Chapter 4
Biological Bases of Visual Perception

This is the first of a series of chapters on the study of visual perception. Because visual perception has been studied for a long time and because it is easier to illustrate visual phenomena in a book than illustrating phenomena involving any other sensory modality, visual perception has traditionally taken a lot of space in textbooks dedicated to the psychology of perception. The importance of vision in the study of perception may also be explained by the obvious place that this sense occupies in everyday life in humans. This chapter is dedicated to the description of the main biological structures and of some of the mechanisms associated with visual perception.

4.1 The Eye

The eye, which is almost spherical and has a diameter of 2–2.5 cm, is a set of structures which allows the transformation of the light into a code that the brain can understand.

4.1.1 The Eyeball

Figure 4.1 shows the main parts of the eyeball. In its front part, there are ligaments, which hold the lens, and the iris, which is controlling the amount of light entering in the eye. In fact, it is the color of the iris that determines the fact of having, for example, brown or blue eyes. With a diameter ranging from 2 to 8 mm and located in the center of the iris, the pupil lets in more or less light, depending on the fact that it is dilated or contracted. One can easily see the direct effect of light on the state of the iris and pupil. Just look at someone in the eyes in the dark and then turn on a light. You will see a reflex activity, called the Whytt reflex, in which the pupil diameter gradually decreases.

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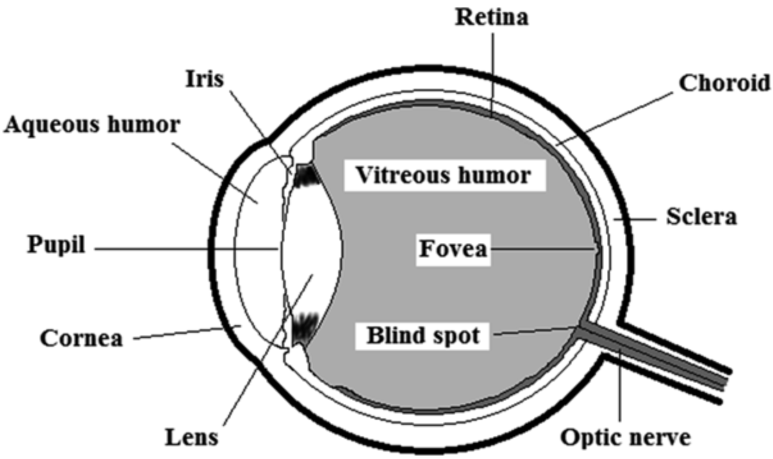

Fig. 4.1 Main structures of the eye

The light rays entering the eye are first bent by a curved membrane, the cornea, before crossing the pupil where they are bent again. Another adjustment of rays is done through an automatic mechanism called accommodation, which consists of a more or less pronounced flattening of the lens. The lens becomes rather round if the object on which we try to focus on is close or very flat if the object is far. Thus, if an object is near, the muscles contract; the lens becomes thicker and the light rays are bent even more.

The outermost part of the eye is the sclera. The sclera is resistant and maintains the shape of the eye. In its anterior part, it is transparent and covered by a thin membrane, the conjunctiva, which has a protecting role. Between the sclera and the retina, there is an intermediate membrane, the choroid, or choroid membrane, which allows to avoid the presence of light reflection (internal) by absorbing light. Highly vascularized, the choroid has a nutritive function for retinal cells.

Note that the spherical shape of the eye is made possible by the presence of two types of fluid. In the anterior part, between the cornea and the lens, this fluid is called the aqueous humor. In the back part, there is a large space filled with a rather gelatinous substance called the vitreous humor.

In the posterior part of the eye, there is a blind spot (or optic disk) caused by the presence of the optic nerve. This spot covers approximately 7.5° on the vertical axis and 5° on the horizontal axis (approximately 2.1 mm × 1.5 mm). The brain manages to compensate for the loss of vision caused by the blind spot (Fig. 4.2).

