

Vision and Visual Navigation in Nocturnal Insects

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apposition compound eye, superposition compound eye, nocturnal
vision, neural summation, homing

Abstract

With their highly sensitive visual systems, nocturnal insects have evolved a remarkable capacity to discriminate colors, orient themselves using faint celestial cues, fly unimpeded through a complicated habitat, and navigate to and from a nest using learned visual landmarks. Even though the compound eyes of nocturnal insects are significantly more sensitive to light than those of their closely related diurnal relatives, their photoreceptors absorb photons at very low rates in dim light, even during demanding nocturnal visual tasks. To explain this apparent paradox, it is hypothesized that the necessary bridge between retinal signaling and visual behavior is a neural strategy of spatial and temporal summation at a higher level in the visual system. Exactly where in the visual system this summation takes place, and the nature of the neural circuitry that is involved, is currently unknown but provides a promising avenue for future research.

Optical sensitivity:

the ratio of the number of photons absorbed by a photoreceptor to the number emitted per steradian of solid angle from a unit area of an extended source (i.e., a measure of the light-gathering capacity of an eye)

INTRODUCTION

Despite their tiny size and comparatively few neurons, the visual systems of insects are remarkably sophisticated. With the help of their compound eyes, insects recognize and react to conspecifics; distinguish and avoid predators; locate food sources and intercept prey; navigate to and from a nest using learned visual landmarks; and walk, swim, or fly through a complicated three-dimensional habitat. Even in the bright sunlit world in which many insects are active, these visual tasks would be demanding enough. But for the vast numbers of insects that are active exclusively at night, when light levels can be up to 11 orders of magnitude lower, such tasks may at first glance seem impossible. However, over the past two decades we have begun to realize that nocturnal insects perform the same visual tasks as their diurnal relatives—and with the same precision and accuracy—despite the difficult light conditions they face. This remarkable fact has led to a new appreciation of the visual abilities of nocturnal insects and to

an impetus to understanding how these abilities are realized in the nervous system.

How is such impressive visual performance achieved in nocturnal insects? Part of the answer clearly lies in behavioral modifications (such as slower locomotion) that enhance the reliability of visual information that reaches the insect at night. Part of the answer also lies in the visual system itself. The optical designs of most nocturnal compound eyes are well suited to high optical sensitivity (e.g., the superposition compound eyes of nocturnal moths and beetles) (**Figure 1a**), but in some rare cases they are not (e.g., the apposition compound eyes of some exceptional species of nocturnal bees and wasps) (**Figure 1b**). Compared to their diurnal relatives, in nocturnal insects optical sensitivity can typically be improved by one (apposition eyes) to three (superposition eyes) orders of magnitude, but rarely more. In addition, the photoreceptors of nocturnal insects tend to respond more slowly and have higher visual gain (roughly five

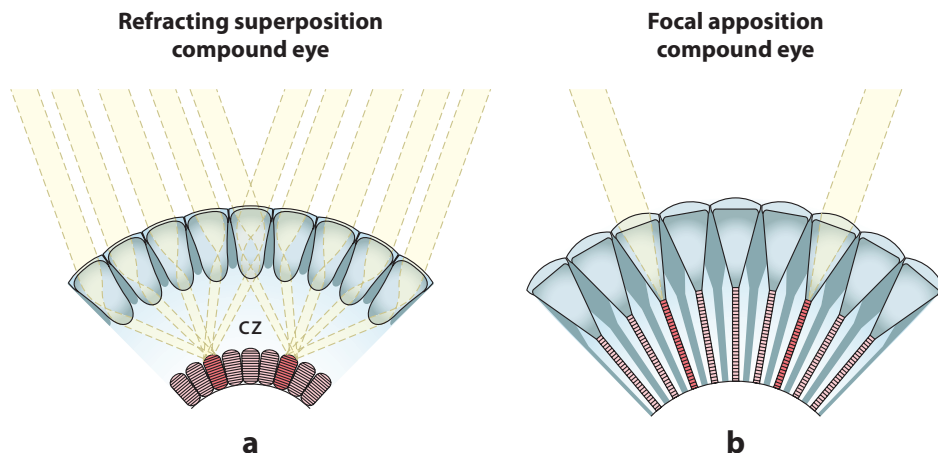


Figure 1

Two compound eye designs in insects. (a) A refracting superposition compound eye. A large number of corneal facet lenses and bullet-shaped crystalline cone lenses (each possessing a powerful internal gradient of refractive index) collect and focus light across the clear zone of the eye (CZ) toward single photoreceptors in the retina. Several hundred, or even thousands, of facets service a single photoreceptor. Not surprisingly, many nocturnal insects have refracting superposition eyes and benefit from the significant improvement in sensitivity. (b) A focal apposition compound eye. Each ommatidium is isolated from its neighbors by a sleeve of light-absorbing screening pigment, thus preventing light from reaching the photoreceptive rhabdom from all but its own small corneal lens, significantly limiting light capture. This eye design is therefore typical of diurnal insects. Diagrams courtesy of Dan-Eric Nilsson.

times higher), physiological adaptations that also improve visual reliability. However, these optical and physiological gains are relatively modest and suggest that peripheral visual mechanisms on their own are unable to explain behavioral visual performance. Higher visual mechanisms—including spatial and temporal summation, and other mechanisms—are thus likely to be responsible. Where this takes place in the visual system, and how the necessary circuitry works, remains largely unknown.

This gap between our knowledge of what nocturnal insects can actually see and our understanding of how it is achieved neurally is thus large. In this review we describe our current understanding of vision and visual processing in nocturnal insects and how the gains in visual performance afforded by these mechanisms appear to fall short of the actual visual performance of freely behaving nocturnal insects. The results of this synthesis suggest several future avenues of fruitful research.

WHAT CAN NOCTURNAL INSECTS SEE?

From the outset it is important to point out that the nocturnal visual world is essentially identical to the diurnal visual world. The contrasts of objects are identical and so (or nearly so) are their colors. The only distinguishing difference is the mean level of light intensity, which can be up to 11 orders of magnitude dimmer at night (58, 88), depending on the presence or absence of moonlight and clouds and whether the habitat is open or closed (i.e., beneath the canopy of a forest). It is this difference that severely limits the ability of a visual system to distinguish the colors and contrasts of the nocturnal world. Indeed, many animals, especially diurnal animals, distinguish little at all. In the end, the greatest challenge for an eye that views a dimly illuminated object is to absorb sufficient photons of light to reliably discriminate it from other objects (51, 85, 86, 88).

Nonetheless, many nocturnal insects have evolved sufficiently sensitive visual systems to

orient themselves and navigate at night. Some navigate under the open sky, and take full advantage of the celestial cues available there. Others navigate in more difficult conditions, such as through the understory of a dense tropical rainforest, analyzing the optic flow of the passing world generated by their own movements in order to hold a stable course, discriminate landmarks, or control flight. Many nocturnal insects even experience the world in color. In all these nocturnal insects, the apparent disadvantages for visual orientation and navigation imposed by low light levels, in particular a decreased visual reliability arising from greater visual noise and lower visual contrast, have been overcome. These facts, inextricably linked to their highly sensitive visual systems, suggest that the visual world experienced by nocturnal arthropods is essentially no different than that experienced by their diurnal relatives. This surprising fact is underscored by an examination of a few case examples, notably the ability of nocturnal insects to see color and their ability to navigate using celestial cues and terrestrial landmarks. Fuller accounts of the impressive visual abilities of nocturnal insects can be found elsewhere (85, 86, 88–90).

