Insect photoreceptor adaptations to night vision

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Abstract

Night vision is ultimately about extracting information from a noisy visual input. Several species of nocturnal insects exhibit complex visually guided behaviour in conditions where most animals are practically blind. The compound eyes of nocturnal insects produce strong responses to single photons and process them into meaningful neural signals, which are amplified by specialized neuroanatomical structures. While a lot is known about the light responses and the anatomical structures that promote pooling of responses to increase sensitivity, there is still a dearth of knowledge on the physiology of night vision.

Retinal photoreceptors form the first bottleneck for the transfer of visual information. In this review, we cover the basics of what is known about physiological adaptations of insect photoreceptors for low-light vision. We will also discuss major enigmas of some of the functional properties of nocturnal photoreceptors, and describe recent advances in methodologies that may help to solve them and broaden the field of insect vision research to new model animals.

Introduction

Visual guidance of behaviour is challenging when photons, the elementary particles of light, are scarce. To produce a reliable representation of the surroundings, the visual system must (1) ensure absorption of a sufficient number of photons into a photoreceptor; (2) house photoreceptors that efficiently convert each photon absorption into a neural signal; and (3) process these signals appropriately. Insects are a numerous and diverse class of arthropods that have evolved to occupy ecological niches from the brightest to the darkest. The accessibility and comparative simplicity of the insect visual system make it an attractive model for studying visual adaptations, including adaptations to vision in dim light.

The main photoreceptive organ of insects is the compound eye. As the name implies, it consists of more or less identical repeating optical units (ommatidia) that contain the photoreceptor cells. The two compound eye types, apposition and superposition, collect light in different ways (figure 1a). In an apposition eye, light is guided through optically isolated ommatidial lenses onto the light-sensitive structures, rhabdoms, lying immediately underneath each lens. This arrangement is thought to favour acuity over sensitivity, making it well-suited for vision in bright light. In contrast, a dark-adapted superposition eye collects light from a wider angle through multiple lenses onto each rhabdom. As a result the number of photons reaching each photoreceptor in a superposition eye can be hundreds of times greater than in an apposition eye [1], albeit at the expense of spatial resolution. Therefore, not surprisingly, superposition eyes are typically found among nocturnal insects. Outstanding examples of nocturnal behaviour with superposition vision include colour discrimination and colour constancy in the hawkmoth *Deilephila elpenor* [2] and orientation to the night sky polarisation pattern and the Milky way [3] by nocturnal dung beetles. Remarkably, against the seemingly apparent logic, also various insects with apposition eyes have adapted to life in darkness. Some hymenopterans and bugs use canopy cues, landmarks, and skylight polarisation for navigation [1,4,5]. The shade response of the American cockroach, *Periplaneta americana*, persists down to at least 0.01 lux [6] and its optomotor turning response to 0.005 lux [7].

The lowest light intensity where a given visually guided behaviour can successfully take place is known as the behavioural threshold. Visual behaviour in dim light can be linked to photoreceptor physiology by determining both the behavioural threshold and the photon absorption rate in a photoreceptor, either by recording intracellularly [7,8] or by estimating it from the photoreceptor optics [9,10]. While the photon absorption rate in *Periplaneta* photoreceptors is 0.1 photons/s at the behavioural threshold, it is 17 times higher in the fly, 50 times higher in the nocturnal bee *Megalopta genalis* and 4400 times higher in the hawkmoth *Deilephila* [1,2,7,8]. This does not mean that these insects need brighter ambient light than the cockroach for seeing or behaviour. *Megalopta*, for example, has its behavioural threshold at one tenth of the absolute light intensity of *Periplaneta*'s threshold [1,7], yet each of its photoreceptors is able to capture 5 photons/s. For flying insects the threshold probably is at higher absorption rates than for walking ones, because flight steering requires more visual information and thus more photons/s than terrestrial locomotion. The differences also emphasize how the moth, with its superposition eyes, is able to capture hundreds of photons/s at an intensity where diurnal flies can no longer be active.

Megalopta and *Periplaneta* have apposition eyes, yet they both are nocturnal, and the bee is even an active flyer. In fact, *Megalopta* retains its flight and landing performance under starlight intensities [1]. Although the apposition eye is traditionally considered as the day active eye type, structural modifications, such as increased lens and rhabdom diameter,

may facilitate its operation at low light conditions. Moreover, various neuroanatomical and functional adaptations, resulting in spatial and temporal summation within the visual pathway from photoreceptors to the brain, can improve information acquisition from unreliable visual inputs. Spatial summation is preferred when temporal resolution cannot be sacrificed, such as during flight and landing in bees [11,12]. Slow tracking of small moving targets in darkness generally relies on temporal summation, as in shore crabs [13]. The hawkmoth visual system likely uses both spatial and temporal summation for the demanding task of hovering at night [14].

