CHAPTER 15
THE CENTRAL VISUAL PATHWAYS

Review: Levels of information processing.

In nearly all sensory systems, information is transmitted from the receptor cell through synapses in the receptor organ, spinal cord, peripheral ganglion, and/or brainstem to a specialized area in the thalamus.

From the thalamus, information is transmitted to a primary sensory area in the cortex, and then to secondary sensory areas and other structures that ultimately may elicit a response.

15.1. INFORMATION PROCESSING IN THE CENTRAL VISUAL SYSTEM

In the visual system, extensive processing takes place in the receptor organ, through the complex connections of the retinal circuitry. Many different aspects of vision and many illusions can be explained solely on the basis of retinal processing, but others cannot. To fully explain how we perceive our visual world, we need to consider the whole system, including the many levels of processing that occur in the brain.

15.1.1. Parallel and hierarchical processing.

In all sensory systems (and other brain systems, for that matter), we can think of processing as either taking place over time in a series of sequential steps, or at the same time but in different places. These two processing strategies can be characterized as:

*Parallel processing*, in which a single set of information is processed simultaneously in multiple parallel systems, or

*Hierarchical (sequential) processing*, in which information is processed first at one level and the output of this level is then further processed at a "higher" level.

In reality, most brain systems perform both types of processing, consisting of multiple parallel pathways, each of which performs multiple steps of hierarchical processing.

15.2. THE CENTRAL VISUAL PATHWAYS

15.2.1. Subcortical pathways.

The optic nerve enters the brain and proceeds as the optic tract to innervate several structures in the brainstem and thalamus. These include the *lateral geniculate nucleus* in the thalamus, the *superior colliculus* in the brainstem (midbrain), and the *suprachiasmatic nucleus* in the hypothalamus.
15.2.1.1. **The lateral geniculate nucleus (LGN).** After leaving the eye, the main projection of the optic nerve in humans is to the *lateral geniculate nucleus*, located in the *thalamus*. The lateral geniculate is the first central relay through which visual information passes on the way to the cortex.

15.2.1.2. **The superior colliculus.** The optic nerve sends a branch to the superior colliculus, a center that initiates and regulates reflex *orientation movements* of the eyes, head and neck.

*Figure 15-1.* The main features of the central visual pathway as they would appear in a horizontal slice through the human brain, viewed from below. Shaded area is external surface of brain, white area is cut surface.

*Figure 15-2.* The main features of the central visual pathway as they would appear in a side view of a slice through the human brain.

15.2.1.3. **The suprachiasmatic nucleus.** The *suprachiasmatic nucleus* is a small group of cells that lie on the ventral side of the brain just above the optic chiasm, the point where fibers from the optic nerves cross to the other side. These cells are involved in regulating daily (*circadian*) rhythms, including our sleep-wake cycles.

15.2.2. **The visual cortex.**
The lateral geniculate nucleus projects directly to primary visual cortex, also called "striate cortex" or "area V1". The cerebral cortex is a 6-layered structure, with different types of cells in each layer. The thalamic sensory areas project to layer 4 of the cortex. Cells in Layer 4 contact cells in other areas that project to other cortical areas, to premotor or motor areas, or back to the thalamus.

In addition to V1 (striate cortex), there are many other visual cortical regions, known as extrastriate visual areas. These include an area specialized for color perception (V4) and one specialized for motion perception (MT).

![Figure 15-3. Side view of the external surface of the cortex, showing the primary visual cortex (V1 or striate cortex), and some of the secondary and tertiary (extrastriate) cortical areas that receive visual input. The numbers on each area refer to "Brodmann’s areas", one system used by neuroanatomists to subdivide the cortex.](image)

### 15.3. INFORMATION PROCESSING IN THE CENTRAL VISUAL SYSTEM.

Although much processing takes place in the retina, even more takes place in the central nervous system. At every level of the visual system, there is one obvious organizational principle. This is the systematic representation of different points in the visual field across a population of neurons. Such an organization is called a topographic representation (or topographic map), as was already discussed in the section on the somatosensory system.

#### 15.3.1. Topographic representations, or "maps" of visual space.

A systematically organized representation of a stimulus parameter (e.g., visual space) is called a topographic representation. In the visual system, the topographic map of visual space begins in the retina, where light from different points in space falls on different parts of the retina. Beginning with the ganglion cells, each level of the visual system projects to the next level in an organized way so that the map of visual space on the retina is preserved.

In the visual system, nearly every area contains a "map" of the visual field. However, in this map is “drawn” at a different scale in different parts. Because of the patterns of convergent and divergent connections beginning with the bipolar and ganglion cells in the retina, parts of the visual field that fall on the cone-rich region of the fovea are expanded relative to parts that fall on the rod-rich areas of the periphery. The resulting representation of the visual field would be comparable to your making a photographic print in which the center was greatly enlarged relative to the edges, something like the view through a “fish-eye” lens.

