The ‘six-eyed’ stomatopod

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Stomatopods (mantis shrimps) possess one of the most complex visual systems in the animal kingdom. Each eye is capable of monocular distance judgement, colour vision involving eight or more primary channels and polarisation vision. This involves a series of eye movements unique among the crustaceans. Furthermore, each eye usually acts almost entirely independently of the other. Colour, in particular, seems to be important to stomatopods. Many live in spectrally diverse tropical coral reef habitats and possess coloured markings which are used in communication between and within species.

Mantis shrimps are a small group of aggressive marine crustaceans rather distantly related to more common shrimps and crabs. The stomatopod lineage diverged from other crustaceans 400 million years ago and today around 350 species are known. Perhaps because these animals have been out on an evolutionary limb for such a long time, their eyes have evolved a complexity unparalleled in the crustaceae. The eye is divided into three clearly distinct regions (figure 1) each assigned one or several different functions. One function made possible by dividing the eye is that of monocular stereopsis, or judging distance with one eye [1]. This is possible as the optical axes of two eye regions are tilted in towards each other so they can triangulate on the same areas in space (figure 1).

Accurate distance judgement is required for the violent method of prey capture and pugnacious nature which stomatopods are famed for. Folded beneath the head are a pair of large raptorial limbs which are shot forward at high speed to stun or stab prey. They are analogous to the forelimbs used by their common name of mantis shrimp. The force of the strike is also fearsome, in one large Californian species, *Hemisquilla califorica*, it approaches the force of a small-calibre bullet. This makes keeping the animals in glass marine aquaria a hazardous task. The ability to determine distance with a single eye enables a quick response to possible competitors, predators or prey. Also, should an eye be lost in a fight, as occasionally happens, the animal is still capable of capturing prey.

For a dwelling, mantis shrimps often choose cavities in coral rubble or live in burrows which they excavate in soft mud and sand. From these jealously guarded homes they ambush prey and fight fiercely to repel other stomatopods. Living space in a busy coral reef is at a premium. In some areas as many as five or six stomatopods can be found living in one small rock. However, despite their aggressive nature, stomatopods are retiring creatures so all that an investigating diver is likely to see of them is a pair of eyes peering out from the burrow or cavity. In order to prevent damaging conflict with rivals, mantis shrimps have evolved accurate assessment mechanisms, involving both odour and visual cues [3]. Battles may be over a mate or, as is quite often the case, an attempted eviction from the head from the raptorial limbs of an opponent could be fatal. As a result, if animals do come to blows, a ritualistic form of combat is used in some species. Aggressor and defender strike at the heavily armoured telson (tail end) of their opponent, causing little actual damage, but enabling them to sort out who is the strongest [2].

Stomatopods are often put into two groups, the spearmen and the smashers, based on the structure of the raptorial limb. In smashers the maxillipeds have become enlarged to form a heavily armoured elbow-like structure used to stun and crack into hard-bodied prey such as molluscs and other crustaceans (figure 2). Fish and soft-bodied prey are favoured by the spearmen, and their raptorial limbs are lined with viciously barbed spines to ensnare prey. Zoologically, however, stomatopods are arranged into four superfamilies: the bathysquilloids, squilloids, lysiosquilliods, and the gonodactyloids [4]. The bathysquilliods, living in the lightless depths of the deep-sea, have reduced or simple eyes. Species from the gonodactyloid and lysiosquillloid superfamilies live in shallow waters, often only a few feet deep. In association with this shallow water habitat, their eyes contain a centrally placed 'mid-band' zone, beneath which lies an astonishingly diverse retina capable of colour and polarisation vision. The mid-band and some of the possible uses of this eye region is the main subject of this article. Unless stated, stomatopod or mantis shrimp henceforth refers to species from these two superfamilies only.

