

Superior visual performance in nocturnal insects: Neural principles and bio-inspired technologies

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ABSTRACT

At night, our visual capacities are severely reduced, with a complete loss in our ability to see colour and a dramatic loss in our ability to see fine spatial and temporal details. This is not the case for many nocturnal animals, notably insects. Our recent work – particularly on fast-flying moths and bees and on ball-rolling dung beetles – has shown that nocturnal animals are able to distinguish colours, to detect faint movements, to learn visual landmarks, to orient to the faint pattern of polarised light produced by the moon and to navigate using the stars. These impressive visual abilities are the result of exquisitely adapted eyes and visual systems, the product of millions of years of evolution. Nocturnal animals typically have highly sensitive eye designs and visual neural circuitry that is optimised for extracting reliable information from dim and noisy visual images. Even though we are only at the threshold of understanding the neural mechanisms responsible for reliable nocturnal vision, growing evidence suggests that the neural summation of photons in space and time is critically important: even though vision in dim light becomes necessarily coarser and slower, it also becomes significantly more reliable. We explored the benefits of spatiotemporal summation by creating a computer algorithm that mimicked nocturnal visual processing strategies. This algorithm dramatically increased the reliability of video collected in dim light – including the preservation of colour – strengthening evidence that summation strategies are essential for nocturnal vision.

Key words: nocturnal vision, spatial summation, temporal summation, sensitivity, compound eye, insect, biomimetics, computer vision

1. INTRODUCTION

All levels of vision – from the simple detection of a tiny point of bioluminescent light at great depths in the ocean, to the negotiation of a complex field of three dimensional obstacles during high-speed flight – are impossible unless eyes can capture a sufficient quantity of light. In a bright sunny terrestrial habitat, this basic requirement is generally met without difficulty. But in a dim rainforest at night, or in the depths of the sea, visual systems may have trouble capturing enough light to see reliably, that is, to extract reliable information from what may be an unreliable visual signal.

Why is vision unreliable in dim light? The basic answer is that visual signals in dim light are contaminated by visual “noise”. Part of this noise arises from the stochastic nature of photon arrival and absorption: each sample of absorbed photons (or signal) has a certain degree of uncertainty (or noise) associated with it. 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^{12,51}. As light levels fall, the fewer the number of photons that are absorbed, the greater the noise relative to the signal and the less that can be seen. Signal reliability in dim light can thus be improved with an eye design of high sensitivity to light.

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† Dedicated to the memory of Professor Matti Weckström (1959-2015) – friend, scholar and a champion in the study of dim light vision in insects.

The eyes of insects living in dim light are usually very sensitive^{43,65,66,68}. However, even with very sensitive eyes capturing as many of the available photons as possible, a reliable signal is only assured if each captured photon is transduced efficiently and reproducibly. This is the task of the photoreceptors, and signal reliability at this level depends on how ideal the receptors are as photodetectors. Even though insect photoreceptors are not perfectly ideal, they are nonetheless remarkably efficient. The reliability of the signals they transmit to higher levels of the visual system can be improved even further by optimal processing designed to minimise the effects of noise, for instance by summing visual signals in space and time. Higher level processing of visual stimuli such as the colour of nectar-bearing flowers, the relative motions of obstacles during flight or the size and shape of learned landmarks, is ultimately used to steer the behaviour of the animal. If, in dim light, such higher level processing is reliable, then nocturnal animals have the potential to see quite well. As we will see below, there is mounting behavioural evidence from a variety of insects suggesting that this is indeed the case^{65,66,69}.

2. SIGNAL, NOISE AND THE RESPONSES OF PHOTORECEPTORS IN DIM LIGHT

The greatest challenge for an eye that views a dimly illuminated object is to absorb sufficient photons of light to reliably discriminate it³³. As mentioned above, the arrival and absorption of photons is stochastic, and this puts an upper limit on the visual signal-to-noise ratio^{12,51}. However, the greater the number of absorbed photons, the greater the signal relative to the noise and the more reliable is visual discrimination. Even though the eyes of animals that live in dim light are usually adapted to capturing and absorbing as many photons as possible (see below), this upper limiting ratio of signal to noise is rarely reached. Other noise sources – intrinsic within the photoreceptors themselves – ensure that visual reliability is rarely as good as predicted by the stochastic nature of photon arrivals. Photoreceptors, it seems, are not ideal photodetectors.

2.1 The efficiency of photoreceptors

How reliable are photoreceptors as detectors of light? At first glance they appear extremely reliable. Ever since the pioneering studies of Yeandle in the horseshoe crab *Limulus* in the late 1950s⁷⁵, we have known that photoreceptors can respond to single photons with small but distinct electrical responses known as “bumps”, responses found in both vertebrates⁸ and invertebrates (Fig. 1A). Apart from the horseshoe crab, bumps have now been recorded from many invertebrates including insects (e.g. flies, locusts and cockroaches; reviewed in 33), crustaceans (e.g. 13) and spiders (e.g. 34). Numerous studies have now established that there is a 1:1 relationship between transduced photons and bumps^{16,37}: a single bump results from the absorption and transduction of no more than a single photon, and a single transduced photon leads to no more than a single bump.

Interestingly, already at the level of their responses to photons, the photoreceptors of nocturnal insects reveal two properties that are uniquely suited to a life in dim light. Firstly, responses to single photons are much larger in nocturnal insects than they are in their closely related diurnal relatives. Large bumps have been demonstrated in nocturnal crane flies³⁶, cockroaches²⁰ and bees¹⁵ and even in other arthropods, notably spiders^{34,45}. This trend can be seen in closely related nocturnal and diurnal sweat bees: in the nocturnal *Megalopta genalis* the bumps are much larger than in the diurnal *Lasioglossum leucozonium* (Fig. 1A¹⁵). The larger bumps of *Megalopta* and other nocturnal species indicate that the photoreceptor’s gain of transduction is greater than in diurnal species (in fact about 5 times greater). This means that for an identical light stimulus (i.e. a single photon) the response of the nocturnal photoreceptor is around 5 times larger than that of the diurnal photoreceptor, allowing the nocturnal photoreceptor a greater likelihood of accurately registering the arrival of photons. Secondly, due to the demands of seeing well in dim light^{15,19,64}, the photoreceptor responses of nocturnal insects tend to be a lot slower than those of diurnal insects (i.e. have a longer time course), a fact that is quite noticeable in the photon bumps of nocturnal and diurnal bees (Fig. 1A).

