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Stomatopod Photoreceptor Spectral Tuning as an Adaptation for Colour Constancy in Water

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Where colour is used in communication absolute judgement of signalling spectra is important, and failures of colour constancy may limit performance. Stomatopod crustaceans have unusual eyes in which the midband contains ten or more classes of photoreceptor. For constancy based on receptor adaptation to a fixed background, elementary theory predicts and we confirm by modelling, that stomatopods' narrow-band receptors outperform more broadly tuned receptors. Similar considerations could account for the small spectral separation of receptors in each midband row. Thus, stomatopods seem to trade-off sensitivity and signal-to-noise ratio for increased colour constancy. © 1997 Elsevier Science Ltd

Colour constancy Visual ecology Spectral tuning Stomatopoda

INTRODUCTION

A valuable principle used to interpret eye design is that early vision is adapted to optimise information capacity for a given investment in neural machinery (Barlow, 1961). An efficient code matches the allocation of channel bandwidth to signal characteristics, and this seems to hold both for the sampling of the optical image and for spatio-temporal filtering at early stages of the visual pathway in both insect and vertebrate eyes (Atick & Redlich, 1990; van Hateren, 1992; Laughlin, 1994). Coding theory predicts how eye design should be optimised given an animal's habitat, the light levels at which it is active and how it moves (Laughlin & Weckström, 1993), but because each bit of pictorial information is accorded equal value it is difficult to infer how specific optical signals are used in behaviour. Here, in contrast, we argue that an appreciation of how signals are used is essential to understanding eye design for colour vision.

Just as spatial vision is concerned with signals that vary in intensity with position, colour vision encodes spectra that vary with wavelength of light, so common principles may apply to spatial coding and to chromatic coding (Barlow, 1982). Optimal codes coding natural spectra can be found, given that phase relations between the spectral frequency components of natural reflectances are random (van Hateren, 1993; Atick *et al.*, 1995). For the 400–700 nm spectral window used by humans, Maloney (1986) found that three principal components, which might be derived from three appropriately tuned photoreceptors, encode over 98% of all the variance in a set of natural spectra measured by Krinov (1953). The advantage from additional receptors is small or negative, because the power of additional signal components encoded is exceeded by receptor noise (van Hateren, 1993). Apart from the number of receptor types, selection may act on the spectral width of the receptors—which is analogous to the spatial aperture of a single receptor. Barlow (1982) observed that given a sampling density of three receptors in the 400–700 nm spectral window rhodopsin tuning curves are narrower than expected by sampling theory, raising the possibility that colour vision is corrupted by aliased chromatic signals. Mammalian eyes have comparatively little intraocular filtering and the spectral width of receptors is at roughly the value for rhodopsin, but in birds and reptiles oil droplets narrow the spectral tuning of individual cones (Partridge, 1989; Maier & Bowmaker, 1993), an arrangement which, according to Barlow's argument, seems maladaptive as it would increase spectral aliasing.

Aquatic spectra and colour vision

Moving from land to the brightly lit shallows of a coral reef does not seem likely to impose radically different demands on vision (see also Lythgoe & Partridge, 1991). But here we find two animals whose very different eyes seem to belie the notion that general principles provided by coding theory can be used to explain their design. These are the cuttlefish, *Sepia*, and the stomatopod, *Odontodactylus*, both of which are territorial diurnal hunters that wait on the bottom to ambush passing prey.

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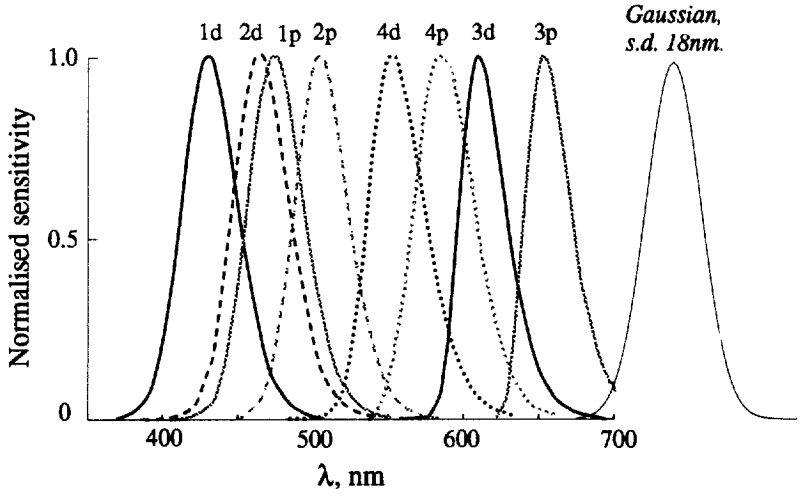

FIGURE 1. Normalised spectral sensitivities of principal receptors in the midband of *Odontodactylus scyllarus*. The label on each curve refers to the midband row in which the receptor resides, and whether it is the distal (d) or the proximal (p) cell. Each receptor contains a different type of visual pigment, but spectral sensitivity is restricted to comparatively long wavelengths compared with the pigment peak. Filtering of short wavelengths is by photostable carotenoid filters and, for proximal receptors, the distal receptors (Marshall, 1988; Cronin & Marshall, 1989; Cronin *et al.*, 1994). Note that row 3 contains a pair of receptors with peaks over 600 nm, but whose rhodopsin peak sensitivities are below 580 nm. Intraocular filtering reduces the sensitivity of the row 3 654 nm receptors to below 2% of that for receptors containing unfiltered photopigment.