For an area in which cells have small receptive fields (e.g., the fovea), a large number of cells (large expanse of cortex) will be required to represent a given area in the visual field. In an
area where cells have large receptive fields, few cells (small expanse of cortex) will be required to represent a given area. The amount by which a point on the retina is expanded in a central representation is called the magnification factor.

**Figure 15-4.** Representation of the visual field, here divided into 12 sections (top), in the primary visual cortex (bottom). Each half of the visual field is represented (mapped) on the opposite side of the cortex. Notice how the small region at the center of the visual field (areas 1-4) is expanded in the cortex so that it occupies about half of the entire cortical representation.

**Figure 15-5.** Mapping visual space in the retina and brain. Light from the large checkered surface at the left falls on the retina, with light from different parts of the surface falling on different parts of the retina. The eye is fixating on the middle (white) square on the right, so this portion of the surface falls on the fovea. In the retinal image (top right), light from each square falls on an equal surface of the retina. However, between the retina and cortex, considerable convergence and divergence of connections takes place, so that in the cortical representation (lower right) certain parts of the field are "enlarged" (those falling on the fovea) and others are reduced (those falling on the periphery.)
15.3.2. Parallel processing.

As mentioned before, parallel pathways begin in the retina with two classes of ganglion cells.

a. The **magnocellular** (magno = large) pathway originates in large ganglion cells with large receptive fields. Cells in the magno pathway are not sensitive to color. They are very sensitive to **motion**.

b. The **parvocellular** (parvo = small) pathway originates in small ganglion cells with small receptive fields. Cells in the parvo pathway are sensitive to **color**. They are also sensitive to fine detail.

The lateral geniculate nucleus is a **layered** structure. Each layer receives a different set of input from the retina.

a. The magno pathway projects to layers 1 and 2. The parvo pathway projects to layers 3-6.

b. Each layer receives input from one eye; layers 1, 4 and 6 from the ipsilateral eye (the eye on the same side) and layers 2, 3, and 5 from the contralateral eye (the eye on the opposite side).

![Figure 15-6](image)

*Figure 15-6. Organization of projections to the layers of the lateral geniculate nucleus. Crossed projections (solid line) go to some layers and uncrossed projections (dotted line) to others within both the magnocellular (M) layers and the parvocellular (P) layers.*

The cortex is a layered structure. LGN cells project to layer 4 of the primary visual cortex (V1). Information relayed via the magno and parvo systems remains somewhat segregated at the visual cortex. The visual cortex is organized into fields that receive information primarily from the magno or parvo pathways.

After going through several different intermediate stages of processing, the magno pathway projects to the medial temporal area (MT), a region where neurons are very sensitive to movement; from there it projects to the **parietal** cortex. The magno stream of processing is often described as being concerned with "where" a visual stimulus is.

After going through several intermediate processing stages, the parvo pathway projects to V4, a region that where neurons are very sensitive to color, and to the **temporal** cortex, where
neurons are very sensitive to form and detail. The parvo stream of processing is often described as being concerned with "what" a stimulus is.

Figure 15-7. Schematic diagram of the flow of information through the M-pathways and the P-pathways to form a "where" (movement sensitive) pathway in the medial temporal (MT) area and parietal cortex, and a "what" pathway sensitive to color in V4 and complex forms in inferotemporal (IT) cortex.

15.3.3. Receptive fields in the central visual system.

Receptive fields of cells in the lateral geniculate are similar to those of the retinal ganglion cells that provide their input.

The receptive fields of neurons in V1 are very different from those of LGN neurons, and include several different types:

"Simple cells" respond best to a bar or stripe of light in a specific orientation. More cells "prefer" vertical or horizontal bars than bars at other angles. Their receptive fields have elongated center-surround organizations, suggesting that their responses may be due to convergence of inputs from parallel bands of neurons in the LGN.

"Complex cells" respond best to a bar in a specific orientation, often one that moves in a specific direction. They do not have straightforward center-surround receptive field organizations.

"Hypercomplex" (or "end-stopped" cells) respond best to an oriented, moving stimulus of a specific length.
**Figure 15-8.** Comparison of center-surround receptive field organization in the lateral geniculate (left) and visual cortex (right). Crosses indicate areas of the visual field in which light evokes "on" responses, triangles indicate areas in which light evokes "off" responses for individual cells.