Despite the apparently remarkable sensitivity of photoreceptors to single quanta of light, not all photons that strike the pupil of an eye are actually absorbed by the photoreceptors and lead to a bump. For a start, a certain percentage of the incident light is immediately reflected from the surface of the eye. In the fly, for instance, only about 90% of the photons that strike the corneal surface of the eye actually reach the fly’s retina. Moreover, the rhodopsin molecules resident in photoreceptors do not absorb all wavelengths of light with equal efficiency. Only light of wavelength matching the absorption peak wavelength λ_{max} of the rhodopsin molecule is absorbed with maximum efficiency. At all other wavelengths photons are absorbed with lower efficiency. Absorption efficiency also depends on the angle relative to the

photoreceptor waveguide axis that light is incident⁵⁹. However, despite these angular and wavelength limitations, it has been estimated that in flies about 80% of the energy of the lens diffraction pattern is transferred to the photoreceptive waveguide⁵⁹. Of these photons, between 86% and 95% are absorbed⁵⁸. Of these absorbed photons, perhaps only 80% are actually transduced since the quantum capture efficiency of the photopigment is around 80%³³. This means that only around 50% of photons that are incident on the external corneal facet lens of each ommatidium of a fly compound eye (see below) lead to a bump (0.90 x 0.80 x 0.86 x 0.80). This is actually quite efficient, and a similarly high efficiency is also found in other arthropods: 45% in the shore crab *Leptograpsus variegatus*¹³ and 59% in the locust *Locusta migratoria*³⁷. In vertebrates the figure tends to be somewhat lower, and in the cat it is probably below 25%⁷.

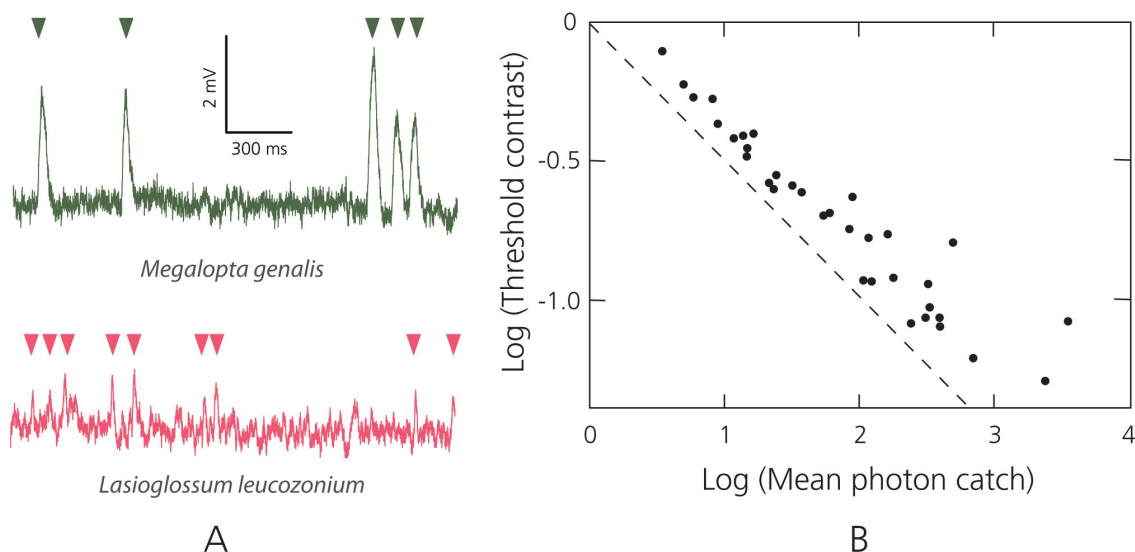


Figure 1. Light detection at visual threshold. **A.** Photoreceptor responses (“bumps”) to single photons of light (arrow heads) in the nocturnal halictid bee *Megalopta genalis* (green trace) and the closely related diurnal bee *Lasioglossum leucozonium* (red trace). Note that the amplitudes of the receptor responses in the nocturnal species are about 5 times the amplitude of those in the day-active species, an adaptation in nocturnal insects that increases visual reliability in dim light. From 15. **B.** Threshold contrasts measured from locust photoreceptors (black dots) as a function of intensity (defined in terms of mean photon catch). If threshold contrast is determined by photon noise alone, the data points would lie along the dashed line. The fact that the points lie above the line implies that additional sources of noise – in this case intrinsic transducer noise – raise the threshold for contrast discrimination. Redrawn from 35.

The remarkably efficient quantal sensitivity of invertebrates is especially obvious at very low rates of photon arrival. Single bumps – the responses to single photons – are sufficient on their own to trigger a response in the second order cells to which the photoreceptors connect. In flies, the photoreceptors connect to monopolar cells in the first optic neuropil of the optic lobe (the lamina), and careful recordings have shown that bumps in the photoreceptor trigger bumps in the monopolar cell¹⁴. Remarkably, this level of quantal sensitivity has also been found in neural pathways involving even more synapses. The well-studied motion-detecting cell of flies – the wide-field movement detector H1, found in the third optic neuropil of the optic lobe (the lobula plate) – also reveals quantal sensitivity at threshold despite being at least three synapses distant from the photoreceptors: single action potentials generated in H1 are correlated with the absorption of single photons in the photoreceptors³⁸. Because H1 and the other motion-detecting cells of the fly lobula plate are thought to steer optomotor behaviour⁴⁶, such quantal sensitivity even has the potential to occur at the level of the behaving animal. This is indeed the case: a housefly (*Musca domestica*) tethered within a rotating optomotor drum lined with vertical stripes reacts to the movements of the stripes when as few as 2 or 3 photons reach each photoreceptor every second^{14,47,48,52}. This remarkable quantal sensitivity is even more pronounced in truly nocturnal insects, such as cockroaches – these insects can react to a rotating optomotor drum when each photoreceptor receives on average around 1 photon every 10 seconds²².