Sepia, the cuttlefish, is a master of camouflage, altering coloration and texture of its body pattern to match the surroundings. Chromophore cells set in a white skin are under neural control, and are of three spectral classes, containing black, yellow or red pigment (Hanlon & Messenger, 1988). Camouflage and camouflage breaking are obvious tasks for colour vision (Cott, 1949; Morgan *et al.*, 1992), but *Sepia*, like most cephalopods, is a monochromat with a receptor sensitivity maximum around 500 nm (Marshall & Messenger, 1996). *Sepia's* camouflage works because the spectra of its chromophores are a good match to those of the sea floor. A cephalopod's camouflage might be better if it had colour vision, but for a human observer mismatches are not a major failing—lightness and texture are critical, the spectrum can be guessed.

Stomatopods, on the other hand, sample the spectrum more finely than any other animal. In these crustaceans a specialised midband of up to six rows of large facets runs about the equator of their compound eyes (Marshall, 1988). Two of these rows are probably used for polarisation vision, with the remainder specialised for chromatic coding (Cronin & Marshall, 1989; Marshall *et al.*, 1991a, b). The ommatidia in a given midband row contain three spectral types of receptor: a small cell sensitive to UV, and two principal receptors. In shallow water species the principal receptors' sensitivity maxima range from about 420 to 660 nm (Fig. 1; Table 1; Cronin *et al.*, 1994), with those in a given midband row being separated by about 40 nm. Intraocular filtering gives narrow spectral sensitivities, and optical measurements of photo-and screening pigments (Cronin *et al.*, 1994) predict that in the species *Odontodactylus scyllarus* the receptors' sensitivity functions approximate gaussians with standard deviations close to 18 nm. (Such estimates of spectral sensitivities have been confirmed by intracellular recording in *Gonodactylus oerstedii*, a close relative of *Odontodactylus*; unpublished observations.) There may be a different UV opsin for each midband row, but as these receptors are probably less sensitive, and are

TABLE 1.

Row	Distal peak	Width (s)	Relative quantal efficiency	Proximal peak	Width (s)	Relative quantal efficiency	Separation
1	428	18	87	475	18	50	47
2	465	18	100	505	18	38	40
3	609	14	15	654	14	2	45
4	554	19	17	584	19	5	30

All measurements in nm.

Spectral sensitivity peaks, for principal photoreceptors in midband rows 1 to 4 in *Odontodactylus scyllarus*. For each midband row we give the wavelength of the peak and approximate standard deviation of the distal and proximal receptors spectral sensitivities, and the separation of the two peaks. Relative sensitivities are normalised to the value for the row 2 distal cell. Estimates of the width of the sensitivity curve are given as standard deviation of gaussian fitted by eye to curves derived from optical measurements (Marshall, 1988; Cronin & Marshall, 1989; Cronin *et al.*, 1994).

