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REVIEW

Stark trade-offs and elegant solutions in arthropod visual systems

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ABSTRACT

Vision is one of the most important senses for humans and animals alike. Diverse elegant specializations have evolved among insects and other arthropods in response to specific visual challenges and ecological needs. These specializations are the subject of this Review, and they are best understood in light of the physical limitations of vision. For example, to achieve high spatial resolution, fine sampling in different directions is necessary, as demonstrated by the well-studied large eyes of dragonflies. However, it has recently been shown that a comparatively tiny robber fly (*Holcocephala*) has similarly high visual resolution in the frontal visual field, despite their eyes being a fraction of the size of those of dragonflies. Other visual specializations in arthropods include the ability to discern colors, which relies on parallel inputs that are tuned to spectral content. Color vision is important for detection of objects such as mates, flowers and oviposition sites, and is particularly well developed in butterflies, stomatopods and jumping spiders. Analogous to color vision, the visual systems of many arthropods are specialized for the detection of polarized light, which in addition to communication with conspecifics, can be used for orientation and navigation. For vision in low light, optical superposition compound eyes perform particularly well. Other modifications to maximize photon capture involve large lenses, stout photoreceptors and, as has been suggested for nocturnal bees, the neural pooling of information. Extreme adaptations even allow insects to see colors at very low light levels or to navigate using the Milky Way.

KEY WORDS: Visual specializations, Insect vision, Optics, Specialized visual systems

Introduction

For humans, vision is a particularly important sense. Notably, among vertebrates, there is a remarkable unity in the design of eyes as image-forming lens eyes, perhaps because evolution took a path from which it is difficult to diverge (Nilsson and Pelger, 1994). In contrast, visual systems in invertebrates are impressively diverse, with many specializations that appear to be mostly constrained by optical limits. Hence, invertebrate visual systems comprise fundamentally different eye designs, from image-forming camera-type eyes (that function similar to our own eyes) to an assortment of compound eye variants (Box 1), and even some visual systems that represent interesting combinations thereof (for excellent in-depth treatment of this topic, see Cronin et al., 2014; Land and Nilsson, 2012; Warrant and Nilsson, 2006). As this diversity has evolved within the constraints set by the physics of light, optical solutions are best understood in view of these constraints. In fact, there are many examples of eyes that operate right at their physical limitations. In this Review, we aim to convey a general overview of visual constraints and related trade-offs, providing many examples that manifest the diversity of invertebrate eyes. We first provide an overview and go on to consider specific visual accomplishments, such as resolution, color vision, polarization vision and adaptations to dark environments, in more detail.

Constraints on the function of visual systems

Light can generally be described by its intensity, wavelength content and polarization (see Glossary) qualities, all of which are known to influence eye design (Land and Nilsson, 2012) (Fig. 1). At low light intensity, the number of photons that are available to be captured by an eye is limited, which sets up critical conflicts regarding how many points in space can be resolved and how fast information can be processed. To improve spatial resolution (see Glossary), an increasing number of points in space must be independently resolved by photoreceptor cells that can transduce the light's energy into neural signals. In invertebrates, this process typically starts with visual pigments that are situated in the rhabdomeres (see Glossary) of photoreceptors. To differentiate between neighboring points, the visual pigments in nearby rhabdoms have to be excited. Therefore, if more points need to be differentiated, more rhabdoms must be situated next to each other. However, only a limited number of rhabdoms can be placed next to each other while still capturing light independently. To function as light guides (as many rhabdoms do; see Glossary), they need to remain wider than the dimension of the wavelength of the captured light (Warrant and McIntyre, 1993). Rhabdoms of the same order of magnitude as the wavelength itself (or smaller) act as waveguides, resulting in some loss of light as it travels outside the rhabdom (Snyder, 1975). In addition, light needs to be properly focused (usually near the top of rhabdoms), which in insects is typically achieved using lenses. If the lens is too small, light is lost as a result of the diffraction limit (see Glossary), which (together with various other optical parameters, such as chromatic and spherical aberration; see Glossary) constrains the efficiency of the system, thereby limiting the number of lenses that can be situated on an eye surface of any size. Hence, the smaller the insect, the more difficult it is to fit high-resolution eyes.

The available light intensity also imposes constraints on the speed at which photoreceptors can function. Light absorption by the chromophore–opsin complex (see Box 2) starts a complex G-protein-coupled signal transduction cascade that ultimately changes the electric potential of the photoreceptor cell (for a recent review, see Hardie and Juusola, 2015). How quickly this process occurs and, equally importantly, how quickly it is turned off again set critical temporal parameters for the eye. Just as the integration time of a camera needs to be adjusted depending on available light levels, the integration time of a photoreceptor (which is the time that a photoreceptor spends sampling incoming light to resolve a point in time) also needs to be adjusted (Weckstrom and Laughlin, 1995). Accordingly, the photoreceptor dynamics greatly vary in different organisms (Howard et al., 1984). For example, the

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Glossary

Acceptance angle
The maximum angle in space at which a photoreceptor can be excited by incident light.

Apposition eye
A type of compound eye (see Box 1).

Chromatic aberration
Inability of a lens to focus different wavelengths of light at the same plane, as each wavelength of light has a slightly different focal length.

Diffraction limit
Optical limit that restricts the highest possible achievable resolution on the basis of the physics of light.

e-Vector
In linearly polarized light, the e-vector orientation defines the plane of vibration of propagating light.

Gain control
In sensory systems, this describes adjustments in sensitivity that allow detection over a large range of a given type of input.

Light guide
A structure that can direct light through total internal reflection. In insect rhabdoms, this is facilitated by the relatively high internal refractive index compared with the surrounding tissue, allowing rhabdoms to function like fiber-optic cables.

Microsaccade
Small, involuntary movement of the eye or head.

Ommatidia
Building blocks of arthropod compound eyes (see Box 1).

Polarization
A physical property of light that relates to directions of vibration of propagating light.

Rhabdomere
The light-absorbing region of certain photoreceptor cells that are commonly found in arthropods (see Box 1).

Spatial resolution
The ability to resolve multiple points in space.

Spherical aberration
Inability of a lens to focus light at the same place, due to the center and periphery of the lens having slightly different focal lengths.

Superposition eye
A type of compound eye (see Box 1).

Temporal resolution
The ability to resolve multiple points in time.

Trichromat
An animal that is able to able to discriminate color based on three different wavelength sensitivities.

ability of many insects to fly quickly and rapidly avoid objects (or chase prey or mates) is facilitated by 'high-speed vision'.

Considering light as photons is helpful when evaluating what is required to activate photoreceptor cells. However, to understand how the visual spectrum has influenced the evolution of any visual system, it is more useful to regard light as waves. Visible light accounts for only a tiny portion of the electromagnetic spectrum, which also includes X-rays, with wavelengths that are too short to be detected by animal eyes, and microwaves, with wavelengths that are too long to be detected by our eyes. In fact, humans can only detect light between ∼400 and 700 nm (Wolfe et al., 2017). Although many insects can also see ultraviolet light (300–400 nm), they are often incapable of seeing red (Briscoe and Chittka, 2001). To achieve color vision, the limited surface space that is available for photoreceptors needs to be subdivided into separate color channels, which further constrains how much light can be captured by any one unit. The owners of digital cameras will have experienced this type of trade-off: one can either capture a high-resolution black and white image or forfeit some resolution to gain color. Finally, light can be polarized, a property that is largely lost on us (apart from those who wear polarized sunglasses) and is therefore less familiar. The polarization of light is determined by the direction of orientation of prevailing light rays, a property that influences characteristics such as how light is scattered in the atmosphere, or how it is refracted from surfaces. Many insects have polarization vision, or at least polarization sensitivity, which can be used to provide valuable directional information for successful migration, for example. However, here too, to detect differences in polarization, multiple photoreceptors must sample overlapping areas in space.

