Integrative and Comparative Biology

Integrative and Comparative Biology, pp. 1–13
doi:10.1093/icb/icx111

Society for Integrative and Comparative Biology

SYMPOSIUM

Intracellular Recordings of Spectral Sensitivities in Stomatopods: a Comparison across Species

Hanne H. Thoen,[1,*] Tsyr-Huei Chiou[†] and N. Justin Marshall[*]

*Sensory Neurobiology Group, Queensland Brain Institute, University of Queensland, St Lucia, Brisbane, Queensland 4072, Australia; [†]Department of Life Sciences, National Cheng Kung University, Tainan City 70101, Taiwan, ROC

From the symposium "Low Spatial Resolution Vision–Function and Evolution" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2017 at New Orleans, Louisiana.

[1]E-mail: h.thoen@uq.edu.au

Synopsis Stomatopods (mantis shrimps) possess one of the most complex eyes in the world with photoreceptors detecting up to 12 different colors. It is not yet understood why stomatopods have almost four times the number of spectral photoreceptors compared with most other animals. It has, however, been suggested that these seemingly redundant photoreceptors could encode color through a new mechanism. Here we compare the spectral sensitivities across five species of stomatopods within the superfamily Gonodactyloidea using intracellular electrophysiological recordings. The results show that the spectral sensitivities across species of stomatopods are remarkably similar apart from some variation in the long-wavelength receptors. We relate these results to spectral sensitivity estimates previously obtained using microspectrophotometry and discuss the variation in the spectral sensitivity maxima (λ_{max}) of the long-wavelength receptors in regard to the previous findings that stomatopods are able to tune their spectral sensitivities according to their respective light environment. We further discuss the similarities of the spectral sensitivities across species of stomatopods in regard to how color information might be processed by their visual systems.

Introduction

Stomatopods, commonly known as mantis shrimp have one of the most complex visual systems known in the animal kingdom, with 12 spectral receptors and the ability to perceive linearly and circularly polarized light (Marshall 1988; Cronin and Marshall 1989a; Kleinlogel and Marshall 2006; Marshall et al. 2007; Chiou et al. 2008). Due to differential attenuation of light with increasing depth it is only the shallow water species within the four superfamilies Pseudosquilloidea, Hemisquilloidea, Gonodactyloidea, and Lysiosquilloidea (Marshall et al. 2007; Porter et al. 2010) that appear to take advantage of the spectral range available to them, while species living in deeper water have lost these specializations (Ahyong and Harling 2000; Cronin and Porter 2008; Porter et al. 2010). The eye of the stomatopod is divided by a band of specialized ommatidia, termed the midband, which separates the rest of the eye into a dorsal and a ventral hemisphere (Fig. 1A, B). The midband consists of six rows of ommatidia; rows 1–4 contain 12 narrow-banded spectral receptors while rows 5 and 6 accommodate achromatic receptors that are sensitive to circular polarized light, a visual modality that no other animal is shown to have (Chiou et al. 2008; Gagnon et al. 2015). The ommatidia in the stomatopod eye are composed of eight retinula cells (R1–R8) with R1–7 making up the main rhabdom underneath a small, four-lobed ultraviolet (UV)-sensitive R8 cell (Fig. 1A). In rows 1–4 of the midband the R1–7 cells are divided into two different tiers: R1, 4 and 5 making up one tier and R2, 3, 6, and 7 making up the other (Marshall et al. 1991a, 1991b). These two tiers have different spectral sensitivities, giving each ommatidium in rows 1–4 a total of three spectral sensitivities: one UV-sensitive R8 cell, and two spectral sensitivities in the "human visible" part of the spectrum (~400–700 nm).

While a diversity of opsin genes are expressed in various stomatopod photoreceptor cells (see Porter et al. 2009, 2010, 2013; Cronin et al. 2010), the

© The Author 2017. Published by Oxford University Press on behalf of the Society for Integrative and Comparative Biology.
All rights reserved. For permissions please email: journals.permissions@oup.com.

