

NOTES FROM MODULE 5.1

GENERAL PRINCIPLES OF PERCEPTION:

You see an object when it emits or reflects light that stimulates receptors that transmit information to your brain. The brain codes information largely in terms of which neurons are active, and how active they are at any moment. Impulses in certain neurons indicate light, whereas impulses in others indicate sound, touch, or other sensations. Johannes Müller (1838) described this as the law of specific nerve energies.

THE EYE AND ITS CONNECTIONS TO THE BRAIN:

Light enters the eye through an opening in the centre of the iris called the pupil. It is focused by the lens (adjustable) and cornea (not adjustable) and projected onto the retina, the rear surface of the eye, which is lined with visual receptors.

In the vertebrate retina messages go from the receptors at the back of the eye to bipolar cells, located closer to the centre of the eye. The bipolar cells send their messages to ganglion cells, located still closer to the centre of the eye. The ganglion cells' axons join together and travel back to the brain. Additional cells called amacrine cells get information from bipolar cells and send it to other bipolar, amacrine, and ganglion cells. Amacrine cells refine the input to ganglion cells, enabling certain ones to respond mainly to particular shapes, directions of movement, changes in lighting, colour, and other visual features.

One consequence of this anatomy is that light passes through the ganglion, amacrine, and bipolar cells en route to the receptors. However, these cells are transparent, and light passes through them without distortion, a more important consequence is the blind spot. The ganglion cell axons join to form the optic nerve that exits through the back of the eye. The point at which it leaves is a blind spot because it has no receptors.

VISUAL RECEPTORS - RODS AND CONES:

The vertebrate retina contains two types of receptors: rods and cones. The rods, abundant in the periphery of the human retina, respond to faint light but are not useful in daylight because bright light bleaches them. Cones, abundant in and near the fovea, are less active in dim light, more useful in bright light, and essential for colour vision.

Characteristic:	Foveal Vision	Peripheral Vision
Receptors	Cones only	Proportion of rods increases toward periphery
Convergence of input	Each ganglion cell excited by a single cone	Each ganglion cell excited by many receptors
Brightness sensitivity	Distinguishes among bright lights; responds poorly to dim light	Responds to dim light; poor for distinguishing among bright lights
Sensitivity to detail	Good detail vision because each cone's own ganglion cell sends a message to the brain	Poor detail vision because many receptors converge their input onto a given ganglion cell
Colour vision	Good (many cones)	Poor (few cones)

Both rods and cones contain photopigments, chemicals that release energy when struck by light. Photopigments consist of opsins, which modify the photopigment's sensitivity to different wavelengths of light.

COLOUR VISION:

Visible light consists of electromagnetic radiation within the range from less than 400 nanometres to more than 700 nanometres. We perceive the shortest visible wavelength as violet. Progressively longer wavelengths are perceived as blue, green, yellow, orange, and red. We call these wavelengths "light" only because the receptors in our eyes are tuned to detecting them.

According to the Young-Helmholtz theory, we perceive colour through the relative rates of response by three kinds of cones, each one maximally sensitive to a different set of wavelengths. He found that people could match any colour by mixing appropriate amounts of just three wavelengths. Therefore, he concluded that three kinds of cones - are sufficient to account for human colour vision.

Ewald Hering (19th century) proposed the opponent-process theory: we perceive colour in terms of opposites. That is, the brain has a mechanism that perceives colour on a continuum from red to green, another from yellow to blue, and another from white to black. After you stare at one colour in one location long enough, you fatigue that response and swing to the opposite.

To account for colour and brightness constancy, Edwin Land proposed the retinex theory: the cortex compares information from various parts of the retina to determine the brightness and colour for each area.

NOTES FROM MODULE 5.2

AN OVERVIEW OF THE MAMMALIAN VISUAL SYSTEM:

The axons of the ganglion cells form the optic nerve, which leaves the retina and travels along the lower surface of the brain. The optic nerves from the two eyes meet at the optic chiasm, where, in humans, half of the axons from each eye cross to the opposite side of the brain.

PROCESSING IN THE RETINA:

Lateral inhibition is the retina's way of sharpening contrasts to emphasise the borders of objects. The receptors send messages to excite nearby bipolar cells and also send messages to horizontal cells that slightly inhibit those bipolar cells and the neighbours to their sides. The net result is to heighten the contrast between an illuminated area and its darker surround.

