22

Vision

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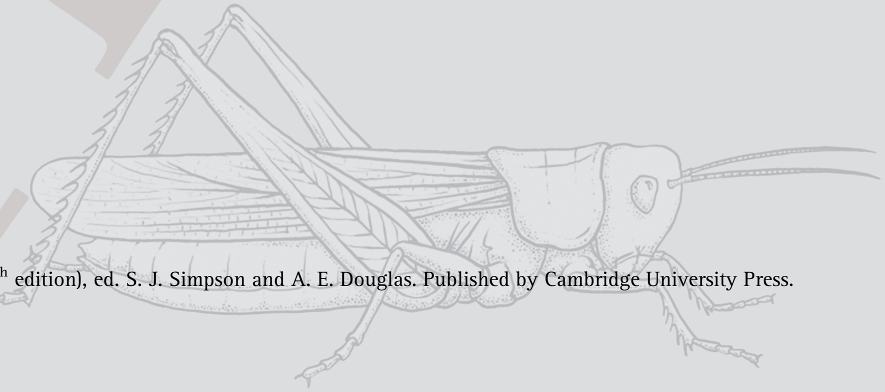
INTRODUCTION

Light is perceived by insects through a number of different receptors. Most adult insects and larval hemimetabolous insects normally have a pair of compound eyes, whose structure (Section 22.1) and function in form and motion vision (Section 22.2) are described below in turn. Section 22.3 covers the molecular and physiological function of photoreceptors and mechanism of regulating light sensitivity before explaining the processes of color vision and polarization vision. Adult insects also typically have three single-lens eyes, called ocelli, whose optics and function are described in Section 22.4. Larval holometabolous insects have one or more single-lens eyes, known as stemmata, on the sides of the head (Section 22.5). Some insects also possess epidermal light receptors, and, in some cases, light is known to have a direct effect on cells in the brain (Section 22.6). Magnetic sensitivity aids orientation in at least some insects, and has known interactions with light sensitivity (Section 22.7).



The Insects: Structure and Function (5th edition), ed. S. J. Simpson and A. E. Douglas. Published by Cambridge University Press.

22.1 Compound eyes

22.1.1 Occurrence

Compound eyes are so called because they are constructed from many similar units called ommatidia. They are present in most adult pterygote insects and the larvae of hemimetabolous insects, but are strongly reduced or absent in wingless parasitic groups, such as the Phthiraptera and Siphonaptera, and in female coccids (Hemiptera). This is also true of cave-dwelling species. Among termites (Isoptera), compound eyes are greatly reduced or absent from stages that are habitually subterranean, and, although present in winged reproductives, the sensory components of the eyes degenerate during the permanently subterranean reproductive life. Among Apterygota, compound eyes are lacking in some Thysanura, but Lepismatidae have 12 ommatidia on each side. Well-developed compound eyes are present in Archaeognatha. In the non-insect orders of Hexapoda, Collembola have up to eight widely spaced ommatidia, while Protura and Diplura have no compound eyes.

Each compound eye may be composed of several thousand ommatidia. There are up to 30 000 in the eyes of dragonflies, 10 000 in drone honey bees, 5500 in worker honey bees and 800 in *Drosophila*. At the other extreme, workers of the ant *Ponera punctatissima* have only a single ommatidium on each side of the head. Usually the eyes are separate on the two sides of the head, but in some insects, such as Anisoptera (Odonata) and male Tabanidae and Syrphidae (Diptera), the eyes are contiguous along the dorsal midline, this being known as the holoptic condition.

22.1.2 Ommatidial structure

Each ommatidium consists of an optical, light-gathering part and a sensory part, which transforms light into electrical energy. The sensory receptor cells of most diurnal insects end close to the lens, and, because of the method of image formation, these are called apposition eyes (Fig. 22.1). Most night-flying insects, however, have eyes with a clear zone between the lenses and the sensory components; they are called superposition eyes, and produce brighter images than apposition eyes. (Fig. 22.2).

The cuticle covering the eye is transparent and colorless and usually forms a biconvex corneal lens. In surface view, the lenses are usually closely packed together, forming an array of hexagonal facets. Each corneal lens is produced by two epidermal cells, the corneagen cells, which later become withdrawn to the sides of the ommatidium and form the primary pigment cells. Beneath the cornea are four cells, the Semper cells, which, in many insects, produce a second lens, the crystalline cone. This is usually a hard, clear, intracellular structure bordered laterally by the primary pigment cells.

The sensory elements are elongate photoreceptor neurons. Generally there are eight receptor cells in each ommatidium, but some species have seven, and others nine. Each receptor cell extends basally as an axon, which passes out through the basal lamina backing the eye and into the lamina of the optic lobe (see Fig. 20.17). The margin of each receptor cell nearest the ommatidial axis is differentiated into close-packed microvilli extending toward the central axis of the ommatidium at right angles to the long axis of the photoreceptor cell. The microvilli of each receptor lie parallel with each other and are often aligned with those of the receptor cell opposite, but are set at an angle to those of adjacent receptor cells (Fig. 22.1d). The microvilli of each receptor cell collectively form a rhabdomere. The visual pigment (rhodopsin) is located within the microvillar membrane. In many insects such as bees and flies (but not butterflies), most receptor cells have a twist along their lengths. Thus, the orientation of the microvilli of each rhabdomere changes regularly through the depth of the eye, eliminating polarization sensitivity where it isn't needed (see below).

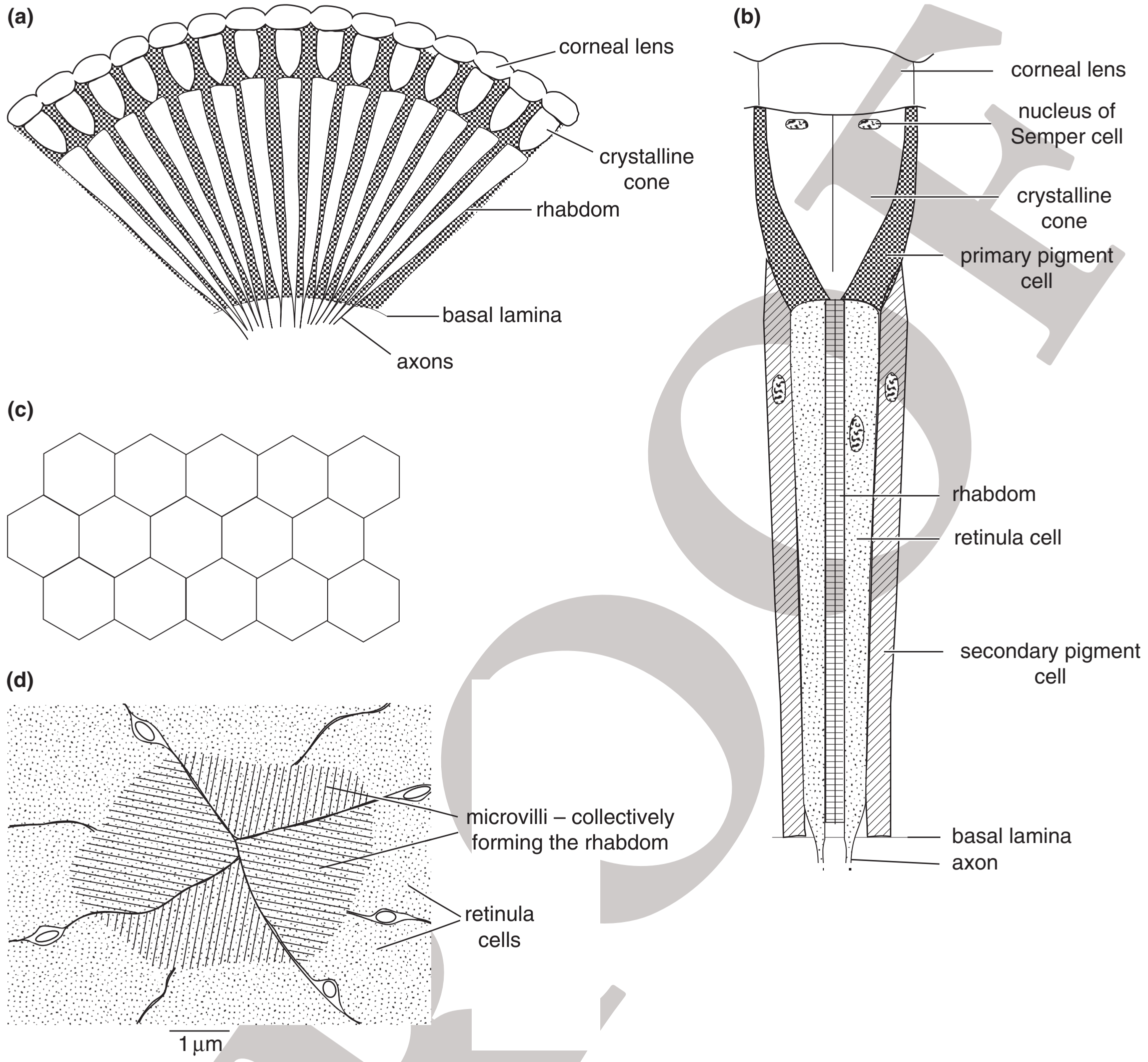


Figure 22.1 Apposition eye. (a) Diagrammatic section through an apposition eye showing the rhabdoms extending to the crystalline cones. (b) Ommatidium. (c) Surface view of part of an eye showing the outer surfaces of some corneal lenses (facets). (d) Cross-section through a fused rhabdom (*Apis*) (after Goldsmith, 1962).

In most insects the rhabdomeres abut on each other along the axis of the ommatidium, forming a “fused” rhabdom (although the cells are not actually fused), but Diptera, Dermaptera, some Heteroptera (Hemiptera) and some Coleoptera have widely separated rhabdomeres forming an “open” rhabdom (Fig. 22.3). Because a fused rhabdom acts as a light guide, all the photoreceptor cells within one ommatidium have the same field of view. In species with open rhabdoms, each receptor cell within an ommatidium has a separate visual field, shared by individual cells in each of the adjacent ommatidia (see Fig. 20.21b).

The rhabdom of apposition eyes usually extends the full length of the photoreceptor cells between the crystalline cone and the basal lamina. It is 150 μm

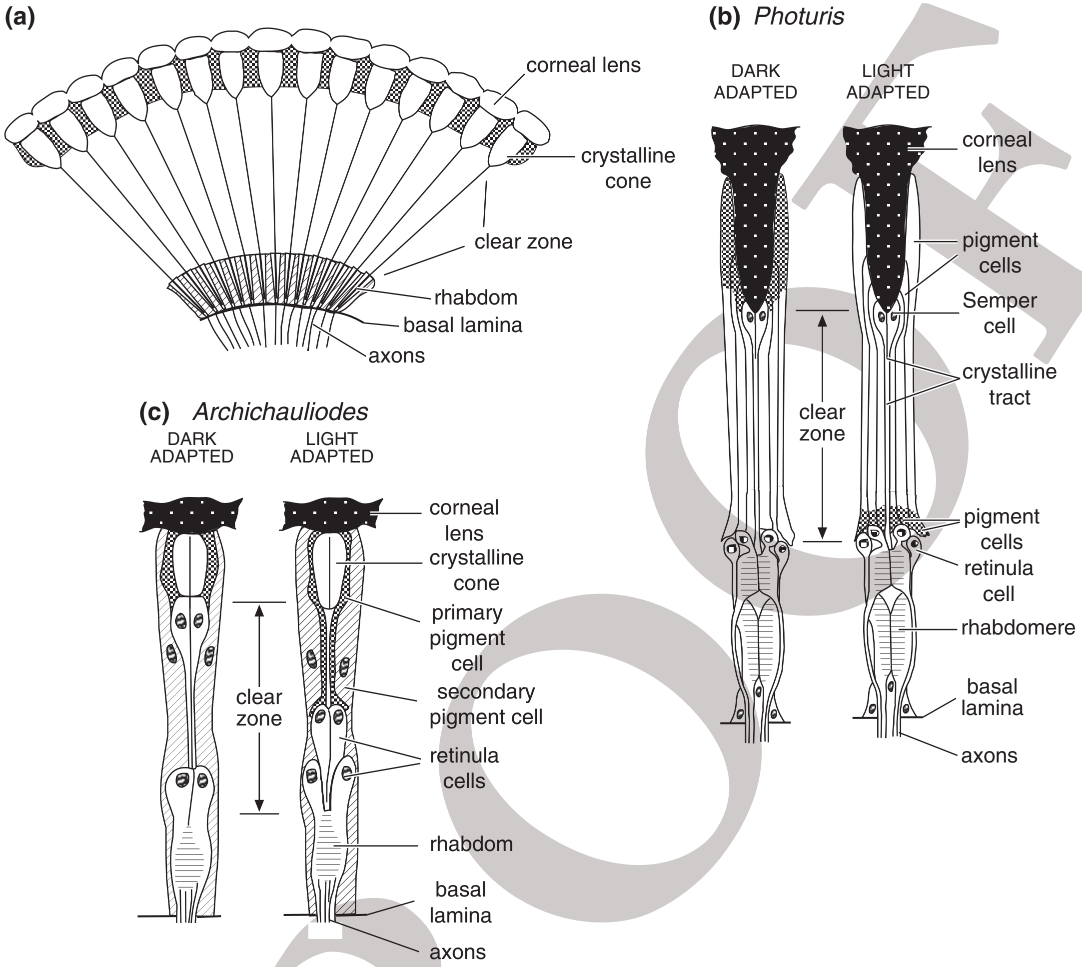


Figure 22.2 Superposition eye. (a) Diagrammatic section through a superposition eye showing the clear zone between the rhabdoms and the lens systems. (b) Exocone eye in which the clear zone is crossed by a tract formed from the Semper cells. Note that there is no crystalline cone in exocone eyes. Left: dark-adapted; right: light-adapted (*Photuris*, Coleoptera). (c) Eucone eye in which the clear zone is bridged by photoreceptor cells. Left: dark-adapted; right: light-adapted (*Archichauliodes*, Megaloptera) (after Walcott, 1975).

long in the ant *Camponotus* and, in *Drosophila*, with an open rhabdom, each rhabdomere is 80 μm long. It is usually shorter in superposition eyes, and even in apposition eyes one of the rhabdomeres may be very short (see Fig. 22.4a, cell 9).

