Commentary

Nocturnal colour vision – not as rare as we might think

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Summary

The dual retina of humans and most vertebrates consists of multiple types of cone for colour vision in bright light and one single type of rod, leaving these animals colour-blind at night. Instead of comparing the signals from different spectral types of photoreceptors, they use one highly sensitive receptor, thus improving the signal-to-noise ratio. However, nocturnal moths and geckos can discriminate colours at extremely dim light intensities when humans are colour-blind, by sacrificing spatial and temporal rather than spectral resolution. The advantages of colour vision are just as obvious at night as they are during the day. Colour vision is much more reliable than achromatic contrast, not only under changing light intensities, but also under the colour changes occurring during dusk and dawn. It can be expected that nocturnal animals other than moths and geckos make use of the highly reliable colour signals in dim light.

Key words: vision, colour vision, sensitivity, colour constancy, night vision.

Preconditions for colour vision

Colour vision is commonly defined as the ability to discriminate between two visual stimuli that only differ in their spectral composition, independent of their relative intensities (e.g. Kelber et al., 2003b). A large number of animals are known to use colour to detect, discriminate and recognise objects such as food sources (for instance flowers or fruit), mating partners (as is the case in butterflies and birds), landmarks or their homes. For colour vision to be possible, an animal needs to possess and use at least two types of photoreceptors, with different spectral sensitivities, to look at an object (stage 1 in Fig. 1A). The signals from these receptors need to be compared by neurons in the visual system (stage 2 in Fig. 1A) to produce a chromatic or colour signal. Alternatively, receptor signals can be summed to produce an achromatic (intensity-related) signal. In human colour vision, brightness refers to the achromatic, and hue and saturation to the chromatic, properties of a colour. For colour discrimination, the signals arising from two different stimuli must then be compared (stage 3 in Fig. 1A) and result in a behavioural reaction in the animal (stage 4 in Fig. 1A). Most animals that possess multiple types of photoreceptors use them for colour discrimination (for references, see Kelber et al., 2003b).

Many invertebrates possess two (cockroaches, ants), three (giant clams, firefly squid, bees, wasps, moths, hunting spiders), four (water fleas), five (flies and some butterflies) or even twelve (stomatopod crustaceans) types of receptor that can be used for colour vision (for references, see Briscoe and Chittka, 2001; Cronin and Hariyama, 2002; Kelber, 2006). However, not all of the receptors are used for colour vision. Flies, a well-studied example, use only four out of their five receptor types for colour vision; the fifth receptor has a broad spectral sensitivity and is used exclusively for achromatic vision, as is obvious from the complete separation of both visual pathways (Strausfeld and Lee, 1991; Osorio and Vorobyev, 2005; Kelber, 2006). The firefly squid has three spectral types of receptor but only two of them are localized in the same part of the retina (Michinomae and Masuda, 1994).

In vertebrates, the situation is somewhat more complicated. Most of them possess a dual retina consisting of rods used for vision in dim light and cones used for vision in bright light. Only cones make a major contribution to colour vision. At scotopic light intensities (below 0.005 cd m^{-2}, see Fig. 1B) only rods contribute to (colour-blind) vision, and at photopic light levels (above 5 cd m^{-2}), most vertebrates including humans use only cones to see colour. At mesopic light levels both cones and rods contribute and colours look less saturated (Ambler and Proctor, 1976).

