The use of different eye regions in the mantis shrimp *Hemisquilla californiensis* Stephenson, 1967 (Crustacea: Stomatopoda) for detecting objects

David L. Cowles *, Jaclyn R. Van Dolson, Lisa R. Hainey, Dallas M. Dick

Department of Biology, Walla Walla College, 204 S College Avenue, College Place, WA 99324, USA

Abstract

A behavioral assay was used to assess the ability of the stomatopod *Hemisquilla californiensis* to perceive and respond to a moving target under different wavelengths and intensities of light illumination. Subjects responded to targets rotating horizontally across their visual field by a brief startle response of their eyes or antennules but did not track the targets. Under white light responses were elicited down to a light intensity of 0.9 μW cm^{-2}. Responses were seen in blue light at intensities as low as 0.5 μW cm^{-2}, and in green light down to 1.0 μW cm^{-2}. The animals were less sensitive to red light, with no responses seen at intensities below 3.0 μW cm^{-2}. Subjects did not respond to the targets at all under infrared light. This response pattern mirrors the computed sensitivity spectrum of ommatidia in the species' peripheral hemispheres but not that in most of the central bands. We conclude that this species uses the monochromatic vision in the peripheral hemispheres of its eyes to recognize objects and that the sharply tuned color receptors of the central band serve to add supplemental information if light conditions allow.
© 2005 Elsevier B.V. All rights reserved.

Keywords: Behavior; Color vision; *Hemisquilla californiensis*; Stomatopoda

1. Introduction

The eyes of stomatopods are structurally and functionally more complex than those of most other crustaceans (Cronin et al., 1988, 2000; Marshall, 1988). In crustaceans such as crabs the ommatidia in different eye regions are similar in structure and contain only 2–3 different types of pigment (Cronin and Forward, 1988; Sakamoto et al., 1996). Stomatopod eyes, in contrast, are divided into several different morphological regions, each with its own ommatidial structure as well as its own type of pigment and characteristic
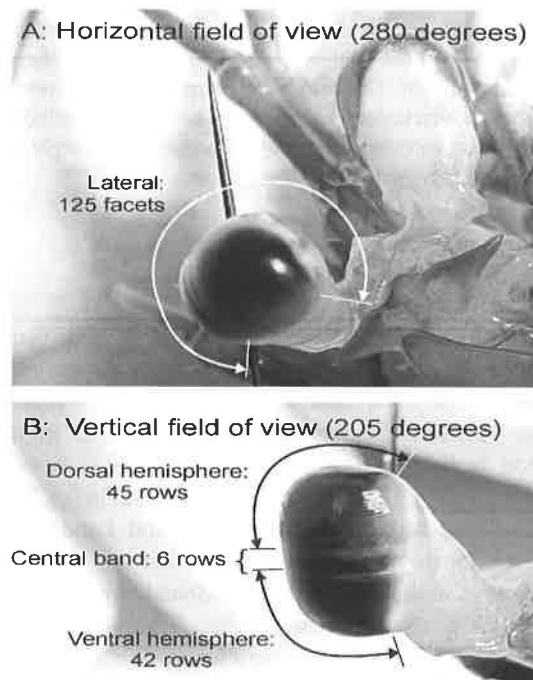
spectral sensitivity. The stomatopod eye is usually elliptical rather than spherical. It has two peripheral hemispheres composed of many rows of ommatidia (Fig. 1). These hemispheres provide a wide angle of vision in both the vertical and horizontal dimensions and probably allow stereoscopic vision in each eye (Milne and Milne, 1961; Marshall and Land, 1993). Except in the deep-sea Bathysquilloidea, the hemispheres are separated by a midband which usually contains 6 rows of ommatidia. The ommatidia in these 6 central rows are parallel to one another and

