1.29 Color in Invertebrate Vision[☆]

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1.29.1 Abstract

Invertebrates have a variety of color vision systems: while mantis shrimps use 12 photoreceptors types for color vision, cephalopods have only one spectral type of photoreceptor and therefore are color blind. Ancestors of all extant invertebrates having color vision have lost during evolution some visual pigments. In arthropods, the numbers spectral receptor types have been subsequently increased due to gene duplication and intraocular filtering, as in some jumping spiders and butterflies. Unlike us, invertebrates do not have separate receptors for photopic and scotopic vision. Therefore, some nocturnal insects discriminate colors in extremely dim conditions. Arthropod rhabdomeric photoreceptors are inherently polarization sensitive. Therefore, some butterflies have mixed sensation of polarization and color. Other arthropods, such as bees, supress polarization sensitivity of photoreceptors used for color by reorienting microvilli in their rhabdoms. While it is unlikely that insect color vision has been evolutionary adjusted to flower colors, color vision of some butterflies probably coevolved with color of butterfly wings.

1.29.2 Glossary

Color is that aspect of visual perception by which an observer may distinguish differences between two structure-free fields of view of the same size and shape, such as may be caused by differences in the spectral composition of the radiant energy concerned in the observation (Wyszecki and Stiles, 1982)

1.29.3 What Is ColorVision?

A human observer is assumed to have color vision if he can discriminate light stimuli of different spectral composition using cues other than their intensity (Wyszecki and Stiles, 1982). Accordingly, we assume that an animal has color vision, if it can discriminate two light stimuli of different spectral composition (but equal in polarization) and continues to discriminate them when the intensity of the stimuli are varied, that is, these stimuli cannot be matched by adjusting their intensity. The first animals demonstrated to have color vision were invertebrates. Lubbock (1888) showed that a water flea *Daphnia*, which is positively phototactic, prefers yellow light to white light of a higher intensity. Some time later, von Frisch (1914) showed that honeybees could discriminate colored stimuli from various shades of gray. Since these pioneering studies, color vision has been demonstrated using behavioral experiments in a variety of invertebrates, including mites, spiders, crustaceans, and insects (for review see Kelber et al., 2003; Kelber, 2006).

Color vision is achieved by comparing the signals of photoreceptor cells sensitive to different parts of the spectrum. Anatomical and physiological studies show that the majority of invertebrates with eyes also have multiple spectral types of photoreceptors (Kelber et al., 2003) However, multiple spectral types of photoreceptors do not necessarily infer color vision – different spectral receptor types can be used for different purposes at different behaviors, giving receptor-specific (or wavelength-specific) behavior

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rather than color vision (Menzel, 1979). Receptor-specific behavior does not require the comparison of signals from different receptors and, therefore, is color blind. Animals that do have color vision can also show receptor-specific behavior in particular tasks. For example, a honeybee uses color vision for discriminating objects at close range (Frisch, 1914; Menzel, 1979; Menzel and Backhaus, 1991), but it uses only a long-wavelength-sensitive photoreceptor for discriminating objects from far away and for motion vision (Srinivasan and Lehrer, 1984; Giurfa et al., 1996; Giurfa and Vorobyev, 1997). It is important to note that, while animals with multiple receptors can, in theory, be color blind in all behavioral contexts, such color blindness has not been revealed behaviorally in any animal so far tested.