The innermost layer of the eye's posterior part is the retina. It is on the retina that the image is formed. Given its importance in vision, the next subsection is devoted to it. On the retina is a point having a diameter of about 1°, the fovea. It is at the fovea that we have the sharpest vision. The fovea is located 2 mm from the blind spot in a small area, the macula lutea (or yellow spot). In this area, there is a high concentration of cones. In fact, at the center of the fovea, there are only cones.

Fig. 4.2 Demonstration about the presence of the blind spot. (1) You need to fixate *X* on the *top row* with your right eye, keeping the left eye closed. From the corner of your eye, you should still be able to see the *black disk* located on the same row. Then, with a movement of your arm that is holding the book, you will vary the distance between your eye and the *X*. At a given distance, the visible *black disk* in the corner of your eye should disappear, although it is possible to see it a little further or a little closer. (2) You should repeat the demonstration with the *bottom row*. This time, if you fixate *X*, you should, at a given distance, perceive a non-interrupted *black line*; this interruption, in *white*, should disappear, the brain having compensate the loss of vision caused by the presence of the *black spot*

Finally, each eyeball is provided with three pairs of muscles that direct the eye in all directions of the visual field. These pairs have actually antagonistic roles. The superior and inferior lower rectus muscles allow the eye to make movements in the vertical direction, from top to bottom and from bottom to top; the lateral and medial rectus muscles make possible the horizontal movements, to the left or to the right; and the inferior (which is smaller) and superior (which is larger) oblique muscles are responsible for torsional movements and are involved in the vertical movements.

4.1.2 The Retina

The retina covers a section of about 200° in the posterior part of the eye and has a surface of about 25 cm^2 and a thickness of about 4 mm. As illustrated in Fig. 4.3, the retina is made essentially of three layers of cells. There are photoreceptor cells, which convert the electromagnetic energy (light) into nerve impulses. This information is transmitted to higher centers through the other two layers: the bipolar and ganglion cells. The retina is also made of horizontal and amacrine cells whose function is to facilitate the transfer of information between neurons of the same level.

There are two types of photoreceptor cells in the retina, the rods and the cones, which have different functions and properties. These types of cells do not have the same sensitivity to light. There are about five million cones and 120 million rods. Because of their high response threshold, the cones are assigned to daytime vision and form the photopic system. The cones are responsive to color and provide better visual acuity than the rods. We find a very large concentration of cones—about 35,000—at the fovea.