Some vertebrates have pure rod retinae (e.g. Douglas et al., 1998), but most have one type of rod and one (marine and some nocturnal mammals), two (the majority of mammals), three
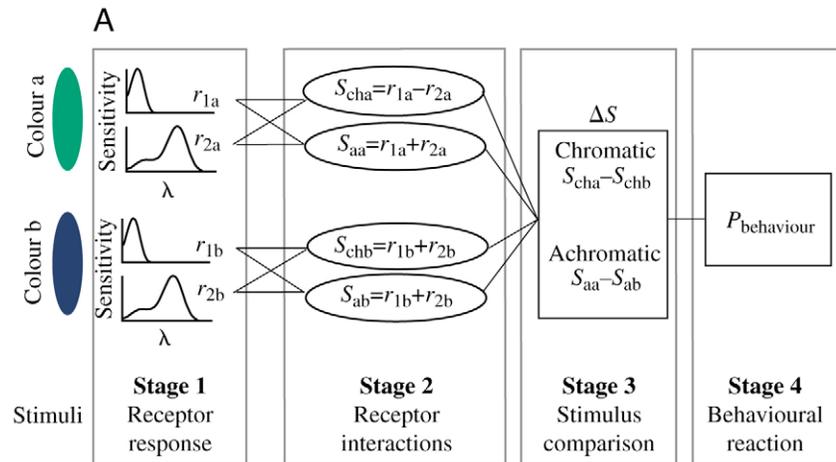
Fig. 1. (A) Simple 4-stage model of colour discrimination with two spectral types of receptors. At receptor stage 1, the signals r_{1a}, r_{1b} and r_{2a}, r_{2b} arise when the animal looks at the two colours a and b. At the subsequent neural stage 2, two neural interactions are possible: summation of the receptor signals, resulting in the achromatic signals S_{aa} and S_{ab}, and subtraction (or comparison), resulting in the chromatic signals S_{cha} and S_{chb}. At stage 3, the signal arising from the two colours a and b are compared, and finally, a behaviour will occur with probability P. (Adapted from Kelber et al., 2003b.) (B) Natural light levels and limits of colour vision in different animals. Humans lose their colour vision ability in dim moonlight and so do diurnal honeybees *Apis mellifera* (Menzel, 1981). Nocturnal hawkmoths (*Deilephila elpenor*, *Hyles lineata* and *H. gallii*) can still see colour at dim starlight levels. Nocturnal geckos (*Tarentola chezaliae*) were tested at dim moonlight levels.
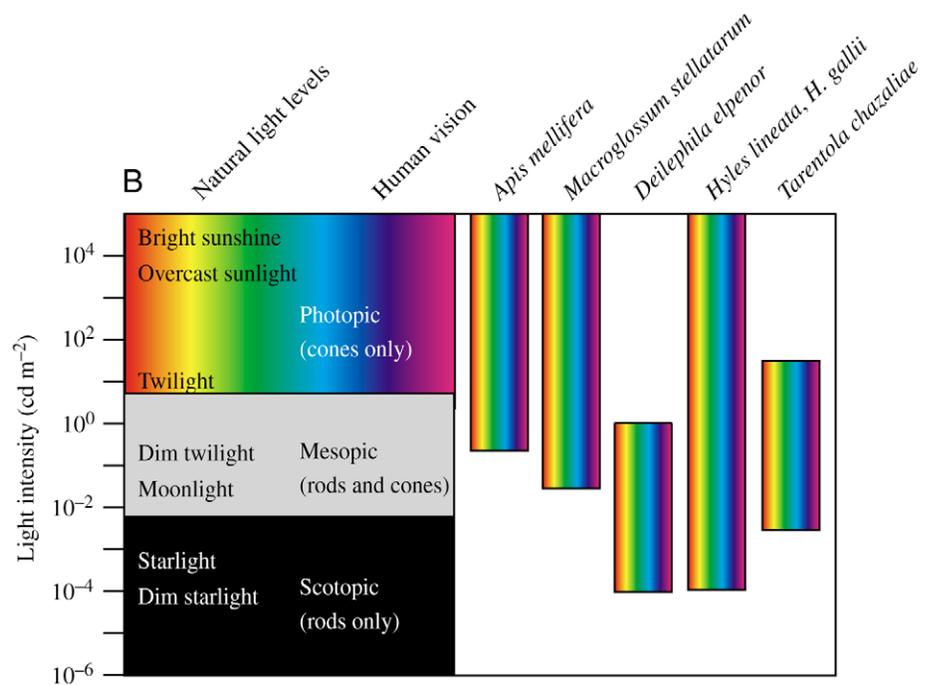
(primates, and some fish, amphibians and reptiles) or four (some fish, most reptiles and birds) types of cone (for a review see Kelber et al., 2003b). Lizards have pure cone retinae (Underwood, 1970).

Animal groups known to lack the preconditions for colour vision include most deep-sea fish and crustaceans, most cephalopods, and some nocturnal and marine mammals (for references see Douglas et al., 1998; Kelber et al., 2003b). Even mammals with two types of photoreceptor (a rod and a cone) are most certainly colour-blind because they use one type, the rods, in dim light and the other type, the cones, in bright light. To prove that an animal uses colour vision, we need therefore to prove behaviourally that it is able to discriminate two colours by means of their spectral distributions and independent of their relative intensities (Kelber et al., 2003b).

Adaptations to nocturnal colour vision

A moonless night is about 100 million times darker than a day with bright sunshine (Fig. 1B). Still, a large number of animal species actively use their eyes at night, to find food, mates, or their homes. At nocturnal light levels, the quantal nature of light has severe consequences for vision. Quanta are distributed randomly and the noise, or uncertainty in an intensity measurement, is equivalent to $\sqrt{n}$ quanta, when an average n quanta reach the eye at any one time interval. Discrimination of low contrasts is therefore severely impaired at low light intensities, and the eyes of nocturnal animals increase quantum capture by having large apertures and short focal lengths (for a review, see Warrant, 2004).

