

Citation:

Cronin TW, Porter ML, Bok MJ, Caldwell RL, Marshall J. 2022 Colour vision in stomatopod crustaceans. *Phil. Trans. R. Soc. B* 377: 20210278. <https://doi.org/10.1098/rstb.2021.0278>

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

BIOLOGICAL SCIENCES

Color Vision in Stomatopod Crustaceans

Journal:	<i>Philosophical Transactions B</i>
Manuscript ID	Draft
Article Type:	Review
Date Submitted by the Author:	n/a
Complete List of Authors:	Cronin, Thomas; UMBC, Department of Biological Sciences Porter, Megan; University of Hawai'i-Mānoa, Bok, Michael; Lund University Faculty of Science, Biological Sciences Marshall, Justin; University of Queensland, School of Biomedical Sciences
Issue Code (this should have already been entered and appear below the blue box, but please contact the Editorial Office if it is not present):	COLVIS
Subject:	Neuroscience < BIOLOGY, Behaviour < BIOLOGY, Physiology < BIOLOGY
Keywords:	Stomatopod, color vision, ultraviolet vision, filtering, visual ecology, visual genetics

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Authors' contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):
All authors contributed equally to the research of the paper. Thomas W. Cronin wrote the paper; the other three authors contributed suggestions for edits.

COLOR VISION IN STOMATOPOD CRUSTACEANS

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Keywords: Stomatopod, color vision, ultraviolet vision, filtering, visual ecology, visual genetics

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Abstract

The stomatopod crustaceans, or mantis shrimps, are colorful marine invertebrate predators. Their unusual compound eyes have dorsal and ventral regions resembling typical crustacean apposition designs separated by a unique region called the midband that consists of from two to six parallel rows of ommatidia. In species with six-row midbands, the dorsal four rows are themselves uniquely specialized for color analysis. Rhabdoms of ommatidia in these rows are longitudinally split into three distinct regions: an apical ultraviolet receptor, a shorter-wavelength distal tier receptor and a longer-wavelength proximal tier receptor. Each of the total of 12 photoreceptors has a different spectral sensitivity, potentially contributing to a color-vision system with 12 primaries. Mantis shrimps can discriminate both human-visible and ultraviolet colors, but with limited precision compared to other color-vision systems. Here, we review the structure and function of stomatopod color vision, examining the types of receptors present in a species, the spectral tuning of photoreceptors both within and across species, the neural analysis of color, and the genetics underlying the multiple visual pigments used for color vision. Even today, after many decades of research into the color vision of stomatopods, much of its operation and its use in nature remain a mystery.

1. Introduction

These days, it seems like everyone “knows” that mantis shrimps (properly called stomatopod crustaceans) have the best color vision in the animal kingdom. This idea, along with stories about their famous predatory strikes, has been promoted widely in popular media. But do these animals even have color vision? If so, what is the physiological and neural basis for this ability?

And if they do discriminate visual objects on the basis of their colors, is their color vision indeed the best of all known animals? This review intends to discuss all these aspects of stomatopod vision, provide a thorough background that covers what we know, and speculate on the limits and abilities of their color vision systems.

The unique retinal structure of mantis shrimp eyes, similar to the typical crustacean design but decidedly more complex, is well described (Marshall et al 1991a,b). The novel retinal design underlies the ability of these animals to have unique color-analysis receptor sets (in addition to receptors devoted to linear and circular polarized-light analysis, not discussed here). Mantis shrimps, crustacean Subclass Hoplocarida, Order Stomatopoda, are taxonomically separated into seven superfamilies (Ahyong and Harling, 2000; Ahyong and Jarman, 2009; Porter et al.; 2010; Van der Wal et al., 2017). Coincidentally, there are seven main eye designs in these animals as well, although eye design in itself is not a reliable taxonomic indicator (Harling, 2000). Almost all mantis shrimp eyes, with the exception of the poorly known deep-sea species, have eyes divided into three distinct regions (see Fig. 1A,B): the distinct dorsal and ventral hemispheres (also referred to as the peripheral retina), which have essentially hexagonal arrays of ommatidia, separated by a central midband region made up of two to six parallel rows of ommatidia.

Stomatopod eyes with two-row midbands, found only in members of the superfamily Squilloidea, apparently have identical photoreceptors throughout the eye, based on their anatomical appearance (Schönenberger, 1977). The eyes with the greatest expansion of photoreceptor types and the greatest variety of receptor classes are those with six midband rows (Figure 1A,B). These occur in all other stomatopods (except for those in the relatively rare species of the Superfamily Parasquilloidea and the deep sea Bathysquilloidea). Here, as far as is known, the photoreceptors throughout the peripheral retina all have identical spectral

sensitivities: an ultraviolet (UV) receptor type, occurring in the 8th retinular cell (R8) at the top of the rhabdom, and a middle-wavelength type in the main rhabdom constructed of the other seven retinular cells (R1-R7; see Fig. 1C) (Cronin and Marshall, 1989a,b; Cronin et al., 1994a; Cronin and Marshall, 2004; Marshall et al., 2007). In contrast, the six rows of the midband are all distinctive. In the dorsal four of these rows, the main rhabdom is broken into two tiers (Figure 1B). Adding to the complexity, the second and third of the tiered rows have photostable filter structures incorporated into the rhabdom at the junctions where rhabdomal tiers meet, which play critical roles in tuning stomatopod color vision (Cronin et al. 1994b, Cronin et al., 2014, Marshall, 1988; Marshall et al., 1991a,b).

2. Color vision in the visible light range

Throughout stomatopods, color vision in the human-visible range is the responsibility of the main rhabdoms, containing retinular cells R1 to R7. The spectral absorbance of these photoreceptors has been established using microspectrophotometry (MSP) in at least 19 stomatopod species. The first to be examined, *Squilla empusa*, turned out to be exceptionally simple, with evidence for only a single visual pigment (peaking at 507 nm) in all receptors throughout the retina (Cronin, 1985). A second squilloid, *Cloridopsis dubia*, was similar, with all receptors peaking at 510 nm (Cronin et al., 1993). The same story holds with the peripheral retinas of all mantis shrimp species with 6-row midbands; in each species, all main rhabdoms have the same spectral absorbance. In stark contrast, the receptor set in the midband is spectacularly diverse (Chiao et al., 2000; Cronin and Marshall, 1989a,b, 2004; Cronin et al., 1993, 1994a, 1994c, 1996, 2002a; Jutte et al., 1998a; Thoen et al., 2014, 2017). Microspectrophotometric work suggests that six-row stomatopod species have ten visual

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3 pigments absorbing in the visible range: one in the peripheral retina, one in main rhabdoms of
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5 the two most ventral rows of the midband, plus eight in just the four dorsal, tiered rows of the
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7 midband (Figure 1B,C).
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10 Main rhabdoms in retinas of all described six-row species have a similar pattern of spectral
11 sensitivities. The peripheral photoreceptors respond in the middle-wavelength spectral range.
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13 Rows 5 and 6 of the midband (the two ventral rows) also have middle-wavelength main
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15 rhabdoms. The four tiered rows, numbered 1-4, are thought to be responsible for color vision.
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17 Here, distal-tier photoreceptors of the rhabdom are always sensitive to shorter wavelengths than
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19 those of the proximal tier of the same rhabdom. Across species, they are invariably arranged in
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21 the same order (going from dorsal to ventral): Row 1, very short-wavelength receptors (the
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23 sensitivities in a typical species, *Neogonodactylus oerstedii*, are graphed as the left-most receptor
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25 pair in Fig. 2B); Row 2, middle-wavelength receptors (the 3rd receptor pair in Fig. 2B); Row 3,
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27 long-wavelength receptors (right-most pair in Fig. 2B); Row 4, short-wavelength receptors
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29 (second pair in Fig. 2B). The spectral maxima of visual pigments have the same distribution in
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31 the receptor sets, although their maxima do not duplicate those of the sensitivity spectra (Fig.
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33 1C,D; this figure also includes two ultraviolet classes, found in R8 cells and discussed in the next
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35 section). The reason for the mismatch between the visual pigment absorbance and the spectral
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37 sensitivity is the heavy filtering of incoming light in the tiered rows. In Rows 1 and 4, the
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39 filtering of the proximal tier is primarily by the visual pigment in the distal tier, which
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41 simultaneously sharpens the spectral shape and shifts it to longer wavelengths (Cronin and
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43 Marshall, 1989a,b). Rows 2 and 3 carry this a step further. Here, strongly absorbing photostable
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45 colored filters between rhabdom tiers act as long-pass filters, shifting spectral sensitivity to
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47 wavelengths far longer than the absorption maximum of the visual pigment in each tier. This
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costs sensitivity, but in the bright shallow waters inhabited by many stomatopod species the payback is a series of eight narrow-band spectral receptors that march across the visible spectrum, covering a 300-nm spectral range (Fig. 2B). To some extent, optical specializations in midband ommatidia such as larger facets, shorter focal lengths, and longer and wider rhabdoms, compensate for the cost of the extensive filtering (Marshall and Land, 1993).

