Spectral tuning and the visual ecology of mantis shrimps

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The compound eyes of mantis shrimps (stomatopod crustaceans) include an unparalleled diversity of visual pigments and spectral receptor classes in retinas of each species. We compared the visual pigment and spectral receptor classes of 12 species of gonodactyloid stomatopods from a variety of photic environments, from intertidal to deep water (> 50 m), to learn how spectral tuning in the different photoreceptor types is modified within different photic environments. Results show that receptors of the peripheral photoreceptors, those outside the midband which are responsible for standard visual tasks such as spatial vision and motion detection, reveal the well-known pattern of decreasing λ_{max} with increasing depth. Receptors of midband rows 5 and 6, which are specialized for polarization vision, are similar in all species, having visual λ_{max}-values near 500 nm, independent of depth. Finally, the spectral receptors of midband rows 1 to 4 are tuned for maximum coverage of the spectrum of irradiance available in the habitat of each species. The quality of the visual worlds experienced by each species we studied must vary considerably, but all appear to exploit the full capabilities offered by their complex visual systems.

Keywords: visual ecology; stomatopod; visual pigment; spectral sensitivity

1. INTRODUCTION

Mantis shrimps, properly called stomatopod crustaceans, possess some of the most highly specialized and unusual visual systems in existence. These marine invertebrates generally inhabit shallow, tropical waters, living either within cracks and crevices of coral reefs or in excavated burrows in muddy or sandy substrates. Unlike most crustaceans, they are cursorial predators that actively hunt down, chase and capture living prey (Caldwell & Dingle 1975). Adaptations for this high-energy lifestyle include a pair of powerful raptorial appendages used to spear, stun or dismember prey and a suite of sense organs—including the highly evolved compound eyes—that enable the detection and recognition of other animals at a distance.

The apposition compound eyes of stomatopods include up to several thousand ommatidia and are always divided into three distinct parts: the dorsal region (or hemisphere), the midband and the ventral region. Eye design varies among stomatopod taxonomic groups (Manning *et al*. 1984). Probably the most interesting eyes are found in members of the superfamilies Gonodactyloidea and Lysiosquilloidea, where the midbands are composed of six parallel rows of ommatidia, and each ommatidial row has unique specializations that enhance the analysis of spectral and polarizational features of light (Marshall 1988; Marshall *et al*. 1991*a,b*). In these animals, vision is critical for signalling between individuals and species (Caldwell & Dingle 1975; Marshall *et al*. 1999).

2. SPECTRAL TUNING IN STOMATOPOD RETINAS

In this paper, we will consider how spectral sensitivities of gonodactyloid stomatopod eyes may be adaptive for species from different photic environments. The stomatopods are uniquely capable of spectrally tuning their visual systems, because rhabdoms in the four dorsal rows of the midband region (termed rows 1 to 4) are divided into a series of tiers, such that light entering a particular layer may have previously passed through several successive optical elements. Each tier includes a particular visual pigment, a photostable and strongly coloured filter pigment, or both. The arrangement leads to sharp spectral tuning of individual receptor classes and produces an unequalled diversity of spectral sensitivity classes in a single retina. Here, we will focus on the receptors in the main rhabdoms (retinular cells 1 to 7). Besides these, the eighth retinular cells include several classes of ultraviolet-sensitive receptors (Marshall & Oberwinkler 1999).

We characterized the spectral visual systems of a dozen gonodactyloid species, using microspectrophotometry of cryosectioned retinas, and computed spectral sensitivity functions for all photoreceptor classes (see, for example, Cronin & Marshall 1989; Cronin *et al*. 1994). A typical example is given in figure 1, which shows data obtained from *Gonodactylaceus mutatus* (formerly *Gonodactylus aloha*), a species that occupies shallow-water habitats in Hawaii.

