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Eye Design and Color Signaling in a Stomatopod Crustacean *Gonodactylus smithii*

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Key Words
Eye design · Color signaling · Color vision · Stomatopod · *Gonodactylus smithii*

Abstract
Many species of stomatopod crustaceans have multiple spectral classes of photoreceptors in their retinas. Behavioral evidence also indicates that stomatopods are capable of discriminating objects by their spectral differences alone. Most animals use only two to four different types of photoreceptors in their color vision systems, typically with broad sensitivity functions, but the stomatopods apparently include eight or more narrowband photoreceptor classes for color recognition. It is also known that stomatopods use several colored body regions in social interactions. To examine why stomatopods may be so 'concerned' with color, we measured the absorption spectra of visual pigments and intrarhabdomal filters, and the reflectance spectra from different parts of the bodies of several individuals of the gonodactyloid stomatopod species, *Gonodactylus smithii.* We then applied a model of multiple dichromatic channels for color encoding to examine whether the finely tuned color vision was specifically co-evolved with their complex color signals. Although the eye design of stomatopods seems suitable for detecting color signals of their own, the detection of color signals from other animals, such as reef fishes, can be enhanced as well. Color vision in *G. smithii* is therefore not exclusively adapted to detect its own color signals, but the spectral tuning of some photoreceptors (e.g. midband Rows 2 and 3) enhances the contrast of certain color signals to a large enough degree to make co-evolution between color vision and these rather specific color signals likely.

Introduction

The color vision systems of animals vary in the number of distinct spectral classes of photoreceptors that are used to extract chromatic information from the outside world. Obviously, two different spectral types of photoreceptor cells are a minimum requirement for color vision. Beyond this minimum, one might ask how much information can be gained by acquiring additional photoreceptor classes in the retina, and what limits the number of classes. Based on Barlow's [1982] consideration of photoreceptor spectral bandwidth, trichromacy extracts almost all possible spectral information in the range 400 to 700 nm. Indeed, most animals (both vertebrates and invertebrates) known to have color vision have 2 to 4 different types of photoreceptors. For example, typical mammals have two [Jacobs, 1993], most primates and honeybees have three [Menzel and Backhaus, 1991; Jacobs, 1991], and most birds, reptiles and many fishes have four; the fourth photoreceptor often accompanying an expansion of the color vision system to include UV [Gold-

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smith, 1990; Neumeyer, 1991; Vorobyev et al., 1998]. However, stomatopods (mantis shrimps) have been found to have as many as sixteen different types of photoreceptors, and at least eight of these are involved in color vision [Cronin and Marshall, 1989a, b; Marshall et al., 1991a, b, 1994; Cronin et al., 1994c]. Behavioral studies [Marshall et al., 1996] have also shown, unsurprisingly, that stomatopods have true color vision – objects can be distinguished by stomatopods using only chromatic information. These results immediately raise the following question: Why do these animals have so many different types of photoreceptors, i.e. what advantages might this visual system have?

Osorio et al. [1997] have postulated that these eight narrow-band spectral classes may help stomatopods to achieve color constancy in environments where illuminants are spatially and temporally variable. Based on theoretical calculations of modeled spectra, Osorio et al. [1997] showed that a photoreceptor pair with narrow-band spectral sensitivities, like that found in each row of the midband, can detect color signals more reliably than a photoreceptor pair that has typically broad-band spectral sensitivities. This reliability of detecting color signals is especially crucial for animals such as stomatopods that use color for their intraspecific communication under various conditions of illumination [Caldwell and Dingle, 1975, 1976]. In this study, we consider in detail the possibility that stomatopod color vision systems may also function to enhance the detection of color signals reflected from the bodies of the animals themselves.

Gonodactylus smithii is a brightly colored species, living in the shallow, clear, tropical waters of the Indo-Pacific. During intraspecific communication, individuals of this species display brightly colored spots on their raptorial limbs and telsons [Caldwell and Dingle, 1975, 1976; Hazlett, 1979]. The perception of color signals may play a major role in determining the status of stomatopods during agonistic interactions and in recognizing conspecifics during male-female interactions [Caldwell and Dingle, 1975; Hazlett, 1979]. It has long been speculated that color signals of animals co-evolve with their sensory systems [Endler, 1992, 1993]. However, there is no conclusive evidence to support that speculation anywhere except in bioluminescent signaling [Partridge and Douglas, 1995; Cronin et al., 2000]. In this study, we examined potential color signals from several individual mantis shrimps, as well as from various reef fishes that *G. smithii* may encounter in its natural habitats, to investigate whether vision in this species is specialized to enhance its own color signals above other color signals from neighboring animals such as reef fishes.

To study color detection in *G. smithii*, we first computed the spectral sensitivity functions of all different photoreceptor classes involved in color vision, namely those in main rhabdoms of Rows 1–4 in the midband (see fig. 1 for a diagram of the retina of *G. smithii*). The reflectance spectra and multispectral images of various body parts from several individuals were also measured, as well as various reflectance spectra of reef fish colors [Marshall, 2000]. Using a model of multiple dichromatic channels for color encoding in stomatopods proposed by Marshall et al. [1996], we estimated the chromaticities in four ommatidial rows (Rows 1 to 4) of the midband of *G. smithii* to test the following hypothesis: The color vision system of *G. smithii* enhances the detection (i.e. the chromaticity) of intraspecific color signals. Note that we use color signals strictly to represent the spectral variation of body colors throughout this study, and chromaticity is used to denote color information encoded in the chromatic channel. The possibility of co-evolution of body coloration and the eye designs in stomatopods will be discussed in the context of animal communication.

Materials and Methods

Animals and Experimental Preparation

Individuals of *Gonodactylus smithii* of both sexes were collected from Coconut Reef flat, near Lizard Island Research Station (Queensland, Australia), in August of 1997 and 1998. All animals are low intertidal animals that probably never experienced ambient light at depths exceeding 3 m. Animals were generally maintained in the laboratory for brief periods before examination and measurement. In the laboratory, animals were kept in marine aquaria at ≈25 °C illuminated by daylight fluorescent lamps and fed fresh and frozen shrimp.

Microspectrophotometry

Absorption spectra of visual pigments and intrarhabdomal filters were obtained using techniques described previously by Cronin and Forward [1988], Cronin and Marshall [1989a] and Cronin et al. [1994a, b]. In brief, eyes were removed from animals dark-adapted overnight or longer, and were immediately flash-frozen using cryogenic spray. Frozen eyes were mounted in a cryostat at ≈ –30 °C and sectioned at a thickness of 14 µm. Individual retinal sections were mounted in pH 7.5 marine crustacean Ringer's solution containing 2.5% glutaraldehyde (visual pigments) or in mineral oil (intrarhabdomal filters) within a ring of silicone grease between coverslips for microspectrophotometry.

The microspectrophotometer (MSP) is of single-beam design, scanning from 400 to 700 nm. A small circular, linearly polarized spot (1.5 µm or 5 µm in diameter) was placed in the material to be scanned. Retinal location was ascertained using the characteristic structure of stomatopod retinas [Marshall et al., 1991a]. A reference scan was first taken in a clear region of the specimen, followed by a measurement scan in the material of interest. Intrarhabdomal filters were identified and positioned under white light and the spectrum was obtained directly. To measure absorbance spectra of visual pigments, rhabdoms were positioned under dim red illumination (Corning CS 2-61 filter; 50% transmission at 619 nm), and two initial scans were made of the dark-adapted rhabdom (to check for physical and photochemical sta-

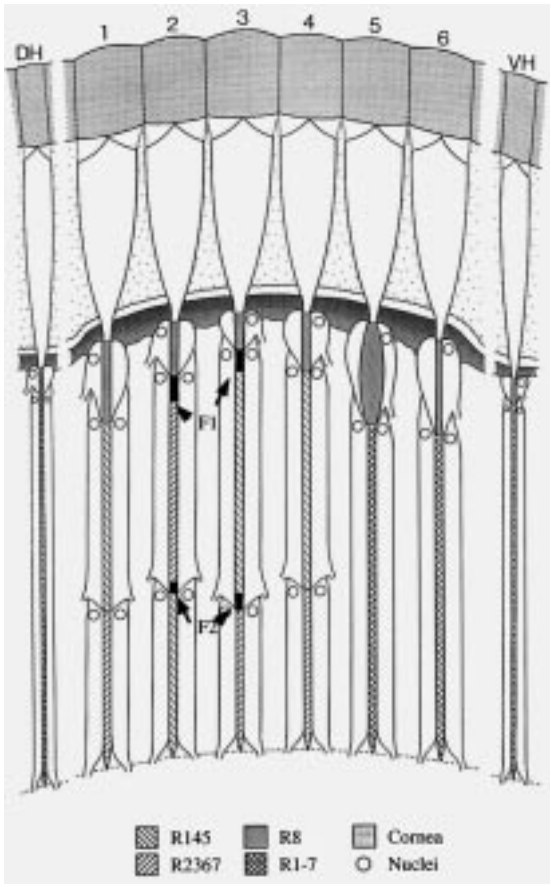


Fig. 1. Diagram of the retina and dioptric apparatus of *Gonodactylus smithii*, showing the cornea, crystalline cones, rhabdoms and intrarhabdomal filters. Crystalline cones are the clear, paraboloid structures between the cornea and R8. Nuclei, indicated by circles, are those of the retinular cells. Abbreviations: 1–6 = Rows of the midband; DH = dorsal hemisphere of peripheral retina; VH = ventral hemisphere of peripheral retina; F1 = distal intrarhabdomal filter; F2 = proximal intrarhabdomal filter; R145 = 3-part rhabdom produced by the 1st, 4th, and 5th retinular cells; R2367 = 4-part rhabdom produced by the 2nd, 3rd, 6th, and 7th retinular cells; R8 = rhabdomere of the 8th retinular cell; R1-7 = 7-part rhabdom produced by the retinular cells number 1 through number 7.

bility). The rhabdom was then exposed to a photobleaching exposure of bright white light for 2–5 min, using the substage illuminator of the photometric microscope, and another scan was taken. The difference between last two scans was considered to be the absorption spectrum of the photobleachable visual pigment in the rhabdom.