Nocturnal Color Vision

The world is as equally colorful at night as during the day, and the usefulness of color for object discrimination (e.g., flower identification; 40) does not decrease with falling light intensities. The nocturnal nectar-feeding hawk moth *Deilephila elpenor* has superposition eyes (**Figure 1a**) with three different spectral classes of photoreceptors, centered in the UV, the violet, and the green parts of the spectrum (33, 73). This moth can not only be trained to associate a sugar reward with a blue disc at starlight levels of illumination (39), but it can also discriminate this blue disc from other discs in various shades of gray with a choice frequency of at least 80%. This hawk moth, despite its tiny eyes and brain, thus has color vision at light levels 100 times dimmer than the dimmest level at

which the human visual system can distinguish color. Moreover, color vision in *D. elpenor* is color-constant, meaning that color discrimination is not affected by moderate shifts in the spectrum of illumination (2). This is a feature of all advanced color vision systems (40). Remarkably, color vision has also been demonstrated in the nocturnal Indian carpenter bee *Xylocopa tranquebarica* (74, 75), which has apposition eyes, the design apparently unsuited to life in dim light (**Figure 1b**). The discovery of nocturnal trichromatic color vision in two widely separated taxa of nocturnal pollinators suggests that color is equally visible and important for both nocturnal and diurnal insects.

Nocturnal Navigation and Orientation

To navigate back to the safety of a nest after a long and tortuous foraging trip, or to optimally orient themselves in order to efficiently escape from rivals or predators, insects require reliable detection of both terrestrial and celestial visual cues (reviewed for insects in References 95 and 98), and this is equally true at night as it is during the day. Most insects rely on hierarchies of both kinds of cues. Thus, in the examples that follow, even though we separately review selected case studies concerning how nocturnal insects use terrestrial and celestial cues for navigation and orientation, in any one species both types of cues are likely to be used in concert.

Navigation and orientation using celestial cues. At night, the brightest and most easily discernable cue in the sky is undoubtedly the moon. Because of its variable rise time and prominence, the moon is a much more complicated orientation cue than the sun (94), but nevertheless its bright disk is used for orientation and navigation in a number of different nocturnal insects, including ants (37, 44), earwigs (82), moths (77), and beetles (8).

A much dimmer and more subtle cue associated with the moon is its pattern of polarized light. This circular pattern, centered around the moon, arises because of the atmospheric

scattering of moonlight as it travels toward Earth (17, 36). Light is most polarized around a circular celestial locus 90° from the moon, and the circular pattern of polarized light moves with the moon. In many day-active insects, such as ants and bees, the equivalent polarization pattern formed around the sun is used as a compass cue when returning to the nest (93, 95, 96, 97) and allows them to hold a constant bearing during their straight-line returns. A similar use of the moon's polarization pattern, which during a full moon is a million times dimmer, should only be limited by the sensitivity of nocturnal eyes.

After the sun sets over the savannah, the nocturnal dung beetle, *Scarabaeus zambesianus*, emerges from its temporary nest in the soil and takes flight in search of fresh dung. Once found, it rapidly makes a dung ball and rolls it away on foot (9), aiming toward a location well away from the ferocious competition of the dung pile, where the beetle can manipulate its ball safe from interference. The safest and most efficient way to escape is to move away from the dung pile along a straight line in any direction, as indeed the beetles do (5, 9, 10). To hold this course in a straight line, beetles rely on compass information from the dim moonlight polarization pattern. If a large linearly polarizing filter is placed above the ball-rolling beetle as it moves along such a straight path, the insect realigns itself as it passes underneath, in accordance with the dominant polarization axis of the filter. When it then rolls back out under the natural sky, it again realigns itself to the natural skylight polarization pattern (9). Thus, nocturnal dung beetles have sufficient visual sensitivity to detect dim polarized moonlight and to use it as a compass cue for orientation. This ability is likely shared by other nocturnal insects, including crickets (28, 71), tenebrionid beetles (4, 66), and bees (20, 42).

Navigation and orientation using terrestrial cues. Just as for diurnal insects, many nocturnal insects rely on terrestrial features and landmarks for orientation, for flight control, or

for homing in on the exact location of a small nest entrance in the dark. The ability of an animal to use terrestrial cues for orientation at night is much more dependent on whether the cues have a sufficient contrast against the background than on their own particular luminance (38).

As shown in numerous excellent studies on diurnal flying insects, such as bees and flies, the ability to accurately analyze optic flow cues visually during flight is crucial for holding a stable course, hovering, landing, and homing (reviewed in References 100 and 101). Visual detection of optic flow is also clearly necessary for controlling nocturnal flight. For instance, in dim light gypsy moths (6) and mosquitoes (18) analyze optic flow cues to control their flight trajectories, and on brighter moonlit nights, nocturnally migrating locusts may be capable of doing the same thing (69).

For insects living in forests, where a clear view of the night sky is impossible, terrestrial features and landmarks seen silhouetted against the brighter night sky, such as the canopy or individual trees, are especially well suited for nocturnal orientation. As the animal moves under the tree canopy, the brighter sky in the gaps of the canopy, together with the darker area under the canopy, has the potential to form a spatial representation of the world above. Thus, an animal leaving its nest can memorize the structure of the canopy above and use it as a landmark for orientation (34), or use it to pinpoint the nest upon return from a longer trip. Indeed, both nocturnal (35, 79) and diurnal ants (1, 13, 34, 64) navigate to and from their nests using the rainforest canopy pattern as a navigational cue. Recently, the same ability has been demonstrated in a nocturnal shield bug, *Parastrachia japonensis* (29, 30, 31, 32).

Females of the Japanese subsocial shield bug *P. japonensis* forage on the floors of heavily wooded forests and look for food (stone fruits dropped from nearby trees) to take back to their nymphs in the home burrow. The outbound trip is typically tortuous, but the bug returns with fruit to the burrow along a straight course. To test if the shield bugs orient themselves

with respect to the spatial pattern of gaps in the canopy, a nesting female was placed on the floor of a large closed box having a single round opening at one end of the box's dorsal lid (30). This opening, representing an artificial canopy gap, was always exposed to an overcast night sky to eliminate other celestial cues. For several days prior to testing, the bug was allowed to forage for fruit in this box and to home after finding it (Figure 2*a,b*). During the test, the bug was allowed to forage for fruit as usual, but at the moment the fruit was found, the lid of the box was rapidly rotated by 180° so that the canopy gap was now positioned at the other end of the box. The shield bug, not realizing the change, homed in a direction exactly opposite the direction of the burrow (Figure 2*a,c*). This shows that in nocturnal as well as in diurnal insects the canopy pattern provides a powerful

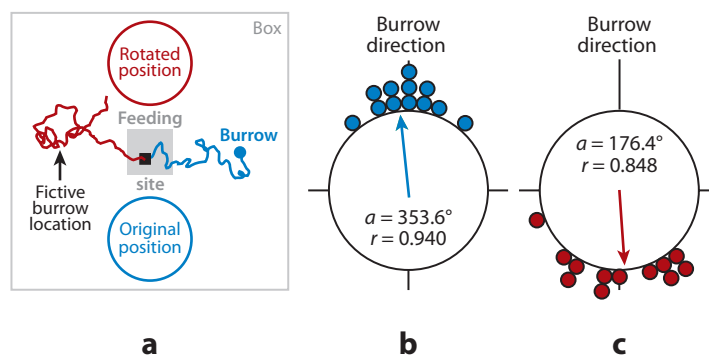


Figure 2

Nocturnal homing using canopy cues in the shield bug *Parastrachia japonensis*. (a) The typical homing route (red line) of a bug exposed to a sudden 180° rotation of an artificial canopy gap (circular hole, 90 cm in diameter; blue circle indicates original position, red circle indicates new position) in the roof of its box (large square: box measured 3 × 3 m, height 2 m). The bug was allowed to forage from its burrow to the feeding site where it located fruit (outbound foraging route shown by the blue line). At the moment the fruit was located, the canopy gap was rotated to its new position (red circle). The rotation caused the bug to home in the opposite direction to normal (red line) and to search for its burrow at its fictive location (arrow). (b) The distribution of homing directions in 12 bugs (blue dots) relative to the canopy gap (blue circle in panel a shows one of three original positions: four bugs were tested at each). In tests, all bugs oriented toward the real burrow. (c) The distribution of homing directions in 12 bugs (red dots) following a sudden 180° rotation of the canopy gap position (red circle in panel a). All bugs oriented 180° away from the real burrow. In panels b and c: a is the mean angle of orientation, r is the length of the mean resultant vector ($r = 1$ equates to perfect orientation at angle a). Adapted with kind permission from Reference 30.