Light striking the rods and cones decreases their spontaneous output, and the receptors make inhibitory synapses onto the bipolar cells. Therefore, light on the rods or cones decreases their inhibitory output. A decrease in inhibition means net excitation.

Lateral inhibition is the reduction of activity in one neuron by activity in neighbouring neurons. Lateral inhibition heightens contrast. When light falls on a surface, the bipolars just inside the border are most excited, and those outside the border respond the least. Lateral inhibition is important for many functions in the nervous system. In olfaction, a strong stimulus can suppress the response to another one that follows slightly after it, because of inhibition in the olfactory bulb. In touch, stimulation of one spot on the skin weakens the response to stimulation of a neighbouring spot, again by lateral inhibition. In hearing, inhibition makes it possible to understand speech amid irrelevant noise.

FURTHER PROCESSING:

Each cell in the visual system of the brain has a receptive field, an area in visual space that excites or inhibits it. the receptive field of a rod or cone is simply the point in space from which light strikes the cell. Other visual cells derive their receptive fields from the connections they receive.

A rod or cone has a tiny receptive field in space to which it is sensitive. One or more receptors connect to a bipolar cell, with a receptive field that is the sum of the receptive fields of all those rods or cones connected to it (including both excitatory and inhibitory connections). Several bipolar cells report to a ganglion cell, which therefore has a still larger receptive. The receptive fields of several ganglion cells converge to form the receptive field at the next level, and so on.

Primate ganglion cells fall into three categories: parvocellular, magnocellular, and koniocellular. The parvocellular neurons, with small cell bodies and small receptive fields, are mostly in or near the fovea. They are well suited to detect visual details. They also respond to colour, each neuron being excited by some wavelengths and inhibited by others. The high sensitivity to detail and colour relates to the fact that parvocellular cells are located mostly in and near the fovea, which has many cones.

The magnocellular neurons, with larger cell bodies and receptive fields, are distributed evenly throughout the retina. They respond strongly to movement and large overall patterns, but they do not respond to colour or fine details. Magnocellular neurons are found throughout the retina, including the periphery.

The koniocellular neurons have small cell bodies, similar to the parvocellular neurons, but they occur throughout the retina. They have several functions, and their axons terminate in several locations.

Axons from the ganglion cells form the optic nerve, which proceeds to the optic chiasm, where half of the axons cross to the opposite hemisphere. Most of the axons go to the lateral geniculate nucleus of the thalamus. Cells of the lateral geniculate have receptive fields that resemble those of the ganglion cells - an excitatory or inhibitory central portion and a surrounding ring with the opposite effect. After the information reaches the cerebral cortex, the receptive fields become more complicated.

THE PRIMARY VISUAL CORTEX:

Information from the lateral geniculate nucleus of the thalamus goes to the primary visual cortex in the occipital cortex. People with damage to this area report no conscious vision, no visual imagery, and no visual images in their dreams. In contrast, adults who lose vision because of eye damage continue to have visual imagery and visual dreams.

People often show blindsight, the ability to respond in limited ways to visual information without perceiving it consciously. Within the damaged part of the visual field, they are unaware of visual input, unable even to distinguish between bright sunshine and utter darkness. Nevertheless, they might be able to point accurately to something in the area where they cannot see, or move their eyes toward it, while insisting that they are "just guessing".

cell has a receptive field with fixed excitatory and inhibitory zones. The more light shines in the excitatory zone, the more the cell responds. The more light shines in the inhibitory zone, the less the cell responds.

Unlike simple cells, complex cells, located in areas V1 and V2, do not respond to the exact location of a stimulus. A complex cell responds to a pattern of light in a particular orientation anywhere within its large receptive field. Most complex cells respond most strongly to a stimulus moving in a particular direction. The best way to classify a cell as simple or complex is to present the stimulus in several locations. A cell that responds to a stimulus in only one location is a simple cell. One that responds equally throughout a large area is a complex cell.

End-stopped, or hypercomplex, cells resemble complex cells with one exception: an end-stopped cell has a strong inhibitory area at one end of its bar-shaped receptive field. The cell responds to a bar-

shaped pattern anywhere in its broad receptive field, provided the bar does not extend beyond a certain point.