In lens eyes, high sensitivity is achieved by large pupils in combination with a short focal length. Examples of nocturnal animals with highly sensitive lens eyes include owl monkeys,

Fig. 2. (A) Schematic drawing of an apposition compound eye. The aperture (A) is defined by the diameter of a single corneal lens (c). Pigment (p) between the crystalline cones (cc) isolates ommatidia optically. Rhabdom (rh) length (l) and diameter (d) influence sensitivity; f, focal length. (B) Schematic drawing of a superposition compound eye. The clear zone (cz) interspaced between the crystalline cones and rhabdoms allows light entering through a large number of facets to be focussed on one rhabdom. This enlarges the aperture by factor of up to 1000. (C) Superposition eye of *Deilephila elpenor* (photo courtesy of Pär Brannström). cz, clear zone; re, retina. (D) Schematic drawings of the structure of the rhabdom of *D. elpenor* (adapted from Schlecht et al., 1978). B, basement membrane; Rh, rhabdom; Tr, tracheal tapetum, N, nucleus. Receptors 1 and 2 are blue- or UV-sensitive; receptors 3–9 are green-sensitive. (E) About 1000 facets of *D. elpenor* that build the superposition aperture glow when the eye is illuminated and viewed from the same direction. Photo courtesy of Michael Pfaff.
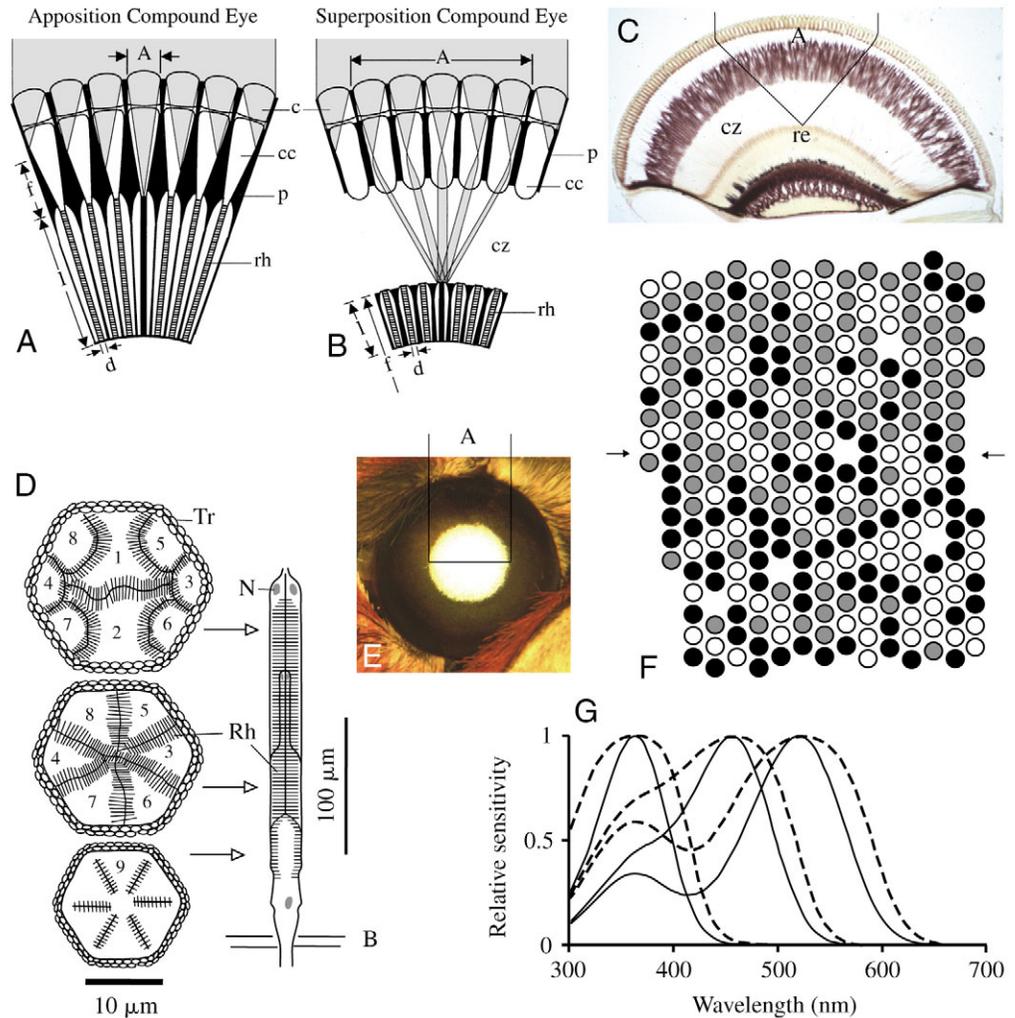
(F) Random arrays of ommatidial types in the crepuscular hawkmoth *Manduca sexta* (redrawn from White et al., 2003). White circles, ommatidia with all three receptor types; black circles, ommatidia with green and blue receptors; grey circles, ommatidia with green and UV receptors. Arrows show the eye horizon. (G) The effect of filtering in the long fused rhabdom of a dark-adapted nocturnal hawkmoth. The broken lines represent the sensitivities that would result from self-screening, if the long photoreceptors of *D. elpenor* had open rhabdoms. The solid lines represent the sensitivities resulting from filtering in the fused and tiered rhabdom.