Lamina: first optic ganglion of the optic lobe of insects

Lobula: third optic ganglion of the optic lobe of insects

compass cue for orientation. In shield bugs this ability seems particularly interesting: For an overcast nocturnal sky the contrast between the gap and the understory is at its minimum, implying that the bug possesses significant visual contrast sensitivity in dim light.

Visual landmarks in a forest, such as nearby bushes and tree trunks, typically have much lower visual contrast than bright gaps in the forest canopy. Nonetheless, two species of nocturnal bees, the Central American sweat bee (*Megalopta genalis*) and the Indian carpenter bee (*X. tranquebarica*), use such landmarks for homing after a foraging trip. Both species are active in extremely dim light and forage at long distances from their tiny nests at night, returning home without getting lost in the dark forest. While the involvement of canopy cues for this remarkable navigational ability remains to be tested, recent behavioral investigations reveal that both species perform orientation flights to visually learn landmarks around the nest entrance at night (74, 91). In *M. genalis* the nest is a hollowed-out stick. When a nest stick was placed in the middle of a row with four empty nest sticks (which could act as visual landmarks), the bee learned the spatial arrangement of these and would effortlessly return to its own stick in the center of the nest array after a foraging flight. If, when the bee was away, the positions of the bee's nest and an empty nest were swapped, the bee would still fly directly into the central unoccupied nest—the spatially correct nest—but after a couple of seconds would fly out again. This continued until the nest stick was returned to its original position in the middle of the array, after which the bee no longer emerged. This experiment shows that *M. genalis* is capable of using visually learned landmarks at night to find its way home, an ability that nocturnal carpenter bees also share (74). From studies of these homing behaviors at different light levels, it has been determined that *M. genalis* can find and land accurately on its nest when as few as five photons every second are absorbed by each photoreceptor of its apposition eye (80, 91). We return to this impressive performance below.

EYES AND VISION IN NOCTURNAL INSECTS

Most of our current knowledge of visual processing in nocturnal insects is confined to the optics and retina of the compound eye, although in recent years a small amount of data have also come from the first and third visual neuropiles of the optic lobe (the lamina ganglionaris of nocturnal bees and the lobula plate of nocturnal hawk moths). The following general conclusion can be drawn from these studies: Vision in nocturnal insects is made possible by having eyes with an enhanced optical sensitivity to light and visual neurons that sacrifice spatial and temporal resolution to improve visual reliability for the slower and coarser features of the world.

The Optical Designs of Nocturnal Compound Eyes

We have known for more than a century (14) that nocturnal insects typically possess superposition compound eyes (**Figure 1a**) and thereby gain a considerable optical sensitivity to light. A superposition eye can have optical sensitivity 100–1000 times higher than that of an apposition compound eye (the design typically possessed by diurnal insects) of the same size (**Figure 1b**).

In apposition compound eyes, each ommatidium is isolated from its neighbors by a sleeve of light-absorbing screening pigment, thus preventing light from reaching the photoreceptive rhabdom from all but its own small corneal lens. This tiny lens, typically some tens of micrometers across, represents the pupil of the apposition eye, and not surprisingly this eye design is typical of insects living in bright habitats. Remarkable exceptions do exist, including nocturnal mosquitoes (48, 49) and crane flies (52, 55), various species of nocturnal and crepuscular ants (e.g., within the bull ant genus *Myrmecia*; 21, 62), tropical nocturnal wasps (within the genera *Provespa* and *Apoica*; 19, 89), and nocturnal and crepuscular bees (41, 87, 89), including the central American sweat bee,

M. genalis (Halictidae), and the Indian carpenter bee, *X. tranquebarica* (Apidae). We discuss the latter two species below. Superposition eyes (Figure 1a) are better known for their high sensitivity. In this eye design, typical of nocturnal insects, the pigment sleeve is withdrawn in the dark-adapted state, and a wide optically transparent area, the clear zone (Figure 1a), is interposed between the lenses and the retina. The clear zone, and specially modified crystalline cones, allows light from a narrow region of space to be collected by a large number of ommatidia (comprising the superposition aperture) and to be focused onto a single rhabdom. Unlike the crystalline cones of most apposition eyes, those of superposition eyes of nocturnal insects have evolved powerful refractive index gradients (7, 14, 59) that allow as many as 2,000 lenses to collect light for a single photoreceptor (as in some large nocturnal moths). The width of this superposition aperture, which effectively acts as the pupil of the eye, is much larger than the width of a single corneal facet lens and represents a massive improvement in sensitivity.

The area of the pupil (diameter A) is not the only determinant of an eye's optical sensitivity (S) to a spatially extended source of broad-spectrum light. S , expressed in units of $\mu\text{m}^2 \text{ sr}$, is given by (43, 47, 92):

$$S = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{d}{f}\right)^2 \left(\frac{kl}{2.3 + kl}\right), \quad 1.$$

where l is the length of the rhabdom, k is the peak absorption coefficient of the visual pigment, f is the focal length of the ommatidium, and d is the diameter of the rhabdom. This equation predicts that good sensitivity to a spatially extended scene results from a pupil of large area ($\pi A^2/4$) and photoreceptors that each view a large solid angle of visual space ($\pi d^2/4 f^2$ steradians) and absorb a substantial fraction of the incident light ($kl/2.3 + kl$). The compound eyes of nocturnal insects tend to show all three trends.

To see how nocturnal life has affected the optical structure, and sensitivity, of insect compound eyes, consider the apposition eyes of the nocturnal sweat bee *M. genalis*. This bee has

larger eyes and larger facets (diameters up to $36 \mu\text{m}$) than the strictly day-active and similarly sized European honey bee, *Apis mellifera* (diameters up to $20 \mu\text{m}$). Moreover, in *A. mellifera* the rhabdoms have a width of only $2 \mu\text{m}$, whereas in *M. genalis* they reach an extraordinary $8 \mu\text{m}$, resulting in a receptive field more than seven times greater in solid angular extent (23, 91). These differences in receptive field and facet size allow *M. genalis* an optical sensitivity that is roughly 27 times greater than that of *A. mellifera*: $2.7 \mu\text{m}^2 \text{ sr}$ versus $0.1 \mu\text{m}^2 \text{ sr}$, a fact confirmed by measurements of responses to single photons in both species (15). Similar differences in sensitivity can be seen in the apposition eyes of nocturnal and diurnal carpenter bees (76), wasps (19), and ants (21, 60, 61). Even though nocturnal apposition eyes have a significantly higher optical sensitivity than diurnal apposition eyes, it is still modest compared to that found in a typical superposition eye, such as those of the nocturnal hawk moth *D. elpenor* ($S = 69 \mu\text{m}^2 \text{ sr}$). This finding exposes the inherent optical limitations of the apposition design for vision in dim light.

Photoreception and the Reliability of Vision in Dim Light

A general property of both vertebrate and invertebrate photoreceptors is their ability to respond to single photons of light with small but distinct electrical responses known as bumps (as they are called in the invertebrate literature) (Figure 3a,b). At higher intensities, the bump responses fuse to create a graded response whose duration and amplitude are proportional to the duration and amplitude of the light stimulus. At very low light levels, a light stimulus of constant intensity is coded as a train of bumps generated in the retina at a particular rate, and at somewhat higher light levels the constant intensity is coded by a graded potential of particular amplitude. At the level of the photoreceptors, the reliability of vision is determined by the repeatability of this response: For repeated presentations of the stimulus, the reliability of vision is maximal if the rate of bump

S: optical sensitivity

Rhabdom: in an ommatidium of a compound eye the light-sensitive structure formed by the microvilli of the retinula cells (contains the visual pigment rhodopsin)

Steradian (sr): one steradian is the solid angle subtended at the center of a sphere of radius r by a portion of the surface of the sphere whose area equals r^2

generation, or the amplitude of the graded response, remains exactly the same for each presentation. In practice this is never the case, especially in dim light.

