**Chapter 4**

**VISUAL SYSTEM: THE BRAIN**

Complex visual pathways exist in the brain to allow us to see. The optic nerves of each eye meet at the optic chiasm, where each optic nerve splits in half such that axons from the right half of each retina combine and axons from the left half of each retina combine to form right and left optic tracts, respectively. The left part of the visual field goes to the right brain, and vice versa, in an organization called contralateral representation of visual space. About 90% of the optic tract of each eye goes to the six-layer lateral geniculate nucleus (LGN) in the thalamus. Neurons in each layer of the LGN show retinotopic organization, meaning ganglion cells from adjacent parts of the retina project to cells in adjacent areas of the LGN. Neurons in the LGN have receptive fields similar to retinal ganglion cells, with center-surround organization. The remaining 10% of the optic tract goes to the superior colliculus, whose main function is the control of rapid eye movements like smooth pursuit and saccades. From the LGN and superior colliculus, projections are made to the primary visual cortex (or V1). The researchers Hubel and Wiesel (1959) identified two distinct types of cells are found in V1, simple cells which respond to stimuli with particular orientations to objects within their receptive field and complex cells which respond best to moving stimuli and may be involved in depth perception. Other parts of V1 are important for each specific eye (ocular dominance columns), orientation (orientation columns), color (blobs), and responding to simple cells (interblobs). From V1, information is sent to V2, which is involved in representing the world. In the visual cortex, two distinct pathways exist, the ventral pathway (the “what” pathway) and the dorsal pathway (the “where pathway). Currently, it is not known where the two pathways come together to give us common perception. One possibility is that it results from the integration of perceptions stemming from constant feedback loops. Finally, the visual system seems to develop as a combination of innate patterns and experiences in the early environment.

Introduction

* Torsten Wiesel and David Hubel completed revolutionary work on the visual cortex.
  + Specifically, they discovered neurons in the brain that have specific visual fields, respond to some patterns of stimuli but not others, and that they are organized into predictable columns.
* This chapter considers the brain’s involvement in the visual system.

The Optic Nerve and Chiasm

* About 1 million retinal ganglion cells form the optic nerve of each eye.
* The optic nerves of each eye meet behind the eyes at the **optic chiasm.**
  + At the optic chiasm, each optic nerve splits in half.
  + Axons from the right half of each retina combine, forming the right **optic tract**, which goes on to the right hemisphere of the brain.
  + Axons from the left half of each retina also combine, forming the left optic tract, which goes on to the left hemisphere.
  + The left part of the visual field goes to the right brain, and the right part of the visual field goes to the left brain in an organization called **contralateral representation of visual space.**

The Lateral Geniculate Nucleus

* The **lateral geniculate nucleus (LGN)** is a bilateral structure in the thalamus that relays information from the optic nerve to the visual cortex.
* It is divided into six layers.
  + The **magnocellular layers** are layers 1 and 2.
  + The somewhat smaller **parvocellular layers** are layers 3 through 6.
  + **Koniocellular layers** are made of very small cells and are between the magnocellular and parvocellular layers.
* Each LGN layer receives input from only one eye.
  + Magnocellular layer 1 and parvocellular layers 4 and 6 receive input from the contralateral eye, whereas magnocellular layer 2 and parvocellular layers 3 and 5 receive input from the ipsilateral eye.
  + The koniocellular layers under each of these receive input in the corresponding fashion.
  + Thus, the LGN maintains information about both where in the visual world information originates and which eye detects that information.
* Particular retinal ganglion cells project to particular layers in the LGN.
* Neurons in each layer of the LGN show retinotopic organization, meaning ganglion cells from adjacent parts of the retina project to cells in adjacent areas of the LGN.
  + In turn, the LGN is organized so that it is oriented to the visual world.
* Three unique pathways, corresponding to each type of layer, start in the retinae and continue to the visual cortex.
  + The **parvocellular pathway (P pathway)** is characterized by **midget retinal ganglion cells (P cells)**, which project to the parvocellular layers.
    - P cells usually receive input from a single cone in the fovea, carrying information necessary for visual acuity.
    - P cells are sensitive to wavelength (basis for color perception) and show a sustained response when stimulated.
  + The **koniocellular pathway (K pathway)** is characterized by **bistratisfied retinal ganglion cells (K cells)**, whichproject to the koniocellular layers.
    - K cells also receive input from cones, but there is more convergence, so they show lower acuity than P cells.
  + The **magnocellular pathway (M pathway)** is characterized by **parasol retinal ganglion cells (M cells)**, whichproject to the magnocellular layers.
    - M cells receive input from both rods and cones.
    - They have large receptive fields and are sensitive to light and motion, but not color.

