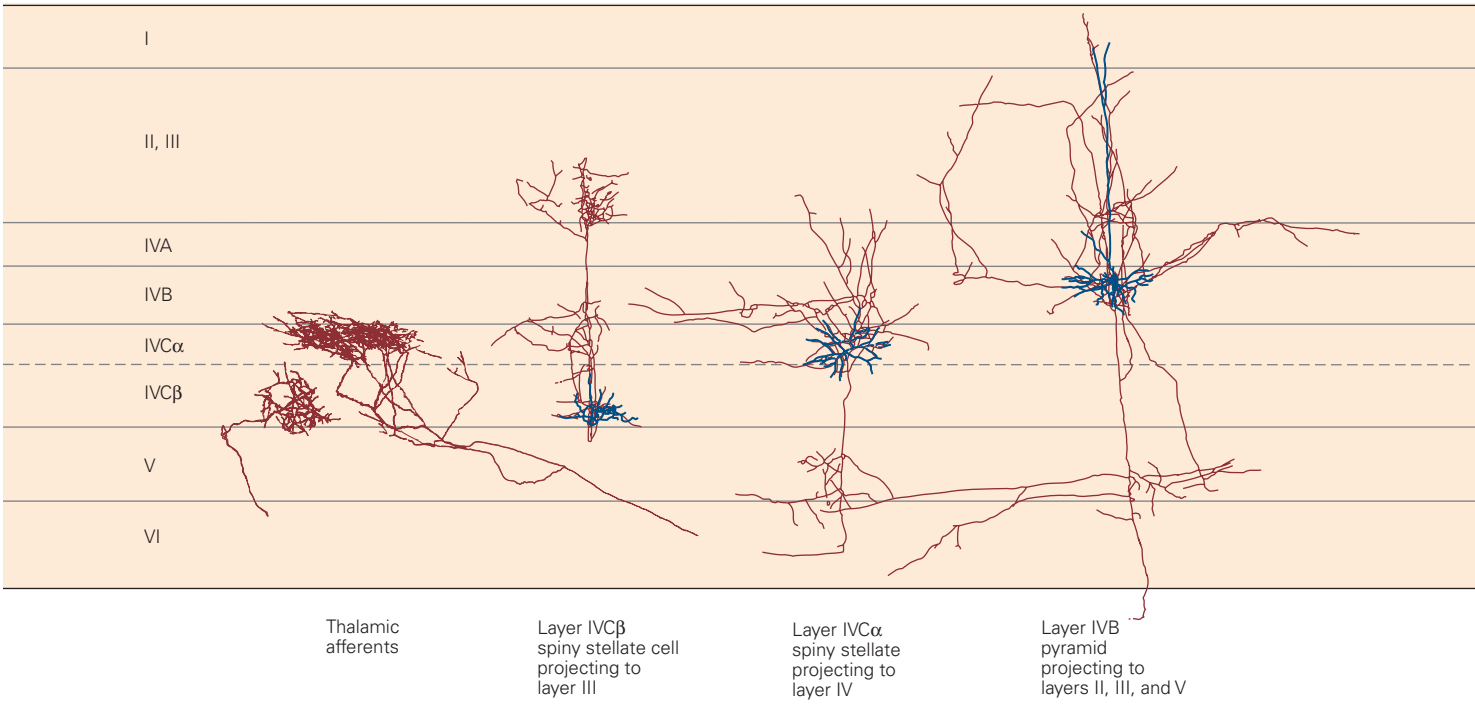
magnocellular layers project to layer IVCα and 6, while the koniocellular neurons project to layer 1 and to the cytochrome oxidase blobs in layers 2 and 3. From there, a sequence of interlaminar connections, mediated by the excitatory spiny stellate neurons, processes visual information over a stereotyped set of connections (Figure 21–15).

This characterization of parallel pathways is only an approximation, as there is considerable interaction between the pathways. This interaction is the means by which various visual features—color, form, depth, and movement—are linked, leading to a unified visual percept. One way this linkage, or binding, may be accomplished is through cells that are tuned to more than one attribute.

At each stage of cortical processing, pyramidal neurons extend output to other brain areas. Superficial-layer cells are responsible for connections to higher-order areas of cortex. Layer V pyramidal neurons project to the superior colliculus and pons in the brain stem. Layer VI cells are responsible for feedback projections, both to the thalamus and to lower-order cortical areas.