As long as it is very bright and an eye can be large, vision can take advantage of many of the above-mentioned properties through the careful tuning of various trade-offs. However, the situation is more extreme when the surface space for eyes is limited (as is the case for small insects) and when light is less abundant (as in densely forested areas or at night). The number of available photons varies dramatically between day and night, by at least 100,000 times (Tierney et al., 2017). Most visual systems are astonishingly well adapted to such massive changes. To see in the dark, major adjustments to several different regions of the eyes are necessary and typically come at the cost of other visual attributes. Nevertheless, the visual systems of some insects can function even at the lowest light levels (see below).

Taken together, there are many constraints on the design of visual systems, and it is simply impossible to have a system that does it all. Instead, the many niches in the environment have resulted in the evolution of a diversity of highly specialized visual systems that excel in some aspects of vision to the detriment of others. In the following sections, we examine the solutions that are available for specific constraints and highlight arthropods that have evolved particularly elegant solutions.

To discern detail, an eye needs to resolve many points in space

Spatial resolution, the ability to independently evaluate and compare different points in space, is arguably among the most important properties of highly functional eyes. To attain spatial resolution, adjacent points in space need to be resolved independently by different photoreceptors or groups of photoreceptors. To achieve this, the main axis of each photoreceptor needs to be aligned at a slightly different angle with respect to the surrounding space. There are two principal ways to do this: (1) invert the eye surface (Fig. 2A), as is the case for single-chamber eyes, or (2) evert the eye surface, as is best known for compound eyes (Fig. 2B).

Single-chamber eyes are typically associated with vertebrates and are also relatively well known for cephalopods, but they also exist in arthropods as they include insect ocelli (Simmons, 1982), the stemmata of many insect larvae (Buschbeck, 2014; Gilbert, 1994) and the primary eyes of most arachnids (Land, 1985a; Loria and Prendini, 2014). Although the degree to which these eyes achieve high levels of spatial resolution varies greatly, there are some examples of arthropods with impressively high levels of resolution. These include the predatory larvae of tiger and diving beetles (Mandapaka et al., 2006; Mizutani and Toh, 1995) and the principal (anterior median or AM) eyes of jumping spiders (Land, 1969).

Compound eyes come in many different shapes and follow several different design types (Nilsson, 1989) (see Box 1). Regardless of the type, one way to enhance spatial resolution is to add building blocks, ommatidia (see Glossary). However, as outlined in the Introduction, there are optical limits to how small ommatidia can be. Therefore, a good way to gain resolution is to make the eye bigger.

The biggest well-studied compound eyes with high resolution are those of dragonflies (Fig. 2D), which can have as many as 30,000

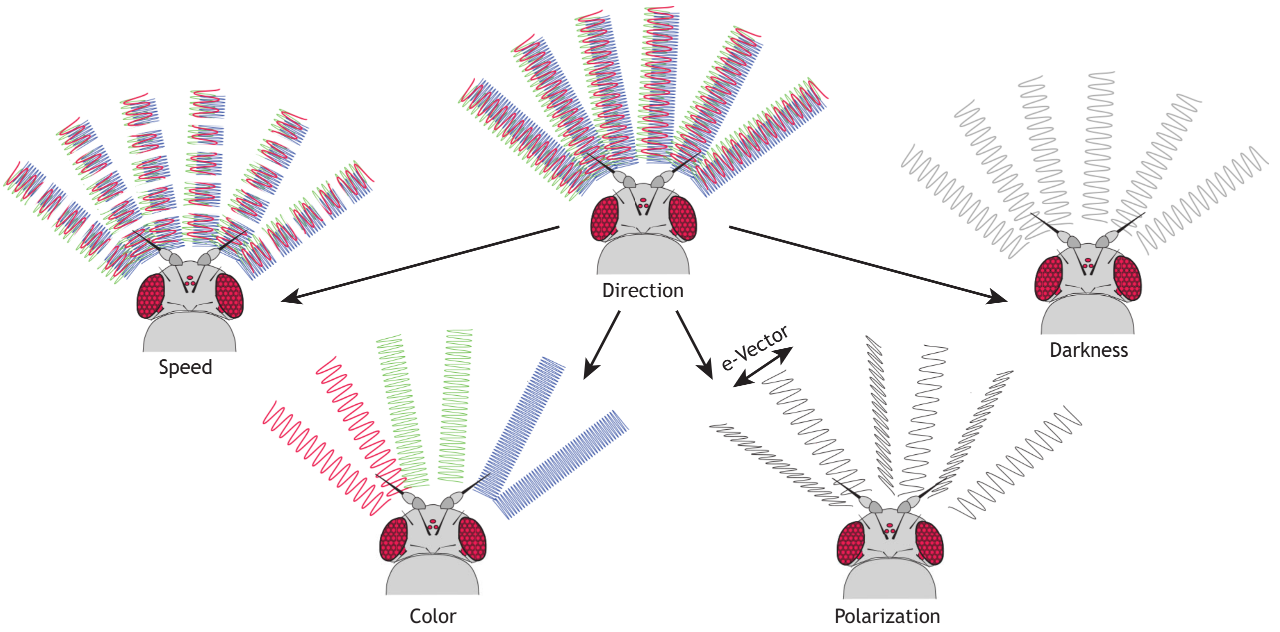


Fig. 1. Schematic diagram highlighting trade-offs between visual modalities that eyes need to accommodate. For example, one of the key properties of image-forming eyes is the ability to independently resolve points from different directions in space. This requires splitting available light into many independently resolved channels. However, especially when it gets dark, the limited availability of photons may restrict how many channels can be resolved, what kind of information (such as color or polarization) can be acquired within each channel, or how fast the eye can respond to changes. Breaks in the light waves here delineate bins of light that are temporally integrated. It is these physical limitations that are the basis for many specializations.

ommatidia (Sherk, 1978). As a result, dragonflies have 360 deg vision with relatively high levels of resolution on all sides. Nevertheless, as is the case for many apposition (see Glossary) compound eyes, there are regional specializations. For example, the dorsal eye region of the genus *Sympetrum* has particularly large ommatidia and shows specializations that allow for locally increased resolution, facilitating prey detection against the sky (Labhart and Nilsson, 1995). One common way to enhance spatial resolution locally is the introduction of a high-resolution region, a phenomenon that in vertebrate eyes is known as a fovea.

Basically, the addition of a fovea carves out a specialized area of particularly high resolution. However, if the eye size is kept constant, this added resolution in one place comes at the cost of resolution elsewhere. An extreme example of this optical trick is the presence of a negative lens (that adds to the resolution of the system by diverging light rays), a phenomenon that has evolved in vertebrates and invertebrates alike. In arthropods, this phenomenon is well known from the AM eyes of jumping spiders (Blest et al., 1988; Land, 1969; Williams and McIntyre, 1980). In these spiders, the AM eyes are movable and their relatively narrow high-resolution area of view overlaps with that of the neighboring anterior lateral (AL) eyes. In fact, in some well-designed experiments, it has recently been shown that the AL eyes are able to direct the gaze of the AM eyes (Jakob et al., 2018). Hence, the jumping spider eye system is a particularly elegant solution to the sampling problem, wherein a lower resolution eye surveys the visual space for important stimuli. This information is then used to direct the high-resolution eye towards this area to gain specific information. This organization represents a bandwidth-efficient system that might yet inspire engineers. In functional terms, the principle here is similar to any movable, foveated eye and highlights how eye movements themselves can be used as a clever trick to obtain high-resolution views of an area of interest (Land, 1999), even if the remaining portions of the eye exhibit relatively low spatial resolution.