Processing in the LGN

* LGN neurons have receptive fields similar to retinal ganglion cells, with center-surround organization.
  + LGN neurons show specific responding to edges and spots.
* There are many feedback loops from the visual cortex to the LGN and the LGN connects to other parts of the brain.
* During sleep, the thalamus is inhibited, meaning that information can be registered on the retina and is sent to the LGN but it stops there.
* To learn all this about the LGN, most single-cell recording experiments on the LGN use rhesus macaques, whose visual brains are very similar to human brains.

The Superior Colliculus

* A **superior colliculus** is located at the top of the brainstem, just beneath the thalamus on each side.
* Like the LGN, it receives information contralaterally and has a retinotopic organization.
* Approximately 90% of retinal ganglion cells project to the LGN, but the other 10% go to the superior colliculus.
* Many projections go to and from the superior colliculus, including to and from the LGN and visual cortex.
* The main function of the superior colliculus is the control of rapid eye movements.
  + That is, it is necessary for **smooth pursuit** and **saccades.**
* The superior colliculus also receives input from other sensory systems, allowing us to orient to the direction of a sound or a touch.

The Primary Visual Cortex

* The primary visual cortex is referred to by several names, depending on the context.
  + *Primary visual cortex* and *V1* refer to its position along the flow of information in the visual system—the first place in the cortex to receive visual information.
  + *Striate cortex* refers to the way the brain cells look under certain staining conditions—they appear striated.
  + *Area 17* and *BA 17* refer to the area’s position on Brodmann charts.
* The cortex is the outer surface of the brain. The occipital lobe is the visual cortex. At the back of the visual cortex is the area known as V1.

Mapping the Eye on the Brain

* V1 is a bilateral structure.
* Where the left and right V1s meet in the middle of the brain is the area that represents the fovea.
* Like the LGN and superior colliculus, V1 has a **retinotopic map** of the retina.
  + Some areas of the retina take up more space on V1 than others, a feature called **cortical magnification**.
  + In particular, the fovea (1% of the retina) is represented on over 50% of V1.
* V1 is a six-layered structure, like all of the cerebral cortex.
  + Layer 4 is the critical layer that receives information from the LGN.
  + Most anatomists subdivide this layer into at least three sublayers, one of which is further divided into still smaller sublevels.

Receptive Fields of V1 Cells

* Cells seem to line up in columns sensitive to the orientation of objects in particular areas in the visual field.
* Cells are of two distinct kinds in V1, simple cells and complex cells.

Simple Cells

* **Simple cells** are V1 neurons that respond to stimuli with particular orientations to objects within their receptive field.
* Like LGN cells, they have clear excitatory and inhibitory regions.
* Unlike LGN cells, they have orientation selectivity rather than center-surround visual fields.
* Hubel and Wiesel (1959) found that lengthened stimuli that looked like bars seemed to be particularly effective stimuli for simple cells.
* Any particular simple cell has its own preferred orientation, which is the orientation that produces the strongest response.
* Single-cell recording experiments demonstrate **orienting tuning curves** for any particular simple cell.
* V1 indicates the orientation of lines in the visual world by having select simple cells respond to different angles of orientation.

Complex Cells and V1 Responses to Visual Features

* **Complex cells** also respond optimally to stimuli with particular orientations, but they also respond to a variety of stimuli across different locations.
* Complex cells do not have peak location sensitivity.
* They respond best to moving stimuli and may be involved in depth perception.
* **End-stopped neurons** respond to stimuli that end within the cell’s receptive field.
  + If the pattern continues beyond the receptive field, these cells do not respond as greatly.
  + Given this pattern, end-stopped neurons are thought to be involved in detecting corners and boundaries.