Visual noise. Why is this so? The basic answer is that the visual response (and as a result its

repeatability) is degraded by visual noise. Part of this noise arises from the stochastic nature of photon arrival and absorption (governed by Poisson statistics): Each sample of N absorbed photons (the signal) has a certain degree of uncertainty (or noise) associated with it ($\pm\sqrt{N}$ photons). The relative magnitude of this uncertainty is greater at lower rates of photon absorption, and these quantum fluctuations set an upper limit to the visual signal-to-noise ratio (i.e., $N/\sqrt{N} = \sqrt{N}$; 70, 83). As light levels fall, the fewer photons absorbed, the greater this shot noise relative to the signal and the less that can be seen. This is the famous Rose-de Vries or square root law of visual detection at low light levels: The visual signal-to-noise ratio, and thus the finest contrast that can be discriminated, improves as the square root of photon catch. Signal reliability in dim light can thus be

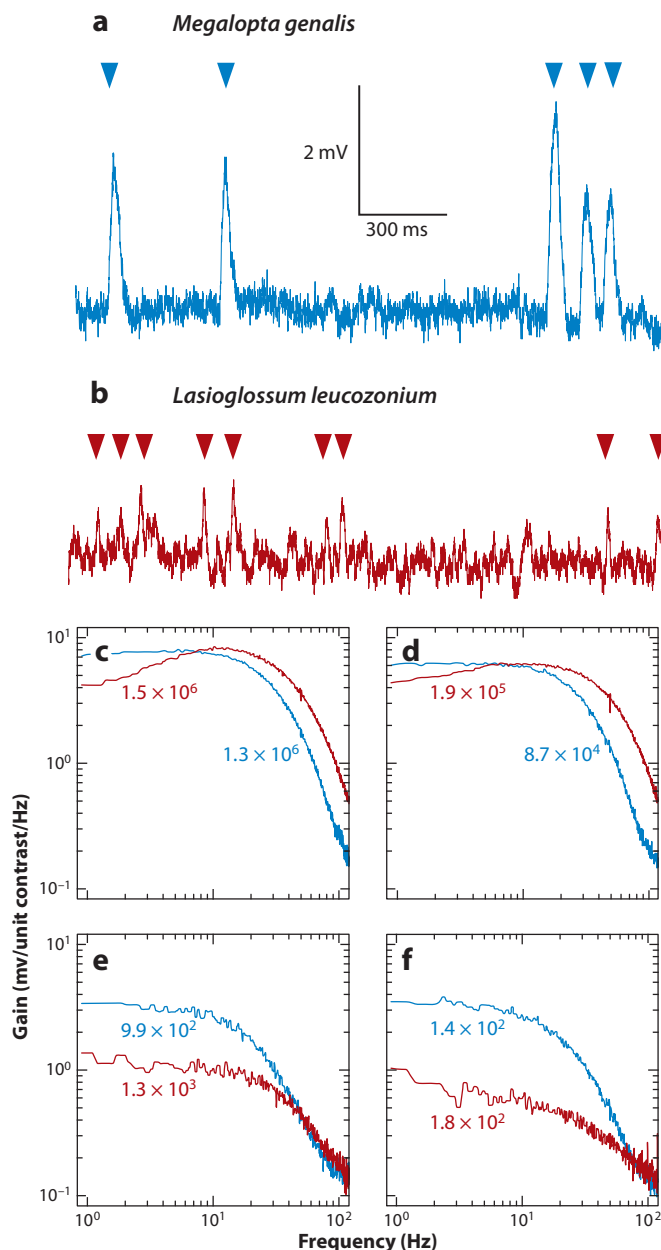


Figure 3

Adaptations for nocturnal vision in the photoreceptors of the nocturnal Central American sweat bee, *Megalopta genalis*, compared with photoreceptors in the closely related diurnal sweat bee *Lasioglossum leucozonium*. (a, b) Responses to single photons (or photon bumps, red and blue arrowheads) recorded from photoreceptors in (a) *M. genalis* and (b) *L. leucozonium*. Note that the bump amplitude is larger, and the bump time course much slower, in *M. genalis* than in *L. leucozonium*. (c–f). Average contrast gain as a function of temporal frequency in *M. genalis* (blue curves, $n = 8$ cells) and *L. leucozonium* (red curves, $n = 8$ cells) at different adapting intensities, indicated as effective photons per second in each panel for each species. [For each species, each stimulus intensity was calibrated in terms of effective photons, i.e., the number of photon bumps per second the light source elicited, thereby eliminating the effects of differences in the light-gathering capacity of the optics between the two species, which is about 27 times greater in *M. genalis* (57).] In light-adapted conditions (c, d), both species reach the same maximum contrast gain per unit bandwidth, although *L. leucozonium* has broader bandwidth and a higher corner frequency (the frequency at which the gain has fallen off to 50% of its maximum). In dark-adapted conditions (e, f), *M. genalis* has a much higher contrast gain per unit bandwidth. All panels adapted with kind permission from Reference 16.

improved with an eye design of higher sensitivity to light.

There are two other sources of noise that limit the reliability of nocturnal photoreception. The first source, transducer noise, arises because photoreceptors are incapable of producing identical bumps of fixed amplitude, latency, and duration to each (identical) photon of absorbed light. This source of noise, originating in the biochemical processes leading to signal amplification, degrades the reliability of vision (54, 56, 57). The second source of intrinsic noise, dark noise, arises because the biochemical pathways responsible for transduction are occasionally activated, even in perfect darkness (3). These activations are due either to spontaneous conversion of rhodopsin to metarhodopsin or to spontaneous activation of G-protein-coupled steps in the transduction chain. Irrespective of their origin, these activations produce dark events, electrical responses that are indistinguishable from those produced by real photons, and are more frequent at higher retinal temperatures. Even though dark noise is much lower in invertebrates than in vertebrates (11, 12, 25, 57), at very low light levels this dark noise could still significantly contaminate visual signals in insects.

Retinal adaptations for nocturnal vision.

To investigate the effects of visual noise on the reliability of vision in dim light, a useful method is to measure the visual signal-to-noise ratio of the photoreceptors by electrophysiologically recording their responses to Gaussian-distributed white-noise light stimuli (45). As a result of such experiments, the photoreceptors of insects reveal several properties uniquely suited to a life in dim light.

First, photoreceptor responses to single photons (i.e., bumps) are much larger in nocturnal insects than in their closely related diurnal relatives. Large bumps have been demonstrated in nocturnal crane flies (55), cockroaches (27), and bees (16), as well as in other arthropods, notably spiders (53, 65). This trend can be seen in closely related nocturnal and diurnal sweat bees: The quantum bumps are much larger

in the nocturnal *M. genalis* than in the diurnal *L. leucozonium* (Figure 3a,b) (16). The larger bumps of *M. genalis* and other nocturnal species indicate that the photoreceptor's gain of transduction is greater compared with diurnal species. This higher transduction gain manifests itself as a higher contrast gain, that is, in a greater photoreceptor voltage response per unit change in light intensity (or contrast). Contrast gain is plotted for the bees *M. genalis* and *L. leucozonium* as a function of temporal frequency in Figure 3c-f: At all levels of light and dark adaptation, at a frequency range both species can discriminate, the visual gain of *M. genalis* is always higher than that of *L. leucozonium*, and at the lowest intensities it is up to five times higher (Figure 3e,f). This higher gain results in greater signal amplification. Unfortunately, it also amplifies the noise, and thus on its own the higher gain does not alter the visual signal-to-noise ratio.