There is much variation in the way that the clear zone in superposition eyes is bridged. In many Lepidoptera and Coleoptera, the receptor cells extend to the crystalline cone as a broad column, but the rhabdom is restricted to the basal region (Fig. 22.2c), but, in Carabidae and Dytiscidae, one of the receptor cells also has a short distal rhabdomere just below the cone. In other Lepidoptera (the Bombycoidea and Hesperioidea), the receptor cells of each ommatidium forms a thin strand, which may be only 5 μm across, to the lens. Beetles with exocone eyes (see below) have a similar structure, but it is formed by the Semper cells and the receptor cells are restricted to a

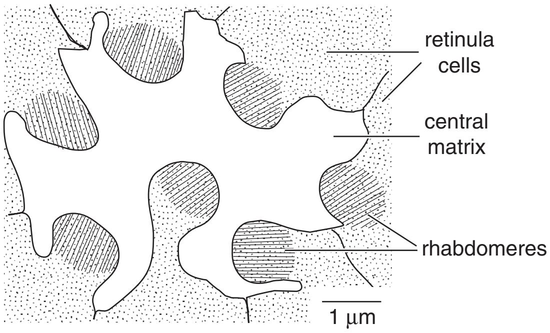


Figure 22.3 Open rhabdom. A section through the rhabdomeres of *Drosophila* (after Wolken *et al.*, 1957).

basal position in the ommatidium (Fig. 22.2b). The sensory parts of each ommatidium are usually surrounded by 12–18 secondary pigment cells so that each ommatidium is isolated from its neighbors.

Tracheae pass between the ommatidia proximally in some species, and, in many Lepidoptera, closely packed tracheae form a layer at the back of the eye. This layer, which reflects light back into the eye, is called a tapetum. The tracheoles forming the tapetum are flattened and enlarged, providing alternating layers of cytoplasm and air. These form a stack in which each layer is about one-quarter of the wavelength of light in optical thickness. In such a structure light reflected from every interface interferes constructively, resulting in a high reflectance and interference colors (Section 25.2.2). In butterflies the reflected light from the back of the eye doubles the effective length of each rhabdom as the light passes through it twice. In moths, with superposition eyes, the basal region of each ommatidium is surrounded by tracheae. Here, their function is probably to contain the light within the rhabdom, increasing sensitivity and also resolution via isolating the ommatidia from each other (sheathing).

In insects with fused rhabdoms, the axons passing back from each ommatidium are kept together in the lamina of the optic lobe, each ommatidium being represented by a separate cartridge (Section 20.4). In general, 6–7 retinal axons terminate in the lamina cartridge, while 1–3 others pass through the lamina, ending in the medulla. The arrangement is different in the open rhabdom of Diptera. Here, well-developed cartridges are present in the lamina, but instead of being derived from the axons of a single ommatidium, they are formed around the axons of receptor cells with the same field of view (see above). Thus they contain axons from each of seven adjacent ommatidia and bring together information about a particular area in the visual field (see Fig. 20.21b). By analogy with superposition eyes, which bring together information from a number of ommatidia (see below), these eyes are called neural superposition eyes. Axons from all the green-sensitive cells end in the cartridge; those sensitive to other wavelengths pass through the cartridge to the medulla, usually without making synaptic connections (see Fig. 20.21a). The open rhabdoms of Heteroptera and Dermaptera are not known to be associated with neural superposition.

Variation of ommatidial structure within species The form and arrangement of ommatidia differ in different parts of the eye in many, and perhaps all, insects. For example, in apposition eyes of the praying mantis, *Tenodera*, the facet diameter is greatest in the forwardly directed part of the eye, and decreases all around (Fig. 22.5). Because the radius of curvature of this same part of the eye is greater (so the surface is flatter) than elsewhere, the angle between the optical axes of adjacent ommatidia (the interommatidial angle) is less than elsewhere and the rhabdoms are longer, but thinner. This area of the eye (the acute zone) is functionally equivalent to the vertebrate fovea (see below) and similar regions are known to be present in the eyes of other insect species with a particular need for good resolution. In dragonflies, for example, there is a wedge of enlarged facets across the fronto-dorsal region of the two eyes, which provides a strip of high resolution for detecting prey insects against the sky. In water-surface living insects, such as the pond skater *Gerris* and empid flies that scavenge over the surface,

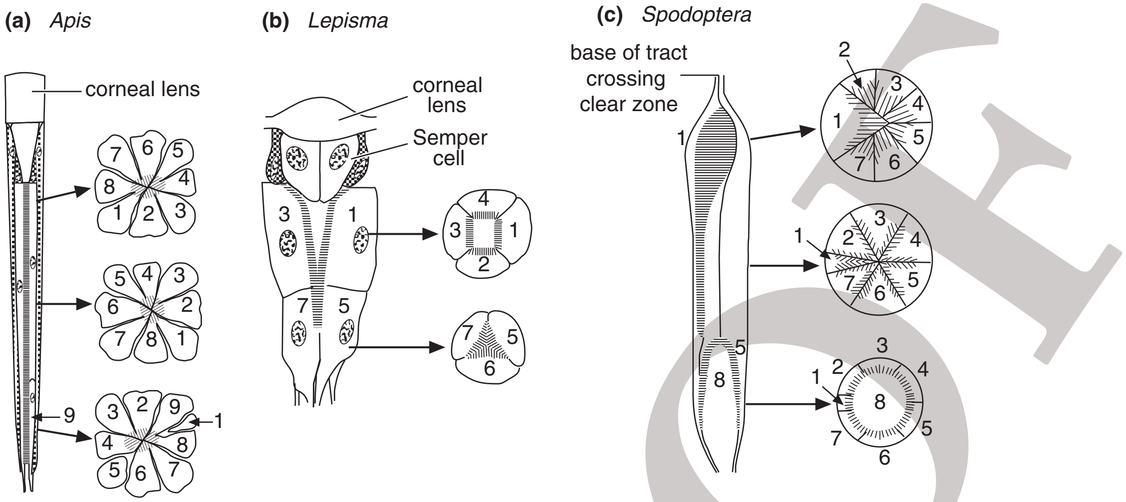


Figure 22.4 Different rhabdoms showing a longitudinal section of an ommatidium with transverse sections at the positions shown. Numbering of photoreceptor cells is for clarity; the numbers have no other significance. (a) Twisted rhabdom. The receptor cells twist through 180° from top to bottom of the rhabdom. Each receptor cell is given the same number in cross-sections at different levels in the eye. Twisting is not shown in the longitudinal section, but note the short ninth cell which only contributes to the rhabdom proximally (*Apis*). (b) Tiered rhabdom. Four photoreceptor cells contribute to the more distal rhabdom, three others to the proximal rhabdom (*Lepisma*, Thysanura) (after Paulus, 1975). (c) Tiered rhabdom in a superposition eye. Only the proximal part of the eye is shown. Cell 8 only contributes to the rhabdom proximally; distally, cell 1 contributes a major proportion (*Spodoptera*, Lepidoptera) (after Langer *et al.*, 1979).

the high-resolution strip is around the equator of the eye, imaging the horizon.

In males of many species, the eye is differentiated into a dorsal region with relatively large facets and small interommatidial angles and a ventral region with much smaller facets and bigger interommatidial angles. In drone honey bees and hoverflies the change in facet size is gradual, but in others, such as male bibionids (Diptera), it is abrupt. The division is complete in the male of *Cloeon* (Ephemeroptera), where each eye is in two parts quite separate from each other. Not only are the ommatidia in these two parts different in size, they are also different in structure. Those of the dorsal part are relatively large and of the superposition type, while in the lateral part the ommatidia are smaller and of the apposition type. The eyes are also divided into two in the aquatic beetle *Gyrinus*, where the dorsal eye is above the surface film when the insect is swimming and the ventral eye is below the surface. The significance of these differences is discussed below.

Many species have a band of ommatidia along the eye's dorsal rim which differ from those in the rest of the eye. Here, the photoreceptor cells are not twisted and the microvilli of different receptor cells are at right angles to each other (Section 22.3.4). This area of the eye is polarization-sensitive (Section 22.3.4). Differences may also occur in the nature of the screening pigments in different parts of the eye. These differences relate to the wavelengths absorbed by metarhodopsin and the regeneration of rhodopsin (Section 22.3.1).

Interspecific variation in ommatidial structure The origin and form of the crystalline cone vary in different insects. Most species have eucone eyes in which the structure is intracellular in the Semper cells. It is usually conical, but in some groups, notably in Collembola and Thysanura, it is

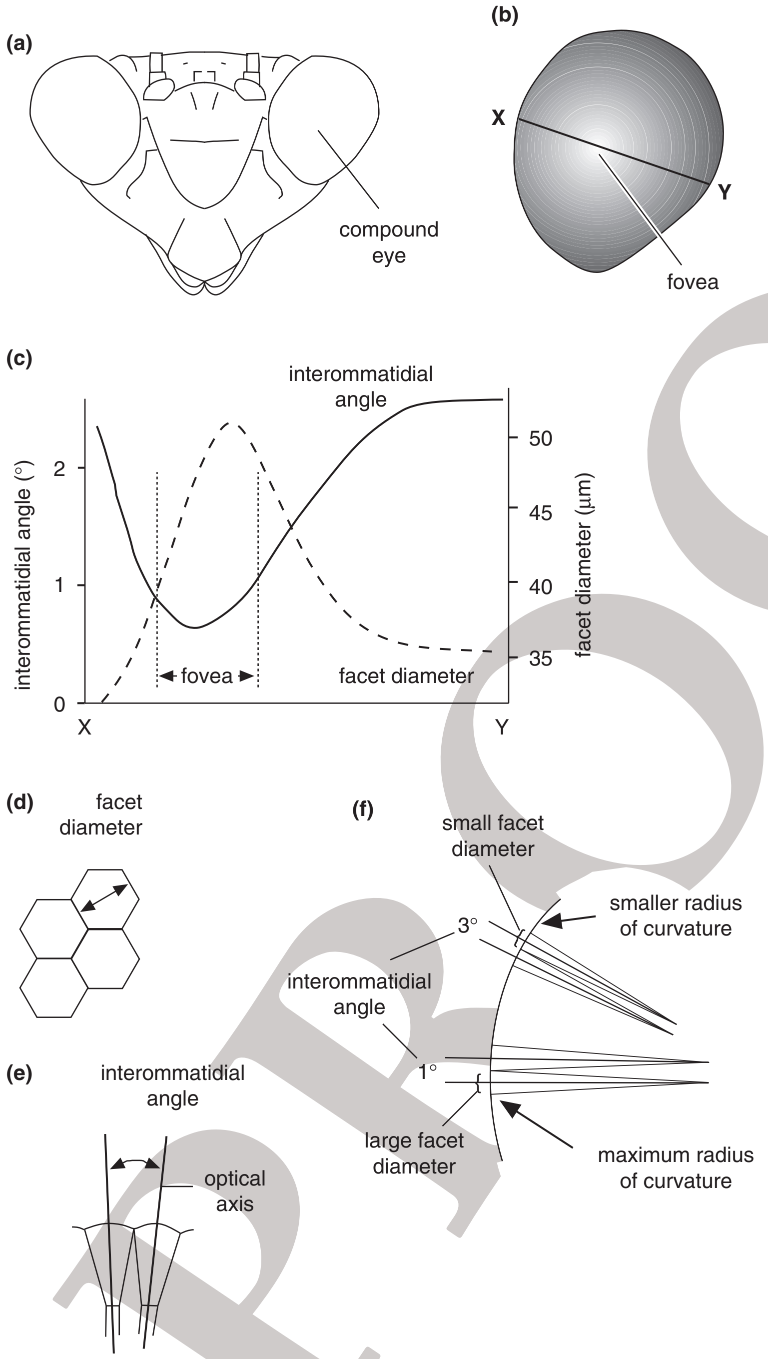


Figure 22.5 Variation in ommatidia within an eye (*Tenodera*, Mantodea) (after Rossel, 1979). (a) Frontal view of the head showing the compound eyes. (b) Compound eye. White area is the fovea in which facet diameter is greatest and interommatidial angle smallest. Increasing density of shading shows decreasing facet size and increasing interommatidial angles. (c) Variation in facet size and interommatidial angle along the transect X–Y shown in (b). (d) Facet diameter. (e) The interommatidial angle is the angle between the optical axes of adjacent ommatidia. (f) Diagrammatic section through the eye showing variation in the curvature of the surface of the eye and the associated differences in facet diameter and interommatidial angle.

more or less spherical. In a few beetles, some Odonata and most Diptera, the Semper cells secrete an extracellular cone which is liquid-filled or gelatinous rather than crystalline. Ommatidia with this type of lens are called pseudocone ommatidia. The Semper cells do not produce a separate lens in some species, but their cytoplasm is clear and they occupy the position of the cone. These acone eyes are present in various families of Coleoptera – for example, Coccinellidae, Staphylinidae and Tenebrionidae – in some Diptera and in Heteroptera (Hemiptera). In Elateridae and Lampyridae (Coleoptera), the Semper cells do not contribute to the lens. Instead, the corneal lens forms a long cone-shaped projection on the inside (Fig. 22.2b). This is known as the exocone condition.