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

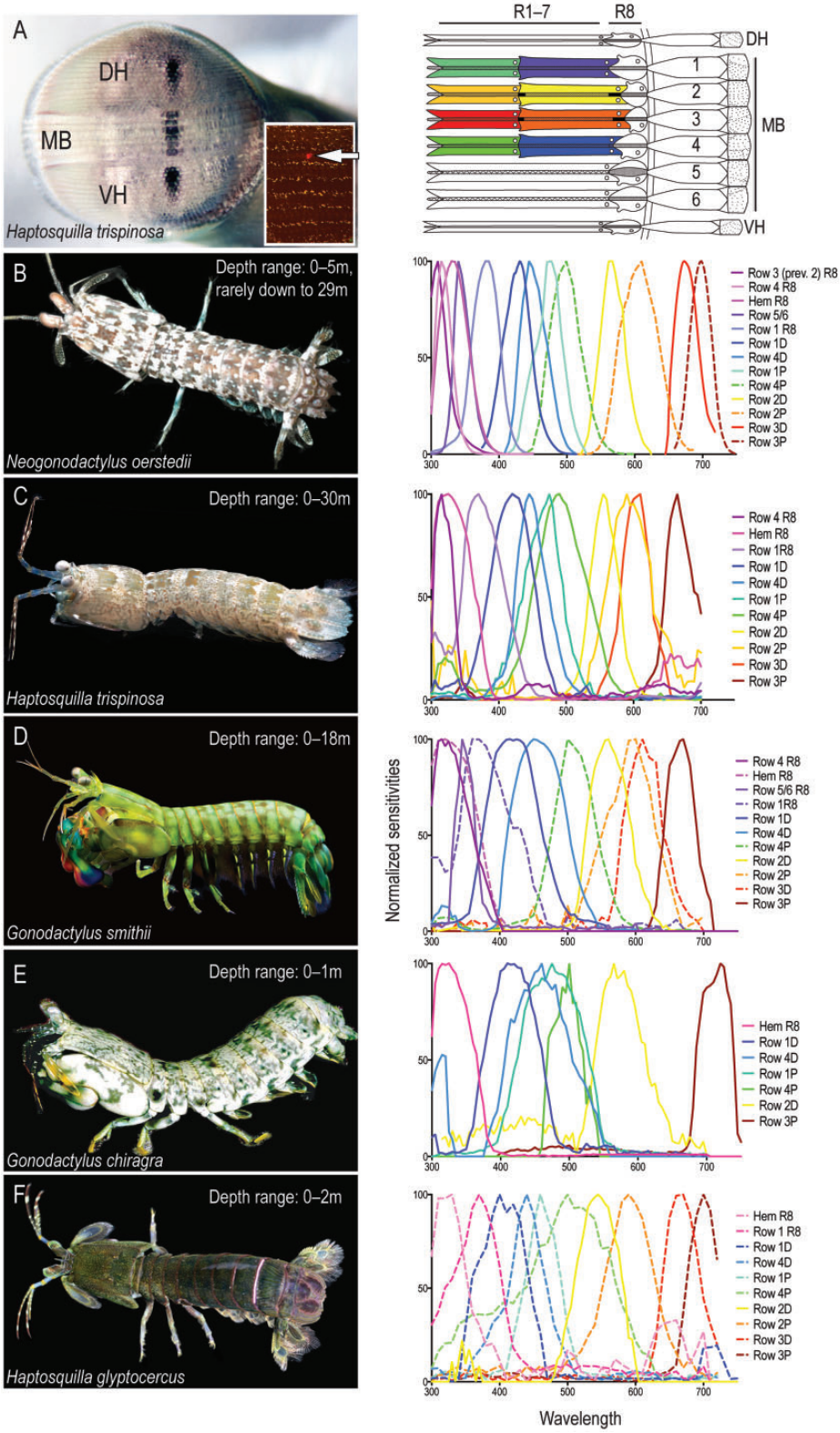

Fig. 1 Overview of the stomatopod eye, midband organization, species used, and their spectral sensitivity curves. (**A**) Left: Illustration showing the eye of *Haptosquilla trispinosa* with the equatorial midband (MB), dorsal (DH), and ventral hemisphere (VH). Inset shows a cell in midband row 1D filled with fluorescent dye (arrow). Right: A sagittal section through the six rows of midband (MB) ommatidia in a stomatopod eye. Rows 1–4 have divided the R1–7 cells (R1–7) into two different tiers, each with a different spectral sensitivity (indicated by color). Rows 5 and 6 are sensitive to circularly polarized light. UV-sensitive R8 cells surmount each row. Achromatic and linearly polarization sensitive photoreceptors are found in the dorsal (DH) and ventral hemisphere (VH) which are indicated on each

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

overall λ_{max} of these visual pigments are surprisingly conservative among different stomatopods, ranging from 330 to 550 nm (Bok et al. 2014; Cronin et al. 2014). The total range of λ_{max} of stomatopod photoreceptors spans from ~315 to 720 nm. The extra extension at either end of the spectrum being the result of selective filtering using both photostable filters and overlying rhabdomeres (Cronin and Marshall 1989a, 1989b; Marshall and Oberwinkler 1999; Bok et al 2014). Rows 2 and 3 have intra-rhabdomal filters located between tiers that are long-pass filters in the 400–700 nm range (Marshall 1988; Cronin et al. 1994a). Depending on the species up to a total of four filters can be found in these two midband rows. These filters successively narrow the spectrum of light passing through the rhabdom, thus increasing the λ_{max} of the long-wavelength sensitive cell at each step. Rows 1 and 4 do not have these intra-rhabdomal filters, therefore the proximal (P) tiers rely on the distal (D) tiers which absorb relatively short wavelengths and act as a long-pass filter. In addition to filtering in the rhabdom itself, stomatopods also utilize UV long- and short-pass optical filters which are located in the crystalline cones (Bok et al. 2014; Cronin et al. 2014) to tune the UV-sensitivities further and diversify them into as many as six distinct UV-receptor types in some species (Marshall and Oberwinkler 1999).

The functional role of the stomatopods numerous spectral sensitivities has puzzled scientists ever since they were discovered in the late 1980s (Marshall 1988; Cronin and Marshall 1989b). Most other animals have between two and three spectral sensitivities enabling them to discriminate colors well within the majority of the "visual" spectrum (Kelber and Osorio 2010). Some animals have one or two additional spectral sensitivities increasing their discrimination abilities into the UV or far-red range of the spectrum (Collin et al. 2009; Marshall and Arikawa 2014). Theoretical modeling shows the ideal number of spectral sensitivities for sampling the whole spectrum (from UV to far-red) to be between 4 and 7 and that more spectral sensitivities would not be beneficial due to diminishing returns in terms of spectral discrimination (Barlow 1982; Maloney 1986). Osorio et al. (1997) suggested that the stomatopods multiple spectral sensitivities could give them better color constancy (i.e., the ability to perceive colors under varying illumination) under water. Stomatopods are known for using different colored signals on their body parts for communication, especially during territorial fights (Dingle and Caldwell 1969; Adams and Caldwell 1990) and sexual interactions (Chiou et al. 2011). Good color constancy may therefore allow them to achieve fast and reliable color identification. Recent behavioral experiments, however, found that stomatopods have surprisingly poor spectral discrimination (i.e., the ability to discriminate between monochromatic light of closely positioned wavelengths) suggesting that they may potentially use an entirely different system to perceive color (Thoen et al. 2014). This putative system is suggested to be based on an interval-decoding system where the perceived color corresponds to the peak sensitivity of the most responsive photoreceptor (Zaidi et al. 2014) or function as a spectral pattern recognition system (Marshall and Arikawa 2014; Thoen et al. 2014).

The spectral sensitivities of stomatopod photoreceptors have previously been extensively investigated using microspectrophotometry (MSP) (Cronin and Marshall 1989a, 1989b; Cronin et al. 1993, 1994a, 1994b, 1994c, 1994d, 1996; Chiao et al. 2000; Marshall et al. 2007). Based on the absorption spectra of the visual pigments and intra-rhabdomal filters in a tissue section, one can model the photoreceptors spectral sensitivity. It does, however, not take any other modifications in the optic pathway into account. Intracellular electrophysiological recordings of individual photoreceptor cells provide a more accurate method as it measures the spectral response of the individual photoreceptor cell within an intact ommatidium, including all the modifications in the optic pathway. With the tiering and color filters within the retina and diverse opsin gene expression patterns, one might expect a high degree of variability of the spectral sensitivities across species. The objective of this study was therefore to investigate the spectral sensitivities across several species of stomatopods using intracellular electrophysiology to determine whether the diverse arsenal of visual modifications does generate variability among species. A summary of electrophysiological data of stomatopod spectral sensitivities, including both

Fig. 1 Continued
side of the midband. (**B**)–(**F**) The images of the species used in this study with the corresponding spectral sensitivities on the right side. Recordings performed with the scan method are shown in solid line while recordings performed with the flash method are shown in dashed lines. Data from *Neogonodactylus oerstedii* were previously published in Marshall and Oberwinkler (1999) and Marshall et al. (2007). Recordings from *H. trispinosa* were published in Thoen et al. (2014). Image credit: B and E, Roy Caldwell; C, Eivind A. B. Undheim; D, Michael Bok; F, Tsyr-Huei Chiou.

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

previously published and unpublished data is presented. The findings are discussed both in relation to previous models of spectral sensitivities obtained using MSP, retinal anatomy, ontogenetic changes, and reference to the ecology of the different species.

Materials and methods

Animals

The species used were *Haptosquilla trispinosa*, *Haptosquilla glyptocercus*, *Gonodactylus smithii*, *Gonodactylus chiragra*, and *Neogonodactylus oerstedii* (Fig. 1A–F). The first four are all Australian species collected from Lizard island research station on the northern Great Barrier Reef (GBRMPA Permit No. G12/35005.1, Fisheries Act no. 140763), while *N. oerstedii* was collected on the reef flats in Florida Keys, USA. Animals were all collected from waters of 0–5 m depth, shipped back to the laboratory and kept in saltwater aquaria in a 12:12 h-light/dark cycle with UV-enhanced full-spectrum lighting.

Intracellular electrophysiology

Spectral sensitivities were recorded using a setup described in Marshall and Oberwinkler (1999) or Kleinlogel and Marshall (2006) and based on the design of Menzel et al. (1986): At least half an hour before each experiment the animal was placed in total darkness to dark-adapt, and all the following steps were performed in dim red light. The animal was anesthetized by cooling before decapitation, and the eyestalk was removed from the body. The eyestalk was attached to a plastic rod using cyanoacrylate glue and placed in a Petri dish containing stomatopod saline (Watanabe et al. 1967). A small hole (approximately five facets wide) was cut through the cornea in the dorsal hemisphere using a sharp razorblade, taking care not to disturb the underlying photoreceptor cells. The eye was then seated in a spherical glass vial filled with saline, with a hole in the top allowing electrode placement (see Fig. 1 in Kleinlogel and Marshall [2006]).