Second, as in slowly moving nocturnal ants (78), crane flies (55), and cockroaches (27), the dark-adapted photoreceptors of fast-flying nocturnal *M. genalis* are slow. In the frequency domain, this is equivalent to stating that the temporal corner frequency is low—this is the frequency at which the gain has fallen to 50% of its maximum value, and lower values indicate slower vision. In dark-adapted conditions, the corner frequency is around 7 Hz for *M. genalis*. In diurnal *L. leucozonium* it is about three times faster, at around 20 Hz (Figure 3f). Because both bees fly at similar speeds, their difference in temporal properties—most likely due to different photoreceptor sizes and to different numbers and types of ion channels in the photoreceptor membrane (52)—can be related only to the difference in light intensity experienced by the two species.

The slower vision of *M. genalis* in dim light, despite compromising temporal resolution, is beneficial because it increases the visual signal-to-noise ratio and improves contrast discrimination at lower temporal frequencies by suppressing photon noise at frequencies too high to be reliably resolved (26). Despite compromising temporal resolution, this low-pass

Contrast gain:
amplitude of the
electrical response of a
photoreceptor per unit
contrast

Information rate:
the number of bits of
information that are
conveyed or processed
per unit time

Supplemental Material

filtering (which is evident in **Figure 3c-f**) improves visual reliability in dim light. However, the narrower bandwidth possessed by nocturnal *M. genalis* (**Figure 3c-f**) has a devastating effect on the visual information rate (calculated in units of bits per second): At all intensities, the intrinsic rate of visual information is significantly greater in the photoreceptors of *L. leucozonium* than in the photoreceptors of *M. genalis* (**Figure 4a**). It is only when the approximately 27 times greater optical sensitivity of *M. genalis* apposition eyes is accounted for (**Figure 4b**) that the rate of information is greater in *M. genalis* than in *L. leucozonium*, but then only at the lowest intensities. Information, it seems, has been sacrificed in *M. genalis* for a greater absolute sensitivity.

FROM RETINA TO BEHAVIOR: A MISSING LINK

There is now little doubt that nocturnal insects have superb night vision, due to their ability (among other things) to see color, fly through complicated forests, and navigate using celestial cues and visual landmarks, all at light levels at least eight orders of magnitude lower than those experienced by their diurnal relatives when performing similar tasks. Neither is there any doubt that the compound eyes of nocturnal insects are well adapted to a life in dim light, with high optical sensitivity and photoreceptors that enhance visual reliability by having higher gains and slower responses. But is this the end of the story? Are the optical and neural adaptations of nocturnal insect eyes alone sufficient to explain nocturnal visual behavior?

To answer these questions, it is necessary to revisit our earlier case studies. Consider the nocturnal hawk moth *D. elpenor*, which can distinguish a blue disk from various gray disks in starlight. Despite having sensitive superposition eyes, its photoreceptors can absorb no more than 16 photons during each visual integration time when the moth performs this task. Theoretically (47), this photon catch is insufficient to reliably distinguish color (39). At similar intensities, each photoreceptor in the apposition eyes of the nocturnal bee *M. genalis* absorbs on average only a single photon every six visual integration times (91)! Yet at these light levels *M. genalis* lands accurately on its nest (80; **Supplemental Film**, follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>) and distinguishes visual landmarks. For *M. genalis*, this level of photon absorption is theoretically (47) about 100 times too low for the bee to distinguish the dark entrance hole of its nest (91). Even diurnal house flies (*Musca domestica*), tethered within a rotating optomotor drum lined with vertical stripes, react to the movements of the stripes when as few as two or three photons reach each photoreceptor every second (11, 67, 68, 72).

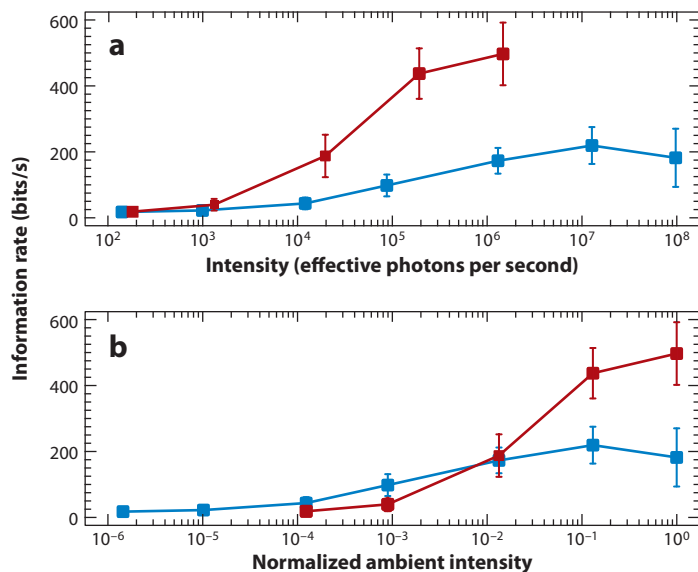


Figure 4

The average rates of information transmission (in bits per second) in the photoreceptors of the sweat bees *Megalopta genalis* (nocturnal) (blue curves, $n = 8$ cells) and *Lasioglossum leucozonium* (diurnal) (red curves, $n = 8$ cells). (a) When photoreceptors alone are considered (via a light source calibration in effective photons absorbed by the photoreceptor per second), it is evident that at all intensities *L. leucozonium* has a higher information rate than *M. genalis*. (b) When light sources are instead calibrated to external ambient intensities (a normalized intensity of 100 corresponds to the light intensity on an overcast day, or around 180 candela m^{-2}), *M. genalis* has a higher information rate in dim light. This results because the optics of *M. genalis* is 27 times more sensitive than that of *L. leucozonium*, not because an intrinsic adaptation is present within the photoreceptors. Error bars show \pm standard deviation. Both panels adapted with kind permission from Reference 16.

Another anomaly concerns nocturnal photoreceptors themselves. Even though they respond more slowly than diurnal photoreceptors, thereby improving visual reliability in dim light (26), the narrower temporal bandwidth of nocturnal photoreceptors significantly reduces the intrinsic information rate (**Figure 4**) (16). Moreover, their higher contrast gain, while providing beneficial signal amplification, also amplifies the noise and thus leads to no improvement in the visual signal-to-noise ratio.

Spatial and Temporal Summation

How can this wide gap between the performance of the retina and the visual performance of freely behaving nocturnal insects be explained? Currently we have only one hypothesis, supported by growing indirect evidence but still lacking definitive proof: Visual signals leaving the retina might neurally be summed in space and time (50, 84). We have already discussed summation in time above: When light gets dim, the visual systems of nocturnal insects can improve visual reliability by integrating signals over longer periods of time (**Figure 3**) (26, 51). This can be achieved by having slower photoreceptors. Even slower vision could be obtained by neurally integrating (summing) signals at a higher level in the visual system. This temporal summation comes at a price: It can drastically degrade the perception of fast-moving objects, which is potentially disastrous for a fast-flying nocturnal animal (such as a nocturnal wasp or bee) that needs to negotiate obstacles. Not surprisingly, temporal summation is more likely to be employed by slowly moving animals (84).

Summation of photons in space can also improve visual reliability. Instead of each ommatidium collecting photons in isolation (as in bright light), the transition to dim light could activate specialized laterally spreading neurons that couple the outputs of the ommatidia together into groups. Each summed group—now comprising a super ommatidium—could collect considerably more photons over a much wider

visual angle, albeit with a simultaneous and unavoidable loss of spatial resolution. Despite being much brighter, the image would become necessarily coarser. Evidence for such laterally spreading neurons has been found in the first optic ganglion (lamina ganglionaris) of nocturnal cockroaches, fireflies, and hawk moths (88), and these neurons have been interpreted as an adaptation for spatial summation (50). *M. genalis* also appears to have such neurons. The wide lateral branches of its laminar monopolar cells L2, L3, and L4, which spread to 12, 11, and 17 lamina cartridges, respectively, are considerably wider than the homologous cells of the diurnal honey bee *A. mellifera*, which spread to 2, 0, and 4 cartridges, respectively (22, 24).