Although it is common for all the receptor cells to be of similar length and to form a rhabdomere all along the inner margin, this is not always the case. The ommatidia of *Apis* have nine receptor cells. Eight of them have more or less similar rhabdomeres distally, but proximally two cells (cells 1 and 5 in Fig. 22.4a) do not contribute to the rhabdom while the rhabdomere of the short, ninth cell is present. Many other insects have photoreceptor cells of different lengths so that they have a tiered arrangement, as in *Lepisma* (Thysanura) (Fig. 22.4b), or as in *Spodoptera* (Lepidoptera) (Fig. 22.4c). Many other arrangements are known.

22.2 Form and motion vision

22.2.1 Image formation

Image formation depends on the optical properties of the corneal lens and the crystalline cone. Refraction of light occurs at any interface with a difference in refractive index on the two sides. In most apposition eyes, the outer surface of the corneal lens is the principal or only refracting surface, although in butterflies further refraction occurs in the crystalline cone.

In an apposition eye, each ommatidium is separated from adjacent ommatidia by screening pigment, so each functions as an independent unit. Each lens produces a small inverted image of the object in its field of view, which is in focus at the tip of the rhabdom (Fig. 22.6a). Because the rhabdoms of apposition eyes are fused, they function as light guides, within which image detail is lost, and all the photoreceptor cells from one ommatidium share the same small field of view. The light reaching the rhabdom in each ommatidium has an overall intensity which varies from one ommatidium to the next, depending on the amount of light reflected by objects in the field of view, and so collectively the rhabdoms transmit an erect mosaic image made up of the adjacent contributions from all the ommatidia.

By bringing the light to a focus at the tip of the rhabdom, the insect maximizes the amount of light entering the rhabdom. In flies, with neural superposition eyes, the amount of light available from each point in space enters through seven ommatidia (see Fig. 20.21b), so the signal contains more photons than light entering through a single lens. Consequently, flies have greater sensitivity at low light intensities than insects with fused rhabdoms, without this compromising the eye's resolution.

Dark-adapted superposition eyes function in a very different way from apposition eyes. The screening pigments are withdrawn so that light leaving one lens system is not confined within a single ommatidium, but can reach the rhabdoms of neighboring units (Fig. 22.6b). This enables the eye to function at low light intensities. Whereas, in apposition eyes, stray light is absorbed by the screening pigment, in superposition eyes it is optically redirected and utilized for image formation.

The superposition eye forms a single upright image. This requires that light is refracted not just on entering each lens, but also within it, so that it follows a curved pathway. The lenses of superposition eyes each possess a gradient of refractive index from the lens axis to its edge (Fig. 22.7). This gradient causes light rays to undergo greater refraction as they travel toward the lens axis, and less refraction as they travel away

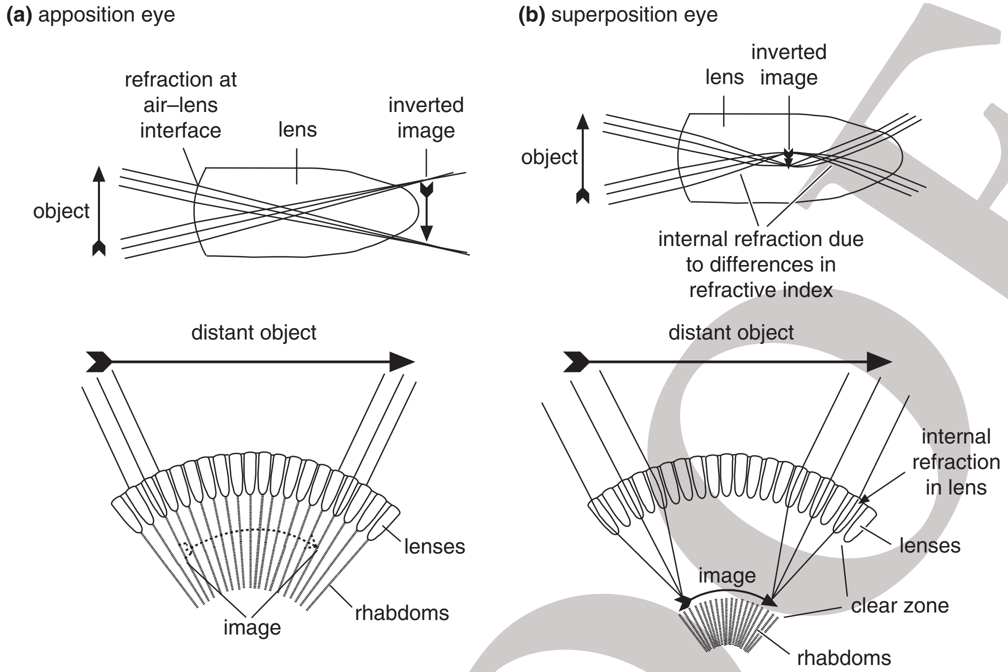


Figure 22.6 Image formation. (a) In an apposition eye each lens forms an inverted image at the tip of the rhabdom (above), but because the rhabdomeres function as a single unit the impression of this image is not retained. Consequently, the output from each rhabdom is a response to the overall intensity of light that reaches it. Information concerning the object is thus represented as a series of spots differing in intensity (below; suggested by the dotted arrow). (b) In a superposition eye light rays are refracted internally within the lens (above). They are unfocused as they exit the lens, but collectively form a single upright image at the tips of the rhabdoms (below).

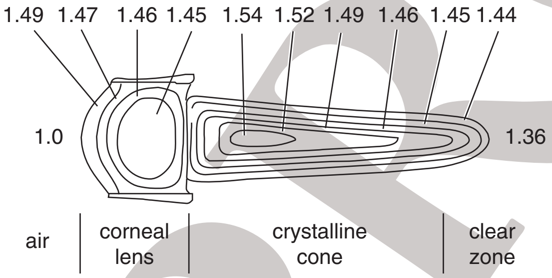


Figure 22.7 Lens cylinder from a superposition eye. The refractive index changes within the corneal lens and crystalline cone so that refraction occurs within the lenses as well as at the air–corneal lens and crystalline cone–clear zone interfaces (after Horridge, 1975).

from the axis, thus making the light path curved. The effect of this is to bend light continuously as it passes down the lens, and the whole structure behaves as though it were a two-lens telescope, accepting parallel light, focusing it internally, and then emitting it again as a redirected parallel beam (Fig. 22.6b). Sigmund Exner, who first described superposition optics, referred to such a structure as a lens-cylinder. The net result is that parallel light passing through many elements converges in the clear zone onto the same rhabdom.

The eyes of butterflies are interesting in that they operate as apposition eyes with optically isolated ommatidia, but their optical system is essentially of the superposition type, with a lens-cylinder type of lens, and light emerging parallel into the rhabdom, rather than focused as in a typical apposition eye. Such a system is known as afocal apposition.

22.2.2 Resolution

Resolution refers to the degree of fineness with which an eye forms an image of an object. In compound eyes, resolution is determined by the interommatidial angle (Δϕ), and by the angle over which each ommatidium accepts light (Δρ; Fig. 22.8a). For diurnal insects these two angles are approximately matched.

The interommatidial angle is the angular separation of the visual axes of adjacent ommatidia. In apposition eyes where each rhabdom functions as a unit, the fineness of the image will be greater the smaller the interommatidial angle. The interommatidial angle is often between 1° and 3°, but is greater than 5° in many beetles, and as little as 0.24° in parts of the eye of the dragonfly *Anax* (Odonata). In many insects it varies in different parts of the eye (see above). Resolution generally decreases when the eye becomes dark-adapted, because the ommatidial acceptance angle expands to admit more light (Section 22.3.2).

There is nothing to be gained, in terms of resolution, by having interommatidial angles smaller than the acceptance angle (Δρ) of individual ommatidia. This angle is determined partly by the angular width of the rhabdom (*d*/*f* in Fig. 22.8a), and partly by the spread of light in the image (Fig. 22.8b).

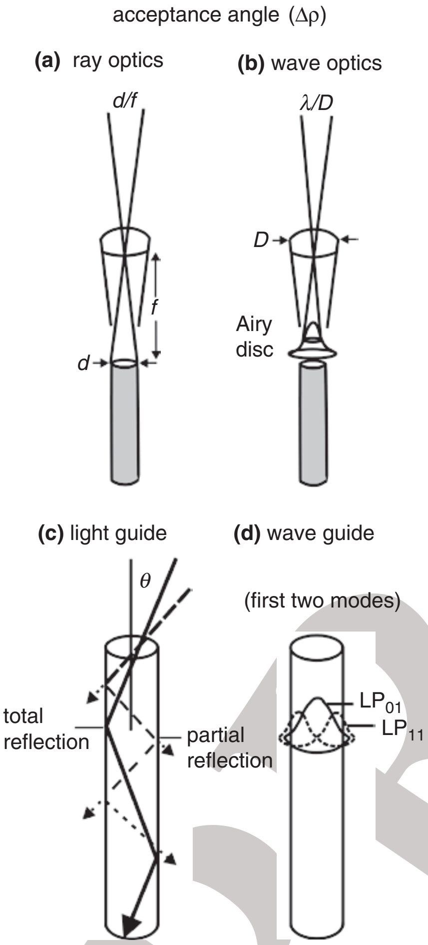


Figure 22.8 Ommatidial optics. (a) Ray and (b) wave optical components of the acceptance angle of an ommatidium (Δρ). By ray optics the acceptance angle is the angle subtended by the rhabdom (diameter *d*) at the nodal point of the lens (focal length *f*). In wave optics a point source produces a diffraction pattern (known as the Airy disc) whose angular diameter at half-maximum intensity is given in radians by the wavelength of light (λ) divided by the lens diameter (*D*). The interaction between the Airy disc and the wave guide modes in the rhabdom (Fig. 22.8d) is complex (see Stavenga, 2006). For most purposes ray optics (a) gives a good approximation to the true acceptance angle, although ultimately it is diffraction (b) that limits the available resolution. (c), (d) Rhabdoms can behave as light guides and wave guides. Light guides (c) will trap all rays up to the critical angle (θ) which for a rhabdom is about 12°. For rays making larger angles with the rhabdom axis reflection is only partial and so their light is progressively lost from the rhabdom. In a wave guide (d) light travels down the structure in the form of transverse interference patterns known as modes. The number of modes present depends on the diameter, wavelength and refractive index difference. Thus for a fly rhabdomere with a diameter of 0.9 μm the first two modes are present (known as LP_{01} and LP_{11} as depicted) at $\lambda = 400$ nm, but at $\lambda = 600$ nm only a single mode (LP_{01}) is present. Wider rhabdoms sustain more complex modes. Note that a proportion of the modal energy lies outside the rhabdom, and this is available for capture by screening pigment (Fig. 22.13). Because this proportion is greater for the higher-order modes they are lost first, which has the effect of narrowing the acceptance angle.

This spread is a consequence of the wave nature of light, and it occurs because different parts of the wave converging on the focus interfere with each other. The result is a diffraction pattern known as the Airy disc, after its discoverer. The angular width of this pattern (in radians; 1 radian is 57.3°) is given by λ / D, where λ is the wavelength of light (about 0.5 μm) and D is the diameter of the lens. In compound eyes D is small, typically around 25 μm, which means that the finest resolvable image point is about 0.5 / 25 radians, or just over 1°. For comparison, humans, with a 2.5 mm pupil, can resolve better than 1 minute of arc, 100 times finer than a bee. The only way to improve the resolution of a compound eye is to increase the diameters of the facets (D), and this can only be achieved for small regions of the eye if the size of the eye as a whole is not to become impossibly large. High resolution is needed in predatory insects such as dragonflies (Odonata: Anisoptera) and robber flies (Diptera: Asilidae) that hunt insects on the wing, and male insects of various orders that capture their mates on the wing. They have all developed limited "acute zones" of enlarged facets. An overall increase in resolution is not an option for a compound eye because this would require both larger facets and larger numbers of facets; the size of the eye increases as the square of resolution, so that a compound eye with 1 minute resolution would have a diameter of 12 meters!