A major site of spatial (neural) summation is probably the 1st optic ganglion, lamina, where many insects have a retinotopic array of cartridges corresponding to individual ommatidia in the retina. The dendrites of 2nd order large monopolar cells connect lamina cartridges laterally in nocturnal fireflies, bees, and moths [15–17], and photoreceptor axon bundles in the cockroach [18]. However, the first steps in processing visual inputs occur in the photoreceptors that are responsible for the conversion of light information into relevant neural representations. Therefore, reliable vision in dim light does not come down to having appropriate optical and anatomical adaptations only, but also crucially relies on the ability of photoreceptors to transduce photon absorptions efficiently. In this review, we will highlight the known functional properties that can facilitate insect photoreceptors to succeed in this task, and provide examples from nocturnal insects with apposition eyes.

Light responses in microvillar photoreceptors

The compound eye surface of an insect consists of small corneal lenses belonging to ommatidia, the optical units of a compound eye (figure 1a). Additionally, an ommatidium consists of a crystalline cone, pigment cells surrounding the ommatidium, and 8-9 photoreceptors. Each photoreceptor has a soma and a brush-like rhabdomere made of thousands of bristle-like microvilli, hence insect photoreceptors are often referred to as *microvillar* or *rhabdomeric*. Photoreceptors within an ommatidium are usually organized in a circle, with rhabdomeres facing each other and forming a rod-like structure known as the rhabdom.

When a photon of visible light enters the rhabdom, it may get absorbed by the visual pigment rhodopsin embedded in the microvillar membrane. This triggers the phototransduction cascade, a chain of biochemical reactions leading to the generation of a membrane voltage response known as a quantum bump. Quantum bumps were first described in the lateral compound eye of the horseshoe crab *Limulus* by Yeandle [19]. Later on, together with Fuortes, he confirmed that stimulation of dark-adapted *Limulus* photoreceptors with steady dim light or short flashes produce discrete voltage bumps with Poisson-distributed timing and occurrence [20]. Similar findings in locust eyes confirmed that these single photon absorption events occur also in insects [21].

The stochastic nature of photon arrival and absorption in the photoreceptor causes variance or noise of $\sqrt{N}$ photons for every N photons absorbed. This *shot noise* increases relative to the signal with decreasing photon availability, until photoreceptors can no longer detect contrast [22]. Another source of noise is the inability of the photoreceptors to produce identical responses to sequentially absorbed photons. This *transducer noise*, i.e. variation in phototransduction, manifests itself as differences in bump latency, duration, and amplitude. Fuortes and Yeandle also reported bumps appearing in total darkness. This *dark noise*, arising from the spontaneous (thermal) activation of phototransduction components, can severely limit vision. However, insect eyes generally have very little dark noise. For example, locust photoreceptors show a dark noise rate of only 10/h [21]. In *Drosophila*, the dark noise rate is clearly higher (~2/s), but unlikely to limit visual capabilities due to the fly's diurnal lifestyle [23].

Quantum bumps in nocturnal photoreceptors tend to be much larger than in diurnal photoreceptors. An example of this is provided by the tropical sweat bees *Megalopta* and *Lasioglossum* (figure 1d). They have apposition eyes and share a similar lifestyle but the former is nocturnal producing large quantum bumps, while the latter is diurnal with small quantum bumps [24]. Importantly, similar findings are reported from nocturnal and diurnal *Onitis* dung beetles, both equipped with superposition eyes [25]. Other nocturnal insects with large bumps include the cockroach [26,27], locust [21], carpenter ant [28], crane fly [29] and stick insect [30]. Microvillar photoreceptors of spiders *Dinopis* [31] and *Cupiennius* [32] also produce very conspicuous bumps. The reason for having larger quantum bumps may be the need to ensure sufficiently undistorted delivery of single photon signals to the optic lobes. With increasing light intensity more photons are absorbed and thus more quantum bumps start to appear. Eventually quantum bumps become so numerous that they start to overlap, fuse and build on each other to form a graded light response. Consequently, the size and shape of a graded light response will depend on the size and shape of the quantum bumps. Following this logic, having large quantum bumps may not be beneficial for a diurnal insect as its photoreceptors could become more easily blinded by bright light.

