INTRODUCTION
Sense of vision is a complex function of the two eyes and their central connections. The physiological activities involved in the normal functioning of the eyes are:
- Maintenance of clear ocular media,
- Maintenance of normal intraocular pressure,
- The image forming mechanism,
- Physiology of vision,
- Physiology of binocular vision,
- Physiology of pupil, and
- Physiology of ocular motility.

MAINTENANCE OF CLEAR OCULAR MEDIA
The main prerequisite for visual function is the maintenance of clear refractive media of the eye. The major factor responsible for transparency of the ocular media is their avascularity. The structures forming refractive media of the eye from anterior to posterior are:
- Tear film,
- Cornea,
- Aqueous humour,
- Crystalline lens, and
- Vitreous humour

PHYSIOLOGY OF TEARS
Tear film plays a vital role in maintaining the transparency of cornea. The physiological aspects of the tears and tear film are described in the chapter on diseases of the lacrimal apparatus (see page 388).

PHYSIOLOGY OF CORNEA
The cornea forms the main refractive medium of the eye. Physiological aspects in relation to cornea include:
- Transparency of cornea,
- Nutrition and metabolism of cornea,
- Permeability of cornea, and
- Corneal wound healing.
(For details see page 90).

PHYSIOLOGY OF CRISTALLINE LENS
The crystalline lens is a transparent structure playing main role in the focussing mechanism for vision. Its physiological aspects include:
- Lens transparency
- Metabolic activities of the lens and
- Accommodation.
(For details see page 40 and 178).
PHYSIOLOGY OF AQUEOUS HUMOUR AND MAINTENANCE OF INTRAOCULAR PRESSURE

The aqueous humour is a clear watery fluid filling the anterior chamber (0.25 ml) and the posterior chamber (0.06 ml) of the eyeball. In addition to its role in maintaining a proper intraocular pressure it also plays an important metabolic role by providing substrates and removing metabolites from the avascular cornea and the crystalline lens. For details see pages 219-222.

PHYSIOLOGY OF VISION

Physiology of vision is a complex phenomenon which is still poorly understood. The main mechanisms involved in physiology of vision are:

- **Initiation of vision** (Phototransduction), a function of photoreceptors (rods and cones),
- **Processing and transmission of visual sensation**, a function of image processing cells of retina and visual pathway, and
- **Visual perception**, a function of visual cortex and related areas of cerebral cortex.

PHOTOTRANSDUCTION

The rods and cones serve as sensory nerve endings for visual sensation. Light falling upon the retina causes photochemical changes which in turn trigger a cascade of biochemical reactions that result in generation of electrical changes. Photochemical changes occurring in the rods and cones are essentially similar but the changes in rod pigment (rhodopsin or visual purple) have been studied in more detail. This whole phenomenon of conversion of light energy into nerve impulse is known as phototransduction.

Photochemical changes

The photochemical changes include:

**Rhodopsin bleaching.** Rhodopsin refers to the visual pigment present in the rods – the receptors for night (scotopic) vision. Its maximum absorption spectrum is around 500 nm. Rhodopsin consists of a colourless protein called opsin coupled with a carotenoid called retinine (Vitamin A aldehyde or 11-cis-retinal). Light falling on the rods converts 11-cis-retinal component of rhodopsin into all-trans-retinal through various stages (Fig. 2.1). The all-trans-retinal so formed is soon separated from the opsin. This process of separation is called photodecomposition and the rhodopsin is said to be bleached by the action of light.

**Rhodopsin regeneration.** The 11-cis-retinal is regenerated from the all-trans-retinal separated from the opsin (as described above) and vitamin-A (retinal) supplied from the blood. The 11-cis-retinal then reunites with opsin in the rod outer segment to form the rhodopsin. This whole process is called rhodopsin regeneration (Fig. 2.1). Thus, the bleaching of the rhodopsin occurs under the influence of light, whereas the regeneration process is independent of light, proceeding equally well in light and darkness.

![Fig. 2.1. Light induced changes in rhodopsin.](image-url)
Electrical changes
The activated rhodopsin, following exposure to light, triggers a cascade of complex biochemical reactions which ultimately result in the generation of receptor potential in the photoreceptors. In this way, the light energy is converted into electrical energy which is further processed and transmitted via visual pathway.

PROCESSING AND TRANSMISSION OF VISUAL IMPULSE
The receptor potential generated in the photoreceptors is transmitted by electrotonic conduction (i.e., direct flow of electric current, and not as action potential) to other cells of the retina viz. horizontal cells, amacrine cells, and ganglion cells. However, the ganglion cells transmit the visual signals by means of action potential to the neurons of lateral geniculate body and the later to the primary visual cortex.

The phenomenon of processing of visual impulse is very complicated. It is now clear that visual image is deciphered and analyzed in both serial and parallel fashion.