The pigments and spectral sensitivities in the different regions of stomatopod eyes have been well characterized. Stomatopods have as many as 11 different visual pigments, which through a combination of receptor stacking and screening pigments may have as many as 16 different patterns of absorbance, each with its own maximum spectral sensitivity (S_{max}) (Marshall et al., 1999). In the peripheral hemispheres, rhabdoms are similar to those seen in other crustaceans, with a short R8 cell distally placed over a longer R1–7 rhabdom tier (Marshall et al., 1999). These ommatidia have a single broad peak of spectral sensitivity, mostly in the blue and blue-green (Fig. 2). The 6 rows of midband ommatidia have a much more complex structure and sensitivity. The first 4 rows seem to be specialized for color vision (Marshall et al., 1999). In a pattern unusual for crustaceans, the photoreceptor segments are two-tiered within the rhabdoms, with different visual pigments in each tier, plus have colored intrarhabdomal filters between the two tiers. This arrangement results in a very sharp spectral tuning of each retinal area, which may allow sensitive discrimination of colors. The maximum sensitivity of each row and tier is different from that of the others. Together they are sensitive to an unusually wide spectrum of colors for aquatic species, especially in the Gonodactyloids in which S_{max} in these rows ranges from 400 to nearly 700 nm (Cronin et al., 1994b, 2000; Marshall et al., 1999). The bottom two rows of ommatidia appear to be specialized for polarization vision (Marshall, 1988; Marshall et al., 1991, 1999; Cronin et al., 2000, 2002, 2003). In addition, the R8 cells in several different regions of the eye are sensitive to ultraviolet light (Marshall et al., 1999).

Stomatopods are highly visually oriented and are primarily tropical species. Many species, especially Gonodactyloids, inhabit shallow water and are exposed to a broad spectrum of light (Cronin and Marshall, 1989; Cronin et al., 1994b). Many species rely on colored spots on their exoskeleton for intraspecific signaling (Caldwell and Dingle, 1975, 1976; Hazlett, 1979; Marshall et al., 1996; Chiao et al., 2000). They can learn to discriminate different colors in response to a food reward (Marshall et al., 1996). Their specialized eyes, sensitivity to a broad spectrum of color, and obvious visually influenced behavior make them appropriate models for investigating the correlation between their behavior and the visual inputs from different regions of their eyes.

Hemisquilla californiensis is a deep-living gonodactyloid stomatopod found off the coast of California and the Pacific coast of Central America. It is often found in relatively turbid warm temperate water, and may be found down to 114 m depth (Schiff and Hendrickx, 1997). Its preferred habitat is silty sand, in which it digs a home burrow (Basch and Engle, 1989). At these depths and in warm temperate water, light is much more attenuated than at the surface and spectrally narrowed into blues and greens. Nevertheless, the animals have well-developed eyes and visual interactions with their surroundings are very important. The animals are brightly colored, including pink, yellow, red, and iridescent blue. Their eyes, although the absorbance peaks are shifted more toward blue and green than in most gonodactyloids, still have a broad range of maximum sensitivities ranging from below 400 nm to beyond 650 nm (Cronin et al., 1994a, 2000). As in other stomatopods, different portions of the eye have quite different color sensitivities (Fig. 2). Assuming that rhabdoms may generate a usable signal at all wavelengths for

A: Horizontal field of view (280 degrees)

Lateral: 125 facets

B: Vertical field of view (205 degrees)