In compound eyes, foveas are typically referred to as acute zones. They are well known in apposition eyes but are typically absent in optical superposition eyes (see Glossary and Box 1), with one remarkable exception, which we will discuss briefly here. In contrast to most optical superposition eyes, those of the hummingbird hawkmoth, *Macroglossum stellatarum*, are aspherical, which allows them to locally alter resolution and sensitivity (Warrant et al., 1999). This facilitates the presence of an acute zone that would be impossible with the typical spherical organization of optical superposition eyes. These Lepidoptera have particularly high resolution in their equatorial and frontal visual fields (Warrant et al., 1999). To help trap light rays within the photoreceptor rhabdoms, *M. stellatarum* has mirror-like structures, tapeta, which are formed by trachea and reflect light back, trapping it within the rhabdoms.

Acute zones are common in apposition compound eyes. They are easy to spot as a flattened region of the eye surface. This flattening narrows the interommatidial angle of neighboring units, and hence allows for additional ommatidia that can more finely dissect the relevant visual space (Fig. 2C). Together with a reduction in the acceptance angle (see Glossary) of the underlying photoreceptors, this ultimately leads to a gain in spatial resolution. A beautiful and relatively extreme example is the compound eye of a small robber fly, *Holcocephala fusca* (Fig. 2D,E), which has a flattened frontally facing eye region with a spatial resolution of just over a quarter of a degree (Wardill et al., 2017). As is frequently the case, this region is also characterized by particularly large ommatidia that are more efficient at gathering light; this is essential, as aerial prey capture is necessarily fast, and hence requires a high level of temporal resolution (see Glossary). As demonstrated for the hover fly *Eristalis tenax*, which also has a region with enlarged facets (a specialized 'bright zone'), such enlargement can be specifically geared towards improved light gathering (Straw et al., 2006). For the hover fly, this provides better contrast sensitivity and faster motion detection rather than spatial resolution.

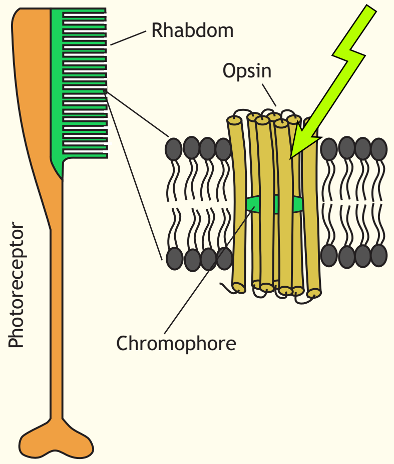
Box 1. Types of compound eyes in arthropods

Arthropod compound eyes can be divided into two broad types: apposition eyes and superposition eyes. Apposition compound eyes (Nilsson, 1989) are a common eye type in diurnal insect species. They are composed of ommatidia, processing units that, in this eye type, are optically isolated from each other. Each ommatidium is served by its own lens that focuses light onto (in focal apposition eyes) or near (in afocal apposition eyes) the distal tips of the photoreceptors. The photoreceptors of each ommatidium only receive light from one direction, while other light is absorbed by screening pigment. As photoreceptors are restricted to receiving light from only one lens, this eye design is inherently less sensitive than optical superposition compound eyes, but one subtype, the neural superposition compound eye, enhances sensitivity through neural pooling.

Neural superposition (Nilsson and Ro, 1994) is an eye design that is unique to certain flies (Diptera). To enhance sensitivity, input from the photoreceptors of neighboring ommatidia (sampling the same direction in space), is pooled neurally in the first processing area of the visual pathway, the lamina. Some variation exists in how neighboring units are pooled (Warrant and McIntyre, 1993; Zeil, 1983), but they have in common that such pooling is possible because each ommatidium houses multiple rhabdomeres that are physically separated from each other, sampling slightly different regions in space. The outcome of this organization is that the sensitivity of the eye is dramatically increased without sacrificing spatial resolution, as the eye can resolve an image point for each ommatidium, despite pooling neighboring units (Nilsson and Ro, 1994). Optical superposition eyes (Nilsson, 1989), the second broad type of compound eyes, are found in insects and crustaceans. They function by optically superimposing – through either refraction (Fig. 4A,B) or reflection – parallel light that enters several ommatidia, onto a set of photoreceptors. Each set of photoreceptors is only excited by light from a specific direction. Depending on the adaptation state, this light could have entered through the lenses of many ommatidia before being focused on selected photoreceptors. It is this pooling that enhances sensitivity, and is made possible by a clear zone that separates the retina and lenses. Visual sensitivity can be further increased with this optical design by allowing light to enter each rhabdom from a relatively wide angle (Warrant, 1999); however, this reduces the spatial resolution. The degree to which pooling takes place can be regulated by screening pigment that migrates along the borders of ommatidia between dark- and light-adapted states (Kunze, 1972).

Box 2. Visual pigment and photoreception

Rhabdomeric photoreceptors of invertebrates are characterized by stacks of membrane that are formed by microvilli that give rise to rhabdoms. Visual pigments are embedded within the membrane: these pigments absorb and react to particular wavelengths of light. Specifically, a chromophore (a light-absorbing molecule such as retinal) interacts with incoming light, leading to a change in conformation that triggers a chain of events, first in the surrounding opsin protein and then through a G-protein-coupled mechanism that ultimately leads to a depolarization in the photoreceptor cell. Wavelength specificity is achieved through differences in opsin molecules.



Apart from their relevance for prey capture, high-resolution and high-sensitivity regions are often also found in the eyes of males that engage in the aerial pursuit of a potential mate; such eye regions are often referred to as 'love spots' (Perry and Desplan, 2016). There are many examples of this phenomenon, including some that are quite extreme. The most prominent examples are black flies (Ogrady and McIver, 1987), march flies (Zeil, 1983) and mayflies (Alba-Tercedor, 2016).

The successful pursuit of a small target such as a mate or prey requires the input of distinct optic flow patterns that result from a combination of those arising from one's own movement and those generated by the movement of the target. How the resulting complex flow patterns are decomposed and used by insects has been a rich topic of investigation, as recently reviewed by Mauss and Borst (2020). The fly visual system has been particularly helpful, as molecular advances have allowed the role of specific circuit elements to be elucidated (Kim et al., 2017). At the same time, comparative studies have revealed remarkable conservation. For example, distinct specializations of the eye and nervous system that facilitate target detection are even found in phylogenetically distant species (Gonzalez-Bellido et al., 2016).

Even in insects without the above-mentioned specializations, high spatial resolution is often accompanied by high temporal resolution. This is important for successful flight, which requires the rapid resolution of highly detailed images to avoid collisions with objects in complex, cluttered environments. The study of exactly how insects navigate their environments has recently been advanced through the development of virtual reality environments that simulate the insect's visual input during free flight (Stowers et al., 2017). Such a setup allows researchers to study animals in complex environments that can be constructed to represent specific visual illusions and can be altered in response to the animal's behavior. Finally, recent findings have suggested that fast vision can be used to further improve spatial resolution, as the compound eyes of at least some insects operate at higher levels of spatial resolution than was thought possible based on the photoreceptor array alone. Specifically, it has been suggested that microsaccades (see Glossary) can be taken advantage of to shift the detailed visual field slightly and add acuity, as long as a fast eye can resolve them separately (Juusola et al., 2017; Viollet, 2014). Targeted muscle movements might further contribute to such hyperacute vision (L. Fenk, personal communication).

Color and polarization vision add versatility and facilitate species-specific communication

As discussed above, arthropod eyes can demonstrate high spatial and temporal resolution. Furthermore, certain qualities of light, if explored by vision, can provide additional information, albeit with trade-offs between visual sub-modalities. In this section we discuss two of these features – the wavelength composition of light and its e-vector (see Glossary) orientation, which can be detected by organisms with color vision and polarization vision, respectively.

