Visual Perception

Visual Perception

The Eye

Detailed Anatomy

The eyeball is held in place and moved by six muscles within the eye socket. Light passes through the cornea and the pupil and reaches the lens, which focuses the rays onto the retina in the most posterior part of the eye. Retinal photoreceptors transduce light rays into neural information that is conveyed through the optic nerve to the brain.

Cornea
The cornea is a transparent, dome-like outer layer of the eye, covering the pupil and the iris. It protects the eye and helps focus light.

Iris
The iris is a circular muscle located behind the cornea. At the center of the iris is a round aperture, the *pupil*. The iris regulates the amount of light that enters the eye by controlling the diameter of the pupil. The iris contains pigments that determine the eye's color. This pigmentation reduces the amount of ultraviolet radiation penetrating the eye. People with blue eyes have less pigmentation than people with brown eyes and are therefore more sensitive to light.

Pupil
The pupil is a circular opening at the center of the iris that allows light to enter the eye and reach the retina. The muscles of the iris control the size of the pupil and in this way regulate the amount of light that enters the eye. In the dark the pupil expands and lets in a greater amount of light, while under regular lighting conditions the pupil contracts and lets in a limited amount of light.

Eyeball
The eyeball is held in place and moved by six muscles within the eye socket. The eyeball's external layer, which covers it completely (except for the cornea), is known as the "white of the eye," or sclera. This layer is opaque and provides the eye with the rigidity necessary for its protection.

Optic Nerve
The optic nerve is a cluster of axons extending from the ganglion cells of the retina and conveying visual information through the optic chiasm to the thalamic LGN (lateral geniculate nucleus). The optic nerve is cranial nerve II.

Rectus Muscles
Along with the oblique muscles (described below), the rectus muscles are the exterior muscles that move the eyeball. There are two pairs of rectus muscles: the superior and the inferior rectus muscles, which control the vertical movement of the eye (up and down); and the lateral and the medial rectus muscles, which control the horizontal movement of the eye (toward the nose or the temple).

Oblique Muscles

Along with the rectus muscles (described above), the oblique muscles are the exterior muscles that move the eyeball. This pair of muscles controls the circular movement of the eye.

Lacrimal Gland
The almond-shaped lacrimal gland secretes tears via thin ducts onto the upper eyelid. The lacrimal liquid is a watery solution containing salts, mucus, and an antibacterial enzyme. Tears serve to lubricate the eye and keep it clean and moist. When a foreign body enters the eye, a reflex of eyelid lowering and tear secreting is activated, thus helping to remove the foreign body.

Lens
The lens is located behind the iris and is made of a series of transparent layers arranged one on top of the other like the layers of an onion. The lens focuses the light rays on the retina. The ciliary muscles within the eye control the shape of the lens to enable the eye to adjust its focus to different viewing distances.

Vitreous Chamber
The vitreous chamber is located between the lens and the retina, and contains the vitreous humor, a gel-like liquid that holds the retina in place and provides the eye with volume. The light passing through the lens crosses the vitreous humor on its way to the retina.

Fovea
The fovea is a small area at the center of the retina that enables acuity (sharpness) of vision and perception of bright colors. When our gaze shifts and focuses on a certain point, the light rays radiating from that point fall onto the fovea. The acuity of the fovea depends on several unique characteristics: a) The fovea includes only *cone*-type *photoreceptors* specialized in daytime vision and responsible for all color vision. b) The *ganglion cells* and the bipolar cells in the fovea are displaced laterally, so that the light strikes the cones directly. c) The *receptive field* of ganglion cells in the fovea is small, as relatively few photoreceptors feed information directly to a ganglion cell (low convergence), as opposed to the periphery, where a large number of *receptors* feed information into a single ganglion cell (high convergence). The less the convergence, the better the resolution and the sharper the vision.

Ciliary Muscle
The ciliary muscle is located within the eye and allows changes in the curvature of the lens. When the eye is focusing on a close object, the curvature of the lens increases by contraction of the ciliary muscle; this process is called accommodation. In contrast, when the eye is focusing on a distant object, the ciliary muscle relaxes and the lens is flattened.

Optic Disc—Blind Spot
The optic disc is where the axons of all ganglion cells *converge* and exit the eyeball as the optic nerve. This is also the point where blood vessels enter and leave the eye. Since this spot contains no *photoreceptors*, we cannot see an image that strikes the blind spot. We are usually unaware of the blind spot, as information from the other eye and constant saccadic eye movements compensate for the missing information. Nevertheless, the existence of the spot can be demonstrated by means of a simple exercise (click the “Blind Spot” button on this screen).

Blood Vessels

Blood vessels supply nerve cells with oxygen and nutrients and remove waste products. Blood vessels enter and exit the eye in the optic disc area. They are mainly arranged along the periphery and are much fewer in the center of the retina.

Blind Spot

The blind spot is where the axons of all ganglion cells *converge* and exit the eyeball as the optic nerve. Since this spot contains no photoreceptors, we cannot see an image that strikes the blind spot. We are usually unaware of the blind spot as information from the other eye and constant *saccadic eye movements* compensate for the missing information. Nevertheless, the existence of the spot can be demonstrated by means of a simple exercise: Cover your left eye and fixate your right eye on the plus (+) sign. Bring your face very close to the computer screen and begin slowly withdrawing from it until the white circle disappears. The circle disappears because its image falls on the blind spot.

Image Formation on the Retina

The cornea and the lens focus images on the retina. The image falling on the retina is inverted by the lens both right-left and top-bottom. For this reason, the right half of the visual field falls onto the left half of each retina, and vice versa. Despite this inversion of the retinal image, we perceive the world as it is. This is because during the first years of life, the nervous system learns through experience where each object is located relative to the observer. This kind of learning requires observations and actions in the world. When wearing inverting spectacles (through which the world looks upside down), a person is only capable of adjusting to the new situation if he/she interacts with the surrounding environment, thus modifying connections between the tactile and visual senses. However, a person with inverting spectacles who only passively looks at the world (while lying in bed, for example) will not adjust to the new situation.

The Retina

Laminar Organization

The retina is located in the back of the eye. It is comprised of a single layer of pigmented epithelium (a light absorbing layer) and three main layers of neurons: photoreceptors, bipolar cells, and *ganglion cells*. Additional types of nerve cells, horizontal cells and amacrine cells, are located in the bipolar layer. The photoreceptors are located at the back of the retina, so that the light must pass through the other layers before it reaches them. The complex relationships among cells of the retina are simplified in the illustration.

Ganglion Cell Layer

The layer closest to the center of the eyeball is composed of ganglion cells. It receives information from the bipolar cells and the amacrine cells. The axons of the ganglion cells extend from the retina to form the *optic nerve*, which carries visual information through the optic chiasm into the brain. Among the various cells that comprise the retinal layers, ganglion cells are the only ones where action potentials are generated.

In primates, it is customary to classify retinal ganglion cells into two main types: M cells (“magno” or large cells) and P cells (“parvo” or small cells). M cells have large receptive fields. They react quickly and briefly to changes in brightness but are insensitive to changes in color—they are “color blind”. Thus, they are particularly

sensitive to moving objects within the visual field. P cells are more numerous, and they have smaller receptive fields. They mainly receive information from certain photoreceptors (cones) and are sensitive to varying colors. They have greater spatial resolution capabilities and seem to be mainly involved in form and color processing.

Bipolar Cell Layer
Bipolar cells receive information from both photoreceptors and horizontal cells. This information is conveyed to ganglion cells by the secretion of a transmitter from the bipolar cells. The secretion is regulated by graded changes in the membrane potential (rather than firing action potentials): Depolarization leads to increased secretion, while hyperpolarization reduces transmitter secretion.

Photoreceptor Layer
The layer of photoreceptors is farthest from the center of the eyeball and is located at the back of the retina. Photoreceptors synapse with bipolar cells and horizontal cells. Light passes through the other retinal layers before it strikes the receptors, where it is transduced into neural activity.

