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N. J. Marshall · J. P. Jones · T. W. Cronin

Behavioural evidence for colour vision in stomatopod crustaceans

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Abstract If an organism can be taught to respond in a particular way to a wavelength of light, irrespective of that light's intensity, then it must be able to perceive the colour of the stimulus. No marine invertebrate has yet been shown to have colour vision. Stomatopod crustaceans (mantis shrimps) are colourful animals and their eyes have many adaptations which indicate that they are capable of such spectral analysis. We adopted an associative learning paradigm to attempt to demonstrate colour vision. Stomatopods readily learnt to choose some colours from arrays of greys, even when the correct choice colours were darker than the ones they had been trained to. Possible mechanisms underlying colour vision in these animals, and their ecological significance are discussed. A simple model is presented which may help interpret the complex-stomatopod colour vision system and explain some of the learning anomalies.

Key words Stomatopod · Colour vision · Crustacean behaviour

Abbreviations *ND* neutral density · *OD* optical density · *R8* Retinular cell 8 · *R1-7* Retinular cells 1-7 · *e.g. R1D* Distally placed R1-7 retinular cells in mid-band row 1 · *e.g. R1P* Proximally placed R1-7 retinular cells in mid-band row 1 · *D/P* Estimate of chromatic signal ratio

Introduction

The mantis shrimp *Odontodactylus scyllarus* lives in the spectrally rich environment of the reef top which it views with large apposition compound eyes. Each eye is hemisected by six clearly visible rows of specialised ommatidia called the mid-band (Manning et al. 1984; Marshall et al. 1991a). Four of these rows show adaptations which are strongly suggestive of colour vision (Marshall 1988; Cronin and Marshall 1989a; Marshall et al. 1991b). These specialisations include more than eight different visual pigments (Fig. 2b), tiered receptor cells and densely coloured filter blocks (Marshall et al. 1991b; Cronin and Marshall 1989b; Cronin et al. 1994b). *O. scyllarus* is astonishingly colourful and in common with other species in its superfamily (Gonodactyloidea), it shows off coloured areas of cuticle during threat displays (Caldwell and Dingle 1976; Hazlett 1979). Based on these varied observations it is likely that *O. scyllarus* possesses some form of colour vision.

To demonstrate colour vision, a behavioural test is needed in which the animal recognises objects of differing spectral properties irrespective of intensity (Menzel 1979; Burkhardt 1983; Neumeyer 1991; Thompson et al. 1992). Such tests have been performed on insects and a wide variety of vertebrates but rarely on crustaceans (Menzel 1979; Menzel and Backhaus 1991; Jacobs 1981). Studies of crustaceans colour vision generally examine phototaxis in relation to colour and are difficult to interpret as they may reflect what are known as wavelength specific behaviours rather than 'true' colour vision (von Frisch and Kupelwieser 1913; Smith and Baylor 1953; Stearns 1975; Hyatt 1974, 1975). Wavelength specific behaviours are stereotyped motor patterns, underlying various behaviours, which are triggered by photoreceptors responding to specific wavelengths (Menzel 1979). They are described in a variety of insects and exist in other animals instead of or as well as 'true' colour vision (Scherer and Kolb 1987a, b; Menzel and Backhaus 1991). As a result some caution is needed in interpreting results involving colour stimuli.

Within the Crustacea there are also a number of studies describing the possibility of colour vision based

N. J. Marshall (✉) · J. P. Jones
Sussex Centre for Neuroscience, University of Sussex,
Brighton BN1 9QG, Sussex, UK

T. W. Cronin
Department of Biological Sciences, UMBC Catonsville,
Baltimore, MD 21228, USA

solely on retinal anatomy and visual pigment diversity (Stowe 1980; Leggett 1979; Lall and Cronin 1987; Smith and Macagno 1990; Marshall 1988). Such claims for colour vision are necessarily speculative. However tests on animals designed to demonstrate colour vision where diverse photoreceptor types exist have almost always proved positive. With over eight visual pigments and colour filters (Marshall et al. 1991b; Cronin and Marshall 1989a), it would be odd if stomatopods did not possess some form of colour vision.

The task required of our shrimps exploits the prey capture and defence mechanism of the so called 'smashing' stomatopods like *O. scyllarus.* Using enlarged, hardened second maxillipeds, these mantis shrimps crack open hard bodied prey and inflict lethal blows on rivals. Raptorial limbs use a storage-release muscle mechanism to generate enormous force for the rapid forward strike, one of the fastest animal movements known (Burrows 1969; Caldwell and Dingle 1976). Animals were given hollow plastic cubes containing food with the 5 open sides sealed by glass coverslips and the remaining solid side covered with coloured or grey plastic. They learned within seconds to pick up cubes and within minutes to crack them open, gaining entry usually through the replaceable glass sides (Fig. 1).