Color vision

Color vision, which is thought to have evolved many times independently, relies on information that is obtained from the

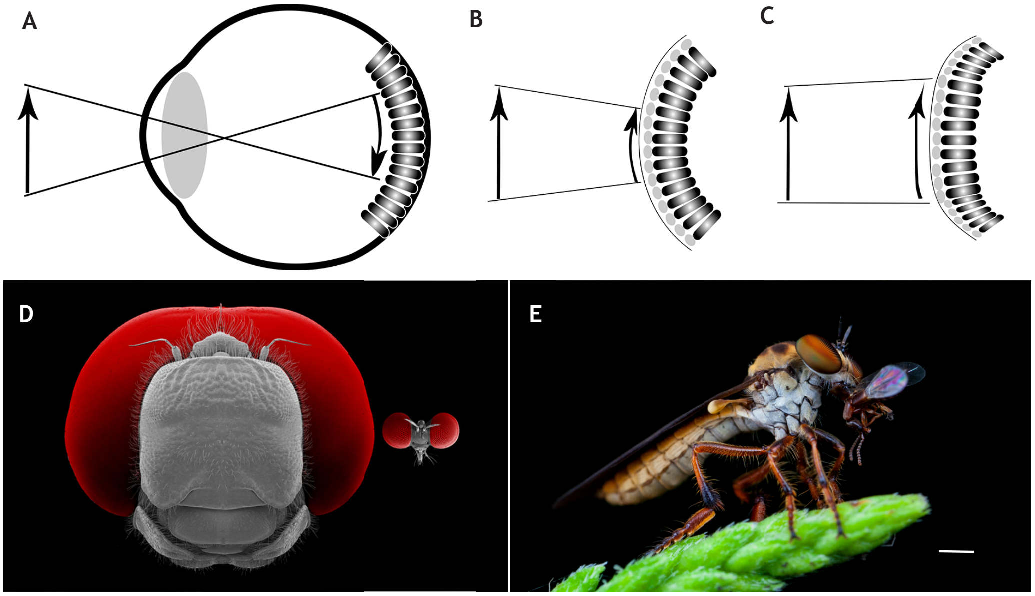


Fig. 2. Spatial resolution requires the placement of photoreceptors along curved surfaces. (A) Concave surface with photoreceptors at the back of a single-chamber eye, allowing for the resolution of independent points along the arrow. (B) Photoreceptors on a convex surface that can resolve points independently. (C) Regional flattening of the eye surface (resulting in a fovea or acute zone), a common strategy for enhancing the spatial resolution of one region of the eye. Note, in equally sized compound eyes, this leads to compressed ommatidia in the periphery. As a result of locally increased curvature, these tend to have larger ommatidial angles leading to regionally reduced resolution. (D) Comparison of the high-resolution eyes of a dragonfly (left) and the eyes of a small predatory robber fly of the genus *Holcocephala* (right). The latter has much smaller eyes but locally achieves comparable levels of resolution (Wardill et al., 2017) by the mechanism described in C. (E) Side view of the robber fly, clearly showing its flattened eye shape. Scale bar: 1 mm. Photo credit for images in D and E: Sam Fabian.

specific wavelength composition of light (Kelber, 2006). It is used for a wide variety of tasks, such as phototaxis, orientation, object detection and communication with and selection of conspecifics (for a review, see Briscoe and Chittka, 2001). For any visual system to successfully discern colors, at least two types of photoreceptor cells (sensitive to different wavelengths of light) need to sample the same visual space (Fig. 3A), so that these inputs can be compared at a later stage of visual processing. Wavelength specificity typically originates from visual pigments, such as opsin–retinal-based chromophore pairs (see Box 2), which are relatively well understood across the animal kingdom. Studies over the past few decades have revealed the great diversity of these visual pigments (Porter et al., 2020, 2012), with sensitivities that cover the visible as well as the UV spectral region (Briscoe and Chittka, 2001). The number of receptor types ranges from two in insects such as cockroaches, ants and many crustaceans to 12 in stomatopods (mantis shrimp) (Kelber, 2006).

One of the most-studied insect visual systems is that of the honeybee (Fig. 3A), in which color vision was behaviorally demonstrated more than a century ago (Turner, 1911; von Frisch, 1914). Bees are trichromats (see Glossary) (Peitsch et al., 1992), with maximal sensitivity in the UV (344 nm), blue (436 nm) and green (556 nm) wavelengths. Intracellular recordings from bee retina have revealed a heterogeneity in the spread of these receptor types across the retina, with the dorso-frontal part containing only UV and blue receptors and the ventral part containing additional green photoreceptors (Peitsch et al., 1992). Apart from some species with added red sensitivity, there is little variation in the receptor types in other hymenopterans, with UV, blue and green being omnipresent in this order (Peitsch et al., 1992). Many other insects, including Lepidoptera (butterflies) and Odonata (dragonflies and damselflies), also have the three above-mentioned color receptor classes, but the specific wavelength sensitivities can vary (Briscoe and Chittka, 2001; van der Kooi et al., 2021). It has been demonstrated that these wavelength domains allow the optimal differentiation of the colors of common flowers (Chittka and Menzel, 1992), possibly suggesting an ancient evolutionary adaptive fine-tuning of photoreceptor sensitivity.

In compound eyes, the expression of specific opsins tends to correlate with specific photoreceptor types that are situated in distinct positions within the ommatidia. Photoreceptor cells are classified into short visual fibers that project into the first optic neuropil (the lamina), and long visual fibers that project into the second optic neuropil (the medulla). As exemplified in flies, short visual fibers tend to have broad sensitivity (in this case, blue–green) with additional UV sensitivity (Salcedo et al., 1999) and have traditionally been considered analogous to vertebrate rod cells (Pichaud et al., 1999; Strausfeld and Lee, 1991). Long visual fibers express different types of opsins, depending on the type of ommatidia, and have traditionally been linked to color vision and considered analogous to vertebrate cones. More recent evidence, however, indicates that chromatic and achromatic circuits are not as clearly separated, with short visual fibers also contributing to color vision (Schnaitmann et al., 2013) and long visual fibers also contributing to the motion vision circuit that is otherwise governed by photoreceptors with short visual fibers (Wardill et al., 2012). Typically, each individual photoreceptor expresses only one type of opsin; however, there are many exceptions where multiple opsins are expressed in selected photoreceptors. For example, among insects, this is the case for several Lepidoptera, including *Papilio xuthus* (Arikawa et al., 2003) and lycaenid butterflies (Sison-Mangus et al., 2006). Among Crustacea, it has been observed in the brachyuran crab *Hemigrapsus sanguineus* (Sakamoto et al., 1996) and the fiddler crab *Uca pugilator* (Rajkumar et al., 2010).