The stomatopod eye

In fundamental design, stomatopod eyes are like those of many other crustaceans or insects. They are apposition compound eyes consisting of several thousand individual units, or ommatidia [5]. Ommatidia in apposition eyes act as individual photoreceptors. Each one views only a small angle of the world and looks in a slightly different direction from its neighbours to allow spatial discrimination. An ommatidium is made up of a lens (the outer hexagon visible on the surface of the eye) which focuses light onto a stack of membrane tubes, the rhabdom (figures 3 and 4). The membrane tubes (microvilli) hold visual pigment molecules, collectively called rhodopsins, which enable eyes to absorb light and transmit this event to the brain. Rhabdoms are the arthropod equivalent of rods and cones in vertebrates, and perform exactly the same function of converting light absorption into an electrical signal. In many crustaceans, including stomatopods, the rhabdom in each ommatidium is constructed from eight cells. Usually, a small portion of rhabdom, made by a single retinular cell (R8) overlies a longer rhabdom made collectively by seven cells (R1-7, figure 3).

An advantage of making an eye of individual units is that it can easily be subdivided into zones of ommatidia which are functionally distinct from each other. Although common among the arthropods [6], nowhere is subdivision better illustrated than in the gonodactyloid and lysiosquillloid stomatopods. Their eyes consist of two 'hemispheres' divided by a centrally placed mid-band of six rows of ommatidia (figures 1 and 2). The lens facets of mid-band ommatidia are often larger than those in the hemispheres, immediately suggesting some...
Figure 1 The eyes of two stomatopods. *Odontodactylus scyllarus*, a gonodactyloid (top) and *Lysiosquilla maculata*, a lysiosquilloid (bottom). (a) and (b) are the living eyes — the black ommatidia, (the pseudopupil) are the ones looking at the observer (the camera); (c) and (d) are sections of the front part of the eye — the dark crescent is the retina onto which light is focused by the dioptric portion to the right; (e) and (f) are the viewing directions of every fifth ommatidium, drawn from (c) and (d). The area which the receptors of the mid-band view has been coloured in to represent their coloured and polarised light sensitivity. The ommatidia in the hemispheres which overlap in their field of view are shaded in.

Functional difference, such as a need for greater sensitivity [7]. However it is at the level of the light-absorbing rhabdoms that the amazing modifications of the stomatopod mid-band become apparent. Rhabdoms in rows one to four (numbered from the top down) are made up of three, rather than two, tiers. A small distally placed R8 cell, as usual, is followed more proximally by two tiers. In each, the rhabdom is constructed by three or four cells, which normally form the single R1–7 cell complex (figure 3 and [8]). In rows two and three the tiers are separated by intensely coloured filters, which look and behave rather like tinted sunglasses (figure 5 and [8]). As these filters lie in the path of light passing down the rhabdom (they are called intrarhabdomal filters), they must alter its spectral quality, allowing through only those wavelengths they transmit. In gonodactyloid stomatopods each filter is a different colour.

Colour vision
The presence of these coloured filters first suggested to us that some form of colour vision was possible using the mid-band photoreceptors. However subsequent investigation of the mid-band tiers exceeded our wildest expectations. The retina can be sectioned in a fresh-frozen state (figure 5). Then, using the technique of microspectrophotometry (like spectrophotometry but using a 2 μm beam), the absorbance of any portion of the retina, whether it be filters or a part of a rhabdom containing visual pigments, can be measured. The results of this analysis for several species, for instance *Gonodactylus oerstedii* (figure 6), indicate that rows one to four of the mid-band contain at least nine different visual pigments and that in total there are more than 12 visual pigments throughout the eye [9]. Each of the lower two tiers in rows one to four contains a different visual pigment. The overlying R8 cells contain different visual pigments, absorbing light in the ultra-violet (UV), a part of the spectrum we are blind to. In other retinal areas, the hemispheres and rows five and six of the mid-band, there are three more visual pigment types. As the UV visual pigments are not fully described yet, all we can say at the moment is that there are more than 12 visual pigments in the retina (possibly as many as 16!). However, it is probably only those in rows one to four of the mid-band which mediate colour vision.