Neurons in different layers have distinctive receptive-field properties. Neurons in the superficial layer of V1 have small receptive fields, whereas neurons in deeper layers have large ones. The superficial-layer neurons are specialized for high-resolution pattern recognition. Neurons in the deeper layers, such as those in layer V that are selective for the direction of movement, are specialized for the tracking of objects in space.

A Distribution of cell types in the primary visual cortex



B Simplified diagram of intrinsic circuitry

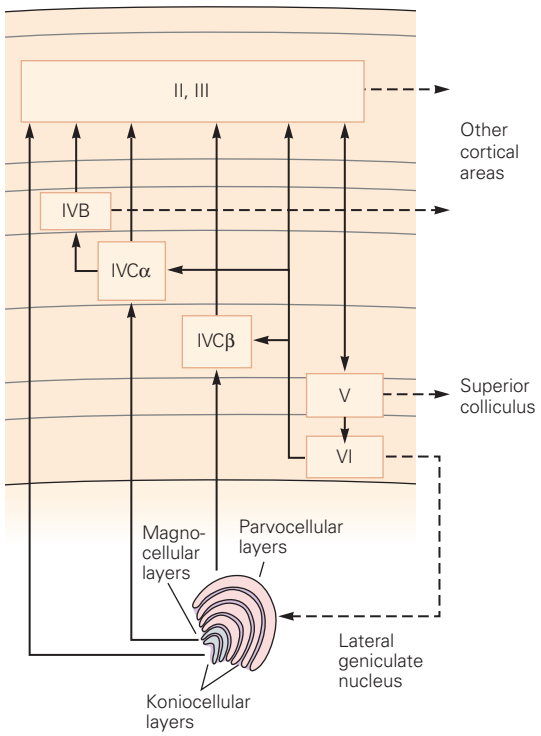
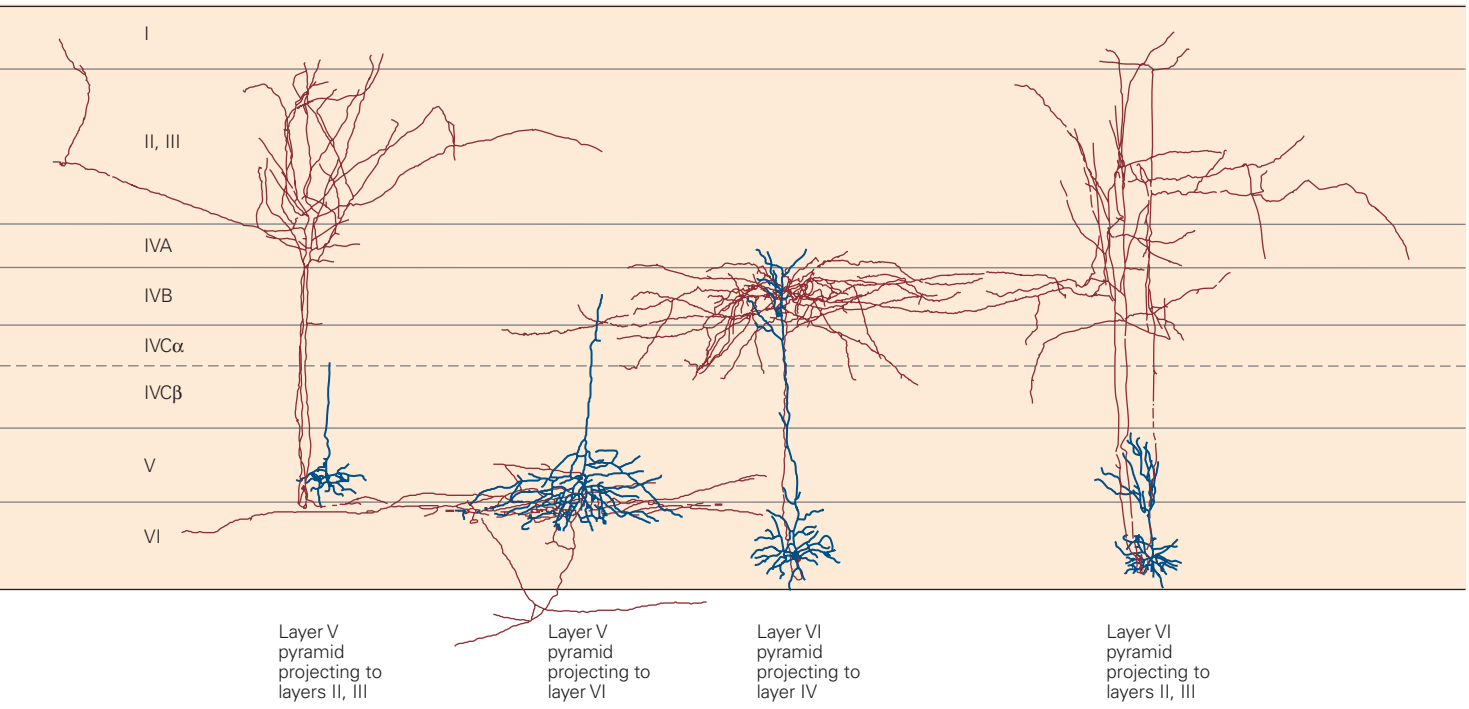