The spectral sensitivities portrayed in Fig. 2B are from a Caribbean, shallow-water species. Species from other habitats have different sets of sensitivities that are appropriately tuned for their specific photic environments (Cronin et al., 1994a,c, 2000). The general pattern with increasing depth is that sensitivities tend to move slightly to longer wavelengths in the shortest-wavelength receptors of Row 1, to remain about the same in Row 4, and to decrease in the wavelength of peak sensitivity in Row 2 and 3 (Fig. 3). The changes in sensitivity among species are produced both by using different sets of visual pigments (Cronin et al., 1996; Jutte et al., 1998a) and different sets of photostable filters (Cronin et al., 1994c, 2002b, 2014; Jutte et al., 1998a). The visual pigment variation in spectral absorbance is much less significant in environmental tuning than the changes in the filters, however. In single species that inhabit a range of depths, the visual pigment sets are invariant, but the retinal photostable filter sets vary depending on the depths inhabited by different individuals (Cronin et al., 2002a,b). The result is a diversity of populations of the same species, each appropriately tuned to the light available at the depth of its habitat. This habitat-specific tuning allows all species to maintain color vision, despite variations in the spectral properties of the environment they inhabit.

Mantis shrimps are often strikingly colorful, and there is strong behavioral evidence that they use true color vision. Marshall et al. (1996) trained *Odontodactylus scyllarus* to recognize cubes marked with a colored face that contained food and to discriminate them from cubes marked

with a range of neutral grays. Later, Thoen et al. (2014) trained members of a different species, *Haptosquilla trispinosa*, to discriminate paired spectral lights from each other. Most recently, Patel et al. (2021) demonstrated that individuals of *Neogonodactylus oerstedii* can discriminate identical objects of different colors (red vs. green), choosing the correct color. All these tests involved a food reward, but it seems likely that stomatopods also use their color vision in species recognition and signaling, although these situations have not yet been investigated.

3. Color vision in ultraviolet light

Up to this point, the discussion has presented the potential for color vision in human-visible light. Beyond this, the six classes of R8 cells (e.g. peripheral, Row 1, Row 2, Row 3, Row 4, and Rows 5&6; Bok et al., 2018; Marshall et al., 1991a) add at least five UV-specialist spectral classes to the mélange (Bok et al., 2014, 2018; Marshall and Oberwinkler, 1999; Marshall et al., 2007) (Fig. 2A). In contrast to the visual pigment diversity in visible-light color receptors in Rows 1 to 4, however, these cells express only two UV visual pigments (Bok et al., 2014; Porter et al., 2020), and possibly only one in some species! One of these visual pigments has an absorbance peak at about 385 nm, but the other is very unusual, peaking at the very short wavelength of ~334 nm (Bok et al., 2014; Cronin et al., 1994d).

As in some of the midband photoreceptors, the diverse spectral tuning of UV receptors is produced using photostable filters, in this case ones that absorb in the ultraviolet. These filters have several unique features (see Bok et al., 2014, 2015). First of all, they are located in the crystalline cones, not in the actual photoreceptors. They consist of mycosporine-like amino acids (MAAs) – compounds that are most commonly used in animals for UV photoprotection, as they are strong absorbers of UV light. This property, of course, also makes them effective UV

filters for use in vision, although only the mantis shrimps have been shown to use them in this way. In contrast, the filters in the rhabdoms probably are formed from carotenoproteins (Cronin et al., 1994b). The absorbance spectra of MAAs are rather narrow. Consequently, they can be used either as short-pass or long-pass filters. Mantis shrimps use them in both ways, depending on the spectral match of the MAA's transmission spectrum and the UV visual pigment's absorption spectrum. The use of short-pass light filters in vision is possibly unique to mantis shrimps, as they have not been reported in any other animals. Most visual filters are carotenoids, as in the cone oil droplets of numerous vertebrates or carotenoproteins, and are used as long-pass filters. Like filters of the midband, the specific set of MAA filters in any given species is dependent on the depth range inhabited by that species. Since water is an effective absorber of UV light, the filters in deeper-water species transmit more of it to underlying R8 photoreceptors. This is achieved by switching to filters that long-pass a broad range of UV and by decreasing the optical density of the filter (Bok et al., 2015). Overall, in both the visible and ultraviolet range, more of the ambient irradiance is passed to the photoreceptors of deeper-living species by using filters that are increasingly transmissive of wavelengths in the restricted range of the irradiance spectrum. Besides acting in ultraviolet vision, the MAA filters and the UV visual pigments in R8 cells remove UV light, filtering the light arriving at the underlying main rhabdom color receptors.

Not surprisingly, given our UV blindness, studies of color vision in the UV are rarely done. Many animals, both vertebrates and invertebrates, take advantage of potentially "secret" intraspecific UV signals, and their various UV "colors" could be meaningful (Cronin and Bok, 2016). Once again using food as a reward, individual *Haptosquilla trispinosa* were found to

discriminate 351 nm from 378 nm and from 314 nm (Bok et al., 2018). This is the first documented case of wavelength discrimination solely among UV wavelengths.

4. Flexibility in the mantis shrimp color vision system

We've already discussed how mantis shrimp color vision is evolutionarily tuned for effective function in the range of ambient photic conditions produced by water quality and depth. For example, we noted how species vary to some extent in their visible-wavelength-absorbing visual pigment complement (Cronin et al., 1996, 2002a). In general, deep-living species have slightly longer-wavelength visual pigments in their shortest-wavelength visible-light receptors and shorter-wavelength pigments in the long-wavelength receptor set (Cronin et al., 1994c, 2000). Much more aggressive tuning of the visible-light color receptors is executed by using a diversity of colored intrarhabdomal filters (Cronin et al., 1994a, 2002b). As noted, these are responsible for the spectral-sensitivity placements of photoreceptors in Row 2 and especially Row 3 illustrated in Fig. 3. Similarly, tuning of filters for enhanced UV sensitivity is produced by variations in the MAA filters in appropriate crystalline cones (Bok et al., 2015). Very few measurements have been made of UV photoreceptor visual pigment absorbance spectra (Bok et al., 2014; Cronin et al., 1994e), so at this point we don't know whether the UV visual pigments spectrally vary among species.

Adaptive, presumably evolutionary, spectral variation among tuning filters across species living in different photic environments is interesting, though perhaps expected. More surprising is the observation that filter sets can vary within a single species, depending on where the adults live (Cronin et al., 2002b). In contrast, visual pigments do not vary at all within species (Cronin et al., 2002a). Not all species seem to be capable of making these filter tuning adjustments; those

with restricted habitat ranges appear to have fixed filter sets (Cheroske et al., 2006). Whenever changes do exist, they invariably occur in the distal and proximal filters of midband Row 3 (Cheroske et al., 2003, 2006; Cronin et al., 2001, 2002b).

We originally thought that the filter set was fixed within an individual, and that the choice of the specific filter was made at the time of metamorphosis, depending on the light environment experienced at that time (Cronin et al., 2001). A chance observation made on a population of animals (*Gonodactylopsis spongicola*) collected at 15 m depth but maintained in bright white light revealed to our surprise that a single retina could contain a variety of filter types. Furthermore, the longer the animals were kept on the lab bench, the greater the proportion of filters with far-red-shifted long-wavelength transmission (Cronin et al., 2002b). Experiments subsequently showed that individual adult animals of a single species (*Pullosquilla litoralis*) tuned the placement of their Row 3 filters to shorter wavelengths when placed in either blue or dim white light compared to their placement in bright white light. This indicates that the tuning response is controlled by the level of stimulation in the photoreceptor paired with the filter, not by the wavelength content of the light. Interestingly, similar experiments with *Haptosquilla trispinosa*'s ultraviolet filter sets found no differences between individuals maintained in natural light vs. complete darkness (Bok et al., 2015). These results suggest that the UV filter sets are relatively inflexible. As far as we know, mantis shrimps are the only invertebrates that can flexibly retune their color vision as adults.