Like most gonodactyloid stomatopod species, retinas of *G. mutatus* include four classes of intrarhabdomal filters, two each in all ommatidia of midband rows 2 and 3 (see
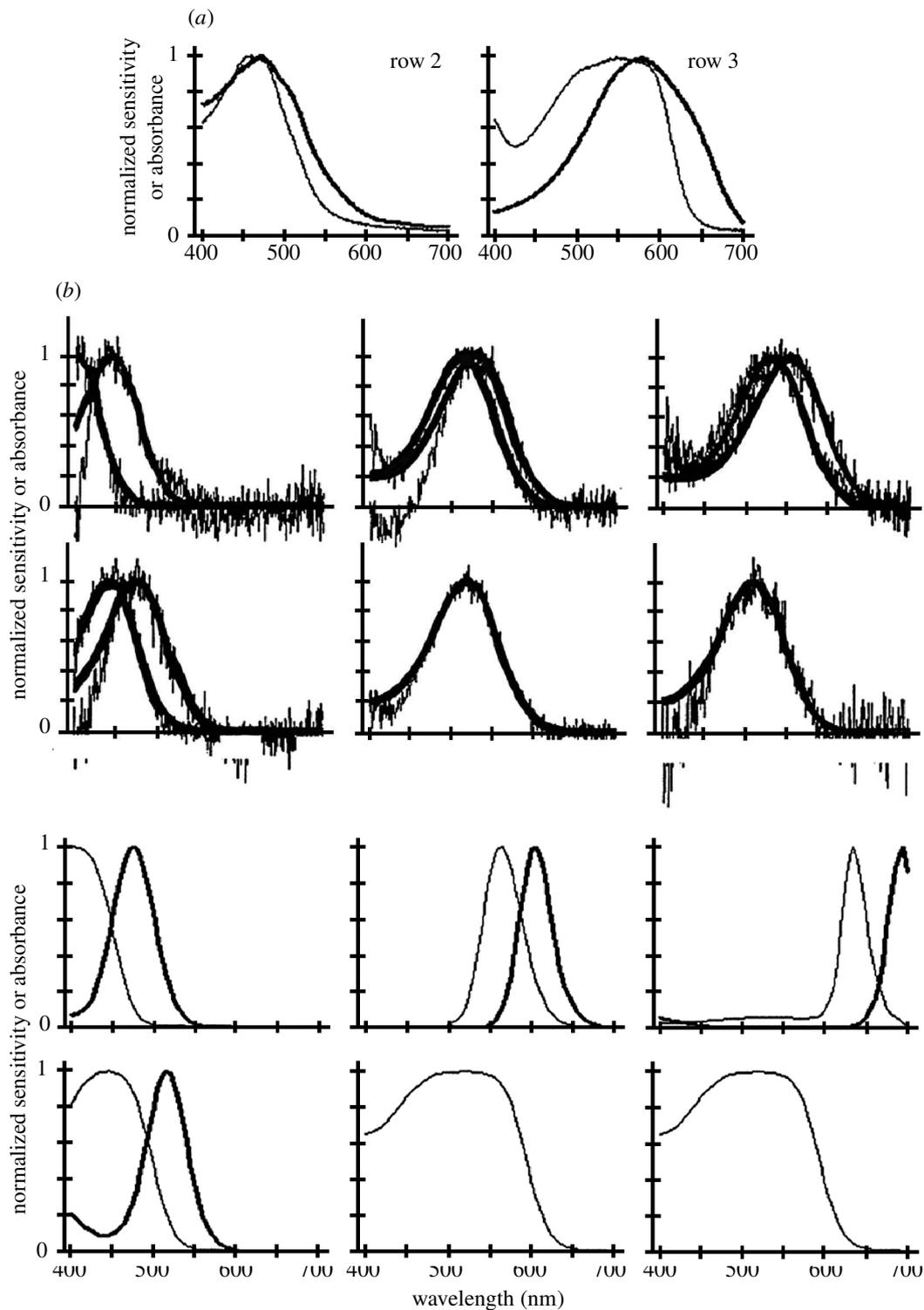
Figure 1. *G. mutatus*. (*a*) Normalized absorbance spectra of intra-rhabdomal filters in rows 2 and 3 of the midbands of the compound eyes. Each panel illustrates the filters from one row. Light trace, distal filter; dark trace, proximal filter. (*b*) Normalized absorbance spectra (light, jagged traces) and best-fit templates (dark, smooth traces) of visual pigments in the main rhabdoms of each retinal region of the compound eyes. Rows 1 to 6 refer to the midband region (rows 5 and 6 contain the same visual pigment); 'periphery' refers to the peripheral retina. The main rhabdoms in rows 1 to 4 have two tiers, each with a different visual pigment; the visual pigment of the proximal tier always absorbs at longer wavelengths than that of the distal tier. Best-fit template spectra have the following maxima: row 1 distal tier, 400 nm; row 1 proximal tier, 443 nm; row 2 distal tier, 513 nm; row 2 proximal tier, 527 nm; row 3 distal tier, 532 nm; row 3 proximal tier, 553 nm; row 4 distal tier, 443 nm; row 4 proximal tier, 475 nm; rows 5 and 6, 518 nm; peripheral retina, 510 nm. (*c*) Computed spectral sensitivities of all main rhabdoms or tiers. Each panel shows the sensitivity of one retinal region, as for visual pigments (above). In panels for rows 1 to 4, light traces illustrate sensitivities of distal tiers and dark traces illustrate proximal tiers. Sensitivity maxima (rounded to the nearest 5 nm) are as follows: row 1 distal tier, 400 nm; row 1 proximal tier, 465 nm; row 2 distal tier, 560 nm; row 2 proximal tier, 605 nm; row 3 distal tier, 635 nm; row 3 proximal tier, 695 nm; row 4 distal tier, 445 nm; row 4 proximal tier, 515 nm; rows 5 and 6, 520 nm; peripheral retina, 510 nm.