Stimulating a photoreceptor with incremental series of light flashes enables recording an intensity-response relation. For dim light flashes the relation is linear, but with brighter flashes compressive nonlinearities set in. In the linear range it is possible to record so-called impulse responses resulting from the superposition of a small number of quantum bumps. Since impulse response shape reflects photoreceptor dynamics, they have been commonly used for comparative studies. Like quantum bumps, impulse responses are typically slower in nocturnal than in diurnal species [28,33]. With increasing light intensity nonlinearities caused by photo- and electrochemical adaptation mechanisms gradually start to have more and more effect on the intensity-response relation. These nonlinearities allow a photoreceptor to compress a range of light intensities, spanning from starlight to daylight, into its narrow operating range (~60 mV).

Photoreceptor dynamics, including light adaptation, can be studied using longer light pulses with varying intensities (figure 1e). In a dark-adapted photoreceptor a dim light pulse produces a rectangular graded light response with superimposed bump noise on top of it. With higher intensities the noise subsides and the graded response is characterized by a fast initial transient followed by a plateau with much reduced amplitude. This peak-to-plateau transition stems from the photoreceptor light adaptation mechanisms. Interestingly, a seminal comparative study on dipteran species by Laughlin and Weckström showed that nocturnal flies not only had slower responses than their diurnal counterparts, but also poorer ability to adapt to increasing light levels [29].

These differences in quantum bumps and macroscopic responses raise two essential questions: (1) what mechanisms underlie the differences and (2) why are they different? The answer to the first question has two parts, phototransduction and electrical properties of the photoreceptor membrane.

Phototransduction in the diurnal *Drosophila*

The starting point of phototransduction is the visual pigment rhodopsin embedded in the microvillar membrane. Photon absorption and thus light sensitivity depend on the concentration of these molecules in the rhabdomere. Unsurprisingly, nocturnal insects have developed means to adjust the expression of rhodopsins with suitable spectral sensitivities [34] and translocate them in and out of the rhabdomere according to the prevailing light levels [35]. Despite investigation in many insects, everything downstream of rhodopsin activation by light has relied heavily on research on the photoreceptors of *Drosophila*. Ever since patch-clamping could be combined with molecular genetic tools [36], *Drosophila* phototransduction has been the single most important model representing all insects [37]. It was also the visually severely impaired *Drosophila transient receptor potential* (*trp*) mutant [38,39] that led to finding a whole superfamily of TRP ion channels.

When a rhodopsin (R) absorbs a photon, it isomerizes into metarhodopsin (M; figure 1bi,ci). M causes the heterotrimeric G_q protein complex to release its alpha subunit ($G_q\alpha$), which in turn activates the phospholipase C (PLC). The active PLC hydrolyses a phospholipid phosphatidylinositol-4,5-bisphosphate (PIP_2) into a proton [40], a hydrophilic inositol-1,4,5-trisphosphate (IP_3) and a hydrophobic diacylglycerol (DAG). The released proton [40] and the mechanical contractions caused by PIP_2 hydrolysis [41] result in the opening of ~15 TRP and TRP-like (TRPL) channels and a flow of cations into the microvillus, generating an ionic current responsible for the generation of a quantum bump, i.e. the bump current [42,43]. The majority of the ~10 pA [43] bump current is mediated by relatively Ca^{2+}-selective TRP channels [44], which are 10 times more abundant in the photoreceptors than the non-selective TRPL [45].

Bump current generation is a fast process, characterized by a 20-100 ms latency and ~20 ms bump half-width [43]. In bright light, these kinetics become even faster and bump amplitudes attenuate minimizing transducer noise [46]. The rapid kinetics are enabled by the scaffolding protein INAD, binding together protein kinase C (PKC), PLC, and TRP channels into a signalling complex [47], and the tight compartmentalization of the whole phototransduction machinery into single microvilli [37]. This has two major advantages. Firstly, the tight compartmentalization minimises diffusional delays. Secondly, Ca^{2+} influx via a single open TRP channel can quickly increase microvillar Ca^{2+} levels [48] to facilitate the rapid opening of the remaining TRP/TRPL channels [49]. Also, IP_3-induced Ca^{2+} release (IP_3-Ca^{2+}) from submicrovillar cisternae (SMC) of the endoplasmic reticulum, which are closely associated to microvilli, may be essential for sensitizing PLC for efficient channel activation [50]. Ca^{2+} build-up in the microvillar lumen provides negative feedback by stimulating Ca^{2+}-dependent mechanisms that inactivate the bump current [51–54]. After the bump current has inactivated, the microvillus remains refractory for 50-150 ms before another bump can be initiated [53], possibly due to the high Ca^{2+} concentration and the reversible dissociation of INAD from PLC and TRP [55]. Responsiveness is recovered after excess Ca^{2+} has been extruded and INAD reassociates with TRP and PLC. Since the differences in the size of bump currents are relatively small [43] and derive from differences between microvilli, the major determinants of the transducer noise are the latency and refractory period. Presumably, the variable latency is caused by diffusion-limited reactions of M and PLC with G_q [37], whose spontaneous activity creates most of the dark noise [56]. Although the refractory period varies, possibly mostly due to INAD complex reassociation time, it might also prevent more severe transducer noise by providing time for recovery processes, such as the replenishment of the PIP_2 reserve [37].