There are two general types of photoreceptors—rods and cones. In general, there are fewer cones than rods (6 million as compared with 120 million photoreceptors), and they are mainly concentrated around the *fovea* at the center of the retina. Cones are important for daytime vision, providing good visual acuity and color vision. They are insensitive to dim light and are therefore inactive under conditions of low illumination or in the dark. Photoreceptors of the rod type are mainly located in the periphery of the retina. They are highly sensitive to dim light, providing for night vision, which is less sharp and "color blind."

Fovea
The fovea is a small area at the center of the retina that enables acuity (sharpness) of vision and perception of bright colors. When our gaze shifts and focuses on a certain point, the light rays radiating from that point fall onto the fovea. The acuity of the fovea depends on several unique characteristics: a) The fovea includes only cone-type photoreceptors specialized in daytime vision and responsible for all color vision. b) The ganglion cells and the bipolar cells in the fovea are displaced laterally, so that the light strikes the cones directly. c) The *receptive field* of ganglion cells in the fovea is small, as relatively few photoreceptors feed information directly to a ganglion cell (low convergence), as opposed to the periphery, where a large number of receptors feed information into a single ganglion cell (high convergence). The less the convergence, the better the resolution and the sharper the vision.

Detailed Anatomy
Light waves reaching the retina are transduced into neural activity by the retina's photoreceptors—the rods and cones. The neural information is conveyed from the receptors to the ganglion cells by bipolar, horizontal and amacrine cells. The *axons* of the ganglion cells extend from the retina to form the optic nerve, which carries visual information through the optic chiasm via the optic tract into the brain.

Ganglion Cell
Ganglion cells convey neural information by means of *action potentials*. They receive nerve impulses from both amacrine and bipolar cells. The number of bipolar cells that send information to a single ganglion cell varies: the greater the number (i.e., the more bipolar cells converging on a single ganglion cell), the greater the *receptive field* of that particular ganglion cell. The receptive field is the area of the visual field to

which the cell responds. Ganglion cells at the center of the retina (in the area of the fovea) have a small receptive field that provides high spatial resolution—the ability to differentiate fine details. In contrast, ganglion cells in the periphery of the retina have a large receptive field (due to the convergence of many bipolar cells), and the information obtained by these cells provides only a low level of spatial resolution.

The receptive field of a ganglion cell is organized in a round center surrounded by a ring. This organization provides for high sensitivity to contrast in brightness between the center and the surround. There are two main types of cells that code brightness contrast: cells with a light-activated center (On-center) and cells with a light-inhibited center (Off-center).

Amacrine Cell
Amacrine cells are intermediate neurons that link bipolar cells and ganglion cells. They lack *axons* and convey neural information via dendrites linked to the synapses between bipolar cells and ganglion cells. More than twenty types of amacrine cells have been discovered, but their precise function is yet unknown.

Bipolar Cell
A bipolar cell receives neural information from photoreceptors, either directly or indirectly, via horizontal cells. The greater the number of photoreceptors that send neural information to a bipolar cell (a phenomenon known as *convergence*), the larger its receptive field. Bipolar cells in the area of the fovea have smaller receptive fields than cells in the periphery of the retina, and consequently their spatial resolution is better.

The receptive field of a bipolar cell is organized in a round center surrounded by a "ring". This organization provides for high sensitivity to brightness contrast between the center and the surround. There are two main types of cells that code brightness contrast: cells with a light-activated center (On-center) and cells with a light-inhibited center (Off-center). For example, on-center cells are maximally activated when the center of the receptive field is stimulated by light, while the periphery remains in the dark; and they are inhibited when the periphery of the receptive field is stimulated by light, while the center remains in the dark (see the animation "On/Off Center").

Bipolar cells' sensitivity to contrast between the center and surround of the receptive field allows them to distinguish contours based on brightness differences of adjacent surfaces. The reaction of bipolar cells to color is also usually based on the contrast between the center and surround of the receptive field.

Horizontal Cell
Horizontal cells are intermediate neurons that link photoreceptors and bipolar cells. Like amacrine cells, horizontal cells have no axons, and they convey neural information via *dendrites* linked to the synapses between photoreceptors and bipolar cells.

Horizontal cells are large and so are their receptive fields. A bipolar cell receives information from the surround of its receptive field via the horizontal cells. The bipolar cell sums up the information arriving from the horizontal cell, along with the information arriving directly from the receptors at the center of its receptive field.

Cones

There are about 6 million photoreceptors of the cone type in the retina. Although the number of cones is small compared to the number of rods (1:20), they provide us with most of the visual information about our environment. Cones are specialized for daylight vision, color perception, and the perception of fine details (spatial resolution). There are three types of cones, each containing a photopigment that is maximally sensitive to a different wavelength: short waves of 420 nm, medium waves of 530 nm, or long waves of 560 nm. The cones that respond to short, medium, or long wavelengths are known as “blue”, “green”, and “red” cones, respectively. The retina contains an almost equal number of red and green cones, and only a small number of blue cones (about 8 percent of all cones). Most cones are located in the *fovea* at the center of the retina. Because cones are insensitive to dim light, our night vision cannot distinguish fine details or colors.

Rods
There are about 120 million *photoreceptors* of the rod type in the retina. Rods are located outside the *fovea*, in the periphery of the retina. Rods cannot distinguish colors, because their photopigment is insensitive to varying wavelengths. In addition, they are insensitive to bright light because they quickly become saturated.

Rods are highly sensitive to dim light. They contain a great amount of photopigment—about 10 million molecules of photopigment in a single human rod. Consequently, even a single photon of light is capable of evoking an electrical reaction, as compared to the hundreds of photons required to stimulate a similar response in a cone. Thus, when the environment is dim, our vision is mainly dependent on the rods. A dim light flickering in the distance may be perceived out of the corner of the eye (i.e., in the receptive field of the rods), but when the gaze is focused on the source of dim light, the cones are unable to detect it and the flickering image disappears.

Pigment Epithelium
The pigment epithelium is located in the back of the eye, between a network of blood vessels and the photoreceptors. The photoreceptors are imbedded in this layer. The pigment epithelium contains the black pigment melanin, also found in the skin. Melanin absorbs the light rays that were not absorbed by the photoreceptors, thus preventing the light from reflecting back to the retina and impairing the quality of the received image.

Optic Nerve Axons
The axons of the optic nerve are in fact ganglion cell axons, converging and leaving the retina as a single tract. At the point of egress, they form the optic disc .The two optic nerves (one from each eye) are partially crossed in the optic chiasm, after which they become the *optic tracts* and continue to the brain.

Physiological Processes

Photo Transduction
The animation presents a rod-type photoreceptor. The receptor is in the dark and is depolarized, which is represented in the animation by a red color. Along the outer segment, a disc *membrane* (one of many) and sodium channels are shown. Along the inner segment there are potassium channels and a sodium-potassium pump. At the top of the inner segment are *synaptic vesicles*.

Segment 1:

The animation shows a rod-type photoreceptor in the dark. Sodium channels, which are mediated by cyclic GMP (cGMP), are open in the dark, enabling the entry of sodium ions into the cell. Within the interior segment of the photoreceptor there are open potassium channels through which potassium ions flows out. A *sodium-potassium pump* helps maintain the membrane potential at -30mV by pushing out sodium ions and taking in potassium ions. This potential is depolarized compared to the *resting potential* of nerve cells, and is therefore represented in the animation in red. The flow of sodium ions entering the cell in the dark is called "the dark current." Because the cell is depolarized, a transmitter is released from the *synaptic vesicles* located at the top of the photoreceptor.

Segment 2:
Light reaches the photoreceptor and is absorbed by the photopigment located on the discs in the outer segment. Following the absorption of light, sodium channels close. Potassium channels remain open, potassium continues to flow out of the cell, and the cell is *hyperpolarized* to -70mV (represented by a change in the cell's color to blue). As a result of the hyperpolarization the *transmitter* is no longer released by the photoreceptor.

Segment 3:
Once illumination shuts off and the photoreceptor is in the dark again, sodium channels reopen. Sodium flows into the cell and the *membrane potential* returns to its depolarized state of -30mV, represented in the animation by red. This leads to renewed *transmitter* release.