also Marshall 1988; Marshall *et al.* 1991*b*; Cronin *et al.* 1994). These act as long-pass spectral filters, with those of row 2 transmitting light in a shorter wavelength range than those of row 3 (figure 1*a*). Since each filter lies above its own photoreceptor tier, they alone are sufficient to produce a well-tuned, spectrally diverse receptor set. Additional complexity, however, is afforded by the diverse assortment of visual pigments present in the same retina (figure 1*b*). Each tier of the main rhabdoms in rows 1 to 4 has its own visual pigment. Main rhabdoms of rows 5 and 6 include another visual pigment, and a tenth visual pigment class occurs throughout the main rhabdoms of all peripheral (dorsal and ventral region) ommatidia.

In midband rows 1 to 4, the visual pigments of the distal tiers themselves act as long-pass filters for the proximal tiers. Thus, in every case the distal pigment absorbs at shorter wavelengths than the proximal pigment, by about 25 nm. The arrangement sharpens spectral sensitivity functions of proximal tier photoreceptors, and the effect is augmented by the action of the filters in rows 2 and 3. Computed spectral sensitivity functions resulting from these combinations, taking the pigment absorbances and retinal dimensions into account, are plotted in figure 1*c*. Each tier contains one narrowly tuned spectral receptor class, that collectively cover the spectral range from below 400 to beyond 700 nm. Receptors in rows 1 and 4, which are sensitive at the shortest wavelengths, are tuned by the tiering of visual pigments alone. Receptors in rows 2 and 3 are more strongly influenced by the presence of the intra-rhabdomal filters. For instance, in row 3, where the filters are transmissive only at very long wavelengths, spectral sensitivities peak at wavelengths 100 nm or more beyond the $\lambda_{\max}$-values of the associated visual pigments. Here, tuning causes a great loss of absolute sensitivity (see also Cronin *et al.* 1994). In contrast to the tiered receptors, those of the ventral midband rows and the rest of the retina have the broad, flat-topped sensitivity functions characteristic of long photoreceptors.

3. SPECIES PATTERNS OF VISUAL PIGMENTS AND SPECTRAL SENSITIVITIES

Stomatopod visual pigments vary extensively even among closely related species (Cronin *et al.* 1996). To illustrate variations on a broader taxonomic and ecological scale, we have plotted $\lambda_{\max}$-values of visual pigments (figure 2*a*) and spectral sensitivity functions (figure 2*b*) in 12 gonodactyloid species. (Spectral sensitivity functions are computed as in figure 1; see also Cronin *et al.* 1994.) Each major panel of the graph shows data for all retinal regions (including both main rhabdomal tiers in rows 1 to 4) for all species.

Considering first the $\lambda_{\max}$-values of visual pigments (which cover the spectral range from 400 nm to just over 550 nm), we see an overall consistency in the pattern of deployment throughout the retina. As in *G. mutatus*, visual pigment $\lambda_{\max}$ tends to increase in the tiered rows in the sequence row 1, 4, 2 and 3, and proximal tiers absorb at longer wavelengths than distal tiers. Rows 5 and 6 and the periphery tend to have visual pigments absorbing near the middle of the visual spectrum. There is considerable interspecific diversity within this overall pattern,

such that visual pigments from any given receptor class commonly vary in $\lambda_{\max}$ over a 20–50 nm range, with the rhabdoms of the peripheral retina showing the greatest variation.

Filtering by visual pigments and the stable intra-rhabdomal filters spreads spectral sensitivity $\lambda_{\max}$-values over twice the range occupied by the visual pigments and separates sensitivity maxima of the proximal and distal tiers. In row 3, particular pairings of filters with visual pigments lead to interspecific variations of nearly 75 nm. In contrast, the structurally simpler receptors in rows 5 and 6 and the periphery are most sensitive at the $\lambda_{\max}$ of the visual pigment.