22.2.3 Form perception

The eye's ability to detect the form of an object depends on its resolving power (Section 22.2.2). As, in diurnal insects, the interommatidial angle, and hence the angular resolution, is often 1° or less in some parts of the eye. This sets the limits of resolution. In predatory insects, such as mantids (Fig. 22.4), the acute zone provides a region of high-quality form perception in the front of the eye where prey is detected before the strike. In other insects, ommatidia in the dorsal part of the eye have small angles of acceptance, giving better form perception than other parts of the eye. If an object subtends an angle at the eye which is less than the ommatidial angle, it will be seen only as a spot.

Bees provide a good model for understanding form perception because they can be trained to discriminate between different shapes. They cannot only distinguish between shapes and patterns that differ in fine spatial detail, but also categorize vertical visual patterns by stripe angular orientation (independently of the color or width of stripes) or by plane of symmetry. Bees are also able to bind separate features of an image into a coherent image. In an example reminiscent of top-down image recognition in primates, bees can detect a camouflaged object only after exposure to a non-camouflaged object of the same type, and subsequently manage to break the camouflage of novel objects (Fig. 22.9); attention-like processes have been found in honey bees and other insects, such as fruit flies. In the wasp *Polistes dominulus*, which has relatively small colonies, individuals have highly distinct facial patterns, and these are used for individual recognition of the members of a colony.

22.2.4 Field of view

Insects with well-developed compound eyes generally have an extensive field of view. For example, in the horizontal plane *Periplaneta* has vision through 360°, with binocular vision in front and behind the head (Fig. 22.10). In the vertical plane the visual fields of the two eyes overlap dorsally, but not ventrally. The visual fields of grasshoppers and many other insects are similar to that of the cockroach.

22.2.5 Distance perception

Insects are able to judge distance with considerable accuracy. This is most obvious in insects such as grasshoppers, which jump to a perch, or in visual predators like mantids, but is also true for any insect landing at the end of a flight. Two possible

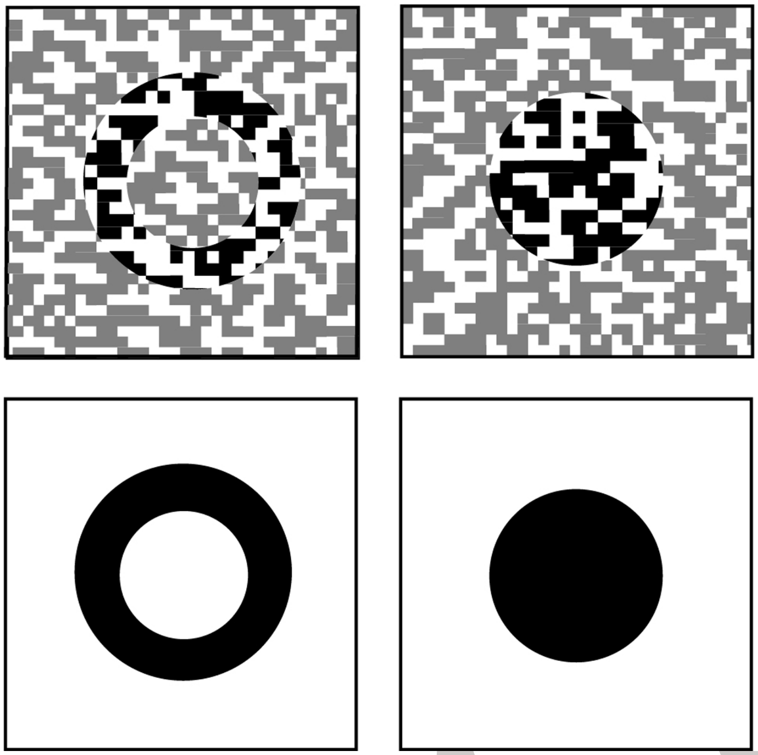


Figure 22.9 Pattern recognition by honey bees involves cognitive processes. Bees are typically trained to associate a visual pattern with a reward, and in a subsequent unrewarded test, must discriminate the trained from a different pattern. If bees are tested for discrimination of two camouflaged targets (top panels), they fail even after extensive training. However, the task can be introduced using non-camouflaged objects (bottom panels), guiding bees so that they “know what to look for.” If bees so entrained are then tested with the camouflaged objects in the top row, they will discriminate them with high accuracy (after Zhang and Srinivasan, 1994).

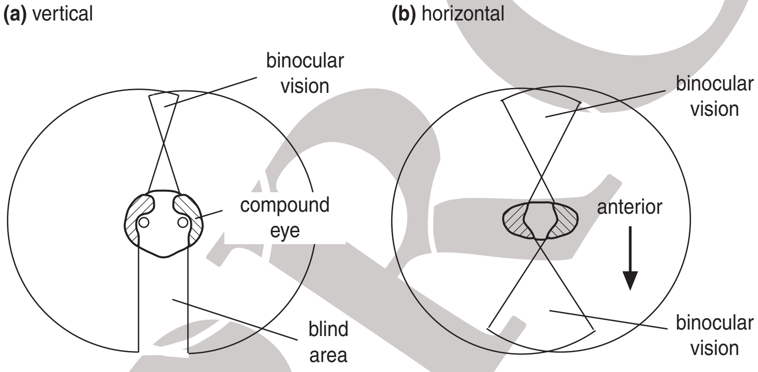


Figure 22.10 Visual field of *Periplaneta* (after Butler, 1973). (a) In the vertical plane, the visual fields of the two eyes overlap above the head, giving binocular vision. (b) In the horizontal plane, the visual fields of the two eyes overlap in front of and behind the head, giving binocular vision in both directions.

mechanisms exist that enable insects to estimate distance: a stereoscopic mechanism and motion parallax.

Some large insects with high spatial resolution have binocular vision in front of the head and so have the potential to assess distance stereoscopically – for example, praying mantids. This depends on the angle which the object subtends at the two eyes (Fig. 22.11). Errors can arise in the estimation of distance due to the size of the interommatidial angle, as this is important in determining resolution. Fig. 22.11 shows the error of estimation which might arise if the interommatidial angle was 2°; larger interommatidial angles will result in greater errors.

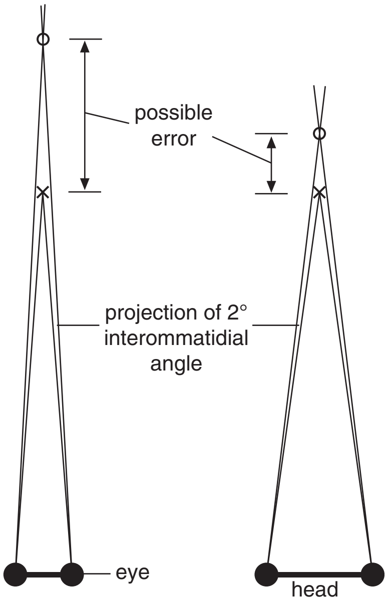


Figure 22.11 Distance perception. Diagrams illustrate how a wider head with greater separation of the eyes improves the estimation of distance. If the interommatidial angle is 2°, an object might lie anywhere between the cross and the open circle. Doubling the width of the head greatly reduces the possible error.

Errors will also be larger if the distance of the insect from its prey is long relative to the distance between the eyes, and in many carnivorous insects which hunt visually, such as mantids and Zygoptera (Odonata), the eyes are wide apart.

Insects, such as grasshoppers, that jump to perches and need to judge distances accurately, make peering movements while looking at their proposed perch. Peering movements are side-to-side swayings of the body, keeping the feet still and with the head vertical, but moving through an arc extending 10° or more on either side of the body axis. In such cases distance is estimated by motion parallax, the extent of movement over the retina as the head is swayed from side-to-side; big movements indicate that the object is close to the insect, while small movements show that it is at a greater distance. Grasshoppers are able to judge distances even when blinded in one eye, which is consistent with the idea that they are using motion parallax.

22.2.6 Visual tracking

Visual tracking refers to an animal's ability to keep a moving target within a specific area of the retina, often when the animal itself is also moving. It occurs, for example, when a predator such as a mantis or dragonfly catches its prey, or when a male fly pursues a female. To do this, the insect must move its head or body to minimize the angle subtended by the object relative to some reference point on the retina. This point is usually in the center of an acute zone where the ommatidia have bigger facets and smaller ommatidial angles than elsewhere in the eye, giving better resolution of the object.

When watching slowly moving prey against a homogeneous background, a mantis moves its head smoothly to keep the image in the high-acuity regions (Fig. 22.12). If the prey moves rapidly, however, or the background is heterogeneous, the insect makes rapid intermittent (saccadic) head movements. Between these movements, the head is kept still until the image has moved some distance from the center of the acute zone, when another rapid change occurs.

Male flies pursuing females exhibit these same two types of behavior, but there are differences between species. The hover fly *Syritta pipiens* tracks smoothly at low angular speeds but saccadically when the female moves faster. Houseflies (*Musca*) and the dolichopodid, *Poecilobothrus*, appear to reorient their bodies continuously in flight, but are probably making head saccades at the same time. This saccadic behavior was also demonstrated in blow flies (*Calliphora*). Small-target motion detectors responding selectively to target motion against the motion of the background have been identified in the lobula of *Eristalis tenax* hoverflies

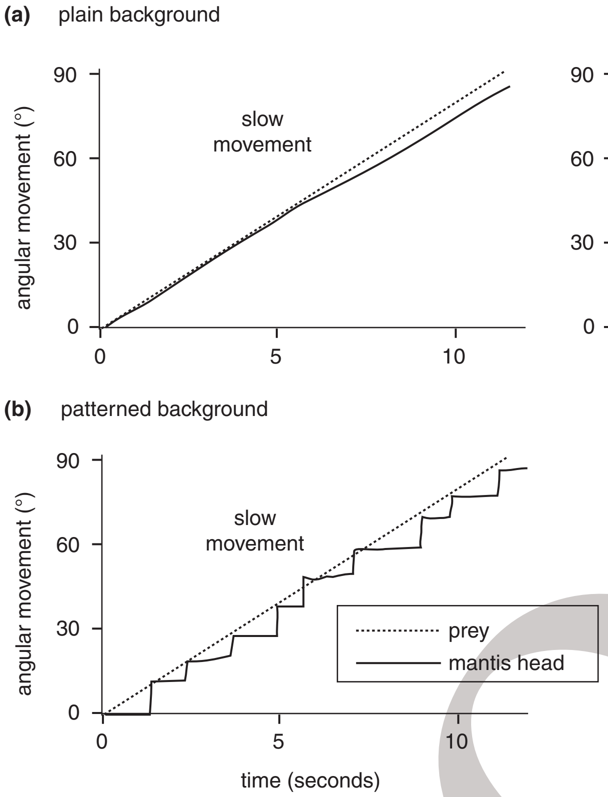


Figure 22.12 Visual tracking of prey by a mantis. The dotted line shows the steady movement of a potential prey item; the solid line shows the orientation of the mantid's head (after Rossel, 1980). (a) When the prey moves slowly against a plain background, the mantis moves its head steadily, keeping the prey within the foveal areas of the eyes (left). When the prey moves quickly (right), the mantis makes saccadic movements of the head. (b) With the prey against a patterned background, the mantis makes saccadic movements whatever the speed of the prey. In a saccade, the head remains still (horizontal lines) until the image of the prey has passed outside the fovea; it is then moved rapidly (vertical lines) so that the image of the prey is now in its original position. In this example, each movement of the head is through approximately 10°.

22.2.7 Visual flow fields

During forward locomotion, objects in the environment appear to move backwards with respect to the organism. This is especially important in flight, and insects are unable to make controlled flights without visual input, requiring image movement across the eye from front to back. Like all other behaviors associated with vision, response to the visual flow field is possible because the neural circuitry within the optic lobe permits the extraction of the appropriate information from image movement over the retina. In flies this is mediated by the lobula plate tangential cells, which have large receptive fields and are specialized for detecting particular directions of motion. Specific interneurons within the central nervous system relay appropriate information to the circuits controlling locomotion.