5. Do mantis shrimp larvae have color vision?

In common with many marine crustaceans, mantis shrimp have a planktonic larval phase in life before settling out on the sea-bed. In many ways these zooplankton are like the adults, in that

they are predatory and have large compound eyes with several unusual adaptations (Feller and Cronin 2017), but do they have color vision? The short answer to this question is “We don’t know”!

The compound eyes of the planktonic larvae of mantis shrimps are quite simple, resembling those of most crustacean larvae (but see Feller and Cronin, 2014; Feller et al., 2019). This fundamental design is amenable to remodeling into the various types of adult eyes (Nilsson et al., 1983; see also Cronin et al., 2017). But unlike all other crustaceans, the larval eyes are NOT remodeled into the far more complex eye structure of the adult eye. Instead, at metamorphosis, the larval eye begins to degenerate and the adult eye with its associated neural centers of the optic lobe form medially to it. At the molt to the “postlarva” (which is essentially a tiny adult), the two retinas are about equal in size, but very soon the larval eye begins to regress. Within a few days the entire eyecup is occupied by the fully formed adult eye, with a midband and its intrarhabdomal filters in place. For a brief period, both retinas are physiologically active (Feller et al., 2015), but within a week all signs of either the physiological or the anatomical presence of the larval eye and its series of optic neuropils have disappeared (Lin and Cronin, 2017; Cronin et al., 2017). This odd process of completely replacing a larval compound eye retina and all its associated optic lobe neuropils with an adult retina and neural apparatus that develops simultaneously with the larval eye’s disappearance is unknown in any other arthropod.

The larvae, naturally, must be fully functioning animals during their time in the plankton, where they survive, feed, and avoid predators over several developmental stages before metamorphosing. Their well-developed eyes certainly suggest that vision is important to them. MSP studies of stomatopod larval rhabdoms suggest that each species has a single middle-wavelength visual pigment which is invariant throughout the retina and often different from any

adult pigment (Cronin and Jinks, 2001; Feller and Cronin, 2016). Behavioral experiments based on phototactic responses of larvae of other crustaceans suggest that there are probably two receptor classes, a middle-wavelength type and an ultraviolet type (Forward and Cronin, 1979). The presence of UV sensitivity has recently been confirmed in the eyes of *N. oerstedii* larvae using both molecular and physiological research approaches (McDonald et al., in press).

A recent study found good evidence for color recognition in a larval prawn (Kawamura et al., 2016). The larvae strongly preferred blue- or white-colored beads (spectral reflectance unspecified) over beads of any other color, include a range of shades of gray. This behavior demonstrates color preference, not color vision, and is thus akin to wavelength-specific behavior (see Menzel, 1979). Still, it suggests the possibility of color processing in stomatopod larvae, and this would certainly be an interesting research project.

6. Color processing in optic lobe neuropils of stomatopod crustaceans

Most animals that have a high-quality color-vision system process color information using opponent channels, in which one color input (generally from a single spectral class of photoreceptor but sometimes a combination of classes) is set in opposition to another particular color input. The interneurons onto which these two inputs synapse receive stimulatory input from one color receptor class and inhibitory input from its opponent. Thus, the output from the interneuron indicates the balance between the two inputs. This provides a simplified information flow which is specific and high contrast between the inputs, enhancing color analysis. Aside from the wavelength-specific behaviors just mentioned, this sort of color processing was thought to be ubiquitous among animals. But as in many other aspects of their vision, mantis shrimps may process color using a different mechanism. Unexplained aspects of the original color-vision

experiments of Marshall et al. (1996), considered with the coarse wavelength discrimination discovered by Thoen et al. (2014) suggest that another mechanism may be at play. An alternative path to color vision is simply to encode each color by the receptor type from which it originates. In this case, a color is simply a pattern of individual receptor class stimulations, much like a bar code (Marshall and Arikawa, 2014; Thoen et al., 2014). One way to verify color encoding by stomatopods is to examine how the multiple receptors in the color-vision system, with eight visible-light classes plus up to four ultraviolet classes, are neurally connected to the neuropils of the optic lobes in the eyestalks of each eye.

In all ommatidia, each of the eight retinular cells that make up the rhabdom forms an axon. Axons from retinular cells R1-R7 directly reach the first optic neuropil below the retina, the lamina, where they synapse onto optic cartridges, one cartridge per ommatidium. This arrangement holds true for all ommatidia in stomatopod compound eyes; similar arrangements are seen in compound eyes of other crustaceans as well as of insects. In stomatopods, cartridges below midband Rows 1 to 4 are particularly large and have an unusual rectangular cross section. Axons from one tier of the midband, built from cells R1, R4, and R5, synapse in the upper level of this cartridge, and R2, R3, R6, and R6 synapse slightly lower, potentially setting up the circuitry for opponency (Kleinlogel and Marshall, 2005; Marshall et al., 2007; Thoen et al., 2017). Each of the two levels of the cartridge is linked to a monopolar cell that in turn sends its axon to the next layer of neuropil, the medulla. Here, inputs from the midband reach an expanded, specialized subsection of the medulla, which is so enlarged it creates a hernia-like extension outward from the medullar surface. Axons from here encounter several layers of the medulla before travelling further into the optic pathway.

Clearly, this arrangement hints at the processing of color into four distinct opponent channels, one for each midband row. This argues against the bar-code hypothesis. There's a wrinkle, however, due to the unusual wiring of the UV-sensitive R8 cells. In common with other arthropods, axons from R8 cells send long projections, mostly bypassing the lamina and terminating in the medulla, the second neuropil layer in the optic lobe. However, as axons of R8 cells of Rows 1 to 4 pass through the lamina, they laterally synapse onto the cartridges via extensions from the upper levels of their axons. This suggests the possibility of an additional opponency, leading Kleinlogel and Marshall (2005) to hypothesize visible/UV opponency.

All this complexity makes it difficult to understand mantis shrimp color vision. Color information could travel in four sets of opponent channels, with UV information incorporated in some unknown way. Alternatively, each single class of reticular cell could signal via a dedicated pathway. For instance, the monopolar cells from each layer of the lamina could encode a spectral channel, for a total of eight that reach the medulla, and the R8 axons extending to the medulla would add eight more. At this point, what we do know is that the retina is unusual, as is color vision at the behavioral level. While the neural organization of color vision has similarities with other arthropods that suggest a typical type signal processing with opponent mechanisms, there is also added - and unexplained - complexity. It is fair to say that our understanding of color vision in stomatopods is still a work in progress.

Experimental evidence currently supports the barcoding model, with 12 individual color channels. Thoen et al. (2014) clearly demonstrated that stomatopods discriminate spectral lights in the human-visible range only if they are separated by 15 to 25 nm, the worst color-vision performance system ever recorded. Predictions based on an opponent system perform far better than this. Butterflies and humans, for example, are able to discriminate 1-2 nm of spectral

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3 difference in some spectral regions. Still, while these data suggest that color is encoded as a
4 series of individual measurements, they were obtained in a single research project based on
5 paired lights, in which the experimental animal had to remember the correct color as well as
6 respond to it correctly to be rewarded with food. In a different experimental system, perhaps
7 targeting visual signal colors, or in another reward setting other than food, different results could
8 occur. Nevertheless, if stomatopods do categorize color immediately at the receptor level, this
9 would surely enhance their decision-making and simplify demands on the central nervous system
10 (see Marshall and Arikawa, 2014; Zaidi et al., 2014).
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22 7. Genetics of color vision in stomatopods

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26 Knowing that most stomatopods have a dodecachromatic color-vision system, a simple hypothesis
27 would postulate that each color class is based on a single visual pigment and thus a single opsin
28 protein type. Therefore, one would expect to find 12 color opsins expressed in the retina.
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30 Adding the two middle-wavelength visual pigments in Rows 5&6 and in the peripheral retina,
31 plus two UV visual pigments in these same regions gives a total of 16 opsins total.
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38 Surprisingly, however, even the first study of opsin expression in stomatopod retinas,
39 limited to middle-wavelength and long-wavelength types, recovered from ten to 15 unique
40 sequences in various species with 6-row midbands (Porter et al., 2009). The same study even
41 found six opsin genes expressed in the seemingly monochromatic eyes of *Squilla empusa*.
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43 Follow-up research suggested that the color opsins had diverged from those responsible for
44 polarization and spatial vision, but did not determine where the color opsins were expressed
45 (Cronin et al., 2010). The first transcriptomic study of the expressed opsins in these animals
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revealed the presence of up to 33 opsin transcripts, far more than the known photoreceptor diversity (Porter et al., 2013). What were all these opsins doing there, anyway?