For the best estimate of the spectral position of each type of photopigment, all photobleach data from each rhabdom were averaged. Each resulting curve was tested for fit against rhodopsin template functions derived by Palacios et al. [1996]. The best fit was defined as that producing the least sum of squares of deviations, from 25 nm below the wavelength of the maximum absorbance to 75 nm above. For maxima below 425 nm, the sum of squares was computed from 400 nm, to 75 nm beyond the maximum, and corrected for the reduced number of squared deviations. See Cronin and Marshall [1989a] for details.

Computation of Spectral Sensitivity Functions of Rows 1–4 of the Midband

It has been shown previously that photoreceptors in Rows 1–4 of the midband of stomatopods are specialized for color vision [Cronin and Marshall, 1989b; Marshall et al., 1991b]. For the purpose of modeling chromaticities in this study, only the spectral sensitivity functions from both tiers of main rhabdoms in Rows 1–4 of the midband were considered. The computation of spectral sensitivity functions was based on the absorbance spectra of the intrarhabdomal filters and visual pigments derived above, retinal dimensions of the appropriate photoreceptors and filters, and optical data from a closely related species *(Gonodactylus chiragra)* in Marshall et al. [1991a]. See Cronin et al. [1994c] for details.

Hypothetical Spectral Sensitivity Functions of Rows 1–4 of the Midband

To test whether color signals can be enhanced by visual systems of *G. smithii*, we also generated two sets of hypothetical spectral sensitivity functions of Rows 1–4 of the midband. These hypothetical spectral sensitivity functions represent possible primitive forms of spectral sensitivity functions in stomatopods. Because the tiering and filtering effects are the main factors that shape spectral sensitivities of Rows 1–4 of the midband, our hypothetical spectral sensitivity functions were computed based on the absorption spectra of the actual visual pigments of *G. smithii* and the consideration of (1) no intrarhabdomal filtering effects for Rows 2 and 3, (2) neither tiering nor filtering effects for all Rows 1–4. In the first case, therefore, only filtering by overlying photoreceptors acts to tune spectral sensitivity functions in Rows 2 and 3 (as is normal in Rows 1 and 4). In the second case, the retina is considered to contain a set of 8 typical, untiered, photoreceptor classes. By comparing chromaticities provided by real spectral sensitivity functions with those of hypothetical functions, we examine how the spectral sensitivities of multiple photoreceptor classes in the midband of the eyes of *G. smithii* affect the detection of color signals.

Measurements of Reflectance Spectra and Multispectral Images of G. smithii

All spot measurements of reflectance spectra from various body parts were made with 'Sub-Spec', a custom-built spectroradiometer (Andor Technology/Oriel), and were referenced to a 99% diffuse white reflection standard [see Marshall et al., 1996, for details]. The reflectance spectra reported in this study were obtained from 5 individuals, and include samples from raptorial appendages (both blue and pink areas, meral spots), maxillipeds, and the orange spots on the last segment of the abdomen.

Multispectral images were recorded from 6 individuals using a custom-made device composed of a CCD camera (Electrim, EDC-1000TE camera, 191 × 164 elements, 8 bits resolution) and a variable interference filter (OCLI semicircular). Typically, we captured 43 frames of images at 7 to 8 nm intervals from 405 to 718 nm. The reflectance spectrum of each pixel in the images was determined by comparison with white (Spectralon, Labsphere) and black (3% diffuse reflector, MacBeth) standards [see Chiao et al., 2000, for details]. Comparisons among images collected at different wavelengths showed no evidence of systematic magnification or registration errors within the resolution of the system [see Osorio et al., 1998]. Multi-

spectral images collected in this study include views of the cephalothorax (showing raptorial appendage, maxillipeds, and meral spots), the abdomen, and the tail region (telsons and uropods) of stomatopods.

Calculations of Stomatopod Color Signals in Rows 1–4 of the Midband

Based on the observation that axons of both distal and proximal tiers of each row in the midband project to the same laminar cartridge (the first interneurons in the visual systems of crustaceans), Marshall et al. [1996] suggested that color signals may be processed independently in each row of Rows 1–4 at the laminar level. Following this suggestion, we predicted the chromaticities that would be given by each row. We first calculated the quantum catch, Q_t, of each tier viewing a body part of a conspecific animal (Eq. 1),

$$Q_t = \sum I(\lambda)R_t(\lambda)S(\lambda) \quad (1)$$

where $I(\lambda)$ is the illuminant spectrum [a CIE standard daylight illuminant, D65, was used in this analysis to represent the combination of light from sun and sky; Wyszecki and Stiles, 1982], $R_t(\lambda)$ is the reflectance spectrum of a particular body part, and $S(\lambda)$ is the spectral sensitivity function of each tier of Rows 1–4 of the midband. The summation is over the range of 400–750 nm for the Sub-Spec data, and 405–718 nm for the multispectral imaging data.

To restrict responses to the middle part of each receptor's operating range, all photoreceptors were considered to be adapted to the background. The quantum catch for a tier viewing the background, Q_b, is given by Eq. 2

$$Q_b = \sum I(\lambda)R_b(\lambda)S(\lambda) \quad (2)$$

Here we define the spectrum of the background $R_b(\lambda)$ as that reflected from a 10% neutral density reflector for the Sub-Spec data, or as the average of all reflectance spectra in the image for the multispectral imaging data.

Thus, the adapted neural response, P, of each tier can be computed by dividing Q_t by Q_b (Eq. 3).

$$P = Q_t/Q_b \quad (3)$$

By dividing by the quantum catch of the background, we are able to access the responses without regard to an overall illumination level. This is analogous to a von Kries adaptation mechanism [von Kries, 1905], where the response of each photoreceptor class is normalized independently.

The chromaticity, C, in each row (of Rows 1–4) of the midband is defined as the difference between the responses of distal, P_{dist}, and proximal tiers, P_{prox}.

$$C = \log P_{dist} - \log P_{prox} \quad (4)$$

Note that the use of a logarithmic scale of response in each tier is simply to give a biologically realistic dynamic range for chromaticity estimation, and that the logarithmic subtraction is equivalent to division of the two responses. In the computation of chromaticities from the Sub-Spec data, the signs of chromaticities were made positive to simplify comparison (see fig. 6, 9). In the calculation of chromaticities from the multispectral imaging data, the signs of chromaticities were left intact for adjusting suitable dynamic ranges (see fig. 7).

Calculations of Reef Fish Color Signals in Rows 1–4 of the Midband

Over 1,000 reflectance spectra (including 200 species from 36 families) of reef fishes collected from Great Barrier Reef were used in this study [see Marshall, 2000, for detail]. Chromaticities in Rows 1–4 of the midband viewing 26 subjective categories of reef fish colors were computed individually using the same formula described above (Eqs. 1–4). Both real and hypothetical sensitivity spectra of *G. smithii* were used in the computation of chromaticities. Results were compared to examine whether the vision systems of stomatopods can also enhance the detection of color signals from reef fishes.

Results

Our primary objective was to examine the relationship between the color signals and the color vision system of the gonodactyloid stomatopod species, *Gonodactylus smithii*. To do this, we required objective assessments both of color signals and of the color vision system [see Endler, 1990]. We characterized the visual system of *G. smithii* and measured potential color signals from conspecific individuals and reef fishes. Thus, the chromaticities which stomatopods might obtain using their visual systems can be objectively evaluated.

Absorption Spectra of Visual Pigments and Intrarhabdomal Filters

The retinas of *Gonodactylus smithii* include 11 classes of photoreceptors below the level of the 8th retinular cell: two tiered classes in each midband row from Row 1 to Row 4 plus the main rhabdoms of midband Row 5 and 6 and of the peripheral retina (see fig. 1). We examined each class of photoreceptor in retinas of this species, and identified a total of 10 different visual pigments (fig. 2a–f). The distribution of visual pigments throughout the retina was qualitatively similar to what is observed in other stomatopods with 6-row midbands [Cronin and Marshall, 1989a; Cronin et al., 1993, 1994a, 1996].

