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VISUAL SYSTEM

THE RETINA

Visual processing starts in the retina, a 0.4-millimeter-thick, bowl-shaped sheet of neurons at the back of the eye, which converts photons into electrochemical signals. The Spanish neuroanatomist Ramón y Cajal (1852–1934) revealed the retina's organization in the late 1800s: Three main layers of neuronal bodies, namely the nuclear layers, contain the photoreceptors, the bipolar cells, and the ganglion cells; these three main layers are separated by two other layers, i.e., the plexiform layers, containing the horizontal cells and the amacrine cells, in addition to the neuronal fibers that interconnect the network.

The photoreceptor layer lies farthest from the front of the eye. Two classes of photoreceptors, cones and rods, transduce the incoming light into electrical signals. Cones, which work under bright light, are the source of daytime vision. Rods work in dim light, but not in daylight conditions (i.e., they saturate at high light levels). Old World primates, including humans, have three types of cones and one type of rod, thus allowing color vision only in daylight. The different cone types are most sensitive to different segments of the light spectrum. L (or red) cones are most sensitive to long wavelengths, M (or green) cones are most sensitive to middle wavelengths, and S (or blue) cones are most sensitive to short wavelengths. Color blindness results from the lack or deficiency of a particular cone type. Cone concentration is highest in the fovea (a small region in the rear, central part of the retina) and becomes sparse in the periphery; thus, visual acuity is highest at the center of vision. Rods are absent from the fovea. The optic disc, the retinal area where the optic nerve—a bundle of nerve fibers comprising the axons of retinal ganglion cells—leaves the eye, has no photoreceptors, producing a blindspot.

A ganglion cell's receptive field (i.e., the area of the visual field that can influence the cell's response) is circular and has two distinct functional regions, called center and surround. Differential illumination of center and surround leads to strong neuronal responses, whereas diffuse illumination of the whole receptive field produces weak or absent responses. ON-center receptive fields respond best to light in the center and darkness in the surround, and OFF-center receptive fields respond best to darkness in the center and light in the surround. Center-surround processing is perceptually linked to edge detection in the visual environment.

The optic nerve encloses the axons of two predominant morphological ganglion cell types: midget and parasol cells. Both have center-surround receptive fields, but present important functional differences. Midget cells are highly sensitive to spatial frequency and color contrast, whereas parasol cells are most sensitive to temporal frequency and luminance contrast. The anatomical and functional differences between these two types of ganglion neurons lead to two different parallel visual pathways that remain largely segregated through the visual system. The midget cells (also called P cells) give rise to the parvocellular pathway, and the parasol cells (also called M cells) lead to the magnocellular pathway.

The Lateral Geniculate Nucleus. The optic nerve connects 90 percent of the retinal ganglion cells to the lateral geniculate nucleus (LGN) of the thalamus, which then