2.2 Noise and the reliability of vision

At these very low threshold rates of photon absorption – where quantal events can even drive behaviour – photon detection is free of the effects of *intrinsic* noise. The upper limit on the visual signal-to-noise ratio is then set by the *extrinsic* noise associated with the random nature of photon arrival^{12,51}. This extrinsic noise is referred to as photon “shot noise”. Consider a photoreceptor that absorbs N photons during one visual integration time. Due to the random nature of photon arrivals (governed by Poisson statistics), the photoreceptor will experience an uncertainty – or shot noise – of \sqrt{N} photons associated with this sample, that is, $N \pm \sqrt{N}$ photons^{12,30,51,71}. This noise reduces the reliability of intensity discriminations and thereby the ability of the eye to distinguish contrast details in a scene. The ratio of signal to noise – $N/\sqrt{N} = \sqrt{N}$ – thus improves with increasing photon catch, implying that photon shot noise, and contrast discrimination, is worse at lower light levels. 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 contrast discrimination, improves as the square-root of photon catch.

All of our discussions so far seem to suggest that photoreceptors are ideal detectors of photons, being able to detect them individually at threshold with a reliability limited only by the stochastic nature of their arrival. But are photoreceptors truly ideal? To be ideal, a photoreceptor must absorb and transduce every photon incident upon it. It must also produce an identical electrical response, of fixed amplitude and duration, to each of them. Finally, an ideal photoreceptor must never produce an electrical response when photons are absent. As we have seen, the first condition – absorption and transduction of every photon – is not met by any photoreceptor: invertebrate photoreceptors only absorb about half of them, and vertebrate photoreceptors even fewer. Photoreceptors also fail to meet the second and third conditions – that responses are identical and do not occur when photons are absent. Bumps vary in latency, duration and amplitude (as seen in Fig. 1A) and the biochemical pathways responsible for their generation are occasionally activated in the absence of light. These two failures – known as “transducer noise” and “dark noise” respectively – are sources of intrinsic noise that reduce efficiency even further.

Dark noise arises due to the fact that even in perfect darkness, the biochemical pathways responsible for transduction are occasionally activated⁶. These activations produce “dark bumps”, electrical responses that are almost indistinguishable from those produced by real photons, and these are more frequent at higher retinal temperatures. At very low light levels this dark noise can significantly contaminate visual signals. In insects and crustaceans dark bumps are rare, only around 10 every hour at 25°C^{13,14,21,25,39}, and this sets the ultimate limit to visual sensitivity^{1,2}.

Vision can also become unreliable at low light levels because of transducer noise. This source of noise, originating in the biochemical processes leading to signal amplification and represented by variations in the latency, duration and amplitude of bumps at low light levels – degrades the reliability of vision. At higher intensities the quantum bumps fuse to form a continuous but noisy receptor potential which not only results from dark noise and variations in bump waveform (transducer noise), but also from shot noise. By performing very careful experiments in locusts – where the number of photons absorbed from dim light flashes of different intensity was calibrated using direct electrophysiological bump counts from photoreceptors – Lillywhite and Laughlin were able to determine the relative contributions of all types of noise, both intrinsic and extrinsic^{35,37,39}. Their results show that at low light levels the contributions of transducer noise and shot noise are approximately equal (dark noise being negligible), while at higher light levels, transducer noise can even be dominating. However, irrespective of their relative magnitudes, the presence of both types of noise degrades visual reliability: transducer noise raises the contrast threshold for visual discrimination above that resulting from shot noise alone (Fig. 1B).

However, regardless of whether it arises intrinsically or extrinsically, visual noise poses a serious threat to the reliability of vision in dim light. How then can visual reliability be improved? The simple answer is that visual systems improve it by either enhancing the signal or suppressing the noise, strategies that have led to a variety of adaptations, both optical and neural.

3. OPTICAL ADAPTATIONS FOR INCREASED SENSITIVITY TO LIGHT

Most visual scenes on land are extended in nature, meaning that light reaches the eye from many different directions at once. Whereas in principal only a single visual detector is necessary for reliably discriminating a point source, many

visual detectors are required for reliably reconstructing the spatial details inherent in an extended scene. These spatial details – defined by local contrast differences between areas of light and dark in the scene – are nothing more than variations in light intensity on the retina, variations that the orderly matrix of retinal detectors are responsible for measuring. In dim light, these variations in light intensity on the retina are more distinct in eyes capable of capturing more light.

3.1 Sensitive compound eye designs

In insects, there are two major classes of compound eyes, the less sensitive apposition eyes and the more sensitive superposition eyes. All compound eyes, regardless of their design, are constructed of optical units called “ommatidia”, each consisting of an external corneal facet lens (or “facet” for short) that focuses light onto an underlying bundle of photoreceptors. Each of these photoreceptors possesses a microvillous photosensitive rod-like region known as a “rhabdomere”; this it contributes, together with the rhabdomeres of the ommatidium’s other photoreceptor cells, to a collective light-sensitive “rhabdom”. In apposition compound eyes (Fig. 2A), each ommatidium is isolated from its neighbours by a sleeve of light absorbing screening pigment, thus preventing light reaching the photoreceptors (i.e. their rhabdoms) from all but its own small facet lens. In most apposition eyes this lens is tiny, just a few tens of micrometres across. Not surprisingly, this tiny pupil generally restricts apposition eyes to insects and crustaceans living in bright habitats. But remarkable exceptions do exist, including nocturnal mosquitoes^{31,32} and the nocturnal tropical halictid bee *Megalopta genalis* that we will discuss below.