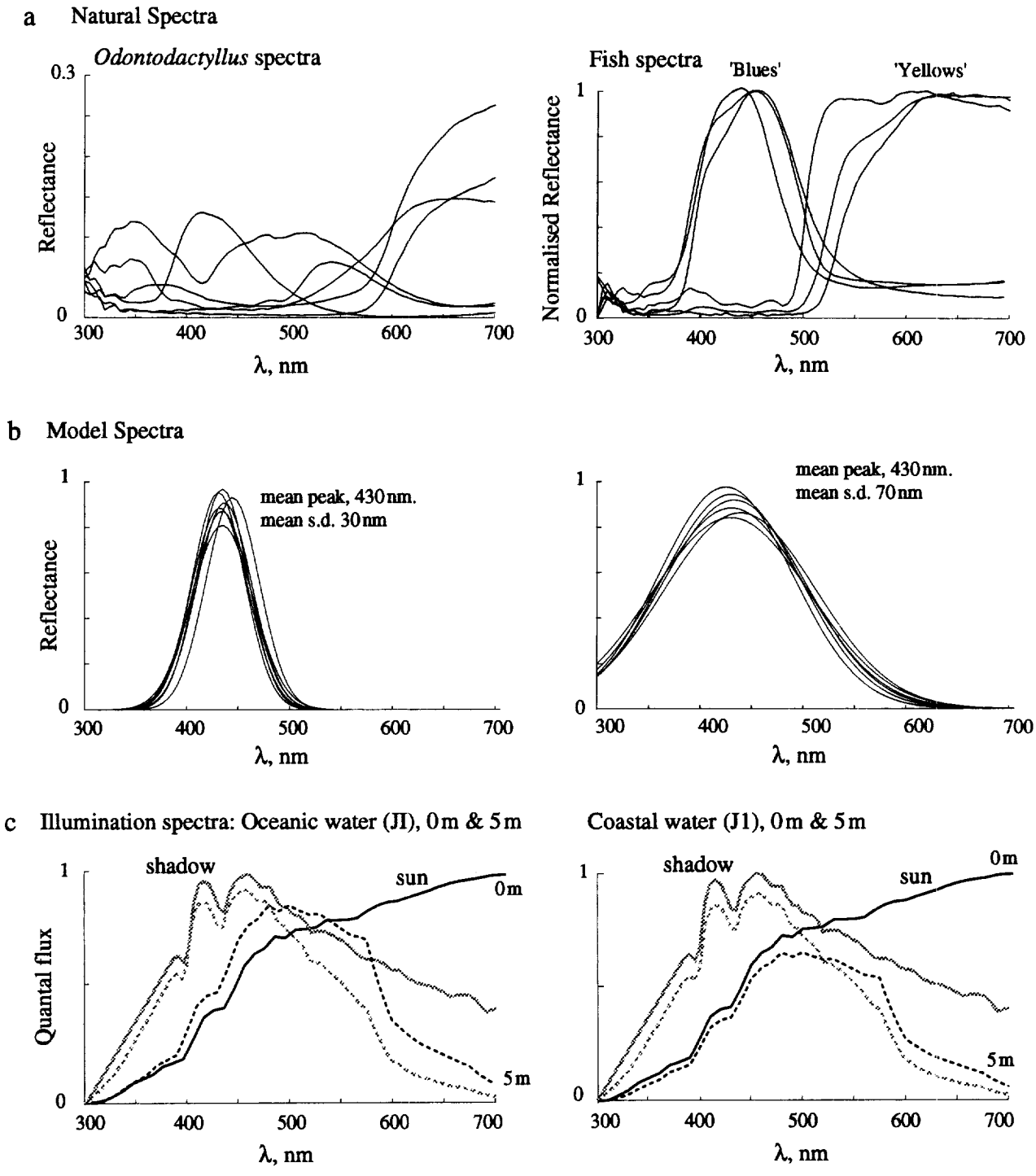

FIGURE 2. Spectra of natural stimuli (a), model stimuli (b), and of illumination in water (c). (a) Left: reflectance spectra for coloured patches of the body of a single individual *Odontodactylus scyllarus*. Right: examples of two commonly encountered spectra on the bodies of coral reef fish taken from a range of species. Measurements made by "Sub-spec", an underwater spectroradiometer (Marshall *et al.*, 1996). The blues are well matched to the peak of down-welling light in clear water (Jerlov, 1976) and are approximately gaussian. The plateau in "yellow" and "red" reflectances above 600 nm is in a part of the spectrum where absorption by water is high (c), so that at a depth of around 5 m, spectra reflected from these latter surfaces have, like the blues, a roughly gaussian form. The prevalence of long wave reflecting pigments in stomatopods may account for the presence of the long wave receptors with peaks at 609 and 654 nm in row 3 of the *Odontodactylus* midband. (b) Examples of model target spectra. These are populations of gaussians whose mean peak values range from 420 to 630 nm, and with mean standard deviations of 30 nm (left) or 70 nm (right). Areas under the curves are normalised as are the r.m.s. differences between the members of the population. Here, for the sake of clarity, the variability of the model spectra is double that used for calculations. (c) Illumination spectra at the surface and at a depth of 5m in clear oceanic water (Jerlov type 1, left) and clear coastal water (Jerlov type I, right), either in direct sunlight (black lines) or in shadow (grey lines; Jerlov, 1976).

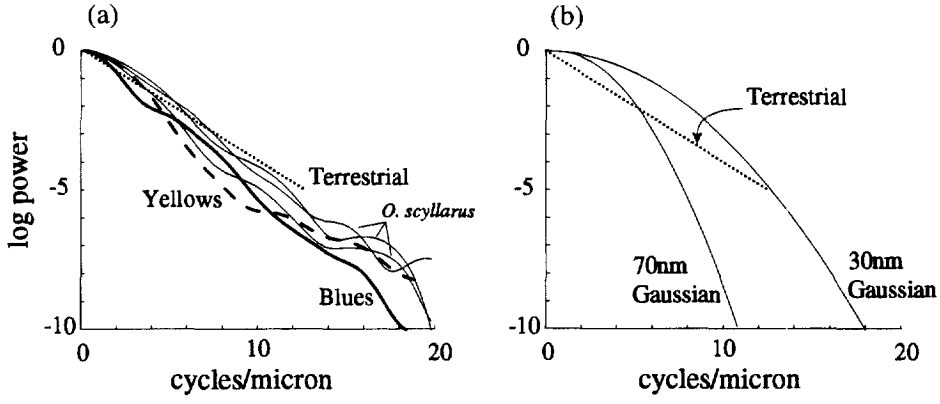

FIGURE 3. Spectral power distributions for natural spectra (a), and model spectra (b) compared with the distributions for terrestrial spectra (..... ; van Hateren, 1993, Fig. 1). Distributions for marine spectra of interest here do not differ substantially from those on land (see Maloney, 1986; van Hateren, 1993). (a) Power distributions for the three *Odontodactylus* colours (_____) with most power at high spectral frequencies [Fig. 2(a), left] and average spectral power distributions 12 fish blues (_____) and ten fish yellows [- - -, e.g. Figure 2(a), right]. (b) Power distributions for gaussian spectra used in the model [Fig. 2(b)]. Natural spectra (a) fall between the values for 30 and 70 nm gaussians.

certainly less well characterised, we do not consider them further.

Why do stomatopods have many narrow-band photoreceptors? Sampling theory predicts that the number of receptor types and their tuning curves will match the bandwidth of the spectral power distribution. Hence, we might infer that stomatopods live in a world of spectra that change more sharply with wavelength than do those on land, where trichromacy will suffice. The colours of coral reef animals are indeed striking, but the bandwidths of chromatic information in spectra from brightly coloured animals that we have measured are comparable with those on land [Fig. 2(a), Fig. 3; van Hateren, 1993], and it is unlikely that an eight-dimensional colour space is necessary for most tasks underwater; not even to break cuttlefish camouflage! In any case stomatopods hide in crevices and ambush prey, which probably give themselves away by moving. A more likely explanation is that stomatopods communicate by displaying brightly coloured insignia [Fig. 2(a); Caldwell & Dingle, 1976; Hazlett, 1979]. For example, the coloration of meral spots on the raptorial limbs varies according to strength or aggression level (both within and between species), and as fights can be fatal, accurate judgement is a matter of life and death.

Identification of communication colours presents a different problem from breaking camouflage. The key task is not detection of these conspicuous colours, but rather to make reliable responses to aspects of spectra that convey information about their bearer. This requires absolute judgement of reflectance spectra. Not only must the eye permit fine discrimination, but judgements must be robust under changing viewing conditions. In other words, colour constancy is important.

Achieving colour constancy is probably more difficult underwater than on land because light absorption by pure water is spectrally selective, and is modified by suspended and dissolved material [Fig. 2(c); Jerlov, 1976]. For a shallow water animal quite small changes in depth with changing tides, passing swell and its own movements have marked affects on illumination spectra. In addition, water colour varies considerably over short periods, especially near the coast, while viewing distance and direction also affect the spectrum reaching the eye.