22.3 Receptor physiology, color and polarization vision

22.3.1 Transduction

The conversion of light to electrical energy involves the visual pigment. Known as rhodopsin, this is a G-protein coupled receptor molecule consisting of seven helices spanning the membrane of the microvilli that make up each rhabdomere. There are between 500 and 2000 rhodopsin molecules on each of the 40 000 microvilli in a *Drosophila* rhabdomere. Bound inside the rhodopsin molecule is a small chromophore; in vertebrates this is 11-*cis* retinal (the aldehyde of vitamin A), but in Diptera and some other insects it is 11-*cis*-3-hydroxy retinal (Fig. 22.13). It is the absorption of a photon by this chromophore that sets in train a cascade of events

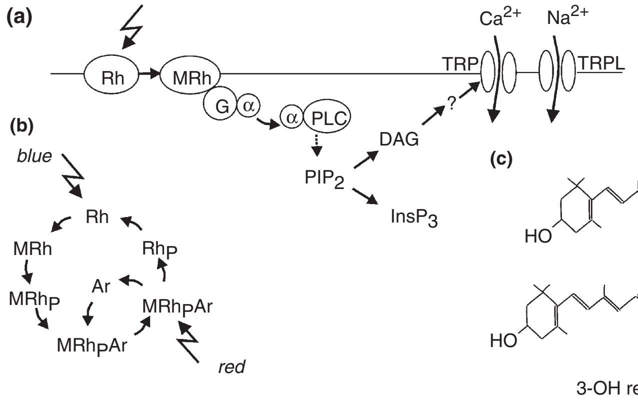


Figure 22.13 Signal transduction. (a) The transduction cascade in *Drosophila*. Rhodopsin (Rh) absorbs a photon and converts to metarhodopsin (MRh). This activates the G-protein whose α subunit is released and bonds to phospholipase C (PLC). This complex enzymatically splits phosphatidyl inositol 4,5-bisphosphate (PIP2) into two molecules, diacylglycerol (DAG) and inositol 1,4,5-trisphosphate (InsP$_3$). DAG acts via an unknown intermediary to open the membrane channels TRP to Ca^{2+} ions and TRPL to Na^{+} and Ca^{2+} ions. (b) The rhodopsin/metarhodopsin cycle. When rhodopsin absorbs a short-wavelength photon it converts to metarhodopsin, which becomes phosphorylated (P) and is inactivated by arrestin (Ar). This complex can be reactivated by a long-wavelength photon, and after losing arrestin and dephosphorylation is reconverted to active rhodopsin. (c) The structure of the chromophore 3-hydroxy retinal in its 11-*cis* and – following photoisomerization – its *all-trans* form. Simplified from Hardie (2006).

leading first to the conversion of rhodopsin to metarhodopsin, and ultimately to the depolarization of the microvillar membrane (Fig. 22.13a,b). In dipteran photoreceptors the situation is complicated by the presence of a second ultraviolet-absorbing chromophore (3-hydroxy retinol). This is a sensitizing pigment that is capable of transferring the energy of the absorbed ultraviolet photons to the primary photopigment, resulting in enhanced overall sensitivity.

The first step in the phototransduction cascade is a change of the 11-*cis* form of the chromophore to the *all-trans* form (Fig. 22.13c), resulting in the conversion of rhodopsin to active metarhodopsin, which can then activate associated G-proteins. Potentially, metarhodopsin can continue to activate G-proteins, but it is inactivated by binding with the small protein arrestin, after activating 5–10 G-protein molecules.

Metarhodopsin is, itself, photosensitive, absorbing light at a different wavelength from the rhodopsin that gave rise to it (Fig. 22.13b). The main rhodopsin in flies absorbs at 480 nm and the corresponding metarhodopsin at 560 nm. Photoactivation reconverts the metarhodopsin to inactive rhodopsin which, after release from arrestin, is available to transduce light again. Thus light of a different wavelength from that to which the photopigment is sensitive contributes to the efficiency of the response by regenerating rhodopsin. Under constant light conditions the amounts of rhodopsin and metarhodopsin are in equilibrium. This is very different from vertebrates, where rhodopsin has to be regenerated via a complex cycle involving the pigment epithelium.

Following the activation of the G-protein the transduction cascade becomes complex, but in outline it proceeds as in Fig. 22.13a. Activated metarhodopsin causes the α subunit of the G-protein to detach and bind to phospholipase C (PLC). This combined molecule then acts as an enzyme that converts phosphatidyl inositol 4,5-bisphosphate

(PIP_2) into two second messenger molecules, diacylglycerol (DAG) and inositol 1,4,5-trisphosphate ($InsP_3$). Current evidence in *Drosophila* favors DAG as the main agent responsible, indirectly, for causing the cation channels in the membrane (the so-called TRP and TRPL channels) to open, resulting in a membrane depolarization. It seems that the components of this cascade do not simply diffuse freely in the microvillar cytoplasm, but many, including PLC and the TRP channels, are anchored onto a protein scaffold known as the INAD complex, which is in turn attached to the actin cytoskeleton of the microvillus.

The Ca^{2+} that enters the microvillus through the TRP and TRPL channels has two opposite effects on the electrical response. Initially it rapidly sensitizes the remaining channels in the microvillus (about 25 per microvillus in flies), which open and thus amplify the response. This further Ca^{2+} influx then causes a complete inactivation of the channels of the microvillus, and a refractory period lasting about 100 ms. For a single photon capture, the net effect of these two process is to produce a single "quantum bump," a rapid electrical depolarization of 1–2 mV, with a current of about 10 pA and lasting about 30 ms. The responses to larger photon numbers sum across the receptor as a whole to give peak responses as high as 70 mv. The range over which a single photoreceptor can operate before reaching saturation is 3–4 decades of light intensity.

The probability that a photon will encounter a visual pigment molecule is increased by the length of the rhabdomere or rhabdom. The proportion of white light absorbed is given approximately by $kL/(2.3 + kL)$ where L is the length and k the absorption coefficient which, for rhabdomeric receptors, is about $0.01\ \mu m^{-1}$. Thus a *Drosophila* rhabdomere 80 μm long absorbs about 26% of the light reaching it. In the much longer rhabdoms of insects such as dragonflies nearly all the incident light is absorbed. A tapetum, when present, reflects light back through the rhabdom and so further increases the chances that the photons and receptor molecules will interact. Rhabdoms have a slightly higher refractive index than the surrounding fluid, and so act as light guides, retaining by total internal reflection most of the light that enters them within about 12° of their long axis (Fig. 22.8c). However, because of their narrow diameter – only a few times greater than the wavelength of light – rhabdoms also behave as wave guides. Within wave guides the light waves interfere, producing a series of stable interference patterns, known as modes, in which the light is not uniformly distributed (Fig. 22.8d). Importantly, a proportion of the modal light travels outside the rhabdom (the boundary wave), and this light is available for capture either by adjacent photoreceptors, or by screening pigment (see Section 22.3.2). This proportion increases as the rhabdoms get narrower, and this limits the useful width of a rhabdom to about 1 μm.

Action potentials are not typically produced by photoreceptor cells and depolarization is transmitted along their axons by passive conduction. In the lamina, most of the receptor cells synapse with large monopolar cells, and with other interneurons (see Fig. 20.21c). The neurotransmitter at these synapses is histamine and the signal is inverted. That is, a depolarization of the receptor cell produces a hyperpolarization of the interneuron. Any new signal is amplified at these synapses while the effects of the general level of illumination are reduced. The mechanisms producing these effects are not fully understood, but involve presynaptic interactions.

22.3.2 Adaptation

The natural change from darkness to full sunlight involves a change in light intensity of some 10 log units: a white surface in bright sunlight reflects about 4×10^{20} photons $m^{-2}\ sr^{-1}\ s^{-1}$ compared with about 10^{10} photons $m^{-2}\ sr^{-1}\ s^{-1}$ on an overcast night with no moon, and 10^{14} photons $m^{-2}\ sr^{-1}\ s^{-1}$ on a moonlit night. However, the response of the photoreceptor cells is fully saturated by an increase

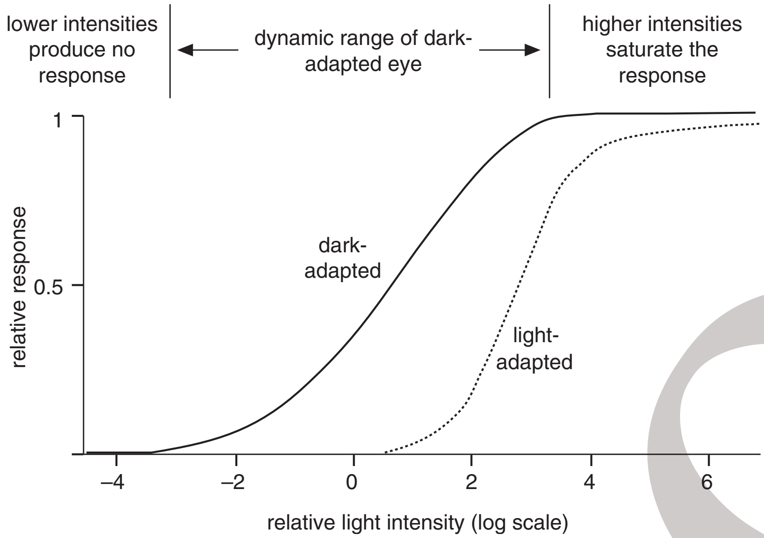


Figure 22.14 Response of visual cells. Different light intensities can only be distinguished within the dynamic range. In the light-adapted eye, the response is shifted to the right (higher intensities). Notice that within the dynamic range of the light-adapted eye a small change in intensity results in a much bigger change in the response level than in the dark-adapted eye. In other words, contrasts are more readily differentiated by the light-adapted eye. Relative response is the receptor potential expressed as a proportion of the maximum response in dark- or light-adapted eyes (based on Matic and Laughlin, 1981).

in intensity of about four log units (Fig. 22.14). Various devices are used to regulate the amount of light reaching the receptors so that the insect can operate over a wider range of intensities. The eye is said to adapt to the light conditions.

This type of adaptation occurs at two different levels in the eye: (1) the amount of light reaching the photoreceptors is regulated; and (2) the receptor sensitivity can be changed. In addition, changes occur at the synapses between receptor cells and interneurons in the lamina. Although the latter does not influence the immediate response to the amount of light, it does influence the information reaching the central nervous system.

Regulation of light reaching the receptors The amount of light reaching the rhabdom is regulated by movement of pigment in the screening cells, sometimes associated with anatomical changes in the ommatidium. Pigment movements are most clearly seen in superposition eyes. In the dark-adapted eye, pigment is withdrawn to the distal ends of the pigment cells and light leaving the lenses can move between ommatidia in the clear zone (Figs. 22.2; 22.6b). At high light intensities, however, the pigment moves so that light can now reach the rhabdom only via a narrow tract across the clear zone and the effective aperture of the ommatidium through which light reaches the rhabdom is very small. The eye is now functioning as an apposition eye with the ommatidia now acting as separate units. In superposition eyes where the photoreceptor cells form a broad column to the lens system, these cells undergo extensive changes in shape (Fig. 22.2c). Dark adaptation results in their extension and in compression of the crystalline cone so that the screening pigment is restricted to the most peripheral parts of the eye. In the light, the receptor cells are short and the primary pigment cells extend below the lens.

Comparable pigment movements occur in apposition eyes of some insects. For example, when the ant *Camponotus* is in the light, the primary pigment cells extend proximally (Fig. 22.15). At the same time, the proximal end of the crystalline cone is compressed to form a narrow crystalline tract surrounded by the pigment cells. Light must pass through the narrow opening to reach the rhabdom. At the same time, the rhabdom shortens, further increasing the likelihood that only light entering the ommatidium directly along its axis will reach the rhabdom.

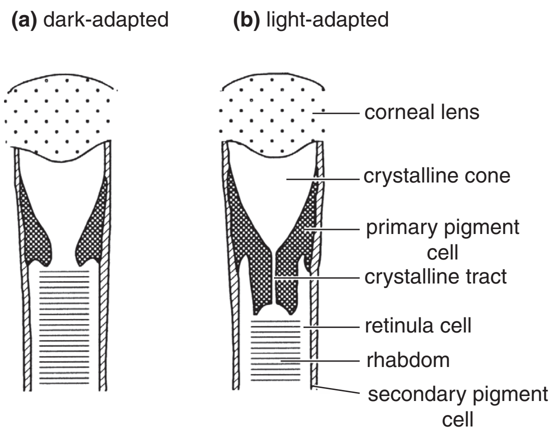


Figure 22.15 Adaptation. Changes in the apposition eye of an ant, *Camponotus*. Only the most distal part of an ommatidium is shown (after Menzi, 1987): (a) dark-adapted; (b) light-adapted.

In the acone eyes of many Diptera and Heteroptera the photoreceptor cells extend in the dark, carrying the distal end of the rhabdom to a more peripheral position and at the same time causing the Semper cells to become shorter and broader. This may involve a movement of 15 μm or even more by the rhabdom. At the same time, the primary pigment cells are displaced laterally so that the aperture of the optic pathway is increased.