The Visual Projection Pathway

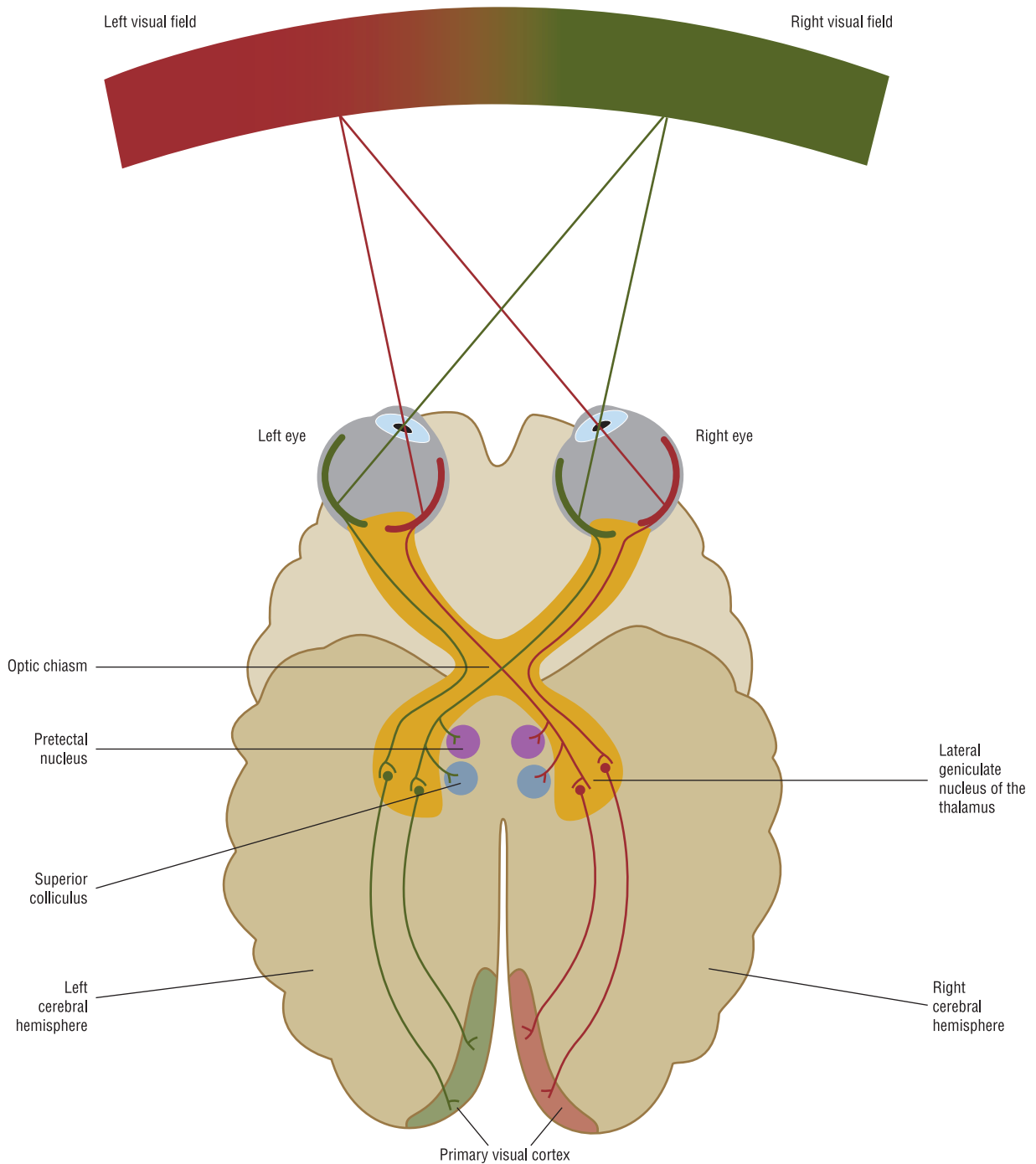


Figure 1. The first three stages of visual information processing: retina, lateral geniculate nucleus of the thalamus, and primary visual cortex. Visual information from each half of the visual field is represented on the opposite side of the visual cortex. © ALILA MEDICAL IMAGES / ALAMY

conveys the visual information to the visual cortex in the occipital lobe, which is situated in the rear of the brain. Before arriving to the LGN, the optic nerve's axons decussate at the optic chiasm, where the retinal axons that come from the nasal halves of the two retinas cross to the opposite side of the brain. The result is that each of the brain's hemispheres processes information from the opposite half of the visual field. Neighboring neurons in the early areas of the visual system (i.e., areas closest to the sensory input) process information from adjacent regions in the visual field, a property called retinotopic organization.

The primate LGN contains six layers of cell bodies. The two bottom or ventral layers receive inputs from the M cells in the retina and contain large cell bodies. They are called magnocellular layers and are involved in motion perception. The four upper or dorsal layers receive inputs from the P cells in the retina and contain smaller cell bodies. They are called the parvocellular layers and are involved in color and shape perception. Each LGN layer receives input from one eye only: layers 1, 3, and 6 from the contralateral (i.e., opposite side) eye, and layers 2, 4, and 5 get input from the ipsilateral (i.e., same side) eye. LGN have center-surround receptive fields, similar to those in retinal ganglion cells.

THE PRIMARY VISUAL CORTEX

The optic radiations are the neural pathways that connect the LGN output to the primary visual cortex, a six-layer cortical region (also called area V1, the striate cortex, and Brodmann area 17), in such a way that the magnocellular and parvocellular pathways that started in the retina remain largely segregated. Two Nobel Prize-winning neuroscientists, Canadian David Hubel (1926–2013) and Swede Torsten Wiesel (1924–), described much of the functional anatomy of area V1 and distinguished two main groups of cells according to their receptive field type: simple cells and complex cells. Simple and complex receptive fields differ from retinal and LGN receptive fields in that they are elongated, rather than circular, and selective to specific orientations of lines and edges. Simple receptive fields are organized in ON and OFF antagonistic subregions. In contrast, complex receptive fields do not have distinctive ON and OFF subregions. Hubel and Wiesel proposed that simple and complex cells represent two successive hierarchical processing stages: simple cells originate from the convergence of inputs from center-surround receptive fields aligned in visual space, and complex cells are generated by the convergence of simple cells inputs with similar orientation preferences.

Hubel and Wiesel showed that V1 cells with similar properties are grouped into columns that are orthogonal

to the cortical layers. Orientation columns group neurons with the same preference for a visual stimulus's orientation. Ocular dominance columns group neurons with the same preference for inputs from one eye versus the other. Orientation and ocular dominance columns are roughly perpendicular to each other, with a full set of orientation and ocular dominance columns constituting a "hypercolumn," a fundamental V1 organizational module.