4. ENVIRONMENTAL ASPECTS OF SPECTRAL TUNING

The availability of data from so many homologous photoreceptor classes of animals from diverse habitats allows us to explore how vision may be tuned for a variety of tasks within specific photic environments. The peripheral retina contains 'general purpose' receptors, responsible for spatial vision, motion detection and general visual tasks throughout the day and night. In this receptor class, visual pigment $\lambda_{\max}$ decreases as habitat depth increases (figure 2, right-hand side). This trend is common in aquatic animals, and it maintains high sensitivity as ambient light becomes bluer at greater depths (see Cronin *et al.* 1994). It is interesting to note that the greatest extremes in $\lambda_{\max}$ are found in two species within the same genus, *Neogonodactylus oerstedii* (528 nm) and *Neogonodactylus curacaoensis* (470 nm); see also Cronin *et al.* (1996).

Photoreceptors in midband rows 5 and 6 are specialized for polarization vision (Marshall *et al.* 1991*a*, 1999). There has been no previous study of variations in polarization vision in aquatic habitats, so the gonodactyloids in our study group provide a unique first opportunity to examine spectral tuning of polarization receptors. Surprisingly, the polarization receptors seem to be spectrally more conservative than the receptors of the peripheral retina (compare 'rows 5 and 6' with 'periphery' in figure 2), although there is again a suggestion of declining $\lambda_{\max}$ with increasing habitat depth. These somewhat unexpected results emphasize that a quantitative description of polarization in water is badly needed; this is particularly true because so many aquatic animals rely on polarization vision. Our data imply that aquatic systems of polarization vision may routinely examine light just beyond 500 nm (note that this does not include the ultraviolet polarization classes, which also exist in stomatopod retinas; see Marshall *et al.* 1991*a*; Marshall & Oberwinkler 1999).