1.29.4   Color Vision and Color Blindness in Different Eye Types

Eye design in invertebrates is diverse and gives rise to a variety of color-vision systems. Simple camera-type eyes, similar in plan to the vertebrate eye, are common in cephalopods and spiders. Compound eyes made up of many units called ommatidia are found in many insects and crustaceans (Land and Nilsson, 2012). The two types of eyes may coexist within the same animal, for example, insects have large compound eyes, which provide spatial, color, and polarization vision, and small camera-type eyes called ocelli. Ocelli detect overall illumination rather than form an image. Interestingly, physiology suggests that ocelli are capable of providing information about color without being able to resolve spatial details (Ruck, 1965; Van Kleef et al., 2005). Usually, camera-type eyes have a better resolution than compound eyes (Land and Nilsson, 2012). The tiny (0.8 mm in diameter) camera-type eyes of the jumping spider *Portia fibriata* have an optical resolution only five times worse than ours and more than five times better than that of the best insect, a dragon fly (Land and Nilsson, 2012). These eyes allow spiders to locate prey with remarkable precision and provide spiders with a sense of color (Land, 1985; Nakamura and Yamashita, 2000). The largest camera-type eyes are found among cephalopods (Land and Nilsson, 2012). While cephalopods have excellent spatial vision, they typically have only one type of visual pigment and, therefore, are color blind. The absence of color vision in cuttlefish and octopus has been questioned, because these animals can adjust body patterns, to match backgrounds consisting of differently colored natural objects, such as stones, sand, and algae. However, it appears that the match is achieved on the basis of brightness cues. When exposed to a background consisting of yellow and blue stones that are matched in brightness for cuttlefish eyes, cuttlefish ignore the difference in color (Marshall and Messenger, 1996; Mäthger et al., 2006) (**Fig. 1**).

Surprisingly, the most sophisticated color vision may be associated with the low resolution compound eyes of ancient marine crustaceans – mantis shrimps (stomatopoda). Mantis shrimps have at least 16 spectral types of photoreceptors, 12 of which are used for color vision including ultraviolet, the remaining four are used for spatial and polarization vision (Cronin and Marshall, 1989; Marshall and Oberwinkler, 1999). The 12 types of spectrally different photoreceptors are located in a narrow strip across the eye – the midband– where photoreceptors used for color vision are combined in the top four rows of ommatidia (**Figs. 1** and **2**). Each of these rows contains an ultraviolet (UV)-sensitive photoreceptor and two spectral types of photoreceptors sensitive in the visible range (Cronin and Marshall, 1989). To be able to register colors of objects in the environment outside this very narrow strip, mantis shrimps move their eyes and scan midband photoreceptors over the image (Land et al., 1990). Such scans indeed allow shrimps to discriminate colors (Marshall et al., 1996). However wavelength discrimination of mantis shrimps is poorer than the wavelength discrimination of animals with fewer number of photoreceptors (Thoen et al., 2014).
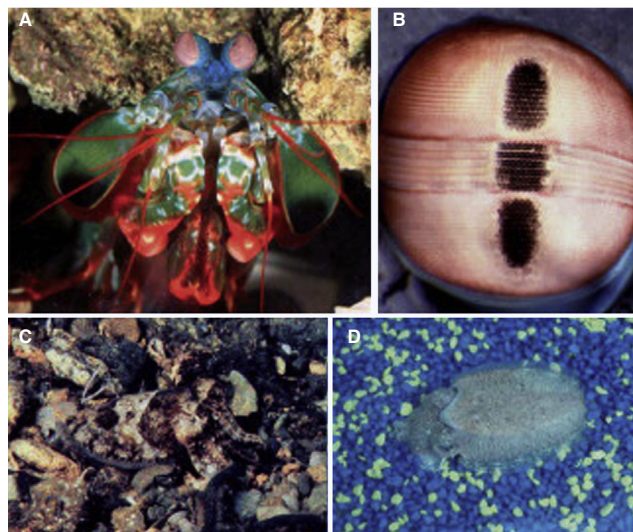
Figure 1   An animal with sophisticated color vision, mantis shrimp *Odontodactilus scyllarus* (A) and a color-blind cephalopod – cuttlefish *Sepia officinalis* (C, D). The frontal eye of a mantis shrimp (B) has a conspicuous stripe of facets – the midband. The four upper rows of the midband are specialized for color vision, its rows contain 12 spectral types of photoreceptors cells (**Fig. 2B**). Color-blind cuttlefish is a master of camouflage – it matches texture, brightness, and color of the substrate – (C) but it fails to imitate the texture of yellow and blue gravel that is matched in brightness for the cuttlefish eye (Marshall and Messenger, 1996). Photographs are courtesy of Justin Marshall and Roger T. Hanlon.
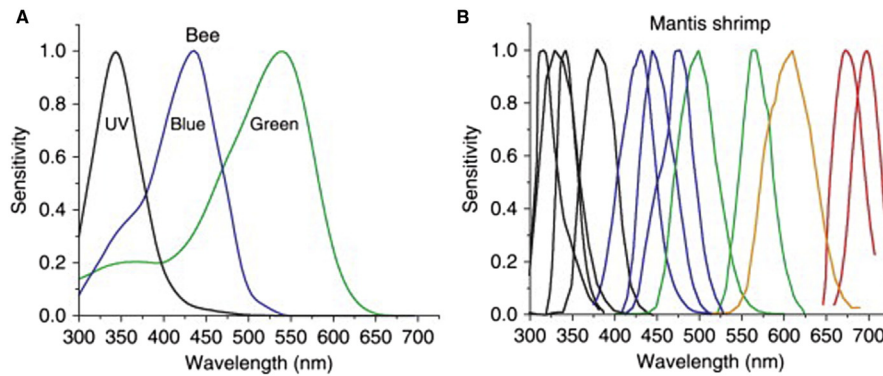
Figure 2   The spectral sensitivities of a honey bee, *Apismellifera* (Menzel and Backhaus, 1991) and of a mantis shrimp, *Neogonodactilus oesredii* (Marshall and Oberwinkler, 1999). In a mantis shrimp, the narrowing of the spectral sensitivities is achieved by intrarhabdomal filtering.