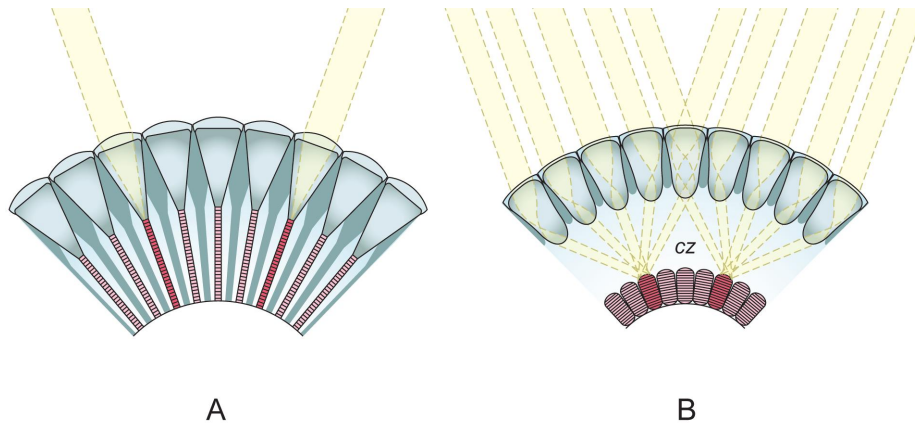


Figure 2. Compound eye designs. Each schematic cross-section through the eye shows nine ommatidia receiving light from two specific directions in visual space – the ommatidia are the optical building blocks of compound eyes. **A.** A focal apposition compound eye. Light reaches the photoreceptors exclusively from the small corneal facet lens located directly above. This eye design is typical of day-active insects. **B.** A refracting superposition compound eye. A large number of corneal facets and bullet-shaped crystalline cones collect and focus light – across the clear zone of the eye (*cz*) – towards single photoreceptors in the retina. Several hundred, or even thousands, of facets service a single photoreceptor. Not surprisingly, many nocturnal and deep-sea animals have refracting superposition eyes, and benefit from the significant improvement in sensitivity. Diagrams courtesy of Dan-Eric Nilsson.

It is, however, the other major class of compound eyes – the superposition eyes (Fig. 2B) – that are better known for their high sensitivity. In this eye design, typical of nocturnal insects and deep-sea crustaceans, the pigment sleeve is withdrawn, and a wide optically transparent area, the clear zone (*cz* in Fig. 2B), is interposed between the lenses and the retina. This 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 focussed onto a single photoreceptor. Unlike the crystalline cones of most apposition eyes, those of superposition eyes have evolved refractive index gradients (in refracting superposition eyes), or reflecting surfaces (in reflecting superposition eyes), or a combination of both (in parabolic superposition eyes). These optical modifications allow as many as 2000 lenses to collect light for a single photoreceptor (as in some nocturnal moths), and this represents a much larger pupil than the single facet lens of an apposition eye.

3.2 The sensitivities of nocturnal and diurnal compound eyes

What optical features of compound eyes maximise sensitivity to light? The answer to this question is embodied in the optical sensitivity (S) of an eye to an extended source of broad-spectrum light. S is given by^{29,30,72}:

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

where A is the diameter of the pupil, l the length of a photoreceptor, k is the peak absorption coefficient of the visual pigment, f is the focal length of the eye and d the diameter of the photoreceptor. This equation predicts that good sensitivity to an 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 ($kl/(2.3 + kl)$). Are these predictions reflected in the eyes of insects active in dim light? The large apertures of superposition eyes – which in some nocturnal moths can comprise thousands of facets – are clearly more sensitive than the single facet apertures of apposition eyes. Moreover, nocturnal rhabdoms are typically wide. In combination with a focal length that is frequently short relative to the width of the aperture (i.e. the “F-number” – f/A – of the eye is low, to borrow the camera term), these photoreceptors often achieve very wide receptive fields.

Many insects make excellent case studies for investigating the optical and neural adaptations that improve sensitivity to an extended source – very closely related species can be either nocturnal or diurnal. Many of these adaptations are well encapsulated in the expression for optical sensitivity (Eq. 1). This sensitivity can vary over several orders of magnitude, and shows very clearly how insects active in dim light, regardless of eye design, have a much greater optical sensitivity than those active in bright light (Table 1). We shall illustrate this point with two case studies, one for superposition eyes and one for apposition eyes.

Table 1: The optical sensitivities S of dark-adapted insect eyes (expanded from an original given in 30). S is given in units of $\mu\text{m}^2\text{sr}$, and the calculation neglects light loss due to reflection, scattering and absorption within the optical media of the eye. A = diameter of aperture [μm]; d and l = diameter and length of the rhabdom, respectively [μm]; f = focal length [μm]. NSup = nocturnal superposition eye; DSUp = diurnal superposition eye; DApp = diurnal apposition eye; NApp = nocturnal apposition eye. Notes: a = rhabdom length quoted as double the actual length due to the presence of a tapetum; b = values taken from frontal eye.