The changes associated with dark adaptation begin within minutes of an insect's entry into darkness, but take longer to complete. In the ant *Camponotus*, the first change is already apparent within 15 minutes of an individual moving from light to dark, but completion takes about two hours. The changes are more rapid in some other insects. In addition to a direct response to environmental conditions, pigment movements are commonly entrained to the light cycle, occurring even in the absence of any environmental change. Thus the eye of the codling moth normally starts to become light-adapted about 30 minutes before sunrise and dark-adapted just before sunset, the process taking about an hour to complete. A consequence of these changes is that the rhabdom receives light from a wide acceptance angle in dark-adapted eyes (Fig. 22.16), resulting in a reduction in image resolution. The range of light intensities over which these pigment movements occur varies according to the insect's normal habits. For example, pigment movements in the eye of the cave-dwelling tenebrionid beetle *Zophobas*, occur at light intensities about five orders of magnitude lower than they do in the diurnal *Tenebrio*. Pigment movements are regulated individually within each ommatidium. In the moth *Deilephila* a structure near the tip of the crystalline cone absorbs ultraviolet light, the principal wavelength producing pigment movements, but how it effects movement is not known.

Regulation of receptor sensitivity Regulation of sensitivity in many apposition eyes is achieved by structural changes in the photoreceptor cells that vary the amount of light available for capture by rhodopsin, and thus act as a pupil. During light adaptation, granules of an absorbing pigment are present within the receptor cells (in addition to that in the screening pigment cells) close to the inner ends of the microvilli of the rhabdoms or rhabdomeres (Fig. 22.17). In the light these pigment granules migrate toward the surface of the rhabdom, and absorb the modal light traveling along the outside (see Fig. 22.8d), thereby bleeding light progressively out of the interior of the rhabdom and so reducing the amount available for photoreception. These movements are rapid, taking only seconds to complete in dipterans and butterflies. In the dark, large vesicles develop in the endoplasmic reticulum so that a clear space, known as the palisade, is formed around the rhabdom, effectively isolating it from the absorbing pigment.

In addition to this pupil mechanism, there are numerous points in the transduction cascade at which sensitivity reduction can occur. One is the rate at which arrestin inactivates metarhodopsin, thereby varying the number of G-protein activations following photon capture. Another is the blocking effect of physiological concentrations of Mg^{2+} on the

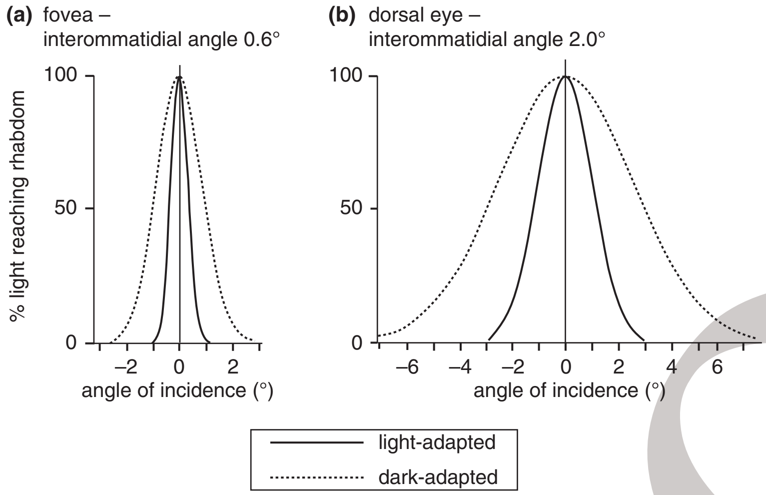


Figure 22.16 Dark adaptation. Effects on the acceptance angles of ommatidia in different parts of the eye of the mantis, *Tenodera*. The acceptance angle is usually measured as the angle over which 50% of the incident light reaches the rhabdom. Compare Fig. 22.4 (after Rossel, 1979). (a) An ommatidium in the fovea, where the interommatidial angle is 0.6°. (b) An ommatidium in the dorsal eye, where the interommatidial angle is 2.0°

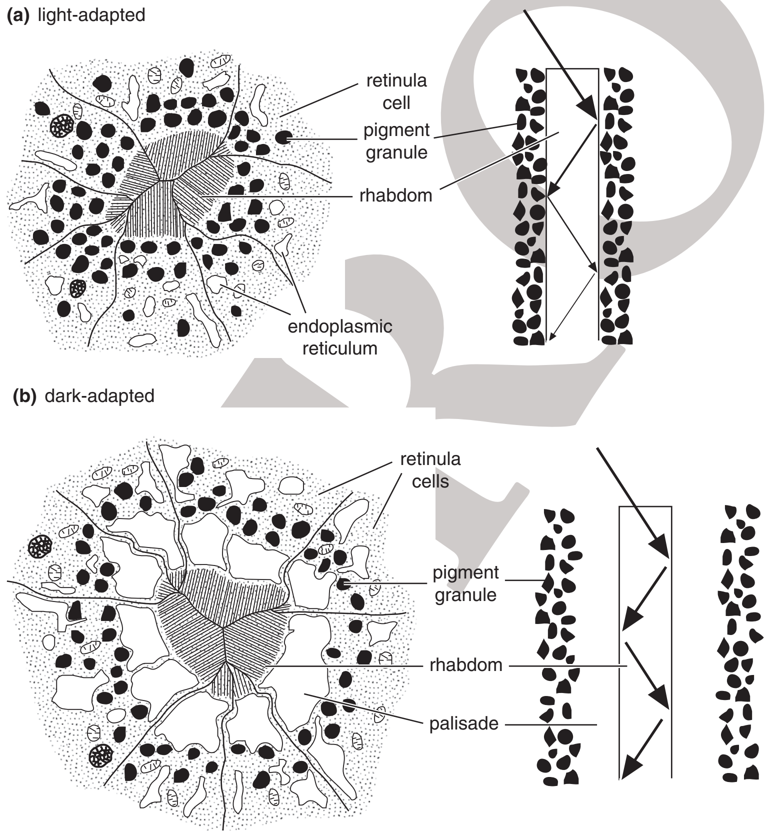


Figure 22.17 Adaptation. Changes in the photoreceptor cells in an apposition eye. Each diagram represents (left) a cross-section of the rhabdom and associated receptor cells, and (right) a longitudinal section showing the extent to which light is internally reflected within the rhabdom (partly after Snyder and Horridge, 1972): (a) light-adapted; (b) dark-adapted.

TRP channels; this intensifies as the cell depolarizes, thus decreasing the channel conductance as a function of light intensity.

Adaptation also occurs at the synapses between the photoreceptor cells and the interneurons in the lamina. The mechanisms are not understood, but probably include modulation of the quantity of transmitter released by the receptor cells. As a result of this adaptation, the input to the lamina is believed to be more or less constant despite differences in overall light intensity. Consequently, changes in stimulation of comparable magnitude are registered by similar activity in the medulla, irrespective of the background level of stimulation.

22.3.3 Spectral sensitivity and color vision

Photoreceptor cells can have wavelengths of maximum sensitivity (λ_{max}) from ~330 nm to 640 nm. When plotted over a linear wavelength scale, photoreceptors typically have roughly Gaussian sensitivity profiles around the peak, with sensitivity falling off smoothly over several dozen nanometers to both sides from the value of maximum sensitivity. In longer wavelength receptors there is a smaller β sensitivity peak at short wavelengths (Fig. 22.18). λ_{max} depends fundamentally on the amino acid sequence of the opsin protein, where specific substitutions at sites interacting with the chromophore will induce spectral tuning.

Other important factors in spectral tuning and the shape of the sensitivity function are the choice of the chromophore (retinal or 3-hydroxy retinal), accessory pigments, tapeta, as well as various filtering mechanisms that limit the spectrum of light available to any one receptor type.

The ancestral set of photoreceptors in the pterygote insects appears to have been am ultraviolet, a blue and a green receptor. This set is retained by many extant insects. These receptor types are distributed over various types of ommatidia, all of which have six green receptors in many species. In bumble bees, honey bees and trichromatic Lepidoptera (*Vanessa*, *Manduca*), type I ommatidia contain a blue and an ultraviolet receptor, type II ommatidia have two ultraviolet receptors and type III ommatidia possess two blue receptors. A modification occurs in flies, which have two types of ommatidia (named "pale" and "yellow"). Both of these contain six receptor cells (R1–6) with unusually broad spectral sensitivities covering the range from 300 nm to 600 nm. This broad sensitivity is mediated by a combination of a blue-sensitive opsin with an ultraviolet-absorbing sensitizing pigment. In addition, "pale" ommatidia contain an ultraviolet (R7p) and a blue receptor cell (R8p), while "yellow" ommatidia contain an ultraviolet (R7y) and a green receptor (R8y). R7 is located directly on top of R8, and where the

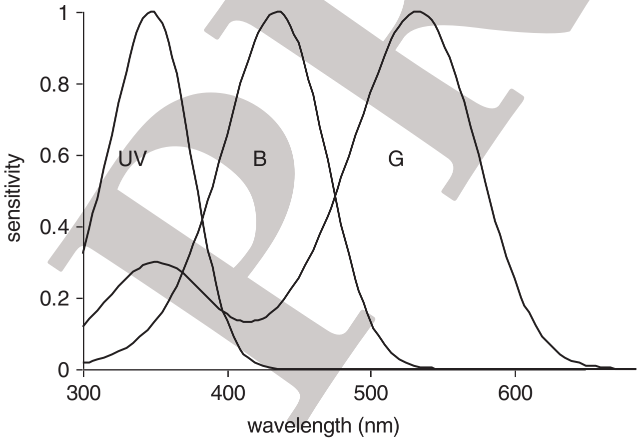


Figure 22.18 Photoreceptor spectral sensitivity. Absorption of light of different wavelengths by three commonly occurring photoreceptor types in insect eyes with peak absorption in the ultraviolet (UV), blue (B) and green (G) ranges of the spectrum, shown here for the bumble bee *Bombus terrestris* (after Skorupski *et al*., 2007). The sensitivity function of each receptor is normalized to a maximum of unity.

rhabdomeres are tiered in such a way (Fig. 22.4b,c) that the distal rhabdomeres function as filters for those situated more proximally. Specialized eye regions aside, the various types of ommatidia are often randomly distributed across the eye, although not necessarily in equal proportions.

In many insects, however, the occurrence of different visual pigments varies in different parts of the eye apparently in relation to the eye's different functions. For example, in the drone honey bee, ommatidia in the dorsal part of the eye have only ultraviolet- and blue-sensitive pigments, whereas, in the ventral part of the eye, green-sensitive pigment is also present. This distinction appears to occur in many flying insects, perhaps because dorsal ommatidia are skyward-pointing and the ventral ones face the vegetation. Sexual differences may also occur, as in the butterfly *Lycaena rubidus*, where the dorsal ommatidia in females have a visual pigment absorbing maximally at 568 nm; this pigment is absent from the dorsal ommatidia of males.

Many Lepidoptera, Odonata and possibly also some Hymenoptera and Coleoptera possess more than three color receptor types – for example, cells with peak sensitivity in the red or in the violet. Such higher diversity of spectral receptor types can be achieved via increases of opsin types (mediated via gene duplication and subsequent spectral tuning) or by systematic usage of filtering mechanisms that control the light reaching the photopigments, or a combination of both strategies. The butterfly *Pieris rapae*, for example, has four opsins, including the typical ultraviolet- and green-sensitive ones, but the blue-sensitive opsin is duplicated so that peak sensitivities are at $\lambda_{\max} = 360$, 425, 453 and 563 nm. However, there exist also red receptors ($\lambda_{\max} = 620$ nm) and deep red receptors ($\lambda_{\max} = 640$ nm), but these express the same visual pigment as the green receptors ($\lambda_{\max} = 563$ nm). Diversity here is achieved by pairing cells containing the same opsin with three different filtering pigments arranged around the rhabdom. Conversely, the swallowtail butterfly, *Papilio xuthus*, has five different opsins where spectral fine-tuning is again achieved by peri-rhabdomal filtering. Here, red sensitivity is mediated by an opsin with peak sensitivity of $\lambda_{\max} = 575$ nm, i.e., at longer wavelengths than the human "red" receptor ($\lambda_{\max} = 565$ nm). Typically, one color receptor type expresses only one opsin, but this species also has receptor cells with a very broad-band spectral sensitivity, and containing two opsins with $\lambda_{\max} = 520$ and 575 nm. In addition, as in flies, *Papilio* photoreceptors are arranged in tiers, meaning that the light reaching more proximal photoreceptors is first filtered by the distal ones.

In a few insects the lenses are colored so that the rhabdoms of the associated ommatidia can receive only those wavelengths transmitted by the lenses. Male dolichopodid flies, for example, have alternating vertical rows of red and yellow facets. As a result, the same visual pigment in different ommatidia will be differentially activated, providing a basis for color vision even if only one type of visual pigment is present. Likewise, differently colored tapeta paired with identical photoreceptors could generate different spectral sensitivities.

Color vision is the ability to see images in which objects have color attributes. This requires image-forming eyes and the ability to recognize targets based on their spectral identity and independently of intensity. A mechanistic requirement is the existence of at least two photoreceptor cell types with distinct spectral sensitivities. This is because a single receptor type, despite its differential sensitivity to different wavelengths, cannot reliably disentangle wavelength from intensity. Information on the wavelength of a photon is lost upon absorption, and all the information that is available for the nervous system is a change in receptor voltage signal. However, an intermediate change can be induced by a weak light at peak sensitivity, or a strong light where the receptor is less sensitive. Thus, the signals from two receptors (at least) must be related to one another in order to extract reliable information about spectral identity, and this is done by so-called color opponent neurons, which have been found, for example, in the optic lobes of flies and bees. In addition, there must be the neural machinery for binding color attributes with other image features.