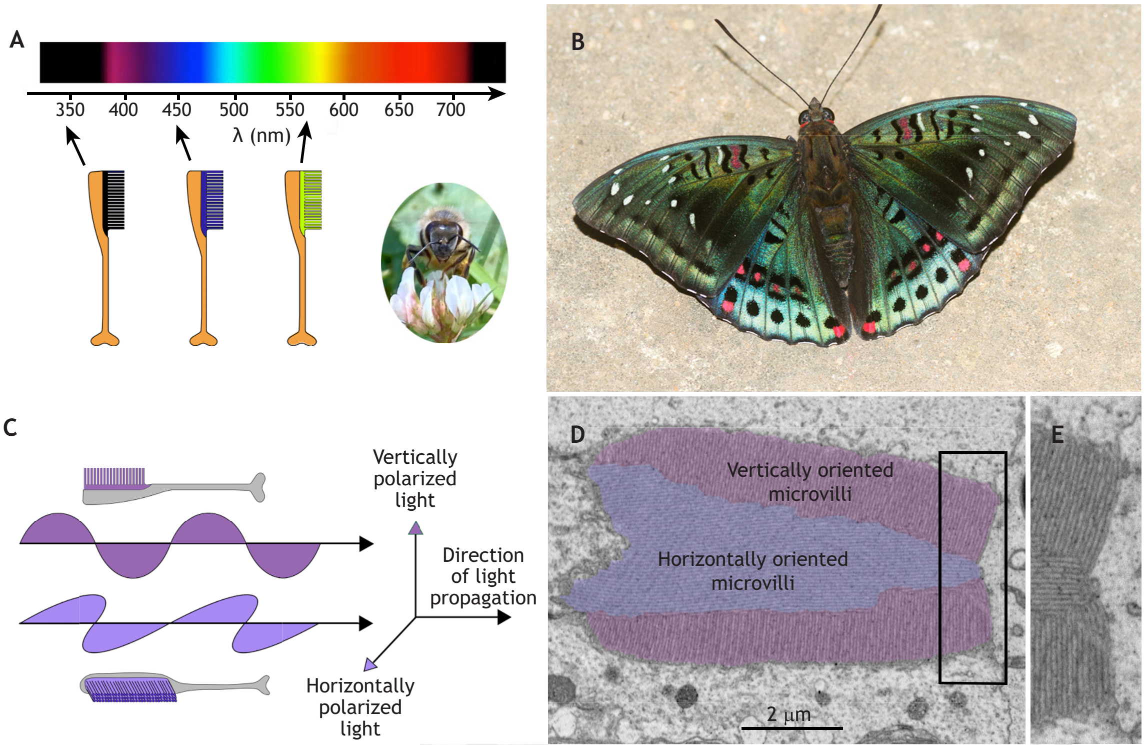


Fig. 3. The addition of parallel channels for the detection of color and polarization allows arthropods to expand vision into further dimensions. (A) To see colors, several photoreceptor classes (lower schematic drawings) are specialized to respond to different wavelengths of light (arrows indicate how specific receptors are reflected within the light spectrum). As exemplified by honeybees, insects are typically better at detecting UV light but worse at detecting red light when compared with vertebrates. (B) Color vision often plays a role in sexual selection, leading to particularly colorful males, as exemplified here by a gaudy baron butterfly (*Euthalia luberntina*). Image credit: Nitin Ravikanthachari. (C) To differentiate linearly polarized light, photoreceptors are needed that respond differentially to the e-vector orientations of polarized light. This is illustrated by the two schematic photoreceptors above and below the two depicted light rays; in each case their microvilli are aligned with the respective e-vector orientation. (D,E) Arthropods with polarization sensitivity often have photoreceptor pairs with orthogonally oriented microvilli. This is exemplified here by the *Thermonectus marmoratus* larval visual system, as shown in a transmission electron microscopy image (with added false colors). An overview of one rhabdom is shown in D and the boxed area is shown in E at a larger magnification, to better visualize the orientation of individual microvilli.

Co-expression of multiple opsins can be advantageous for the detection of light, as it broadens the spectral sensitivity profile.

Perhaps driven at least in part by the relatively high energetic costs associated with vision and color-related processing (Laughlin, 2001), it is common to find region-specific color vision configurations. For example, in the compound eyes of the cricket *Gryllus bimaculatus*, blue- and green-sensitive receptors are abundant in most of the eye, whereas UV-sensitive receptors are restricted to the dorsal rim area, a specialized region for polarization vision. Therefore, crickets have dichromatic color vision at best, despite having three different receptor types (Zufall et al., 1989). In the compound eyes of honeybee workers, the fronto-ventrally directed region is particularly important for color vision and has relatively more color receptors than other eye regions (Peitsch et al., 1992). Another example of regional specialization of the retina is the crepuscular hawkmoth *Manduca sexta*, where the distribution of blue and green receptors varies between the dorsal and ventral parts of the compound eye, blue being higher in the ventral half (White et al., 2003). This corroborates the observation that these moths require blue-sensitive receptors to forage during dusk and night-time (White et al., 2003). Perhaps the most dramatic example of a compound eye with regionalized color vision is found in mantis shrimp, in which color vision is restricted to a few rows of ommatidia (Marshall, 1988). To obtain more global information, these crustaceans scan the visual space for spectral cues with their extremely movable eyes.

Mantis shrimp are very colorful, and the spectral sensitivities of their many different receptor types vary across species (Cronin et al., 1996). Such diversity in coloration often relates to intraspecific signaling, which plays an important role in the evolution of color vision in some butterflies (Fig. 3B) (Arikawa et al., 2005; Stavenga and Arikawa, 2011). An interesting example involves two species of the butterfly genus *Lycaena*, namely, *L. heteronea* and *L. rubidus*. In case of *L. heteronea* (which has blue wings), the ventral part of the compound eye has blue-sensitive photoreceptors among others, whereas for *L. rubidus* (whose wings reflect UV and red wavelengths) the blue-sensitive photoreceptors are absent from that eye region. In both species, sexual dimorphism is also observed in the dorsal part of the compound eye, with males being UV–blue dichromats and females having additional red sensitivity. The ecological relevance of this sexual dimorphism remains elusive (Briscoe and Chittka, 2001). Another example is *Heliconius erato*, where females express an additional UV opsin in their compound eye, resulting in specialized ommatidia with finer UV discrimination (McCulloch et al., 2016). In contrast, males have a higher number of blue receptors than females and are likely to be better able to discriminate shades of blue. This is of ecological importance because it allows *H. erato* (whose wings are monomorphic) to discriminate between conspecifics and their mimics *Eueides isabella* by utilizing the UV signals and the distinct blue-reflecting spectrum of the former's hindwing yellow band (Finkbeiner et al., 2017). Butterflies are also particularly interesting because they are among few arthropods that employ color filters, an organization that allows limiting of the incident light spectrum so as to fine-tune the spectral sensitivities of the underlying photoreceptors (Briscoe and Chittka, 2001; Kelber, 2006). For example, 3-hydroxyretinol narrows and shifts the peak sensitivity from 360 to 400 nm (Arikawa et al., 1999). Interestingly, the same molecule also acts as a UV-sensitizing pigment in the broad-spectrum outer photoreceptors of flies (Hardie, 1986), which foster enhanced sensitivity in the UV domain. Perirhabdomal pigments (which surround the rhabdom) represent another type of filter. For example, such pigments are known to narrow the absorption wavelength range in some butterflies, restricting it tightly to red light (Arikawa, 2017; Stavenga and Arikawa, 2011).

Although this section has primarily focused on compound eyes, it should be mentioned that color vision is relatively rare in single-chambered eyes of invertebrates, with one particularly interesting exception. As might be expected from the beautiful colored diversity of male jumping spiders and their usage of elaborate mating dances, color vision has been demonstrated to be important for their mate selection (Peckham, 1895). Interestingly, there is also evidence for regionalization in their eyes, with the ability to discern colors only in the AM eyes (Land, 1985). In parallel to the above-mentioned Lepidoptera, in some species of jumping spiders, a red filter sharpens and red-shifts the spectral sensitivity of a subset of photoreceptors (Zurek et al., 2015).