To answer this question, Porter and several colleagues launched a research project that identified every single opsin transcript in eyes of *Neogonodactylus oerstedii*, using transcriptomics, and mapped the location of each to the photoreceptor type in which it was expressed using *in situ* hybridization (Porter et al., 2020). This exhaustive project recovered 33 opsin transcripts. Many photoreceptor classes, especially the main photoreceptors (R1-R7) of Rows 5&6 and peripheral ommatidia expressed multiple opsins (for details of their expression patterns, see Porter et al., 2020). On the other hand, there were only two ultraviolet-sensitive opsins expressed in retinal photoreceptors, and only as single transcripts in individual types of R8 photoreceptors. Here, the number of opsins available is less than the receptor diversity, unlike all of the main photoreceptor classes.

Of special significance for this review, opsin expression in the color receptors was relatively simple, totaling 10 types in main rhabdoms (see Fig. 4). Two opsins, designated NoL9 and NoL20, were expressed in all or most color receptor types; both were in the arthropod LWS opsin class (Porter et al., 2020; see Fig. 4 top left area). These two widely distributed opsins, which were not expressed in any other component of the retina, seem somehow connected to the color-vision system, but their roles are unknown. Given that they do not seem to appear in MSP data, it is very possible that their translation into protein is either very weak or that the opsin proteins do not bind chromophore. The other eight opsins that expressed in the color receptors, in arthropod LWS and MWS opsin classes, had a very simple pattern; each located to photoreceptors of only one tier of one row in Rows 1-4 (Fig. 4). In other words, each appears to designate the spectral sensitivity of the visual pigment formed in that tier. If so, their sequences

should be useful in studies of visual pigment tuning in arthropod photoreceptors. See Porter et al. (2020), for a thorough discussion of the significance of opsin types and their diversity in stomatopod retinas.

As mentioned earlier, there are only two ultraviolet opsins expressed in adult retinal photoreceptors, both in the arthropod SWS class (Bok et al., 2014; Porter et al., 2020). These same two opsins are also expressed in larval eyes, although their distributions within photoreceptors has not been established (McDonald et al., in press). Considering only midband photoreceptors, NoUV1 appears in the R8s of all midband rows except Row 1, and NoUV2 is expressed in the Row 1 R8 cell (Fig. 4, lower right). As the rhabdoms of these cells express single visual pigments, these are the only stomatopod visual pigments for which we are confident about their spectral absorbances. MSP reveals that NoUV1's visual pigment absorbs maximally at 334 nm (Bok et al., 2014), making it the shortest-absorbing visual pigment that is thoroughly documented (a similar visual pigment had been tentatively described over two decades earlier in several other stomatopod species, but its spectrum was incomplete; see Cronin et al., 1994d). On the other hand, NoUV2 peaks at 383 nm (Bok et al., 2014), not unusual for an SWS visual pigment. The spectral diversity of the UV photoreceptors potentially active in color vision is determined by the MAA filters that overlie them (Bok et al., 2014, 2015).

8. What is the function of color vision in mantis shrimps?

Given the surprising expansion of the region of the eye devoted to color vision in mantis shrimps, the elaboration of their color receptor complexity and genetics, and the clear demonstration of their ability to discriminate both ultraviolet and human-visible colors, it seems inescapable to conclude that color vision plays a critical role in their biology. Yet proof of the

use of color in specific behaviors in nature such as feeding, predator evasion, navigation, or even mate selection is either weak or completely missing. In this concluding section of the review, we will consider the role of color vision in the lives of mantis shrimps and suggest some possible directions for learning more about its involvement in their behavior.

There's no doubt that mantis shrimps are highly visual animals. Their eyes actively scan the environment, track moving objects, and fix their acute zones onto interesting targets (Cronin et al., 1988; Land et al., 1990; Marshall et al., 2014). While light underwater can be unpredictable and spectrally filtered (Johnsen, 2011), many mantis shrimp species live in, or just beneath, the intertidal zone where illumination is bright and broad-spectrum. Even when species live in deeper water where light has a narrowed spectral range, they adjust their color vision to match the spectrum available. All this implies an active interest in the colors of objects that they encounter.

Thoen et al.'s (2014) discovery that color vision can be quite coarse in mantis shrimps has encouraged a re-evaluation of the primacy of color in their lives. A study on ultraviolet vision showed that these animals do indeed discriminate between very short-wavelength (UVB) spectral lights (314 nm) from UVA lights (379 nm), as well as discriminating 379-nm UVA from 351-nm UVA (Bok et al, 2018). Finer differences were not explored, so we don't yet know whether or not ultraviolet color vision is as coarse as color vision in human-visible light. Both of these studies used food as a reward for a correct choice, and it is quite possible that, in their natural circumstance, color is not an important attribute of food for a mantis shrimp.

An interesting finding in the ultraviolet color vision study was that the species *Haptosquilla trispinosa* showed a strong aversive response to the UVB (314 nm) and was reluctant to make a choice when it was present. This indicates that certain colors can carry intrinsic information, in

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3 this case aversive, if used as visual signals. The behavior is likely the responsibility of a single
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5 receptor, since only one UV receptor class is specifically devoted to UVB light (Bok et al., 2014;
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7 Figure 2A). Such a built-in response is more akin to a wavelength-specific behavior than to true
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9 color vision. At this time, wavelength-specific signals in the human-visible spectral range have
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11 not been documented. In fact, work by Amanda Franklin and colleagues (Franklin et al., 2017,
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13 2019, 2020) suggests that in either camouflage patterning or evaluation of a striking color signal,
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15 the meral spot, visual achromatic contrast is far more significant in shaping behavior than
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17 chromatic contrast. Much earlier work also suggested that the presence of a meral spot is a
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19 significant stimulus, but meral spot color was not evaluated in that study (Hazlett, 1979)
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25 Stomatopods themselves dare to challenge the concept of color's insignificance by being
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27 among the most colorful animals in the ocean, and by flaunting these colors in aggressive and
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29 mating displays. In particular, the just-mentioned meral spot is a highly noticeable and colorful
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31 circular patch, outlined by a strongly contrasting achromatic border, located on the inner side of
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33 the raptorial appendage. It is concealed completely except when the animal suddenly spreads
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35 these appendages laterally in an agonistic display, appearing dramatic and a bit threatening even
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37 to a human. Even if animals evaluate conspecifics by the achromatic contrast of the spot, when
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39 several stomatopod species share a single habitat, the colors of their meral spots vary – perhaps
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41 providing species-specific signals (Caldwell, 1975). At least one stomatopod species
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43 (*Gonodactylus smithii*) varies both its meral spot color and its red-sensitive visual system with
44
45 the changing photic environment at different depths, and in doing so maintains a constant color
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47 signal (Cheroske and Cronin, 2004). In the same species, the meral spot color appears to have
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49 co-evolved with the color-vision system, based on an analysis of its visibility and contrast (Chiao
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51 et al., 2000), once more indicating a role for color signaling. *H. trispinosa* has a brilliant blue
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patch on its first maxilliped, which the male prominently exposes in mating displays. Destroying the color (and also the polarized-light reflection) of this patch lowers mating success in males (Chiao et al., 2011). All this strongly implies that color is a major component of signaling, if not necessarily of other behavioral tasks.