1.29.5   Visual Pigments and Spectral Sensitivities

Animals visual pigments, with a notable exception of a sponge, which uses cryptochrome (Rivera et al., 2012), are constructed from a carotenoid chromophore bound to an opsin protein. The opsins of visual pigments are expressed in photoreceptor cells that belong to two distinct categories. While vertebrates and some invertebrates, such as tunicates and fan worms, use for vision ciliarly photoreceptors, which express *c*-opsins, the two groups of invertebrates that have well developed eyes – arthropods and cephalopods use rhabdomeric photoreceptors, which express *r*-opsins (Porter et al., 2011). Cephalopods have only one *r*-opsin gene and therefore are probably color blind (Porter et al., 2011). Molecular genetic analysis indicates that a common ancestor of arthropods had four or five *r*-opsins named LW1, LW2, MW1, MW2 and SW according to the spectral range of their sensitivity (Cronin and Porter, 2014; Henze and Oakley, 2015). These opsins probably evolved from a single rhabdomeric opsin of a common ancestor of arthropods and color-blind velvet worms (*Onychophora*) (Hering et al., 2012) All extant arthropods so far studied lost some ancestral opsin genes. For example, all winged insects (*Pterygota*) have opsins belonging only to LW2 and SW groups (Cronin and Porter, 2014; Henze and Oakley, 2015). The number of visual pigments has been also increased by gene duplication. Many winged insects are trichromatic due to duplication of a LW2 gene that occurred in the ancestor of all insects (Cronin and Porter, 2014; Henze and Oakley, 2015), in mantis shrimps (Porter et al., 2013), dragon flies (Futahashi, 2017) and butterflies (Arikawa and Stavenga 2014) evolutionarily recent duplications gave rise to a great variety of opsins.

In invertebrates, three types of chromophores are found:(1) retinal, a chromophore found in terrestrial and marine vertebrates, is also found among cephalopods, crustaceans, and in insects such as bees and locusts; (2) 3,4-didehydroretinal, a chromophore typical of freshwater fish and amphibians, is present in several species of squid; (3) 3-hydroretinal, which is common in flies and butterflies. This chromophore is not found among vertebrates (for reviews see Kelber et al., 2003). Generally, colorvision is achieved by expressing different opsins in combination with the same chromophore to generate visual pigments with different sensitivities. However, some cephalopods, such as the firefly squid, *Watasenia scintitalis*, have three visual pigments probably derived from one opsin protein and three different chromophores (Seidou et al., 1990). It remains unclear whether these visual pigments are used for color vision.