![Diagram of receptive field organization](image)

**Figure 15-9.** Examples of the responses of an orientation-sensitive neuron in visual cortex to bars of different orientations. The stimuli are shown in the left column, and the patterns of action potentials recorded from the neuron during presentation of each bar are shown in the center column. Note that the vertical bar elicits the largest response. The graph on the right is a tuning curve for this neuron, showing response magnitude (number of action potentials) on the vertical axis as a function of bar orientation on the horizontal axis.

![Tuning curve diagram](image)

**Figure 15-10.** Example of a neuron in visual cortex that responds best to a bar in a specific orientation, moving at a specific speed. Many cortical neurons are also selective for the direction of motion.

![Speed, orientation, response diagram](image)

One idea is that the different cell types found in visual cortex represent the results of different stages of hierarchical processing, involving the building up of increasingly complex response properties from one level to the next. In some “higher” cortical areas, for example, neurons may respond best to very specific stimuli such as colors, or even entire objects such as faces. One idea is that visual cortical neurons derive their very specific “tuning” through convergence of inputs from many different neurons, each of which has a different pattern of sensitivity. In this scenario, a population of thalamic neurons with adjacent circular receptive
fields would converge to create a cortical neuron that is sensitive to bars oriented in a particular direction. A population of cortical neurons with different direction orientations would, in turn, converge to create selectivity to a specific pattern of lines, and so on.

**Figure 15-11.** Convergence of inputs from arrays of lateral geniculate neurons with circular receptive fields could create cortical neurons with elongated receptive fields. Here, the cortical cell receives three convergent inputs from LGN cells with receptive fields that lie next to each other in the vertical dimension. A vertical bar would stimulate all three receptive fields, leading to spatial summation of inputs but a horizontal bar would stimulate only one LGN neuron.

### 15.4. MODULAR ORGANIZATION OF VISUAL CORTEX

As described earlier, information about color and fine detail is mainly transmitted via the parvocellular pathway; information about movement and large-scale illumination flux across the visual field is transmitted via the magnocellular pathway. These pathways are segregated into specific layers of the LGN, and specific spatial domains within V1.

The visual cortex is organized as an array of spatial domains, or hypercolumns, somewhat like a repeating mosaic pattern of tiles on a floor. Each hypercolumn comprises several different populations of neurons, arranged in a stereotyped 3-dimensional matrix. Each cortical module contains areas that receive information from the LGN via the parvocellular pathway and other areas that receive information via the magnocellular pathway, and from the ipsilateral or contralateral eye. For example, a cortical hypercolumn in V1 includes:

- **Ocular dominance columns**: arrays of neurons, all of which are excited mainly by input from one eye, either the ipsilateral or the contralateral eye. Within each ocular dominance column are:
  - **Orientation columns**: arrays of neurons, all of which are excited by bars of a specific orientation.
  - "Blobs": arrays of neurons that receive input from the parvocellular pathway. The blobs include ocular dominance columns and orientation columns in which neurons are sensitive to color.
  - "Interblob" areas receive input from the magnocellular pathway. The interblob regions include ocular dominance columns and orientation columns in which neurons are insensitive to color but sensitive to movement.
15.5. COLOR-OPPONENT PROCESSING IN CORTEX

In the cortex there are many double-opponent color-sensitive cells. Such a cell would be excited by one color (e.g., red) at the center of its receptive field, but inhibited by the "opposite" color (e.g., green) in the center of its receptive field. In the surround, the situation would be reversed, with the cell excited by green and inhibited by red. Such a cell could arise through convergence of inputs from single color-opponent cells in the LGN. The receptive fields of these color-opponent cells may be circular (in LGN and layer 4 of V1), or shaped like an oriented bar in other cortical layers.

Figure 15-12. A schematic drawing of a hypercolumn in visual cortex. Ocular dominance columns contain cells which are mainly activated by input from either the left eye or the right eye. Within each ocular dominance column are smaller columns or slabs within which neurons are maximally activated by bars of a specific orientation. Each each orientation-specific slab within each ocular dominance column contains aggregations of cells sensitive to color (blobs) and areas insensitive to color but sensitive to motion (interblob areas). The visual cortex contains many hypercolumns, each of which receives input from a different part of the visual field.

Thought question: The idea of hierarchical processing, taken to its extreme, results in neurons so specific that an individual neuron can only respond to one stimulus. Such highly selective neurons have been termed “grandmother cells”, implying that your cortex must contain (among others) a cell that recognizes and responds to your grandmother, but is “blind” to all other visual stimuli. Do you think it is likely that “grandmother cells” exist? Why or why not? What would be the advantages and disadvantages of a system in which a given cell is dedicated to recognizing a single visual object?
Thought question: In what ways is the organization of the visual system similar to that of the somatosensory system? In what ways do the two systems differ? What about the visual system versus the olfactory system?