When associating colored shapes with food, the stomatopod *N. oerstedii* learns the shapes' colors, but if the shape and color are placed in conflict, individuals of this species turn to shape as the primary identifier (Patel et al., 2021). In another example of shifting modes of visual analysis, as the lighting becomes dimmer, individuals of *G. smithii* reduce the use of visual displays and turn to chemoreception when communicating (Cheroske et al., 2009). Ultraviolet communication in *N. oerstedii* is impaired in turbid waters, which could similarly force them to turn to another modality (Franklin et al., 2018). Mantis shrimps remember the chemical signatures of individuals that they have encountered previously (Caldwell, 1979, 1982, 1985), indicating that chemoreception can serve as an alternative means of communicating identity.

In the end, the stomatopods continue to puzzle us with unexpected abilities and paradoxical behavior. Their neatly designed color-vision system, with its tiers, filters, and multiple visual pigments, may in the end be a very elegant design for instantaneous analysis of a specific class of visual stimuli. Alternatively, it could be a delicately tuned instrument for evaluating subtle colors in potential mates or competitors, or perhaps one component of an elegant multimodal sensory channel. Perhaps the entire system's competence and function varies among species in ways that we don't yet appreciate. Whatever the truth may be, stomatopod color vision will continue to serve as an attractive target for evolutionary, physiological, optical, and behavioral research.

Acknowledgement. Much of the research summarized here was made possible by the Lizard Island Research Station in Queensland, Australia. K. Csanadi-Schwartz assisted with editing of this paper. We particularly thank our many graduate students and postdoctoral fellows over the last several decades for their contributions to the research behind this review.

Funding statement. This work is based on research over many years supported by the US National Science Foundation, most recently by grant number 1738567, the British Biotechnology and Biological Sciences Research Council, The Australian Research Council, The Asian Office of Aerospace Research and Development, the Office of Naval Research - Global, and the Air Force Office of Scientific Research, most recently by grant number FA9550-18-1-0278.

References

- Ahyong S. T., Harling C. 2000. The phylogeny of the stomatopod Crustacea. *Austr. J. Zool.* **48**, 607-642.
- Ahyong S. T., Jarman S. N. 2009. Stomatopod interrelationships: preliminary results based on analysis of three molecular loci. *Arthropod Syst. Phylogeny* **67**, 91-98.
- Bok MJ, Porter ML, Cronin TW. 2015. Diversity, ecology, and evolution of ultraviolet filters in stomatopod crustaceans. *J. Exp. Biol.* **218**, 2055-2066.
- Bok MJ, Porter ML, Place AR, Cronin TW. 2014. Biological sunscreens tune polychromatic vision in mantis shrimp. *Curr. Biol.* **24**, 1636-1642.
- Bok MJ, Roberts NW, Cronin TW. 2018. Behavioural evidence for polychromatic ultraviolet sensitivity in mantis shrimp. *Proc. Roy. Soc. Lond. B* **285**, 20181384. (doi:10.1098/rspb.2018.1384)
- Caldwell RL. 1975. Ecology and evolution of agonistic behavior in stomatopods. *Naturwiss.* **62**, 214-222.
- Caldwell, R. L. 1979. Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festai*: Evidence for chemically mediated individual recognition. *Anim. Behav.*, **27**, 194-201.
- Caldwell, R. L. 1982. Interspecific chemically mediated recognition in two competing stomatopods. *Mar. Behav. Physiol.*, **8**, 189-197.
- Caldwell, R. L. 1985. A test of individual recognition in the stomatopod *Gonodactylus festae*. *Anim. Behav.* **33**, 101-106.
- Cheroske AG, Barber PH, Cronin TW. 2006. Evolutionary variation in the expression of phenotypically plastic color vision in Caribbean mantis shrimps, genus *Neogonodactylus*. *Mar. Biol.* **150**, 213-220. (doi:10.1007/s00227-006-0313-5)
- Cheroske AG, Cronin TW. 2005. Variation in stomatopod (*Gonodactylus smithii*) color signal design associated with organismal condition and depth. *Brain. Behav. Evol.* **66**, 99-113. (doi:10.1159/000086229)
- Cheroske AG, Cronin TW, Caldwell RL. 2003. Adaptive color vision in *Pullosquilla litoralis* (Stomatopoda, Lysiosquilloidea) associated with spectral and intensity changes in light environment. *J. Exp. Biol.* **206**, 373-379 (doi:10.1242/jeb.00084)
- Cheroske AG, Cronin TW, Durham MF, Caldwell RL. 2009. Adaptive signaling in stomatopods under varying light conditions. *Mar. Freshw. Behav. Physiol.* **42**, 219-232. (doi:10.1080/102366240903169222)

- Chiao C-C, Cronin TW, Marshall NJ. 2000. Eye design and color signaling in a stomatopod crustacean *Gonodactylus smithii*. *Brain Behav. Evol.* **56**, 107-122.
- Cronin TW. 1985. The visual pigment of a stomatopod crustacean, *Squilla empusa*. *J. Comp. Physiol.* **82**, 679-687.
- Cronin TW, Bok MJ. 2016. Photoreception and vision in the ultraviolet. *J. Exp. Biol.* **219**, 2790-2801. (doi:10.1242/jeb.128769)
- Cronin TW, Bok MJ, Lin C. 2017. Crustacean larvae – vision in the plankton. *Int. Comp. Biol.* **57**, 1139-1150. (doi:10.1093/icb/icx007)
- Cronin TW, Bok MJ, Marshall NJ, Caldwell RL. 2014. Filtering and polychromatic vision: themes in visible and ultraviolet vision. *Phil. Trans. Roy. Soc. Lond. B* **369**, 20130030. (doi:10.1098/rstb.2013.0032)
- Cronin TW, Caldwell RL, Erdmann MV. 2002a. Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. 1. Visual pigments. *J. Comp. Physiol. A* **188**, 179-186.
- Cronin TW, Caldwell RL, Erdmann MV. 2002b. Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. 1. Filter pigments. *J. Comp. Physiol. A* **188**, 187-197.
- Cronin TW, Jinks RN. 2001. Ontogeny of vision in stomatopod crustaceans. *Am. Zool.* **41**, 1098-1107.
- Cronin TW, Marshall NJ. 1989a. Multiple spectral classes of photoreceptors in the retinas of gonodactyloid stomatopod crustaceans. *J. Comp. Physiol. A* **166**, 267-275.
- Cronin TW, Marshall NJ. 1989b. A retina with at least ten spectral types of photoreceptors in a stomatopod crustacean. *Nature* **339**, 137-140.
- Cronin TW, Marshall NJ, Caldwell RL. 1993. Photoreceptor spectral diversity in the retinas of squilloid and lysiosquilloid stomatopod crustaceans. *J. Comp. Physiol. A* **172**, 339-350.
- Cronin TW, Marshall NH, Caldwell RL. 2000. Spectral tuning and the visual ecology of mantis shrimps. *Phil. Trans. Roy. Soc. Lond. B* **355**, 1263-1267.
- Cronin TW, Marshall NJ, Caldwell RL. 1994c. The retinas of mantis shrimps from low-light environments. *J. Comp. Physiol. A* **174**, 607-619.
- Cronin TW, Marshall NJ, Caldwell RL. 1996. Visual pigment diversity in two genera of mantis shrimps implies rapid evolution. *J. Comp. Physiol. A* **179**, 371-384.
- Cronin TW, Marshall NJ, Caldwell RL. 1994b. The intrarhabdomal filters in the retinas of mantis shrimps. *Vision Res.* **34**, 1443-1452.