The spectral sensitivity of invertebrate photoreceptors often deviates substantially from the absorption spectrum of visual pigments. In the compound eyes of insects and crustaceans, rhabdomeric photoreceptors with different visual pigments are usually fused into a common light guide. This leads to mutual filtering of light and narrowing of receptor spectral sensitivity even in the absence of additional filtering pigments (Snyder et al., 1973). In the tired retina of the frontal eyes of a jumping spider, and in many insects and crustaceans, distal rhabdoms filter the light reaching the more proximal ones. However, the most prominent modification of spectral sensitivity is achieved by using additional pigments, which act as filters narrowing the spectral sensitivity, or transfer energy to the visual pigment, thus broadening the spectral sensitivity (for review see Douglas and Marshall, 1999). The broad spectral sensitivity of the R1–R6 photoreceptors in the house fly is achieved by sensitizing pigment 3- hydroxy retinol (Vogt and Kirschfeld, 1984). The same molecule serves as a screening pigment in a moth *Papilio*, where it narrows the spectral sensitivity (Arikawa et al., 1999). Perirhabdomal pigments change the spectral sensitivity of thin rhabdoms by lateral filtering. For example, the red perirhabomal pigment of *Papilio* shifts significantly the peak of the red pigment to the longer wavelength (Arikawa, 2003). A colorful jumping spider, *Habronattus pyrithrix*, which has two visual pigment peaking in UV and green parts of the spectrum, has the third, red sensitive receptor, produced via long-wavelength pass filter (Zurek et al., 2015). In mantis shrimps, intrarhabdomal pigments create narrow spectral sensitivities, thus enabling color vision with 12 spectrally distinct photoreceptors. Interestingly, the spectral transmission of filters in the eyes of mantis shrimps changes as an adaptation to the light environment (Cronin et al., 2001).

1.29.6   Color Vision in the Darkness

In dim light, the signal-to-noize ratio of photoreceptor cells is low, which leads to an unreliability of color vision in darkness (for review see, Osorio and Vorobyev, 2005). Accordingly, vertebrates use one spectral type of rods for scotopic vision and are color blind in dim light, but see (Kelber and Roth, 2006). However, invertebrates do not have a separate set of photoreceptors for nocturnal and diurnal vision. Moreover, nocturnal insects, like hawkmoths, have several spectral types of photoreceptors in their eyes. It appears that nocturnal hawkmoths use color vision at light intensities where we use rod vision only (Kelber et al., 2002). To achieve reliable color discrimination, these insects must sum signals of many ommatidia and in doing so sacrifice spatial resolution. It remains unclear whether other insects that are active at night, such as nocturnal bees, retain their ability to discriminate colors in darkness.

1.29.7   Interaction between Color and Polarization Vision

The rhabdomeric photoreceptors of arthropods and mollusks are inherently polarization sensitive by virtue of their microvillar design (Land and Nilsson, 2012). Because a single polarization-sensitive photoreceptor cannot distinguish between the orientation of polarization and the spectral composition of light, the neural signals caused by changes in polarization cannot be distinguished from those caused by the change of spectral composition of light. Thus, polarization vision may be mixed with color vision inducing false colors, as has been shown for a butterfly *Papilio augeus* (Kelber, 1999). Because *Papilio*'s blue receptors are maximally sensitive to vertically polarized light, whereas green receptors are maximally sensitive to horizontally polarized light, the horizontally polarized light induces a sensation indistinguishable from green light. Papilio prefers to lay eggs on green surfaces to blue ones. It also prefers horizontal polarization to vertical polarization, indicating that polarization and color vision are mixed (Kelber, 1999). However, in the majority of insects and crustaceans, polarization vision is separated from color vision. In many insects, this is achieved by twisting photoreceptors along their longitudinal axis in such a way that microvilli of individual rhabdomers are not aligned (Wehner and Bernard, 1993). For example, the honeybee eye is composed of twisted photoreceptors except for the uppermost dorsal rim of the eye (Wehner et al., 1975). In mantis shrimps, the polarization-sensitive parts of eye are spatially separated from the color-sensitive rows of the mid-band (Land and Nilsson, 2012) (**Fig. 1**).

1.29.8   Spatial Resolution of Color Vision – Random Arrangement of Photoreceptors in Compound Eyes

In our eyes, each photoreceptor cell samples a different point in the space. Since the receptive fields for color should include different spectral types of photoreceptor cells, the random distribution of cones in the human retina leads to a poor spatial resolution of chromatic vision (for review see Lee, 2004). However, because in compound eyes the rhabdomers are fused together into a common light guide, such eyes theoretically allow for higher spatial resolution of color vision, by virtue of locating all spectral types of receptors within each ommatidium. Early studies in the honeybee eye suggested that each ommatidium contains all three spectral types of photoreceptor (UV, blue, and green), indicating that insects have an eye design that optimizes the spatial resolution of color vision (Gribakin, 1969). However later studies found that, in the eyes of butterflies and honeybees, photoreceptors with spectral sensitivities are randomly distributed (Arikawa and Stavenga, 1997; Wakakuwa et al., 2005). Thus, it seems that the random arrangement of photoreceptors is a general pattern characteristic of insect color vision, predicting a significantly poorer resolution for color than for luminance vision.