By allowing the world to become coarser and slower, but more importantly much brighter, spatial and temporal summation could improve visual reliability of these coarser and slower details of the scene. Theoretically, this could explain the ability of nocturnal insects to see color (39), distinguish landmarks (81), and navigate using celestial patterns of polarized moonlight (46). It could also help explain the improved contrast gain of nocturnal photoreceptors (16, 89). The high contrast gain present in the photoreceptors of nocturnal bees amplifies both the signal and the noise. Because the noise is uncorrelated across ommatidia, spatial summation could effectively average out the noise and dramatically increase the visual signal-to-noise ratio in dim light, albeit for a lower range of spatial frequencies. Thus, a high visual gain, followed by spatial summation, could represent a significant strategy for vision in dim light.

Where in the Visual System Does Summation Occur?

The neural circuits responsible for spatial summation could very well be found in the lamina, the first optic ganglion of the optic lobe. Additional circuits might also be found in higher centers of the optic lobe, such as the medulla. Temporal summation, beyond the level already performed in the photoreceptors, could be

performed by temporal integrating mechanisms (e.g., long membrane time constants and neural delays) at many locations in the optic lobe, although exactly where is hard to say and will most likely depend on the type of visual information being processed.

Thus, a promising future avenue of research is to determine the nature of the neural circuitry responsible for summation. A clear question concerns the role of the lamina monopolar cells in spatial summation, and this will require an electrophysiological investigation of their physiological properties in one or more model insect species. Another obvious question involves the nature of the neural mechanisms responsible for temporal summation. This question might best be addressed by studying higher-order cells in which the time domain can be easily investigated. The motion-sensitive cells of the lobula plate

are good candidates: By understanding how the temporal properties of these cells change with light intensity, one may be able to decipher the type of temporal integrating mechanism employed. Other types of higher-order cells may also be useful in this respect, including those that analyze visual depth (99) or moving targets (63).

Although many questions remain unanswered, an undeniable fact remains: The visual systems of insects, despite their small size and comparatively few neurons, are nothing short of remarkable. With their exquisite visual sensitivity, nocturnal insects have evolved the impressive capacity to discriminate colors and navigate at night. It is a sobering thought indeed to realize that these abilities rival, and in some cases even exceed, those of many vertebrates despite the advantages afforded by their orders-of-magnitude larger eyes and brains.

SUMMARY POINTS

1. Nocturnal insects have excellent night vision, with the capacity to discriminate colors, orient themselves using faint celestial cues (such as polarized moonlight), fly unimpeded through a complicated habitat, and navigate to and from a nest using learned visual landmarks. These visual capacities are in all respects similar to those of diurnal insects.
2. Nocturnal insects with advanced visual behaviors possess either superposition compound eyes or apposition compound eyes. Apposition eyes (which are typical of diurnal insects) have an optical sensitivity up to around 1,000 times lower than superposition eyes.
3. At the dim light intensities at which nocturnal insects are visually active, each photoreceptor absorbs photons at extremely low rates.
4. The photoreceptors of nocturnal insects respond more slowly and have a higher contrast gain than those of diurnal insects, adaptations that potentially improve the reliability of vision, especially if visual signals are subsequently neurally summed.
5. A neural strategy of spatial and temporal summation at a higher level in the visual system is hypothesized as the necessary bridge between retinal signaling and visual behavior. Where in the visual system this summation takes place is currently unknown, although the lamina is a strong candidate. The elucidation of these summation strategies provides a fruitful avenue for future research.

DISCLOSURE STATEMENT

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LITERATURE CITED

1. Baader AP. 1996. The significance of visual landmarks for navigation of the giant tropical ant, *Paraponera clavata* (Formicidae: Ponerinae). *Insectes Soc.* 43:435–50
2. Balkenius A, Kelber A. 2004. Color constancy in diurnal and nocturnal hawkmoths. *J. Exp. Biol.* 207:3307–16
3. Barlow HB. 1956. Retinal noise and absolute threshold. *J. Opt. Soc. Am.* 46:634–39
4. Bisch SM. 1999. *Orientierungsleistungen des nachtaktiven Wüstenkäfers* *Parastizopus armaticeps* *Peringuey* (Coleoptera: Tenebrionidae). PhD diss. Rheinischen Friedrich-Wilhelms-Universität Bonn, Ger.
5. Byrne MJ, Dacke M, Nordström P, Scholtz CH, Warrant EJ. 2003. Visual cues used by ball-rolling dung beetles for orientation. *J. Comp. Physiol. A* 189:411–18
6. Cardé RT, Knols BGJ. 2000. Effects of light levels and plume structure on the orientation manoeuvres of male gypsy moths flying along pheromone plumes. *Physiol. Entomol.* 25:141–50
7. Caveney S, McIntyre P. 1981. Design of graded-index lenses in the superposition eyes of scarab beetles. *Philos. Trans. R. Soc. Lond. B* 294:589–32
8. Dacke M, Byrne M, Scholtz CH, Warrant EJ. 2004. Lunar orientation in a beetle. *Philos. Trans. R. Soc. Lond. B* 271:361–65
9. Dacke M, Nilsson D-E, Scholtz CH, Byrne M, Warrant EJ. 2003. Animal behaviour: insect orientation to polarized moonlight. *Nature* 424:33
10. Dacke M, Nordström P, Scholtz CH. 2003. Twilight orientation to polarised light in the crepuscular dung beetle *Scarabaeus zambesianus*. *J. Exp. Biol.* 206:1535–43
11. Dubs A, Laughlin SB, Srinivasan MV. 1981. Single photon signals in fly photoreceptors and first order interneurons at behavioural threshold. *J. Physiol.* 317:317–34
12. Doujak FE. 1985. Can a shore crab see a star? *J. Exp. Biol.* 166:385–93
13. Ehmer B. 1999. Orientation in the ant *Paraponera clavata*. *J. Insect Behav.* 12:711–22
14. Exner S. 1891. *Die Physiologie der facettierten Augen von Krebsen und Insecten*. Leipzig u. Wien: Franz Deuticke
15. Frederiksen R, Warrant EJ. 2008. The optical sensitivity of compound eyes—theory and experiment compared. *Biol. Lett.* 4:745–47
16. Frederiksen R, Wcislo WT, Warrant EJ. 2008. Visual reliability and information rate in the retina of a nocturnal bee. *Curr. Biol.* 18:349–53
17. Gál J, Horváth G, Barta A, Wehner R. 2001. Polarization of the moonlit clear night sky measured by full-sky imaging polarimetry at full moon: comparison of the polarization of moonlit and sunlit skies. *J. Geophys. Res.* 106:22647–53
18. Gibson G. 1995. A behavioural test of the sensitivity of a nocturnal mosquito, *Anopheles gambiae*, to dim white, red and infra-red light. *Physiol. Entomol.* 20:224–28
19. Greiner B. 2006. Visual adaptations in the night-active wasp *Apoica pallens*. *J. Comp. Neurol.* 495:255–62
20. Greiner B, Cronin TW, Ribi WA, Wcislo WT, Warrant EJ. 2007. Anatomical and physiological evidence for polarisation vision in the nocturnal bee *Megalopta genalis*. *J. Comp. Physiol. A* 193:591–600
21. Greiner B, Narendra A, Reid SF, Dacke M, Ribi WA, Zeil J. 2007. Eye structure correlates with distinct foraging-bout timing in primitive ants. *Curr. Biol.* 17:R879–80
22. Greiner B, Ribi WA, Warrant EJ. 2004. Neuronal organisation in the first optic ganglion of the nocturnal bee *Megalopta genalis*. *Cell Tissue Res.* 318:429–37
23. Greiner B, Ribi WA, Warrant EJ. 2004. Retinal and optical adaptations for nocturnal vision in the halictid bee *Megalopta genalis*. *Cell Tissue Res.* 316:377–90

9. First demonstration of an animal that orients itself using polarized moonlight.

16. Demonstrates that nocturnal insects can improve visual reliability at night by sacrificing photoreceptor signal-to-noise ratio and information rate for an increased contrast gain.