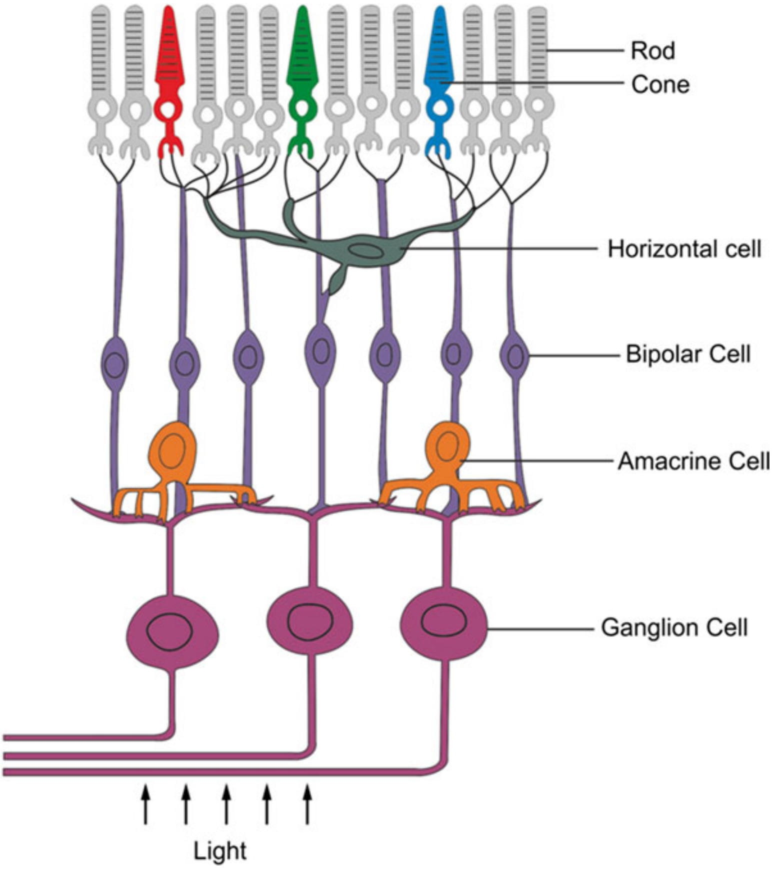

Fig. 4.3 Layers of retinal cells (figure by Leila Aazari)

For their part, the rods are more elongated than cones. Sensitive to low light intensity, the rods are assigned to night vision (the scotopic system). Moving away from fovea to periphery, the rods are more and more numerous, and, unlike the cones, their shape remains almost always the same.

The rods and cones are made of photosensitive pigments. The pigments of the cones are of three types in that the absorption of light of each of these types is maximal at certain wavelengths, long, medium, and short (see Chap. 5 on color perception). The photosensitive pigment of rods, rhodopsin, absorbs wavelengths ranging from 400 to 600 nm. It is therefore a photochemical process that will create an action potential which will be transmitted from the retina to the brain.

Bipolar cells, which can take different forms and different sizes, are involved in the passage of nerve impulses from the photoreceptors to the ganglion cells. Bipolar cells synapse with both rods with cones. Depending on whether it is located at periphery or at the fovea, the number of receptors in contact with the bipolar cells varies. Thus, the bipolar cells of the fovea may receive impulses from only one cone, while a little further at periphery, they may receive information from several photoreceptors. In general, bipolar cells specific to the cones are in contact with less photoreceptors than bipolar cells receiving information from rods. Moreover, the photoreceptors are in contact with each other through the horizontal cells. Some are only in contact with cones, others only with rods; other cells may be in contact with these two types of photoreceptors. These horizontal cells can also synapse with bipolar cells. The reader will find in DeValois and DeValois (1988) additional information about the connections between photoreceptors, horizontal cells, and bipolar cells and about the biological mechanisms underlying vision.

Bipolar cells mainly transmit nerve impulses to the ganglion cells, but also to amacrine cells. The role of the latter is comparable to that of the horizontal cells in that they mainly assume a role of interaction, this time between the ganglion and bipolar cells. For their part, the ganglion cells receive impulses mainly from of one or more bipolar neurons. The farther we get in periphery, the more frequent are the contributions of bipolar and amacrine cells to the excitement of a ganglion cell. The axons of the ganglion cells eventually form the optic nerve. For each eye, there are about one million ganglion cells.

4.2 Receptive Fields

It is important to understand that the retina has a particular organization as it includes more than 125 million receptors, cones, or rods, but does transmit information to the visual cortex cells through only a million ganglion cells. In fact, this particular arrangement of retinal cells refers to the idea of receptive field. To each ganglion cell corresponds a receptive field, which is a surface at the photoreceptor level where the light causes a change on the normal course of the electrical activity.

Early work in neurophysiology has shown that the light projected on the retina causes three types of responses (Hartline, 1940; Hartline & Ratliff, 1957; Kuffler, 1953). Thus, the response recorded at the ganglion cell level using an electrode can be one of the following three (Fig. 4.4). Cell responses show (1) an increase in activity during stimulation, and, from the beginning of the stimulation, then a return to normal activity when the illumination ceases; (2) an interruption of any activity while the light is on, but an acceleration of these responses when the light is turned off; and (3) an increase in activity at the beginning, followed by a decrease, and the repetition of this pattern (increase-decrease) when the light is off. These three types of responses are respectively called "on," "off," and "on-off."