Phototransduction and light-induced currents in nocturnal insects

Recently, through the successful use of the patch-clamp technique on isolated photoreceptors, new insect species with various lifestyles, including nocturnal, have entered into phototransduction research [57]. Bump currents (i.e. the ionic currents underlying the generation of quantum bumps) have been statistically analysed in the field cricket *Gryllus bimaculatus* [58] and the cockroach *Periplaneta americana* [59], both species having apposition eyes and being active in dim light. Compared to *Drosophila*, both cricket and cockroach photoreceptors produce bump currents with ~4-fold higher amplitudes and slower waveforms [43,58,59]. The bump currents of the cricket have also clearly longer latencies, but in the cockroach the latencies and their dispersion are surprisingly close to those in *Drosophila*, suggesting that the phototransduction processes prior to channel opening are similar. The large bump currents are in part responsible for large quantum bumps (i.e. large voltage bumps), facilitating the delivery of messages from absorbed photons to the brain. Although definite evidence is lacking, there are indications that the higher current amplification may be due to higher

expression of TRPL channels. The TRPL channels of *Drosophila* are 10-fold less Ca^{2+}-selective, produce larger currents, and have slower kinetics than TRP [43,44]. Proportionally higher expression of TRPL might also explain some of the Ca^{2+}-dependent properties of the currents in the cockroach [59]. This theory is supported by a study where RNA interference (RNAi) was successfully used to prevent the expression of TRP and TRPL homologues in the photoreceptors of the cockroach [60]. According to this study TRPL is more abundant than TRP in the cockroach retina, and responsible for 75 % of the electroretinographic response amplitude. In *Drosophila*, mutants lacking TRPL do not manifest dramatic changes in responses to bright light, but have trouble adapting to low illumination levels [61]. Also, TRPL channels translocate from the rhabdomere into the cell body in response to prolonged light stimulation [62,63]. All these observations point out to a more significant role for the TRPL in dim light photoreception.

In response to a long, bright light pulse the photoreceptors of *Drosophila* and the cockroach show a conspicuous peak-to-plateau transition, with similar waveform to a corresponding graded voltage response [27,37,59]. When a long light pulse is presented to a *Drosophila trp* mutant the light-induced current (LIC) decays to baseline after the initial transient [39]. Any shortly following light stimulation fails to elicit a new response. This sensitivity loss is due to PIP_2 depletion resulting from the lack of TRP-mediated Ca^{2+} influx necessary for PLC inhibition [51]. Interestingly, a minority of cockroach photoreceptors also shows such transient hyper-adapting behaviour [27,59]. The *trp* phenotype can also be induced by omitting extracellular Ca^{2+} in *Drosophila* [39]. However, this phenotype does not appear in normally responding photoreceptors of the cockroach. When Ca^{2+} is omitted, cockroach LIC shows slow kinetics, large amplitude and no apparent light adaptation, but also no rundown. Only after intracellular Ca^{2+} is chelated, cockroach LIC decays to the baseline while the light is still on [59]. This implies that cockroach photoreceptors might use an intracellular Ca^{2+} source during light responses. If indeed cockroach LIC is largely mediated by TRPL, additional Ca^{2+} sources might be necessary for response amplification and inactivation. The most plausible candidate for the Ca^{2+} release are the SMCs, which undergo light-dependent translocation together with mitochondria and screening pigments [64,65]. In dark-adapted photoreceptors SMCs are situated at the base of rhabdomeres, forming a palisade that helps to gather light more efficiently. Among arthropods, at least the ventral nerve photoreceptors of *Limulus* and the photoreceptors of the honeybee are known to rely on IP_3-Ca^{2+} from SMCs [66,67], possibly due to the lack of sufficient Ca^{2+} influx via light-gated channels in the former. Since a quantum bump in *Limulus* is formed by the activation of several microvilli, and perhaps partially by the widespread Ca^{2+} after IP_3-Ca^{2+} [66], it is possible that the larger bumps in photoreceptors of nocturnal insects might derive from more than one activated microvillus. It should be noted, however, that since the visual function of the extraocular ventral photoreceptors of *Limulus* is not known, and since the honeybee is a diurnal species, the IP_3-Ca^{2+} mechanism might not be an exclusive specialization of nocturnal photoreceptors.