	Simple Cells	Complex Cells	End-stopped Cells
Location	V1	V1 and V2	V1 and V2
Binocular input?	Yes	Yes	Yes
Size of receptive field	Smallest	Medium	Largest
Shape of receptive field	Bar- or edge-shaped, with fixed excitatory and inhibitory zones.	Bar- or edge-shaped, but responding equally throughout a large receptive field.	Same as complex cell, but with a strong inhibitory zone at one end.

Some cells might be feature detectors - neurons whose responses indicate the presence of a particular feature. Supporting the idea of feature detectors is the fact that prolonged exposure to a given visual feature decreases sensitivity to that feature, as if it fatigued the relevant detectors.

DEVELOPMENT OF THE VISUAL CORTEX:

For each aspect of visual experience, researchers identify a sensitive period, when experiences have a particularly strong and enduring influence. The sensitive period depends on inhibitory neurons.

Most neurons in the human visual cortex respond to both eyes - specifically, to approximately corresponding areas of both eyes. By comparing the inputs from the two eyes, you achieve stereoscopic depth perception.

Stereoscopic depth perception requires the brain to detect retinal disparity, the discrepancy between what the left and right eyes see. Experience fine-tunes binocular vision, and abnormal experience disrupts it. Each neuron in the visual cortex becomes responsive to one eye or the other, and few neurons respond to both. The behavioural result is poor depth perception.

Certain children are born with strabismus, also known as "lazy eye", a condition in which the eyes do not point in the same direction. Generally, these children attend to one eye and not the other. The usual treatment is to put a patch over the active eye, forcing attention to the other one. A promising therapy for lazy eye is to ask a child to play three-dimensional action video games that require attention to both eyes. Good performance requires increasing attention to exactly the kind of input we want to enhance. This procedure appears to improve the use of both eyes better than patching does, although neither procedure has much effect on stereoscopic depth perception.

About 70% of all infants have astigmatism, a blurring of vision for lines in one direction (e.g. horizontal, vertical, or one of the diagonals), caused by an asymmetric curvature of the eyes. Normal growth reduces the prevalence of astigmatism to about 10% in 4-year-old children.

NOTES FROM MODULE 5.3

THE VENTRAL AND DORSAL PATHS:

The primary visual cortex (V1) sends information to the secondary visual cortex (V2), which processes the information further and transmits it to additional areas. The connections in the visual

cortex are reciprocal. For example, V1 sends information to V2, and V2 returns information to V1. From V2, the information branches out in several directions for specialised processing.

The ventral stream through the temporal cortex is the perception pathway or the "what" pathway because of its importance for identifying and recognising objects. The dorsal stream through the parietal cortex is the action pathway or the "how" pathway, because of its importance for visually guided movements.

People with damage to the dorsal stream (parietal cortex) have somewhat the opposite problem: they see objects but they don't integrate their vision well with their arm and leg movements. They can read, recognise faces, and describe objects in detail but they cannot accurately reach out to grasp an object. While walking, they can describe what they see, but they bump into objects, oblivious to their location.

DETAILED ANALYSIS OF SHAPE:

As visual information goes from the simple cells to the complex cells and then to other brain areas, the receptive fields become larger and more specialised. In the secondary visual cortex (V2), just anterior to V1 in the occipital cortex, most cells are similar to V1 cells in responding to lines, edges, or sine wave gratings, except that V2 receptive fields are more elongated. Also, some V2 cells respond best to corners, textures, or complex shapes. Areas V2 and V3 have some cells highly responsive to colour, and other cells highly responsive to the disparity between what the left and right eyes see - critical information for stereoscopic depth perception.

Cells in the inferior temporal cortex learn to recognise meaningful objects. A cell that responds to the sight of some object initially responds mainly when it sees that object from the same angle, but after a bit of experience it learns to respond almost equally to that object from other viewpoints. It is responding to the object, regardless of major changes in the pattern that reaches the retina.

Visual agnosia (meaning "virtual lack of knowledge") is an inability to recognise objects despite otherwise satisfactory vision. It is a common result from damage in the temporal cortex. Someone might be able to point to visual objects and slowly describe them but fail to recognise what they are.