Figure 21–15 The intrinsic circuitry of the primary visual cortex.

A. Examples of neurons in different cortical layers responsible for excitatory connections in cortical circuits. Layer IV is the principal layer of input from the lateral geniculate nucleus of the thalamus. Fibers from the parvocellular layer terminate in layer IVCβ, whereas the magnocellular fibers terminate in layer IVCα. The intrinsic cortical excitatory connections are mediated by spiny stellate and pyramidal cells. A variety of γ-aminobutyric acid (GABA)-ergic smooth stellate cells (not shown) are responsible for inhibitory connections. Dendritic arbors are colored **blue**, and axonal arbors are shown in **brown**. (Cortical neurons courtesy of E. Callaway, reproduced with permission. Thalamic afferents adapted, with permission, from Blasdel and Lund 1983. Copyright © 1983 Society for Neuroscience.)

B. Diagram of excitatory connections within the primary visual cortex. Output to other regions of cortex is sent from every layer of visual cortex.



Feedback projections are thought to provide a means whereby higher centers in a pathway can influence lower ones. The number of neurons projecting from the cortex to the LGN is 10-fold the number projecting from the LGN to the cortex. Although this feedback projection is obviously important, its function is largely unknown.

The activity of the excitatory pyramidal and spiny stellate neurons that mediate information flow into or out of cortical regions is also tightly controlled by local networks of inhibitory interneurons. The spike rates of excitatory neurons are constantly nonlinearly balanced by matched inhibition that maintains the stability of the neural response to an input. Inhibitory interneurons come in multiple classes distinguished by their morphology and their coexpression of distinct peptides such as parvalbumin, somatostatin, or vasoactive intestinal polypeptide (VIP). Some of these interneurons form cascading circuits where interneurons of one class target interneurons of another class, which then target excitatory neurons. This leads to multistep control mechanisms in the neural circuit whereby increasing activity in the first class of inhibitory interneurons reduces activity in the second class, disinhibiting and increasing responses in the excitatory targets at the end of the cascade. Such motifs of inhibitory control are likely to be common to multiple cortical sensory areas.

In addition to serial feedforward, feedback, and local recurrent connections, fibers that travel parallel to the cortical surface within each layer provide long-range horizontal connections (Figure 21–16). These connections and their role in the functional architecture of cortex were analyzed by Charles Gilbert and Torsten Wiesel, who used intracellular recordings and dye injection to correlate anatomical features with cortical function. Because the visual cortex is organized visuotopically, the horizontal connections allow target neurons to integrate information over a relatively large area of the visual field and are therefore important in assembling the components of a visual image into a unified percept.

Integration can also be achieved by other means. The considerable convergence and divergence of connections at the synaptic relays of the afferent visual pathway imply that the receptive fields of neurons are larger and more complex at each successive relay and thus have an integrative function. Feedback connections may also support integration, both because of their divergence and because they originate from cells with larger receptive fields.