Electrical properties of the photoreceptor membrane

The conductance created by open TRP/TRPL channels creates a LIC, which changes the photoreceptor membrane potential, resulting in a graded response. LIC amplitude depends on the driving force (i.e. the difference between membrane potential and the LIC reversal potential) and TRP/TRPL conductance. The driving force is reduced during depolarization as membrane voltage approaches the LIC reversal potential, the upper limit of the photoreceptor's operating range, resulting in an effect called self-shunting. Together with other means of light adaptation self-shunting plays an important role in compressing a wide range of light intensities into the narrow functional range of a photoreceptor.

The conversion from conductance to voltage response is governed by the *membrane impedance*, which defines how much amplification a signal receives per temporal frequency [68]. Membrane impedance is formed by capacitive and resistive properties of the photoreceptor membrane, resulting from the lipid bilayer and the ion channel proteins embedded in it, respectively (figure 1 bii & cii). Input resistance (R_{in}) results from *passive resistance* caused by persistently open leak channels, and *active resistance* due to ion channels whose open probability is controlled by a biophysical signal, e.g. chemical ligand or the membrane potential. Together R_{in} and the membrane capacitance (C_m) form a lowpass or bandpass impedance function that filters the phototransduction current signal [69]. The impedance filter is characterized by the upper cutoff frequency $f_c = 1/(2\pi\tau)$, where τ is the membrane time constant $\tau = R_{in} \cdot C_m$, which describes how fast the transmembrane current is converted into a membrane voltage change. By modifying either R_{in} or C_m, τ can be regulated to allow faster voltage changes or to limit the responses to slow signals. C_m is relatively constant, although some variation may occur due to shedding of microvillar membrane [70]. Conversely, R_{in} can be dynamically adjusted by opening and closing ion channels, regulating their expression [71], or by modulating their open probability profile [72].

C_m and R_{in} in nocturnal photoreceptors are large compared to diurnal species (figure 1bii,cii) [29]. The former is partly explained by the larger rhabdom size (see longer microvilli in figure 1c than in 1b) [10,57], and the latter by reduced non-selective leak conductance and smaller voltage-dependent conductance near the dark-resting potential [73]. The large τ and small f_c promote temporal summation, a common property of nocturnal photoreceptors, since the membrane filters out faster signals and amplifies slow ones. Consequently, the photoreceptors will have improved sensitivity for low light signals, but poor temporal resolution.

Kv conductances

Voltage-gated potassium channels, Kv channels, are considered the most important modulators of light-independent membrane impedance in insect photoreceptors [74]. Kv channels opened during the light-induced depolarization can have various functions, such as prevention of voltage response saturation by decreasing the impedance, decreasing the membrane time constant to allow propagation of faster signals, or fine-tuning the time- and voltage-dependent amplification to optimize information processing of the photoresponse [75]. Based on the voltage-dependence of opening and closing kinetics, Kv channels in insect photoreceptors can be categorized roughly into two types: sustained *delayed-rectifier* and transient *A-type* channels.

Kv channels in *Drosophila* photoreceptors were the first to be described in detail [76]. They express at least four Kv channel types contributing to voltage light response modulation. The largest effects come from Shaker, a fast activating and inactivating transient conductance, and Shab, a slowly activating delayed rectifier type conductance. Shaker improves information processing by selectively amplifying graded voltage responses and distributing the responses more effectively into the physiological voltage range [75]. Shab, typically for sustained conductances, prevents saturation during light-induced depolarization and accelerates the photoreceptor temporal properties [77–79].

Since different Kv channels modulate the electrical light response, the expression of specific channels in species with different visual ecologies has received special attention. In *Diptera*, diurnal species express a dominant sustained conductance and crepuscular species a transient Kv conductance [29]. In the locust, the Kv conductance profile follows a circadian rhythm induced by serotonin modulation, with a sustained conductance dominating during the day and a transient conductance during the night [71]. In flies, the Shab delayed-rectifier is up-regulated by light through PIP_2 hydrolysis [80], and serotonin modulates the voltage-dependence of Shab and Shaker conductances [72]. However, fly and locust studies give a simplified view on the relationship between the circadian activity and expressed Kv conductances, as shown by Frolov *et al*. [73]. Their comparative study of 15 species showed that while the fast flying diurnal insects as a rule express a dominant sustained Kv conductance, the nocturnal or crepuscular species may in fact express either a sustained, or both sustained and transient conductance. Moreover, the transient Kv conductances in the nocturnal species do not seem to be active at the physiological voltage levels of light responses, leaving open the question about the significance of such conductances to photoreceptor function. Typecasting insects to specific circadian lifestyles based on Kv conductances is thus difficult and more comparative studies are needed in order to make sense of the Kv channel palette in insect photoreceptors.