Polarization vision

Like color vision, polarization vision requires multiple specialized photoreceptors that sample the same visual space (Wehner and Labhart, 2006), albeit for the e-vector orientation of light rather than the wavelength (Fig. 3C). Polarized light, which emerges from reflection and scattering, can be circular, elliptical or linear (Marshall and Cronin, 2011). Its detection helps arthropods with navigation, object recognition and communication. Many arthropod eyes can detect linearly polarized light (Cronin et al., 2014), which often (but not always) is mediated by UV receptors (Barta and Horvath, 2004). These receptors can be located in specialized regions, such as the dorsal rim area in insect compound eyes (Labhart and Meyer, 1999), but can also be elsewhere in the compound eye retina, as microvilli organized in parallel render photoreceptors inherently sensitive to linearly polarized light. As a prerequisite for detecting linearly polarized light, a minimum of two polarization-sensitive receptors with orthogonally arranged microvilli (Fig. 3D,E) need to be compared (for details, refer to Cronin et al., 2014; Warrant and Nilsson, 2006).

Polarization-dependent navigation was identified decades ago in the compound eyes of honeybees (Frisch, 1949) and the desert ant *Cataglyphis* (Labhart, 1986), which are excellent navigators. Since then, the neural pathways underlying these 'polarization compasses' have been studied in many other insects (Heinze, 2014; Zeil et al., 2014). In addition to insects, certain species of wolf spiders (Lycosidae) and ground spiders (Gnaphosidae) have specialized polarization-sensitive eyes (Dacke et al., 2001). Some ground spiders are even equipped with a reflective tapetum that enhances polarization sensitivity (Mueller and Labhart, 2010). The detection of linearly polarized light can also be used to find water bodies, as exemplified by the water bug *Notonecta glauca* (Schwind, 1984). Other aquatic insects, such as the larvae of the sunburst diving beetle *Thermonectus marmoratus*, can also detect polarized light (Stowasser and Buschbeck, 2012). Another example of polarized light aiding in object detection is the band-eyed brown horse fly *Tabanus bromius*, in which females have ventrally located specialized polarization-sensitive ommatidia that drive polarotaxis towards the fly's food source (Meglič et al., 2019). Recently, several examples have emerged in which the inherent polarization sensitivity of photoreceptors leads to interesting interactions with other visual modalities. For example, *Papilio* butterflies use polarization-dependent color vision to select oviposition sites (Kelber et al., 2001), and the moth *Ostrinia nubilalis* has blue-sensitive receptors that maximally respond to vertically polarized light and may help with object detection (Belušič et al., 2017). The latter has also been observed in the swallowtail butterfly *P. xuthus* (Kinoshita et al., 2011), a species in which polarization contrast furthermore contributes to motion vision (Stewart et al., 2019).

In addition to navigation and object detection, polarization cues are important for communication. For example, in the butterfly *Heliconius cydno*, males are preferentially attracted to females that reflect polarized light from their wings (Sweeney et al., 2003). As for color vision, arguably the most extravagant system has evolved in mantis shrimp compound eyes, which can be oriented to effectively utilize specialized regions for sensing polarized light (Daly et al., 2016). These decapods likely use polarization and color signals in their complex behavioral displays to attract prospective mates (Marshall et al., 2019). They are also among the few known species that take advantage of circular polarization (Chiou et al., 2008), as males of the genus *Odontodactylus* court females with specialized circularly polarizing light reflectors. Circularly polarized light is also known to be reflected by certain scarab beetles (Jewell et al., 2007). Here, polarization vision likely helps recognition of conspecifics that otherwise are well camouflaged (Brady and Cummings, 2010).

The door to the dark: maximizing photon capture

Various insects spend the most active portions of their lives in dim light, using moonlight and the stars to guide them through their environments. This requires the photoreceptors to make the most of the few photons that are available to the eye. Although several adaptations allow insects to overcome this challenge, they often are detrimental to other aspects of vision. For example, light can be pooled spatially to increase sensitivity. This, however, results in a decreased spatial resolution because, on average, fewer points in space are sampled (for an excellent review, see Warrant and McIntyre, 1993). Additionally, temporal resolution can also be decreased in an effort to increase light sensitivity (Warrant, 2017). A longer integration time permits more photons to be absorbed by the photoreceptors, resulting in a better signal-to-noise ratio and enhanced contrast (Greiner, 2006; Warrant, 1999). This longer 'shutter time' provides an animal with improved static vision at the cost of temporal clarity. In addition to adaptations of the optical system and of photoreceptor function, spatial and temporal properties can be altered through neural pooling, as has been beautifully demonstrated for the motion vision pathway of the hawkmoth *Deilephila elpenor* (Stockl et al., 2016). Such summation recently has been demonstrated to take place in the first optic neuropil of the visual pathway (Stockl et al., 2020). It allows insects to dynamically adjust their vision, enabling them to see at a large range of different light levels, and to maintain vision of at least coarser and slower features even when it is too dark to see finer and faster features.

Perhaps the most common solution for nocturnal insects, particularly for beetles and moths (Warrant, 1999), is the optical superposition eye (Fig. 4A,B). This eye type provides greater sensitivity than other types of compound eyes because of its ability to pool light from multiple ommatidia through a clear zone (see Box 1). Here too, trade-offs exist, as resolution in superposition eyes tends to be lost as a result of both optical limitations (such as spherical aberration and the need to precisely bundle light over relatively large distances) and the cross-over of light rays into neighboring ommatidia (Warrant and McIntyre, 1990). As an excellent example of resourceful superposition, the visual system of the dung beetle *Scarabaeus satyrus* is sensitive enough to use starlight to navigate away from a dung pile on nights when the moon is not visible (Dacke et al., 2013). Another dung beetle species, *Scarabaeus zambesianus*, has been observed to navigate away from dung piles using polarized light from the moon and stars (Dacke et al., 2003). Both of these beetles possess optical superposition compound eyes, highlighting how that eye type can facilitate navigation under remarkably dark conditions.

Another common compound eye type is the apposition eye (see Box 1). This eye type can provide high resolution and allows many species to thrive in bright light environments. However, because in apposition eyes each ommatidium receives its own visual input, this eye type tends to be less light sensitive, and several adaptations are necessary for species to be able to function in the dark. Neural superposition has evolved in flies and is a great example of such an adaptation (Box 1). Structurally, neural superposition eyes are of the apposition type, but with a dramatically enhanced sensitivity to light which is achieved through neural pooling.

Apart from different overall eye designs, several other mechanisms have also evolved to improve photon capture in dark environments (Fig. 4C). Among them is increasing the acceptance angle of rhabdoms – for example, by moving the photoreceptors closer to the lens – and increasing the size of the aperture (Warrant and McIntyre, 1993). These configurations allow more light to physically reach the photosensitive region of the eye. Narrow apertures, like those found in many diurnal apposition eyes, result in smaller acceptance angles for rhabdoms, thus causing the eye to be less sensitive. A parameter that can be used to gauge how light is captured is the F-number. The F-number of a given eye can be calculated by dividing the focal length (f) by the aperture width (A, typically equaling the lens diameter), i.e. $F=f/A$. A lower F-number corresponds to a shorter focal length and/or a wider aperture (in both cases leading to a larger acceptance angle) and hence higher sensitivity (Warrant and McIntyre, 1993). A particularly unique animal that is well adapted to a nocturnal lifestyle is the net-casting spider *Deinopis spinosa* (Fig. 4D), which possesses large posterior median eyes that aid in night-time foraging (Stafstrom and Hebets, 2016). These eyes are 200 times more sensitive to light than the human eye and, in fact, they are so sensitive that the rhabdoms have to be largely decomposed in the morning (Blest, 1980) to avoid damage by normal daylight.