Dorsal hemisphere: 45 rows

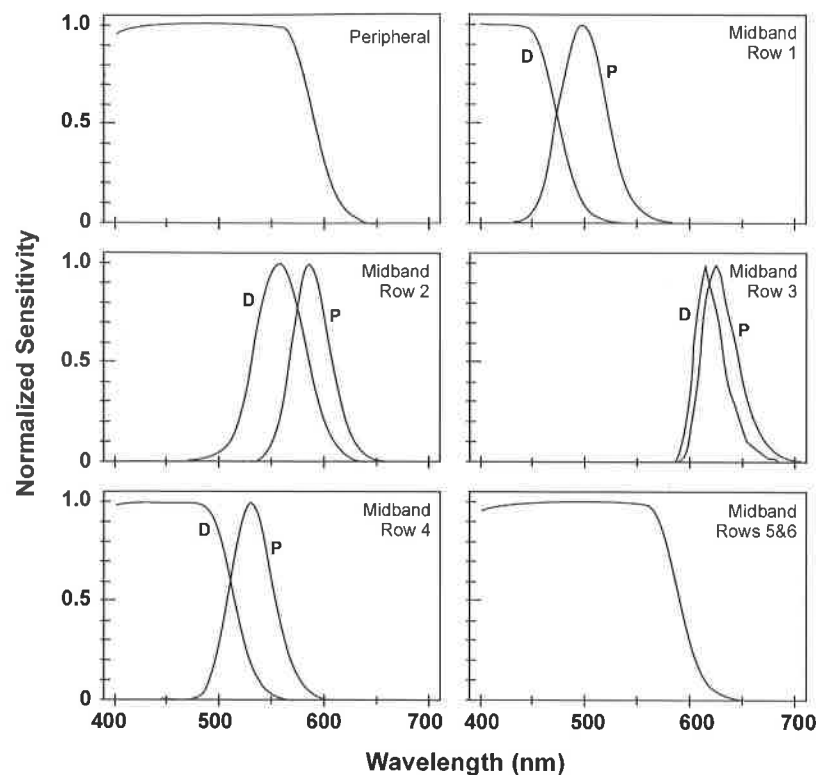Central band: 6 rows {

Ventral hemisphere: 42 rows

Fig. 2. Computed sensitivity functions of photoreceptors in the different regions of *Hemisquilla californiensis* eyes. For eye sections with tiered receptors, P = proximal receptor and D = distal receptor. Adapted with permission from Cronin et al. (1994a; © Springer-Verlag 1994).

the midband, row 1 has a sensitivity range from below 400 to about 550, and could perceive blue and green. Row 2 has sensitivity from about 510 to 650 and could perceive green, yellow, orange, and some red. Row 3 has sensitivity from 600 to 675 and can only perceive orange and red, nearly to the infrared range. Row 4 is sensitive from 475 to 590 and perceives blue, green, yellow, and orange. Rows 5 and 6 have similar sensitivity as do the peripheral hemispheres and perceive blue to orange. Various portions of their eyes, then, are sensitive to different portions of the spectrum from nearly ultraviolet to the edge of infrared, in addition to their R8 receptors which are sensitive to ultraviolet. At the same time, no portion of the eye can see all the colors the animal may be exposed to.

In this paper we used a behavioral assay to determine which wavelengths of light among the many this species is sensitive to are used in perceiving and recognizing

They were maintained in the laboratory in an aerated, recirculating seawater system using Instant Ocean® artificial seawater. The animals were kept in individual sections of the aquarium separated by mesh screens to prevent fighting, and each was provided with a section of plastic drain pipe open on one end for a burrow. Water temperature was between 14 and 20 °C and a 14 h light : 10 h dark cycle was used, similar to the ambient conditions at their time of capture.

Experiments took place in a light-tight chamber. During experiments a subject animal was tethered by elastic bands to an acrylic table which was designed to allow the pleopods to beat freely for respiration. The animal and table were immersed in an aerated, temperature controlled water bath to a depth so that the water barely covered the eyes, which are the highest point on the animal. A 2.5- to 5-cm diameter black-and-white target was rotated 180° across the subject's field of

Table 1
Transmission characteristics of Kodak Wratten filters used in this experiment

Filter	Color	Peak transmission (nm)	Transmission range (nm)
#47	Blue	440	UV–515
#58	Green	530	491–586
#25	Red	>700	588–IR
#87C	IR	950	820–far IR

Data are from Chemical Rubber Company (1974). Transmission range is the range of wavelengths in which the filter transmits at least 10% of its peak transmission. UV = ultraviolet, IR = infrared.

a wall. To prevent habituation at least 15 min intervals were kept between trials (Schiff, 1996) and the direction (left or right) from which the target appeared was varied.

Light was supplied to the experimental chamber through a single port by a Kodak Ektagraphic® projector with a 300 W quartz bulb. After entering the chamber the light was distributed evenly by reflection off a foil diffuser and by reflection from the white chamber walls. Light level was controlled by varying the distance of the projector down a light pipe from the port, by use of neutral density filters at the port, and by varying the power setting on the projector. The spectrum of light was controlled by blue, green, red, and infrared Kodak Wratten® filters (Table 1). The highest levels of infrared light were created using a ProVideo IR-200® infrared illuminator with peak emission at 850 nm and a half-width of 35 nm.

Light levels in each experiment were varied randomly from very dim to daylight levels. All four of the colors plus white (unfiltered) were tested individually. Light levels were calibrated in each configuration with a Newport Power 1815-C® light meter with an 818-SL sensor at the position of the viewing target. During the actual experiments, after it was shown that the animals were not responsive to infrared light a low-level infrared light source was added to the chamber to improve image resolution at the dimmest light levels.