owls, nocturnal geckos and many spiders. Large lenses with short focal lengths suffer from a severe optical problem: longitudinal chromatic aberration. Nocturnal vertebrates have probably solved this problem by having multifocal optics associated with slit pupils (Malmström and Kröger, 2006). Multifocal lenses focus light of different wavelengths in different spherical zones of the lens, thus producing a focussed image for multiple types of cone, and the slit pupil allows light to fall through all zones even when the pupil is closed (Kröger et al., 1999). However, even if this allows for colour vision in photopic and mesopic light intensities when cones are active, animals using a single type of rod in scotopic intensities remain colour-blind at night.

The compound eyes of insects and crustaceans come in two types (Land and Nilsson, 2002). In apposition compound eyes (Fig. 2A), each set of photoreceptors receives light only from its own tiny lens. These eyes are not very sensitive to light and

are not very well adapted to nocturnal vision, yet insects like grasshoppers and some nocturnal bees have driven these eyes to their extremes to cope with dim light levels: they possess large facet lenses, and wide and long rhabdoms (e.g. Warrant et al., 2004). Superposition compound eyes (Fig. 2B,C), possessed by nocturnal moths and beetles, are adapted to dim light vision. These eyes have a clear zone (marked cz in Fig. 2B,C) that allows light passing through a superposition aperture of up to 1000 lenses to be focussed onto one set of photoreceptors, thus enhancing the eye's sensitivity by a factor of up to 1000 (Fig. 2C,E). The photoreceptors of each rhabdom are enclosed by a tracheal tapetum (marked Tr in Fig. 2D) that contributes to the high sensitivity by doubling the light pass.

Besides optical adaptations, nocturnal animals have photoreceptors with large rhabdoms or outer segments (Figs 2D, 3A), and deep-sea fish have banked retinae (for a review, see Warrant, 2004). In addition, many nocturnal eyes

have tapeta, mirrors behind the receptor layer that reflect light that is not absorbed during the first pass through the receptor and thus have the same effect as doubling the length of the receptor (Land and Nilsson, 2002). As a result of self-screening, long receptors have a much broader spectral sensitivity than short receptors (Warrant and Nilsson, 1998).
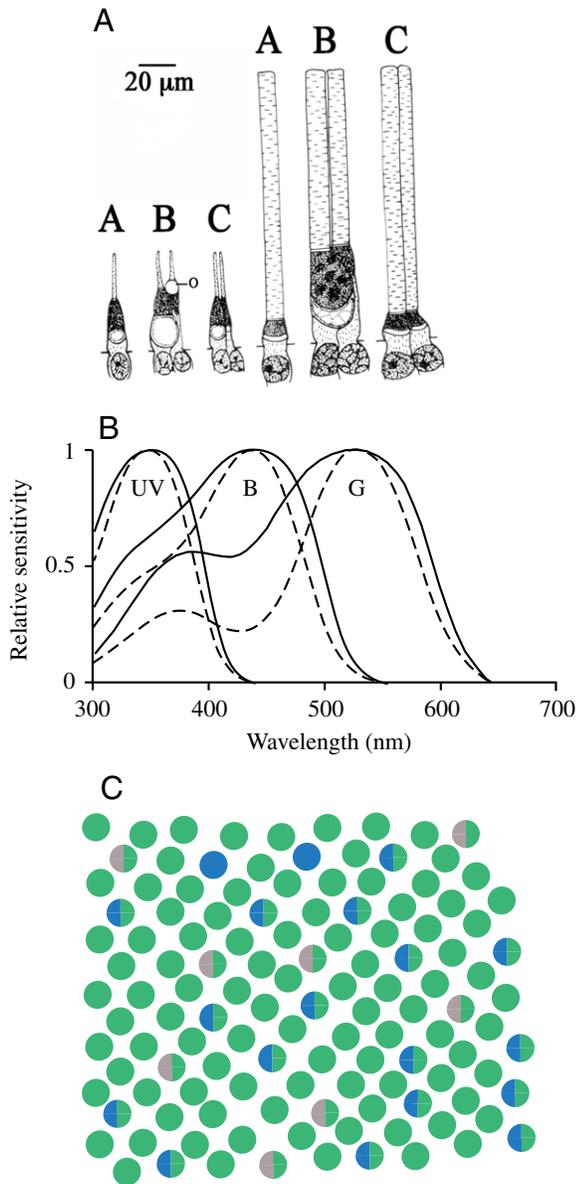

Fig. 3. (A) Anatomy of three anatomical types (A–C) of photoreceptor in diurnal (left) and nocturnal (right) geckos (modified from Underwood, 1970). Note the different lengths of the outer segments that cause different quantum captures. (B) Spectral sensitivities of the 5 μm short cones of a diurnal gecko (broken lines) and the 50 μm long cones of a nocturnal gecko (solid lines). UV, UV receptor; B, blue receptor; G, green receptor. (C) Cone mosaic of the nocturnal gecko *Teratoscincus scincus* (redrawn from Loew et al., 1996). Green circles, green-sensitive cones; blue circles, blue-sensitive cones; blue-green circles, double cones with a green and a blue receptor; grey-green circles, double cones with a green and a UV receptor.