Species	Animal	Eye	A	d	f	l	S	Ref
<i>Deilephila</i>	hawkmoth	NSup	937 ^b	10.3	675	414 ^a	69.0	61
<i>Ephestia</i>	moth	NSup	340	8	170	110 ^a	38.4	9
<i>Onitis aygulus</i>	beetle	NSup	845	13	503	86	58.9	42
<i>Macroglossum</i>	hawkmoth	DSup	581 ^b	7.7	409	362 ^a	37.9	67
<i>Onitis belial</i>	beetle	DSup	309	6.5	338	32	1.9	42
<i>Megalopta</i>	sweat bee	NApp	36	8	97	350	2.7	70
<i>Apis</i>	honeybee	DApp	20	2	66	320	0.1	70

The highly visual hawkmoths (Sphingidae) – which hover in front of flowers and suck nectar on the wing – all have superposition eyes and a well-developed tapetum, irrespective of whether they are nocturnal or diurnal. The remarkable superposition eyes of the diurnal hummingbird hawkmoth *Macroglossum stellatarum* have diffraction-limited optics, and local retinal acute zones that are unique for the superposition design⁶⁷, and like honeybees, they also locate flowers using full trichromatic colour vision²⁶. Most hawkmoths, however, are active in dim light, such as the nocturnal elephant hawkmoth *Deilephila elpenor* (Fig. 3A). The superposition aperture in the frontal eye region of *Deilephila* contains 947 facets, considerably more than the 340 facets found in *Macroglossum*. With a focal length of 675 μm , and photoreceptors of width 10.3 μm ⁶¹, *Deilephila* achieves an optical sensitivity of 69 $\mu\text{m}^2\text{sr}$. In *Macroglossum*, on the other hand, the value is just over half of this – 38 $\mu\text{m}^2\text{sr}$ – a very high sensitivity for a diurnal eye (focal length 409 μm , rhabdom

diameter $7.7 \mu\text{m}^{67}$). Since both hawkmoths have a similar receptive field size ($d/f \approx 1^\circ$), the better sensitivity in *Deilephila* is entirely due to its larger superposition aperture, a sensitivity that is sufficient to allow *Deilephila* to see colour at night, the first animal known that can²⁷.

In the tropical jungles of the world, several remarkable groups of bees and wasps have become nocturnal, despite having apposition compound eyes. The advantages of becoming nocturnal are obvious. The nectar resources of nocturnally flowering plants can be exploited with relatively few competitors at a time of day when there is a lower risk of predation. Despite having apposition eyes, one of these insects – the Central American halictid bee *Megalopta genalis* (Fig. 3B) – can visually learn and use landmarks for homing at night, an impressive feat considering the size and design of its eyes (see below). *Megalopta* is a facultatively social bee, with females living in groups of up to 10 in long bored-out sticks^{3,23,74}. Each day, bees emerge twice from the nest to forage, each trip lasting up to about 35 minutes²⁸. The first

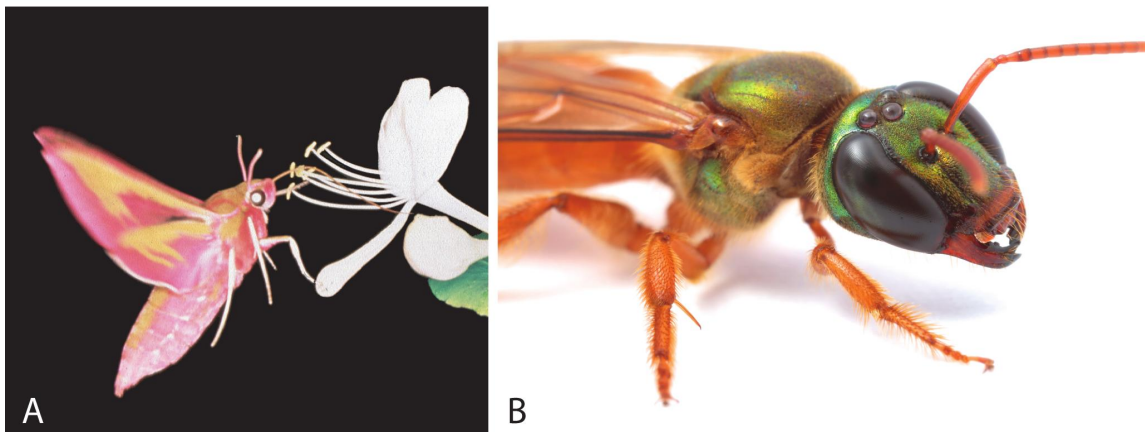


Figure 3. Nocturnal insects with sensitive vision. **A.** The European elephant hawkmoth *Deilephila elphenor*, whose sensitive apposition eyes allow it to distinguish colour at night. **B.** The central American halictid bee *Megalopta genalis*, whose sensitive apposition eyes allow them to forage at night by visually learning landmarks along the foraging route and around the nest entrance. Photographs with the kind permission of the photographers, Drs. Michael Pfaff (A) and Ajay Narendra (B).

foraging trip begins up to an hour before dawn, and the second ends about 40 minutes after sunset, when light levels under the thick rainforest canopy are similar to starlight levels above. This behaviour contrasts strongly with the European honeybee *Apis mellifera*, which is strictly day active. Not surprisingly, this contrast is also reflected in the structure and sensitivity of the eyes. Even though *Megalopta* has larger eyes and larger facets than in *Apis* (facets diameters up to $36 \mu\text{m}$, compared to just $20 \mu\text{m}$), the biggest difference between the two species lies in the size of the rhabdoms^{17,70}. These have a width of only $2 \mu\text{m}$ in *Apis*, but in *Megalopta* they reach an extraordinary $8 \mu\text{m}$, resulting in a receptive field of more than 7 times greater solid angular extent. These differences in receptive field and facet size allow *Megalopta* an optical sensitivity that is almost 30 times greater than in *Apis*: $2.7 \mu\text{m}^2 \text{sr}$ versus $0.1 \mu\text{m}^2 \text{sr}$. Even though this is a significant improvement over *Apis*, sensitivity is still very modest compared to *Deilephila* ($69 \mu\text{m}^2 \text{sr}$) or the nocturnal spider *Dinopis* ($101 \mu\text{m}^2 \text{sr}$). This comparison shows up the inherent limitations of the apposition design for vision in dim light, and begs the question – how can *Megalopta* nonetheless navigate using landmarks at night? The answer, we believe, lies in the brain, the topic to which we turn next.