Stomatopod crustaceans in the superfamily Gonodactyloidea generally have 4 classes of intrarhabdomal filters in their retinas: distal Row 2, proximal Row 2, distal Row 3 and proximal Row 3 [Marshall, 1988; Marshall et al., l991b; Cronin et al., 1994b]. *G. smithii* has all 4 types (fig. 2g, h). These 4 classes of intrarhabdomal filters can significantly shift and narrow the spectral sensitivity functions of photoreceptors in Rows 2 and 3 [Cronin et al., 1993, 1994c].

Spectral Sensitivity Functions of Rows 1–4 of the Midband

With knowledge of the visual pigments, filter absorption spectra, dimensions of the various photoreceptor classes, and optical data from a closely related species [*Gonodactylus chiragra;* see Marshall et al., 1991a], the spectral sensitivity functions of Rows 1–4 of the midband can be com-

puted (fig. 3a). The distribution of spectral sensitivities throughout the Rows 1–4 has the typical gonodactyloid pattern [see Cronin et al., 1994c]. Each ommatidium of midband Rows 1–4 has a pair of spectrally narrow classes separated by 30 to 60 nm at their peaks; the proximal tier is sensitive at longer wavelengths than the distal tier (fig. 3a).

For modeling, we sharpened the spectral sensitivity functions of Rows 1 and 4 distal main rhabdoms (R1D and R4D; fig. 3a) of *G. smithii* on the short wavelength side. As Marshall et al. [1996] pointed out, all midband sensitivities of stomatopods are now believed to have approximately the same shape due to distal filtering. Note that the wavelength range of the spectral sensitivity functions of Rows 1–4 (fig. 3) are provided from 400–750 nm. The spectral range of our MSP data only extended to 700 nm, so the long wavelength limb of the spectral sensitivity function of R3P (fig. 3a) was generated by symmetric flip-over of the short wavelength limb.

Two sets of hypothetical spectral sensitivity functions were generated by removing the absorption spectra of intrarhabdomal filters in Rows 2 and 3 from computation, and by removing all tiering and filtering effects from modeling, respectively (fig. 3b, c). Due to the lack of intrarhabdomal filtering in Rows 2 and 3, the spectral sensitivity functions of distal tiers of these 2 rows now become broader, and shift to shorter wavelengths than actual functions (fig. 3a, b). The bandwidths of spectral sensitivity functions of proximal tiers of Rows 2 and 3 remain narrow (due to the tiering effect), but their values of λ_{max} also shift to shorter wavelengths compared to actual functions (fig. 3a, b). In the condition where all effects of tiering and filtering are excluded (fig. 3c), all spectral sensitivity functions resemble the absorption spectra of rhodopsin-based visual pigments, which have relatively broad bandwidths.

Reflectance Spectra and Multispectral Images of G. smithii

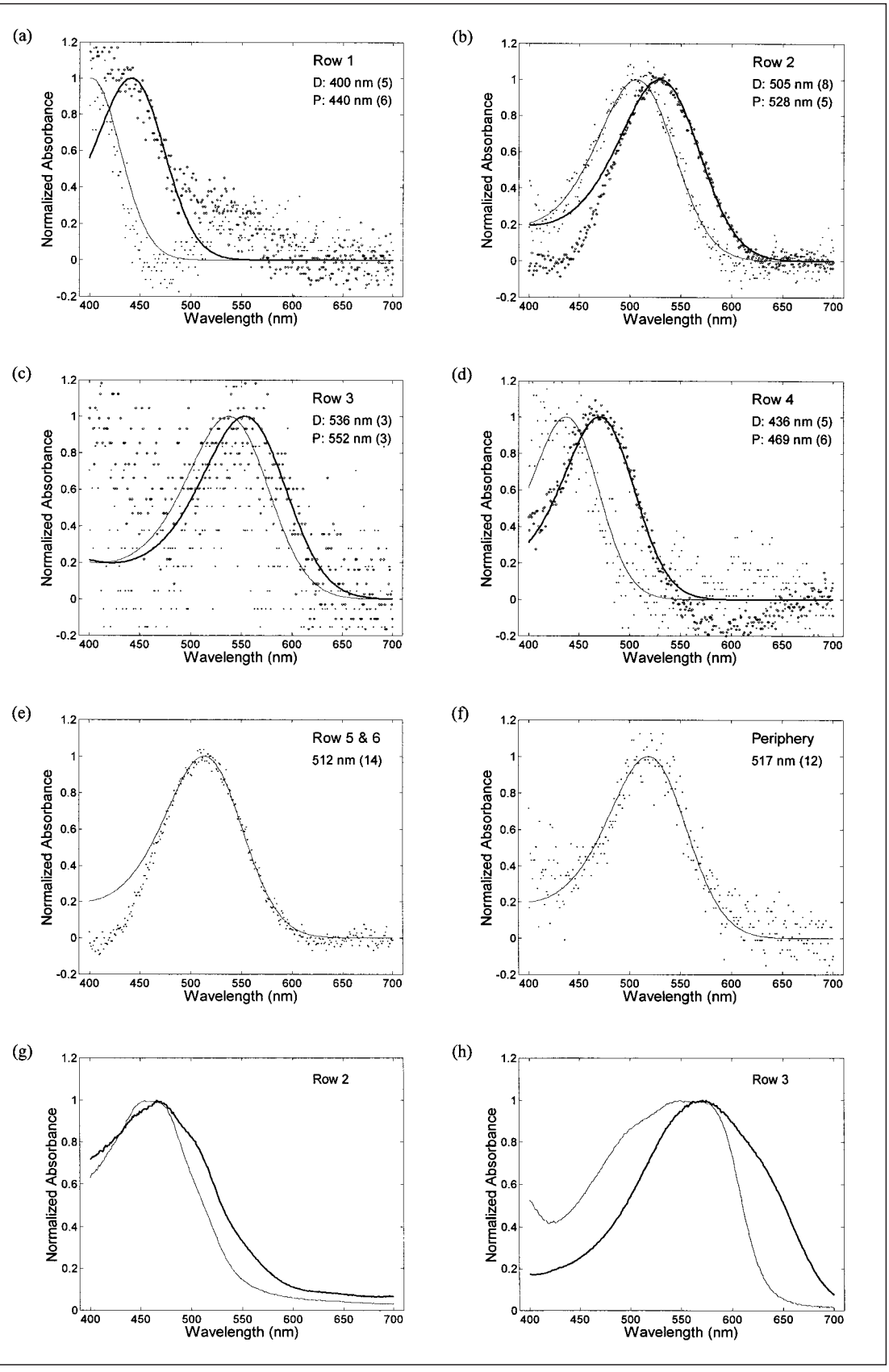
Reflectance spectra of 5 different locations on the bodies of *G. smithii* are illustrated in figure 4. These measurements include meral spots, maxillipeds, raptorial appendages, and the orange spots on the last segment of the abdomen, all of which are thought to be used possibly in intraspecific signaling. Reflectance spectra at the same location were measured from 1 to 5 different individuals, and vary slightly (fig. 4). Note that reflectance spectra of meral spots have been separated into two categories due to the large differences measured among individuals. Also note that most reflectance spectra of *G. smithii* have sharp increases in the spectral range above 700 nm, quite unlike the spectra of most reef fish colors described below (fig. 8).

Multispectral images we recorded include the cephalothorax (showing the raptorial appendage, maxillipeds, and meral spots), the abdomen, and the tail region (telsons and uropods) of *G. smithii* (fig. 5). Each pixel in these multispectral images represents a full reflectance spectrum from 405 to 718 nm. Thus, a total of 31,324 (191×164) reflectance spectra (including the animal body and background) can be simultaneously recorded. Reflectance spectra measured using Sub-Spec or the multispectral imaging device are similar or identical. Images in figure 5 are composite color images of 3 single frames of multispectral images (452, 548, and 649 nm), and are included to illustrate the appearance of these areas to the human visual system.

Color Signals of Stomatopods Viewed by Rows 1–4 of the Midband

We computed the chromaticities in Rows 1–4 of the midband when viewing certain body parts of conspecific animals (see Eqs. 1–4 in Methods). The largest chromaticities (fig. 6; black bars) calculated when using 'real' sensitivity spectra (fig. 3a) in each location vary among Rows 1–4 of the midband. For example, Row 2 produces the largest chromaticities for maxillipeds, the orange spot on the last segment of the abdomen and the pink area on the raptorial limb. Row 3 can generate the largest chromaticities for meral spot (I), whereas Rows 1 and 4 may produce chromaticities slightly better than Rows 2 and 3 in meral spot (II) and the blue area on the raptorial limb. The color processing of stomatopods has not yet been studied, but these results indicate that different color signals may be emphasized by different rows.