While some colours of plastic; green, red and yellow, were easily distinguished from various shades of grey by *O. scyllarus,* the blue plastic chosen was not. A simple model is presented which, based on the colour reflectance characteristics and retinal sensitivities, may help explain this problem. The suggested model system also holds one possible explanation for the tremendous complexity found in the stomatopod retina.

Fig. 1 The stomatopod *Odontodactylus scyllarus* manipulating a feeding cube. Note the presence of the centrally placed mid-band region in the eyes and the enlarged red heel of the raptorial appendage, used to break into cubes

Materials and methods

Odontodactylus scyllarus of both sexes were purchased from tropical fish suppliers and housed individually in standard marine aquaria where half a flower pot acted as a burrow. (Aquastar) fluorescent tubes provided the best possible lighting for the aquaria, including the UV range (Fig 2a).

Food cubes were constructed from white perspex blocks (21 mm^3) with an accessible cavity, drilled from five of the sides, into the centre (Fig. 1). Coloured plastic squares and a range of neutral density (ND) filters (ND-0 – white perspex, no covering filter, ND-A – optical density (OD) 0.3, ND-B – OD 0.6, ND-C – OD 0.9, ND-D – OD 1.2, ND-E – OD 1.8) were attached to the one intact face of individual cubes by using double sided sticky tape. The coloured cubes were primed with a piece of food (usually cockle, shrimp or mussel) for training runs, filled with water and the five open sides closed off with glass coverslips held on with petroleum jelly. In the test situations, all the cubes were empty and these cubes were kept separate from the training cubes to avoid the possibility of remaining odour confounding the visual discrimination task.

At the start of each experiment the animal was partitioned into its burrow with a sheet of black perspex. Three blocks, one coloured and two grey, were then arranged symmetrically in front of the burrow, with their solid faces toward the animal. The relative position of the coloured cube was varied systematically and the neutral density cubes, chosen from a series containing two of each ND type, were both selected at random. A choice was scored as the first cube the animal picked up. Each animal was tested twice a week after an initial four to six week period of training runs which were also conducted twice a week. This test of asking the shrimps to choose a colour from a range of greys follows the basic experimental design used many times in the past (e.g. von Frisch and Kuppelwieser 1913, Fukushi 1990).

Figure 2a illustrates the spectral reflectance of coloured cubes, two of the neutral density cubes used and the emission spectrum of the "Aquastar" florescent lamps which illuminated the arena. All reflection and radiometric measurements were made with "Sub-Spec" a custom-built (Andor Technology/Oriel) spectroradiometer and a "Spectralon" white reflection standard. For the calculations detailed in Fig. 4, radiometric values of light (in photons/ $sec/cm^2/sr/nm$) reflected from each cube were used. "Sub-Spec" was calibrated from 300–800 nm against a known emission standard prior to these measurements. Cube reflectances were measured in the experimental arena and therefore represent our best estimate of the spectrum that reached the shrimp's eyes from each cube.

Results

Stomatopods could learn to discriminate what appeared to us as red, green or yellow, but not blue, from various shades of grey. These results are detailed in Fig. 3 which shows observed versus expected-by-chance results for each cube colour type. Choices of red, green and yellow cubes from greys are significantly higher than the 1:3 chance level. For blue however choice frequencies close to 1:3 were observed. It also proved impossible to train animals to choose a particular shade of grey (ND-A) from a selection of others, a task which would depend solely upon an ability to discriminate and remember intensity (Fig. 3a). In colour preference tests animals also showed no innate preference for any one of the cube colours. There was no preference for cube position.