4. SUMMATION IMPROVES VISUAL RELIABILITY IN DIM LIGHT

Even if the optical sensitivity of an eye is very high, it may still not be enough to allow each visual channel to collect sufficient light from a dim extended scene to guarantee reliable vision. There is however an additional strategy, residing in the neural circuits processing the incoming visual signal, which can potentially solve the problem. This involves neural summation of light in space and time^{33,53-55,64}. As light levels fall vision generally slows down. This increases the visual signal-to-noise ratio and improves contrast discrimination by suppressing photon noise at temporal frequencies that are too high to be reliably resolved¹⁹. For nocturnal insects, slow vision is achieved by either having slower photoreceptors³⁶, or by neurally integrating signals at a higher level in the visual system. But this only comes at a price: temporal summation can drastically degrade the perception of fast-moving objects, potentially disastrous for a fast-flying

nocturnal animal that needs to negotiate obstacles! Not surprisingly, temporal summation is more likely to be employed by slowly moving animals.

Summation of photons in space can also improve visual reliability. Instead of each visual channel collecting photons in isolation (as in bright light), the transition to dim light could activate specialised laterally spreading neurons which couple the channels together into groups (Fig. 4). Evidence of such neurons has been found in the first optic ganglion (lamina ganglionaris) of nocturnal cockroaches⁵⁰, fireflies⁴⁴ and hawkmoths⁶⁰, and these have been interpreted as an

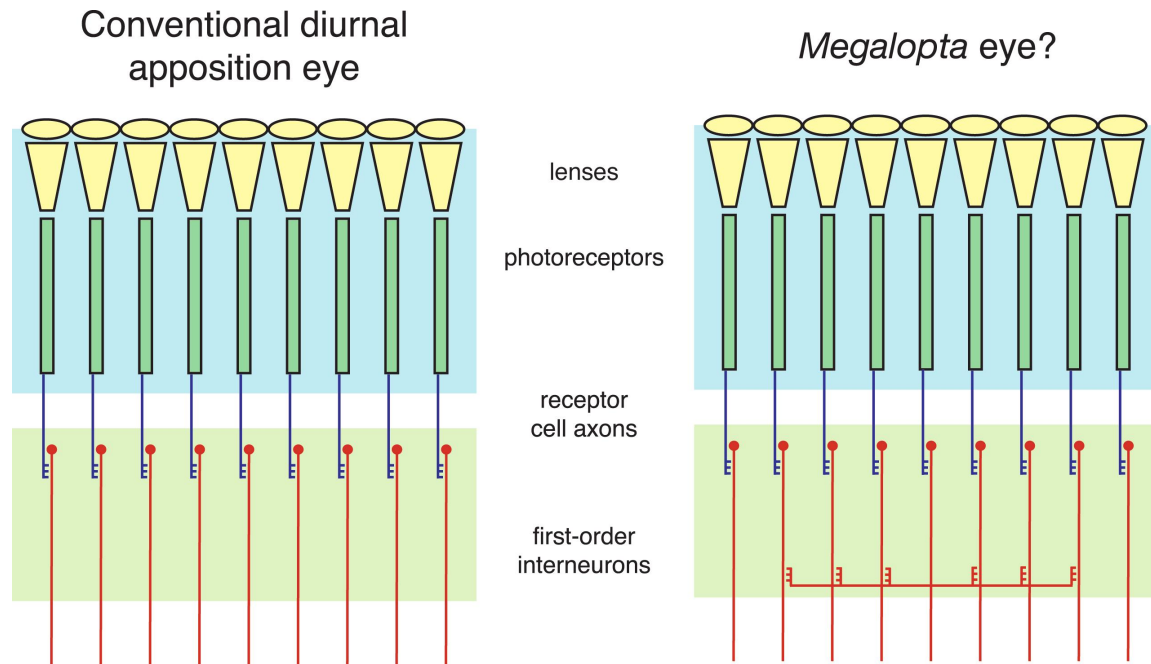


Figure 4. A possible mechanism for spatial summation in *Megalopta's* eye. In a conventional diurnal apposition eye (*left*), the photoreceptors of each ommatidium send their axons to the first optic ganglion, the lamina, where they synapse with lamina monopolar cells (LMCs). The LMCs then send the signal further to the next optic ganglion, the medulla. In bright light, summation is not necessary and the visual channels defined by each ommatidium can remain isolated from each other. In *Megalopta* (*right*), with ommatidia insufficiently sensitive to generate a reliable visual signal in dim light, spatial summation of ommatidial signals is a viable strategy for improving sensitivity. One possibility is that LMCs with modified morphologies provide the neural wiring that couples neighbouring visual channels together. In this scenario, each LMC branches to a group of neighbouring lamina cartridges, each cartridge having cells that process information arriving from a single overlying ommatidium. Thus, if properly arranged, each LMC could connect a group of ommatidia together, and provided that the necessary circuitry exists, this might allow spatial summation. From 70.

adaptation for spatial summation³³. The nocturnal bee *Megalopta genalis* also appears to have such neurons¹⁸ (Fig. 5), as does the nocturnal hawkmoth *Deilephila elpenor*⁶¹. Each summed group – themselves now defining the channels – could collect considerably more photons over a much wider visual angle. The greatly enlarged receptive fields produced by this spatial summation result in a simultaneous and unavoidable loss of spatial resolution. Despite being much brighter, the image becomes necessarily coarser.

Even though summation compromises spatial and temporal resolution, the gains in photon catch are so enormous that vision in dim light can be greatly improved. This is especially true in small eyes like those of arthropods. If a locust, an insect with apposition eyes, employs summation optimally, it has the potential to see reliably at light intensities up to 100,000 times dimmer than those in which they would normally become blind⁶⁴. Similar conclusions can also be drawn for nocturnal bees⁶³. Summation has recently been detected in the responses of wide-field motion-sensitive neurons in the optic lobe of the nocturnal hawkmoth *Deilephila elpenor*, where they maximise the visibility of visual contrasts over four decades of light intensity and allow these moths to see at light intensities 100 times dimmer than they otherwise would have⁶².