The Dorsal and Ventral Visual Pathways. There are at least thirty-two distinct visual areas in the primate visual system. The magnocellular and parvocellular pathways, which remain largely segregated from the retina through V1, blossom into two main processing streams with different capabilities. The dorsal or parietal stream, with similar properties to the magnocellular pathway, projects to MT, MST, and neighboring areas, and includes neurons that are selective to the direction and speed of motion. Often called the "Where" pathway, this stream is involved in the assessment of spatial relationships and has its highest processing stages in the posterior parietal cortex. The ventral or temporal stream, with similar properties to the parvocellular pathway, sends information to V4 and neighboring areas, where many neurons are selective to color and spatial/form features. Usually called the "What" pathway, this stream is involved in shape recognition and has its highest processing stages in the inferotemporal cortex.

The American neuroscientists Leslie Ungerleider and Mortimer Mishkin first proposed the hypothesis of two distinct streams of processing. Their formulation has received overall support from clinical observations and

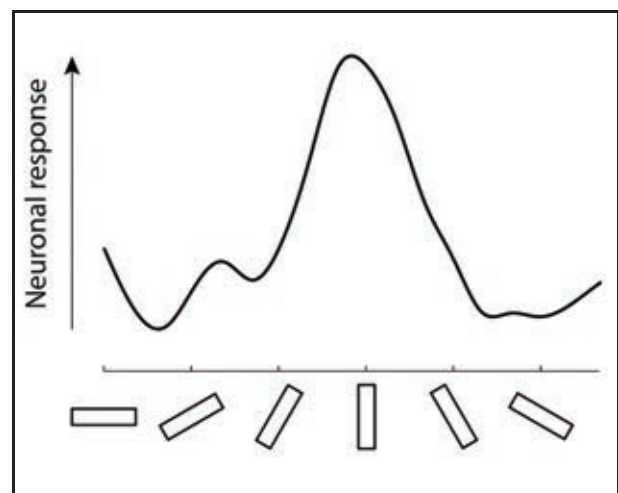


Figure 2. Responses of a primary visual cortex neuron to bars of different orientations. Vertically oriented bars elicited the strongest responses in this particular cell. COURTESY OF THE MACKNIK LABORATORY

lesion studies, but recent evidence indicates that the separation between the two pathways is far from complete, and that there is abundant cross-talk between the two streams.

SEE ALSO *Brain Connectomics, Human; Brain Laterality; Neuronal Structure and Plasticity; Neurons, Electrical Properties of; Neurotransmission.*

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Casimir Funk. Funk was among the first and most articulate to formulate the vitamin doctrine. In 1912, Funk famously proposed that several unknown trace dietary factors were essential for life and, when deficient, resulted in a variety of “deficiency diseases,” including beriberi, pellagra, scurvy, and rickets. He called these substances “vital amines” or “vitamines.” When it was later learned that these substances were not in fact all amines, the term was modified to “vitamins.” SCIENCE SOURCE

VITAMINS AND MINERALS ARE ESSENTIAL TO HEALTH

Diseases resulting from deficiencies of micronutrients—both vitamins and minerals—have been known for millennia, but such disorders were generally attributed to toxic or infectious causes until around the turn of the twentieth century. Before that, a physiologically complete diet was believed to require only sufficient proteins, carbohydrates, fats, certain inorganic salts, and water. Over the last century, multiple essential micronutrients have been identified and found to participate as components of enzymes, or as cofactors in enzymatic reactions, within the body. Deficiencies of micronutrients were found to produce profound health consequences, including sickness and death.

ADVENT OF THE VITAMIN DOCTRINE

From 1880 to 1912, the Russian physician Nicolai Lunin (1853–1937), the Dutch physician-scientist Cornelius Pekelharig (1848–1922), and the British biochemist Sir Frederick Gowland Hopkins (1861–1947) sequentially, though independently, found that animals fed purified mixtures of known food components failed to grow, or even lost weight and died, unless the diet was

supplemented with small amounts of milk. These results suggested that some previously unrecognized substances are required in trace amounts for normal growth. Hopkins labeled these “unsuspected dietetic factors” or “accessory factors” (Hopkins 1912, pp. 425, 450). In 1912 the Polish-American chemist Casimir Funk (1884–1967) suggested that deficiencies of such trace dietary factors were responsible for various diseases, including beriberi, scurvy, rickets, and pellagra. Funk labeled these substances *vitamines* (shortened from *vital amines*), on the mistaken notion that they were not only necessary for life (vital) but were also all of a specific class of organic chemicals (amines) (Funk 1912, p. 342). When it was later recognized that these substances were of varied chemical structure, the term was modified to *vitamins*.