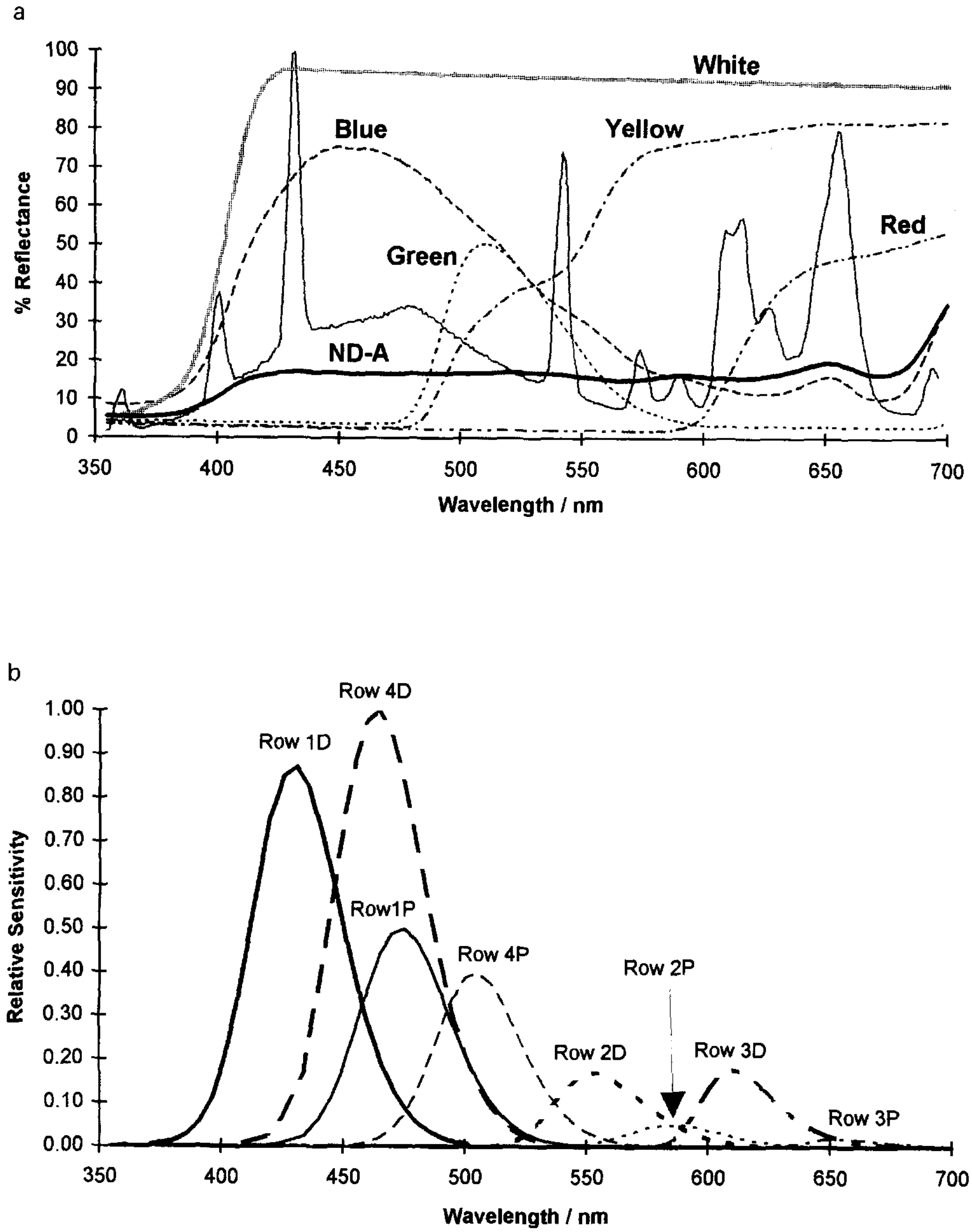


Fig. 2a, b Experimental set-up and estimated retinal sensitivities. **a** *Dotted curves* – spectral reflectance of coloured cubes used, *solid curves* – two of the neutral density cubes used, *sharp-peaked curve* – normalised emission spectrum of the "Aquastar" florescent lamps used to illuminate arena. **b** Spectral sensitivities of the eight regions of the R1-7 retina in rows one to four of *O. scyllarus*. These are normalised to the highest sensitivity found, in row 4 distal receptors (row 4D). The sensitivities of proximal tiers are highly attenuated due to the filtering effect of overlying photoreceptors, and in rows two and three by dense filters (Cronin and Marshall 1989a; Cronin et al. 1994d). Curves for row 1D & 4D are sharpened on the short wavelength side compared to those of Cronin et al. (1994c). See text for details

Although inability to learn brightness and ability to learn colours are together strong evidence for colour vision it still remained possible that the animals were learning the brightness, or some other aspect of the coloured cubes used for training. To control for this, a second series of tests was conducted in which the 'correct' colour choice had its overall reflectance changed, either by being overlaid with one of the ND filters (OD-0.3) transmittance or by using a second layer of identically coloured plastic which increased colour saturation and decreased brightness. The animals saw the altered colours only during the test situations and so had no opportunity to associate the darker colours with the food rewards. Nevertheless, they performed as well in these tests as with the original colours (Fig. 3b). There can therefore be little doubt that the primary cue used in cube identification was colour. As in the initial set of tests, *O. scyllarus* could not learn to discriminate darkened blue cubes from greys.