Segment 4:
The animation now shows a magnified section of the outer segment of the photoreceptor, including a single disc membrane and a single sodium channel. A molecule of the photopigment rhodopsin is shown on the disc membrane. Rhodopsin comprises two components: the protein opsin and retinal, a derivative of vitamin A. Retinal is the molecule that absorbs the light and transduces it into a chemical reaction.

In the dark, cGMP causes sodium channels to open, and sodium ions flow into the photoreceptor. When light strikes the rhodopsin, it causes a conformational change in the structure of retinal, which in turn activates the opsin. Activation of the opsin causes the G-protein to exchange GDP for GTP, which subsequently activates the enzyme cGMP-phosphodiesterase. The enzyme phosphodiesterase breaks down cGMP molecules and reduces their concentration. This leads to closure of the sodium channels. Influx of sodium ions is shut off, and the photoreceptor becomes hyperpolarized. The *hyperpolarization* is represented by the change in the cell's color to blue.

Bipolar and Ganglion On-Center Cells

Bipolar and ganglion on-center cells are particularly sensitive to contrast in brightness between the center and the surround of their receptive fields. On-center cells are maximally excited when stimulated by light in the center of their receptive fields and are inhibited when stimulated in the surround.

Nine photoreceptors are presented in the animation: three at the center of the receptive field of the bipolar cell and six in its surround (center and surround are delineated in yellow). The bipolar cell receives direct input from the photoreceptors in its center and indirect input from the photoreceptors in the surround via the horizontal cells.

While the photoreceptors and bipolar cells respond with graded potentials, the ganglion cell is the first layer in the visual pathway where action potentials are generated.

Segment 1: Total Darkness
In darkness, all photoreceptors are depolarized, as represented by the red color. The photoreceptors in the center of the receptive field inhibit the bipolar cell (inhibition is marked with a blue minus sign in the synaptic cleft). Photoreceptors in the surround of the receptive field excite the horizontal cells, and these in turn excite the bipolar cell (red plus sign). All potentials are summed in the bipolar cell, which is slightly depolarized, as represented by the reddish color. This depolarization leads to spontaneous generation of action potentials at a low frequency (the rate of action potentials are represented by red vertical lines moving along the horizontal axis).

Segment 2: Illumination of the Center
Light is absorbed by photoreceptors in the center of the receptive field causing *hyperpolarization*, as represented by a change of the color to blue. As a result, the inhibition induced by the photoreceptors in the center is removed from the bipolar cell, while the cells in the surround continue to excite the bipolar cell via the horizontal cells. The bipolar cell is more depolarized (as represented by the red color), causing the ganglion cell to fire at a higher frequency.

Segment 3: Illumination of the Surround
Light is absorbed by photoreceptors in the surround of the receptive field causing *hyperpolarization*. As a result, the excitation induced by the photoreceptors in the surround via the horizontal cells is removed from the bipolar cell, while the cells in the center continue to inhibit the bipolar cell. Consequently, the bipolar cell and the ganglion cell are strongly inhibited, and action potentials are no longer generated.

Segment 4: Diffuse Light
Light also falls on the photoreceptors at the center of the receptive field, causing them to hyperpolarize and thus remove the inhibition from the bipolar cell. This leads to a slight excitation of the bipolar cell and the *ganglion cell*, and the latter produces action potentials at a low frequency.

Bipolar and Ganglion Off-Center Cells
Bipolar and ganglion off-center cells are particularly sensitive to contrast in brightness between the center and the surround of their receptive fields. Off-center cells are maximally excited when stimulated by light in the surround of the receptive field and are inhibited when light falls on the center of the receptive field.

Segment 1: Total Darkness
In darkness, all photoreceptors are depolarized, as represented by the red color. The photoreceptors in the center of the receptive field excite the bipolar cell (excitation is marked with a red plus sign in the synaptic cleft). Photoreceptors in the surround of the receptive field excite horizontal cells, and these in turn inhibit the bipolar cell (blue minus sign). All potentials are summed in the bipolar cell, which is slightly depolarized, as represented by the reddish color. This depolarization leads to spontaneous generation of action potentials at a low frequency (the rate of action potentials are represented by red vertical lines moving along the horizontal axis).

Segment 2: Illumination of the Right Side of the Receptive Field

Light is absorbed by photoreceptors in the right side of the receptive field causing hyperpolarization. As a result, the inhibition induced by these photoreceptors via the horizontal cells is removed from the bipolar cell. Once inhibition is removed, the bipolar cell becomes more depolarized (as represented by the red color), causing the ganglion cell to fire at a higher frequency.

Segment 3: Illumination of Two-Thirds of the Receptive Field
The illumination widens and covers the center of the receptive field as well. The light is absorbed by photoreceptors in the center causing hyperpolarization. As a result, the excitation induced by the photoreceptors in the center is removed from the bipolar cell. Consequently, the bipolar cell and the *ganglion cell* are strongly inhibited, and action potentials are no longer generated.

Segment 4: Diffuse Light
Light falls on all photoreceptors, including cells at the left side of the surround, causing *hyperpolarization* of the additionally illuminated cells. These latter photoreceptors cease to excite the left horizontal cell, which in turn stops inhibiting the bipolar cell. This leads to a slight excitation of the bipolar cell, which in turn causes the ganglion cell to produce action potentials at a low frequency.

Contrast Enhancement

Look at the two gray central boxes. The right box, in the black frame, seems to be brighter than the left box, in the light gray frame. Now press the button to remove the background. When the frames are removed, it becomes evident that the two gray boxes are equally bright. Thus, the brightness of an object is perceived relative to its surround, depending on the difference in light intensity between the object and its environment, rather than its absolute intensity.

The on/off-center cells are specialized to detect local differences in light intensity rather than the absolute magnitude of light falling on the retina. For the sake of simplicity, we refer here to on-center ganglion cells. These cells respond maximally when their center is stimulated by light and their surround is in the dark. As the difference in light intensity between the center and surround decreases, so does the response of these cells. Thus, the greater the contrast between the intensity of the light in the center and surround of the receptive field, the stronger the reaction of the cells, resulting in the perception of a brighter center. For this reason, the box within the black frame is perceived as brighter than the box within the light gray frame.

Color Coding in the Retina

The process of color coding begins with *cone*-type photoreceptors located in the retina. There are three types of cones, each containing a photopigment that is maximally sensitive to a different wavelength: short waves of 420 nm, medium waves of 530 nm or long waves of 560 nm. The cones that respond to short, medium, or long wavelengths are known as “blue”, “green”, and “red” cones, respectively. According to the tri-chromatic theory, each color can be created by mixing the proper ratio of red, green, and blue light. The three types of cones make it possible to see all the colors of the rainbow. Colors are perceived by comparing the responses of the three cone types to each wavelength.

The curves in the upper part of the screen presents the spectral sensitivity of the three types of cone pigments. Below each cone type there is a box indicating its response at

different wavelengths.At the level of the retinal ganglion cells, the three-color code gets translated into an opponent pair color system (red-green, blue-yellow, black-white). Each ganglion is excited by one color of the pair (solid arrow) and inhibited by the other (dashed arrow). Thus, for example, the red-green (+R/-G) ganglion cell is excited in response to red light and inhibited in response to green light. Whereas the green- red (+G/-R) ganglion cells is excited in response to green light and inhibited in response to red light. At the top of the screen the entire spectrum is presented. It is possible to move the cursor over the spectrum (to certain wavelengths) and examine color perception at the level of the photoreceptors and the ganglion cells.

Perception of Blue
At a wavelength of 430nm, the blue photoreceptor absorbs most of the light, while the red and green photoreceptors hardly absorb any light at all. Excitation of the blue photoreceptor leads to activation of the blue-yellow *ganglion cells* (+B/-Y), and the perceived color is blue.

Perception of Green
At a wavelength of 490nm, the green photoreceptor absorbs a great deal of light, while the red and blue photoreceptors only absorb a small amount of light.