They are more sensitive to light but the overlap between receptor sensitivities also makes them less useful for spectral discrimination and thus colour vision. Fig. 3B illustrates the difference between the sensitivities of dark-adapted gecko photoreceptors with outer segments of 5 μm and 50 μm length.

With very few photons available, pigment tuning also becomes essential, and should maximise signal-to-noise ratio (for recent discussions of this topic, see e.g. Douglas et al., 1998; Osorio and Vorobyev, 2005) for the visual system. Maximising photon catch and thus signal strength should solve half of the problem, but nocturnal moths, for example, have pigments sensitive to shorter wavelengths than those optimal for high photon catch (Johnsen et al., 2006). Visual pigments of nocturnal geckos are also sensitive to shorter wavelengths than those of related diurnal species (Ellingson et al., 1995; Loew et al., 1996), indicating that minimising noise is indeed an important factor.

Finally, temporal and spatial summation of receptor signals by neurons in the visual pathway can enhance the signal and improve signal-to-noise ratio considerably (Warrant, 1999; Warrant et al., 2004). In contrast, inhibitory interactions between receptors, including those involved in colour vision, lead to a lower signal-to-noise-ratio (Vorobyev, 1997). A single long-wavelength receptor has, under most nocturnal conditions, a higher sensitivity than either a short-wavelength-sensitive receptor or any combination of both (Kelber et al., 2003a; Osorio and Vorobyev, 2005; Johnsen et al., 2006). With very few photons available, a monochromatic eye with an optimally tuned pigment can thus discriminate more shades of colour simply by means of intensity contrast than can a dichromatic or trichromatic eye (Vorobyev, 1997). Many animals, including ourselves, therefore sacrifice colour vision at night (Dusenbery, 1992). However, as demonstrated below, spectral information is just as useful at night as it is during day (Kelber et al., 2002; Land and Osorio, 2003; Johnsen et al., 2006), and some animals capture enough photons to see colours even in dim light.

Nocturnal colour vision for object constancy

How useful colour information can be, compared to the achromatic signal provided by a single type of receptor, is easily demonstrated. One of the most general tasks that animals use vision for is recognition of food items, hosts, mates, landmarks, nests and other objects. As the visual appearance of objects, changes dramatically with changing illumination, however, mechanisms for object constancy are extremely important. Fig. 4 shows how a yellow flower, a blue flower and a typical leaf background change contrast and colour between two illuminations measured at the same place, within less than a minute: direct sunlight and a shadow cast by an observer. The contrasts of both colours to the green background (Fig. 4C) change dramatically; the blue flower looks brighter than the yellow flower in the shadow but darker in direct sunlight. However, in the colour space of an insect (Fig. 4D), both
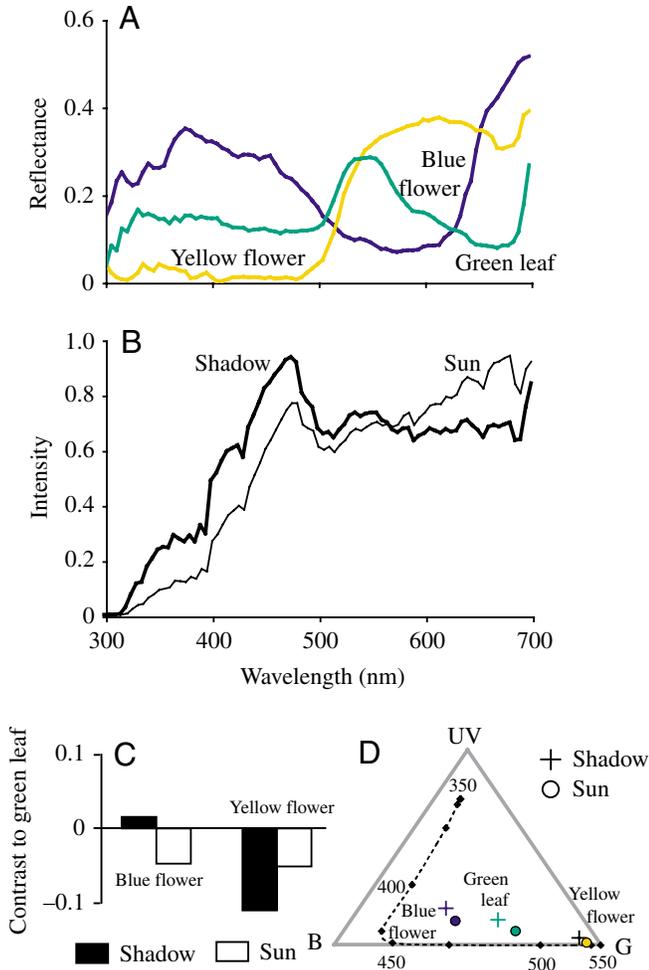
Fig. 4. The use of chromatic vision. (A) The reflectances of a typical yellow and a typical blue flower and a green leaf. (B) The spectral composition of direct sunlight and skylight in a shadow, measured shortly before sunset, on a summer day in Utah, USA. (C) The achromatic contrast between both flowers and the green leaf in both illuminations differ dramatically for the green receptor of *D. elpenor*. (D) The colour loci of all three stimuli in the colour triangle of *D. elpenor* are rather constant in both illuminations, even without the assumption of colour constancy. UV, UV light; B, blue light; G, green light. (For details and methods of all calculations, see Johnsen et al., 2006.)