- Cronin TW, Marshall NJ, Caldwell RL, Pales D. 1995. Compound eyes and ocular pigments of crustacean larvae (Stomatopoda and Decapoda, Brachyura). *Mar. Freshwater Behav. Physiol.* **26**, 219–231.
- Cronin TW, Marshall NJ, Caldwell RL, Shashar N. 1994a. Specialization of retinal function in the compound eyes of mantis shrimps. *Vision Res.* **34**, 2639–2656.
- Cronin TW, Marshall NJ, Quinn CA, King CA. 1994d. Ultraviolet photoreception in mantis shrimp. *Vision Res.* **34**, 1443–1452.
- Cronin TW, Nair JN, Doyle RD, Caldwell RL. 1988. Visual tracking of rapidly moving targets by stomatopod crustaceans. *J. Comp. Physiol. A* **164**, 737–749.
- Cronin TW, Porter ML, Bok MJ, Wolf JB, Robinson PR. 2010. The molecular genetics and evolution of colour and polarization vision in stomatopod crustaceans. *Ophthalm. Physiol. Opt.* **30**, 460–469. (doi://10.1111/j.1475-1313.2010.00762.x)
- Feller KD, Cohen JH, Cronin TW. 2015. Seeing double: visual physiology of double-retina eye ontogeny in stomatopod crustaceans. *J. Comp. Physiol. A* **201**, 331–339. (doi:10.1007/s00359-014-0967-2)
- Feller KD, Cronin TW. 2014. Hiding opaque eyes in transparent organisms: a potential role for larval eyeshine in stomatopod crustaceans. *J. Exp. Biol.* **217**, 3263–3273. (doi:10.1242/jeb.108076)
- Feller KD, Cronin TW. 2016. Spectral absorption of visual pigments in stomatopod larval photoreceptors. *J. Comp. Physiol. A* **202**, 215–223. (doi:10.1007/s00359-015-1063-y)
- Feller KD, Wilby D, Jaucci G, Vignolini S, Mantell J, Wardill TJ, Cronin TW, Roberts NW. 2019. Long-wavelength reflecting filters found in the larval retinas of one mantis shrimp family (Nannosquillidae). *Curr. Biol.* **29**, 3101–3108. (doi:10.1016/j.cub.2019.07.070)
- Forward, RB Jr, Cronin TW. 1979. Spectral sensitivity of larvae from intertidal crustaceans. *J. Comp. Physiol.* **133**, 311–315.
- Franklin AM, Applegate MB, Lewis SM, Omenetto FG. 2017. Stomatopods detect and evaluate achromatic cues in contests. *Behav. Ecol.* **28**, 1329–1336. (doi:10.1093/beheco/arx096)
- Franklin AM, Donatelli CM, Culligan CR, Tytell ED. 2019. Meral spot reflectance signals weapon performance in the mantis shrimp *Neogonodactylus oerstedii* (Stomatopoda). *Biol. Bull.* **236**, 43–54. (doi: 10.1086/700836)
- Franklin AM, Marshall J, Feinstein JD, Bok MJ, Byrd AD, Lewis SD. 2020. Differences in signal contrast and camouflage among different colour variation of a stomatopod crustacean, *Neogonodactylus oerstedii*. *Sci. Rep.* **10**, 1236. (doi:10.1038/s41598-020-57990-z)

- Harling C. 2000. Reexamination of eye design in the classification of stomatopod crustaceans. *J. Crust. Biol.* **20**, 172-185.
- Hazlett BA. 1979. The meral spot of *Gonodactylus oerstedii* as a visual stimulus (Stomatopoda, Gonodactylidae). *Crustaceana* **36**, 196-198 (doi:10.1163/1568540/79X00429)
- Johnsen, S. 2011. *The optics of life: a biologist's guide to light in nature*. Princeton University Press, Princeton New Jersey USA. 368 pp.
- Jutte PW, Cronin TW, Caldwell RL. 1998a. Vision in two sympatric species of *Pullosquilla* (Stomatopoda, Lysiosquilloidea) living in different depth ranges. *Mar. Freshwater Behav. Physiol.* **31**, 231-250.
- Jutte PW, Cronin TW, Caldwell RL. 1998b. Retinal function in the planktonic larvae of two species of *Pullosquilla*, a lysiosquilloid stomatopod crustacean. *J. Exp. Biol.* **201**, 2481-2487.
- Kawamura K, Bagarinao T, Yong ASK, Jeganathan IMX, Lim L-S. 2016. Colour preference and colour vision of the larvae of the giant freshwater prawn *Macrobrachium rosenbergii*. *J. Exp. Mar. Biol. Ecol.* **474**, 67-72. (doi:10.1016/j.jembe.2015.10.001)
- Kleinlogel S, Marshall NJ. 2005. Photoreceptor projection and termination pattern in the lamina of gonodactyloid stomatopods (mantis shrimp). *Cell Tissue Res.* **321**, 273-284. (doi:10.1007/s00441-005-1118-4)
- Land MF, Marshall NJ, Brownless D, Cronin TW. 1990. The eye-movements of the mantis shrimp *Odontodactylus scyllarus* (Crustacea: Stomatopoda). *J. Comp. Physiol. A* **167**, 155-166.
- Lin C, Cronin TW. 2018. Two visual systems in one eyestalk: the unusual optic lobe metamorphosis in the stomatopod *Alima pacifica*. *Devel. Neurobio.* **78**, 3-14. (doi:10.1002/dneu.22550)
- Marshall NJ. 1988. A unique colour and polarization vision system in mantis shrimps. *Nature* **333**, 873-874.
- Marshall NJ, Arikawa K. 2014. Unconventional colour vision. *Curr. Biol.* **24**, R1150-R1154. (doi:10.1016/j.cub.2014.10.025)
- Marshall NJ, Cronin TW, Kleinlogel S. 2007. A review of stomatopod eye structure and function. *Arthropod Struct. Dev.* **36**, 420-448. (doi:10.1016/j.asd.2007.01.006)
- Marshall NJ, Land MF. 1993. Some optical features of the eyes of stomatopods. II. Ommatidial design, sensitivity and habitat. *J. Comp. Physiol. A* **173**, 583-594.
- Marshall NJ, Jones JP, Cronin TW. 1996. Behavioural evidence for colour vision in stomatopod crustaceans. *J. Comp. Physiol. A* **179**, 473-481.

- Marshall NJ, Land MF, Cronin TW. 2014. Shrimps that pay attention: saccadic eye movements in stomatopod crustaceans. *Phil. Trans. Roy. Soc. B* **369**, 20130042. (doi:10.1098/rstb.2013.0042)
- Marshall NJ, Land MF, King CA, Cronin TW. 1991a. The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). I. Compound eye structure: The detection of polarised light. *Phil. Trans. Roy. Soc. Lond. B* **334**, 33-56.
- Marshall NJ, Land MF, King CA, Cronin TW. 1991b. The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). II. Colour pigments in the eyes of Stomatopod crustaceans: Polychromatic vision by serial and lateral filtering. *Phil. Trans. Roy. Soc. Lond. B* **334**, 57-84.
- Marshall J, Oberwinkler J. 1999. The colourful world of the mantis shrimp. *Nature* **401**, 873-874. (doi:10.1038/44751)
- McDonald MS, Palecandra S, Cohen JS, Porter ML. In press. Ultraviolet vision in larval *Neogonodactylus oerstedii*. *J. Exp. Biol.*
- Menzel R. 1979. Spectral sensitivity and colour vision in invertebrates. In *Handbook of sensory physiology, vol VII/6A* (ed H Autrum), pp. 503-580. Berlin:Springer-Verlag.
- Nilsson, D-E. 1983. Evolutionary links between apposition and superposition optics in crustacean eyes. *Nature* **302**, 818-821.
- Patel RN, Khil V, Abdurahmonova L, Driscoll H, Goldwasser T, Patel S, Pettyjohn-Robin O, Shah A, Sparklin B, Cronin TW. 2021. Mantis shrimp identify an object by its shape rather than its color during visual recognition. *J. Exp. Biol.* **224**, jeb224256 (doi:10.1242/jeb.242256)
- Porter ML, Awata H, Bok MJ, Cronin TW. 2020. Exceptional diversity of opsin expression patterns in *Neogonodactylus oerstedii* (Stomatopoda) retinas. *Proc Nat. Acad. Sci.* **117**, 8448-8457. (doi:10.1073/pnas.1917303117)
- Porter ML, Bok MJ, Robinson PR, Cronin TW. 2009. Molecular diversity of visual pigments in Stomatopoda (Crustacea). *Visual Neurosci.* **26**, 255-265. (doi:10.1017/S0952523809090129)
- Porter ML, Speiser KI, Zaharoff AK, Caldwell RL, Cronin TW, Oakley TH. 2013. The evolution of complexity in the visual systems of stomatopods: insight from transcriptomics. *Int. Comp. Biol.* **53**, 39-49. (doi:10.1093/icb/ict060)
- Porter ML, Zhang Y, Desai S, Caldwell RL, Cronin TW. 2010. Evolution of anatomical and physiological specialization in the compound eyes of stomatopod crustaceans. *J. Exp. Biol.* **213**, 3473-3486. (doi:10.1242/jeb.046508)
- Schönenberger N. 1977. The fine structure of the compound eye of *Squilla mantis* (Crustacea, Stomatopoda). *Cell Tissue Res.* **176**, 205-233.