A 150 W xenon-arc lamp (Oriel, Stratford, CT, USA) was used in combination with a computer controlled monochromator (Oriel) with a 1.24 nm slit-width, producing a light stimulus with a spectral composition of ~4 nm half band-width. A circular, computer controlled, neutral density wedge (Edmund Optics, Barrington, NJ, USA) was used for varying the light intensity (over 4 log units) of the light beam, before being passed through an electronic shutter (Uniblitz, Rochester, NY, USA) and into a flexible UV-transmitting liquid light guide. The end of the light guide was mounted on a cardan arm perimeter device, allowing adjustments of the angular position of the stimulus while maintaining a fixed distance to the centrally positioned eye. The optical system was calibrated using a USB 4000 spectrometer (Ocean Optics, Dunedin, FL, USA), and the light had an unattenuated maximal intensity of $\sim 10^{18}$ photons $s^{-1} cm^{-2}$ at the location of the eye.

Microelectrodes (Borosilicate, OD 1.2 mm × ID 0.69 mm) filled with 1 M KCl and with a resistance between 50 and 100 MΩ were inserted into the eye using a one-axis hydraulic micromanipulator (Narishige, Japan). The microelectrode was connected to the headstage of an intracellular amplifier (Axoprobe 1 A, Axon Instruments Ltd, Inverurie, Scotland) with an Ag/AgCl pellet immersed in saline as a ground electrode. A drop in resting potential to between −20 and −50 mV and response to a brief flash of white light (produced by bypassing the grating of the monochromator by a surface-mirror) signified the penetration of photoreceptor cells. Spectral sensitivity curves were recorded using either the spectral scan or the flash procedure as described by Laughlin (1975), Menzel et al. (1986), DeVoe et al. (1997), or McCulloch et al. (2016). The spectral scan method uses a neutral density wedge to adjust the light flux while changing the spectral output of the monochromator in an attempt to clamp the membrane potential of the cell to a preselected threshold (a criterion response). By taking the reciprocal of the number of quanta at each wavelength required to maintain the criterion response one acquires the spectral sensitivity function of the cell. The flash method uses short (50 ms) flashes of monochromatic light of equal intensities over 40 wavelength steps (300–750 nm) and measures the depolarization potential change of the photoreceptor at 2–10 s intervals. Prior to this spectral run a comparison of voltage (V) output to intensity (I), plotted as V/log I allows the absolute spectral sensitivity of the cell to be calculated independent of intensity variation (Laughlin 1975; Menzel et al. 1986; DeVoe et al. 1997; McCulloch et al. 2016).

The spectral scan method was the preferred method for obtaining a spectral sensitivity curve due to reasons listed in DeVoe et al. (1997) such as lengthy data collection and variability in responses of dark-adapted photoreceptors, however, in certain cases we could only obtain recordings using the flash method. A comparison of results from cells recorded with both methods showed little to no differences, specifically none in λ_{max}.

Cell identification

Cell identities according to midband row and distal/proximal position were determined either by

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

injections into the cell using a fluorescent dye, by comparisons to similar spectral sensitivities determined by recordings using MSP and by anatomical order of penetration (the eye was always mounted with midband row 1 uppermost). Injections were performed using the fluorescent dye Alexa Fluor 568 Hydrazide (Molecular Probes, Invitrogen) at 200 µM solutions in 1 M KCl. The tip of the microelectrode was filled with dye and then backfilled with 1 M KCl. The dye was injected into the cell using a hyperpolarizing current between 0.1 and 0.2 nA in a 1 Hz 50% duty regime for between 20 and 30 min. After injection, the cell condition was checked by flashing a brief white light making sure the cell was still responsive and that the resting potential was similar to the resting potential before the injection. The eye was then fixed in 4% paraformaldehyde for 1 h and sectioned on a cryomicrotome (Leica CM 1100) in 8–10 µm thick sections. For the injected cells the distal/proximal position was determined by the number of sections cut from the distal to the proximal position of the retina. A Zeiss Axioskop Microscope with fluorescent filters was used to visualize the filled cells.

Results

Spectral sensitivities

Recordings of photoreceptor spectral sensitivities were obtained from all five species. Only recordings obtained from the photoreceptor cells within midband rows 1–4 and the UV-sensitive R8 cells were included in this study while the broad-banded R1–7 in rows 5 and 6 and both hemispheres were omitted. A total of 13 retinular cells with characteristic spectral sensitivities were identified in *N. oerstedii*, 11 in *H. trispinosa*, 11 in *G. smithii*, 10 in *H. glyptocercus*, and 7 in *G. chiragra* (Figs. 1 and 2; Table 1). The number of photoreceptor cells, number of recordings, and λ_{max} values from each spectral sensitivity class from all five species are summarized in Table 1. A comparison of the normalized spectral response curves from each cell is shown in Fig. 2. Some of the recordings shown here have been published previously: the recordings of the spectral sensitivities of the UV-sensitive R8 cells in *N. oerstedii* were published in Marshall and Oberwinkler (1999) and the remaining spectral sensitivities were published in Marshall et al. (2007). The spectral sensitivities of *H. trispinosa* were published in Thoen et al. (2014). The *G. smithii*, *G. chiragra*, and *H. glyptocercus* recordings presented in this paper have not been published before. Kleinlogel and Marshall (2006) published recordings of the spectral sensitivities of row 2D and rows 5 and 6 in *G. chiragra*, showing both row 2D and row 5 and 6 cells to have a λ_{max} at about 565 nm.

Secondary peaks

In a few recordings, secondary peaks in the UV region appear (Fig. 2F, H, and J). These peaks have mostly been observed in the spectral sensitivity curves with λ_{max} in the shorter wavelength region between 370 and 550 nm. Similar peaks were observed in recordings from all the investigated species, although the λ_{max} of the primary spectral sensitivity varied.

Comparison to previous MSP spectral sensitivity estimates from 300 to 400 nm

We compared the UV spectral sensitivity estimates from R8 cells in *N. oerstedii* obtained using MSP (data obtained from Bok et al. [2014] for the details of visual templates and spectral sensitivity modeling refer to the original articles therein) and our electrophysiological data (Fig. 3). In general, there is good correspondence in λ_{max} values between electrophysiology and MSP for the R8 cells of rows 1, 4, 5, and 6 and the hemispheres. The spectral sensitivity of the row 2 R8 cell obtained using electrophysiology in Marshall and Oberwinkler (1999) was likely misidentified and is shown in Fig. 3A as row 3 R8 (also see the "Discussion" section). For the R8 cells of row 1 the spectral sensitivity curve obtained from MSP (Cronin and Marshall 1989a) appears wider and shifted compared with the spectral sensitivity curve from the electrophysiological data. However, Bok et al. (2014) estimated spectral sensitivity curves of row 1 R8 cells using an alternative visual template (for details see Bok et al. 2014), which results in a much better match between the electrophysiological and MSP data for this cell (Fig. 3A).