colours can easily be separated under both illuminations, even without any assumption of colour constancy. The colour triangle shown here is a two-dimensional projection of the three-dimensional colour space of an insect with three receptor types. It disregards intensity. It shows that colour is a much more reliable and constant property of objects than achromatic contrast. Obviously, the same applies in dim light. The colour of light changes dramatically during dawn and dusk, and between moonlight and starlight, and colour vision allows animals to identify objects more reliably under these conditions (Johnsen et al., 2006). The colour signal changes much less with changing illumination than the achromatic signal (Johnsen et al., 2006).

Scotopic colour vision in crepuscular and nocturnal hawkmoths

Most hawkmoths are active during twilight (crepuscular) or at night (nocturnal). They have superposition compound eyes with a large superposition aperture and tracheal tapeta (Fig. 2B–D), and are therefore well adapted to nocturnal vision. Similar to the well-known honeybee, they rely on one single set of three spectral receptor types that are maximally sensitive to ultraviolet, blue and green light, for vision at all light intensities (Schwemer and Paulsen, 1973). As a result of self-screening, their long photoreceptors should have broadened sensitivity functions when they are dark-adapted (broken curve in Fig. 2G; Warrant and Nilsson, 1998; Kelber et al., 2003a). However, the rhabdomeres of moth photoreceptors are fused and work as spectral filters for each other, thus narrowing the sensitivity functions and making them well suited for colour vision (solid curve in Fig. 2G; for formulae to calculate the curves see Johnsen et al., 2006). Diurnal flower visitors such as honeybees have long been known to use colour to detect, recognise and discriminate the colours of rewarding flowers (Frisch, 1914).

Using a method developed by von Frisch in 1914, we have recently demonstrated colour vision in the crepuscular and nocturnal hawkmoths *Deilephila elpenor*, *Hyles lineata* and *Hyles gallii* (von Frisch, 1914; Kelber et al., 2002; Kelber et al., 2003a). The moths were trained to associate a reward of sucrose solution with the blue or yellow colour of artificial flowers (Fig. 5A). After training, they were able to discriminate the training colour from eight different shades of grey and from two other colours (Fig. 5B,C). As the different shades of grey provided different achromatic cues to the moths, they could only rely on the chromatic signal (or colour) for the discrimination. They were therefore unable to discriminate the training blue (or yellow) from a lighter or darker shade of blue (or yellow, respectively), because these stimuli differed only in the achromatic and not the chromatic signal (right panels in Fig. 5B,C). The results shown in Fig. 5 were obtained at a light intensity similar to light levels on a starlit night (0.0001 cd m^{-2}). Moths also discriminated between two colours looking white to the human eye, one absorbing ultraviolet light and one reflecting it (Kelber et al., 2002). This proves that the nocturnal colour vision of *D. elpenor* also extends into the ultraviolet range. In addition, *D. elpenor* has good colour constancy and is able to recognize rewarding flowers under changed illumination (Balkenius and Kelber, 2004).