Signalling and information transfer in nocturnal photoreceptors

Together the phototransduction and the electrochemical properties of the membrane define the signalling properties of photoreceptors. A useful tool for comparing signalling differences between diurnal and nocturnal photoreceptors is the photoreceptor transfer function. The simplest way is to derive the transfer function from impulse responses by Fourier transformation. Another method is recording responses to a light contrast stimulus modulated by Gaussian-distributed white noise. This provides two temporal frequency-dependent measures, which together constitute the transfer function: *contrast gain* describing the size of a photoreceptor voltage response per unit contrast at a given frequency, and *phase function* describing the phase difference between the stimulus and response. Since the white-noise method allows the analysis of the frequency dependence of the signal-to-noise ratio (SNR) it can be used to estimate photoreceptor information transfer rates, i.e. the number of bits processed per second.

Once again the closely related tropical bees, *Megalopta* and *Lasioglossum*, may serve as an example of differences in diurnal and nocturnal photoreceptor signalling [25]. *Megalopta* photoreceptors discriminate contrasts in dim light better due to higher contrast gain and a relatively narrow signalling bandwidth, which effectively filters out high frequency noise, but also reduces temporal resolution (figure 1f). In a bright background, *Megalopta* photoreceptors retain their lowpass filtering properties, while *Lasioglossum* photoreceptors assume bandpass properties, improving temporal discrimination (figure 1g). However, when information rates are compared, *Lasioglossum* triumphs at all background light levels due to the consistently poorer SNR and bandwidth in *Megalopta* photoreceptors. Only after accounting for the more sensitive optics, has *Megalopta* higher information rates than *Lasioglossum* in the dimmest backgrounds. Similar lowpass filtering (temporal summations) and relatively poor information transfer properties have been reported also in other dark-active insects [27,29,58,81]. In conclusion, nocturnal insects trade temporal (and spatial) resolving power to allow photoreceptors to distinguish meaningful intensity differences from an environment where photons are scarce.

Peculiar properties in cockroach photoreceptors underlie adaptation to dim light

Compared to diurnal and also other studied nocturnal species, the photoreceptors of the cockroach *Periplaneta* have some peculiar features. Light responses adapt with greatly varying kinetics and magnitude [26]. At the extreme, cockroach photoreceptors may enter a dark-adapted-like state within seconds after a prolonged bright light exposure, with the membrane potential returning close to the dark-resting potential value and discrete bumps forming the response despite the bright illumination (the *trp* phenotype).

Contrary to most of the studied insects where light adaptation mechanisms improve photoreceptor performance with increasing light intensity, cockroach photoreceptors do not generate significantly faster or more accurate responses at intensities above ca. 1000 absorbed photons/s [27]. Failure of adaptation to brighter backgrounds has also been observed in nocturnal flies and bees, although to somewhat lesser degrees than in cockroach [24,29]. A possible explanation for the saturation of the performance at modest light levels can be given using the stochastic sampling model by Song et al. [82], and by assuming that in comparison to *Drosophila* photoreceptors, cockroach photoreceptors have either fewer microvilli, longer refractory periods, or both. Activation of several microvilli during the generation of a quantum bump, or the first stage of TRPL channel translocation out of the microvilli [63] could also explain the early saturation.

Presumably to boost signal propagation in the long photoreceptor axons of *Periplaneta*, graded photoreceptor responses recorded from the axon are overlaid with spikes [83]. Although inter-axon variability is large, all of the photoreceptor axons in *Periplaneta* are very long and grouped seemingly randomly into bundles terminating in the optic lobe [26]. The random variation in photoreceptor properties, the random pooling of photoreceptor signals, and the peculiar spiking axons are actually adaptations improving visual reliability in low light [26].

Future perspectives

Drosophila is a useful model organism in vision research because of the vast research toolbox available to be used with it. However, the mainly day active [23] *Drosophila* represents a very narrow group of insects. Mounting evidence [57] warns against making generalisations of visual system functions between insects from different ecological niches.