One part of the parahippocampal cortex responds strongly to pictures of places, and not so strongly to anything else. Part of the fusiform gyrus of the inferior temporal cortex, especially in the right hemisphere, responds more strongly to faces than to anything else. And an area close to this face area responds more strongly to bodies than to anything else.

FACIAL RECOGNITION:

People vary considerably in their ability to recognise faces, and the reason is not just that some people don't care or don't pay attention. People with severe problems are said to have prosopagnosia, meaning impaired ability to recognise faces. That problem can result from damage to the fusiform gyrus, or from a failure of that gyrus to develop fully.

MOTION PERCEPTION:

Two areas especially important for motion perception are area MT (for middle temporal cortex), and an adjacent region, area MST (medial superior temporal cortex). These areas receive input mostly from the magnocellular path, which detects overall patterns, including movement over large areas of the visual field. Given that the magnocellular path is colour insensitive, MT is also colour insensitive. Most cells in area MT respond selectively when something moves at a particular speed in a particular direction. MT cells detect acceleration or deceleration as well as the absolute speed, and they respond to motion in all three dimensions. Area MT also responds to photographs that imply

movement, such as a photo of people running. People who had electrical stimulation of area MT (while they were undergoing exploratory studies to find the cause of their severe epilepsy) report seeing vibrations or other hallucinated movements during the stimulation. They also become temporarily impaired at seeing something that really is moving. Cells in the dorsal part of area MST respond best to more complex stimuli, such as the expansion, contraction, or rotation of a large visual scene. In short, MT and MST neurons enable you to distinguish between the result of eye movements and the result of object movements.

Motion blindness is when you're able to see objects but unable to see whether they are moving or, if so, which direction and how fast. People with motion blindness are better at reaching for a moving object than at describing its motion.

NOTES FROM MODULE 6.1

SOUND AND THE EAR:

Sound waves are periodic compressions of air, water, or other media. Sound waves vary in amplitude and frequency. The amplitude of a sound wave is its intensity. In general, sounds of greater amplitude seem louder, but exceptions occur.

The frequency of a sound is the number of compressions per second, measured in hertz. Pitch is the related aspect of perception. Sounds higher in frequency are higher in pitch. The height of each wave corresponds to amplitude, and the number of waves per second corresponds to frequency.

In addition to amplitude and pitch, the third aspect of sound is timbre, meaning tone quality or tone complexity. Two musical instruments playing the same note at the same loudness sound different, as do two people singing the same note at the same loudness.

People communicate emotion by alterations in pitch, loudness, and timbre. Conveying emotional information by tone of voice is known as prosody.

The outer ear includes the pinna, the familiar structure of flesh and cartilage attached to each side of the head. By altering the reflections of sound waves, the pinna helps us locate the source of a sound. When sound waves reach the middle ear, they vibrate the tympanic membrane, or eardrum. The tympanic membrane connects to three tiny bones that transmit the vibrations to the oval window, a membrane of the inner ear.

When the stirrup vibrates the oval window, it sets into motion the fluid in the cochlea, the snail-shaped structure of the inner ear. The auditory receptors, known as hair cells, lie between the basilar membrane of the cochlea on one side and the tectorial membrane on the other. Vibrations in the fluid of the cochlea displace the hair cells, thereby opening ion channels in its membrane.

PITCH PERCEPTION:

Soft sounds activate fewer neurons, and stronger sounds activate more. Thus, at low frequencies, the frequency of impulses identifies the pitch, and the number of firing cells identifies loudness.

As sounds exceed 100Hz, it becomes harder for any neuron to continue firing in synchrony with the sound waves. At higher frequencies, a neuron might fire on some of the waves and not others. Its action potentials are phase-locked to the peak of the sound waves (i.e. they occur at the same phase in the sound wave).

According to the volley principle of pitch discrimination, the auditory nerve as a whole produces volleys of impulses for sounds up to about 4000 per second, even though no individual axon approaches that frequency.

THE AUDITORY CORTEX:

The auditory system has a pathway in the anterior temporal cortex specialised for identifying sounds, and a pathway in the posterior temporal cortex and the parietal cortex specialised for locating sounds. Patients with damage in parts of the superior temporal cortex become motion deaf. They hear sounds, but they do not detect that a source of a sound is moving.