Comparison to previous MSP spectral sensitivity estimates from 400 to 700 nm

A comparison between our electrophysiological recordings and previously obtained MSP spectral sensitivities from *H. trispinosa* is shown in Fig. 3B, C. The spectral sensitivities from the short part of the spectrum (row 1D and row 4D) are narrower and shifted toward longer wavelengths in the electrophysiological recordings (λ_{max} of 420 and 445 nm, respectively) compared with those obtained using MSP and subsequent absorptance estimates (λ_{max} of 410 and 425 nm, respectively) (Fig. 3A). The long-wavelength spectral sensitivities of rows 2 and 3 show some variability between the intracellular

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

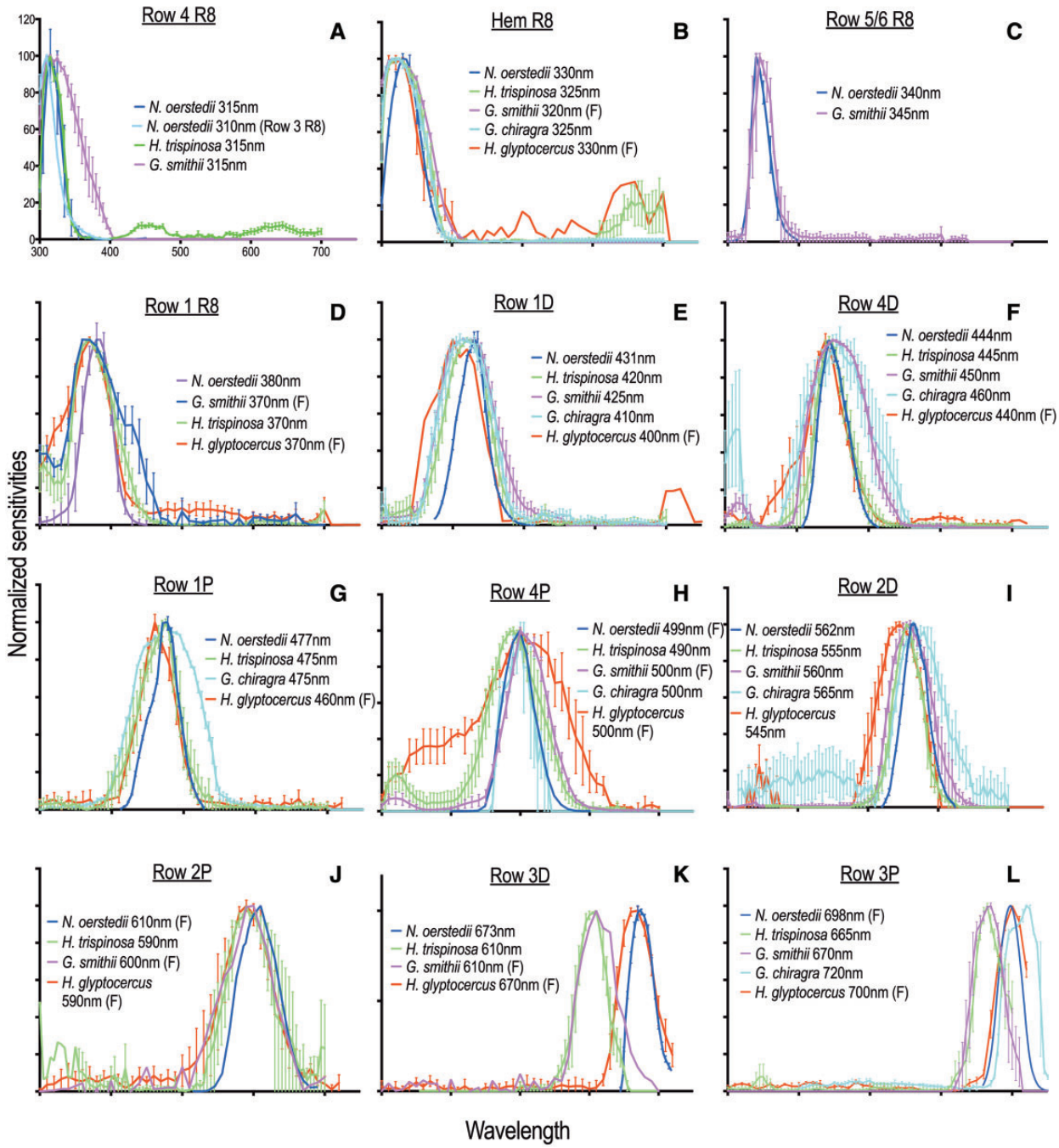

Fig. 2 Comparison of spectral sensitivity curves for each photoreceptor type across species. (**A**)–(**D**) The UV-sensitive R8 cells, (**E**) Row 1 distal, (**F**) Row 4 distal, (**G**) Row 1 proximal, (**H**) Row 4 proximal, (**I**) Row 2 distal, (**J**) Row 2 proximal, (**K**) Row 3 distal, (**L**) Row 3 proximal. Recordings are shown as mean ± SEM. Recordings performed with the flash method are indicated with the letter F. Data from *Neogonodactylus oerstedii* were previously published in Marshall and Oberwinkler (1999) and Marshall et al. (2007). Recordings from *Haptosquilla trispinosa* were published in Thoen et al. (2014).

recordings and the MSP data, with a slight difference in the λ_{max} of row 2P toward shorter wavelengths (~10 nm) in the electrophysiological data. There was also a short-wavelength shift in row 3P λ_{max} of about 30 nm compared with the MSP estimates. Row 3D on the other hand appears very similar using both methods, apart from a long tail of the row 3D MSP estimate. Figure 3B shows the difference in spectral sensitivities from shallow-living *H. trispinosa*, while Fig. 3C shows the spectral sensitivities in row 3 using the same electrophysiological results as in Fig. 3B combined with spectral sensitivity estimates from a

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

Table 1 Summary of all recordings

Cell type	*Neogonodactylus oerstedii*				*Haptosquilla trispinosa*				*Gonodactylus smithii*				*Gonodactylus chiragra*				*Haptosquilla glyptocercus*			
	λ_{max} (nm)	#Cells	#Rec		λ_{max} (nm)	#Cells	#Rec		λ_{max} (nm)	#Cells	#Rec		λ_{max} (nm)	#Cells	#Rec		λ_{max} (nm)	#Cells	#Rec	
			S	F			S	F			S	F			S	F			S	F
Row 3 R8	310	5	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Row 4 R8	315	4	8	—	315	1	4	—	315	4	14	—	—	—	—	—	—	—	—	—
Hem R8	330	9	23	—	325	3	9	—	320 (F)	3	2	4	325	3	3	4	330 (F)	2	—	2
Row 5/6 R8	340	5	12	—	—	—	—	—	345	3	4	1	—	—	—	—	—	—	—	—
Row 1 R8	380	7	18	—	370	5	15	—	370 (F)	3	6	3	—	—	—	—	370 (F)	4	1	7
Row 1D	431	1	2	3	420	6	20	—	425	8	13	4	410	7	13	3	400 (F)	2	1	1
Row 4D	444	1	3	1	445	7	21	—	450	16	33	9	460	3	7	—	440 (F)	4	2	6
Row 1P	477	1	3	—	475	4	12	—	—	—	—	—	475	2	4	3	460 (F)	5	—	9
Row 4P	499 (F)	1	—	1	490	5	16	—	500 (F)	5	—	5	500	1	2	1	500 (F)	2	—	5
Row 2D	562	1	3	3	555	5	18	—	560	5	24	2	565	2	7	—	545	2	3	3
Row 2P	610 (F)	1	—	1	590	2	6	—	600 (F)	2	2	1	—	—	—	—	590 (F)	3	6	7
Row 3D	673	1	3	3	610	2	6	—	610 (F)	1	—	2	—	—	—	—	670 (F)	5	4	9
Row 3P	698(F)	1	—	1	665	5	21	—	670	5	12	2	720	1	2	1	700 (F)	1	—	3