However, the existence of these mechanisms is not in itself sufficient evidence for color vision. For example, two distinct spectral receptor types in an animal might be used for color vision, but they could also be used to each drive a separate behavior routine, such as phototaxis, mate search or oviposition. In many motion-related behavioral contexts (such as edge detection, assessment of speed, motion parallax), insects behave as if color blind – in bees such behaviors are mediated only by green receptor input, whereas in flies the broad-band R1–6 receptors provide the input to such behaviors. Thus behavioral tests are necessary to prove that receptor responses are integrated in a color vision system. It is essential that an animal can respond to targets based on their spectral composition, and independently of intensity. Many insects, including Hymenoptera, Lepidoptera and Diptera can be trained to associate colors with certain outcomes, even some nocturnal insects. The conjunction of color with shape (as required by a strict definition of color vision) requires that insects can disentangle shape from color and moreover to categorize distinctly shaped objects by color; this has been demonstrated in bees and wasps.

Many insects have distinct color preferences when they first search for food; however, these can typically be modified by learning. Interestingly, herbivorous insects often prefer not only green, but more strongly yellow when searching for suitable forage. This bias can be understood when one considers that a spectrally opponent neural mechanism with antagonistic inputs from green receptors and more short-wave receptors drives the behavioral response: typically, yellow targets provide a stronger signal in such a mechanism than the relatively broad-band reflectance of green foliage. Many species of bees prefer colors in the violet to blue range, an evolutionary response to the fact that flowers with such colors often contain high nectar rewards.

22.3.4 Discrimination of the plane of vibration (polarization sensitivity)

Lightwaves vibrate in planes at right angles to the direction in which they are traveling. These planes of vibration may be equally distributed through 360° about the direction of travel, or a higher proportion of the vibrations may occur in a particular plane. Such light is said to be polarized, and if all the vibrations are in one plane the light is plane-polarized.

Light coming from a blue sky is polarized. The degree of polarization and the plane of maximum polarization from different parts of the sky vary with the position of the sun. It is, consequently, possible to determine the position of the sun, even when it is obscured, from the composition of polarized light from a patch of blue sky. Certain insects are able to make use of this information in navigation. It is particularly important in the homing of social Hymenoptera, and is best known in *Apis* and the ant *Cataglyphis*. In other insects, including Odonata and some Diptera, the ability to perceive polarized light probably enables the insects to maintain a constant and steady orientation.

Detection of the plane of polarization is possible because photopigment molecules are preferentially oriented along the microvilli of the rhabdomere and maximum absorption occurs when light is vibrating in the same plane as the dipole axis of the pigment molecule. If the rhabdom is twisted, as in most ommatidia, there can be no preferred plane of absorption; polarization sensitivity depends on a uniform orientation of the visual pigment molecules within a rhabdomere. In ants and bees, and other insects responding to the plane of polarization, straight rhabdomeres are present only in a small group of ommatidia along the dorsal rim of each eye. These polarization-sensitive ommatidia constitute only 6.6% of the total ommatidia in *Cataglyphis*, and 2.5% in *Apis*.

When light is polarized all wavelengths are affected, but the polarization receptors of ants and bees are responsive to ultraviolet light. In *Cataglyphis*, six of the eight photoreceptor cells in the dorsal rim ommatidia are ultraviolet-sensitive; four have a common orientation of their microvilli, those of the other two are at right angles (Fig. 22.19a). Consequently, when one set of cells is responding maximally because its microvilli are parallel with the plane of polarization, the other set is responding minimally. Each ommatidium in the dorsal rim responds maximally to polarization in one plane, and the population of receptors exhibits a range of different orientations (Fig. 22.19b). In the medulla of the optic lobe, the photoreceptor cell axons synapse with interneurons responding maximally to polarization in a particular plane (Fig. 22.19c). It is believed that, by scanning the sky, the insect is able to match the inputs of its polarization receptors to the pattern in the sky. When reorienting, it matches the sky pattern to the remembered neural input. A neural map that could achieve this kind of comparison has been located in the central body of the locust brain.

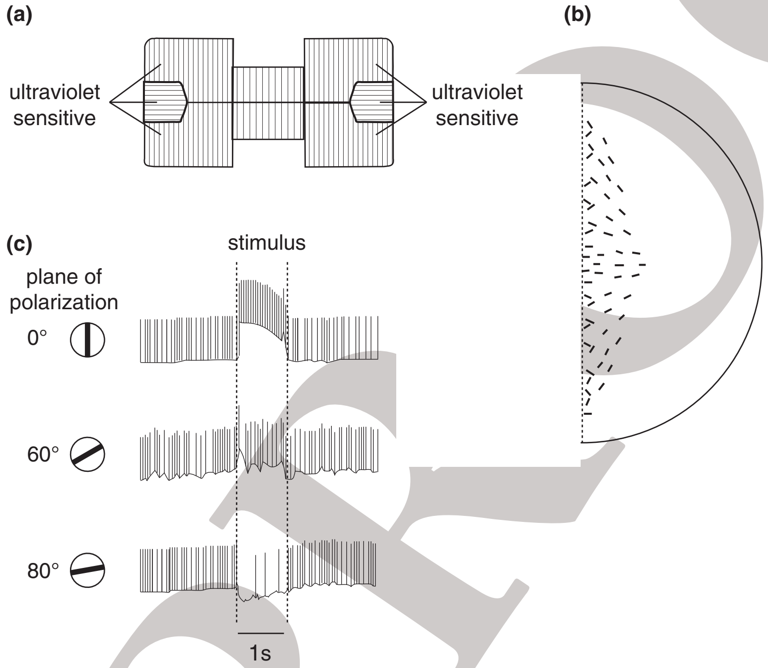


Figure 22.19 Detection of the plane of polarization. (a) Arrangement of microvilli in the rhabdom in the polarization-sensitive area. Six of the eight photoreceptor cells are ultraviolet-sensitive, with orthogonally arranged microvilli (*Cataglyphis*) (after Wehner, 1982). (b) Orientation of the rhabdoms in the polarization-sensitive area along the dorsal margin of the right eye of *Cataglyphis* (after Wehner, 1989). (c) Response of an interneuron in the medulla to stimulation of the eye with light polarized in different planes. Vertically polarized light (0°) results in depolarization of the interneuron and an increase in its firing rate. Near horizontally (80°) polarized light causes a hyperpolarization and inhibition of the cell. These effects are thought to be produced by interaction of the input from receptor cells with different microvillar orientation, as in (a) (*Gryllus*) (after Labhart, 1988).

22.4 Dorsal ocelli

Dorsal ocelli are found in adult insects and the larvae of hemimetabolous insects. Typically there are three ocelli forming an inverted triangle antero-dorsally on the head (Fig. 22.20a), although in Diptera and Hymenoptera they occupy a more dorsal position on the vertex. The median ocellus shows evidence of a paired origin, as the root of the ocellar nerve is double and the ocellus itself is bilobed in Odonata and *Bombus* (Hymenoptera). Frequently, one or all of the ocelli are lost and they are often absent in wingless forms.

A typical ocellus has a single thickened cuticular lens (Fig. 22.20b), although in some species, such as *Schistocerca* (Orthoptera) and *Lucilia* (Diptera), the cuticle is transparent, but not thickened, and the space beneath it is occupied by transparent cells. Each ocellus contains a large number of photoreceptor cells packed closely together without any regular arrangement; in the locust ocellus there are 800–1000. A rhabdomere is formed on at least one side of each receptor cell, and the rhabdomeres of between two and seven cells combine to form rhabdoms. The rhabdomeres usually occupy much of the cell boundary and, in the case of *Rhodnius* (Hemiptera), are present all around the cells, forming a hexagonal meshwork similar to that in the stemmata of *Cicindela* (Coleoptera) (Section 22.5). The structure of the rhabdomeres in the dorsal ocelli is the same as that in the compound eye. Pigment cells sometimes invest the whole ocellus, but in some species, e.g., cockroaches, they are lacking.
A reflecting tapetum, probably consisting of urate crystals in a layer of cells, may be present at the back of the receptor cells.

Each photoreceptor cell gives rise, proximally, to an axon which passes through the basal lamina of the ocellus and terminates in a synaptic plexus immediately behind the ocellus. Two anatomical classes of ocellar interneurons originate here. Some have giant axons up to 20 μm in diameter, often called large (L) fibers, others are of small diameter (S fibers). About ten large fibers and up to 80 small ones are associated with each ocellus. In most insects studied the large interneurons end in the brain, but in bees and flies some extend to the thoracic ganglia

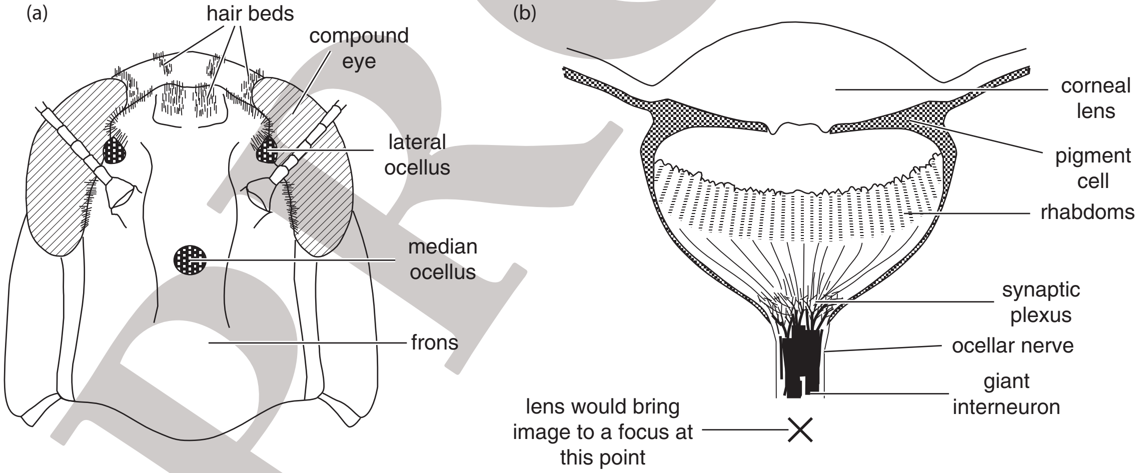


Figure 22.20 Ocellus. (a) Frontal view of the head of a grasshopper, showing the positions of the ocelli. (b) Diagrammatic longitudinal section through an ocellus of a grasshopper. The diagram shows the light-adapted condition with the pigment of the pigment cells restricting the entry of light. Notice that the image is focused below the rhabdoms (after Wilson, 1978).

(Fig. 22.21). Where these descending interneurons are absent, the pathway to the thoracic motor centers is completed by second-order descending interneurons. The small interneurons connect with several other centers in the brain, including the optic lobes, mushroom bodies and the central body.

The receptor cell axons synapse repeatedly and reciprocally with each other and with the interneurons, which also synapse with each other. Some of the synapses between interneurons and receptor cells are input synapses to the receptor cells, indicating that the interneurons may modulate the activity of the receptor cells as well as receiving information from them.

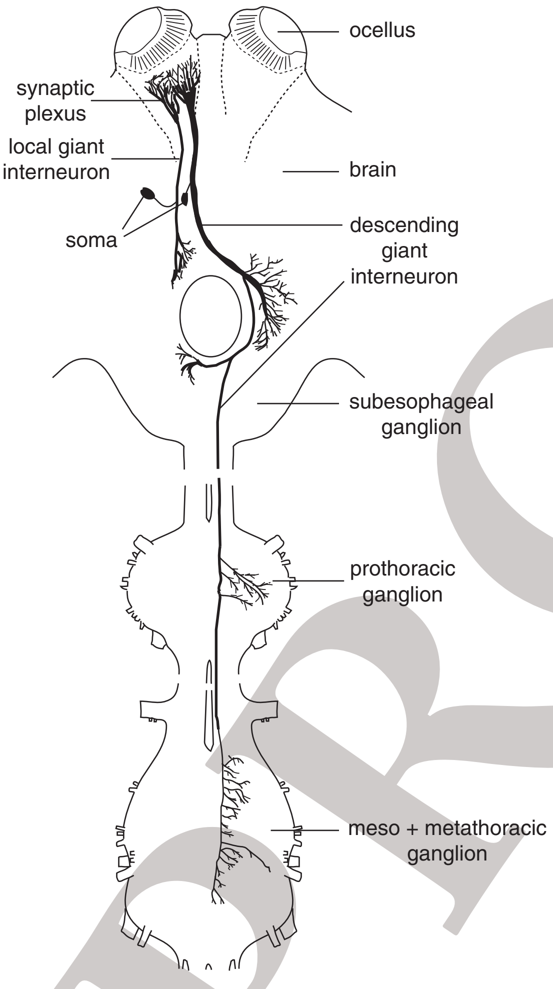


Figure 22.21 Giant interneurons from the ocelli. A diagram of the anterior ganglia of the central nervous system of a honey bee showing examples of giant interneurons, a local neuron that does not extend beyond the brain and a descending neuron that runs from the ocellus to the pterothoracic ganglion (based on Mobbs, 1985).