The human visual system employs four visual pigments: three cone pigments (usually referred to as red, green, and blue cones) for colour vision and a single rod pigment for vision under light-limited circumstances. By placing the absorbance peaks of the cone pigments at different parts of the spectrum, and comparing their relative output on seeing a colour, humans can resolve thousands of different hues [10]. Many other animals have more colour receptors than humans but the closest any come to stomatopods are the five 'cone' types found in some butterflies [11] and birds [12]. As we use three cone types for colour vision, humans are referred to as 'trichromats' or as having 'three-dimensional' colour vision. The nine or more visual pigments, and the colour filters, which stomatopods appear to use for perceiving colour give them the potential for stunningly complex colour vision.

A potential problem with having so many visual pigments is redundancy or overlap in receptive range. This is clear in figure 6(b) which illustrates modelled response curves for the visual pigments of *Gonodactylus oerstedii*. The broad shape of these curves is a characteristic of all visual pigments and is generally thought to be what limits most animals to 3–5 visual pigments [13]. With more than this number, too much overlap in the available 300–700 nm spectral range...
occurs. Stomatopods get around this problem with intrarhabdomal filters and the tiered construction of the retina (figures 3 and 5). The eyes of birds and some reptiles also contain colour filters which spectrally modify the nature of light reaching their photoreceptors [14]. Colour filters can actually be used to multiply the number of spectral channels in an eye although this does not occur in stomatopods. Two receptors containing one visual pigment type, screened by two filter types, a blue and a red say, would be sensitive to blue and red light. Alternatively, if the absorbance of the filters contains a sharp ‘cut-off’, they may be used to sharpen an underlying photoreceptor spectral response [14].

Stomatopod filters do behave as cut-off filters, selectively allowing through only wavelengths beyond a particular, sharply defined value (figure 6). Rows one and four do not contain filters. However, due to the tiered rhabdom system, each tier acts like a filter, transmitting only wavelengths its visual pigment has not absorbed. Thus the spectral response of proximal tiers are sharpened in these two rows also [figure 6(c)]. Starting with eight, rather broad-band, overlapping visual pigments [figure 6(b)], modified by a set of cut-off filters [figure 6(a)], and by arranging the photoreceptors in tiers to sample light serially (figure 3), the final result is eight sharply tuned sensitivities [figure 6(c)]. The ninth spectral sensitivity class in rows one to four is in the ultra-violet range and is located in the distal R8 cells (figure 3). As light passes down the rhabdom it is sequentially absorbed, from short to long wavelengths, by the different photoreceptor tiers, and this information is passed on the brain by axons from each tier [figure 3(b)]. This starts with ultra-violet at the R8 cell level, the next tier absorbs light of longer wavelengths and the most proximal tier, longer wavelengths still. As well as sharpening spectral sensitivity of photoreceptors to help them fit in the 300–700 nm range, another result of serial filtering is to shift the peak sensitivities of more proximal photoreceptor tiers to cover more of the red end of the spectrum [compare figure 6(b) and (c)]. A penalty paid by filtering is a massive loss in sensitivity in the proximal photoreceptors. For exactly this reason mid-band ommatidia are larger to increase their light gathering ability (figure 1 and [15]).

As each of rows one to four contains different visual pigments, and in rows two and three different filter types, the rows are clearly ‘interested’ in different windows in the available light spectrum. In all species examined the same pattern emerges. Row one is generally sensitive to light from 400–500 nm, row four 450–550 nm, row two 500–650 nm, and row three 600–700 nm or more. As well as being able to increase the number of photoreceptor types, sharp spectral sensitivities also enable finer spectral resolution within the range chosen by opponent photoreceptors. At present we hypothesise that the stomatopod eye performs four dichromatic comparisons, one in rows one to four of the mid band, within the ranges detailed above [8]. This would generate areas in the spectrum where very fine discrimination is possible, and areas where poor or no spectral discrimination occurs. Evidence for such a discontinuous, spectral category type of colour vision has recently been provided in the blowfly, which also possesses tiered photoreceptors in its eye [16].