Excitation of the green photoreceptor activates the green-red (+G/-R) ganglion cell, and inhibits the red-green ganglion cell (+R/-G). Cells in the blue-yellow channel receive conflicting information (both excitatory and inhibitory) from the blue photoreceptor and the green and red photoreceptors. These messages cancel out each other. The perceived color is green.

Perception of Yellow
At a wavelength of 550nm, the green photoreceptor and the red photoreceptor absorb an equal amount of light, while the blue photoreceptor does not absorb any light at all. The green and red photoreceptors activate the yellow-blue ganglion cell (+Y/-B). The ganglion cells in the red-green channel receive conflicting messages (both excitatory and inhibitory) that cancel out each other. The perceived color is yellow.

Perception of Orange
At a wavelength of 580nm, the red photoreceptor absorbs a maximum amount of light, the green photoreceptor absorbs a medium amount of light, and the blue photoreceptor does not absorb any light at all. Excitation of the red photoreceptor activates the red-green (+R/-G) ganglion cell and inhibits the green-red (+G/-R) ganglion cell. In addition, the two photoreceptors both excite the yellow-blue (+Y/-B) ganglion cell. In higher cortical areas of the brain, these messages are combined. The perceived color is orange.

Perception of Red
At a wavelength of 650nm, the red photoreceptor absorbs some light, while the green and blue photoreceptors do not absorb any light at all. Excitation of the red photoreceptor activates the red-green (+R/-G) ganglion cell. The perceived color is red.

Perception of Black
At wavelengths above 700nm, which is at the upper limit of visible light, the three types of photoreceptors do not absorb any light at all. *Ganglion cells* in the blue-yellow and red-green channels are not activated, while a black-white (+B/-W) ganglion cell is excited, leading to the perception of black. Ann identical process also

takes place below the lower limit of visible light (wavelengths below 400nm), and the perceived color is also black.

Perception of Black
At wavelengths below 400nm, which is at the lower limit of visible light, the three types of photoreceptors do not absorb any light at all. Ganglion cells in the blue-yellow and red-green channels are not activated, while a black-white (+B/-W) ganglion cell is excited, leading to the perception of black. An identical process also takes place above the upper limit of visible light (wavelengths above 700nm), and the perceived color is also black.

Perception of White
Light that includes all visible wavelengths is absorbed by all three photoreceptors. These convey conflicting messages, both excitatory and inhibitory, to the ganglion cells in the yellow-blue and red-green channels. These messages cancel out each other. At the same time, the three photoreceptors excite the white-black (+W/-B) ganglion cell. The perceived color is white.

The Afterimage Effect

Stare at the flag for about a minute, then press the button below to replace the flag with a white screen. When you do so, you will see an image with the complementary colors, red, white, and blue—the colors of the U.S. flag.

This phenomenon is known as the afterimage effect and is associated with opponent processes of color perception in the ganglion cells. In order to explain the afterimage effect let us take, for example, a yellow surface. Observing the yellow surface for an extended period of time leads to adaptation (reduced responsiveness) of the yellow-blue ganglion cells. When the flag illustration is removed and your gaze is fixed on the white screen (which combines many wavelengths), the blue-yellow cells are stimulated by the white light, while the yellow-blue cells are still less responsive. Thus, the afterimage perceived on the white background is that of a blue opponent color. The red afterimage appearing after looking at the green stripes, and the white afterimage appearing after looking at the black stars, may be explained in a similar way.

The Optic Chiasm

Visual Pathways from the Eye to the Cortex

The visual information in the retina is conveyed through the optic nerves (extending from each eye) to the optic chiasm, where the nerves partially decussate and continue, as the optic tracts, to the lateral geniculate nuclei in the thalamus. From the thalamus, the information continues to travel along the optic radiation to the primary visual cortex in the back of the occipital lobe.

Fixation Point
The point in the visual field upon which the gaze of both eyes is focused is called the fixation point. The light arriving from this point falls on the retinal fovea of both eyes, where the most precise and focused vision takes place.

Right Visual Hemifield
The right visual hemifield is found to the right of the fixation point. The right visual hemifield projects to the nasal part (proximate to the nose) of the retina in the right eye and the temporal part (close to the temple) in the left eye. On the optic chiasm, information from the right visual field is transferred to the left hemisphere of the brain.

Left Visual Hemifield
The left visual hemifield is found to the left of the fixation point. The left visual hemifield projects to the nasal part (proximate to the nose) of the retina in the left eye and the temporal part (close to the temple) in the right eye. On the optic chiasm, information from the left visual field is transferred to the right hemisphere of the brain.

Binocular Visual Field
The portion of the visual field viewed by both eyes is known as the binocular visual field. Binocular vision is important to depth perception.

Projection on the Retina
The retina of each eye receives information from the central, binocular visual field. In addition, each eye receives information from the ipsilateral (same side), monocular visual field.

Optic Nerve
The optic nerve (*cranial nerve* II) is a cluster of axons extending from the *ganglion cells* in the retina, conveying visual information to the optic chiasm.

Optic Chiasm
The optic chiasm is where the optic nerves partially *decussate* and continue, as the optic tracts, to the lateral geniculate nuclei in the *thalamus*. In the optic chiasm, the *axons* extending from the nasal (proximate to the nose) part of both retinas decussate to the contralateral side, while the axons extending from the temporal (proximate to the temple) part of both retinas continue to the ipsilateral side. Thus, each brain hemisphere processes information from the contralateral side of the visual field (the right hemisphere processes information from the left visual field, and vice versa).

The Optic Tract
The optic tract is made up of the axons that link the optic chiasm and the lateral geniculate nucleus in the thalamus. These axons convey information relating to the contralateral side of the visual field.

The Lateral Geniculate Nucleus (LGN)
The lateral geniculate nucleus (LGN) is located in the thalamus and comprises six layers of cell bodies. Each of these layers receives input from one eye only (layers 2, 3, and 5 receive input from the ipsilateral eye, while layers 1, 4, and 6 receive input from the contralateral eye).

Optic Radiation
The optic radiation is collection of axons extending from the lateral geniculate nucleus (LGN) to the primary visual cortex.

Primary Visual Cortex

The primary visual cortex is located in the posterior part of the occipital *cortex*. It consists of six layers. Layer IV receives information from the lateral geniculate nucleus (LGN) and retains the distinction between information arriving from the ipsilateral eye (light strips) and that arriving from the *contralateral* eye (dark strips). This monocular information is then converged into binocular information in other layers of the primary visual field.

Lesions in the Visual Pathways

A specific lesion in the visual pathways causes loss of vision in part of the visual field, according to the damaged area. The screen before you illustrates a number of lesions that may occur in the visual pathway. Selecting each check box on the screen illustrates the visual deficit associated with damage to a certain area. Selecting a number of boxes illustrates the ensuing deficit of a combination of lesions. In order to cancel the effect of a previous selection, click the check box once again, so that the X mark disappears.

Lesion in the Right Optic Nerve
Following a complete section (transection) of the right optic nerve visual information from the right eye will be completely lost, resulting in blindness in the right monocular part of the visual field. The visual information arriving from the central part of the visual field and from the left monocular part is perceived by the left eye. However, due to the loss of information from the right eye, the vision in the binocular part of the visual field becomes monocular.

Lesion in the Left Optic Nerve
Following a complete section of the left optic nerve, visual information from the left eye will be completely lost, resulting in blindness in the left monocular part of the visual field. The visual information arriving from the central part of the visual field and from the right monocular part is perceived by the right eye. However, due to the loss of information from the left eye, the vision in the binocular part of the visual field becomes monocular.

Lesion in the Right Optic Tract
Following a complete section of the right optic tract visual information from the left visual hemifield will be completely lost, resulting in blindness in the left part of the visual hemifield.

Lesion in the Left Optic Tract
Following a complete section of the left *optic tract*, visual information from the right visual hemifield will be completely lost, resulting in blindness in the right part of the visual hemifield.