The responses given by the ganglion cells depend on the stimulated location on the retina. Stimulating the retina at a specific location, or nearby, can result in responses of different types on a given ganglion cell. Indeed, to each ganglion cell corresponds a receptive field. This field could be of two types: on-center or off-center. These two types of field have a circular shape (Fig. 4.5) and are divided in equal number on the retina. For a type of field, stimulation at center causes "on" responses, and around this center, responses are "off." Between these two levels,

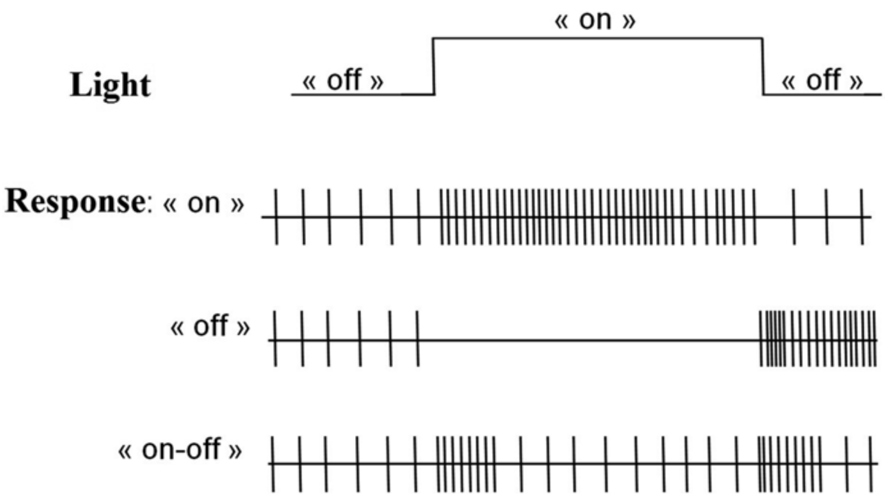

Fig. 4.4 Illustration of activation and inhibition patterns on ganglion cells with the arrival, maintenance, and disappearance of the light stimulation

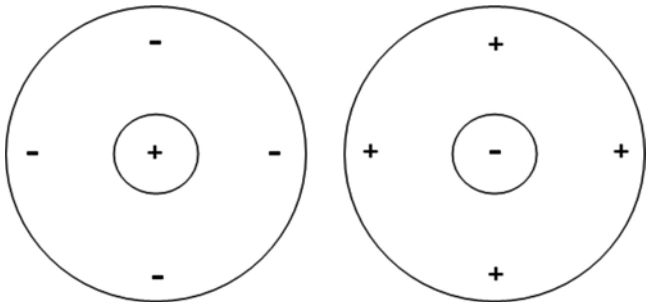

Fig. 4.5 Two types of circular receptive fields: with an "on" *center* (*left*) and with an "off" *center* (*right*)

there are responses of another type, "on-off." For the second type of receptive field, stimulation causes off responses in the center and around this center, on responses. In other words, the ganglion cells are in a position to gather information on the center of their receptive field and on the surrounding region.

In fact, there is critical distinction between two types of ganglion cells: "magno" versus "parvo." About 80 % of ganglion cells are of the parvo type (P cells, sometimes called "X"), and the magno cells (M cells or "Y") represent 10 % of these ganglion cells. There is also a third class of ganglion cells ("W") which would have a receptive field different of those described above and which would have the slowest conduction speed.

Parvo cells have a small receptive field (diameter of 0.01 mm) and a conduction speed of about 20 m/s. In contrast, magno cells have a larger receptive field. For

Table 4.1 Contrasting the characteristics of two types of ganglion cells, magno and parvo

	Magno (Y)	Parvo (X)
Represent (of total)	10 %	80 %
Body cells and axons	Larger	Smaller
Conduction speed	40 m/s	20 m/s
Neural responses	Jerkily	Continuous
Receptive field	Larger	Smaller
Contrast sensitivity	High	Low
Sensitive to	Large objects	Colors
Sensitive to	Movement	Stationary patterns

example, at 10 mm from the fovea, the receptive fields are 50 times larger (0.5 mm). Because their body cell and axon are larger, magno cells have a much greater conduction speed (40 m/s) than parvo cells. Table 4.1 summarizes the main features that differentiate these two types of ganglion cells, P and M.