Any visual system utilising more than one visual pigment is capable of colour vision. Stomatopods with at least 12 visual pigments seem certain to have some form of colour discrimination. However, pedantic though this may seem, true colour vision (the discrimination of colours from each other and from shades of grey) must be shown behaviourally. Such evidence has been provided recently using the large smashing species Odontodactylus scyllarus. The experiment takes advantage of the animal’s violent method of prey capture, as this species can be trained to break into small
Figure 3 Internal structure of the stomatopod eye. (a) is a transverse section of the mid-band and hemispheres at the retinal level. The dark squares and circles are sections through the rhabdoms and the ‘petals’ around each of these are the cells which make the rhabdom. The letters c, e, f & g mark portions of the retina shown enlarged in this figure; (b) is a diagrammatic representation of the stomatopod eye with ommatidia in longitudinal section. The six rows of the mid-band are labelled 1–6, dorsal to ventral. DH — dorsal hemisphere, VH — ventral hemisphere. Retinular cell tiers are called R8, R1–7, R2, 3, 4 and 7, and R1, 4 and 5 depending on the number of cells responsible for their construction. R1, 4 and 5, for instance, is a tier in a rhabdom made by three cells. Letters on the figures (a), (c), (d), (e), (f) and (g) mark sections shown in the photographs. x and y are section levels illustrated in figure 4; (c)–(g) are transmission electron micrographs of parts of the retina labelled in (a) and (b). (c) is an intrarhabdomal filter coloured yellow like that of figure 5(b). The small ‘empty’ vesicles here and the dark vesicles in (d) contain coloured pigment; (d) is a longitudinal section of filter coloured blue like that in figure 5(c); (e) is a rhabdom in the ventral hemisphere made by seven cells; (f) and (g) are rhabdoms from different tiers in the mid-band made by four and three cells, respectively.

plastic cubes to get at food placed within them (figure 7). One side of the cube can be coloured or given a particular shade of grey and, for training, food is placed only in the coloured cubes. An individual rapidly learns to associate food with the colour to which it has been assigned, and breaks into the appropriate cube as opposed to grey or other coloured cubes given in a test. This is the first real demonstration of colour vision in any crustacean. Possible uses for colour vision in mantis shrimps are discussed later.

Polarisation vision

Rows five and six of the mid-band contain photoreceptors which are specifically designed to be sensitive to polarised light. Many invertebrate photoreceptors have this ability, due to the geometry of their construction [17]. The finger-like microvillar membranes of the rhabdom contain rhodopsin molecules which are mostly oriented parallel to their long axis. As a result the receptors respond best to light polarised in a plane containing the microvillar axis (figure 4). With two sets of receptors whose microvillar directions are at an angle, of say 90°, to each other, it is possible to ‘compute’ polarisation contrast. This works in much the same way as the colour opponent mechanisms outlined above where two receptors are needed to see colour. Such an orthogonal arrangement of receptor microvilli is typical of most crustacean rhabdoms and those in rows five and six of the mid-band are illustrated in figure 4. These two rows in fact contain three microvillar directions with the overall arrangement in row five rotated 90° relative to row six. As the R8 cells are sensitive to ultra-violet light and the R1–7 cells (which in these rows are not split into different tiers) to green light there is also the potential for polarised light analysis in different regions of the spectrum. This sense is not available to humans as our visual pigment molecules are arrayed randomly within the membrane of the photoreceptors. Therefore it is rather difficult for us to conceptualise how polarisation vision might be useful. Actually the sky and in particular the shallow water marine environment is full of polarised light, mainly derived from reflected or scattered light [18]. We use polaroid sunglasses to reduce glare from reflecting surfaces such as the sea. Suggested uses for polarisation vision
in the arthropod world include: navigation (using the natural pattern of polarised light in the sky), glare reduction, detecting water surfaces, camouflage breaking of silvery surfaces and haze reduction for contrast enhancement where there is a high proportion of scattered light [19].