Illumination produces a sustained depolarization of the photoreceptor cell which is proportional to light intensity. No action potentials are produced in the receptor cells, and graded receptor potentials are transmitted along the axons to the synapses. As at the first synapses behind the compound eye, the signal is amplified and the sign is reversed. Also as in the compound eye, the input signals arising from contrasts in illumination are of similar amplitude even though the background level of illumination is different. The giant interneurons transmit information to the brain, either electrotonically, or by spiking.

Because the image produced by the lens is not in focus on the retina in some species, the function of ocelli was long thought to be only light detection. However, it is now known that in dragonflies and nocturnal wasps, the median ocelli are focused, and, at least in dragonflies, adapted for accurate detection of the horizon. Here, the median ocellus can even detect the direction of moving gratings and is involved in early-stage motion processing and subserving pitch control. Even in species where the lens is underfocused there is still potential for form vision. In the locust the ocelli are involved in detecting roll, their sensitivity to rapid changes in light intensity being well suited for the perception of changes in the position of the horizon.

22.5 Stemmata

Stemmata are the only visual organs of larval holometabolous insects. They are sometimes called lateral ocelli, but this term is better avoided as it leads to confusion with the dorsal ocelli from which they are functionally and often structurally distinct. Extraocular photoreceptor organs in the optic lobes of adult insects are also sometimes called stemmata, and indeed it appears that they are developmentally based on larval precursors (Section 22.6.2). Larval stemmata occur laterally on the head and vary in number from one on each side in tenthredinid larvae (Hymenoptera: Symphyta) to (most typically) six on each side, for example in larval Lepidoptera (Fig. 22.22). The larvae of fleas and most hymenopterans, other than Symphyta, have no stemmata. In larval Cyclorrhapha (Diptera) they are represented only by internal receptors. Some stemmata are simple visual organs, while others are complex camera-type eyes.

Stemmata are of two types, those with a single rhabdom, and those with many rhabdoms. The former occur in Mecoptera, most Neuroptera, Lepidoptera and Trichoptera. They are also present in Diptera, but in some species several stemmata are fused together to form a compound structure with a branching rhabdom. In Coleoptera the stemmata of many species have a single rhabdom, but some species, such as those of larval Adephaga (Coleoptera) have multiple rhabdoms. Stemmata with multiple rhabdoms also occur in larval Symphyta (Hymenoptera).

In caterpillars each stemma has a cuticular lens beneath which is a crystalline lens (Fig. 22.22b,c). Each lens system has seven photoreceptor cells associated with it. Commonly, three form a distal rhabdom and four form a proximal rhabdom. A thin cellular envelope lies around the outside of the sense cells and is, in turn, shrouded by the extremely enlarged corneagen cells. All the distal cells contain a visual pigment with maximal absorbance in the green part of the spectrum, while some proximal cells contain a blue- or ultraviolet-sensitive pigment. The rhabdomeres within the stemmata of caterpillars have different visual fields, and the acceptance angles of the distal rhabdomeres are close to 10° so they have low spatial resolution. The proximal rhabdomeres have much smaller acceptance angles of less than 2°. This, together with the fact that the focal plane of the lens is at the level of the proximal cells, gives them better spatial resolution. The visual fields of adjacent stemmata do not overlap so the caterpillar perceives an object as a very coarse mosaic, which is improved by side-to-side movements of the head, enabling it to examine a larger field. It is known that caterpillars can

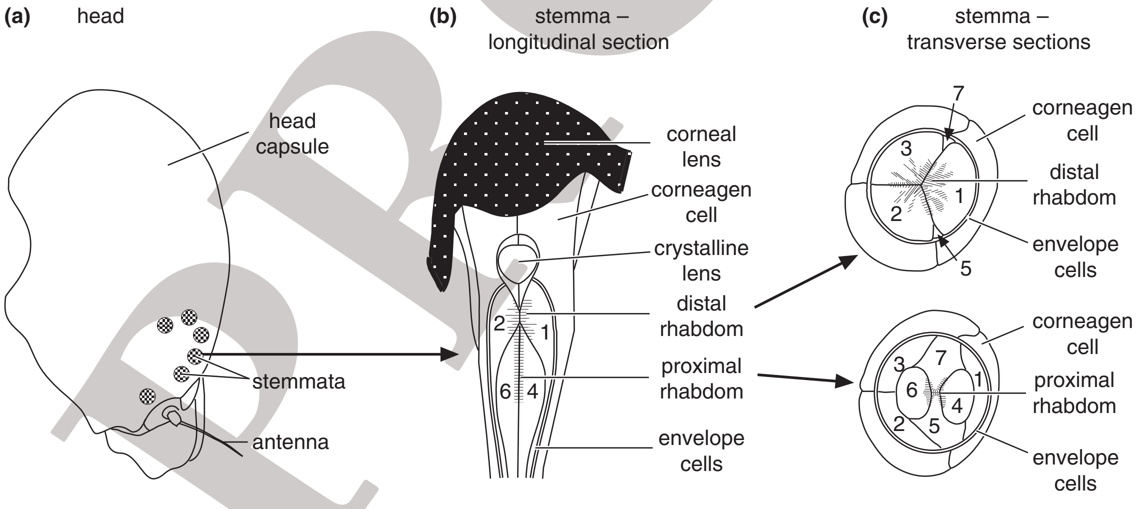


Figure 22.22 Stemmata with a single rhabdom in a caterpillar (mainly after Ichikawa and Tateda, 1980). (a) Side of the head showing the positions of the stemmata. (b) Longitudinal section of one stemma. (c) Transverse sections through the distal and proximal rhabdom.

differentiate shapes and orient toward boundaries between black and white areas.

The situation is different in larval symphytans (Hymenoptera), which have only a single stemma. These have large numbers of rhabdoms, each formed by eight photoreceptor cells and each group of cells is isolated by pigment from its neighbors. The lens produces an image on the tips of the rhabdoms which, in *Perga*, are oriented at about 5° from each other (equivalent to the interommatidial angle in compound eyes). Consequently, this type of eye is capable of moderately good form perception.

The larvae of the tiger beetle, *Cicindela*, have six stemmata, like caterpillars, but with a large number of photoreceptor cells in each stemma, as in the Hymenoptera. The largest of the stemmata has about 5000 receptor cells, each of which forms a rhabdomere on all sides so that the rhabdoms are in the form of a lattice (Fig. 22.23). It is possible that spatial resolution in these eyes is limited because of optical pooling and perhaps electrical coupling. In the larvae of the visual-oriented, predatory sunburst diving beetles *Thermonectus marmoratus*, several of the 12 stemmata have multiple retinae so that, together with two lensless eye-patches, this species has 28 retinae. Four of the stemmata are long and tubular, with horizontally extended but vertically very narrow retinae. When the larva approaches a potential prey the whole head and body move up and down in the sagittal plane so that the four horizonal retinae scan vertically across the target before a strike is made. The remaining stemmata probably act as movement detectors, allowing the animal to orient the tubular stemmata toward potential prey.

The optic lobes of larval insects consist of a lamina and medulla comparable with those associated with compound eyes of adults and, at least in caterpillars, each stemma connects with its individual cartridge in the lamina. In all these types of stemmata, the photoreceptor cells contain screening pigment granules in addition to the visual pigment. Movement of the granules – away from the rhabdomeres in the dark and toward them in the light – provides sensitivity adjustment. Caterpillars have three visual pigments and the neural capacity to distinguish colors. The larvae of several holometabolous species have been shown, experimentally, to respond to the plane of polarization of incident light. In neither case is the behavioral importance of these abilities understood.

22.6 Other visual receptors

22.6.1 Dermal light sense

A number of insects, such as *Tenebrio* larvae, respond to light when all the known visual receptors are occluded. The epidermal cells are apparently sensitive to light. This is also suggested by the

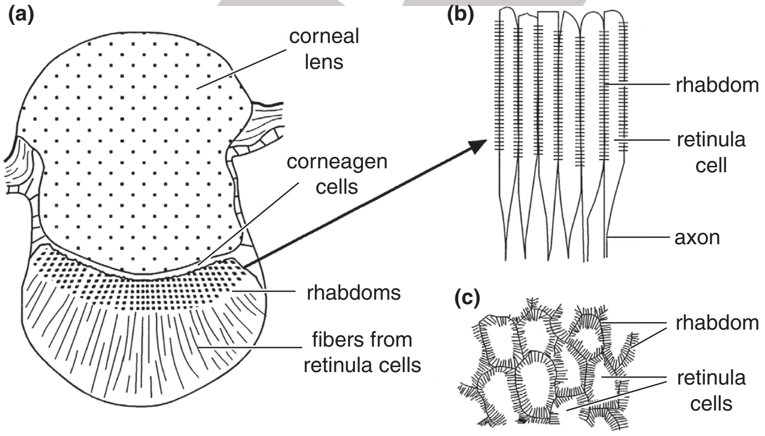


Figure 22.23 Stemma with multiple rhabdoms in the larva of a tiger beetle (based on Toh and Mizutani, 1994).
(a) Diagrammatic longitudinal section.
(b) Diagrammatic longitudinal section through the photoreceptor cells, showing the rhabdoms.
(c) Diagrammatic transverse section through the receptor cells showing the rhabdomeres forming a continuous lattice.

pigment movements which occur in isolated epidermal cells of some insects, i.e., cells which do not receive neural input from the central nervous system (Section 25.5.1), and by the production of daily growth layers in the cuticle (Section 16.2).

Several families of butterflies are known to have photoreceptors on the genitalia of both sexes. In *Papilio* there are two receptors on each side, each consisting of a single neuron lying on a nerve a short distance below the epidermis. The cuticle above the neuron is transparent. The cells are called phaosomes and they probably monitor the positions of the genitalia during copulation.

22.6.2 Sensitivity of the brain

In several insect species, light affects neural activity directly by acting on the brain, not via the compound eyes or ocelli. This commonly occurs in the entrainment of diurnal rhythms. In some species day length – regulating diapause or polyphenism – is registered directly by the brain. Typically, such rhythmicity is mediated by cerebral cell clusters containing rhabdomeric structures and sometimes screening pigments, sometimes called adult stemmata. One such structure, the Hofbauer-Buchner eyelet in *Drosophila*, has been identified as an essential circadian photoreceptor. Similar structures have been found in several species of beetles, bees and hawk moths, where they contain two classes of opsin, sensitive to ultraviolet and blue. Other extraretinal cells in the optic lobes express green-sensitive opsin. Together, these various spectral inputs potentially facilitate the detection of changes in ambient light to control various photoperiodic rhythms.

22.7 Magnetic sensitivity and photoreception

A number of insect species have been shown to respond to changes in magnetic field, and it is possible that they use the earth's magnetic field in navigation. Two mechanisms have been proposed to account for this response. Some insects are known to contain particles of magnetite, an iron oxide, which might be affected by the magnetic field. In worker honey bees, the magnetite is contained in innervated trophocytes in the abdomen. In many species, however, geomagnetic orientation has been demonstrated to depend on the spectral composition of ambient light, suggesting a role of photoreceptor proteins. The blue-light photoreceptor cryptochrome protein (CRY), also involved in setting the circadian clock in insects, is required for magnetoreception in *Drosophila*. This protein is expressed in various parts of the body, but also in the eyes, which, at least in birds, seem to mediate sensitivity to the earth's magnetic field by generating a neural map of this field. In insects, CRY is also expressed in the eyes, but the precise location and physiology of magnetoreception, as well as its complex interaction with light sensitivity, remains to be determined.

Summary

- Insects have compound eyes, which in part mediate capacities similar to those of lens eyes in vertebrates, but sometimes with wholly different mechanisms. However, some of the visual abilities of insects are wholly different to those of humans – for example, the sensitivity to polarized and ultraviolet light, and the capacity (found in some insects) for 360° vision.

- Compound eyes typically have relatively poor spatial resolution when compared with vertebrate eyes, which can be compensated in part by relatively higher temporal resolution and rapid scanning of the visual scene.
- Many components of compound eyes, such as the resolution of the ommatidial array and color vision, show dramatic variation between species and are often exquisitely tuned to the environment in which their bearers operate.
- Insects also have single-lens eyes, the dorsal ocelli, which typically occur in triplicate in adults. Their function is in motion processing and horizon detection, but also the potential for form vision, albeit at relatively poor spatial resolution. Many insect larvae have stemmata (sometimes called larval ocelli) which enable form detection in at least some species.
- In addition, many insects have extraocular photoreceptors in a variety of locations, with varied functions related to magnetoreception, circadian rhythm control and sexual behavior.

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