To test the hypothesis that the narrow band spectral sensitivity functions of *G. smithii* enhance the detection of color signals from conspecific animals, we compared the chromaticities of Rows 1–4 of the midband using real (fig. 3a) and two hypothetical (fig. 3b, c) sets of spectral sensitivity functions that vary in a number of ways. Chromaticities produced by receptor pairs with real, narrow-band spectral sensitivity functions (fig. 3a) are greater than those produced by receptors with untiered and unfiltered spectral sensitivity functions (fig. 3c, 6, black vs. white bars). On the other hand, chromaticities in Row 2 of the midband are increased by intrarhabdomal filtering when viewing all areas (Row 2 in fig. 6, black vs. gray bars), but chromaticities in Row 3 of the midband are actually decreased by intrarhabdomal filtering when viewing the pink area of the raptorial limbs and the orange spots on the last segment of the abdomen, although they are increased by intrarhabdomal filtering when viewing meral spot (I) (Row 3 in fig. 6, black vs. gray bars). It is worthwhile to note that intrarhabdomal


(a)
Row 1
D: 400 nm (5)
P: 440 nm (6)
(b)
Row 2
D: 505 nm (8)
P: 528 nm (5)
(c)
Row 3
D: 536 nm (3)
P: 552 nm (3)
(d)
Row 4
D: 436 nm (5)
P: 469 nm (6)
(e)
Row 5 & 6
512 nm (14)
(f)
Periphery
517 nm (12)
(g)
Row 2
(h)
Row 3
Normalized Absorbance
Wavelength (nm)

2

filtering in Row 3 greatly increases the chromaticities from meral spots (I), producing the largest signals of any row at that location. Note that meral spots are considered to be among the most important features for signaling in stomatopod communication.

To demonstrate how the patterns of color-contrast that *G. smithii* displays might appear when viewed by conspecific animals, we took advantage of multispectral imaging, that includes both spectral and spatial information. Based on the same computation of chromaticities for Rows 1–4 of the midband described above (see also Eqs. 1–4 in Methods), we calculated chromaticities of all pixels in the images, representing them by the intensity value at that pixel in each image. To facilitate the interpretation of these images, the intensity values in the images are scaled according to the maximum and minimum values of chromaticities in the images of all rows and then expanded to a 0–255 gray scale

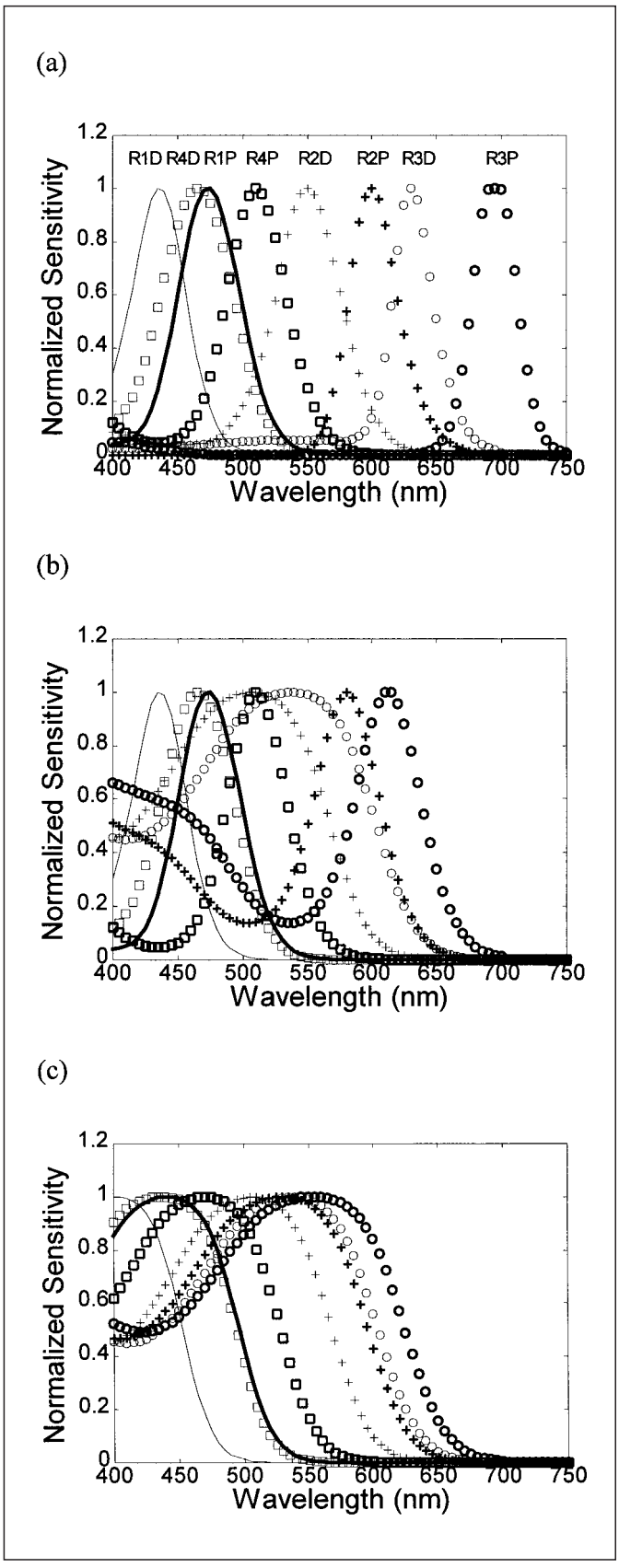


Fig. 2. Absorption spectra of visual pigments and intrarhabdomal filters of *Gonodactylus smithii*. **a**–**f** Normalized average spectra for photobleaching of visual pigments in all retinal regions below the level of the rhabdomere of the 8th retinular cell. Mean absorbance change from 651 to 700 nm is set to 0 in each curve. Retinal location and number of photobleaches included in the curve are indicated in the upper right part of each panel. The smooth curves represent the best-fit template spectrum (see text), with the λ_{max} for each curve given on the panel. In the 4 dorsal tiered ommatidial rows of the midband (Rows 1–4), data of both tiers are given; the proximal tier is represented by the small points and thin curve, whereas the distal tier is represented by the large points and thick curve. Data from ventral 2 rows of the midband (Rows 5–6) are combined, as these ommatidia contain identical visual pigments. D = Distal tier; P = proximal tier. **g**–**h** Normalized average absorption spectra for the intrarhabdomal filters of Rows 2 and 3 in the midband. Distal filters are plotted with thin lines and proximal filters with thick lines. Maximum absorbances for these filters are as follows: Row 2 distal, 1.68; Row 2 proximal, 6.64; Row 3 distal 0.88; Row 3 proximal, 6.67.

Fig. 3. Spectral sensitivities of photoreceptors of *Gonodactylus smithii*. **a** Normalized spectral sensitivities of both distal tiers (D) and proximal tiers (P) of Rows 1 to 4 of the midband of *G. smithii*. These spectral sensitivities were computed based on the microspectrophotometric measurements of visual pigments and filters, and optical data (see text for details). Distal tiers are plotted with thin curves or markers, and proximal tiers with thick curves or markers. **b** Hypothetical spectral sensitivities of both tiers of Rows 1–4 of the midband of *G. smithii*, without the effect of intrarhabdomal filtering in Rows 2 and 3. Note that the spectral sensitivities of Rows 1 and 4 remain intact as in **a**. Spectral sensitivities of Rows 2 and 3 become broader (especially the distal tiers), and λ_{max} shifts to shorter wavelengths. **c** Hypothetical spectral sensitivities of both tiers of Rows 1–4 of the midband of *G. smithii*, without both the filtering (intrarhabdomal filters and R8 cells) and tiering effects. Spectral sensitivities of all tiers become broader, and λ_{max} also shifts to shorter wavelengths in most classes.