Lesions in Part of the Primary Visual Cortex (Scotoma)
A small *lesion* in part of the primary visual cortex causes a scotoma, a region of blindness, in the contralateral visual field. Sometimes the scotoma results in a syndrome known as blindsight, which is the ability to identify the location, motion, and even form and color of an object, while remaining unconscious of the object itself. The ability to identify the features of an object although unaware of its existence may depend on indirect connections that convey information from the superior colliculi and the lateral geniculate nucleus (LGN) to the associative visual cortex, bypassing the primary visual cortex.

Lesions in the Right Primary Visual Cortex (Hemianopia)
Lesions of the right primary visual cortex lead to total blindness in the left hemifield. This type of blindness is known as *hemianopia* (see the video clip "Hemianopia" under "Brain Lesions in the Visual Cortex" section).

Lesions to the Left Primary Visual Cortex (Hemianopia)
Lesions of the left primary visual cortex lead to total blindness in the right hemifield. This type of blindness is known as *hemianopia* (see the video clip "Hemianopia" under "Brain Lesions in the Visual Cortex" section).

Lesions in the Optic Chiasm
Following a complete section of the optic chiasm the crossing fibers from the nasal part of both retinas will be completely lost, resulting in blindness in the peripheral monocular visual field in both eyes. Moreover, the vision in the central part of the visual field becomes monocular instead of binocular.

The Lateral Geniculate Nucleus (LGN)

Detailed Anatomy

The lateral geniculate nucleus (LGN) receives its name from its similarity in appearance to a bent knee (*genu* means "knee"). The LGN is located within the thalamus and comprise six layers of neuronal cell bodies. It receives visual information from the optic tracts and conveys this information to visual cortical areas, particularly to the primary visual cortex. Each of these layers receives input from one eye only (layers 2, 3, and 5 receive input from the ipsilateral eye, while layers 1, 4, and 6 receive input from the *contralateral* eye), so that these layers are monocular.

The somas of the neurons in the two innermost layers are larger than the somas of neurons in the four outer layers. For this reason, the two inner layers are known as the magnocellular layers (magno refers to the large size of the cells), while the four outer layers are known as the *parvocellular* layers (parvo refers to the small size of the cells). The two types of layers belong to two separate systems that are responsible for the analysis of different forms of visual information. Each system receives input from one type of ganglion cells in the retina: M-type ganglion cells project to the magnocellular layers, and P-type ganglion cells project to the parvocellular layers. Cells in the LGN retain the same arrangement of center and surround *receptive fields* as is found in the ganglion cells associated with them.

(Image is taken from Hubel, D.H. "Layering of the lateral geniculate," in *Eye, Brain, and Vision*. Page 65.. By kind permission of Dr. David Hunter Hubel, Department of Neurobiology, Harvard University.)

Magnocellular Layers
Layers 1 and 2 of the LGN are the magnocellular layers. Similar to M-type retinal ganglion cells, neurons in the magnocellular layers have large center-surround receptive fields and are insensitive to differences in wavelength. Their response to stimulation of the receptive field centers is fast but brief. In general, these cells are sensitive to rapid changes in brightness and are particularly important for detection of

stimulus movement. The magnocellular system is found in all mammals, while the parvocellular system exists in primates only.

Parvocellular Layers
Layers 3 to 6 of the LGN are the parvocellular layers. Similar to P-type retinal ganglion cells, neurons in the parvocellular layers have small center-surround receptive fields and are sensitive to differences in wavelength. Their response to stimulation of the receptive field centers is slow but sustained. In general, these cells are specialized in the perception of color and fine details.

Retinal Input

Each LGN layer receives information from a single eye. Three layers receive information from the right eye and three from the left eye. Each LGN receives complete representation of the contralateral hemifield.

Right LGN
The right LGN receives information from the left visual hemifield.

Input from the Left Eye
Layers 1, 4, and 6 of the right LGN receive information from the nasal part of the retina of the left eye.

Input from the Right Eye
Layers 2, 3, and 5 of the right LGN receive information from the temporal part of the retina of the right eye.

Left LGN
The left LGN receives information from the right visual hemifield.

Input from the Left Eye
Layers 1, 4, and 6 of the left LGN receive information from the nasal part of the retina of the right eye.

Input from the Right Eye
Layers 2, 3, and 5 of the left LGN receive information from the temporal part of the retina of the left eye.

The Superior Colliculi

The superior colliculi (Latin for “mounds”), which resemble two hills, are located in the *tectum* area of the *brain stem.* They are involved in saccadic movements of the eyes and in the orientation of the eyes and head toward objects in the visual field.

The superior colliculi receive visual information from the retina through a neural pathway that branches out from the *optic nerves*. They also receive information from the visual cortex and other sensory systems, such as the somatosensory and the auditory systems. Each superior colliculus receives information from the contralateral side of the visual field, and this information is represented in a retinotopic organization, that is, adjacent retinal areas are represented by adjacent cells within the

superior colliculi. This representation map is distorted such that more cells of the superior colliculus are devoted to analysis of the center of the visual field.
(The illustration is based on a drawing taken from Bear & Connors & Paradiso. *Neuroscience: Exploring the Brain*. Figure 10.7.Retinotopic map of the superior colliculus. By permission of Waverly/Williams & Wilkins/Urban & Schwarzenberg, Baltimore, MD.)

The Primary Visual Cortex

Laminar Organization

The primary visual cortex, also known as the striate cortex, is located in the area surrounding the calcarine fissure, at the back of the occipital lobe. This cortex comprises six main layers (1-6) and a number of sublayers (4A, 4B, 4C), arranged parallel to the cortex surface. The information arriving from the lateral geniculate nucleus (LGN) enters sublayer 4C within the striate cortex. Layer 4 is unique in that its input is monocular, that is, cells of this layer each receive input from a single eye. Half the cells receive information from the right eye, while the other half receive information from the left eye (note the ocular separation of light-brown areas and dark-pink areas in layer 4). Cells in the other layers of the striate cortex receive binocular information. Binocular disparity, the slight differences between the views of the two eyes, is important for depth perception. The figure also presents the blobs and interblobs in layers 2 and 3 of the striate cortex.

Selecting each of the check boxes presents the flow of information into and out of the striate cortex, and the intralayer connections. In order to cancel the effect of a previous selection, click the check box once again, so that the X mark disappears.

Blobs Area
In the primary visual cortex (particularly in layers 2 and 3) there are neural clusters that look like blobs that are mainly concerned with color processing. The blobs in layers 2 and 3 receive input from cells in sublayer 4Cβ and also receive direct information from the *lateral geniculate nucleus (LGN).* Blob cells are monocular and insensitive to orientation columns (see “Orientation Columns” section).

Interblobs Area
Between the blobs in the primary visual cortex there are interblob regions. Just like neurons in the blobs, neurons in the interblob areas in layers 2 and 3 receive input from sublayer 4Cβ. Unlike the blobs however, most of the cells in the interblobs are binocular and are insensitive to varying wavelengths. Interblob cells are sensitive to orientation, movement, spatial frequency, and retinal disparity.

Input
Most of the visual input into the primary visual cortex originates in the lateral geniculate nucleus (LGN) and terminates in sublayer 4C. It is possible to distinguish two sublayers within sublayer 4C: The upper part (sublayer 4Cα) receives input from the two *magnocellular* layers of the LGN, while the lower part (sublayer 4Cβ) receives input from the four *parvocellular* layers of the LGN. In addition to the input from the LGN, the primary visual cortex also receives visual information from higher cortical areas. From sublayer 4C axons extend to higher and lower layers within the striate cortex.

Interconnections Between Layers
Interconnections within the primary visual cortex allow the exchange of information between all cortical layers. Sublayer 4Cα (which receives input from the magnocellular layers of the LGN) sends output to layer 4B, which in turn conveys information to layers 2 and 3. Sublayer 4Cβ (which receives input from the parvocellular layers of the LGN) also sends output to layers 2 and 3, which transfer the information to layer 5, which projects onto layer 6 and also returns information to layers 2 and 3. Output from layer 6 returns to sublayer 4C.