We do not know the purpose of polarisation vision in stomatopods. Using the pattern of polarised light in the sky seems unlikely as it is greatly disrupted by surface waves. Several fish species are silivered as a form of camouflage, their mirrored sides reflecting general ambient light, making them less visible against the background. A predator which could reduce this reflection may be able to crack this camouflage [19]. Many stomatopods live in the turbid sand-particle filled waters of the coral reef where scattered light from these particles creates a veilng haze. A polarising filter or a receptor sensitive to light in one polarisation plane only, would help to cut through this haze and enable the animal to see further.
coloured meral spots, pink, white, orange, yellow, purple, or red being just a few examples [figure 2(a) and 2(b)]. In some species, there is also a coloured spot on the first maxilliped. This colour-coding apparently serves for species recognition and may also encode other information such as breeding state or readiness for combat. Although the general colour of the spot is the same for one species, different individuals do show some colour variation. We cannot be sure, but it is possible that interspecific differences in meral spots mean something to another stomatopod. Individual recognition by colour may help in making important decisions at a safe distance from the striking power of an opponent’s raptorial clubs or spears. It is also worth bearing in mind that colour differences may exist that are not discernable to the human colour vision system.

Camouflage is an important consideration, especially for many of the smaller stomatopod species. Figure 8 illustrates three different individuals of the small gonodactyloid Gonodactylus oerstedii. The yellow animal was found living in a rock covered in yellow sponges, the others from more variegated rocks. Although not true for all species, many stomatopods can change colour to match their local background, or microhabitat, with remarkable accuracy (see also figure 9). Unlike cephalopods or chameleons, this change is not instantaneous but occurs over a number of moults. One important function of the stomatopod colour vision system may be to enable them to fit in wherever they go. Also, other reef creatures, including most of the crustaceans, are known to specialise in cryptic colouration (in this case by direct evolutionary design) [22]. It may be that, along with background recognition, general colour vision, and colour signalling, the enhanced spectral discrimination in stomatopods helps to break the colour crypts of potential prey items or even other stomatopods on the reef. Such multi-tasking of colour-related visual problems may explain the diversity of mantis shrimp photoreceptors. If forced to choose one explanation for this complexity, our money would go on the chromatic subtleties of the stomatopod colour markings and communication.

**Optics and eye movements**

Anyone seeing a stomatopod for the first time probably will not notice the six-row mid-band and may even miss the often concealed coloured markings. However, what is immediately noticeable about these animals is their extraordinary eye movements. The eyes are in almost continuous motion, moving up and down, side to side, and rotating about the eye stalk axis, all the time examining the world in a most inquisitive manner. That the eyes move at all is unusual for a crustacean. A frightened crab may retract its eye suddenly and, in common with all animals, will make optokinetic
Figure 7. Colour vision, the behavioural proof. (a) Is a drawing of the behavioural training/test arena where a shrimp in a burrow (flower-pot) is presented with three glass-sided perspex cubes; (b) results of colour vision tests. A positive choice in a test is when a shrimp picks up the coloured cube first to smash into it.

By subdivision and optical rearrangement, the mantis shrimp eye has evolved into a one-dimensional strip sampler. Other ommatidia are needed to cover the rest of the visual field (when the eyes are static) but these are non-specialised and lack the high spatial acuity of those within the strip [15]. Objects examined by the strip can simultaneously be analyzed for colour, polarised light content, spatial detail, and distance from the eye, the latter two functions being the job of the hemispheres. Such parallel processing is obviously desirable but creates a problem. Any object falling outside the visual strip will be examined only by ommatidia from one hemisphere. As a result, to fill in the image, the strip must be scanned over objects literally to colour in their detail. This explains the slow deliberate eye movements of stomatopods. The speed of scanning is slow, around $40^\circ$ s$^{-1}$ to allow the photoreceptors time to respond (figure 10 and [24]).