Notes: The spectral sensitivity maxima (λ_{max}), the number of recorded cells (#Cells), and the number of recordings per cell (#Rec), from each photoreceptor. For the recorded cells, the number of scan and flash recordings are indicated by (S) and (F), respectively. Rows 1–4 indicate midband row number, and distal (D) or proximal (P) position of the photoreceptor cell. (Hem) indicates hemispheral cell position. Total number of animals successfully recorded from: *N. oerstedii*: 30, *H. trispinosa*: 40, *G. smithii*: 29, *G. chiragra*: 7, *H. glyptocercus*: 16. Both eyes were used from each animal and in general, no more than three cells were recorded from each eye. When cells were filled with fluorescent dye only one cell per eye were recorded from. Cells with both scan and flash recordings and with λ_{max} denoted by an (F) behind the number indicate that the flash recording has been shown in the figures.

Table 2 Species ecology and physiology

Species	Location	Habitat depth range	Filters	Ecology/habitat
Neogonodactylus oerstedii	Florida Keys	Generally shallow (0–5 m), very rarely down to 29 m	4	Reef flats and coralline algae
Haptosquilla trispinosa	Lizard island	0 to at least 30 m	4	Burrows in coral rubble
Gonodactylus smithii	Lizard island	0 to at least 18 m	4	Reef flats and in coral rubble
Gonodactylus chiragra	Lizard island	0–1 m	4	Reef flats
Haptosquilla glyptocercus	Lizard island	0–2 m	4	Burrows in coral rubble

Notes: Overview of species, collections sites, depth range, total number of rhabdomal filters in midband rows 1–4, and the habitat they occupy. Depth estimates: *N. oerstedii*: Manning 1969, *H. trispinosa*: Cronin et al. 2001, *G. smithii*: Cheroske and Cronin 2005, *G. chiragra*: Marshall et al. 2007, *H. glyptocercus*: Marshall et al. 2007.

deep-living population of *H. trispinosa* obtained using MSP (Cronin and Caldwell 2002). Here the MSP spectral sensitivity estimates of the deep-living *H. trispinosa* row 3D has actually shifted toward longer wavelengths (~15 nm) while the deep-living spectral sensitivity estimate of row 3P has shifted a total of 55 nm toward shorter wavelengths, more than 25 nm further than the electrophysiologically measured spectral sensitivity of row 3P. This results from changes in intrarhabdomal filtering with depth as described in Cronin et al. (2002).

Discussion

Similarities in λ_{max} across species of stomatopods

The spectral sensitivities recorded from the five stomatopod species in this study in general show very similar λ_{max} values, particularly the ones in the part of the spectrum covering 300–550 nm. Variability in λ_{max} here normally ranged between 5 and 20 nm. There was more variability in the longer wavelength part of the spectrum, with λ_{max} values in row 3D and 3P in *H. trispinosa* (610 and 665 nm, respectively) and *G. smithii* (610 and 670 nm, respectively) shifted toward shorter wavelengths compared with *N. oerstedii*, *G. chiragra*, and *H. glyptocercus*. One of the striking aspects of this study (and previous studies of spectral sensitivities in stomatopods using MSP) is that it demonstrates how similar the λ_{max} values are across species of stomatopods.

In a few recordings with λ_{max} between 350 and 550 nm a secondary peak in the UV was observed suggesting that there could be an interaction between the UV-sensitive R8 cells and the R1–7 cells in rows 1–4. Kleinlogel and Marshall (2005) showed that the UV-sensitive R8 cell axons demonstrated varying degrees of arborizations in the lamina (the first optic neuropil) with rows 1–4 having extensive arborizations compared with the smooth axons of rows 5 and 6. These secondary peaks may result from a connection between the dendrites of the R8 cell and the terminals of the R1–7 cells, however this needs further anatomical examination. The secondary peaks are unlikely to be β-bands of the visual pigment as there is short-wave filtering in all cases from overlying photoreceptors that would preclude this. Other explanations for the secondary UV-peak in these recordings could be due to cross-recordings between the R8 cell and the R1-7 cells or it could be a case of opsin coexpression within one photoreceptor.

Correspondence to previously obtained spectral sensitivity estimates from MSP

Short wavelength spectral sensitivities: The results from this study correspond well with the photoreceptor spectral sensitivity estimates obtained from previous studies using MSP, with variations evident mainly in the short and long wavelength part of the spectrum. The spectral sensitivity curves of photoreceptors recorded from rows 1D and 4D are markedly narrower than the curves obtained using MSP and anatomical estimates. The reason for this is likely due to the fact that the MSP estimates do not take into account the filtering performed by the crystalline cones and the UV-sensitive R8 cells positioned above the R1–7 cells. Bok et al. (2014) modeled the spectral sensitivity of the row 4D photoreceptor in *N. oerstedii* using MSP absorption spectra together with new data about the filtering performed by the crystalline cones and showed that the modeled spectral sensitivities fit well with the recordings obtained using electrophysiology (data not presented here, for details see Bok et al. [2014]). The shifted λ_{max} and narrower shape of the row 1D and 4D spectral sensitivity curves in this study compared with the results from MSP is likely due to this filtering effect. The differences in the modeled and the measured row 2 R8 are likely due to a misidentification of the row 2 R8 cell in the electrophysiological results in Marshall and Oberwinkler (1999). Bok et al. (2014) suggest that the misidentified row 2 R8 is actually a row 3 R8, while the λ_{max} of the row 2 R8 obtained using MSP was at 359 nm.