Several nocturnal and crepuscular bee and wasp species have evolved a low-light lifestyle, even with apposition compound eyes, the eye type less suitable for nocturnal vision. Two such species are the Indian carpenter bee *Xylocopa tranquebarica* and the Central American sweat bee *Megalopta genalis* (Warrant, 2008). As is the case for many nocturnal species with superposition eyes, such species operate near the physical limit of their eyes, requiring some degree of bright moonlight or twilight to properly navigate their environments. The apposition eyes of *M. genalis* show several adaptations for enhanced light capture (Greiner et al., 2004). At the optical level, this includes large ommatidial lenses and thick

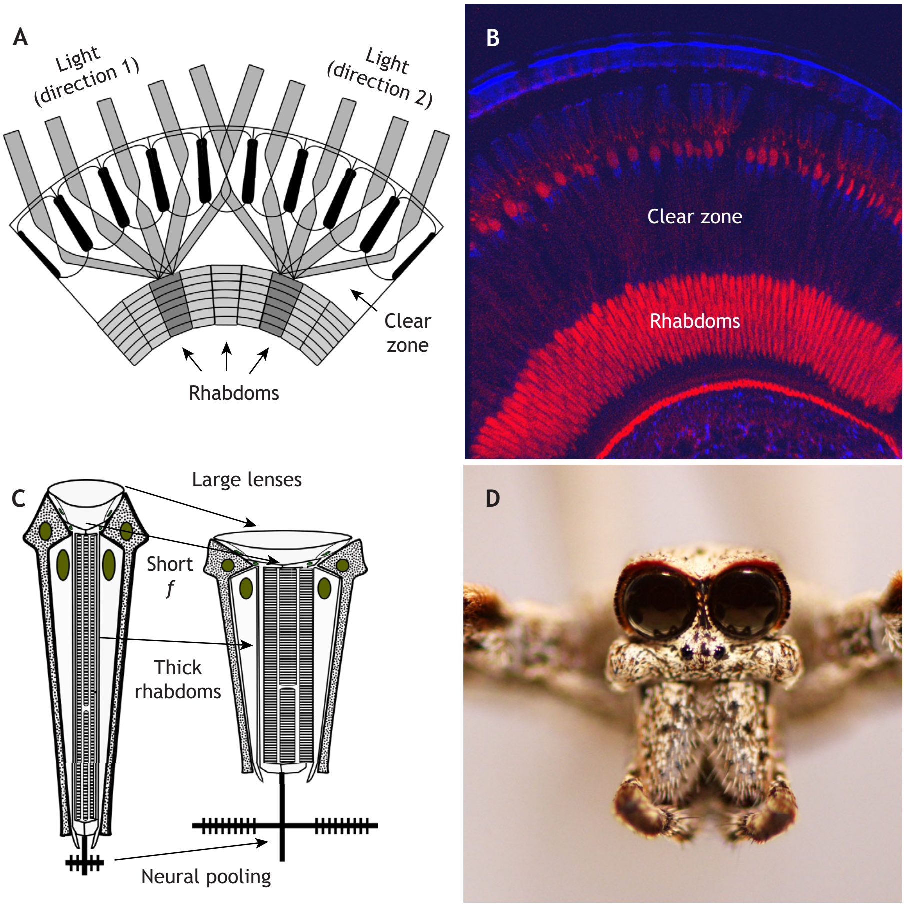


Fig. 4. Many arthropod eyes are designed to function well in the dark. (A) A schematic diagram of the optical superposition organization, which allows pooling of parallel light over relatively large areas and thus functions well in the dark (modified after Nilsson, 1989). (B) Key features of the optical superposition eye organization include the presence of a clear zone through which light can pass, and the placement of photoreceptors deep into the eye, as exemplified by a phalloidin-stained (and DAPI-counterstained) image of the *T. marmoratus* compound eye. (C) Although apposition compound eyes generally are better suited for diurnal vision, some insects with this eye type have evolved adaptations that allow for nocturnal vision. As illustrated by the schematic diagram (with an ommatidium suitable for diurnal vision on the left, and one for nocturnal vision on the right), nocturnal apposition eyes typically include some or all of the following characteristics: (1) large lenses, which have large apertures and hence capture more light; (2) short focal lengths (f), which result in larger acceptance angles of photoreceptors, and hence enhanced light capture; and (3) thick rhabdoms that allow for a larger volume of light-capturing rhabdoms. Neural pooling allows for the summation of neural signal over larger areas of the eye. (D) Net-casting spider, *Deinopis subrufa*, one of the champions of nocturnal vision. Photo credit: Jay Stafstrom.

rhabdoms, which increase the acceptance angle of light for each rhabdom. *Megalopta genalis* also has a significantly longer integration time for its photoreceptors (approximately 30 ms) than the diurnal sweat bee *Lasioglossum leucozonium*, and it likely uses spatial summation to further increase sensitivity (Warrant, 2008). The Indian carpenter bee also displays multiple adaptations to its nocturnal lifestyle when compared with its diurnal relatives. For example, the ocelli of *X. tranquebarica* are more than twice the size of those of similarly sized diurnal bees (Warrant, 2008).

The introduction of strategically placed mirrors, or tapeta, is yet another solution to improve light capture. Some of the light that passes through the photoreceptors without being absorbed is reflected back through the retina by tapeta, providing a second chance for absorption. Tapeta have been observed in single-chamber eyes of nocturnal arthropods (including arachnids) and in optical superposition eyes (Miller and Bernard, 1968), but they appear to be absent from the apposition eyes of nocturnal insects (Greiner, 2006). For nocturnal insects with apposition eyes, temporal integration is another common strategy to increase light sensitivity.

It has been theorized that color vision is uncommon in low-light scenarios; humans are color blind in dim lighting, and this was assumed to be true for other species until an elegant behavioral study on a moth showed otherwise (Kelber et al., 2002). The elephant hawkmoth, *Deilephila elpenor*, has been shown to discriminate colors in light intensities as low as 0.0001 and 0.01 cd m^{-2} (equivalent to dim starlight and dusk, respectively). Other champions of nocturnal color vision are *X. tranquebarica* (Warrant, 2008) and glow-worms (which are beetles), the latter thought to use chromatic cues to find mates (Booth et al., 2004). The obvious advantage of nocturnal color vision parallels that of diurnal animals, as color vision provides an animal with crucial information that goes beyond what can be captured by achromatic systems, in addition to providing enhanced contrast (Kelber and Roth, 2006). Alas, vision that is both sensitive to small quantities of light and allows color discernment comes at a cost. As multiple parallel channels (devoted to different spectral content) need to gather sufficient light, this can have a cost in regards to spatial or temporal resolution (Kelber and Lind, 2010).

Additional ways to become a specialist: visual adaptations to specific challenges

Whereas the previous sections outlined the major challenges that drive the visual ecology of most arthropods, this section highlights a few additional challenges, such as those posed by environments with variable light intensity, variations in the refractive index of the external medium, effects of eye size and visual requirements of predatory behavior.

Variable light environments

In many cases, it is not enough to be well adapted to light or dark environments; instead, it is necessary to adapt well to highly variable light environments. Imagine an insect that arrives at a clearing after emerging from the deep, relatively dark forest (Fig. 5A). Within a fraction of a second, its visual system needs to adjust to around two orders of magnitude of additional light (Tierney et al., 2017). This requires a rapid down-regulation of the gain control (see Glossary) of the eye. Generally, visual systems profit from a G-protein-mediated visual transduction mechanism that allows for impressive adjustments to immensely different light environments (Hardie and Raghu, 2001). In addition, pigment movement is a well-known adaptive mechanism (Warrant and McIntyre, 1993), as discussed above. Another way to function in highly variable light levels is to have an eye that contains components that are well adjusted for vision in bright environments and other components that are better suited for darker environments. Such an organization has been described in backswimmers (Immonen et al., 2014), which tend to be active not only in different environments (aerial and aquatic) but also at different times of the day. A combination of substantial movement of screening pigment and the existence of specialized intrinsic photoreceptors allows the eye to remain functional across different light levels.