Many of the 'negative' results in both initial and darkened cube experiments stem from one or two idiosyncratic animals which picked up cubes at random order and removed them to their home burrow before opening. Training stomatopods presents a number of difficulties not often encountered with other arthropods. They are very inquisitive animals, especially for a crustacean, and on being presented with an object will usually spend some time examining it visually, pick it up to manipulate and tap at with their raptorial limbs. However some individuals are more cautious than others, perhaps due to past experiences, which

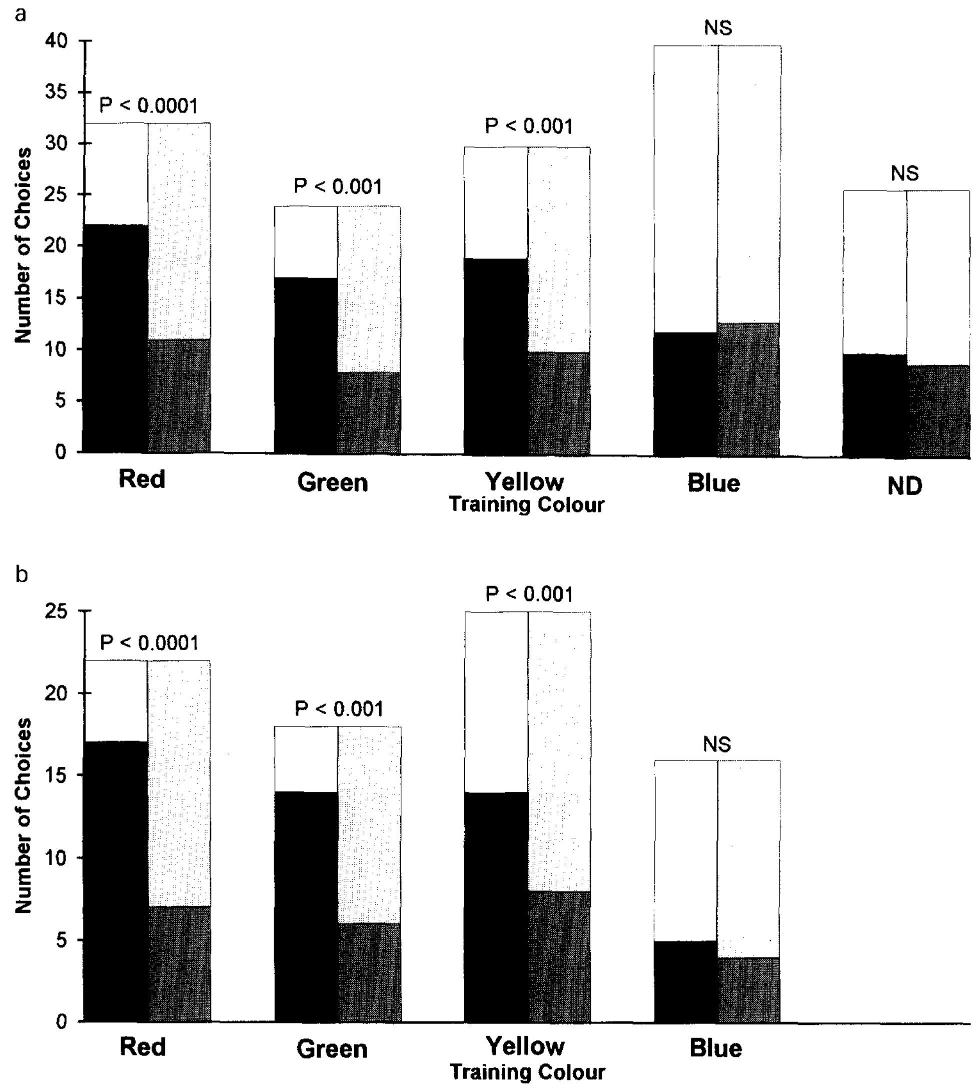


Fig. 3a, b Choice test results **a** Histogram showing the performance of 14 animals which were tested with their training colour. For each cube colour the left-hand bar represents the observed data whilst the right-hand shows the results expected from random choice (rounded to the nearest whole choice). Each *bar* plots positive results in dark areas beneath, light areas which are 'negative' results. *p* values are from contingency chi-squared tests. **b** Histogram showing the results obtained when the test cubes were darkened, either with ND-A or another layer of identically coloured gel. Conventions are as in **a**

they are known to remember for a considerable time (Caldwell 1982). These are the individuals that rush out and remove all cubes to their flower pot, apparently without prior examination. Despite this difference in behaviour, such animals choices were retained in the data set.

A further problem with stomatopods is that to maintain motivation to feed, training and tests must be performed twice a week only. As a result building a statistically testable data set takes a considerable amount of time.

Discussion

Stomatopods and other crustaceans

O. scyllarus is good at discriminating the red, green and yellow plastics from a range of greys, but not blue. This is the first demonstration of 'true' colour vision in a crustacean.