24. Provides the possible neural substrate for spatial summation in the lamina of a nocturnal bee.

39. First demonstration of nocturnal color vision.

24. Greiner B, Ribi WA, Warrant EJ. 2005. A neural network to improve dim-light vision? Dendritic fields of first-order interneurons in the nocturnal bee *Megalopta genalis*. *Cell Tissue Res.* 323:313–20
25. Hardie RC, Martin F, Cochrane GW, Juusola M, Georgiev P, Raghu P. 2002. Molecular basis of amplification in *Drosophila* phototransduction: roles for G protein, phospholipase C, and diacylglycerol kinase. *Neuron* 36:689–701
26. Hateren van JH. 1993. Spatiotemporal contrast sensitivity of early vision. *Vision Res.* 33:257–67
27. Heimonen K, Salmela I, Kontiokari P, Weckström M. 2006. Large functional variability in cockroach photoreceptors: optimization to low light levels. *J. Neurosci.* 26:13454–62
28. Herzmann D, Labhart T. 1989. Spectral sensitivity and absolute threshold of polarization vision in crickets: a behavioral study. *J. Comp. Physiol. A* 165:315–19
29. Hironaka M, Filippi L, Nomakuchi S, Horiguchi H, Hariyama T. 2007. Hierarchical use of chemical marking and path integration in the homing trip of a subsocial shield bug. *Anim. Behav.* 73:739–45
30. Hironaka M, Inadomi K, Nomakuchi S, Filippi L, Hariyama T. 2008. Canopy compass in nocturnal homing of the subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Parastrachiidae). *Naturwissenschaften* 95:343–46
31. Hironaka M, Nomakuchi S, Filippi L, Tojo S, Horiguchi H, Hariyama T. 2003. The directional homing behavior of the subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Cydnidae), under different photic conditions. *Zool. Sci.* 20:423–28
32. Hironaka M, Tojo S, Nomakuchi S, Filippi L, Hariyama T. 2007. Round-the-clock homing behavior of a subsocial shield bug, *Parastrachia japonensis* (Heteroptera: Parastrachiidae) using, path integration. *Zool. Sci.* 24:535–41
33. Höglund G, Hamdorf K, Rosner G. 1973. Trichromatic visual system in an insect and its sensitivity control by blue light. *J. Comp. Physiol.* 86:265–79
34. Hölldobler B. 1980. Canopy orientation: a new kind of orientation in ants. *Science* 210:86–88
35. Hölldobler B, Taylor RW. 1983. A behavioral study of the primitive ant *Nothomyrmecia macrops* Clark. *Insectes Soc.* 30:381–401
36. Horváth G, Varjú D. 2009. *Polarized Light in Animal Vision: Polarization Patterns in Nature*. Berlin/Heidelberg/New York: Springer. 447 pp.
37. Jander R. 1957. Die optische Richtungsorientierung der Roten Waldameise (*Formica rufa*). *Z. Vergl. Physiol.* 40:162–238
38. Kaul RM, Kopteva GA. 1982. Night orientation of ants *Formica rufa* (Hymenoptera: Formicidae) upon movement on routes. *Zool. Zb.* 61:1351–58
39. Kelber A, Balkenius A, Warrant EJ. 2002. Scotopic color vision in nocturnal hawkmoths. *Nature* 419:922–25
40. Kelber A, Balkenius A, Warrant EJ. 2003. Color vision in diurnal and nocturnal hawkmoths. *Integr. Comp. Biol.* 43:571–79
41. Kelber A, Warrant EJ, Pfaff M, Wallén R, Theobald JC, et al. 2006. Light intensity limits the foraging activity in nocturnal and crepuscular bees. *Behav. Ecol.* 17:63–72
42. Kerfoot WB. 1967. The lunar periodicity of *Sphecodogastra texana*, a nocturnal bee (Hymenoptera; Halictidae). *Anim. Behav.* 15:479–86
43. Kirschfeld K. 1974. The absolute sensitivity of lens and compound eyes. *Z. Naturforsch.* 29C:592–96
44. Klotz JH, Reid BL. 1993. Nocturnal orientation in the black carpenter ant *Camponotus pennsylvanicus* (De Geer) (Hymenoptera: Formicidae). *Insectes Soc.* 40:95–106
45. Kouvalainen E, Weckström M, Juusola M. 1994. A method for determining photoreceptor signal-to-noise ratio in the time and frequency domains with a pseudorandom stimulus. *Vis. Neurosci.* 11:1221–25
46. Labhart T, Petzold J, Helbling H. 2001. Spatial integration in polarization-sensitive interneurons of crickets, a survey of evidence, mechanisms and benefits. *J. Exp. Biol.* 204:2423–30
47. Land MF. 1981. Optics and vision in invertebrates. In *Handbook of Sensory Physiology*, ed. H Autrum, VII/6B:471–592. Berlin: Springer
48. Land MF, Gibson G, Horwood J. 1997. Mosquito eye design, conical rhabdoms are matched to wide aperture lenses. *Proc. R. Soc. Lond. B* 264:1183–87