The animal's reactions to the appearance and movement of the target were filmed with a Sony Hi-8 video camera positioned over the animal's head. The video sequences were captured on a Pentium computer using the Pinnacle DVD500 plus® system, and digitized in Adobe Premiere® 6.0. These sequences were later

exposed to a variety of conditions. Data for every intensity and wavelength were compiled from the responses of several different animals.

3. Results

A total of 177 tests were performed on 8 animals. Unlike *Gonodactylus oerstedii* (Cronin et al., 1988), the eyes of *H. californiensis* did not physically track the target. The most frequent response was a startle response of one or both eyes or of the first antennae (antennules) on appearance of the target. In the eye response, one or both eyes (usually the eye nearest the target) briefly turned toward the target. The antennular response was a sudden rapid flick of the antennules toward the target. After the initial brief response, neither eye nor antennules followed the target for more than a few degrees.

In the absence of tracking, subject responses were tabulated on the basis of presence or absence of the startle response when the target appeared. If a subject responded all 3 times to the target at a particular wavelength and intensity, the animal was rated as having a full response. A response at least once but less than 3 times was rated as a partial response. A full or partial response by at least one animal, while other test subjects did not respond at a particular wavelength and intensity was rated as a partial response for those conditions. An intensity of light was also recorded as sufficient to elicit a response if at least some animals responded to a lower intensity of the same wavelength.

The behavioral response of the subjects followed a consistent pattern for all the wavelengths tested (Fig. 3).
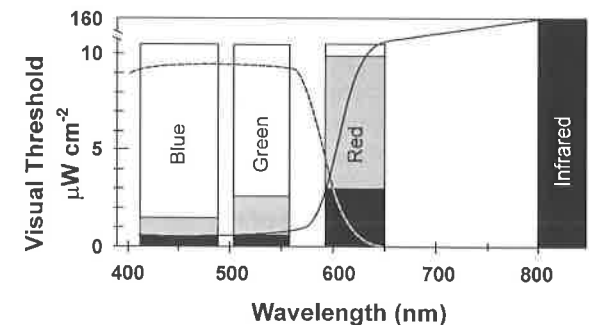

Fig. 3. Visual thresholds in *Hemisquilla californiensis* determined by

Under bright light, nearly all animals had a full response. At an intermediate intensity, some subjects ceased responding while others still had a full or partial response. Below a threshold intensity none of the subjects responded. The subjects gave clear indication of seeing the target under white light. Nearly all subjects responded at white light intensities above 3.0 μW cm^{-2}; intensities between 0.9 and 3.0 μW cm^{-2} elicited a partial response, and no subject responded at intensities below 0.9 μW cm^{-2}. The subjects' responses were different under different colors of light. The response pattern to blue light paralleled that to white light, if not slightly more sensitive. Most subjects had a full response at blue light intensities above 1.6 μW cm^{-2}, a partial response down to 0.5 μW cm^{-2}, and no response below that intensity. Green light elicited a similar pattern as blue, though the subjects may have had slightly less sensitivity. Most subjects had a full response to green at intensities above 1.9 μW cm^{-2} and a partial response was observed down to 1.0 μW cm^{-2}. The subjects had a sharply reduced response to red light. Most had a full response at intensities above 9.8 μW cm^{-2} and a partial response down to 3.0 μW cm^{-2}, below which no response was observed. As expected, subjects gave little indication of any vision in the infrared. In fact, no animal had a response at any infrared intensity, even the brilliant intensity of 163 μW cm^{-2}. This in spite of the fact that the high-intensity infrared light source could be dimly but clearly seen by human eye.

4. Discussion

Hemisquilla's behavioral response in this experiment parallels the spectral sensitivity pattern of its peripheral hemispheres (and rows 5–6 of the midband), but not that of other eye regions (Fig. 3). The animals appeared to detect blue and green light even more sensitively than they did white light. Red light, on the other hand, had to be much brighter before it elicited a response. The fact that this response pattern mirrors the spectral sensitivity of the peripheral hemispheres (Fig. 3) suggests that the animal interprets sensory input from that region to recognize an object. Although the moving target's path was such that it should cross the visual

do the peripheral hemispheres, anatomical evidence suggests that these rows are specialized for detection of polarized light (Marshall, 1988; Marshall et al., 1991, 1999; Cronin et al., 2000, 2002, 2003) and so may not play a primary role in object recognition. These results are consistent with those of Schiff (1996), who recorded the behavioral effects of covering different regions of stomatopod eyes. In her experiments several species of stomatopods could still readily locate a snail with the midbands covered, but with the peripheral eye covered they appeared to find the snails mostly by searching with their antennae.