Cladocerans such as *Daphnia magna* are known to have four spectral classes of photoreceptor (Smith and Macagno 1990) and both *D. magna* and *D. pulex* perform different swimming responses to different wavelengths of light in what have been called "colour dances" (von Frisch and Kupelwieser 1913; Smith and Baylor 1953; Stearns 1975). These are phototactic responses and are generally interpreted as a means of detecting and orienting to the surface or finding places to hide under algae; they may best be thought of as wavelength specific behaviours (Menzel 1979). Wavelength specific behaviours are stereotyped actions such as egg laying or feeding, induced by stimulation of one or more classes of spectrally distinct photoreceptor. They are generally not thought of as 'true' colour vision and are well documented in the Lepidoptera and Hymenoptera (Scherer and Kolb 1987a, b; Lunau and Maier 1995; Cutler et al. 1995). Lepidopterans and hymenopterans also exhibit 'true' colour vision where, as with the experiments described here, different colours must be learned in association with a particular task (Menzel 1979; Goldsmith 1990; Lunau and Maier 1995).

Stomatopods often show off coloured areas of cuticle, e.g. the "meral spot" (Hazlett 1979), so in principle a fixed response to such a signal could be an economic way of organising behaviours. However different species possess differently coloured meral spots, and other coloured body regions, and live in close proximity to one another on coral reefs. As stomatopods must make important decisions based on colour (Caldwell and Dingle 1976) some degree of real colour discrimination is desirable.

Another group of crustacean in which wavelength related behaviour seems likely are the fiddler crabs. *Uca pugilator*, for instance, waves coloured chelepeds as part of sexual and territorial displays making them attractive candidates for colour vision. However as with cladocerans, only their spontaneous phototactic reactions to light of different wavelengths has been studied (Hyatt 1974, 1975) making any firm conclusions regarding colour vision difficult (Lunau and Maier 1995). These, like other crabs examined, possess only one or two spectrally different types of photoreceptor. There are the main R1-7 photoreceptors which have their maximum sensitivity at around 500 nm and sometimes a small distal R8 cell sensitive to shorter wavelengths around 400 nm, each sensitivity being based on a different visual pigment (Cronin and Forward 1988; Lall and Cronin 1987). Coloured screening pigments also exist in the retinae of crabs and other crustaceans and these, in conjunction with two visual pigments, could perhaps mediate colour vision (Leggett 1979; Stowe 1980; Lall and Cronin 1987).

Why is blue not recognised by *O. scyllarus*?

It is curious that blue can't be distinguished by *O. scyllarus* as to our eyes the blue is distinct, well saturated and as a category of colour is as persuasive as the others. To find possible reasons for this, we examined the colour receptors of *O. scyllarus*, using the available data (Marshall et al. 1991b; Cronin et al. 1994c), and have begun to model what the shrimp sees when looking at the cubes. The relative photon catch by each receptor type was estimated by summing the product of the reflectance of the cubes in photons/sec/cm^2/sr/nm and the modelled sensitivity of each of the eight receptor types at 1 nm intervals (Fig. 2 and see Cronin and Marshall 1989a; Cronin et al. 1994c). Figure 2a illustrates cube's colour in percent reflectance and the illumination emission. This gives more information about the materials used than giving absolute reflectances for each cube, which are the values used for these calculations.

It may be that the relatively broad reflectance function of the blue cubes prevents accurate discrimination by the stomatopod visual system (see on). Only the wavelength range 400–700 nm was considered as the white perspex used has a negligible UV reflectance (Fig. 2a) and although *O. scyllarus* does have UV photoreceptors these are as yet not fully characterised (Cronin et al. 1994e). The results from these calculations are given in Fig. 4. However before discussing these, and attempting an answer to the blue cube confusion problem, some clarification of the retinal sensitivities used is needed.