Could the demands of colour constancy have influenced the evolution of stomatopods' eyes, leading to a different eye design from the ideal for vision under fixed illumination? To answer this question we assume that colour constancy is attributable to adaptation of photoreceptors independently to a uniform, or average, background. (Methods, equations (1, 2); von Kries, 1905 cited in Wyszecki & Stiles, 1982, p. 430; Worthey & Brill, 1986). Receptor adaptation gives a normalisation, or von Kries transformation, which presumably precedes any "special purpose" constancy mechanisms. On land this transformation gives effective constancy, and can account for some aspects of human colour perception (Dannemiller, 1993; Foster & Nascimento, 1994). Nonetheless, where failures occur (e.g. Osorio, 1997) narrow-band receptor sensitivities are advantageous (Worthey & Brill, 1986; Foster & Nascimento, 1994). For the limiting case of a monochromatic receptor viewing a target on a background the contrast signal is simply the ratio of target and background reflectances at that wavelength, and is independent of the illuminant [equation (2)]. Consequently, the chromatic (i.e., difference) signal encoded by a pair of monochromatic receptors is itself independent of illumination, giving perfect colour constancy.

To try and understand the function of the stomatopod eye, we assume that the animal needs to identify members of a population of spectra [Fig. 2(b)]. A simple model of chromatic coding predicts the reliability of chromatic signals generated by pairs of receptors, either narrowly tuned as in *Odontodactylus* midband, or more broadly tuned like human red and green cones. The model estimates relative quantal catches to a given target and an achromatic background to which the receptors are

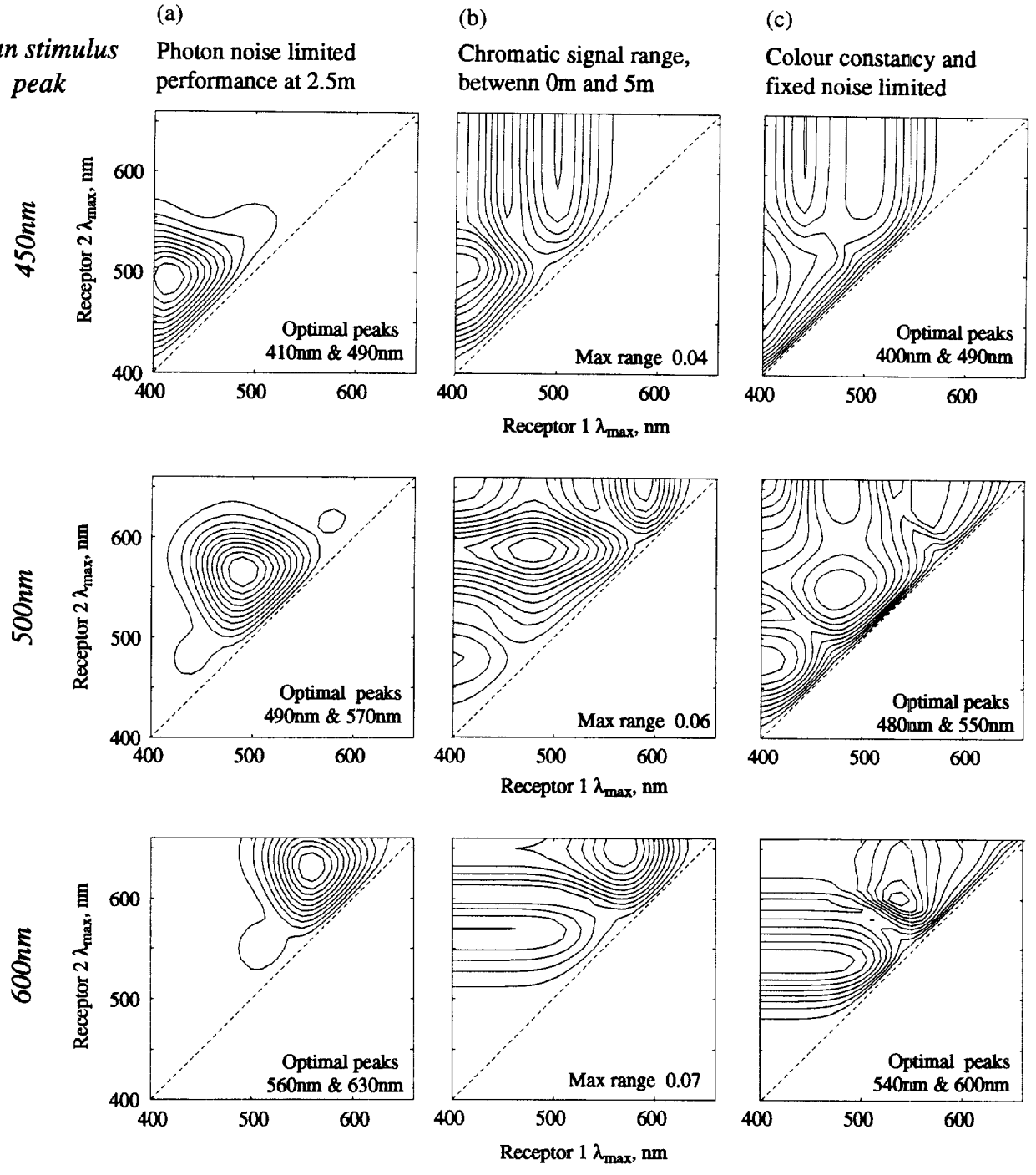

FIGURE 4. Examples of model calculations for populations of targets with peaks at 450, 525 and 600 nm and mean SD of 30 nm [Fig. 2(b)] in oceanic water (JI) at depths of zero to 5 m [Fig. 2(c)]. Chromatic signals are for targets viewed on an achromatic adapting background, and are derived from all possible pairs of receptors with peaks ranging from 400 to 660 nm. Contours are equally spaced. (a) Discriminability of members of target populations by chromatic signals, where performance is limited by photon noise. Optimal performance is for chromatic signals derived from receptors whose peaks lie either side of the mean target peak. Illumination is direct sunlight at a depth of 2.5 m. (b) Average ranges of chromatic signals for target populations under varying illumination [Fig. 2(c)] allowing receptor adaptation to an achromatic background [equation (3) and equation (4)]. This is a measure of failures of colour constancy. (c) Discriminability of members of target populations by chromatic signals derived from pairs of receptors. Failures of colour constancy shown in the centre column are added to a fixed discrimination threshold of 0.02 [equation (6)].