4.3 Central Mechanisms

The grouping of ganglion cell axons forms the optic nerve. The distance between the exit of the eye and the optic chiasm is about 5 cm. At the optic chiasma level, a shift occurs in the routing of a part of the information arriving from the eye. As indicated by the word chiasma, there is a crossing of information. Approximately 50 % of the information from one eye is transferred to the opposite side of the brain. It is the information received in the nasal portion of the retina (the part of the retina closest to the nose) that is intersecting at the optic chiasm level. The fibers from the temporal region of the retina remain on the same side. Whether the optic nerve fibers cross or not, there is no synapse at the optic chiasm location. Also, beyond the optic chiasm, the optic nerve is called the optic tract.

The information carried by each optical track therefore comes from each eye and is directed to one of the following two structures, the lateral geniculate nucleus (LGN) and the superior colliculus, most of the visual information being routed to the LGN. The superior colliculi, which are a primitive structure of the brain, have no role in the detection of the exact nature of the stimuli, but would be used to locate their source. The superior colliculi also exert control on the movement of the eyes when they should be moved to look at an object in periphery.

As for the LGN, this structure has a much greater contribution to the whole visual processing. As the name suggests, they are located on each side of the brain and have the shape of a flexed knee. Each of the LGN, the left and right, has a receptive field similar to that of ganglion cells. They also have a retinotopic organization, that is to say, that the representation on the retina is maintained at the LGN level. The other features of the LGN include the fact that they are made up of six separate layers that do receive information from only one eye, that they have a key role in the perception of form, and, more than the superior colliculi, that they receive a lot of information from the fovea. Consequently, the LGN are involved in the perception of color.

4.3.1 The Visual Cortex

The visual cortex is located in the occipital part of the brain and has an area of approximately 64 cm^2. The cerebral organization in the brain also preserves the spatial organization of retinal cells (retinotopic organization), but the amount of space occupied in the brain depends on the location stimulated on the retina. About 65 % of the visual cortex is associated with the activity on the retina corresponding to 10 % of the visual field.

The terms V1–V5 are now used for describing the different regions of the visual cortex, and two main sections should also be kept in mind, the primary visual cortex and the secondary visual cortex (Table 4.2). The primary visual cortex, or striate cortex, is also sometimes called area 17. This corresponds to the visual 1 (V1) area. The V1 area receives information from LGN, which also has a spatial arrangement corresponding to a retinotopic organization. The V1 area is divided into six layers designated by the numbers 1–6. The information from the LGN arrives at the fourth layer (specifically 4c) in V1.

The second section, the secondary visual cortex or extrastriate cortex, includes areas V2 and V3 (or area 18) and V4 and V5 (or area 19). It is in these areas that are routed nerve impulses coming from superior colliculi. Similarly, some information already processed in V1 will reach certain areas of the secondary visual cortex. Finally, the processing of visual information also involves the contribution of another part of the visual cortex called the associative cortex. It is in this part of the visual cortex that some learning and some past associations intervene in the overall perception.

Some other features of the visual cortex are noteworthy. The knowledge of these features relies essentially on the pioneer work of two neurobiologists, David Hubel and Torsten Wiesel, who won the Nobel Prize in Physiology in 1981 (Hubel & Wiesel, 1959, 1962). Essentially, Hubel and Wiesel used a technique allowing the recording of the activity of one cell at a time in the visual cortex. They found that the receptive fields in the visual cortex are not necessarily circular. For example, they are sometimes elongated. They identified three types of cells in the visual cortex to which they gave the name of simple cells, complex cells, and hypercomplex cells.

Table 4.2 Names given to areas in the primary and secondary visual cortex

	Primary visual cortex	Secondary visual cortex
Other name	Striate visual cortex	Extrastriate visual cortex
Brodmann classification	Area 17	Areas 18 and 19
Common nomenclature	Area V1	Areas V2, V3, V4, and V5

The response of simple cells is maximal when an observer is presented with a specific orientation. Simple cells in layer 4c of the area V1 have for their part a circular receptive field. The selectivity for orientation (bars placed more or less vertically or horizontally) is a fundamental feature of these simple cells. A change of a few degrees of a bar significantly reduces the electrical activity, or neural response made by a given cell, but increases the activity of another of these simple cells located in V1.