Although research with dark-active insects lags behind *Drosophila* studies in available molecular methods, some advances have been made. RNA interference (RNAi) is a method of targeted gene silencing via a cascade initiated by introduction of double stranded RNA into the cell. RNAi has been successfully used in concert with ERG recordings to determine the functional consequences of silencing visual opsins or channel proteins in the compound eye of *Periplaneta* [60]. Next, TRP and TRPL channel silencing by RNAi should be combined with behavioural and electrophysiological experiments in controlled environment [7] to resolve whether TRPL channel prevalence in the photoreceptor membrane really is a prerequisite for vision in low light. *Periplaneta* has two green opsins [60] but the function, or lack thereof, of the less abundant duplicate is unknown. Its possible role in light adaptation could be examined with protein expression studies and immunohistochemistry (e.g. [35]). Also, the possibility of the recruitment of multiple microvilli during a quantum bump, possibly in conjunction with IP_3-Ca^{2+}.

Superposition compound eyes, typical of many nocturnal insects such as moths, pose a problem of their own for electrophysiology. Poor success of patch clamp experiments on superposition photoreceptors means their electrical properties and phototransduction mechanisms are practically unknown. Also, conclusions about spatiotemporal pooling in the optic lobes have until recently [14] relied mainly on lamina cell anatomy (e.g. [16,18]).

The ideal animal model for studying night vision, or any vision for that matter, would manifest visual behaviour suitable for behavioural experiments, have visual system fit for both various electrophysiological recording methods and histological and immunohistochemical studies, and be yielding to various molecular methods. The cockroach *Periplaneta americana* is joining *Drosophila* in the ranks of vision research workhorses meeting all these demands, but other model organisms are badly needed as well. Comparative studies between species possessing different eye types and behavioural needs will lead the way into a more thorough understanding of photoreception in dim light.

Conclusion

The compound eyes of night active insects produce bigger quantum bumps relative to the eyes of their diurnal counterparts. Big bumps are characterised by slow kinetics, and high phototransduction gain due to high input resistance and membrane capacitance. The high capacitance is partially explained by larger rhabdomeres and thus larger photoreceptive membrane area in the night active eyes. Together with the high-gain phototransduction these electrical properties adjust nocturnal photoreceptors to have high sensitivity to light with the cost of reduced temporal resolution and information transfer. Efficient adaptation mechanisms -such as trafficking organelles, screening pigments, rhodopsin, and ion channels- are needed to optimise the vision to changing photic conditions during dusk and dawn. As more insects are being studied, it is becoming evident that the division between night- and day active photoreceptor physiologies is not as straightforward as was thought. A varied set of experimental tools and new animal models are needed for the thorough study of dim light vision in insects.

Figure legends

Figure 1. (a) Schematic structure of an insect compound eye. An ommatidium (middle; from *Periplaneta americana*), the functional unit of the compound eye, consists of the corneal lens C, crystalline cone CC, pigment cells PC, the photoreceptive rhabdom R made up by the photoreceptor cells RC, and the RC axons A traversing the basement membranes B and the tracheal layer T. A cross section of light- (LA) and dark-adapted (DA) cockroach ommatidium demonstrating pigment migration. In an apposition eye (left) ommatidia are optically isolated and each rhabdom (purple)

receives light through a single lens. In a superposition eye (right), several lenses focus light onto a rhabdom across the clear zone, CZ. (b) & (c) Simplifications of a transverse slice of a diurnal (b) and a nocturnal (c) photoreceptor. The schematics consist of rhabdomere microvilli MV, and cell soma S. Note the size difference of the microvilli between (b) and (c). Simplified representations of (i) the phototransduction cascade and (ii) the electrical properties of the photoreceptor membrane with their molecular constituents (see chapter *Phototransduction* for full explanation). Note the hypothetical difference in TRP/TRPL channel expression between (b,i) and (c,i), and the IP_3-induced Ca^{2+} release from submicrovillar cisternae, SMC. Also note that C_m (due to larger rhabdomeres) and R_{in} (voltage-gated and leak channels combined) are larger in (c,i) than in (b,i). (d) Single photon responses, quantum bumps, intracellularly recorded from dark adapted photoreceptors of the diurnal bee *Lasioglossum leucozonium* (blue) and the nocturnal bee *Megalopta genalis* (red). A quantum bump and its shape are the combined results of (i) and (ii). (e) Intracellularly recorded graded voltage responses of *P. americana* photoreceptor to 300 ms light pulses with incremental intensity. (f) & (g) The average contrast gain functions of *Lasioglossum* (blue) and *Megalopta* (red) photoreceptors to (e) a dim and (f) a bright white-noise modulated light stimulus. The nocturnal photoreceptors are more low-passing and provide more response amplification in dim light. Panels (d), (f) & (g) are modified from Frederiksen et al. 2008. *Curr Biol* **18**, 349-358. (doi:10.1016/j.cub.2008.01.057) with permission. Panel (e) is modified from Heimonen et al. 2006. *J Neurosci* **26**, 13454-62. (doi:10.1523/JNEUROSCI.3767-06.2006)

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Authors' contributions

All authors contributed equally.