fully adapted [equations (1) and (2)]. Performance of chromatic signals [equation (3)] derived from pairs of receptors with peaks ranging from 400 to 660 nm is calculated either where photon noise is limiting under fixed illumination [equations (4, 5)], or, alternatively, for varying illumination with a fixed discrimination threshold in the chromatic channel [equation (6)]. These models give the best pair of receptors for identifying the

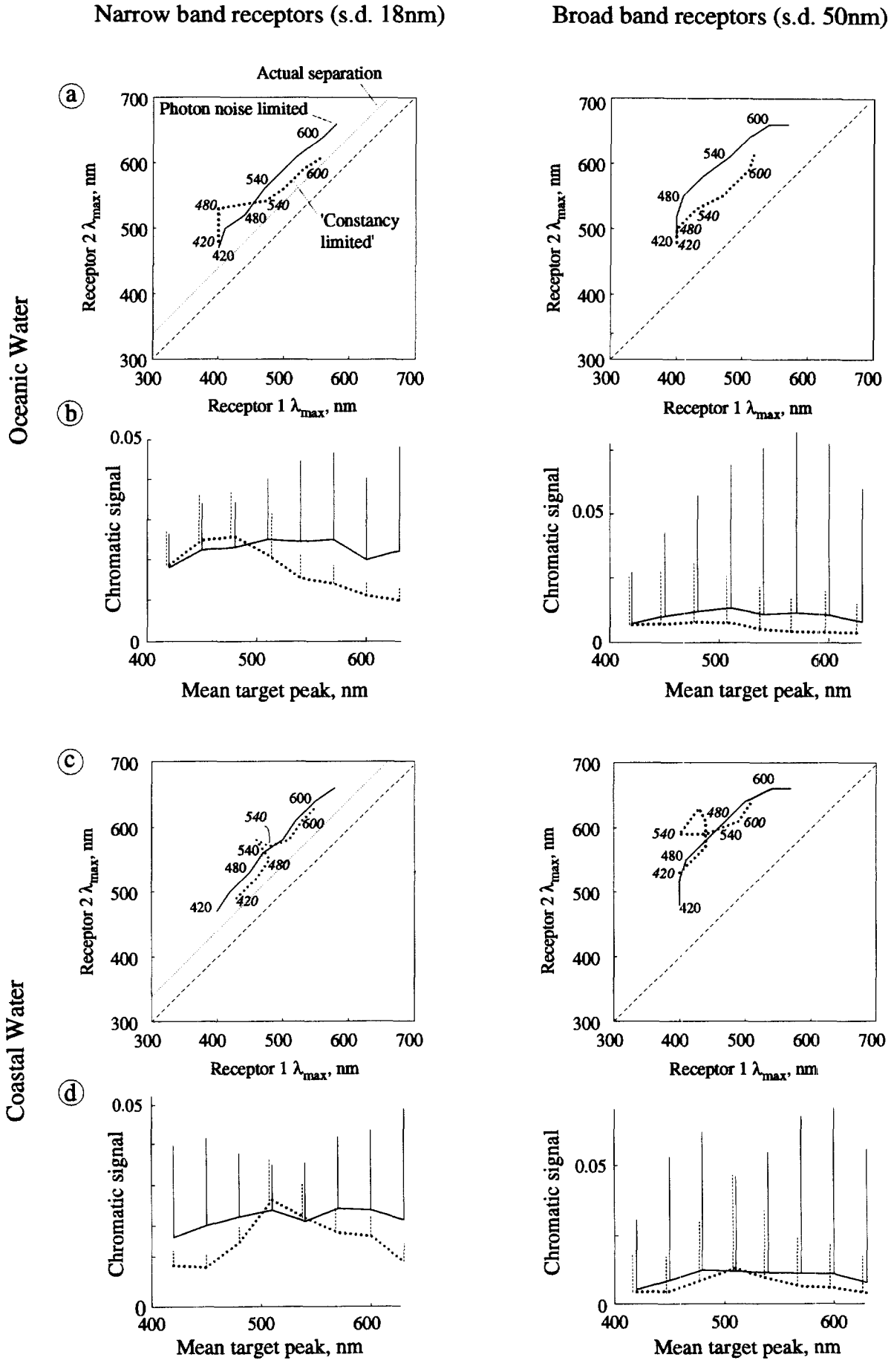

FIGURE 5—*Legend opposite.*

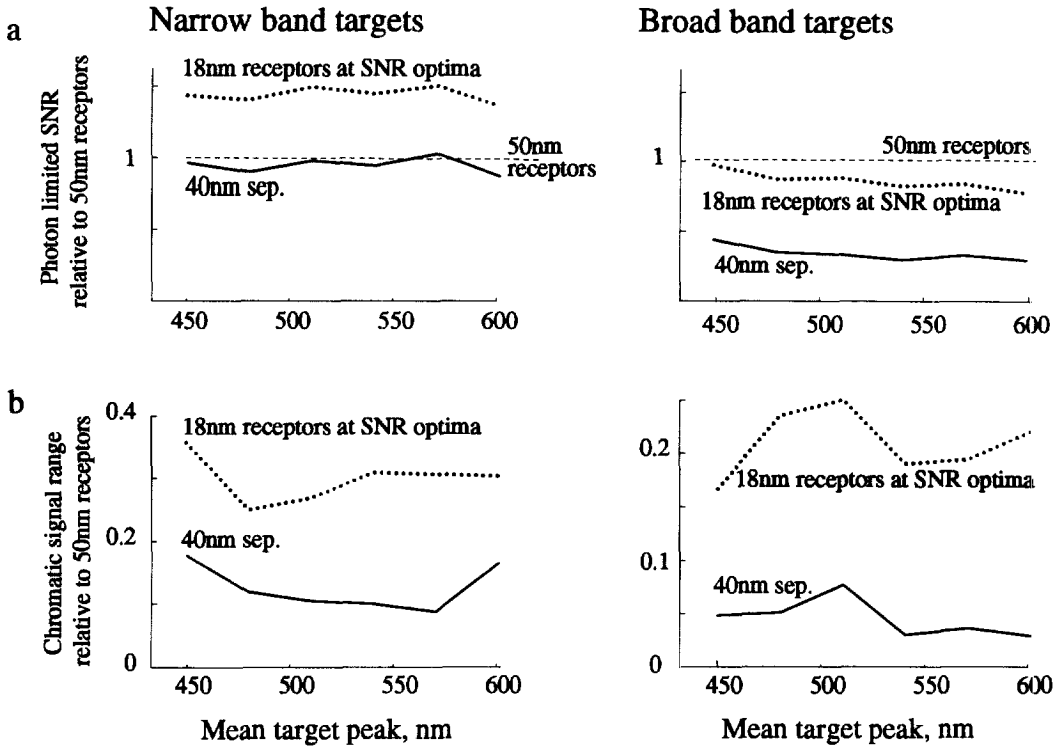

FIGURE 6. Comparison of the performance of narrow-band receptors (SD 18 nm) relative to those for 50 nm receptors for discrimination either under photon-noise-limited conditions (a) or where failures of von Kries constancy limit performance (b). Chromatic signals are either for photoreceptor pairs optimised for photon-noise-limited performance under a fixed illuminant either without restriction on the spectral separation of the inputs [Fig. 5(a), ...), or with a fixed separation of 40 nm (_____). (a) Photon noise limited performance. Discriminability of the narrow-band targets is 1.5-times better with narrow-band receptors at optimum separation than with broad-band receptors. (b) Chromatic signal range, [Fig. 4(b), Fig. 5(b, d)], a measure of failure of colour constancy for chromatic signals (low values meaning better colour constancy). As in (a), chromatic signal ranges derived from 18 nm receptors are compared with those for signals derived from 50 nm receptors. Narrow-band receptors convey a substantial advantage over broad-band, where failures of von Kries constancy limit performance. With receptor separation set to 40 nm this advantage is especially pronounced, rising to around 20-times the value for 50 nm receptors.

members of a target population under these respective conditions (Fig. 4, Fig. 5), and show qualitatively how changing spectral tuning and separation of receptor inputs to a chromatic signal may influence performance (Fig. 5, Fig. 6).

MODEL

Receptors with peak sensitivities ranging from 400 to 660 nm at 10 nm intervals are modelled as gaussians, with maxima normalised to unity and standard deviations (SDs) of either 18 nm or 50 nm. For a receptor type K viewing a target, t, the number of quanta captured $q_{k(t)}$ is given by:

$$q_{k(t)} = \int I(\lambda) \cdot S(\lambda) \cdot R_k(\lambda) d\lambda, \qquad (1)$$

where $I(\lambda)$, is number of incident photons wavelength per

(FIGURE 5 opposite)