The Organization of V1

* Hubel and Wiesel found that some cells prefer to respond to inputs from one eye, whereas other cells prefer to respond to the other eye, a concept known as ocular dominance of the cell.
* Hubel and Wiesel also found that simple cells all selected bars at particular locations.
  + The simple cells were organized into vertical arrangements of columns
  + **Ocular dominance columns** are made up of neurons that respond to only one eye.
  + Perpendicular to ocular dominance columns are **orientation columns**, which selectively respond to small variations in orientation.
  + When ocular dominance columns and orientation columns are combined, they form a **hypercolumn**, which is a 1-mm block of V1 for a particular region of space.
* In the 1980s, **blobs** and **interblobs** were discovered interspersed throughout V1.
  + Blobs are sensitive to color.
  + Interblobs are sensitive to the orientation of an object and respond to simple cells.

V2 and Beyond

V2

* V1 is not the end of visual processing.
* Information travels from V1 to other areas of the occipital lobe, which are collectively called the **extrastriate cortex** or **secondary visual cortex.**
* One of the major pathways is from V1 to the adjacent **V2** region.
* V2 seems to be involved in representing the world rather than making sense of it.

Functional Pathways in the Visual Cortex

* In V1, the P pathway and the M pathway show distinct organization.
* Referred to as the **ventral pathway,** the P pathway is described as the “what” pathway**.** V1 projects to the other areas of the occipital lobe and then to the inferotemporal cortex.
* Referred to as the **dorsal pathway,** the M pathway is described as the “where” pathway. V1 projects to V2 and then to the parietal cortex.
* Two things are striking about these pathways:
  + Very early in the visual system, information is sorted and channeled into different directions.
  + The pathways are anatomically distinct and functionally separate.
* In a classic study, Mishkin et al. (1983) trained rhesus monkeys to complete a task requiring monkeys to either remember the location of an event (landmark task) or to learn a particular object (object task). Then, lesions to either the inferotemporal cortex or parietal lobe were made. Monkeys with damage to the inferotemporal cortex showed normal performance on the landmark task but were impaired on the object task, whereas monkeys with damage to the parietal lobe showed normal performance on the object task but were impaired on the landmark task. This study suggests that the inferotemporal cortex is important for object recognition, whereas the parietal lobe is important for spatial relation of objects.
* In humans, accidents have essentially replicated Mishkin et al.’s study.

The Ventral Pathway

* The “what” pathway
* After being processed in Layers 2, 3, and 4cβ of V1, information is sent to V2 and then along to V3 and V4 in the extrastriate cortex.
  + V4 neurons are sensitive to **binocular disparity**, useful for identifying 3-dimensional objects in space. Thus, V4 is critical for shape recognition.
  + V4 is also important in color vision.
* V4 then sends information to the inferotemporal cortex.
  + The inferotemporal cortex has neurons that respond to specific features such as hands and faces.
  + For example, the fusiform face area is specifically dedicated to recognizing familiar faces.

The Dorsal Pathway

* The “where” pathway
* After information leaves V2, it is sent to an area in the occipital lobe known as **MT** (middle temporal), also known as **V5**.
  + Neurons in MT are important for motion perception.
* After leaving MT, information is sent to several areas of the parietal lobe.
  + These areas are involved in the visual guidance of reaching and grasping.

Where Does Vision Come Together?

* Though there are two visual pathways, humans perceive a cohesive world.
* Currently, it is not known where the two pathways come together to give us common perception.
* One possibility is that it results from the integration of perceptions due to the constant feedback loops from higher to lower levels.

Development of the Visual System

* There is much flexibility in the development of the visual system with some patterns being fixed and others altered by the early environment.
* Correlational studies in humans and experimental studies in cats suggest that early visual experience is necessary for fully elaborating innate patterns of vision.

***In Depth: Blindsight***

* **Blindsight** is the paradoxical presence of visual abilities in the absence of the visual cortex. The patient claims to be blind but makes visual responses.
* A **scotoma** is an area of partial or completely destroyed cells resulting in a blind spot in a particular region of the visual field.
* The predominant view of blindsight is that it is mediated by mechanisms in the superior colliculus that continue to get input from the retina.