Serial processing. The successive cells in the visual pathway starting from the photoreceptors to the cells of lateral geniculate body are involved in increasingly complex analysis of image. This is called sequential or serial processing of visual information.

Parallel processing. Two kinds of cells can be distinguished in the visual pathway starting from the ganglion cells of retina including neurons of the lateral geniculate body, striate cortex, and extrastriate cortex. These are large cells (magn or M cells) and small cells (parvo or P cells). There are striking differences between the sensitivity of M and P cells to stimulus features (Table 2.1).

<table>
<thead>
<tr>
<th>Stimulus feature</th>
<th>Sensitivity</th>
<th>M cell</th>
<th>P cell</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colour contrast</td>
<td>No</td>
<td>Yes</td>
<td></td>
</tr>
<tr>
<td>Luminance contrast</td>
<td>Higher</td>
<td>Lower</td>
<td></td>
</tr>
<tr>
<td>Spatial frequency</td>
<td>Lower</td>
<td>Higher</td>
<td></td>
</tr>
<tr>
<td>Temporal frequency</td>
<td>Higher</td>
<td>Lower</td>
<td></td>
</tr>
</tbody>
</table>

The visual pathway is now being considered to be made of two lanes: one made of the large cells is called magnocellular pathway and the other of small cells is called parvocellular pathway. These can be compared to two-lanes of a road. The M pathway and P pathway are involved in the parallel processing of the image i.e., analysis of different features of the image.

VISUAL PERCEPTION
It is a complex integration of light sense, form sense, sense of contrast and colour sense. The receptive field organization of the retina and cortex are used to encode this information about a visual image.

1. The light sense
It is awareness of the light. The minimum brightness required to evoke a sensation of light is called the light minimum. It should be measured when the eye is dark adapted for at least 20-30 minutes.

The human eye in its ordinary use throughout the day is capable of functioning normally over an exceedingly wide range of illumination by a highly complex phenomenon termed as the visual adaptation. The process of visual adaptation primarily involves:

- Dark adaptation (adjustment in dim illumination), and
- Light adaptation (adjustment to bright illumination).

Dark adaptation
It is the ability of the eye to adapt itself to decreasing illumination. When one goes from bright sunshine into a dimly-lit room, one cannot perceive the objects in the room until some time has elapsed. During this period, eye is adapting to low illumination. The time taken to see in dim illumination is called ‘dark adaptation time’.

The rods are much more sensitive to low illumination than the cones. Therefore, rods are used
more in dim light (scotopic vision) and cones in bright light (photopic vision).

**Dark adaptation curve** (Fig. 2.3) plotted with illumination of test object in vertical axis and duration of dark adaptation along the horizontal axis shows that visual threshold falls progressively in the darkened room for about half an hour until a relative constant value is reached. Further, the dark adaptation curve consists of two parts: the initial small curve represents the adaptation of cones and the remainder of the curve represents the adaptation of rods.

![Fig. 2.3. Dark adaptation curve plotted with illumination of test object in vertical axis and duration of dark adaptation along the horizontal axis.]

When fully dark adapted, the retina is about one lakh times more sensitive to light than when bleached. **Delayed dark adaptation** occurs in diseases of rods e.g., retinitis pigmentosa and vitamin A deficiency.

**Light adaptation**

When one passes suddenly from a dim to a brightly lighted environment, the light seems intensely and even uncomfortably bright until the eyes adapt to the increased illumination and the visual threshold rises. The process by means of which retina adapts itself to bright light is called light adaptation. Unlike dark adaptation, the process of light adaptation is very quick and occurs over a period of 5 minutes. Strictly speaking, light adaptation is merely the disappearance of dark adaptation.

**2. The form sense**

It is the ability to discriminate between the shapes of the objects. Cones play a major role in this faculty. Therefore, form sense is most acute at the fovea, where there are maximum number of cones and decreases very rapidly towards the periphery (Fig. 2.4). Visual acuity recorded by Snellen’s test chart is a measure of the form sense.

**Components of visual acuity.** In clinical practice, measurement of the threshold of discrimination of two spatially separated targets (a function of the fovea centralis) is termed visual acuity. However, in theory, visual acuity is a highly complex function that consists of the following components:

- **Minimum visible.** It is the ability to determine whether an object is present or not.
- **Resolution (ordinary visual acuity).** Discrimination of two spatially separated targets is termed resolution. The minimum separation between the two points, which can be discriminated as two, is known as minimum resolvable. Measurement of the threshold of discrimination is essentially an assessment of the function of the fovea centralis and is termed ordinary visual acuity. Histologically, the diameter of a cone in the foveal region is 0.004 mm and this, therefore, represents the smallest distance between two cones. It is reported that in order to produce an image of minimum size of 0.004 mm (resolving power of the eye) the object must subtend a visual angle of 1 minute at the nodal point of the eye. It is called the minimum angle of resolution (MAR).