Visual function in air and water

Aquatic environments introduce another challenge to visual systems. Although relatively few insects have conquered water, several remarkable adaptations are worth highlighting. In regard to optics, the very different refractive indices of air and water must be considered. Typically, arthropod eye lenses are curved at their interface to the exterior world (Land and Nilsson, 2012). Hence, the focus of the optical system is influenced by the refractive index of the medium that surrounds the lens. The lower refractive index of air results in a relatively high refractive power. Water, by contrast, has a higher density, and the reduced refractive index difference leads to less refractive power. Depending on the curvature, the difference between media can be dramatic, so that eyes typically can only function in water or in air. One way around this problem is to flatten the outer surface of the lenses and to off-load refraction to inner structures, as has been observed in water striders, which are able to operate in both water and air (Schwind, 1980). Another strategy is to divide the eye into different regions, one that is well adjusted for vision in air and another that is suited to seeing underwater (Fig. 5B). This organization is seen in whirligig beetles (Wachmann and Schröer, 1975); while these beetles swim on the surface of the water, the dorsal portion of the eye stays above the water and functions in air, whereas the ventral portion is submerged. Each eye portion is adapted to its respective medium (Burghause, 1976).

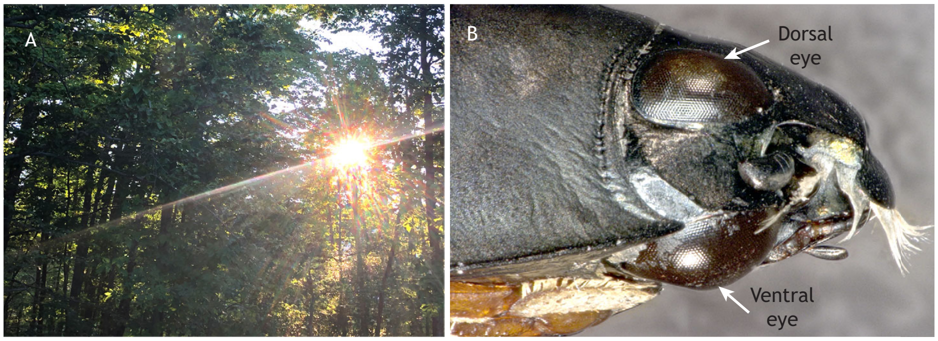


Fig. 5. Special environments add additional challenges for visual systems. (A) Insects that inhabit dense forests often need to rapidly adjust their sensitivity over many orders of magnitude as they fly between dark and light patches. (B) Several aquatic insects have evolved specializations to see well in both air and water, as exemplified by a whirligig beetle with dorsal eyes that function well in air and ventral eyes that function well in water.

More recently, these beetles have been shown to even have different nanocoatings on the dorsal and ventral eye surfaces to accommodate the two different media (Blagodatski et al., 2014). How the development of insect eyes accounts for the ability to focus correctly remains unclear. However, recent evidence suggests that effective developmental mechanisms tend to be in place in arthropods, because they do not require visual feedback for the development of proper focusing (Owens et al., 2020).

Effects of eye size

The kind of trade-offs that we have outlined in this Review become particularly conspicuous when eyes are small and the eye surface area is limited. This has recently been beautifully demonstrated in ants (Palavalli-Nettimi et al., 2019), where a species (*Rhytidoponera inornata*) with relatively small eye size (when compared with eyes of other ant species) is able to maintain an impressive level of spatial resolution, albeit at the cost of contrast sensitivity. Consistent with this finding, ant species with a reduced eye size move closer to an object before avoiding it than those with larger eyes (Palavalli-Nettimi and Narendra, 2018). The question of how such trade-offs are resolved when size becomes limiting has also been addressed in an elegant study in which *Drosophila* were raised to different sizes (Currea et al., 2018). Here, smaller flies had fewer and smaller ommatidia, with slightly larger interommatidial angles. Optically, the reduction in contrast sensitivity was dominant over the reduction in spatial resolution (the latter being influenced by the interommatidial angle). However, further examination revealed that these flies lost little spatial acuity overall. Moreover, they could even recover contrast sensitivity neurally, albeit at the cost of temporal resolution. Incidentally, the neural control of contrast sensitivity has also been highlighted in bumblebees (Chakravarthi et al., 2016, 2017).

Anatomically, a recent study on small beetles (Ptiliidae) highlights how optical limits can shape the eye surface. Here, miniaturization has been shown to have a more profound effect on the number of ommatidia than on the size of the ommatidia, possibly because optical limits restrict further reduction of the lens diameter (Makarova et al., 2019).

A particularly interesting eye organization has been found in the parasitic twisted-wing insect *Xenos peckii* (Buschbeck et al., 1999, 2003), another group of typically very small insects. Their eyes consist of arrays of small image-forming eyes (Maksimovic et al., 2007), each of which samples a small region of space (as opposed to the one point in space that is typical for compound eyes). This organization is particularly space efficient: as many sample points are served by each lens, these lenses are less prone to being restricted by diffraction limits. In fact, this design principle is so space efficient that it has inspired the development of novel microcameras (Keum et al., 2018).

Visual requirements for predatory behavior

Successful prey detection and related predatory behavior have also led to the evolution of other extraordinary eyes. In this context, we have already highlighted robber flies and dragonflies in relation to having to be fast, and jumping spiders with sophisticated high-resolution eyes. Other eyes that deserve mentioning as having evolved to accommodate prey capture are those of the diving beetle larvae *T. marmoratus*, which have two pairs of highly specialized (Stowasser and Buschbeck, 2014; Stowasser et al., 2010) tubular eyes on each side of the head (Mandapaka et al., 2006). Among their specializations is the ability to correctly gauge the distance of prey (Bland et al., 2014), a capability that, within insects, has been most closely examined in another prominent predator – praying mantis (Collett, 1996; Rossel, 1983). Using miniature 3D glasses, praying mantises were presented with visual illusions that confirmed their ability to use stereopsis for distance vision (Nityananda et al., 2016). Stereopsis requires that the same region in space be viewed independently from two eyes, with minor disparities detected and successfully interpreted as distance cues. This brings up an additional constraint to arthropod visual ability; namely, that some tasks require sampling of the visual field with multiple eyes.

Conclusions

Above, we have discussed how diverse arthropod visual systems have developed interesting solutions to a variety of visual challenges. Many more examples could be highlighted, but they are beyond the scope of this Review. Some of these challenges relate to the environment, such as maintaining adequate vision despite limited availability of light, while others relate to specific needs, such as that of flying insects to track rapidly changing visual input. Further adaptations explore specific physical aspects of light, such as its wavelength or polarization content so as to gain additional information from the environment, or to communicate with conspecifics. Some of these adaptations are relatively subtle and hence have been overlooked until recently, as exemplified by sex-specific expression of specific visual pigments that leads to regional specialization of retinas. It is generally the case that many of the discussed adaptations closely reflect specific ecological needs of organisms. Undoubtedly, the extremely rich and diverse visual ecology of insects and other arthropods will continue to reveal interesting new solutions to specific problems that animals encounter. In addition, recent advances in molecular biology, especially in regard to non-model organisms, has opened the door to additional explorations. Therefore, one of the aims of this Review is to open the floor to multi-tiered questions regarding arthropod visual system adaptations such as: how are specific visual adaptations encoded genetically?; to what extent are genetically encoded adaptations conserved within different eye types, e.g. among arthropods that share similar habitats?; and how do niche-specific adaptations of eyes correlate with those of other sensory systems? Answering these and other related questions will help us to gain further insights into the rich visual ecology of insects and other arthropods.

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Competing interests

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