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

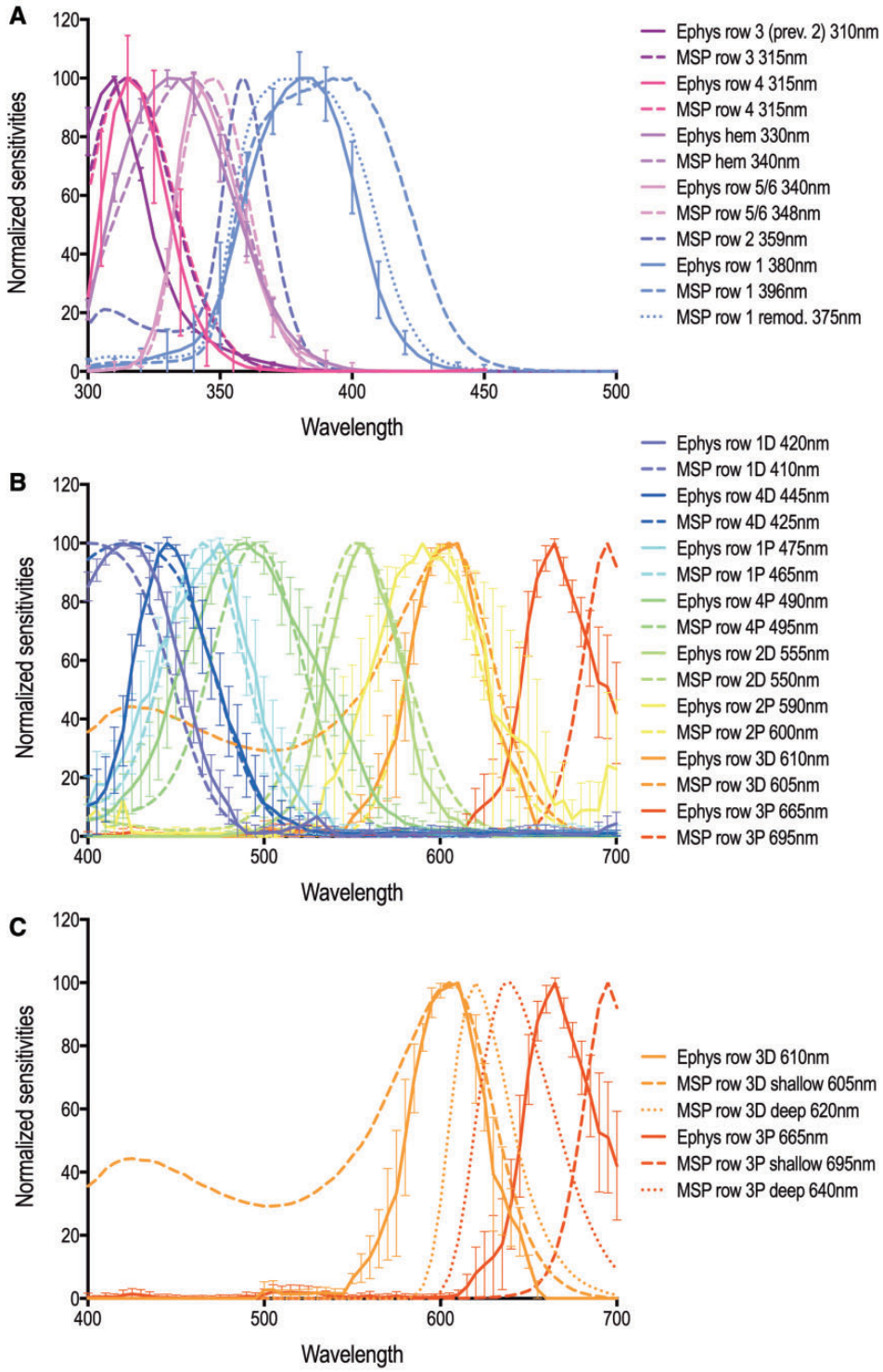

Fig. 3 Comparison of electrophysiologically recorded spectral sensitivity curves and spectral sensitivity estimates obtained using MSP. (**A**) Spectral sensitivity curves for the UV-sensitive R8 cells from *Neogonodactylus oerstedii* determined using electrophysiology (solid lines [Ephys]) and MSP (dashed lines [MSP]). The electrophysiological recordings are presented as mean ± SEM. The MSP spectral sensitivity estimates are from Bok et al. (2014). The dotted line illustrates a row 1 R8 spectral sensitivity curve estimated using an alternate visual pigment fit. For details see text and Bok et al. (2014). The legend showing Ephys row 3 (prev. 2) indicates the misidentified row 2 R8 in Marshall and Oberwinkler (1999) which is actually row 3 R8. For details see text and Bok et al. (2014). (**B**) Spectral sensitivity curves for midband rows 1–4 for *Haptosquilla trispinosa* determined using electrophysiology (solid lines [Ephys]) and MSP (dashed lines [MSP]). MSP data from a shallow-living population obtained from Cronin and Caldwell (2002). (**C**) Comparison of spectral sensitivity curves of the long-wavelength receptors of *H. trispinosa* from shallow- and deep-living populations determined using MSP (data from Cronin and Caldwell [2002]). Dashed lines indicate shallow-living populations while dotted lines indicate deep-living populations. Electrophysiologically recorded spectral sensitivity curves from shallow-living animals are also shown in solid lines (mean ± SEM).

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

Long wavelength spectral sensitivities: Previous studies (Cronin et al. 2001, 2002; Cronin and Caldwell 2002; Cheroske et al. 2003, 2006; Cheroske and Cronin 2005) have shown that stomatopods are able to tune or adjust their spectral sensitivities according to the light-environment they occupy. This tuning is performed by intrarhabdomal filters, where the optical density and spectral shape of the filter is adjusted according to the dominating light environment (Cronin and Caldwell 2002). The visual pigments themselves do not show any differential expression according to habitat depth (Cronin et al. 2002), and as it is only midband rows 2 and 3 that contain filters, rows 1 and 4 remain the same under different light conditions. Differences among the filters within the midband are also evident, with filters in row 2 using a different pigment in each major stomatopod lineage while row 3 filters use flexible interconversion and mixing of pigments, making these filters tunable within an individual (Cheroske et al. 2006; Porter et al. 2010). As red light attenuates faster than blue light with increasing depth this system is adaptive on a short time-scale, and it enables stomatopods to tune the spectral range of their color vision system according to their environmental depth.

The largest variability in λ_{max} found in this study occurs in midband rows 2 and 3. The recordings from *H. trispinosa* reveal that the row 3P λ_{max} have shifted toward shorter wavelengths, though not as much as the calculated MSP spectral sensitivities from *H. trispinosa* at 18 m depth (Cronin and Caldwell 2002) (Fig. 3B). The species included in this study were all collected in shallow water (0–5 m), but despite keeping the animals in a light environment as close as possible to natural and recording from them as quickly as possible after bringing them to the laboratory, some changes to their spectral sensitivities may have occurred between the time of collection and recording. Both Cronin et al. (2001) and Cheroske et al. (2006) found that individuals of *H. trispinosa*, *Neogonodactylus wennerae*, and *Neogonodactylus bredini* kept in restricted light environment (lacking wavelengths longer than 550 nm) for about 3 months changed their filters to resemble filters of deep-water living animals, indicating that their color vision encompasses a significant level of phenotypic plasticity. Such a change has also been observed on even shorter timescales (within a few weeks) (T. W. Cronin, personal communication). *Gonodactylus smithii* are likewise able to tune their color vision, as well as being able to change their body coloration according to depth (Cheroske and Cronin 2005). *Neogonodactylus oerstedii* on the other hand did not change its filters significantly (Cheroske et al. 2006), suggesting a more limited ecological variation in habitat depth for this species. This is in agreement with our results, which showed no shift toward shorter wavelengths in row 3 receptors in *N. oerstedii*. *Haptosquilla trispinosa* and *G. smithii* are known to more commonly inhabit depths from 0 to between 18 and 30 m, and could exhibit a larger amount of tuning ability in their color vision, while the normally shallower living *N. oerstedii*, *G. chiragra*, and *H. glyptocercus* may have no need for this tuning ability.