Competing interests

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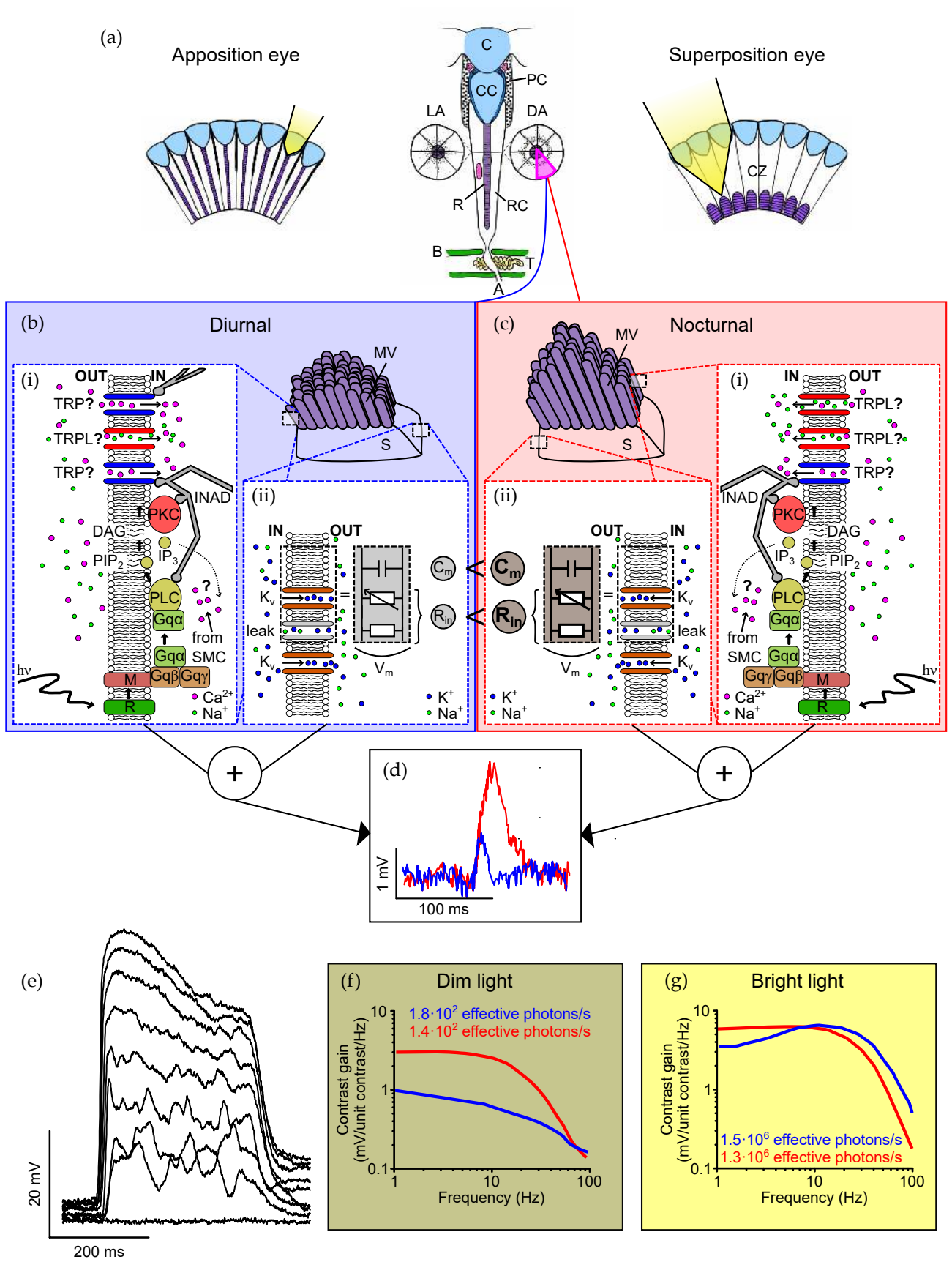
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Contrast gain (mV/unit contrast/Hz)
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