FIGURE 5. (a) Loci of optimal receptor pairs contributing to dichromatic signals for discrimination of members of target populations with mean peaks ranging from 420 to 630 nm [SD 30 nm, Fig. 2(b)], in clear oceanic water [Fig. 2(c), left]. Simulations consider either photon noise limited performance under a fixed illuminant [_____; e.g. Figure 4(a)], or taking account of failure of colour constancy under variable illumination with a fixed chromatic signal threshold of 0.02 [.....; e.g. Figure 4(c)]. Models are for dichromatic signals derived from narrow-band (SD 18 nm; left) or for broad-band receptors (SD 50 nm; right) whose peaks vary from 400 to 660 nm. Mean spectral peaks of target populations are indicated (at 60 nm intervals), in roman type where performance is photon noise performance, and in italics where colour constancy is limited with a fixed threshold of 0.02. Where failures of colour constancy limit performance, comparatively small receptor separations are generally favoured. The optimal separation predicted by the model can be compared with the line parallel to the leading diagonal which gives the approximate separation of principal receptors in stomatopod midband rows (Table 1, see also Fig. 6). (b) Chromatic signals vs mean target peak in clear oceanic water (Jerlov type I). Either for signals optimised for SNR at 2.5 m (_____), or for signals optimised for colour constancy as in Fig. 5(a) (.....). Vertical lines give half the signal range under variable illumination for each condition. Chromatic signals are for narrow-band receptors (left) and broad-band receptors (right). (c, d) As (a, b) but for clear coastal water (Jerlov type 1).

unit time, $S(\lambda)$ the surface reflectance and $R_k(\lambda)$ the spectral sensitivity of K at wavelength λ.

Receptor responses are modelled by a Lipetz (1971) function which approximates the intensity response function of light-adapted stomatopod midband receptors (Matic & Laughlin, 1981; unpublished observations). Where quantal catches of a receptor class K to the adapting background and target are $q_{k(b)}$ and $q_{k(t)}$, respectively, the adapted receptor response to the target, r_k, is given by:

$$r_{k(t)} = \left[\left(R \cdot q_{k(t)}\right)^n\right] / \left[\left(R \cdot q_{k(t)}\right)^n + 1\right], \qquad (2)$$

with $R = 1/q_{k(b)}$ and the exponent, n, unity. This gives a range of zero to one with a response of 0.5 to the background intensity. The adaptation to a mean intensity giving a von Kries type mechanism for colour constancy is implemented by this model of the receptor response.