1.29.9   Separation of Chromatic and Achromatic Vision

In humans, the chromatic aspects of color (hue and saturation) remain largely invariant when the intensity of a light stimulus varies. However, because color vision can be achieved by neural mechanisms that are sensitive to changes in light intensity (Brandt and Vorobyev 1997) animals that evolved color vision independently from the ancestors of humans can process color by neural mechanisms that do not permit separation of chromatic and achromatic vision. Therefore, invertebrates may have color vision that differs substantially from ours. Interestingly, behavioral experiments reveal striking similarities between color coding in bees and humans. Similar to humans, bees have three spectral receptor types, all of which are used for chromatic vision that is not sensitive to changes in stimulus intensity (Menzel, 1979; Menzel and Backhaus, 1991). Bees also have achromatic vision, which is mediated by their green receptor alone (for review see Giurfa and Vorobyev, 1997). In bees, as in humans, the spatial resolution of achromatic vision is better than that of chromatic vision. Bees detect and discriminate large stimuli (subtended angle >15 degrees) on the basis of chromatic cues alone (Giurfa et al. 1996, 1997), whereas small stimuli (subtended angle <15 degrees) are detected and discriminated on the basis of achromatic cues alone (Giurfa and Vorobyev, 1998). Low spatial resolution may be a general feature of chromatic vision, because the signal-to-noise ratio can be improved by spatial summation of receptor signals. Indeed, comparisons of physiological recordings of receptor noise with behavioral thresholds shows that honeybees sum signals of individual photoreceptor cells to improve the signal-to-noise ratio (Vorobyev et al., 2001). The random arrangement of receptors may be a consequence of the low spatial resolution of chromatic vision, because there is no selective advantage in arranging all spectral receptor types

within one ommatidium, if the receptive field for chromatic vision summates signals from many ommatidia. On the other hand, where receptors are arranged randomly in the retina, chromatic vision must utilize signals averaged over large areas. It remains unclear whether the separation of chromatic and achromatic vision is widespread among invertebrates.

1.29.10   Why ColorVision?

Color vision is useful for many tasks, and it is difficult to pinpoint one particular reason for the origin of color vision in animals (Vorobyev, 2004; Lind et al., 2017). However, two hypotheses explaining the origin of color vision have been widely discussed in the literature.

1. Color vision could have appeared as a general adaptation for seeing objects in conditions of patchy and changing illumination (Maximov, 2000). Since shadows yield strong variations in the intensity of illumination, achromatic vision is unreliable.Chromatic signals provide much more information about object material and can be used for reliable discrimination of objects from their backgrounds.
2. Color vision could have appeared as a specific adaptation for looking at colorful signals of plants and animals, which in turn could have coevolved with color vision. In the late 19th century, a prominent Canadian writer, Grant Allen, summed up the coevolution hypothesis for the origin of color vision in the following condensed formula: "Insects produce flowers. Flowers produce the color-sense in insects. The color-sense produces a taste for color. The taste for color produces butterflies and brilliant beetles" (Allen, 1879).

Analysis of relationship between insect spectral sensitivities and flower spectra does not support the hypothesis that "flowers produce color-sense in insects" (e.g. Vorobyev and Menzel, 1999). In particular, it appears that the photoreceptors in flower foraging bees are practically identical to those in predatory wasps (Peitsch et al., 1992). Therefore, it is more likely that flowers exploited the preexisting color vision systems, which could have evolved for general tasks such as detection and identification of a variety of objects in conditions of patchy and changing illumination (Maximov, 2000; Vorobyev, 2004). On the other hand, in accordance with a co-evolution hypothesis, color vision of some colorful butterflies probably coevolved with wing coloration (e.g. Briscoe et al., 2010).

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