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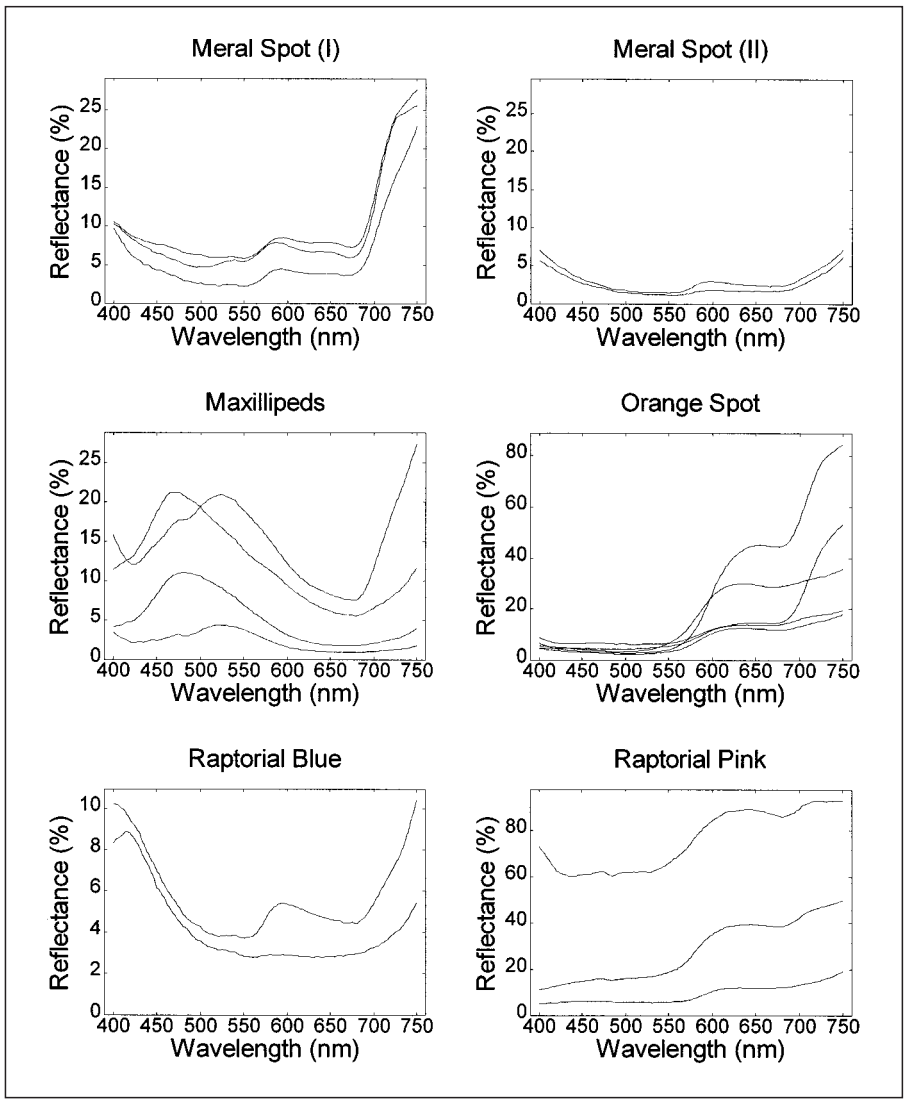

Fig. 4. Reflectance spectra measured from various locations on the bodies of *Gonodactylus smithii.* Location names are indicated on the top of each panel. Each curve in the panel represents one reflectance measurement from a single animal. Number of animals measured for different locations varies from 2 (meral spot II and raptorial blue) to 5 (orange spot).

display (fig. 7). The lighter areas in the images indicate that the responses of distal tiers are larger than those of proximal tiers, and the darker areas in the images represent responses of proximal tiers that are larger than those of distal tiers (the signs chosen here are arbitrary). Backgrounds in the images are generally gray, showing little or no difference between the responses of distal and proximal tiers (this is a natural consequence of the fact that the receptors are adapted to the overall intensity of the image, as in Eq. 3).

In the multispectral images, color signals from many different locations can be compared simultaneously. When *G. smithii* views the cephalothorax of a conspecific animal from the side (fig. 7, the upper left set), the chromaticities in Rows 1 and 4 obviously enhance regions of the raptorial appendages, whereas those in Row 2 significantly highlight parts of the maxillipeds (solid arrow in the Row 2 image of the upper left set of fig. 7). Although the chromaticities in Row 3 also slightly emphasize the maxillipeds, the enhancement is far less dramatic than that available in the Row 2 signals. When *G. smithii* views the cephalothorax of a conspecific animal from above (fig. 7, the upper right set), the images produced by Rows 1 and 2 have higher contrasts for meral spots (two solid arrows in the Row 2 image of the upper right set of fig. 7) than those produced by Rows 3 and 4. In our multispectral imaging system, reflectance spectra of stomatopods can be collected only up to 718 nm. Note that meral spot (I) reflects strongly above 718 nm (see fig. 4). As a result, the chromaticities in Row 3 may be underestimated in multispectral images. When *G. smithii* views the tail fan (telsons and uropods) of a conspecific ani-

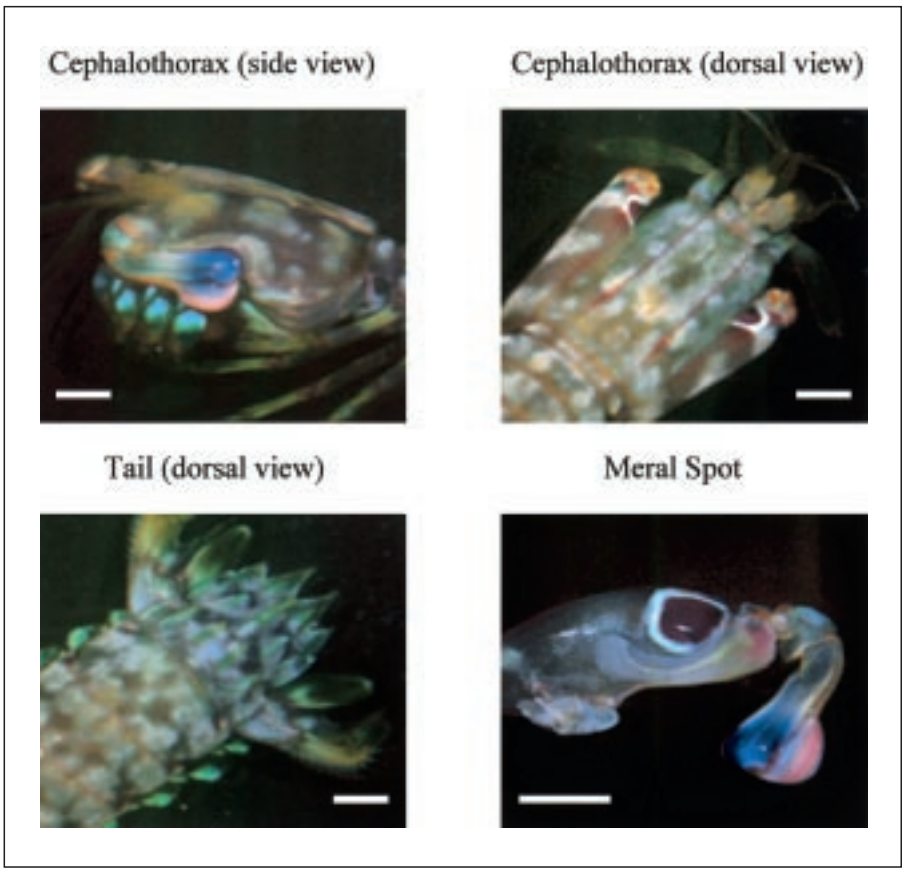

Fig. 5. Color images of *Gonodactylus smithii* selected from 4 different individuals in our data sets of multispectral images. Each image shows various colorful parts of their bodies (e.g. raptorial appendages, maxillipeds, orange spots, uropods, and meral spots). These images were generated by combining 3 single frames of multispectral images (452, 548, and 649 nm). The white bar in the lower corner of each panel represents 5 mm.

mal (fig. 7, the lower left set), the appearance of orange spots (circled in the Row 2 image of the lower left set of fig. 7) is enhanced primarily in the chromaticities in Rows 2 (especially) and 3; they are essentially invisible in the chromaticities in Rows 1 and 4. Finally, when *G. smithii* views the medial portion of the raptorial appendage of a conspecific animal (fig. 7, the lower right set), the meral spot is strongly enhanced by chromaticities produced in all rows. Again, the spectral limitation of our imaging device might cause an underestimation of chromaticities in Row 3. In addition, the chromaticities in Rows 1 and 4 also emphasize the blue areas of the raptorial appendages (open arrow in the Row 2 image of the lower right set of fig. 7), which are not apparent in the chromaticities in Rows 2 and 3.

Color Signals of Reef Fishes Estimated from Rows 1–4 of the Midband

Six out of 26 subjective categories of reef fish colors [Marshall, 2000] are shown in figure 8. In each category, only 5 reflectance spectra are plotted. Note that the reflectance spectra of most fish colors, unlike stomatopod colors, are flat above 700 nm, except for 'wrasse purple' and some 'wrasse green' (fig. 8). Furthermore, the color vision system of *G. smithii* enhances color contrast not only of its own signals (fig. 6), but those of reef fishes as well (fig. 9, black vs. white bars), to degrees that vary among the midband rows. However, intrarhabdomal filtering in Rows 2 and 3 does not always increase the total chromaticities of reef fish colors (fig. 9, black vs. gray bars).