O. scyllarus spectral sensitivities

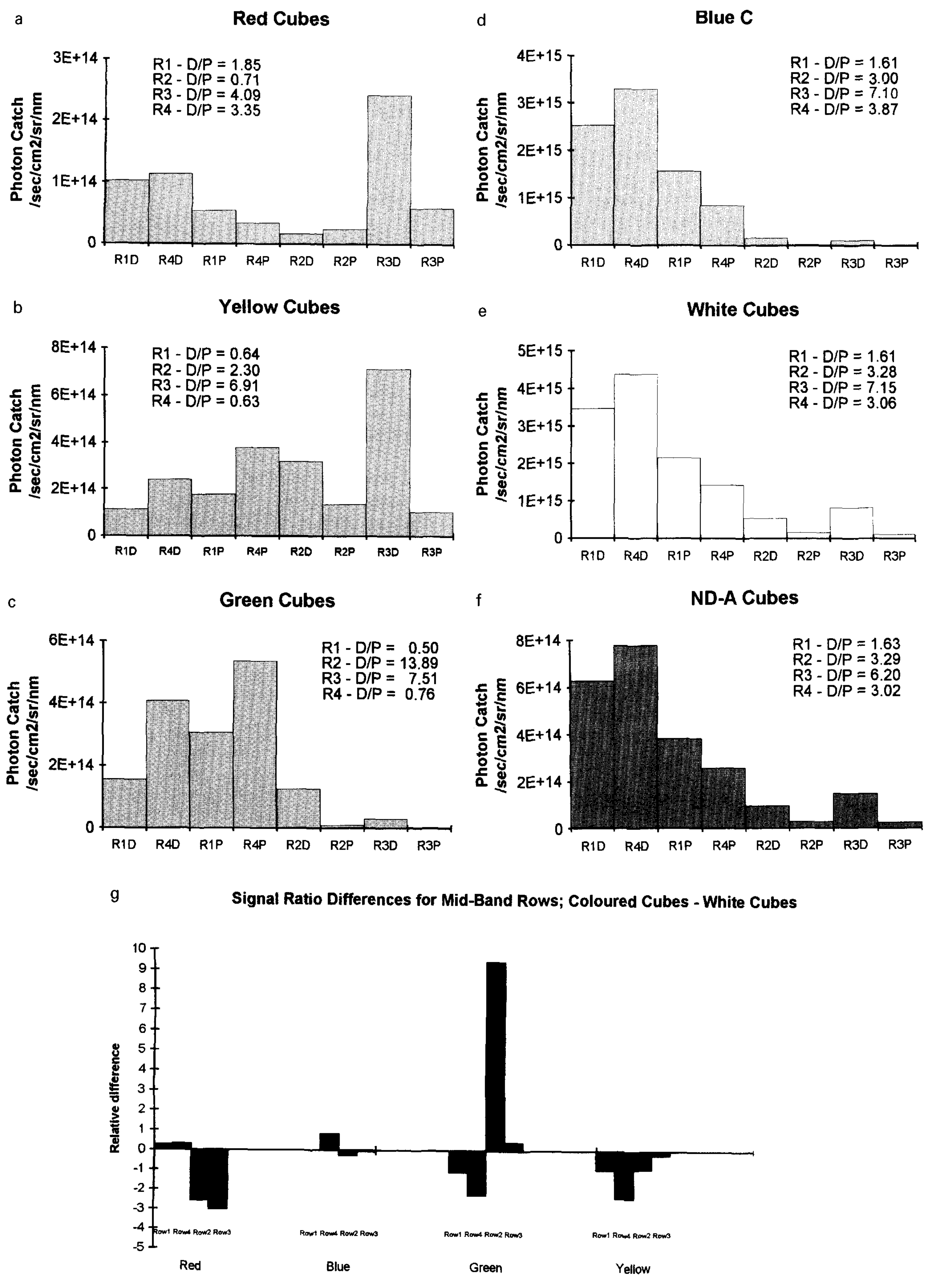
The relative sensitivities of the different mid-band row 1–4 photoreceptors are estimates from microspectrophotometric measurements of axial density, filtering properties and anatomical measures, of the different eye regions (Cronin and Marshall 1989a; Cronin et al. 1994c). The sensitivities of proximally placed photoreceptors are lower due to the filtering by overlying retina. This is particularly so in rows 2 and 3 because of the dense intrarhabdomal filters which overlay both distal and proximal photoreceptor types (Marshall 1988; Cronin et al. 1994b). In rows 1 and 4 the more proximally placed photoreceptors are filtered only by overlying distal photoreceptors and hence their sensitivity is attenuated less.

Spectral sensitivity curves for rows 1 and 4 distal main rhabdom (R1D & R4D, Fig. 2b) are sharpened more on the short wavelength side compared to those presented in Cronin et al. (1994c), as we now believe all mid-band sensitivities are approximately the same shape due to distal filtering. Filtering in these rows is from overlying R8 retinular cells (not considered in Cronin et al. 1994c) and the dioptric apparatus. Where known, the R8 cells of stomatopods contain visual pigment absorbing maximally in the 300–400 region of the spectrum (Cronin et al. 1994e) and would thus act as filters of the short wavelength limbs of the relatively short wavelength R1D and R4D visual pigments. Unpublished electrophysiological evidence from a closely related species indicates UV spectral sensitivities in the R8 cells of rows 1 and 4 and sharp sensitivities in the distal part of the main rhabdom similar to those in Fig. 2b.