It is interesting that in general, while the range of spectral sensitivities in the stomatopod species here may have become narrowed, particularly at long wavelengths, no photoreceptors are lost. Fish, birds, and other animals living in spectrally narrowed environments are known to shed cone types (Lythgoe 1979; Losey et al. 2003). Stomatopods from the deeper living superfamily Squilloidea have lost the entire complexity of the six-row midband, reducing to two midband rows or to "normal crustacean" rhabdoms, such as the ones found in the hemispheres (Ahyong and Harling 2000). Beyond a certain point in spectral narrowing, it is clearly no longer energetically valuable to maintain such complex color vision (Sterling and Laughlin 2015). Shallow-living species of stomatopods such as the ones investigated in this study are all fast-moving animals that appear to use color (and polarized signals) for a variety of communication signals and live in complex and spectrally rich environments such as the coral reef (Steger and Caldwell 1983; Adams and Caldwell 1990; Mazel et al. 2003; Cheroske and Cronin 2005; Chiou et al. 2005, 2011; Cheroske et al. 2009; Cronin et al. 2009). *Haptosquilla trispinosa* and *H. glyptocercus* live in cavities in hard substrate such as rock or coral rubble, acting as sit-and-wait predators at the burrow entrance (Caldwell and Dingle 1977; Reaka and Manning 1981; Ahyong 2001). *Neogonodactylus oerstedii*, *G. smithii*, and *G. chiragra* on the other hand live a more exposed lifestyle where they roam around hunting for prey on exposed reef flats, seeking shelter in coralline algae and coral rubble (Caldwell and Dingle 1975; Reaka and Manning 1981; Ahyong 2001). Despite these lifestyle differences, all the species clearly have need for a quick and reliable color vision system both when interacting with conspecifics and during encounters with possible predators and prey.

Proposed color processing systems

Stomatopod clearly construct their color world differently to other animals. Previous suggestions on

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

color vision using 12 spectral sensitivities include the hypothesis of within-row opponency (Marshall 1988; Cronin and Marshall 1989b), where the tiered retinula cells (R1, R4, R5 vs. R2, R3, R6, and R7) in a single ommatidium could provide a narrow dichromatic opponent pair without substantial re-wiring (see Marshall et al. [2007] for further explanation). This idea of within midband-row opponent channels (providing a total four potential dichromacies) has since been replaced or added to by the hypothesis of a more unconventional color sense discussed below, however, the two systems are not necessarily mutually exclusive. Thoen et al. (2014) carried out behavioral experiments on the color vision system of stomatopods and found that, despite the large number of photoreceptors, stomatopods have poor spectral resolution. This has led to the proposition that stomatopods may process color differently to other animals, possibly using a system based on a "winner takes it all" principle coupled with interval decoding, as proposed in Zaidi et al. (2014) or using a spectral pattern recognition system as proposed in Marshall and Arikawa (2014) and Thoen et al. (2014). Either system would necessitate photoreceptor spectral sensitivities that are evenly distributed through the spectrum to enable sufficient sampling of the available colors. This examination of color could also be viewed as working more like the cochlea in the vertebrate ear, an encoding mechanism that looks for a frequency pattern across a sound/color frequency continuum (Marshall et al. 2007). The narrow shape of each spectral sensitivity would determine the spectral resolution of such a system, which would provide an explanation for the poor behavioral wavelength discrimination reported by Thoen et al. (2014) and the apparently excessive number of spectral sensitivities found in stomatopods. Further speculation requires a better understanding of how color information is used by stomatopods in a variety of behavioral contexts.

Conclusion

This study supports the conclusions from previous studies of stomatopod spectral sensitivities; they have a high number of spectral sensitivities and they appear to strive to keep their spectral sampling range as numerous and wide as possible within the available light environment. Their color vision also appears, at least in some species, to be tunable. Further electrophysiological work is needed to disentangle the spectral tuning abilities across species, depths, and time scales. Investigations into the neural architecture beneath the complex retina and electrophysiological recordings of neurons involved in the various stages of color processing are also required to provide a more comprehensive understanding of how stomatopods see colors.

Acknowledgments

The authors thank Assoc. Prof. Anders Garm for the gracious invitation to participate in this symposium. They also would like to thank Prof. Tom Cronin and Dr. Michael Bok for supplying the MSP spectral sensitivity estimates and the two anonymous reviewers for their helpful comments.

Funding

This work was supported by the grants from the Asian Office of Aerospace Research and Development [Grant number: AOARD-12-4063] and the Australian Research Council [Grant number: FL140100197] to N. J. M, and a Doctoral Fellowship (2013) from the Lizard Island Research Foundation, a facility of the Australian Museum to H. H. T. Financial support was also granted from the Society for Integrative Biology (SICB) and from the Company of Biologists.

References

Adams E, Caldwell R. 1990. Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. Anim Behav 39:706–16.

Ahyong ST. 2001. Revision of the Australian stomatopod Crustacea. Rec Aust Mus 26(Suppl):1–326.

Ahyong ST, Harling C. 2000. The phylogeny of the stomatopod Crustacea. Aust J Zool 48:607–42.

Barlow HB. 1982. What causes trichromacy? A theoretical analysis using comb-filtered spectra. Vision Res 22:635–43.

Bok MJ, Porter ML, Place AR, Cronin TW. 2014. Biological sunscreens tune polychromatic ultraviolet vision in mantis shrimp. Curr Biol 24:1636–42.

Caldwell RL, Dingle H. 1975. Ecology and evolution of agonistic behavior in stomatopods. Naturwissenschaften 62:214–22.

Caldwell RL, Dingle H. 1977. Variation in agonistic behavior between populations of the stomatopod, *Haptosquilla glyptocercus*. Evolution 31:220–3.

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 150:213–20.

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.

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 206:373–9.

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

Cheroske AG, Cronin TW, Durham FM, Caldwell RL. 2009. Adaptive signalling behaviour in stomatopods under varying light conditions. Mar Freshw Behav Physiol 42:219–32.

Chiao CC, Cronin TW, Marshall NJ. 2000. Eye design and color signaling in a stomatopod crustacean *Gonodactylus smithii*. Brain Behav Evol 56:107–22.

Chiou T-H, Cronin TW, Caldwell RL, Marshall J. 2005. Biological polarized light reflectors in stomatopod crustaceans. Proceedings of the SPIE, Polarization Science and Remote Sensing II, p. 58881B–58881B-9.

Chiou TH, Kleinlogel S, Cronin TW, Caldwell R, Loeffler B, Siddiqi A, Goldizen A, Marshall NJ. 2008. Circular polarization vision in a stomatopod crustacean. Curr Biol 18:429–34.

Chiou TH, Marshall NJ, Caldwell RL, Cronin TW. 2011. Changes in light-reflecting properties of signalling appendages alter mate choice behaviour in a stomatopod crustacean *Haptosquilla trispinosa*. Mar Freshw Behav Physiol 44:1–11.

Collin SP, Davies WL, Hart NS, Hunt DM. 2009. The evolution of early vertebrate photoreceptors. Philos Trans R Soc Lond B Biol Sci 364:2925–40.

Cronin TW, Bok MJ, Marshall NJ, Caldwell RL. 2014. Filtering and polychromatic vision in mantis shrimps: themes in visible and ultraviolet vision. Philos Trans R Soc Lond B Biol Sci 369 published online (doi: 10.1098/rstb.2013.0032).

Cronin TW, Caldwell RL. 2002. Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. II. Filter pigments. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 188:187–97.

Cronin TW, Caldwell RL, Erdmann MV. 2002. Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. I. Visual pigments. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 188:179–86.