During scanning, the optokinetic stabilising mechanism must be turned off, and both these visual functions cannot operate during rapid acquisitional eye movements or tracking. It appears then that a time-share system must operate for the eyes to function in other modes. An object is acquired and, if necessary tracked, by

1. stabilising eye movements to fix an image on the retina. More unusual still, each one of a stomatopod's eyes moves (almost) entirely independently of the other. Trying to decide what the animal is looking at is a bewildering task but has been accomplished with the aid of a computer modelled eye (figure 11). Frame by frame analysis of video film using the computer eye, suggests that the types of eye movement made are rather like those of a primate. There are rapid saccades (targetting eye movements) to look at new objects of interest (figure 10),

moving objects are tracked by one or both eyes (figure 11) and for part of the time, optokinetic eye movements are used to stabilise an image of the world on the retina. Saccadic and tracking eye movements imply the presence of an acute zone, or foveal eye region, within which spatial acuity, and possibly other visual capabilities, are heightened. Objects of particular interest are 'foveated' by saccades and, if they move, they are tracked to allow closer examination. Stomatopods do possess pronounced acute zones whose spatial acuity is around three times finer than most of the rest of the eye (figure 12 and [15]). Although quite common in the insects [7], stomatopods are among less than a handful of crustaceans with a fovea-like acute zone [23].

Strangely, however, the majority of eye movements made by mantis shrimps are too slow to be useful for object acquisition or following. They are slow, deliberate scanning movements, and are almost unique to the stomatopods [24]. The function of scanning becomes clear when one considers the optical arrangement of the eye, in particular the strip-like nature of the mid-band.

Mid-band ommatidia, and many of those from both of the hemispheres look into the same narrow strip in visual space (figure 1). We know this from examining the pseudo-pupil, the black-appearing eye regions (figures 1 and 12) which correspond to those ommatidia looking in the direction of the observer. The three black ommatidial regions of figure 1(a) for instance, indicate that the eye views the observer (the camera) three times, once with the mid-band and once with each of the two hemispheres. Figures 1(e) and (f) illustrate the directions in which ommatidia look in the eyes of two stomatopod species. The visual axes of the six rows in the mid-band are essentially parallel to each other. Those on either side of the mid-band are tilted in towards the centre of the eye and consequently a strip in front of the eye is viewed by ommatidia from all three eye regions. The spacing of the ommatidia is not even; in both hemispheres over half have their visual axes crammed into the same narrow zone as those of the mid-band, resulting in high spatial acuity.

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acute zone. Its distance, colour, and polarisation content are determined by scanning and when there is nothing special to look at, optokinetic stabilisation takes over to reaffirm the shrimps position in the world.

The neural processing behind scanning eye movements has the added problem of needing an internal image (or in this case, possibly two internal images, as the eyes operate independently) of the world which is continuously renewed over time like a radar image. Such vision must involve the cognitive abilities of higher processing brain areas. As yet we know very little about this side of vision in any invertebrate. One aim for the future is to understand how neuronal processing interprets, and communicates, the mass of information reaching the retina. Also we would like to know something about the nature of this information. Are colour signals as important as they seem? What behaviours are linked to the astonishing colour and polarisation vision capabilities? What do stomatopods actually see in the world around them?

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Figure 9 Mantis shrimps in their natural habitat. (Photos R. L. Caldwell). (a) and (b) Pseudosquilla ciliata and Gonodactylus affinis well camouflaged against their microhabitat; (c) and (d) Gonodactylus glabrous and Haplosquilla stilurus showing orange and blue markings probably used in communication.

References

Figure 10 Some results of eye movement analysis. (a) Scanning eye movements are mostly made at around 90° to the mid-band to allow serial sampling by all receptors; (b) and (c) Scanning eye movements are slow, around 40° s⁻¹, to allow serial intake of information. Saccadic eye movements are to 'acquire' new objects of interest and are fast, 200–600° s⁻¹. The speed of saccades varies between the two species shown, probably because the eyes of Odontodactylus scyllarus are substantially larger than those of Pseudosquilla ciliata, and therefore have greater inertia.

Figure 11 Tracking eye movements of Pseudosquilla ciliata. The target was oscillated from side to side in front of the shrimp and the eye movements analysed as shown in figure 11. Tracking from side to side (longitude) is performed by both eyes in a rather loose manner.

Figure 12 Analysis of stomatopod eye movements. (a)–(f) Video frames of the eye movements of Odontodactylus scyllarus; (g) and (h) a single video frame demonstrating the way eye movements are measured by fitting a computer model eye to the real eye, frame-by-frame.