Because it is more difficult to know what determines their activity, a second type of cells is called “complex cells.” They are found in the layers 2, 3, 5, and 6 of V1. It is known that they are sensitive to movement, some to movement in one direction, the others to movement in another direction. In brief, we are referring here to a case of selectivity for motion perception.

Even more difficult to understand, the hypercomplex cells appear to be end-stopped cells. They respond only to edges having a specific orientation or moving in a certain direction.

In their work, Hubel and Wiesel also identified an important feature of the organization of cells in V1. The visual cortex is built with architecture in columns. Thus, when inserting an electrode vertically, beginning from layer 1 up to the layer 6, it is always the bars of the same orientation that give maximal responses. That sequence of six layers is called a column. When moving the electrode on a horizontal plane, there is a gradual change about the cell preference to stimuli ranging from horizontal to vertical: this sequence of columns are called hypercolumn and have an area of about 2 mm^2. There are about 6400 hypercolumns composed of 15,000 cells each.

There are in the brain several specialized processing areas for specific functions or features. In other words, there is a segregation of the various functions related to visual processing and an assignment of these functions to specific areas in the visual cortex. Areas V1 and V2 are alike as they both have small receptive fields and form, according to some authors, a V1–V2 complex. In addition to the characteristics described above, it should be noted that in V1, the segregation applies according to shape, color, and movement. Area V2 receives some information directly from the LGN but mostly receives information via relays from V1.

Area V3 is very closely linked to the activity at the fovea and is specialized in the processing of form. This area however would also contain information about the position changes of the form or object. Area V4 is specialized in the processing of color, more specifically in the processing of reflected light. Area V5 processes movement; more specifically, most of the cells in this area would respond to movement in a particular direction.

4.3.2 Visual Pathways

We distinguish two major pathways in the processing of visual information. Their name refers to the origin of the stimulation and where it ends up. Thus, the first pathway is called magnoparietal. It is also referred to as the median temporal pathway or dorsal pathway (or even *geniculostriate*). This pathway provides information about the “where” and “how” aspects of vision and requires the contribution of

10 % of ganglion cells. As this pathway passes through V5, it is not surprising that it is associated with motion perception.

The other pathway is called parvotemporal or ventral (*tectopulvinar*). It is also known as the "what" pathway. This pathway requires the contribution of areas V2 and V4, the latter indicating that it involves color processing. In fact, this pathway allows to scrutinize images or objects for identifying them correctly.

Finally, this chapter on the biological bases of visual perception would be incomplete without the presentation of some principles. For example, relatively to a fixation point straight ahead, what is located on the left will be processed in the right cerebral hemisphere, and what is located on the right will be processed in the left hemisphere. Figure 4.6 illustrates in what position the information captured from