1
2
3 Thoen HH, Chiou T-H, Marshall NJ. 2017. Intracellular recordings of spectral sensitivities in
4 stomatopods: a comparison across species. *Integr. Comp. Biol.* **5**, 1117-1129.
5 ([doi:10.1093/icb/ix111](https://doi.org/10.1093/icb/ix111))
6

7
8 Thoen HH, How MJ, Chiou T-H, Marshall NJ. 2014. A different form of color vision in mantis
9 shrimp. *Science* **343**, 411-413. (doi:10.1126/science.1245824)
10

11 Thoen HH, Strausfeld NJ, Marshall J. 2017. Neural organization of afferent pathways from the
12 stomatopod compound eye. *J. Comp. Neurol.* **525**, 3010-3030. (doi: 10.1002/cne.24256)
13

14 Van Der Wal C, Ah Yong ST, Ho SY, Lo N. 2017. The evolutionary history of Stomatopoda (Crustacea:
15 Malacostraca) inferred from molecular data. *PeerJ*, **5**, e3844. ([doi:10.7717/peerj.3844](https://doi.org/10.7717/peerj.3844))
16

17 Zaidi Q, Marshall J, Thoen H, Conway BR. 2014. Evolution of neural computations: mantis
18 shrimp and human color decoding. *i-Perception* **5**, 492-496. (doi:10.1068/i0662sas)
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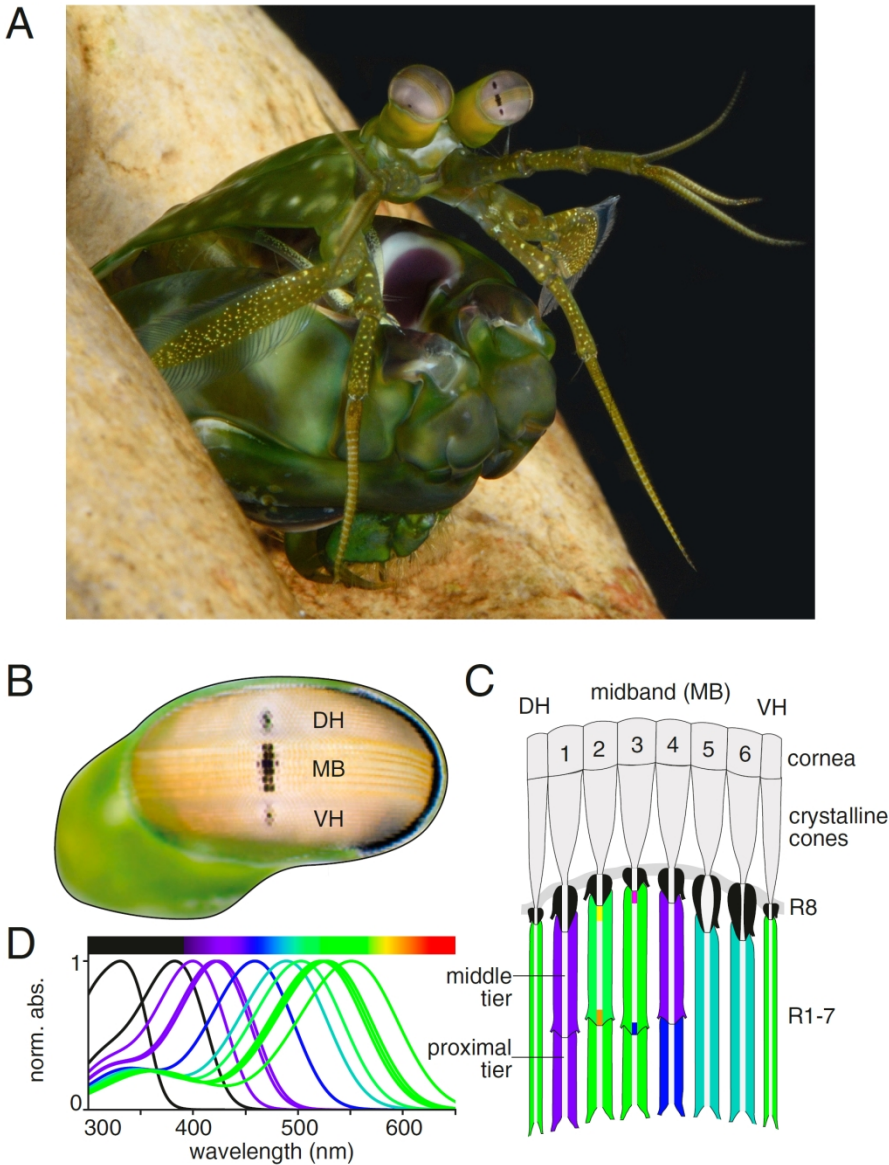
FIGURE CAPTIONS

Figure 1. **A.** A typical Caribbean reef stomatopod, *Neogonodactylus oerstedii* (photo by RL Caldwell). **B.** A close-up view of one of its compound eyes, showing the dorsal hemisphere (DH), ventral hemisphere (VH), which together make up the peripheral ommatidial of the eye, and the 6-row midband. **C.** A schematic diagram to show the organization of each ommatidium in the hemispheres and the midband. Midband rows are numbered 1 to 6, from dorsal to ventral. The color-vision region of the eye is thought to be contained in the tiered Rows 1 to 4. The retinular cells are colored to show the spectral region absorbed by the visual pigment they contain (UV-sensitive cells are colored black); colored filters are present in Rows 2 and 3 and are illustrated as they appear to the human eye. **D.** Absorbance spectra of all 12 visual pigments in this eye as measured by MSP. Visual pigment spectra are colored to approximately match the spectral range sensed by retinular cells, and the same colors show where they are expressed as seen in panel C. (After Porter et al., 2020).

Figure 2. Sensitivities of the color-sensitive photoreceptors in the retina of *Neogonodactylus oerstedii*, obtained from intracellular recordings (Oberwinkler and Marshall, 1999; Thoen et al., 2017). The row number where each sensitivity was measured is indicated. **A.** Spectral sensitivities of the UV-sensitive R8 cells. Note that the sensitivity for R8 cells in Row 3 is not yet known. **B.** Spectral sensitivities in the eight main rhabdom photoreceptors of the four tiered rows of the midband. In the tiered Rows 1 to 4, the distal tier's sensitivity (D) always peaks at shorter wavelengths than the proximal tier's (P).

Figure 3. Peak sensitivities in color photoreceptors of 12 stomatopod species from various habitats. Each group of points represents the sensitivity maxima of the 12 retinas in the retinal region indicated at the bottom of the figure. Point types vary by primary habitat of the species: intertidal, open circles; shallow subtidal (<5 m), hatched circles; species found in a range of depths from shallow to deep, half-filled circles; deep water (> 5 m), fully filled circles. (After Cronin et al., 2000).

Figure 4. Tissue expression patterns of opsins in *Neogonodactylus oerstedii*, revealed by *in situ* hybridization. Expressions are grouped into opsin types: LWS, long-wavelength sensitive; MWS, middle-wavelength sensitive; SWS, short- wavelength and ultraviolet sensitive. A schematic showing the retina is given for each expression panel, see description in Figure 1 caption. In this schematic the expression location of the associated opsin is indicated by the colored cells. Cell colors suggest the approximate region of the spectrum for which the cell is responsible; black indicates UV. See text for details. (After Porter et al., 2020).