The drop in sensitivity which results from the type of sequential filtering seen here indicates that stomatopods are trading sensitivity for spectral coverage (Cronin and Marshall 1989a). This is no problem for tropical reef animals such as *O. scyllarus* due to the bright sunlight they enjoy for much of the day.

Photon catch in the retina

Estimates of the photon catch by each of the eight mid-band row 1–4 receptors as they view the coloured


a
Red Cubes
R1 - D/P = 1.85
R2 - D/P = 0.71
R3 - D/P = 4.09
R4 - D/P = 3.35
Photon Catch /sec/cm2/sr/nm
3E+14
2E+14
1E+14
0
R1D R4D R1P R4P R2D R2P R3D R3P
b
Yellow Cubes
R1 - D/P = 0.64
R2 - D/P = 2.30
R3 - D/P = 6.91
R4 - D/P = 0.63
Photon Catch /sec/cm2/sr/nm
8E+14
6E+14
4E+14
2E+14
0
R1D R4D R1P R4P R2D R2P R3D R3P
c
Green Cubes
R1 - D/P = 0.50
R2 - D/P = 13.89
R3 - D/P = 7.51
R4 - D/P = 0.76
Photon Catch /sec/cm2/sr/nm
6E+14
4E+14
2E+14
0
R1D R4D R1P R4P R2D R2P R3D R3P
d
Blue C
R1 - D/P = 1.61
R2 - D/P = 3.00
R3 - D/P = 7.10
R4 - D/P = 3.87
Photon Catch /sec/cm2/sr/nm
4E+15
3E+15
2E+15
1E+15
0
R1D R4D R1P R4P R2D R2P R3D R3P
e
White Cubes
R1 - D/P = 1.61
R2 - D/P = 3.28
R3 - D/P = 7.15
R4 - D/P = 3.06
Photon Catch /sec/cm2/sr/nm
5E+15
4E+15
3E+15
2E+15
1E+15
0
R1D R4D R1P R4P R2D R2P R3D R3P
f
ND-A Cubes
R1 - D/P = 1.63
R2 - D/P = 3.29
R3 - D/P = 6.20
R4 - D/P = 3.02
Photon Catch /sec/cm2/sr/nm
8E+14
6E+14
4E+14
2E+14
0
R1D R4D R1P R4P R2D R2P R3D R3P
g
Signal Ratio Differences for Mid-Band Rows; Coloured Cubes - White Cubes
Relative difference
10
9
8
7
6
5
4
3
2
1
0
-1
-2
-3
-4
-5
Row1 Row4 Row2 Row3
Row1 Row4 Row2 Row3
Row1 Row4 Row2 Row3
Row1 Row4 Row2 Row3
Red
Blue
Green
Yellow

and neutral grey cubes are plotted in Fig. 4, each cube producing a distinct stimulation profile across the mid-band rows. For red, green and yellow cubes these profiles are quite different from each other and the greys (Fig. 4a, b, c) whereas for the blue and grey neutral density cubes the stimulation profiles are rather similar (Fig. 4d, e, f). The high degree of correlation between blue and grey stimulation profiles suggests why this blue spectrum can't be learned as a colour distinct from greys. This similarity is, at least in part, because the blue spectrum has rather 'shallow sloped' characteristics compared to the other colours (Fig. 2a). It may be that the stomatopod visual system requires more abruptly changing spectra to function properly. Such colours are found on many the coral reef animals such as fish and on stomatopods themselves (Marshall, unpublished data). Before such ecological considerations are discussed further, examination of the number of chromatic channels in the retina gives further insight into the blue cube confusion problem.

Why so many chromatic channels?

By comparison with other animals, the stomatopod colour vision system with eight or more spectral receptor types seems unnecessarily complex. However our present working hypothesis provides a relatively simple explanation for the number of receptors and can explain why the blue cubes were poorly distinguished. We propose that stomatopods employ four separate dichromatic colour channels, one in each of mid-band rows 1 to 4, with inputs from distal and proximal main retinular cells (R1-7). As a result of the narrow spectral sensitivities, each dichromatic channel has a narrow spectral window to analyse, row 1 processing light in the blue region of the spectrum, row 2 yellow, row 3 red and row 4 green (Fig. 2b).

Support for this hypothesis is found from examination of the organisation in the lamina ganglionaris, the first neural integration site beneath the retina. Axons from crustacean R1-7 retinular cells project to the lamina ganglionaris where information from the ommatidium is integrated (Stowe 1977; Sabra and Glantz 1985). Retinal information may be directly projected onto the lamina preserving retinotopicity and therefore spatial information (that is one lamina cartridge receives all 7 axons from one ommatidium – R8 axons generally project through the lamina to the next neural integration site, the medulla externa – see Strausfeld and Nässel 1979). Alternatively the seven axons may project to different lamina cartridges (Nässel 1976).