The greatest spectral diversity of receptor classes occurs, of course, in the tiered midband rows 1 to 4. In general, the spectral sensitivity range encompassed by midband receptors tends to be compressed in species living at greater depths (see also Cronin *et al.* 1994). Thus, in the deeper-living species, receptors in rows 1 and 4 may show a slight tendency to increase $\lambda_{\max}$, while those of the proximal tier of row 2, and both tiers of row 3, move to shorter wavelengths. In rows 2 and 3, these changes are primarily due to variations in intra-rhabdomal filters.
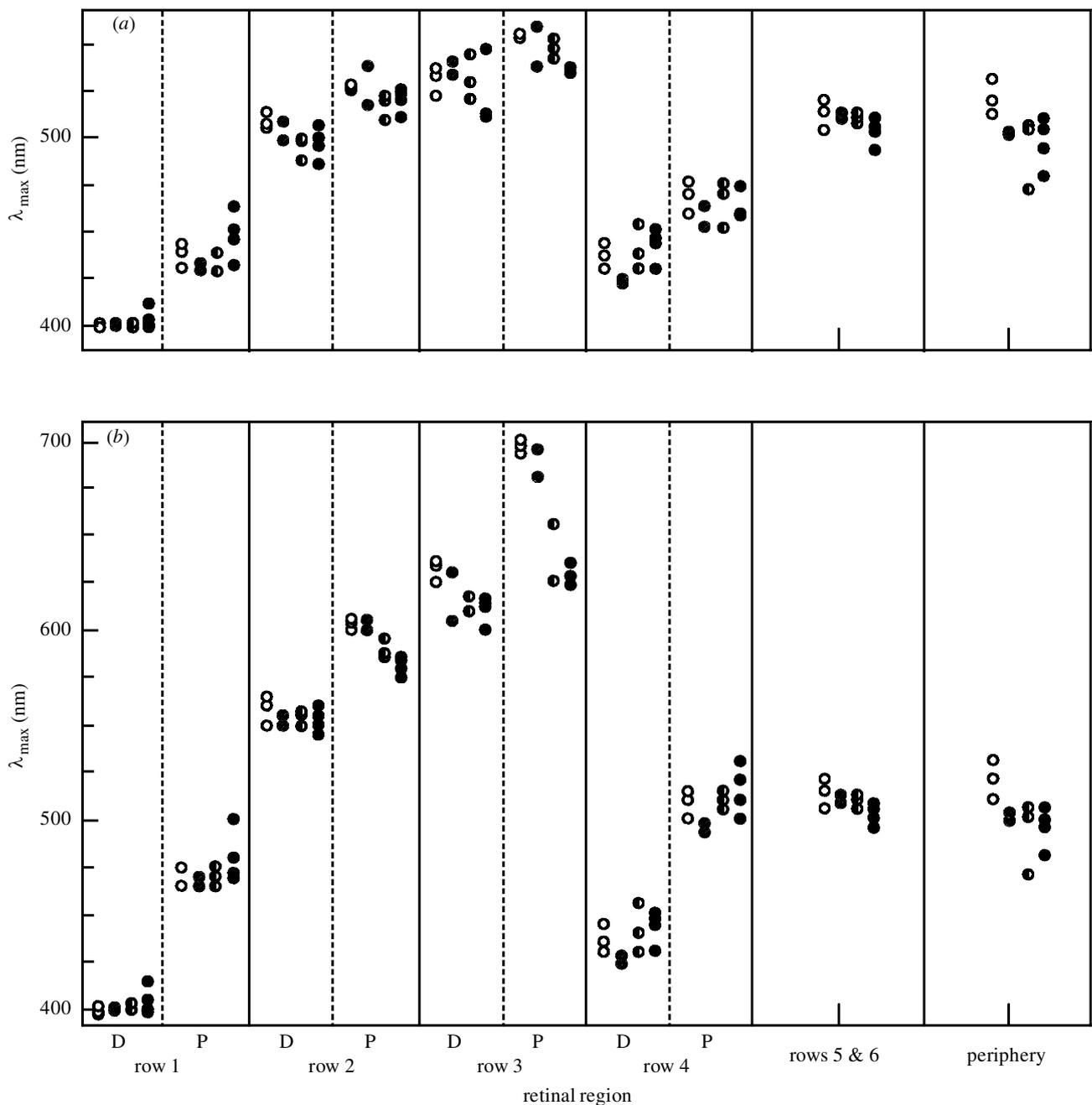
Figure 2. Spectral maxima of (*a*) visual pigment absorbances and (*b*) spectral sensitivities in 12 species of gonodactyloid stomatopod crustaceans from four classes of photic environments. Each panel of the figure includes data from main rhabdoms of all retinal regions, with each plotted point representing data from one class of receptor from one species. Each retinal region is plotted in an enclosed rectangle; in the tiered rows 1 to 4, this area is subdivided by a dashed vertical line so that each tier is plotted separately (D, distal tier; P, proximal tier). Species have been assigned to four photic environmental classes, based on their most common depths of occurrence: open circles, intertidal; hatched circles, shallow subtidal (< 5 m); half-filled circles, inhabiting a range of depths from shallow to deep; filled circles, deep (5–50 m). Included species and their environmental class assignments are as follows: intertidal, *Gonodactylus smithii*, *Gonodactylaceus mutatus* and *Neogonodactylus oerstedii*; shallow subtidal, *Pseudosquilla ciliata* and *Haptosquilla trispinosa*; range of depths, *Gonodactylellus affinis*, *Gonodactylopsis* sp. A and *Odontodactylus scyllarus*; deep, *Hemisquilla ensigera*, *Neogonodactylus curacaoensis*, *Odontodactylus brevirostris* and *Odontodactylus havanensis*.

Osorio *et al.* (1997) hypothesized that the narrowly tuned spectral classes in stomatopod retinas are specialized for robust colour constancy in a photically variable world. Matching the spectral range of receptors to local irradiance clearly is consistent with such a hypothesis. An odd consequence of this is that closely related species may have quite different visual worlds (at least, in terms of

colour appearance), which must complicate interspecific signalling (see Caldwell & Dingle 1975). Gonodactyloid stomatopods apparently go to some extremes to preserve their long-wavelength receptor classes in row 3, which often operate at the very edge of photon starvation. Indeed, in the deep-living populations of some species, receptors in row 3 degenerate or contain no measurable

visual pigments (Cronin *et al.* 1996). Clearly, in species living near the photon limit, selection for complete spectral coverage in some individuals must be strong enough to override partial loss of visual function in others that may live only a few metres deeper.

5. CONCLUSIONS

The polychromatic visual systems of gonodactyloid stomatopods vary with depth in patterns that are likely to be adaptive. Spectral range of the narrowly tuned receptors in the tiered, filtered receptor classes is matched to the bandwidth of ambient light at different depths, maintaining function even at the very limits of the available spectrum. Visual pigments in the receptors of the peripheral retina (responsible for pattern and motion vision) are most likely adapted for high sensitivity at the preferred depth of each species. Polarization receptors, on the other hand, are spectrally among the least variable of all classes we examined, implying that the analysis of polarized light is optimally performed at wavelengths near 500 nm at all depths. An unusual consequence of the tuning of spectral function in these animals is that colour space may vary wildly among species, complicating interspecific signalling.

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