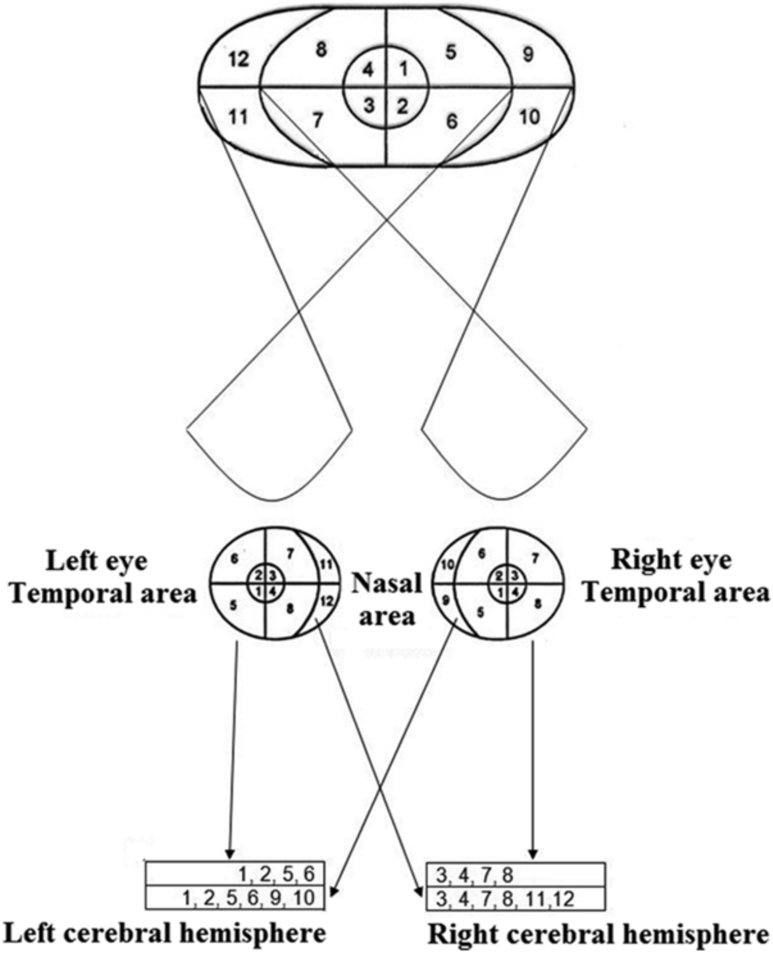

Fig. 4.6 In relation to the visual field, each eye receives information that is upside down and mirrored; also, what is located to the right of the fixation point arrives in the left cerebral hemisphere, and what is located to the left of the fixation point arrives in the right cerebral hemisphere

the visual field arrives on the retina and in the cerebral hemispheres. Thus, it is possible to observe that, relative to the visual field, the image on the retina is upside down and mirrored. Also, the properties of the optic chiasm lead to (1) the passage of information from the nasal region of the left eye (information contained in the left side of the visual field) to the right side of the brain and (2) the passage of information from the nasal region of the right eye (information contained on the right side of the visual field) to the left side of the brain. This crossover explains why each cerebral hemisphere is responsible for processing the visual information presented to the opposite side.

4.4 Clinical Aspects

Different problems may arise that will impede the proper functioning of the visual system. We can distinguish various categories of disorders that lead to poorer vision. The most common are listed here. Color vision disorders are presented in the following chapter.

A first major category of problems, and the most frequent indeed, is related to the capacity of focusing. Refraction problems (or refractive errors) prevent the light rays to reach the retina so that the picture is clear. One type of refraction problem is called *hypermetropia*. This occurs when the distance between the lens and the retina is too short (Fig. 4.7). The image is formed behind the fovea. The person suffering from hypermetropia will have difficulty to see near objects. Glasses with a biconvex lens allow to correcting this problem.

Conversely, a person suffers from *myopia* when the distance between the lens and the retina is too large; the image is formed in front of the fovea. Sometimes, a distinction is made between refractive myopia, which means that the light rays are too deflected by the cornea or by the lens, and axial myopia, which means that the eyeball is too long. The person suffering from myopia, or nearsighted, does not see clearly distant objects and will benefit from the use of biconcave lenses. This very common problem can be corrected by photorefractive keratectomy. This is a laser surgery for changing the curvature of the cornea. After the operation, the light rays reach the retina correctly and vision is in focus.

There are rarer cases where a person suffers from *astigmatism*, which means that this person does not have clear vision in all directions of the visual field. A part of the visual field always remains out of focus. This is caused by a nonspherical curvature of the cornea or lens.

Furthermore, *presbyopia* refers to a difficulty to focus on an object that is nearby and is caused by the hardening of the lens with age. It is common that people in their forties, who until then had never experienced any vision problem whatsoever, may need glasses. You may have noted that, without their glasses, older people tend to hold a book at arm's length for reading it. The reduction of the lens' plasticity eventually makes reading much more difficult.