49. Land MF, Gibson G, Horwood J, Zeil J. 1999. Fundamental differences in the optical structure of the eyes of nocturnal and diurnal mosquitoes. *J. Comp. Physiol. A* 185:91–103
50. Laughlin SB. 1981. Neural principles in the peripheral visual systems of invertebrates. In *Handbook of Sensory Physiology*, ed. H Autrum, VII/6B:133–280. Berlin: Springer
51. Laughlin SB. 1990. Invertebrate vision at low luminances. In *Night Vision*, ed. RF Hess, LT Sharpe, K Nordby, pp. 223–250. Cambridge, UK: Cambridge Univ. Press
52. Laughlin SB. 1996. Matched filtering by a photoreceptor membrane. *Vision Res.* 36:1529–41
53. Laughlin SB, Blest AD, Stowe S. 1980. The sensitivity of receptors in the posterior median eye of the nocturnal spider, *Dinopis*. *J. Comp. Physiol.* 141:53–65
54. Laughlin SB, Lillywhite PG. 1982. Intrinsic noise in locust photoreceptors. *J. Physiol.* 332:25–45
- 55. Laughlin SB, Weckström M. 1993. Fast and slow photoreceptors—a comparative study of the functional diversity of coding and conductances in the Diptera. *J. Comp. Physiol. A* 172:593–609**
56. Lillywhite PG. 1981. Multiplicative intrinsic noise and the limits to visual performance. *Vision Res.* 21:291–96
57. Lillywhite PG, Laughlin SB. 1979. Transducer noise in a photoreceptor. *Nature* 277:569–72
58. Martin GR. 1990. *Birds By Night*. London: Poyser. 227 pp.
59. McIntyre P, Caveney S. 1985. Graded-index optics are matched to optical geometry in the superposition eyes of scarab beetles. *Philos. Trans. R. Soc. Lond. B* 311:237–69
60. Menzi U. 1987. Visual adaptation in nocturnal and diurnal ants. *J. Comp. Physiol. A* 160:11–21
61. Moser JC, Reeve JD, Bento JMS, Della Lucia TMC, Cameron RS, Heck NM. 2004. Eye size and behavior of day- and night-flying leafcutting ant alates. *J. Zool. Lond.* 264:69–75
62. Narendra A, Reid SF, Hemmi JM. 2010. The twilight zone: ambient light levels trigger activity in primitive ants. *Proc. R. Soc. Lond. B* 277:1531–38
63. Nordström K, O'Carroll DC. 2009. Feature detection and the hypercomplex property in insects. *Trends Neurosci.* 32:383–91
64. Oliveira PS, Hölldobler B. 1989. Orientation and communication in the neotropical ant *Odontomachus bauri* Emery (Hymenoptera, Formicidae, Ponerinae). *Ethology* 83:154–66
65. Pirhofer-Walzl K, Warrant EJ, Barth FG. 2007. Adaptations for vision in dim light: impulse responses and bumps in nocturnal spider photoreceptor cells (*Cupiennius salei* Keys). *J. Comp. Physiol. A* 193:1081–87
66. Rasa OAE. 1990. Evidence for subsociality and division of labor in a desert tenebrionid beetles *Parastizopus armaticeps* (Puey). *Naturwissenschaften* 77:591–92
67. Reichardt WE. 1965. Quantum sensitivity of light receptors in the compound eye of the fly, *Musca*. *Cold Spring Harb. Symp. Quant. Biol.* 30:505–15
68. Reichardt WE, Braitenburg V, Weidel G. 1968. Auslösung von Elementarprozessen durch einzelne Lichtquanten im Fliegenauge. *Kybernetik* 5:148–69
69. Riley JR, Kreuger U, Addison CM, Gewecke M. 1988. Visual detection of wind-draft by high-flying insects at night: a laboratory study. *J. Comp. Physiol. A* 169:793–98
70. Rose A. 1942. The relative sensitivities of television pickup tubes, photographic film and the human eye. *Proc. Inst. Radio Eng. New York* 30:293–300
71. Rost R, Honegger HW. 1987. The timing of premating and mating behavior in a field population of the cricket *Gryllus campestris* L. *Behav. Ecol. Sociobiol.* 21:279–89
72. Scholes JH, Reichardt W. 1969. The quantal content of optomotor stimuli and the electrical responses of receptors in the compound eye of the fly *Musca*. *Kybernetik* 6:74–80
73. Schwemer J, Paulsen R. 1973. Three visual pigments in *Deilephila elpenor* (Lepidoptera, Sphingidae). *J. Comp. Physiol.* 86:215–29
- 74. Somanathan H, Borges RM, Warrant EJ, Kelber A. 2008. Nocturnal bees learn landmark colours in starlight. *Curr. Biol.* 18:R996–97**
75. Somanathan H, Borges RM, Warrant EJ, Kelber A. 2008. Visual ecology of Indian carpenter bees I: light intensities and flight activity. *J. Comp. Physiol. A* 194:97–107
76. Somanathan H, Kelber A, Borges RM, Wallén R, Warrant EJ. 2009. Visual ecology of Indian carpenter bees II: adaptations of eyes and ocelli to nocturnal and diurnal lifestyles. *J. Comp. Physiol. A* 195:571–83
77. Sotthibandhu S, Baker BB. 1979. Celestial orientation by the large yellow underwing moth, *Noctua pronuba* L. *Anim. Behav.* 27:786–800

55. Compares the responses and membrane properties of photoreceptors in 20 species of flies and demonstrates that temporal coding is matched to the visual ecology of the species.

74. First demonstration of nocturnal color vision in an insect with apposition compound eyes, an eye design more typical of diurnal insects.

83. First demonstration of the relationship between the quantal nature of light and human visual threshold. Introduces the “square root law” of visual detection at low light levels.

91. First demonstration of an insect that navigates at night using visual landmarks.

78. Souza de JM, Ventura DF. 1989. Comparative study of temporal summation and response form in hymenopteran photoreceptors. *J. Comp. Physiol. A* 165:237–45
79. Taylor RW. 2007. Bloody funny wasps! Speculations on the evolution of eusociality in ants. In *Advances in Ant Systematics (Hymenoptera: Formicidae): Homage to E.O. Wilson – 50 Years of Contributions*, Memoirs of the American Entomological Institute, ed. RR Snelling, BL Fisher, PS Ward, 80:580–609. Gainesville, FL: Am. Entomol. Inst.
80. Theobald JC, Coates MM, Weislo WT, Warrant EJ. 2007. Flight performance in night-flying sweat bees suffers at low light levels. *J. Exp. Biol.* 210:4034–42
81. Theobald JC, Greiner B, Weislo WT, Warrant EJ. 2006. Visual summation in night-flying sweat bees: a theoretical study. *Vision Res.* 46:2298–309
82. Ugolini A, Chiussi R. 1996. Astronomical orientation and learning in the earwig *Labidura riparia*. *Behav. Process.* 36:151–61
83. Vries de H. 1943. The quantum character of light and its bearing upon threshold of vision, the differential sensitivity and visual acuity of the eye. *Physica* 10:553–64
84. Warrant EJ. 1999. Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vision Res.* 39:1611–30
85. Warrant EJ. 2004. Vision in the dimmest habitats on earth. *J. Comp. Physiol. A* 190:765–89
86. Warrant EJ. 2006. Invertebrate vision in dim light. In *Invertebrate Vision*, ed. EJ Warrant, D-E Nilsson, pp. 83–126. Cambridge, UK: Cambridge Univ. Press
87. Warrant EJ. 2007. Nocturnal bees. *Curr. Biol.* 17:R991–92
88. Warrant EJ. 2008. Nocturnal vision. In *The Senses: A Comprehensive Reference, Vision II*, ed. T Albright, RH Masland, AI Basbaum, A Kaneko, GM Shepherd, G Westheimer, 2:53–86. Oxford: Academic
89. Warrant EJ. 2008. Seeing in the dark: vision and visual behavior in nocturnal bees and wasps. *J. Exp. Biol.* 211:1737–46
90. Warrant EJ, Dacke M. 2010. Visual orientation and navigation in nocturnal arthropods. *Brain Behav. Evol.* 75:156–73
91. Warrant EJ, Kelber A, Gislén A, Greiner B, Ribi W, Weislo WT. 2004. Nocturnal vision and landmark orientation in a tropical halictid bee. *Curr. Biol.* 14:1309–18
92. Warrant EJ, Nilsson D-E. 1998. Absorption of white light in photoreceptors. *Vision Res.* 38:195–207
93. Waterman TH. 1981. Polarization sensitivity. In *Handbook of Sensory Physiology*, ed. H Autrum, VII/6B:281–469. Berlin: Springer
94. Wehner R. 1984. Astronavigation in insects. *Annu. Rev. Entomol.* 29:277–98
95. Wehner R. 1992. Arthropods. In *Animal Homing*, ed. F Papi, pp. 45–144. London: Chapman and Hall
96. Wehner R. 2001. Polarization vision—a uniform sensory capacity? *J. Exp. Biol.* 204:2589–96
97. Wehner R, Labhart T. 2006. Polarisation vision. In *Invertebrate Vision*, ed. EJ Warrant, D-E Nilsson, pp. 291–47. Cambridge, UK: Cambridge Univ.
98. Wehner R, Srinivasan M. 2003. Path integration in insects. In *The Neurobiology of Spatial Behavior*, ed. KJ Jeffery, pp. 9–30. Oxford, UK: Oxford Univ. Press
99. Wickklein M, Strausfeld NJ. 2000. Organization and significance of neurons that detect change of visual depth in the hawk moth *Manduca sexta*. *J. Comp. Neurol.* 424:356–76
100. Zeil J, Boeddeker N, Stürzl W. 2009. Visual homing in insects and robots. In *Flying Insects and Robots*, ed. D Floreano, pp. 87–100. Berlin: Springer-Verlag
101. Zeil J, Boeddeker N, Hemmi JM. 2009. Visually guided behaviour. In *Encyclopaedia of Neuroscience*, ed. LR Squire, 10:369–80. Oxford: Academic



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