Output
The primary visual cortex sends information to higher visual cortical areas and to other brain areas. Layers 2, 3, and 4B project information to areas of the associative visual cortex, such as V2, V3, V4, and MT (V5). Layer 5 projects to subcortical areas, including the pulvinar in the *thalamus*, the superior colliculi, and the pons. Layer 6 projects back to the lateral geniculate nucleus (LGN) and the claustrum.

Modular Organization in the Primary Visual Cortex (V1)
The primary visual cortex (V1) includes hundreds of basic processing units called modules. Each module comprises tens of thousands of neurons concerned with the analysis of various features of visual perception within a small area of the visual field. The illustration presents a number of modules within the primary visual cortex (the highlighted segment within the illustration represents a single module). Each module consists of ocular dominance columns (left and right), orientation columns arranged in pinwheel patterns (each orientation is represented by a different color), and blobs (white circles interspersed among the pinwheels), which are specialized in color analysis. Layer 4, marked as a white strip within the depths of the columns (especially sublayer 4C), is unique in that its nerve cells are monocular, lack blobs, and are insensitive to line orientation.

In addition to depth, orientation, and color processing, module cells are sensitive to other stimulus features such as motion and spatial frequency. A relatively extensive area within the striate cortex (about 25 percent) is devoted to the analysis of input arriving from the fovea, which represents only a small part of the retina.
(Image provided by Grinvald, A., Weizmann Institute of Science, Rehovot, Israel.)

Analysis of Visual Information

Ocular Dominance
Cells within the primary visual cortex are specifically sensitive to information arriving from one of the eyes, a trait known as ocular dominance. These cells are organized in columns according to the dominant eye (left or right). Cells of layer 4 are exceptional in that they receive only monocular information. The video clip presents an experiment showing ocular dominance columns in a segment of the *striate cortex* of a live monkey. The experiment is based on a camera recording of changes in the blood flow reflected from the cortex when the monkey is watching a checkerboard presented on a computer screen, with one eye closed. The presentation of visual stimuli (the checkerboard) on the screen activates neurons in the striate cortex. This activity is associated with dilation of blood vessels and increased oxygen supply, which appears in the clip as dark blotches over the surface of the cortex.

The first part of the clip shows the cortex while the monkey is looking at the checkerboard with his left eye only (the right eye is covered). First shown are the blood capillaries that cover the surface of the cortex. The next frame shows the same cortical area after the signal-to-noise ratio has been enhanced. The main artery seen in the previous frame and its two branches can still be seen in the center of the picture. The dark blotches over the surface of the cortex represent the active areas involved in processing information from the left eye.

In the second part of the clip, the screen is split in two: the upper frame presents the same image of the cortex as before while the monkey is looking with just the left eye; the lower frame presents an image of the same area while the monkey is looking with the right eye. Despite the similarity between the two pictures, a close inspection reveals differences in the location of the dark blotches (which indicate higher cortical activity). What appears dark in the upper frame appears bright in the lower frame, and vice versa, showing that clusters of cells that react forcefully to stimuli presented to one eye hardly react to stimuli presented to the other eye.

Now the upper frame presents again an image of the cortex while the monkey is looking with just the left eye. The lower frame presents an image derived by a subtraction of the image recorded when the monkey is looking with left eye from the image recorded when the monkey is looking with the right eye. This subtraction reveals the ocular dominance columns. The black strips represent areas with left eye ocular dominance, while the white strips represent areas with right eye ocular dominance.
(Clip courtesy of Grinvald, A., &Maloned D., Weizmann Institute of Science, Rehovot, Israel.)

Orientation Columns

This experiment demonstrates the existence of orientation columns in the primary visual cortex. The images are based on a camera recording of changes in blood flow reflected from the cortex when the monkey is watching a line in various orientations on a computer screen (represented by a purple line in the upper-right-hand corner of the video clip). When the monkey observes the line, neurons sensitive to its orientation are activated. This activity is associated with dilation of blood vessels and increased oxygen supply, which appears in the clip as dark blotches over the surface of the cortex. When the orientation of the line is slightly changed, adjacent cells sensitive to the new orientation are activated, and a new pattern of dark patches is seen over the cortex. During the experiment, the orientation of the line is changed in a circle. The results show that each orientation of the line activates a group of cells. These groups are spatially arranged in a pinwheel pattern. The video clip presents three such pinwheels (delineated by three purple circles) that rotate around their centers (purple points).
(Video clip provided by Grinvald, A., and Bonhoeffer, T. Weizmann Institute of Science, Rehovot, Israel.)

Orientation Pinwheels (image)

This illustration presents an optical imaging recording of the primary visual *cortex* of a monkey. The imaging is based on a camera recording of changes in blood flow reflected from the cortex while the monkey is watching lines in various orientations. Cells that respond to a particular orientation are recorded by the camera and are then assigned a certain color. Each color represents a cluster of cells sensitive to a specific line orientation (see legend along the side of the picture). The different colors are

arranged in a pinwheel pattern. Each of the pinwheels contains cells for all possible line orientations, and adjacent segments in each pinwheel react to adjacent line orientations (see magnification). Note that each orientation is represented only once within a pinwheel.
(Image courtesy of Grinvald, A., Weizmann Institute of Science, Rehovot, Israel.)

Simple Cell

Simple cells are found within a number of layers in the primary visual cortex. They have rectangular receptive fields with discrete excitatory and inhibitory zones. Each simple cell is particularly sensitive to a bar of light with a particular axis of orientation that corresponds to the axis of the cell's receptive field.

The video clip presents a recording of the activity in a simple cell in the primary visual cortex . The cell's response to a moving bar of light is recorded by means of a microelectrode. The neural activity (*action potentials*) is translated into auditory signals, so that each action potential is heard as a single shot, while a sequence of action potentials sounds like a barrage.

In the first stage of the experiment, a simple cell responds with a burst of action potentials to a bar of light with a particular axis of orientation presented in its excitatory zone. (The excitatory zone is identified with X marks). In the second stage, the inhibitory zones of the cell are marked (with triangles) on both sides of the excitatory zone. The cell is inhibited when a bar of light stimulates the inhibitory zones, and it responds with a burst of action potentials when the light is removed. Next, the cell's reaction to various line orientations is examined. The cell's response to a bar of light is strongest when the orientation of the bar is parallel to the axis of the excitatory zone. Other orientations of the bar of light are less effective. Finally, the cell's reaction to a rectangle of light covering the entire receptive field is examined. The simple cell does not respond when the light illuminates the entire receptive field, because it is inhibited by the inhibitory zones. When the area of the light is reduced, and it once more stimulates the excitatory area with the preferred axis, the cell reacts once again with a burst of action potentials.
(Clip courtesy of Hubel, D. H., Harvard Medical School, Boston, MA; and Wiesel, T., Rockefeller University, NY.)

Complex Cell

Complex cells are found in layers 2, 3, 5, and 6 of the primary visual cortex. Their *receptive fields* do not have discrete excitatory and inhibitory zones. They respond to specific orientations of the image, regardless of its position in the receptive field. Some complex cells are sensitive to the direction of movement of the image. They respond maximally when a line with the preferred orientation moves in a certain direction within the receptive field; the response becomes weaker when the same line moves in the opposite direction. Some complex cells are also sensitive to line ends, a trait known as end-stopping. They react maximally when one end (at least) of the line terminates within their visual field, but do not respond when the line is longer than the boundaries of the receptive field.

The video clip presents a recording of the activity of a complex cell in the primary visual cortex of a cat. The cell's response to a moving bar of light is recorded by means of a microelectrode. The neural activity (action potentials) is translated into auditory signals, so that each action potential is heard as a single shot, while a sequence of action potentials sounds like a barrage.