We now believe that summation strategies like these – together with eye designs of high optical sensitivity – are able to explain the impressive vision found in many nocturnal insects, including their ability to visually avoid obstacles during

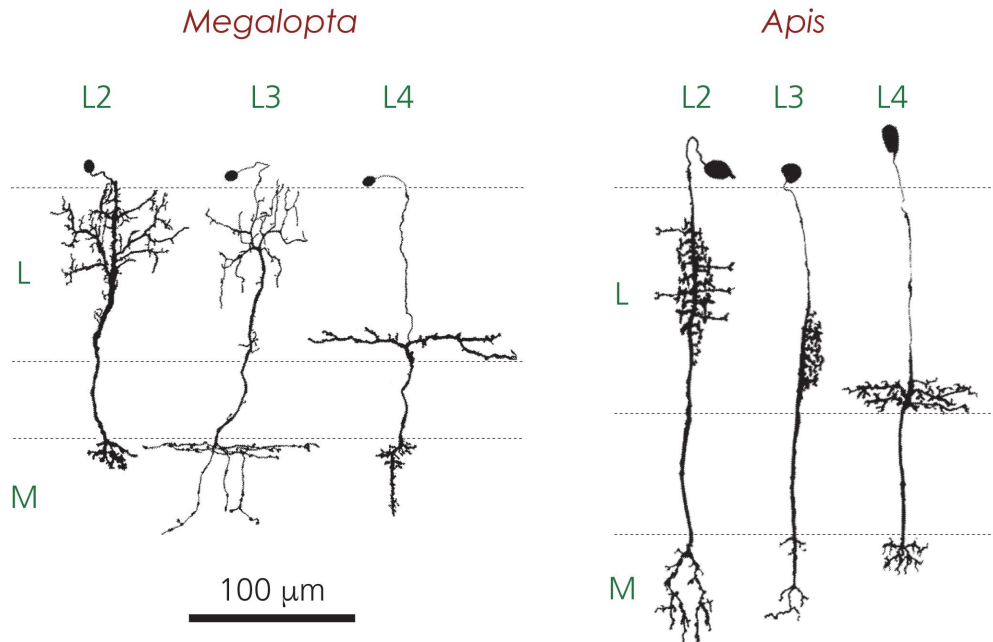


Figure 5. The possible neural substrate for spatial summation in nocturnal bees. Compared to the worker honeybee *Apis mellifera* (right), the horizontal branches of the first-order L-fibres (types L2, L3 and L4) in the nocturnal *Megalopta genalis* female (left) connect to a much larger number of lamina cartridges, suggesting a possible role in spatial summation. L = lamina, M = medulla. Reconstructions from Golgi-stained frontal sections. Adapted from 18 and 49.

flight, discover and pursue prey, escape predators or orient towards a goal⁶³. Indeed, our recent research has revealed that nocturnal insects can see very well, being able to distinguish colours^{27,57}, perceive optic flow^{22,62} and use it to control flight^{4,5}, home using learned landmarks^{56,70} and to navigate by the dim celestial pattern of polarisation formed around the moon^{10,24} or by using the Milky Way¹¹.

If these summation strategies provide nocturnal insects with such impressive visual abilities, can the same strategies even improve the quality of video sequences collected in very dim light? The answer it turns out is yes, as we discuss further in the next section.

5. A BIO-INSPIRED NIGHT VISION ALGORITHM

Despite their tiny and relatively insensitive compound eyes, many insects have successfully conquered the nocturnal niche, and taken advantage of the benefits that this niche provides for foraging and the avoidance of enemies, feats that require reliable vision in dim light. As we have discussed above, this reliability is the result of the combined action of a variety of adaptations within the eyes and visual system. Greatly enlarged corneal facet lenses and rhabdoms, and slow photoreceptors with high contrast gain, ensure that visual signal strength is maximal as it leaves the eye and travels to the brain. Visual signals are then spatially and temporally summed, resulting in an enhanced signal and reduced noise. The greatly improved signal-to-noise ratio that this strategy affords, whilst sacrificing spatial and temporal resolution would ensure that nocturnal visual reliability is maximised for the slower and coarser features of the world.

Like nocturnal eyes, artificial imaging systems operating in dim light also suffer from limitations in detection reliability. And like nocturnal eyes, these systems should benefit from the same strategies for improving reliability. Thus, our idea was to take visual solutions resulting from countless millions of years of biological evolution and to incorporate them in a computer algorithm that radically improves the quality of video sequences collected in dim light.

The algorithm mimics several of the key steps of nocturnal visual processing^{40,41,73} (Fig. 6). The first step involves an amplification of the dim image sequence, in a manner not unlike the amplification (or gain) in photoreceptor response amplitude we discussed above (see Fig. 1A). The downside of this amplification is that it amplifies both the signal and