The *KL* chromatic signal derived from a pair of receptors, K and L, is defined as:

$$KL = r_{k(t)} - r_{l(t)}. \qquad (3)$$

Given a set of such dichromatic signals derived from all possible combinations of photoreceptors we can compare their performance for identification of reflectance spectra drawn from a population of target spectra [e.g. Figure 2(a, b)], either under fixed or under variable illumination.

Fixed illumination

Under fixed illumination (e.g. constant depth) the discriminability of a population of targets, $t_{1:n}$, by their *KL* chromatic signals is proportional to:

$$\frac{\sigma(KL_t)}{N}, \qquad (4)$$

where N is the mean noise in the chromatic signals.

If performance is photon-noise-limited the relative signal-to-noise ratio (SNR) in a set of chromatic channels can be predicted. Photon capture is a Poisson process so that the variance in quantal capture by a receptor per unit time is equal to the mean. The photon noise limit to contrast discrimination in the response of a single receptor, K, is proportional to the ratio of mean to standard deviation, $1/\sqrt{q_{k(t)}}$, so that the additive noise, N, in a *KL* dichromatic signal to a target, t, is given by:

$$N \propto \sqrt{\frac{1}{q_{k(t)}} + \frac{1}{q_{l(t)}}}. \qquad (5)$$

Variable illumination

The model assumes that colour constancy relies on adaptation of the receptors to a background [equation (2)]. Failures of constancy occur where shifts in the response to a given target add uncertainty to the chromatic signal. Our measure of this uncertainty, U, is the mean of the *maximum* shift in *KL* for each target in the population under the range of illuminants used [Fig. 2(c)].

To compare the performance of chromatic signals under variable illumination [Fig. 4(c), Fig. 5(a, c)] it is necessary to take account of other sources of uncertainty (i.e., noise) in the signal. In this case the chromatic signal threshold, T, is assumed to be independent of illumination intensity (i.e., the contrast threshold is constant); for the calculations shown $T = 0.02$. A measure of the utility of the *KL* chromatic signal for distinguishing a population of target spectra, $t_{1:n}$, under variable illumination is then:

$$\frac{\sigma(KL_t)}{T + U}, \qquad (6)$$

where U is the uncertainty in the signal due to failure of colour constancy.

Illumination and target spectra

To cover the spectral range used by the principal midband receptors in the stomatopod eye a series of simulations were run for populations of closely similar spectra, with mean peaks set at 30 nm intervals between 420 and 630 nm (Fig. 5, Fig. 6). For each simulation a population of 100 gaussian spectra was generated with mean standard deviations of either 30 or 70 nm [Fig. 2(b)]. Within a population, both peaks and standard deviations were normally distributed. The root mean square (rms) values of the differences between spectra in target populations were normalised so that for ideal detectors broad and narrow-band targets were equally discriminable. The two classes of model spectra were chosen because the spectral power distribution of the 30 nm gaussian is somewhat broader, while that of the 70 nm gaussian somewhat narrower than the distributions of naturally occurring spectra [Fig. 2(a, b), Fig. 3; van Hateren, 1993]. Consequently, model calculations (Fig. 5, Fig. 6) for these two classes of spectra roughly bracket those expected for natural colours.

The model considers targets viewed against a uniform background from a negligible distance. Illumination at the water surface is either direct sunlight or blue sky [i.e., the target is in shadow; Fig. 2(c)], and receptor responses calculated for depths of zero to 5 m in a uniform column of Jerlov's (Jerlov, 1976) type I (oceanic) or type 1 (coastal) water. The fixed illumination condition is for direct sunlight at the midpoint in this depth range. For the variable illumination condition, performance of chromatic signals is disregarded where the photon-limited SNR falls below a threshold fraction (0.1) of that in the best signal for a given target population.

RESULTS

Stomatopods have eight types of principal midband receptors giving 28 possible dichromatic signals, although in practice comparisons may be between pairs of receptors within in a midband row (Fig. 1; Marshall *et al.*, 1991b, 1996). To investigate why such an unusual eye has evolved, the utility of chromatic signals for discrimination of targets is modelled under two conditions, either for fixed illumination where photon noise is limiting [Fig. 4(a)], or under variable illumination, where

failures of a von Kries type constancy mechanism [Fig. 4(b)] are added to a fixed chromatic threshold of 0.02 [equation (6); Fig. 4(c)].

Discrimination thresholds under fixed illumination

Bearing in mind that spectral power distributions of 30 and 70 nm gaussians used to model targets roughly bracket the range of natural colours on stomatopods (Fig. 3) we can compare the performance of chromatic signals derived from narrow (18 nm; resembling stomatopod midband) and broad (50 nm; resembling unfiltered rhodopsin) receptors for discrimination of populations of model targets under fixed illumination. For narrow-band targets (SD 30 nm) viewed by 18 nm receptors target discriminability is optimised when receptor inputs to the chromatic channels are separated by about 110 nm, with peaks lying either side of the mean target peak [Fig. 5(a, c)]. The optimal peak separation for 50 nm receptors is about 200 nm. The modelled discriminability of narrow-band targets is about 1.5-times greater for 18 nm than for 50 nm receptors [Fig. 6(a)], but in reality the advantage of narrow-band receptors will be reduced because intraocular filters reduce peak sensitivity (Table 1). Unsurprisingly, for broad-band targets (SD 70 nm) 18 nm receptors convey no advantage over 50 nm receptors [Fig. 6(a)].

Variable viewing conditions

The model shows how the need to limit failures of colour constancy may influence receptor and chromatic signal design. Consider narrow-band targets (mean SD 30 nm) in coastal water [Jerlov type 1; Fig. 2(b, c)] at depths ranging from zero to 5 m, and with blue sky or sunlight as the illuminant. Where receptors contain unfiltered visual pigment (SD 50 nm) and chromatic channels are optimised for discrimination under a fixed illuminant, chromatic contrast signals for a fixed target under variable illumination vary by 0.07 to 0.25, depending on the spectral peak of the target. Absolute values of these ranges will depend upon the specific details of the animal's behaviour and habitat, but the range of illumination modelled is not unrealistically large. It is evident, therefore, that failure of colour constancy may degrade communication signals in shallow water.