Discussion

Color Vision Systems of Stomatopods

In stomatopods, the color vision system involves at least eight different classes of photoreceptors in the midband region of the retina operating in the visible spectral range [Cronin and Marshall, 1989a; Marshall et al., 1991a]. In addition to these, there are multiple UV-sensitive receptor classes present in the 8th retinular cells [see Cronin et al., 1994d; Marshall and Oberwinkler, 1999]. Comparisons between spectral sensitivity functions of Rows 1–4 (fig. 3a)

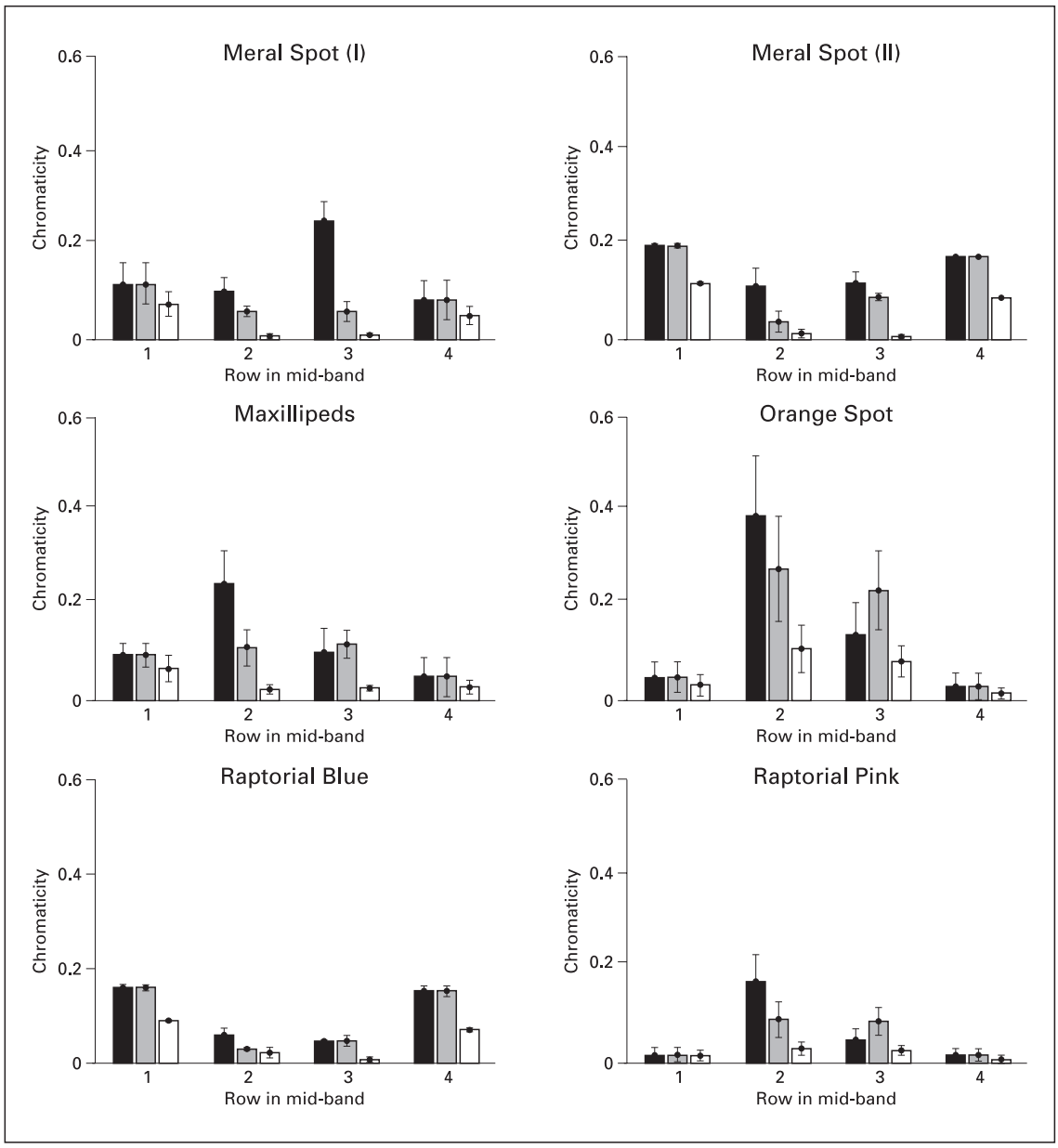

Fig. 6. Chromaticities provided by Rows 1–4 of the midband of *Gonodactylus smithii* when viewing various spots of the bodies of conspecifics. Location name of each spot is indicated on the top of the panel. These chromaticities are computed based on a model of a multiple dichromatic channel system (see text). The black bars represent chromaticities calculated from real spectral sensitivities (see fig. 3a). The gray bars represent chromaticities calculated from hypothetical spectral sensitivities without the consideration of intrarhabdomal filters in Rows 2 and 3 (see fig. 3b). The white bars represent chromaticities calculated from both un-tiered and un-filtered hypothetical spectral sensitivities (see fig. 3c). The line on each bar denotes the standard deviation.

and two hypothetical (possibly primitive) spectral sensitivity functions of Rows 1–4 (fig. 3b, c) show that the span in λ_{max} of the 8 different spectral sensitivities is considerably increased by filtering and tiering. In the absence of both filtering and tiering, the λ_{max} range is the same as that of the visual pigments themselves, about 400–550 nm (fig. 3c). However, with filtering and tiering, the values of λ_{max} extend from 436 to 695 nm (fig. 3a). The filtering and tiering effects not only shift the λ_{max} of spectral sensitivities, but also significantly reduce the bandwidths of spectral sen-

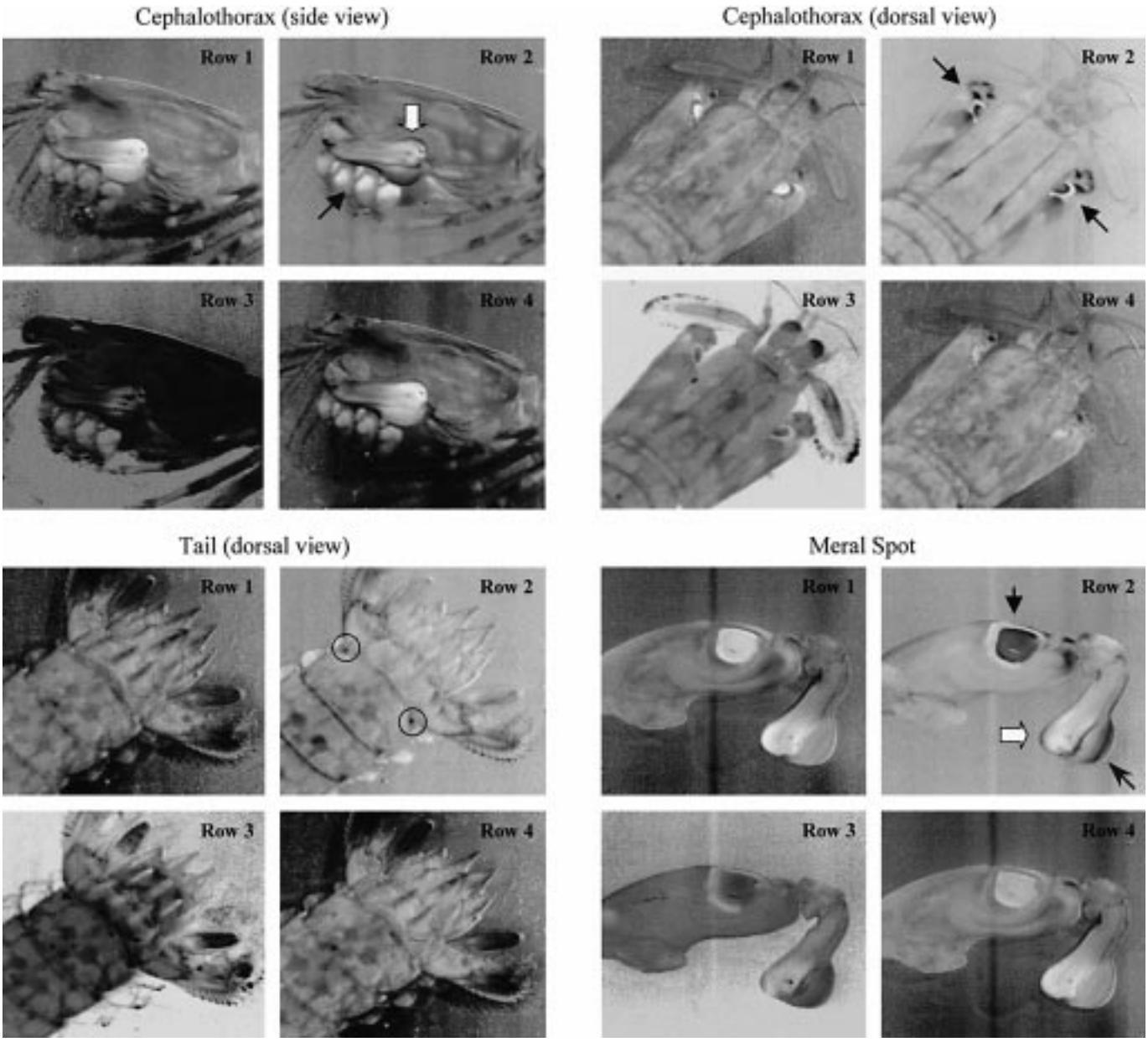

Fig. 7. Color contrast images of various body regions of *Gonodactylus smithii* provided by Rows 1 to 4 of the midband of this species. Four sets of images corresponding to figure 5 are shown here. Each image in each set is generated by subtracting distal tier responses from proximal tier responses (see text). The intensity values in each image are scaled according to the maximum and minimum values of color signals in the images of all rows to fit a 0–255 gray scale display. The lighter or darker areas in the images represent the differences between the responses of distal and proximal tiers. The solid arrow in the Row 2 image of the upper left set indicates the maxillipeds; the open arrow indicates the raptorial appendage. The two arrows in the Row 2 image of the upper right set indicate the meral spots on the raptorial appendages. The orange spots on the last segment of abdomen are indicated by two circles in the Row 2 image of the lower left set. The solid arrow in the Row 2 image of the lower right set indicates the meral spot, the open arrow indicates the raptorial blue area, and the stealth arrow indicates the raptorial pink area.