In the first stage of the experiment, the receptive field of a complex cell is identified and marked. A bar of light with a given orientation is swept across the receptive field, and the cell's response is recorded. The area where the cell responds to the visual stimulus is delineated with lines forming a rectangle. In the second stage, an arrow marks the selective direction to which the cell responds maximally. Note that the cell is totally unresponsive to movement in the opposite direction. Following this, the reaction of the cell to various lengths of the light bar is examined. The cell does not respond to light bars with the preferred orientation extending over the boundaries of its receptive field (end-stopping). This may be explained in the following way: Three complex cells with similar receptive field properties lined up one below the other converge on another complex cell (the recorded end-stopping cell). The central cell (of the three) is excitatory, while the two on both sides are inhibitory. Activation of all three cells inhibits the recorded cell. However, when at least one end of the light bar is within the receptive field, the inhibition is reduced and the cell responds once again. Thus, the recorded complex cell is sensitive to orientation, specific movement direction, and to ends of the line within its receptive field (end-stopped).
(Clip courtesy of Hubel, D. H., Harvard Medical School, Boston, MA; and Wiesel, T. N., Rockefeller University, NY.)

Associative Visual Cortex

Detailed Anatomy

The associative visual cortex receives visual information mainly from the primary visual cortex (V1). The associative visual area is located along the occipital, inferior temporal, and posterior parietal cortex. It is divided into a number of sub-areas. Each sub-area selectively responds to a specific dimension of visual information. For example, area V4 specializes in the processing of form and color, while area V5 specializes in the processing of motion. In general, two visual processing streams extend from the primary visual cortex: the dorsal visual stream (the "where" or "how" stream) extends to the parietal lobe and is specialized in spatial vision and in the coordination between vision and body movements; and the ventral stream (the "what" stream) extends to the temporal lobe and is specialized in identifying the form, color, and meaning of objects.

Primary Visual Cortex (V1)

The primary visual cortex (the striate cortex) surrounds the calcarine fissure. Functionally, V1 is organized in modules, each of which processes a variety of visual features within a very small area of the visual field. Most neurons in the striate cortex are binocular and produce response patterns that probably contribute to depth perception. Simple cells and complex cells contribute to the perception of orientation, location, and size of lines within their receptive fields. The blob areas are probably associated with the perception of color.

V2 Area

The V2 area is adjacent to the primary visual cortex (V1). Cells of the V2 area are organized in a retinotopic organization and are sensitive to all visual features. In monkeys, the V2 area includes cells organized in the form of thin and thick stripes separated by interstripe areas. The neural pathway specializing in the processing of color extends from the parvocellular system in the lateral geniculate nucleus (LGN)

proceeds to the blobs in the primary visual cortex, and continues from there to the thin stripes in V2. The pathway specializing in the processing of form mainly extends from the parvocellular system, proceeds to the interblob areas in V1, and continues from there to the interstripe areas in V2. The pathway specializing in motion and depth processing extends from the magnocellular system, continues into the interblob areas, and continues from there to the thick stripes in V2.

V3 Area
The V3 area is organized in a retinotopic organization and is mainly involved in the processing of form. Many cells in the V3 area of monkeys are sensitive to orientation, direction of motion, and retinal disparity; but are insensitive to color.

V3a Area
The V3a area is similar in function to V3 and is also organized in a retinotopic organization. Cells in V3a are sensitive to orientation and retinal disparity but not to color. A number of findings indicate that in humans, unlike monkeys, the cells in V3a are also sensitive to form.

Ventral Posterior (VP) Area
The VP area is organized in a *retinotopic organization* and seems to be involved in both form and color processing.

V4 Area—Form and Color Processing
Neurons in the V4 area of monkeys mainly receive information from the parvocellular system. These cells are sensitive to orientation and are specialized in form processing. The information processed in V4 is subsequently transferred to the inferior temporal cortex (ventral visual stream), where the objects are identified. Area V4 is also involved in color processing. Like ganglion cells in the retina and the *parvocellular* neurons in the lateral geniculate nucleus (LGN), V4 cells respond to pairs of opponent colors, but their response patterns are far more complex. Lesions in area V4 can lead to color blindness, or achromatopsia. Achromatopsic patients cannot imagine colors and they describe what they see as a "black and white film."

Lateral Occipital (LO) Area
The lateral occipital (LO) area in the human brain specializes in perception of objects, faces, and complex shapes. PET and fMRI studies in humans have shown that cells in this area mainly respond to meaningful visual stimuli, such as faces, figures, and objects. Their responsiveness decreases when simple stimuli (lines, dots) or non-object stimuli (various textures) are presented. (See the "Form Perception" video clip.)

V5 – Processing Movement
The V5 area is also known as the Medial Temporal (MT) area. In the monkey brain this area receives input directly from the striate cortex (V1) and from areas V2, V3, and V4. It also receives input from the superior colliculi, which are related to visual reflexes and tracking objects in motion.

Most cells in the V5 area are arranged in a patchy distribution and exhibit a preference for one direction over the opposite direction of motion. Experiments in monkeys have demonstrated that perception of motion direction can be changed by brain stimulation with microelectrodes inserted into V5. Lesions in this area in monkeys severely impair the ability to perceive moving stimuli. In humans, the area responsible for perception of motion (corresponding to V5 in monkeys) seems to be

located at the junction of the occipital, parietal, and *temporal lobes*. As in monkeys, patients with lesions in the corresponding area experience difficulties in motion perception, a condition known as motion agnosia.

Dorsal Visual Stream (The "Where" or "How" Stream)
The dorsal visual streamis one of the two main streams of visual processing. The dorsal stream mainly receives input from the magnocellular system, which extends from the *striate cortex* (V1) to the V5 area and continues to the posterior parietal lobe. The dorsal visual stream is specialized in perception of object location in space, perception of spatial relations between objects, and perception of motion. The ability to direct attention to a certain stimulus or area in space is also ascribed to the posterior parietal lobe. Some researchers claim that the role of the dorsal stream is not only to identify the movement and location of objects in space, but also, and perhaps mainly, to guide motor-visual activities associated with objects and their location in space. In other words, this stream assists in coordinating between vision and behavior, and is therefore also called the "how" stream. This hypothesis is corroborated by the fact that the parietal lobe has many connections with higher motor areas in the frontal lobe. In optic ataxia syndrome, which is caused by *lesions* in the dorsal stream, the patient's ability to reach out his/her hand and hold an identified object is impaired (see the "Optic Ataxia" video clip in "Brain Lesions in the Visual Cortex").

Ventral visual stream (The "What" Stream)
The ventral visual stream extends from the *striate cortex* (V1) to the extrastriate cortex (mainly V4), then continues downward until it reaches the inferior temporal lobe. The ventral stream is associated with visual recognition of objects and is therefore called the "what" stream. In the past, it was thought that this stream receives input solely from the parvocellular system, but new studies have shown that it also receives input from the magnocellular system.

The inferior temporal lobe of primates carries out complex processing of form and color; this seems to help the perception and identification of three-dimensional objects. Among monkeys, the inferior temporal cortex comprises two central sub-areas, the TEO (occipital temporal) and the IT (inferior temporal) areas. Neurons in these areas have large receptive fields (that can cover almost the entire field of vision) and are maximally sensitive to objects or object parts. Some neurons in the IT selectively respond to specific complex stimuli (such as faces) presented across varying angles, colors, or sizes. In humans, the lateral occipital (LO) area on the boundary between the occipital lobe and the temporal lobe seems to correspond functionally to the IT area in monkeys. PET and fMRI studies in humans have shown that LO cells, like IT cells in monkeys, mainly respond to visual stimuli such as faces, figures, objects, and parts of objects (see the video clip "Form Perception.")

Form Perception in Associative Visual Areas

The video clip demonstrates how associative areas within the ventral visual stream participate in the identification of complex figures. A subject's brain is scanned by an MRI scanner while the subject is looking at visual stimuli presented on a computer screen. The coronal MRI section shows the posterior part of the brain. In the lower part of the section one can see the cerebellum— at the center are the primary visual areas, while on both sides are the ventral associative visual areas in the lateral occipital lobe.

Superimposed on the MRI section are data based on –an fMRI—a technique used for the detection of oxygen consumption by active brain regions. Activation of certain brain areas by the experimental stimulus is associated with increased neural activity, increased blood flow, and increased oxygen consumption. The increased oxygen consumption is represented in the clip by blotches of color that appear across the brain section (the brighter, white-yellow hues denote the highest level of brain activity).