◄

Fig. 4a–f Relative photon catch for each photoreceptor type viewing different cubes. In each panel the histogram shows the estimated relative photon catch of each tier of the mid-band retina (Rows 1–4). Figures are calculated by multiplying retinal sensitivity curves by cube reflectance's (in Photons/sec/cm^2/sr/nm) and summing the resultant curve area. Responses are plotted in order of tier sensitivity, from short to long wavelengths. With each graph, ratios of distal photoreceptor/proximal photoreceptor photon catch are given for each row (Row1 D/P – row one, Row 2 D/P – row two, etc). **g** Histogram of relative difference in D/P photon catch ratios for each mid-band row looking at each colour, versus grey. Each *bar* is calculated in the following way:

$$\text{e.g. Row 1 red} = \left(\frac{\text{Row 1 D sensitivity} \times \text{Red cube Reflectance}}{\text{Row 1 P sensitivity} \times \text{Red cube Reflectance}}\right) - \left(\frac{\text{Row 1 D sensitivity} \times \text{ND Reflectance}}{\text{Row 1 P sensitivity} \times \text{ND Reflectance}}\right)$$

In mid-band rows 1–4 of *O. scyllarus* all axons from the R1-7 cells project to a single lamina cartridge thus keeping the chromatic content, as well as spatial information of that ommatidium discrete, at least to this level (Marshall and Horwood, unpublished results). This isolation of each row's outputs suggests signal comparison or opponency of some kind between distal and proximal cells within one row (Marshall et al. 1991b). Such two channel opponent processing is believed to occur in many decapod crustaceans between the two sub-populations of retinular cells which are sensitive to perpendicular E-vectors of polarised light (Sabra and Glantz 1985; Marshall et al. 1991a). It is exactly these two populations of retinular cells which, within the spectral window for the row, are sensitive to shorter and longer wavelengths. That is, the putative polarisation opponency system has been swapped for colour. What lies beyond the lamina ganglionaris is not known. There may be some degree of mixing and comparison between channels below the level of the lamina making our suggested 4 dichromatic systems simplistic.

From this anatomical evidence we assume that chromatic opponent signals are based on comparison between receptors from a single row, and can estimate chromatic signal ratios for each row as; distal R1-7 photon catch divided by the proximal R1-7 photon catch. These ratios, (inserts – D/P for each row looking at each cube type – Fig. 4) indicate, at the retinal level, how distinguishable each cube colour is to each mid-band row. On their own, however, they are relatively meaningless as they often yield large numbers simply because of apparent relative sensitivity differences between distal and proximal photoreceptors within one row. The difference between these D/P ratios for one cube compared to another is a better estimate of how different the colours or greys appear to the stomatopod retina. This can be done by comparing the blocks of calculated D/P ratios in Fig. 4. For instance Row 1 D/P values for blue, 'white' and ND-A cubes are 1.61, 1.61 and 1.63 respectively, indicating this row on its own may have difficulty differentiating these cubes.

To make this comparison clearer, Fig. 4g plots these differences for coloured cube values minus a grey cube, in fact the 'white' (e.g. Row 1 looking at red: value = (Row 1 D/P Red) – (Row 1 D/P White)). To all four of our presumed dichromatic channels, it is the blue cubes that look the least different from the greys in this analysis. This may be why the blue of the cubes chosen is indistinguishable from greys to *O. scyllarus*. As there are some blue – grey differences between photoreceptor catch D/P ratios, this hypothesis makes some assumptions. For instance for it to work, there must be a threshold value for colour detection.

'Spectral Windows' and stomatopod colour vision

Two interacting steep sloped spectral sensitivities potentially enable fine colour discrimination within the window of overlap between photoreceptors. For any small change in the spectral content of an object being examined, there may (depending on the colour reflectance profile of the object) be a larger differential change in the output of the two photoreceptors, than if they were shallow sloped. Clearly only a small amount of the spectrum is covered by any one dichromatic system. As a result stomatopods such as *O. scyllarus*, which live where there is a broad spectrum of light available to them, must increase the number of receptor types if they are to use all spectral regions. This potentially explains the large number of spectral receptor types in the stomatopod eye.

Spectral window or 'categorical' systems are known in the fly and may benefit from fine discrimination in specific regions but, as only a small number of spectrally different photoreceptors are involved, they suffer from a loss of spectral resolution elsewhere (Troje 1993). For the stomatopod, with eight interleaved receptor classes spanning much of the visible spectrum, this may not be a problem.

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