Cover illustration

Superman on the reef

Superman is alive and well in the warm, bright, shallow seas of the coral reef. He is faster than a speeding bullet, more powerful than a locomotive, and capable of seeing into a realm we cannot begin to understand. The mantis shrimp (*Odontodactylus scyallurus*), a misnamed stomatopod, is the captivating creature gracing this month's cover, and he has an array of talents and stealth so impressive as to make him a decathlete of unprecedented prowess. For those interested in vision, this creature is truly world class, with few if any competitors. Eyes in these species should be considered the invertebrate equivalent of the avian eye in vertebrates—top of the line in the phylum.

As can be seen from the arresting photograph on this page, the compound eyes of *Odontodactylus scyallurus* have a belt-like region that seems to divide the eye in half. This equatorial belt is called a mid-band and has six specialised rows of ommatidia, the individual units of every compound eye. An ommatidium contains eight separate retinular cells arranged in a petaloid fashion when seen in cross section. Each retinular cell provides microvilli with photopigments in its membranes. Each set of microvilli is called a rhabdomere and creates the rhabdom at the core of these cells. The rhabdom, then, is the light sensitive portion of the ommatidium and is composed of elements of eight separate cells. Rhabdoms in ommatidia in four of these six mid-band rows are arranged in successive tiers of two pair of rows. The remaining two rows, in the ventral aspect of the mid-band, have specialised ommatidia for analysis of linear polarised light. In these two ventral rows, the most distal portion of the rhabdom is the ultraviolet sensitive portion and is provided by the rhabdomere of only one of the retinular cells. The remaining seven cells provide the rhabdomeres with appropriate orientation and a visual pigment for the detection of linear polarised light in the middle wavelengths with a peak at approximately 500 nm. These ommatidia in the ventral two rows, then, provide polarised vision in two separate spectral regions. Additionally, the single cell providing the distal rhabdomere of these ommatidia could, in principle, convert circularly polarised light to linearly

polarised light. Circularly polarised light is found reflecting from, among other sources, the crustacean cuticle, and probably helps confirm prey species.

Two of the dorsal two rows of ommatidia become more interesting in their processing. In addition to the distal ultraviolet receptor, these receptors have two visual pigments contained in rhabdomeres of three and four retinular cells respectively, in a tiered fashion. The ultraviolet receptor is the most distal visual receptor followed serially by a short wavelength pigment in three rhabdomeres, which then becomes a spectral filter with its absorption of some of the photons. The final most proximal visual pigment tier composed of the remaining four rhabdomeres, absorbs at a longer wavelength making the first pigment after the ultraviolet receptor a long pass filter. This tunes and sharpens the spectral sensitivity of the last and more proximal visual pigment producing a set of spectrally specialised, narrow band photoreceptors.

The other two dorsal rows have another intriguing elaboration. These rhabdoms intercalate coloured filters containing tightly packed vesicles with strongly absorbing, photostable pigments at each successive junction between tiers. The photons that enter each tier are altered not only by absorption by the visual pigments at all higher levels, but by the coloured filters that the photons have transited. This absorption makes these proximal rhabdoms in the central rows particularly suitable for producing middle to long wavelength receptor classes (Cronin *et al*, *Vis Res* 1994;**34**:2639).

Each row has different photopigments in each tier with different ultraviolet receptors, and together with the polarisation cells in the ventral two rows provide as many as 16 different visual pigments across the entire eye (Cronin and Marshall, *Nature* 1989;**339**:137) (Marshall *et al*, *Nature* 1999;**401**:873).

The superior and inferior halves delimited by the mid-band are also highly organised. The dorsal and ventral halves of ommatidial arrays contain one middle wavelength and one ultraviolet sensitive pigment in the rhabdoms of each ommatidia. Some of the ommatidia of each half and of the mid-band are directed towards the same point in space providing monocular range finding abilities, or even uniocular "stereopsis." All of that would be plenty, of course, but there is more.

Because of the specialisations of the ommatidia, and heavy skewing of ommatidial line of sight in the upper and lower eye regions, the visual field of this creature is largely limited to a narrow strip in space. As a result, to achieve a complete visual image, he must scan his environment. His stalked eyes allow for a peculiar ability to look in almost all directions and to rotate his eyes in all six possible axes even to the point of having one mid-band vertical, and perpendicular, to the opposite mid-band and direct the stalks in almost any direction. These abilities betoken a curious, even intelligent and gentle animal. But, don't be fooled. This is a solitary rapacious predator with a thunderous attack who can either patiently lie in wait because he possesses the blinding speed necessary for capture or he can prowl the reef like a street thug chasing down his quarry.

To subdue his prey, the mantis shrimp, like a well conditioned pugilist, uses his hammer-like arm with the force of a small calibre bullet, a force that can break the glass of an aquarium (Caldwell, *et al*, *Sci Am* 1976;**234**:81). This arm has perhaps the fastest acceleration in the animal kingdom. He uses this ability to break open clams, or stun fish.

So, superman is indeed alive and well, flashing vibrant colours for intraspecific communication, using multiple visual pigments to see in other realms, and employing the momentum and power of a speeding bullet.

I R Schwab
University of California, Davis, Department of Ophthalmology, 4860 Y Street, Suite 2400, Sacramento, CA 95817, USA; irschwab@ucdavis.edu

Photographs by James Brandt, MD. Advice and counsel by Roy Caldwell, PhD, Thomas Cronin, PhD, and Justin Marshall, PhD.

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I R Schwab

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