The subject is presented with two alternate types of stimuli: a grid of black and white lines in different orientations, or a figure-like image at the center of the screen. Looking at the grid of lines mainly activates the central areas of the occipital lobe (areas V1, V2, and V3), while looking at the figure-like image mainly activates the lateral and inferior parts of the occipital lobes (areas V4 and LO). Thus, primary and secondary visual areas mainly react to simple lines with sharp contrast, while higher associative areas mainly respond to visual stimuli such as faces, figures, objects, and parts of objects.

(Animation based on data from Malach, R., & Grill-Spector, K., Weizmann Institute of Science, Rehovot, Israel; and Kushnir, T., & Yaakov, I., The Chaim Sheba Medical Center, Tel Hashomer, Israel.)

Brain Lesions in The Visual Cortex

Human Head Injuries

This section presents a number of patients suffering from various neuropsychological impairments. Such impairments serve as an important tool in the study of higher brain functions. At the same time, one should not forget the suffering and agony experienced by patients and their families due to the loss of essential cognitive abilities. All video clips presented in the CD were taken with the consent of the patients appearing in the clips.

Hemianopia

Hemianopia is a loss of vision in half of the visual field caused by lesions of the contralateral primary visual cortex or the optic radiation fibers that carry visual information into this area. The video clip shows a patient suffering from hemianopia affecting the right hemifield. Looking forward, the patient can see the physician's finger only when wiggled across the left half of his visual field. However, the patient does not see the finger once it shifts to the right visual hemifield.
(Movie provided by Rafal, R., School of Psychology, University of Wales, Bangor, UK and Sharon Posner, Perpetua Productions, "Deficits of Mind & Brain".)

Simultanagnosia

Simultanagnosia (one of three symptoms included within Balint's syndrome) is an inability to perceive more than one object at a time. The patient is capable of focusing on and identifying an object, while at the same time failing to perceive another object, even when the latter object is close to the first one. In the clip, a simultanagnosia patient easily identifies a comb when presented alone, but cannot identify a teaspoon presented across the comb. Later on, the patient reports seeing the teaspoon, but now fails to see the comb, and vice versa. At the end of the clip, the patient's attention is suddenly drawn to the blackboard behind the physician. Now the patient can only see the marks on the board, but cannot see the teaspoon or the comb, although they are presented before him.

Although simultanagnosia patients can see objects in the entire visual field, they find it difficult to pay attention to a number of objects simultaneously. When they perceive an object, it is liable to spontaneously disappear and be displaced by another object. For example, the patient in the clip suddenly lost sight of the teaspoon and the comb, while the blackboard popped out in his visual field. In addition, simultanagnosia patients find it hard to track objects in motion or identify spatial relations between objects. This condition is usually caused by bilateral *lesions* in the parietooccipital cortex or lesions in the inferior occipitotemporal area of the left hemisphere.
(Movie provided by Rafal, R., School of Psychology, University of Wales, Bangor, UK and Sharon Posner, Perpetua Productions, "Deficits of Mind & Brain".)

Impaired Perception of the Whole

Lesions in the associative visual cortex can lead to difficulties in the perception of objects and the relationships among identified objects (perception of the whole). In the video clip, a patient is looking at a photograph of a room decorated for Christmas. The patient, whose voice is heard, describes what he sees in the photograph. The description is slow and halting, as the patient scans each detail in the picture one at a time. Since he fails to comprehend the general context of the picture (the inside of a room decorated for Christmas), he finds it difficult to identify the objects in the photograph. For example, the patient hesitates as to the identity of the dog (real or a model) and of the fir tree (a tree or a bush). In the case of the tree, the patient ignores the decorations hanging on it, and does not recognize it as a Christmas tree. Instead, he assumes that what he sees is a tree in the garden outside the house. He identifies the painting on the wall in the photograph, but then immediately changes his mind and says that it is actually a window, for otherwise, conflict would arise with his prior understanding that the photograph has been taken outside the house. Following the same line of reasoning, he identifies the gifts under the Christmas tree as a collection of decorative stones along the garden path. The patient's difficulty in perception of the meaning of the scene as a whole subsequently affects the identification of the objects in the picture.
(Movie derived from Broken Images The BBC)

Prosopagnosia

Prosopagnosia is an inability to identify faces (the word *prosopon* means "face"). The patient is usually aware of the fact that he is looking at a face and can even describe the features and the expression, but is unable to identify a familiar face, even if the face is that of a family member or a close friend. Such a patient can identify faces by special visual characteristics (such as a mustache or special glasses) or by other sense modalities (such as the voice of a person). The following video clip presents a French prosopagnosia patient who finds it difficult to identify the face of a well-known French figure, Charles de Gaulle. She describes precisely the specific features of the face, such as the look in his eyes, but these details are not integrated into a recognized face. In the second part of the clip, she is shown a picture of the physician who is sitting by her side. Here, too, the patient focuses on facial details but fails to recognize the face of the physician talking to her.

Prosopagnosia can occur even when the patient has no apparent difficulty recognizing other objects. The precise site of brain lesions causing prosopagnosia is still in dispute. Some evidence suggests that this condition is associated with lesions in the junction of the parietal and occipital lobes (parietooccipital area); other evidence ascribes the lesion to the inferior occipitotemporal area. The lesion is usually bilateral, but there are known cases with lesions in the right hemisphere alone.

(Video clip derived from *The Brain Modules: The Two Brains*, The Annenberg/CPB Projects, 901 E Street, NW, Washington, D.C. 20004.)

Optic Ataxia

Optic ataxia (one of the three symptoms included in Balint's syndrome) is a difficulty in reaching objects under visual guidance. People suffering from visual ataxia are capable of seeing a certain object, identifying it, and even describing it in detail, but are unable to reach out with their hand and grasp it. Their reaching movement does not correspond to the direction and distance of the object. The problem does not arise from any motor defect, but from an inability to coordinate between eye and hand movement. The brain lesion leading to optic ataxia is usually located in the upper part of the parietal lobe. The damage can be either unilateral or bilateral.

The following video clip presents a patient suffering from optic ataxia who finds it difficult to reach his right hand to a teaspoon presented before him. When the physician wiggles the teaspoon, the patient's ability to grasp the teaspoon with his right hand somewhat improves.
(Movie provided by Rafal, R., School of Psychology, University of Wales, Bangor, UK and Sharon Posner, Perpetua Productions, "Deficits of Mind & Brain".)

Neglect Syndrome

A patient suffering from neglect syndrome finds it difficult to report, respond, or orient to information in the visual field contralateral to the lesioned hemisphere. The difficulty is usually explained as a reduced ability to direct attention to the neglected area. The patient is often unaware of his condition and in certain cases the patient may even deny or disown half of his body. For example, a patient with neglect syndrome may shave only one side of his face or wear just the right sleeve of his shirt, ignoring the left sleeve. In many cases, symptoms of neglect are moderate and could be noticed only in certain contexts. For example, a patient with neglect syndrome is capable of reporting a single stimulus presented in the neglected visual hemifield, but fails to perceive such a stimulus when another stimulus is presented simultaneously in the ipsilateral visual field. This type of neglect is known as "extinction." Although neglect syndrome can occur following *lesions* in the right or left hemispheres, it is most commonly associated with lesions in the right hemisphere. The lesions are usually in the inferior posterior parietal lobe. Additional areas associated with this syndrome are the frontal lobe, the basal ganglia, and certain parts of the thalamus.

The following clip presents a number of neglect syndrome characteristics. The clip first presents neglect of information within the left-sided space, showing drawings made by neglect syndrome patients, such as a clock with numbers on the right side only or a flower without petals on its left side. The next example presented in the clip is that of object neglect, characterized by the neglect of details located in the left part of an object, even if the entire object is within the right visual field. Note how the picture drawn by the neglect syndrome patient lacks some of the details of the tree and the house, although these details are located in the right and central part of the picture.
(Video clip derived from *The Experience of Visual Neglect*, by Halligan, P., Rivermead Rehabilitation Center, John Radcliffe Hospital, Oxford Medical Illustration: University of Oxford.)