The clinical tests determining visual acuity measure the form sense or reading ability of the eye. Thus, broadly, resolution refers to the ability to identify the spatial characteristics of a test figure. The test targets in these tests may either consist of letters (Snellen’s
chart) or broken circle (Landolt’s ring). More complex targets include gratings and checker board patterns.

**Recognition.** It is that faculty by virtue of which an individual not only discriminates the spatial characteristics of the test pattern but also identifies the patterns with which he has had some experience. Recognition is thus a task involving cognitive components in addition to spatial resolution. For recognition, the individual should be familiar with the set of test figures employed in addition to being able to resolve them. The most common example of recognition phenomenon is identification of faces. The average adult can recognize thousands of faces.

Thus, the form sense is not purely a retinal function, as, the perception of its composite form (e.g., letters) is largely psychological.

**Minimum discriminable** refers to spatial distinction by an observer when the threshold is much lower than the ordinary acuity. The best example of minimum discriminable is **vernier acuity**, which refers to the ability to determine whether or not two parallel and straight lines are aligned in the frontal plane.

**3. Sense of contrast**

It is the ability of the eye to perceive slight changes in the luminance between regions which are not separated by definite borders. Loss of contrast sensitivity results in mild fogginess of the vision.

Contrast sensitivity is affected by various factors like age, refractive errors, glaucoma, amblyopia, diabetes, optic nerve diseases and lenticular changes. Further, contrast sensitivity may be impaired even in the presence of normal visual acuity.

**Measurement of contrast sensitivity:** In clinical practice the contrast sensitivity can be measured by using any of the following charts with letters or stripes represented in various shades of gray:

- Arden gratings,
- Cambridge low-contrast gratings,
- Pelli-Robson contrast sensitivity chart which consists of low contrast letters with same size (Fig. 2.5),
- The Visitach chart, and
- Functional acuity contrast test (FACT).

**4. Colour sense**

It is the ability of the eye to discriminate between different colours excited by light of different wavelengths. Colour vision is a function of the cones and thus better appreciated in photopic vision. In dim light (scotopic vision), all colours are seen grey and this phenomenon is called **Purkinje shift.**

**Theories of colour vision**

The process of colour analysis begins in the retina and is not entirely a function of brain. Many theories have been put forward to explain the colour perception, but two have been particularly influential: 1. **Trichromatic theory.** The trichromacy of colour vision was originally suggested by Young and subsequently modified by Helmholtz. Hence it is called **Young-Helmholtz theory.** It postulates the existence of three kinds of cones, each containing a different photopigment which is maximally sensitive to one of the three primary colours viz. red, green and blue. The sensation of any given colour is determined by the relative frequency of the impulse from each of the three cone systems. In other words, a given colour consists of admixture of the three primary colours in different proportion. The correctness of the Young-Helmholtz’s trichromacy theory of colour vision has now been demonstrated by the identification and chemical characterization of each of the three pigments by recombinant DNA technique, each having different absorption spectrum as below (Fig. 2.6):
Red sensitive cone pigment, also known as erythrolabe or long wavelength sensitive (LWS) cone pigment, absorbs maximally in a yellow portion with a peak at 565 nm. But its spectrum extends far enough into the long wavelength to sense red.

Green sensitive cone pigment, also known as chlorolabe or medium wavelength sensitive (MWS) cone pigment, absorbs maximally in the green portion with a peak at 535 nm.

Blue sensitive cone pigment, also known as cyanolabe or short wavelength sensitive (SWS) cone pigment, absorbs maximally in the blue-violet portion of the spectrum with a peak at 440 nm.

Thus, the Young-Helmholtz theory concludes that blue, green and red are primary colours, but the cones with their maximal sensitivity in the yellow portion of the spectrum are at a lower threshold than green.

It has been studied that the gene for human rhodopsin is located on chromosome 3, and the gene for the blue-sensitive cone is located on chromosome X. The genes for the red and green sensitive cones are arranged in tandem array on the q arm of the X chromosomes.

2. Opponent colour theory of Hering. The opponent colour theory of Hering points out that some colours appear to be ‘mutually exclusive’. There is no such colour as ‘reddish-green’, and such phenomenon can be difficult to explain on the basis of trichromatic theory alone. In fact, it seems that both theories are useful in that:

- The colour vision is trichromatic at the level of photoreceptors, and
- Colour opponency occurs at ganglion cell onward.

According to opponent colour theory, there are two main types of colour opponent ganglion cells:

- Red-green opponent colour cells use signals from red and green cones to detect red/green contrast within their receptive field.
- Blue-yellow opponent colour cells obtain a yellow signal from the summed output of red and green cones, which is contrasted with the output from blue cones within the receptive field.

Colour vision tests
(See page 326)