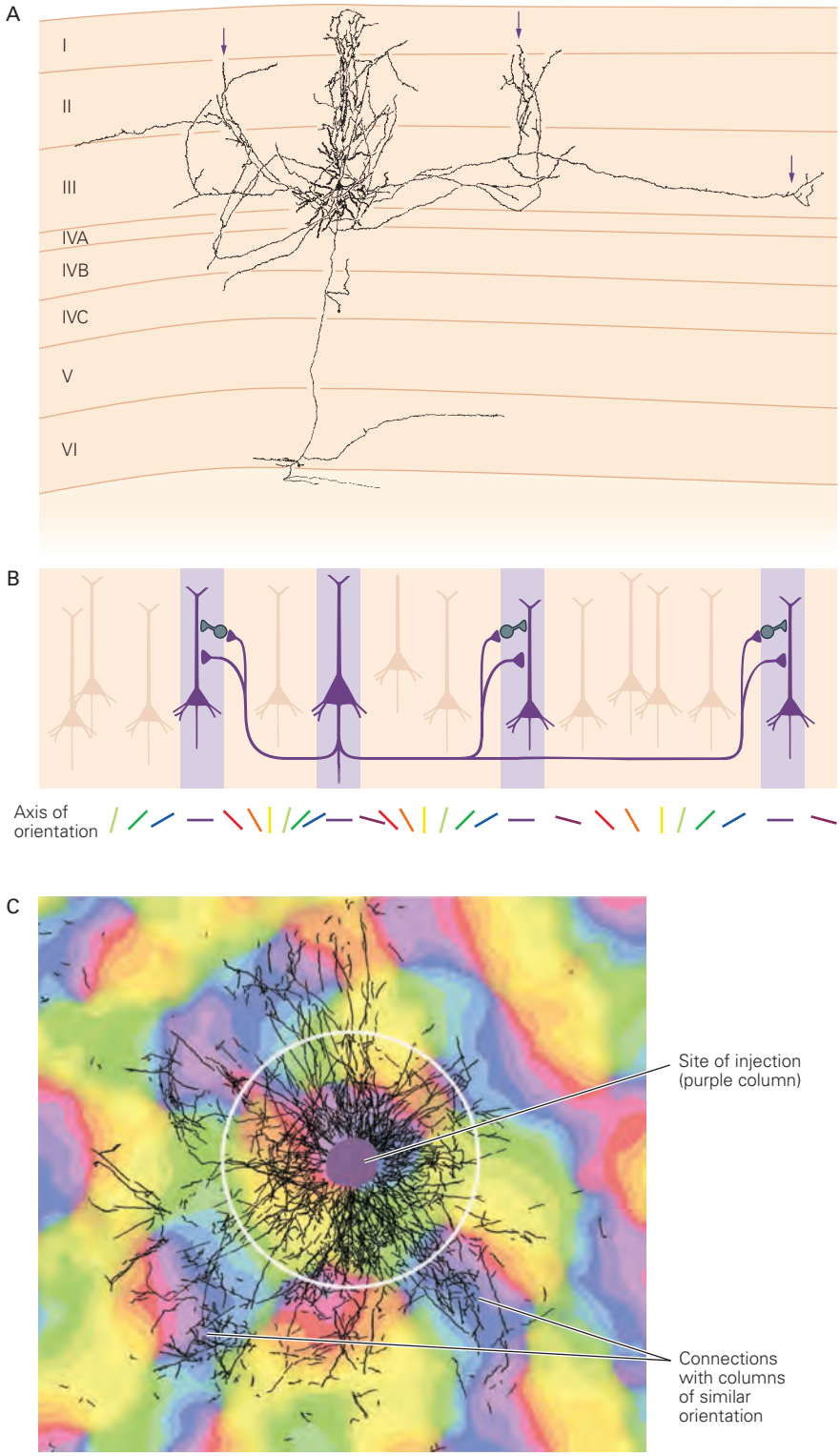


Figure 21–16 Long-range horizontal connections in each layer of the visual cortex integrate information from different parts of the visual field.

A. The axons of pyramidal cells extend for many millimeters parallel to the cortical surface. Axon collaterals form connections with other pyramidal cells as well as with inhibitory interneurons. This arrangement enables neurons to integrate information over large parts of the visual field. An important characteristic of these connections is their relationship to the functional columns. The axon collaterals are found in clusters (**arrows**) at distances greater than 0.5 mm from the cell body. (Reproduced, with permission, from Gilbert and Wiesel 1983. Copyright © 1983 Society for Neuroscience.)

B. Horizontal connections link columns of cells with similar orientation specificity.

C. The pattern of horizontal connections is visualized by injecting an adenoviral vector containing the gene encoding green fluorescent protein into one orientation column and superimposing the labeled image (**black**) on an optically imaged map of the orientation columns in the vicinity of the injection. (Diameter of white circle is 1 mm.) (Reproduced, with permission, from Stettler et al. 2002.)