Maximum behavioral sensitivity to blue and green is appropriate given that these are the predominant wavelengths at depth, especially near dawn and dusk when this species is most active (Basch and Engle, 1989). At depths shallow enough for broad-spectrum lighting, the other color receptors in the midband ommatidia may provide optional, supplemental information about the object once it is detected by the peripheral hemispheres and recognized as an object of interest. The highly motile eyes may scan the midband across objects and "paint" them with color (Marshall, 1988; Land et al., 1990; Cronin et al., 1994b; Cronin and Marshall, 2001), in a similar manner as cones in the human fovea are used for color vision. In this context it is interesting that Marshall et al. (1996) found that another stomatopod, *Odontodactylus scyllarus*, could learn to distinguish red, green, and yellow, but not blue objects from gray. They attributed this to the color vision system located in midband rows 1 to 4.

The response behavior shown by *H. californiensis* when presented with a moving target in this experiment has been observed in other species as well. Similar eye or antennular flicks have been reported for *Squilla empusa* (Cronin et al., 1988), for *Squilla mantis* (Schiff et al., 1986), and for several species during agonistic interactions (Caldwell and Dingle, 1975). While the eyes of some stomatopod species such as *G. oerstedii* track nearby moving targets, others such as *S. empusa*, do not (Cronin et al., 1988). This may be related to the architecture of the eye. Some stomatopods such as *Gonodactylus* and *Pseudosquilla* hold the long axis of their eye horizontal so that the peripheral hemispheres are on the right and left and the midband is vertical;

(Jones, 1994). With such a horizontal midband, objects moving nearly anywhere along the horizon can be kept in the trifocal area with little eye movement. This arrangement is analogous to that seen in some fish species with a horizontal visual streak in their retina (Land, 1990; Collin and Partridge, 1996) and has also been referred to as a visual streak in stomatopods (Marshall and Land, 1993). These species have a panoramic, sharp view of their environment without the need for horizontal saccadic eye movements. Stomatopod species such as *Gonodactylus* with vertical midbands, on the other hand, would need to track a horizontally moving target in order to keep it in the trifocal area. The scanning direction in stomatopod eyes is almost always perpendicular to the midband (Land et al., 1990; Marshall and Land, 1993). The extreme wide angle of view for each eye in *Hemisquilla* also doubtless contributes to its ability to track objects with minimal movement. In one representative individual that we examined, for example, a row of 125 ommatidia just under the central band subtended 280° horizontally. Vertically a count of 93 ommatidial rows subtended 205°, which included the dorsal and ventral hemispheres as well as the 6 midband rows (Fig. 1).

Acknowledgements

References

Basch, L., Engle, J., 1989. Aspects of the ecology and behavior of the stomatopod *Hemisquilla ensigera californiensis* (Gonodactyloidea: Hemisquillidae). In: Ferraro, E.A. (Ed.), Biology of Stomatopods, Selected Symposia and Monographs U.Z.I., vol. 3. Mucchi, Modena, pp. 199–212.

Caldwell, R.L., Dingle, H., 1975. Ecology and evolution of agonistic behavior in stomatopods. Naturwissenschaften 62, 214–222.

Caldwell, R.L., Dingle, H., 1976. Stomatopods. Sci. Am. 2343, 80–89.

Chiao, C.C., Cronin, T.W., Marshall, J., 2000. Eye design and color

Cronin, T.W., Forward Jr., R.B., 1988. The visual pigments of crabs. I. Spectral properties. J. Comp Physiol., A 162, 463–478.

Cronin, T.W., Marshall, N.J., 1989. Multiple spectral classes of photoreceptors in the retinas of gonodactyloid stomatopod crustaceans. J. Comp. Physiol., A 166, 261–275.