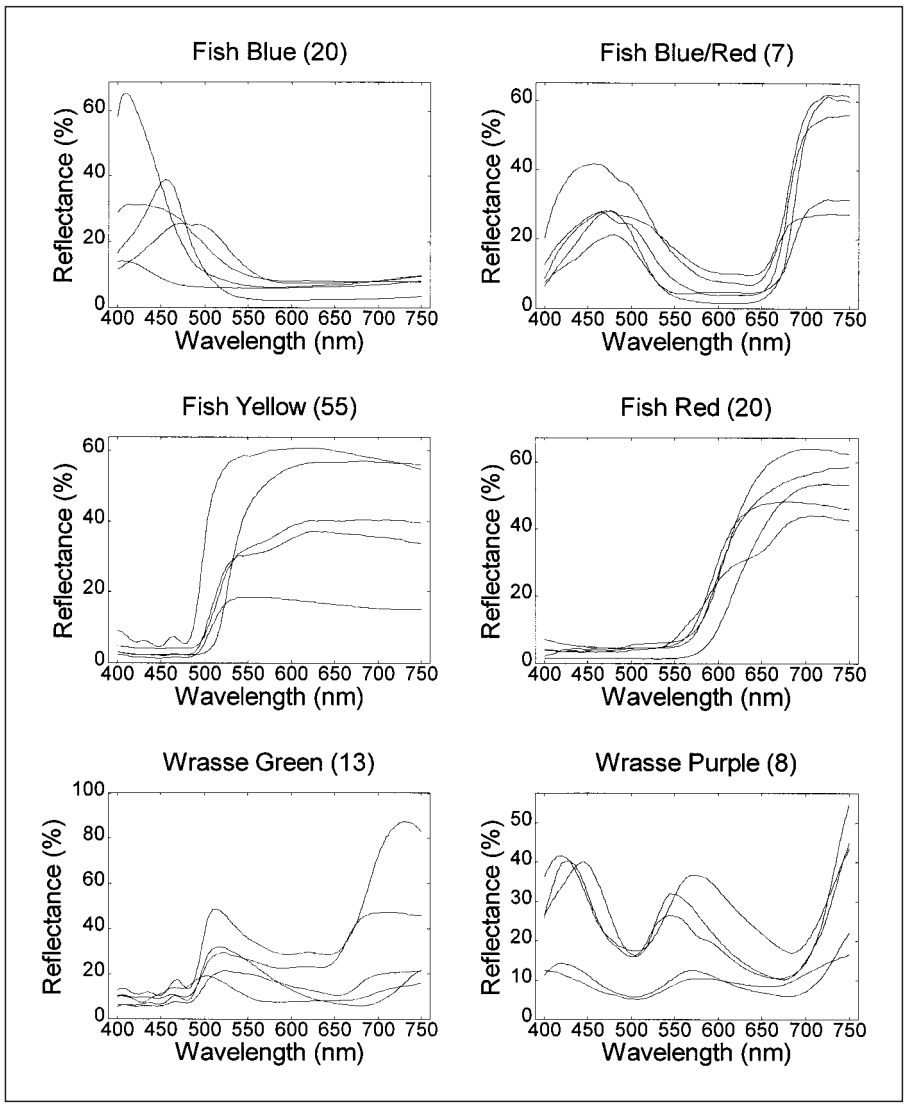

Fig. 8. Reflectance spectra of various reef fish colors. The name of each subjective color category is indicated at the top of each panel [see Marshall, 2000, for details]. Only 5 reflectance spectra are plotted for each color category. The number on the top of each panel indicates the actual number of reflectance spectra used in the analyses.

sitivity functions, and additionally, decrease the photon catches of receptors. Thus, the color vision systems of stomatopods trade photon catch for spectral coverage and narrow tuning.

There is some speculation that these eight different, narrow-band, spectral sensitivity systems in the retinas of stomatopods may function as spectral frequency detectors, analogous to hair cells in auditory systems [Marshall et al., 1989; Neumeyer, 1991; Marshall and Oberwinkler, 1999]. Despite its attractiveness, there is no physiological evidence to support this hypothesis directly, as we know very little about post-receptor visual processing in stomatopods. An alternative idea is that the spectral information that stomatopods encounter in their natural environments might include an unusually high content of high spectral frequency components [Marshall et al., 1991b, 1996; van Hateren, 1993]. If so, a large number of narrowly tuned spectral classes would be required to detect this high spectral frequency information. However, analyses of the spectral power distributions of naturally occurring spectra [Osorio et al., 1997] show that the color signals that stomatopods encounter have typical natural spectra, with only low-frequency components [Buchsbaum and Gottschalk, 1984; Lythgoe and Partridge, 1989]. Thus, the significance of having so many different color classes of photoreceptors in stomatopods seems unclear. Our results demonstrate that besides the improvement of color constancy [Osorio et al., 1997], this multiple receptor system can enhance the detection of intraspecific color signals.

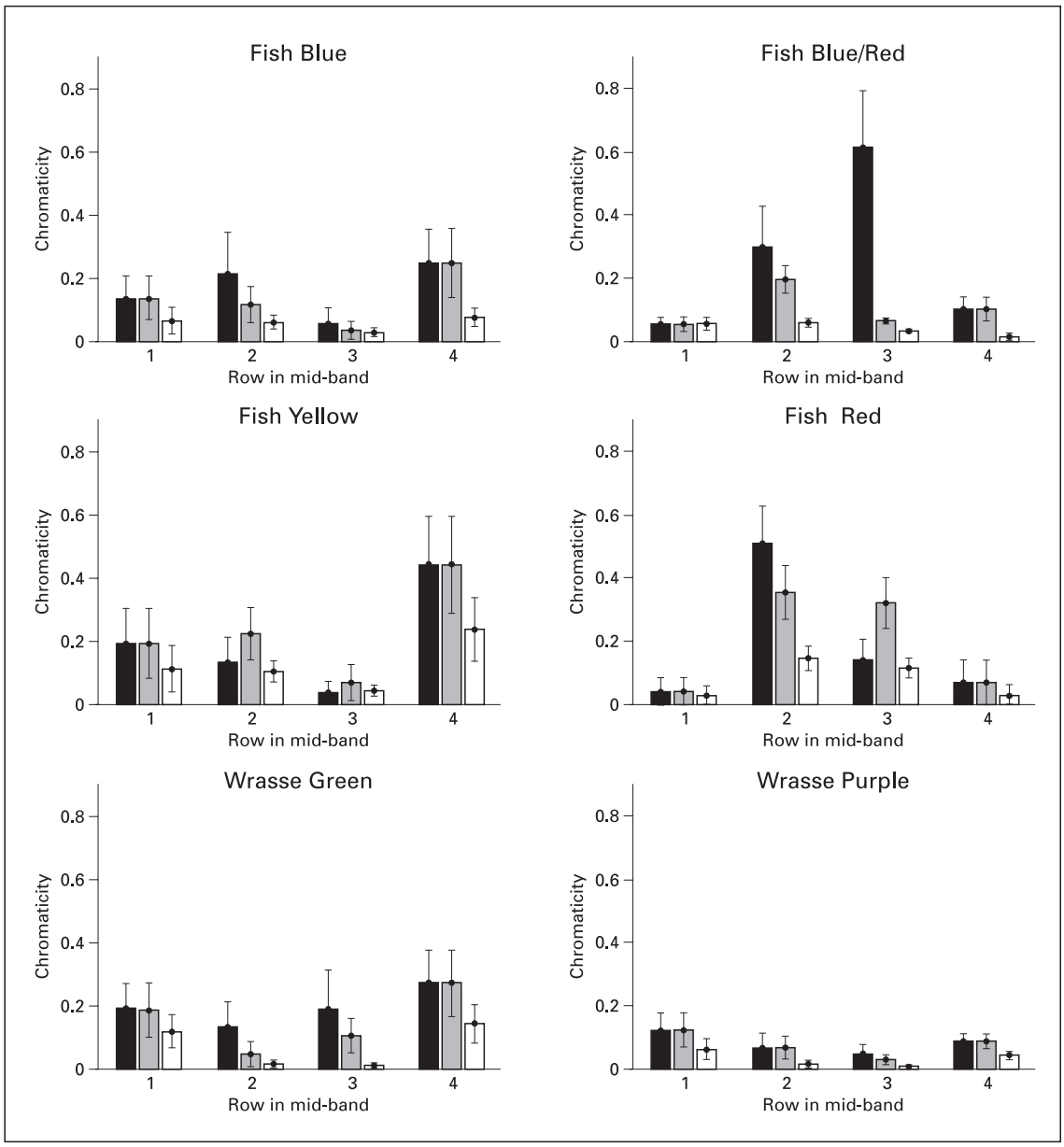

Fig. 9. Chromaticities provided by Rows 1–4 of the midband of *Gonodactylus smithii* when viewing various colors of reef fishes. The name of each color category is indicated on the top of the panel. These chromaticities are computed based on a model of a multiple dichromatic channel system (see text). The black bars represent chromaticities calculated from real spectral sensitivities (see fig. 3a). The gray bars represent chromaticities calculated from hypothetical spectral sensitivities without the consideration of intrarhabdomal filters in Rows 2 and 3 (see fig. 3b). The white bars represent chromaticities calculated from both un-tiered and un-filtered hypothetical spectral sensitivities (see fig. 3c). The line on each bar denotes the standard deviation.