Cronin TW, Caldwell RL, Marshall NJ. 2001. Sensory adaptation. Tunable colour vision in a mantis shrimp. Nature 411:547–8.

Cronin TW, Chiou T-H, Caldwell RL, Roberts NW, Marshall NJ. 2009. Polarization signals in mantis shrimps. In: Joseph A, Shaw J, Scott T, editors. SPIE optical engineering + applications. San Diego: The International Society for Optical Engineering. p. 74610C-1–10.

Cronin TW, Marshall NJ. 1989a. Multiple spectral classes of photoreceptors in the retinas of gonodactyloid stomatopod crustaceans. J Comp Physiol A 166:261–75.

Cronin TW, Marshall NJ. 1989b. A retina with at least ten spectral types of photoreceptors in a mantis shrimp. Nature 339:137–40.

Cronin TW, Marshall NJ, Caldwell RL. 1993. Photoreceptor spectral diversity in the retinas of Squilloid and Lysiosquilloid stomatopod crustaceans. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 172:339–50.

Cronin TW, Marshall NJ, Caldwell RL. 1994a. The intrarhabdomal filters in the retinas of mantis shrimps. Vision Res 34:279–91.

Cronin TW, Marshall NJ, Caldwell RL. 1994b. The retinas of mantis shrimps from low-light environments (Crustacea; Stomatopoda; Gonodactylidae). J Comp Physiol A 174:607–19.

Cronin TW, Marshall NJ, Caldwell RL. 1996. Visual pigment diversity in two genera of mantis shrimps implies rapid evolution (Crustacea; Stomatopoda). J Comp Physiol A 179:371–84.

Cronin TW, Marshall NJ, Caldwell RL, Shashar N. 1994c. Specialization of retinal function in the compound eyes of mantis shrimps. Vision Res 34:2639–56.

Cronin TW, Marshall NJ, Quinn CA, King CA. 1994d. Ultraviolet photoreception in mantis shrimp. Vision Res 34:1443–52.

Cronin TW, Porter ML. 2008. Exceptional variation on a common theme: the evolution of crustacean compound eyes. Evo Edu Outreach 1:463–75.

Cronin TW, Porter ML, Bok MJ, Wolf JB, Robinson PR. 2010. The molecular genetics and evolution of colour and polarization vision in stomatopod crustaceans. Ophthalmic Physiol Opt 30:460–9.

DeVoe RD, de Souza JM, Ventura DF. 1997. Electrophysiological measurements of spectral sensitivities: a review. Braz J Med Biol Res 30:169–77.

Dingle H, Caldwell RL. 1969. The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* manning (Crustacea: stomatopoda). Behaviour 33:115–36.

Gagnon YL, Templin RM, How MJ, Marshall NJ. 2015. Circularly polarized light as a communication signal in mantis shrimps. Curr Biol 25:3074–8.

Kelber A, Osorio D. 2010. From spectral information to animal colour vision: experiments and concepts. Proc Biol Sci 277:1617–25.

Kleinlogel S, Marshall NJ. 2005. Photoreceptor projection and termination pattern in the lamina of gonodactyloid stomatopods (mantis shrimp). Cell Tissue Res 321:273–84.

Kleinlogel S, Marshall NJ. 2006. Electrophysiological evidence for linear polarization sensitivity in the compound eyes of the stomatopod crustacean *Gonodactylus chiragra*. J Exp Biol 209:4262–72.

Laughlin SB. 1975. Receptor function in the apposition eye—an electrophysiological approach. In: Snyder AW, Menzel R, editors. Photoreceptor optics. Berlin, Germany: Springer. p. 479–98.

Losey GS, McFarland WN, Loew ER, Zamzow JP, Nelson PA, Marshall NJ. 2003. Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. Copeia 2003:433–54.

Lythgoe JN. 1979. The ecology of vision. Oxford: Clarendon Press.

Maloney LT. 1986. Evaluation of linear models of surface spectral reflectance with small numbers of parameters. J Opt Soc Am A 3:1673–83.

Manning RB. 1969. Stomatopod Crustacea of the Western Atlantic. Studies in Tropical Oceanography, Miami 8:1–380.

Marshall NJ. 1988. A unique colour and polarization vision system in mantis shrimps. Nature 333:557–60.

Marshall NJ, Arikawa K. 2014. Unconventional colour vision. Curr Biol 24:R1150–4.

Marshall NJ, Cronin TW, Kleinlogel S. 2007. Stomatopod eye structure and function: a review. Arthropod Struct Dev 36:420–48.

Marshall NJ, Land MF, King CA, Cronin TW. 1991a. The compound eyes of mantis shrimps (Crustacea,

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017

Hoplocarida, Stomatopoda). I. Compound eye structure: the detection of polarized light. Philos Trans R Soc Lond B Biol Sci 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. Philos Trans R Soc Lond B Biol Sci 334:57–84.

Marshall NJ, Oberwinkler J. 1999. Ultraviolet vision: the colourful world of the mantis shrimp. Nature 401:873–5.

Mazel CH, Cronin TW, Caldwell RL, Marshall NJ. 2003. Fluorescent enhancement of signaling in a mantis shrimp. Science 303:51.

McCulloch KJ, Osorio D, Briscoe AD. 2016. Determination of photoreceptor cell spectral sensitivity in an insect model from in vivo intracellular recordings. J Vis Exp (108):53829.

Menzel R, Ventura DF, Hertel H, Desouza JM, Greggers U. 1986. Spectral sensitivity of photoreceptors in insect compound eyes—comparison of species and methods. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 158:165–77.

Osorio D, Marshall NJ, Cronin TW. 1997. Stomatopod photoreceptor spectral tuning as an adaptation for colour constancy in water. Vision Res 37:3299–309.

Porter ML, Bok MJ, Robinson PR, Cronin TW. 2009. Molecular diversity of visual pigments in Stomatopoda (Crustacea). Vis Neurosci 26:255–65.

Porter ML, Speiser DI, Zaharoff AK, Caldwell RL, Cronin TW, Oakley TH. 2013. The evolution of complexity in the visual systems of stomatopods: insights from transcriptomics. Integr Comp Biol 53:39–49.

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 213:3473–86.

Reaka ML, Manning RB. 1981. The behavior of stomatopod Crustacea, and its relationship to rates of evolution. J Crustacean Biol 1:309–27.

Steger R, Caldwell RL. 1983. Intraspecific deception by bluffing: a defense strategy of newly molted stomatopods (Arthropoda: Crustacea). Science 221:558.

Sterling P, Laughlin S. 2015. Principles of neural design. Cambridge (MA): MIT Press.

Thoen HH, How MJ, Chiou TH, Marshall NJ. 2014. A different form of color vision in mantis shrimp. Science 343:411–3.

Watanabe A, Obara S, Akiyama T. 1967. Pacemaker potentials for the periodic burst discharge in the heart ganglion of a stomatopod, *Squilla oratoria*. J Gen Physiol 50:839–62.

Zaidi Q, Marshall NJ, Thoen HH, Conway BR. 2014. Evolution of neural computations: mantis shrimp and human color decoding. i-Perception 5:492–6.

Downloaded from https://academic.oup.com/icb/article-abstract/doi/10.1093/icb/icx111/4096521/Intracellular-Recordings-of-Spectral-Sensitivities
by University of Queensland user
on 05 September 2017