How can moths achieve colour vision at light intensities where humans are colour-blind? The number of photons captured by the receptors in each ommatidium, at starlight intensities, ranges between 1 and 25 photons, per receptor channel and receptor integration time. With these numbers of photons, the noise level ($\sqrt{N}$ equivalent to between 1 and 5 photons) would make discrimination impossible. We therefore have to propose that nocturnal moths use spatial and/or temporal summation (Warrant, 1999) to improve the signal-to-noise ratio and allow the colour discrimination we observed.
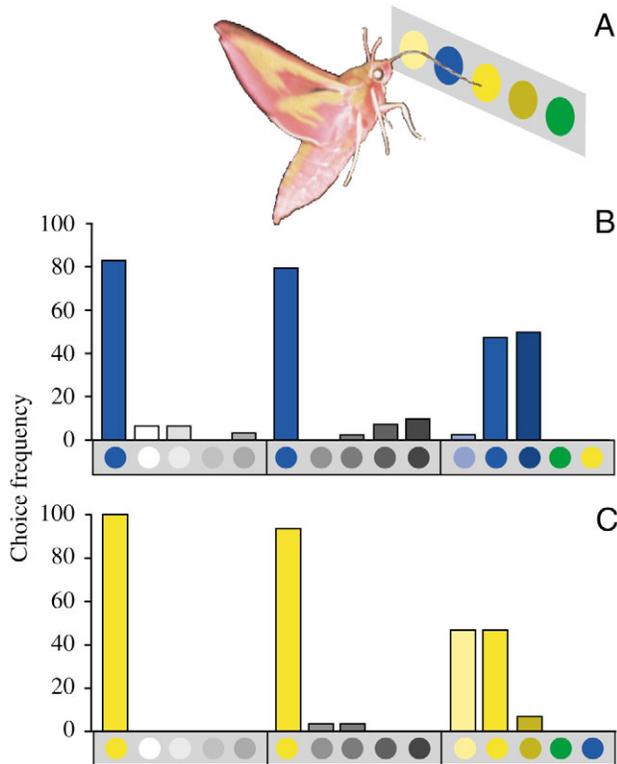
Fig. 5. At starlight intensities of illumination, nocturnal hawkmoths of the species *Deilephila elpenor* learned to discriminate a training colour from eight different shades of grey and from two other colours but not from brighter or darker shades of the training colour. (A) The animal choosing one of the stimuli in the set-up. Discrimination occurred when the training colour was blue (B) or yellow (C). (Data from Kelber et al., 2002.)

Calculations show that by having three spectral types of receptor, the hawkmoths sacrifice absolute sensitivity, and this indicates that colour vision is highly relevant for them, just as it is for diurnal flower visitors (Kelber et al., 2003a; Johnsen et al., 2006).

Colour vision in nocturnal geckos

Among vertebrates, lizards have lost their dual retina during evolution, and are now left only with cones (Underwood, 1970). Nocturnal geckos have evolved from diurnal lizards and thus have a similar retina: no rods but three spectral types of cone sensitive to ultraviolet, blue and green light (360, 440 and 520 nm, respectively, Fig. 3B,C) (Loew et al., 1996). Adaptations to the nocturnal life-style include very long cone outer segments (Fig. 3A) and a combination of large pupil and short focal length. Since this condition results in severe chromatic aberration it is assumed that geckos may have multifocal lens optics (Kröger et al., 1999). Being ambush predators, geckos use motion vision to detect prey, and motion vision tends to be colour-blind in most animals (Kelber et al., 2003b). Are geckos nonetheless able to use colour as a cue?

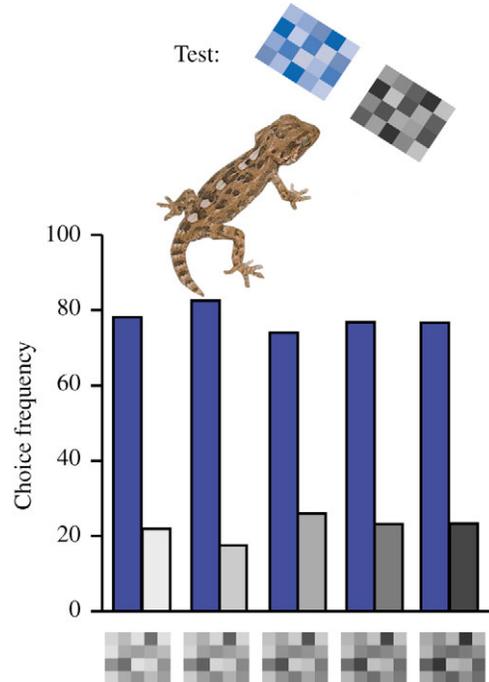It is difficult to convince geckos to use colour cues but it

Fig. 6. Two nocturnal geckos of the species *Tarentola chezaliae* learnt to take a cricket from forceps decorated with a pattern made from blue squares (right). The forceps decorated with a grey pattern (left) always held a salted cricket, which geckos always refused. Both geckos predominantly chose blue in all tests, independent of the overall intensity of the grey pattern (represented by the different shades of the grey patterns on the abscissa). (Data from Roth and Kelber, 2004.)

was possible using a method similar to that used with nocturnal hawkmoths (Roth and Kelber, 2004). A well-tasting cricket was presented in front of a blue pattern, and a salty (badly-tasting) cricket in front of a grey pattern (inset in Fig. 6). The shades of grey and blue were made equally bright for the geckos, thus making discrimination by means of achromatic cues very unlikely. To make intensity completely unreliable for the geckos, we varied it between training trials leaving only colour as the signal to be learned. Two geckos learned to discriminate between both colours, at light intensities mimicking dim moonlight (Fig. 6; 0.002 cd m^{-2}). They might well be able to use colour even at lower light intensities. Their anatomical adaptations thus allow nocturnal geckos to use cone-based colour vision at night (Roth and Kelber, 2004). The question as to why a predator should preserve and use colour vision, even in dim light, remains to be answered. Most probably, object constancy is important even for predators.