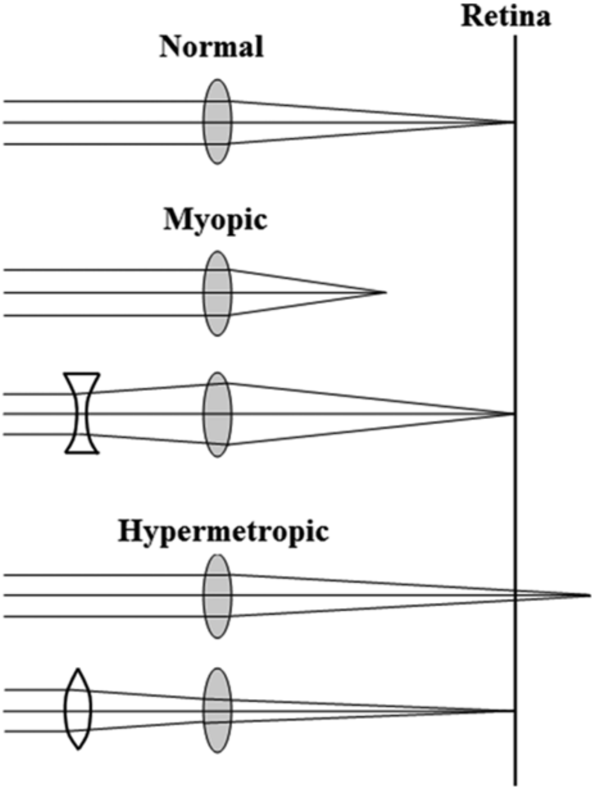

Fig. 4.7 Refraction problems often caused by an anormal shape of the eyeball. After passing through the lens (*gray*), light rays arrive at the retina in front of a myopic eye or behind the hypermetropic eye. Normal view could be recovered with a biconcave lens, for myopia, or a biconvex lens, for hypermetropia

Sometimes, instead of being improperly refracted, the light that enters the eye is rather blurred. This can be caused by certain injuries or diseases. It may happen that the cornea is infected, causing vision problems. Furthermore, there are various cases of *cataract*, which refers to the opacity of the lens. The gradual loss of lens transparency in some cases may cause a loss of vision. Cataracts may be congenital or caused by disease (secondary cataract) or injuries (traumatic cataracts). Most often, cataracts are caused by aging. It affects 75 % of people aged 65 and older, and 95 % of those aged 85 and older. Problems caused by cataracts can be corrected with a surgery when the reduction of vision becomes too severe.

Some vision problems are caused by a problem specific to the retina. One such problem is the age-related macular degeneration. With such a problem, a person sees somehow very well everywhere except where he or she is looking, i.e., where the focus is made! There are also cases of retinopathy caused by diabetes. Problems often develop after several years of diabetes. Older people who have long suffered from diabetes can have serious vision problems. Also, poor vision may result from a poor flow of information at the optic nerve; this problem might be caused by an intoxication or inflammation. Finally, vision can be disrupted by a displacement of the retina. In addition, certain injuries can cause a retinal detachment and impair severely sometimes peripheral vision, sometimes central vision.

Another group of eye problems is *glaucoma*. This is a common cause of blindness. Glaucoma is a degeneration of optic nerve sometimes caused by a very large pressure within the eye. Glaucoma usually occurs in people aged over 60 years.

Note in conclusion that there are many other problems that can affect vision. Some of these are related to muscles. That is the case of *strabismus*, which consists of a poor centering of the image (which does not arrive at the fovea) and which causes double vision. It is caused by a disorder in the extraocular muscles, for example, by a paralysis of the muscles of an eye. *Nystagmus*, which refers to a continuous movement of the eyes, is another problem having of muscular origin, this time due to the presence of plaques in the eyes. Finally, *scotoma* is the name given to visual field defects. These deficits can be more or less important and may affect specific portions of the field. In rare cases, this problem can be caused by a lesion to the visual cortex.