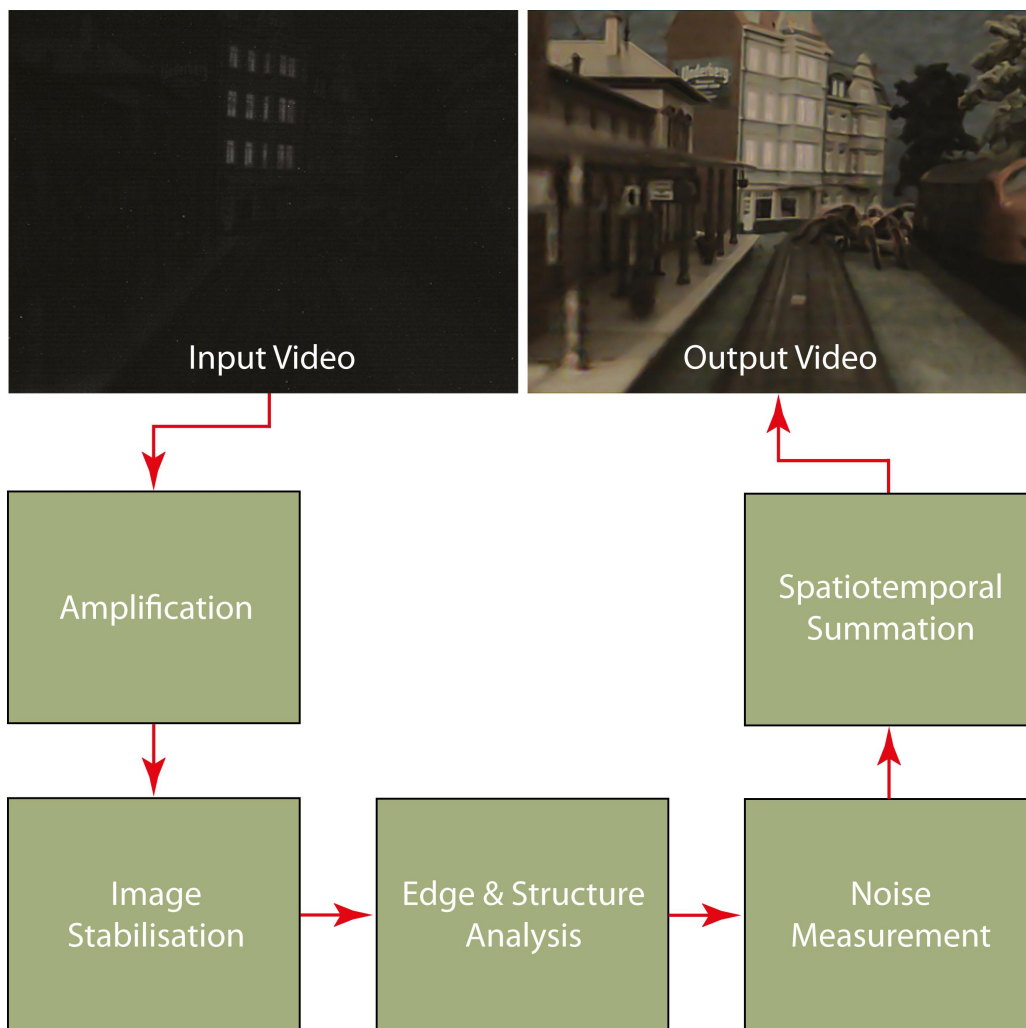


Figure 6. The main steps in the night vision algorithm. The algorithm consists of a contrast enhancement step (amplification) and a noise reduction step based on optimal spatial and temporal summation. It adapts automatically to the local intensity distribution and preserves as much of the structure in the scene as possible. It also adapts to the local noise level, which depends on the ambient light level. Further, it sharpens edges in the output at appropriate places to prevent over-smoothing (via a lateral inhibition algorithm not dissimilar to lateral inhibition in the retina). A still frame (*upper left*) from a dim input video sequence can be compared to a still frame (*upper right*) from the significantly enhanced output video sequence that resulted from processing with the algorithm.

the noise, and thus does not improve the signal-to-noise ratio *per se*. To get around this, another crucial step in the algorithm involves spatial and temporal summation – this results in signal information (which is correlated between frames in the video sequence) being summed and reinforced and noise (which is uncorrelated) being averaged out. The result is a dramatic improvement in the signal-to-noise ratio. Moreover, because this summation is done separately (and in parallel) for the R, G and B channels, the result of this summation preserves colour information (as is evident in the output video frame in Fig. 6). A similar separate and parallel summation of colour channels in nocturnal animals is likely the reason that many are able to see colour at night²⁷.

A disadvantage of even radial spatial summation is that it doesn't preserve edges and boundaries, the contrast elements of visual scenes that define and localise objects. These edges and boundaries exist between neighbouring areas of the visual

scene that differ in intensity, colour or texture, and spatial summation has the potential to blur these and thus make the visual scene less distinct. Likewise, temporal summation, if done indiscriminately, has the potential to obscure the correlated motion of an object moving in a particular direction from one film frame to the next (or the correlated motion of the entire scene if the movement is due to the movement of the camera rather than of something in the scene). To deal with this problem, the algorithm performs a real-time structure tensor analysis of the intensity structure (in space and time) of the scene contained within the film and constructs local smoothing kernels for each location in the film frame. These kernels adapt to the local spatiotemporal intensity structure, being large (i.e. summing more) in directions where there are no spatiotemporal edges, and being small (i.e. summing less) in directions where there are strong edges. Moreover, because dimmer video sequences require greater extents of summation, the volumes of these kernels become larger for videos filmed at lower light levels. By measuring the magnitude of the average noise in the film frame, the algorithm is able to determine the light level in which the video was made and adjust the kernel accordingly, adapting to light intensity in an automatic manner, in much the same way an animal visual system would do it.

By mimicking the way nocturnal visual systems process information, the night-vision algorithm dramatically restores the quality of video sequences recorded in very dim light (for a deeper and more formal description of the algorithm, please see 73). Not only are spatial and temporal details – obscured by noise in the original video – restored, colour information is preserved. Our hypothesis that spatial and temporal summation is a crucial strategy in nocturnal visual processing is very well supported by the algorithm – the output of the algorithm (Fig. 6) suggests that summation can greatly enhance nocturnal visual performance.

6. CONCLUSIONS

Insects have conquered the terrestrial world's dimmest habitats, and they have done so with some of the most sensitive eyes found in the animal kingdom. This sensitivity – coupled to neural summation mechanisms at higher levels in the optic lobes – has allowed nocturnal insects to experience the world in much the same way as their day-active relatives. They can see colour and negotiate dimly illuminated obstacles during flight. They can also navigate using learned terrestrial landmarks, the constellations of stars or the dim pattern of polarised light formed around the moon. In other words, nocturnal insects have evolved sufficient visual sensitivity to exploit various sources of visual information in their never-ceasing struggle to survive and reproduce. The strategies they use – and the benefits to visual reliability they bestow – are directly applicable to algorithms for processing video sequences captured in very dim light.

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