Cronin, T.W., Marshall, N.J., 2001. Parallel processing and image analysis in the eyes of mantis shrimps. Biol. Bull. Mar. Biol. Lab. Woods Hole 200, 177–183.

Cronin, T.W., Nair, J.N., Doyle, R.D., 1988. Ocular tracking of rapidly moving visual targets by stomatopod crustaceans. J. Exp. Biol. 138, 155–179.

Cronin, T.W., Marshall, N.J., Caldwell, R.L., 1994a. The retinas of mantis shrimps from low-light environments (Crustacea; Stomatopoda; Gonodactylidae). J. Comp. Physiol., A 174, 607–619.

Cronin, T.W., Marshall, N.J., Caldwell, R.L., Shashar, N., 1994b. Specialization of retinal function in the compound eyes of mantis shrimps. Vis. Res. 34 (20), 2639–2656.

Cronin, T.W., Marshall, N.J., Caldwell, R.L., 2000. Spectral tuning and the visual ecology of mantis shrimps. Philos. Trans. R. Soc. Lond. (B Biol. Sci) 355, 1263–1267.

Cronin, T.W., Caldwell, R.L., Erdmann, M.V., 2002. Tuning of photoreceptor function in three mantis shrimp species that inhabit a range of depths. I. Visual pigments. J. Comp. Physiol., A. doi:10.1007/s00359-002-0291-0.

Cronin, T.W., Shashar, N., Caldwell, R.L., Marshall, J., Cheroske, A.G., Chiou, T.-H., 2003. Polarization vision and its role in biological signaling. Integr. Comp. Biol. 43, 549–558.

Hazlett, B.A., 1979. The meral spot of *Gonodactylus oerstedii* Hansen as a visual stimulus (Stomatopoda, Gonodactylidae). Crustaceana 36, 196–198.

Jones, J., 1994. Architecture and composition of the muscles that drive stomatopod eye movements. J. Exp. Biol. 188, 317–331.

Land, M.F., 1990. Optics of the eyes of marine animals. In: Herring, P.J., Campbell, A., Whitfield, M., Maddock, L. (Eds.), Light and Life in the Sea. Cambridge University Press, Cambridge, pp. 149–166.

Land, M.F., Marshall, N.J., Brownless, D., Cronin, T.W., 1990. The eye-movements of the mantis shrimp *Odontodactylus scyllarus* (Crustacea: stomatopoda). J. Comp. Physiol., A 167, 155–166.

Marshall, N.J., 1988. A unique colour and polarization vision system in mantis shrimps. Nature 333, 557–560.

Marshall, N.J., Land, M.F., 1993. Some optical features of the eyes of stomatopods. I. Eye shape, optical axes and resolution. J. Comp. Physiol., A 197, 473–481.

Marshall, N.J., Land, M.F., King, C.A., Cronin, T.W., 1991. The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). I. Compound eye structure: The detection of polarised light. Philos. Trans. R. Soc. Lond. (B Biol. Sci.) 334, 33–56.

Marshall, N.J., Jones, J.P., Cronin, T.W., 1996. Behavioral evidence for colour vision in stomatopod crustaceans. J. Comp. Physiol., A 179, 473–481.

Marshall, J., Kent, J., Cronin, T., 1999. Visual adaptations in crustaceans: spectral sensitivity in diverse habitats. In: Archer, S.N.,

Sakamoto, K., Hisatomi, O., Tokunaga, F., Eguchi, E., 1996. Two opsins from the compound eye of the crab *Hemigrapsus sanguineus*. J. Exp. Biol. 199, 441–450.

Schiff, H., 1996. Influence of different eye regions on striking, size discrimination and habituation in mantis shrimps. Ital. J. Zool. 63, 139–148.

Schiff, H., Hendrickx, M.E., 1997. An introductory survey of ecology and sensory receptors of tropical eastern Pacific crustaceans. Ital. J. Zool. 64, 13–30.

Schiff, H., Abbott, B.C., Manning, R.B., 1986. Optics, range-finding, and neuroanatomy of the eye of a mantis shrimp, *Squilla mantis* (Linnaeus) (Crustacea: Stomatopoda: Squillidae). Smithson. Contrib. Zool. vol. 440. Smithsonian Institution Press, Washington, D. C.