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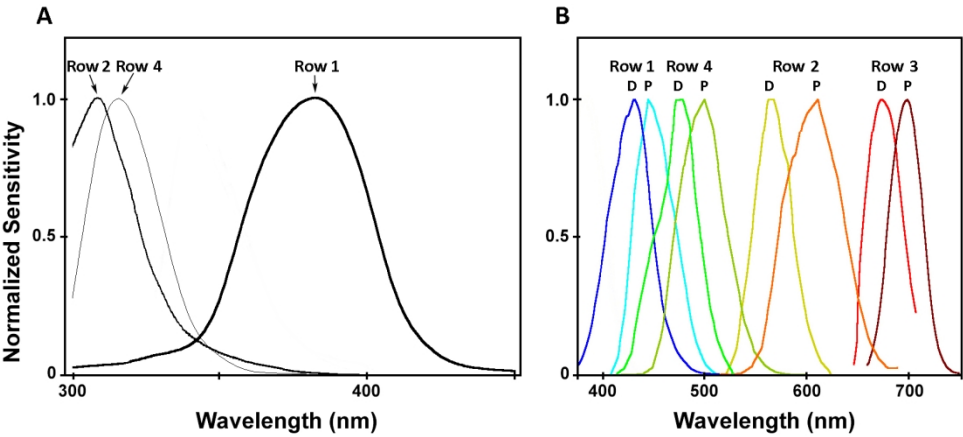


Figure 2. Sensitivities of the color-sensitive photoreceptors in the retina of *Neogonodactylus oerstedii*, obtained from intracellular recordings (Oberwinkler and Marshall, 1999; Thoen et al., 2017). The row number where each sensitivity was measured is indicated. A. Spectral sensitivities of the UV-sensitive R8 cells. Note that the sensitivity for R8 cells in Row 3 is not yet known. B. Spectral sensitivities in the eight main rhabdom photoreceptors of the four tiered rows of the midband. In the tiered Rows 1 to 4, the distal tier's sensitivity (D) always peaks at shorter wavelengths than the proximal tier's (P).

159x71mm (300 x 300 DPI)

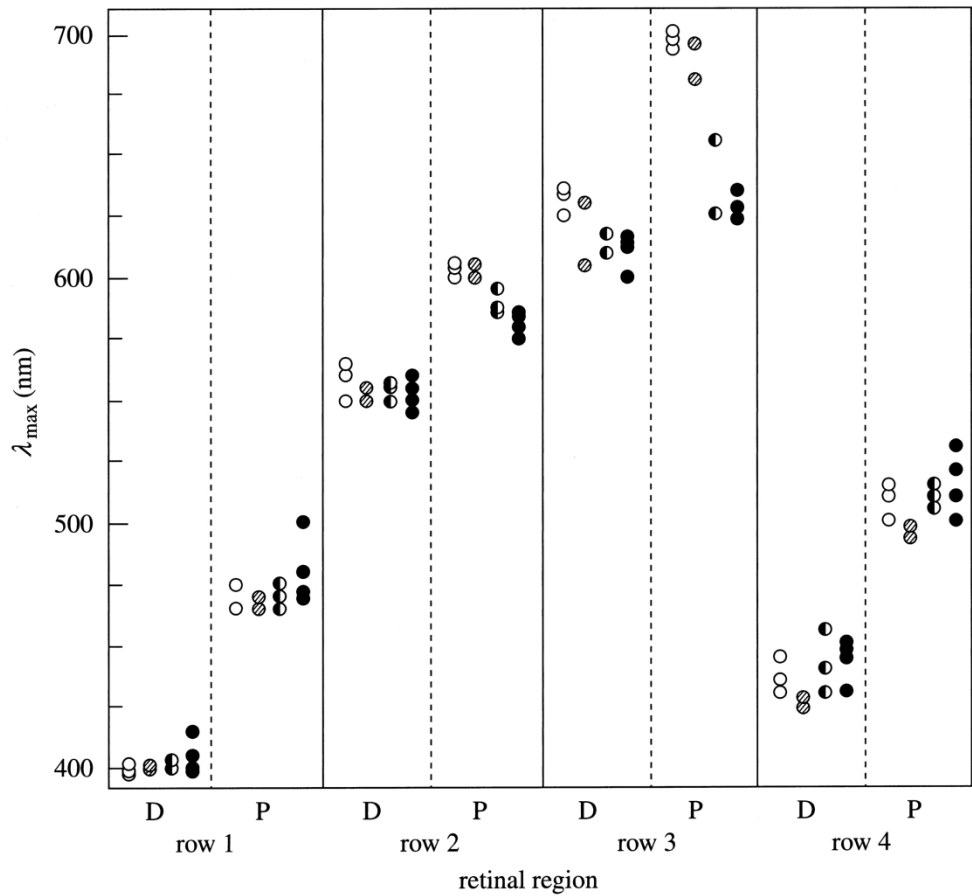


Figure 3. Peak sensitivities in color photoreceptors of 12 stomatopod species from various habitats. Each group of points represents the sensitivity maxima of the 12 retinas in the retinal region indicated at the bottom of the figure. Point types vary by primary habitat of the species: intertidal, open circles; shallow subtidal (<5 m), hatched circles; species found in a range of depths from shallow to deep, half-filled circles; deep water (> 5 m), fully filled circles. (After Cronin et al., 2000).

121x112mm (600 x 600 DPI)

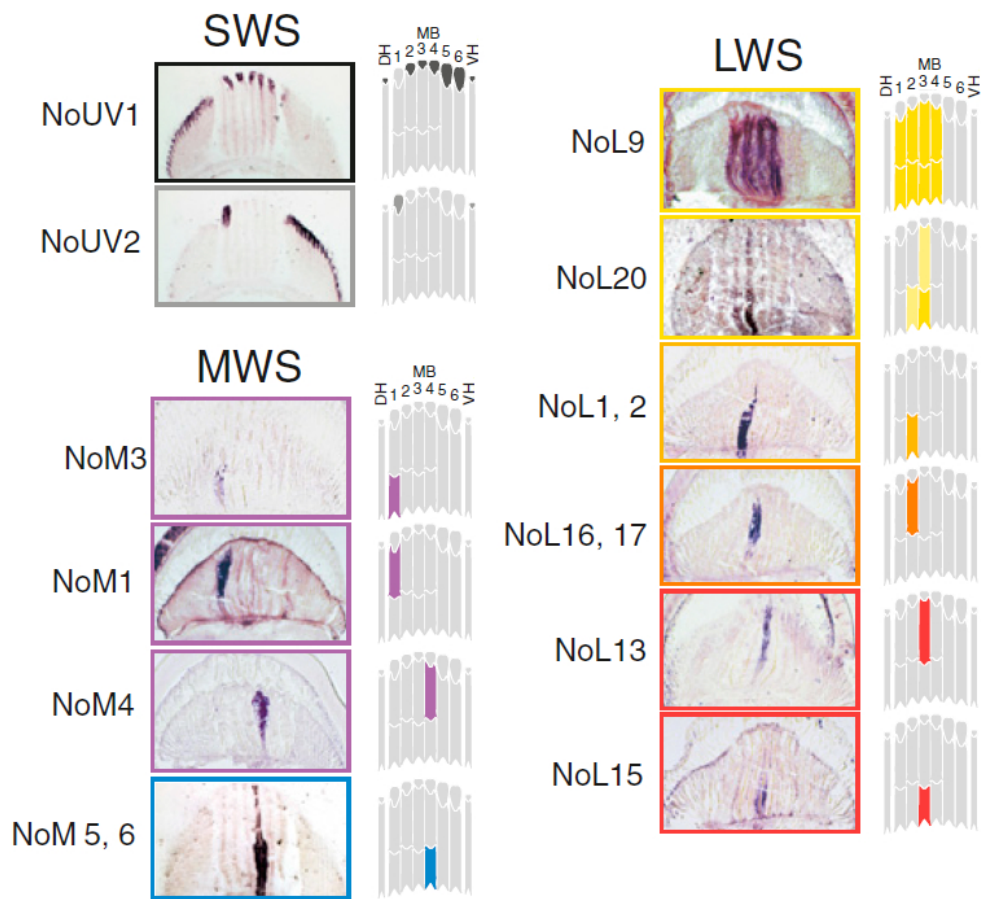


Figure 4. Tissue expression patterns of opsins in *Neogonodactylus oerstedii*, revealed by in situ hybridization. Expressions are grouped into opsin types: LWS, long-wavelength sensitive; MWS, middle-wavelength sensitive; SWS, short- wavelength and ultraviolet sensitive. A schematic showing the retina is given for each expression panel, see description in Figure 1 caption. In this schematic the expression location of the associated opsin is indicated by the colored cells. Cell colors suggest the approximate region of the spectrum for which the cell is responsible; black indicates UV. See text for details. (After Porter et al., 2020).

98x91mm (200 x 200 DPI)