Bioluminescence and colour vision

Glow worms and fireflies, and many fishes, crustaceans and cephalopods living in the deep sea, produce their own light to be seen in the darkness: bioluminescent signals. They are bright light sources, the intensity of which should make detection a simple task. It is therefore commonly thought that

bioluminescent communication is based on achromatic matched filtering: the spectral sensitivity of the eye is matched to the mate's signal, and the temporal patterns of flashes are species-specific. However, in fireflies (*Photinus* sp.) and glow-worms (*Lampyris noctiluca*), there is good evidence that colour vision is involved. In fireflies, behavioural data (Lall and Worthy, 2000) can only be explained by assuming a chromatic interaction between the blue and green receptors. Recent experiments prove this to be the case for the European glow-worm *Lampyris noctiluca* (Booth et al., 2004). The Central-American click beetle *Pyrophorus plagiophthalmus* (Elateridae) has two dorsal light organs emitting green light and a third ventral organ emitting orange light (Stolz et al., 2003). Behavioural data are missing, but we may speculate on their use of colour.

Behavioural evidence is also lacking for firefly squids, but it is known that these molluscs and some deep-sea crustaceans and fish possess two receptor types that may allow them to discriminate between the colour of the down-dwelling daylight and the colour of their bioluminescence (for references see Kelber, in press; Douglas et al., 1998).

Some deep-sea dragon fish have two-coloured bioluminescence in the blue and far-red, and photoreceptors sensitive to the red fluorescence (Douglas et al., 1998). Whether they compare signals from this red receptor and the blue-sensitive rod for colour vision or just use the red receptor as a parallel channel may remain their secret since these animals are difficult to access and hard if not impossible to study in behavioural tests (Douglas et al., 1998). In general, however, bioluminescent stimuli are bright, and the eyes of these animals do not have to be quite as sensitive as those of nocturnal moths or geckos.

Other species might join the club

Are moths and geckos special or do more species have the capability to see colour at night? We can assume that other large nocturnal insects with superposition eyes, including large moths and beetles, should be able to see colour in dim light. Even insects with highly sensitive apposition eyes, including grasshoppers and large nocturnal bees such as the carpenter bee *Xylocopa (Nyctimelitta) proximata* that forages on moonless nights (Somanathan and Borges, 2001; H. Somanathan and R. Borges, unpublished observations), and the Halictid bee *Megalopta genalis* that forages during dawn and dusk under the canopy of the tropical rain forest (Warrant et al., 2004), might possess this ability, but this remains to be studied. Large arthropods with lens eyes and three types of photoreceptors in the retina, such as the nocturnal wandering spider *Cupiennius salei* (Walla et al., 1996), might also have colour vision in dim light.

Among the vertebrates, another nocturnal group besides the geckos might see colour at night. In contrast to other vertebrates, toads and frogs have two types of rod (Liebman and Entine, 1968), maximally sensitive to 432 nm and 502 nm, respectively. They use colour vision for mate recognition in bright light (for references, see Kelber et al., 2003) and might

use rod-based colour vision for the same purpose in dim light. Alternatively, they might only use the achromatic signal that results from summing the signals in both rods types. The latter has been shown to be the case for the optomotor response in the green treefrog *Hyla cinerea* (King et al., 1993). Finally, in some fish, the red-sensitive cones are more sensitive to light than the other cone types and can interact with rods (Roessel et al., 1997). This has been proved by classical conditioning experiments in anaesthetised goldfish (Powers and Easter, 1978) and it might apply to other species as well. It is, however, unknown whether and how the chromatic signal derived from rods and red cones is used by the fish.

Conclusions

Colour vision is just as useful at night as it is during the day. The reason for this probably lies in the dramatic changes in the colour of light that animals experience both between sun- or moonlit areas and shadows, and during the twilight period. Animals with highly sensitive eyes can see colour in very dim light, if their eyes have the preconditions: several types of receptor that are active simultaneously. Direct evidence for nocturnal colour vision only exists for nocturnal hawkmoths and geckos, but more species need to be studied. Rather than asking why some animals do have colour vision at night, we may have to ask why many others, among them most vertebrates, do not!

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