In our analyses, spectral sensitivity functions of Rows 1 and 4 distal main rhabdoms (R1D and R4D, fig. 3a) of *G. smithii* were arbitrarily sharpened on the short wavelength side. Filtering in the distal tiers of Rows 1 and 4 is from the overlying 8th retinular cells [not considered in Cronin et al., 1994c, but in Marshall et al., 1996] and by the dioptric apparatus. The 8th retinular cells of stomatopods contain visual pigments absorbing maximally in the 300–400 nm region of the spectrum [Cronin et al., 1994d; Marshall and Oberwinkler, 1999], and such visual pigments

could potentially act as filters of the short wavelength limbs of the relatively short wavelength R1D and R4D visual pigments. The long wavelength limb of the spectral sensitivity function of Row 3 proximal main rhabdom of *G. smithii* (R3P, fig. 3a) was also generated by symmetric flip-over of the short wavelength limb to extend the spectral range up to 750 nm. Comparison between the shape of spectral sensitivity functions of R3P generated here and measured electrophysiologically from a closely related species *(Neogonodactylus oerstedii)* showed that this approach is justified.

In the lamina ganglionaris (the first layer of interneurons beneath the retina) of another gonodactyloid stomatopod species, *Odontodactylus scyllarus*, the axons of the two main rhabdomal tiers of each ommatidium in Rows 1–4 of the midband are projected onto the same lamina cartridge [Marshall and Horwood, unpubl. results]. This organization suggests that chromatic signal comparison in stomatopods may begin at the level of the lamina. Although there is no direct electrophysiological evidence to support such chromatic processing, other lines of evidence from crayfishes and stomatopods indicate the possibility of polarized light opponent processing in the lamina [Sabra and Glantz, 1985; Marshall et al., 1991a]. It might be that the neural wiring that is responsible for the opponent processing of polarized light signals is similarly used for opponent processing of color in Rows 1–4 of stomatopods [Marshall et al., 1996]. Based on the assumption of chromatic opponent processing, a model of multiple dichromatic channels for color vision of stomatopods was proposed by Marshall et al. [1996]. Although further investigation is necessary to validate this model, it is a reasonable first step to assume that chromatic signals are initially processed in four parallel dichromatic channels. Thus, this model allows us to estimate chromaticities that visual channels arising from Rows 1–4 of the midband might produce when viewing conspecific animals.

Marshall and Oberwinkler [1999] have found recently that there are multiple UV photoreceptors in the eye of *Odontodactylus scyllarus* (a closely related species), but the involvement of these UV sensitive 8th retinular cells in color vision of stomatopods is not clear. Neuroanatomical evidence also indicates that the axons of the 8th retinular cells bypass the lamina cartridge and project directly onto the medulla layer [Marshall and Horwood, unpubl. results]. Furthermore, our multispectral imaging measurement is currently limited to the visible range. Thus, color vision of *G. smithii* in the UV range is not considered in this study.

The simple algorithm of estimating chromaticities used in this study (Eqs. 1–4) is widely used in studies of animal color vision systems. It includes the considerations of von Kries adaptation (Eq. 3) and opponent interaction of receptor inputs (Eq. 4). Although the weighting functions of chromatic coding for an interaction between responses of two tiers in each dichromatic channel are not known, reasonable variations in these numbers affect our results only slightly. Furthermore, although we use a logarithmic scale in computing color signals (Eq. 4) to approximate the physiological responses, a simple linear estimation gives similar results. In general, the approach used here provides a robust way to estimate chromaticities in the color vision system of stomatopods.

Eye Design and Color Signaling

Color signals seem to be very important in the communication systems of stomatopods [Caldwell and Dingle, 1975, 1976; Hazlett, 1979]. Thus, one function of the unusual eye design of stomatopods might be to perceive reliable color signals or to increase fine color discrimination of conspecifics (or heterospecifics) under various illumination conditions underwater [Osorio et al., 1997; Marshall and Oberwinkler, 1999]. Stomatopods are not closely related to decapod crustaceans and they appear to have branched off from the leptostracan stock some 400 million years ago. Their visual systems have evidently evolved in unique directions since that time, trading photon catch and overall sensitivity for increased spectral range and color constancy [Marshall et al., 1996; Osorio et al., 1997; Marshall and Oberwinkler, 1999].

In animal communication systems, receiving mechanisms can evolve in directions that improve the detectability of information [Endler, 1993]. This implies that biological signals affect the evolution of sensory systems. Good examples include the calling signals of cricket frogs [Wilczynski et al., 1992], the electrical signals of electric fishes [Hopkins, 1999], and the bioluminescent signals of deep-sea fishes [Partridge and Douglas, 1995; Douglas et al., 1998] and fireflies [Lall et al., l988; Cronin et al., 2000], where conspecific sensory systems are well tuned to improve the detectability of biological signals. It is interesting that there are very few potential examples of coevolution of color vision and color signals aside from bioluminescence. Color vision is very probably too general a task for it to become over specialized. There are possible examples of co-evolution of color vision and color signals in the wavelength-specific behaviors of butterflies, such as oviposition [Kelber, 1999]; however, these are hard to assign to specific photoreceptors. Good evidence that other color vision systems are adapted for a general sense of color rather than specific color signals comes from bees [Chittka and Menzel, 1992]. Based on the comparative studies of spectral sensitivities of many different species of bees, Chittka [1996] suggested

that color vision systems of honeybees predate the evolution of flower colors. Many species of stomatopods, regardless of their variations in body coloration (some of them have only dull colors), all show eight rather similar narrow-band spectral sensitivity functions in Rows 1–4 of the midband [Cronin and Marshall, 1989a; Cronin et al., 1993, 1994c]. Thus, it is unlikely that color vision systems of stomatopods are designed exclusively to maximize the color signals of conspecific animals. The examination of color signals of reef fishes encoded in Rows 1–4 of *G. smithii* (fig. 9) indicates that the narrow spectral sensitivities of *G. smithii* enhance not only the color signals of conspecific animals, but also the color signals of other animals as well. Therefore, we conclude that the stomatopod eye is designed for a variety of tasks that utilize color vision.

We did find one clear case in which a stomatopod color signal is strongly enhanced by a stomatopod visual system. As shown in figures 4 and 6, there are two different varieties of meral spots (although some intermediate colors of meral spots can occur), one of which gives higher chromaticity in Row 3 than does the other. Because meral spots have been speculated to play an important role in agonistic behavior [Caldwell and Dingle, 1975, 1976; Hazlett, 1979], it is possible that the meral spot signals might exploit color vision systems of *G. smithii*, and Row 3 may give the best color discrimination of various meral spots. Body coloration of *G. smithii* can vary significantly depending on the depths of their habitats [Cronin, Marshall, and Caldwell, unpubl. observ.]. The reflectance spectra of meral spots might also vary depending on the aggressiveness of different species in agonistic behaviors [Caldwell and Dingle, 1975, 1976]. Thus, more measurements of reflectance spectra from various meral spots in different depths, as well as appropriate ethological experiments, are needed in order to clarify the relationship between color signals of meral spots and spectral tuning of receptors in Rows 2 and 3.

In conclusion, we measured reflectance spectra and recorded spectral images from various parts of the body of the stomatopod, *Gonodactylus smithii*. Using a multiple dichromatic channel model first suggested by Marshall et al. [1996], we estimated chromaticities in Rows 1–4 of the midband from many body parts of *G. smithii*. Our results indicate that the narrow-band spectral sensitivities of photoreceptors of stomatopods can enhance the contrast of their color signals. Similarly, color signals of other reef animals, such as teleosts, can be enhanced by *G. smithii*'s visual system as well. Although the stomatopod eye does not exclusively enhance conspecific color signals, the specific spectral tuning of some photoreceptors (i.e. Rows 2 and 3 in the midband) via filtering might increase the discriminability of some behaviorally relevant color signals (e.g. meral spots). Therefore, the color signals of stomatopods might adapt to their color vision system for maximizing the reliability of signal detection in animal communication.

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