Consistent with theoretical prediction (Worthey & Brill, 1986) the model shows that narrow-band receptors (SD 18 nm; Fig. 1) optimised for signal discrimination under variable illumination and assuming a fixed chromatic signal threshold of 0.02 [equations (3, 6); Fig. 5(b, d)] reduce the failures of a constancy by about three times [Fig. 6(b)]. Constancy improves further if separation of receptor peaks is reduced. For receptor separations limited to 40 nm, roughly that in a stomatopod midband row (Fig. 1; Table 1) the constancy failure is around one-twentieth of that for unfiltered rhodopsin (Figs 4–6).

DISCUSSION

To try and understand the design of the stomatopod compound eye midband (Fig. 1) we have assumed that the function of their colour vision is to make precise judgements about spectra used in intraspecific communication. We assume also that judgements are based on chromatic signals derived from pairs of photoreceptors (Marshall *et al.*, 1996). It could be that one type of behaviour is influenced by the outputs of specific midband row to a specific colour; for example, whether to be dominant or submissive. There is no direct evidence for this type of colour vision in stomatopods, but comparable wavelength specific behaviours are well known in butterflies, for example (Scherer & Kolb, 1987).

What factors could have led to the evolution of chromatic channels driven by narrow-band receptors with small spectral separations? One possibility is that the chromatic signals they encode maximise the discriminability of spectra, where performance is limited by receptor noise (Osorio & Vorobyev, 1996). However, it is implausible that their communication spectra contain sufficient spectral detail to account for the number or the 18 nm gaussian tuning of *Odontodactylus* receptors (see Introduction). Moreover, intraocular filtering reduces peak sensitivity as well as the spectral width of receptors (Fig. 1; Table 1; Cronin *et al.*, 1994) and in consequence the performance of narrowly tuned receptors under photon-noise-limited conditions will, in reality, be lower than that estimated here (Fig. 6; Table 1).

Apart from receptor noise, failures of constancy under variable illumination may limit the reliability of colour vision [Fig. 2(c)]. Where constancy is based on a von Kries transformation (Wyszecki & Stiles, 1982), unfiltered visual pigments—approximated here as gaussian spectral sensitivities with SD of 50 nm—suffer from chromatic distortion, which under the range of illuminants modelled are equivalent to chromatic contrast signals of 0.07–0.25 depending on the target population [Fig. 2(c), Fig. 4, Fig. 5(b, d)]. Stomatopod eyes will suffer a substantially, perhaps 20-fold lower distortion than this, because of the narrow spectral tuning of their receptors and (if inputs to a chromatic channel are from a single midband row) the small separation of receptor inputs to chromatic mechanisms [Fig. 6(b)]. Because reducing receptor separation worsens the photon-limited SNR [Table 1; Fig. 6(a, b)], the small separation of receptors in each stomatopod midband row as well as their narrow tuning may reflect a trade-off for sensitivity against constancy.

An alternative explanation for the occurrence of narrow-band-receptors also based on the need to achieve colour constancy, but not assuming a von Kries transformation may also be relevant. Barlow (1982) noted that for humans the cone receptors' spectral curves are narrower than predicted by sampling theory (see Introduction). To account for this anomaly, Maloney (1986) pointed out that receptors of comparatively narrow-bandwidth are again advantageous for a mechan-

ism of colour constancy which (unlike a von Kries transformation) requires the spectra of illuminants and surface spectra to be reconstructed independently. The relevance of this type of constancy model to stomatopods is unclear, but the small UV receptors in each midband row would be suited to an estimate of the illumination spectrum independent of the chromatic signal derived from the two principal receptors (Maloney, 1986).

Comparisons with other eyes

Stomatopod midbands are an extreme of eye design, but do similar principles apply elsewhere? The difference between stomatopods and the eyes of vertebrates does not simply reflect invertebrates' stereotyped behaviours and small brains. Honeybees and other hymenopteran insects, for example, nearly all have three spectral receptor types with peaks around 340, 430 and 540 nm, and rhodopsin tuning is not greatly modified by intraocular filtering (Peitsch *et al.*, 1992). Honeybees are chromatic generalists who visit all kinds of flower, but their receptor sensitivities do not differ from bees that visit a few species, or from predatory wasps. Most likely, hymenopteran trichromacy evolved before flower visiting (Chittka & Menzel, 1992), and conforms rather well to the principle that early stages of vision are evolved to encode natural stimuli economically (Barlow, 1982; Buchsbaum & Gottschalk, 1983; Chittka *et al.*, 1993; van Hateren, 1993).

Other eyes seem to fall between the stomatopod and the hymenopteran models. For example, in trichromat primates the small spectral separation of the red and green cone peaks limits failures of (von Kries) colour constancy which may degrade judgement of fruit ripeness (Osorio, 1997; Vorobyev and Osorio, in preparation). An more interesting comparison with stomatopods is in the role of oil droplets in vertebrates, especially birds (Partridge, 1989). The passerine *Leiothrix* has four receptor pigments in two types of cone (Maier & Bowmaker, 1993). Double cones have a rhodopsin with peak sensitivity peak at 568 nm, and a short wavelength oil droplet that cuts off light only below 420 nm, perhaps to prevent UV photodamage. However. on single cones, oil droplets cut closer to the receptor sensitivity maxima, especially in the two longer wavelength cones. In consequence, *Leiothrix's* four single cones types have comparatively narrow spectral tuning. From the stomatopod perspective, the unfiltered double cones may be analogues to the dorsal and ventral eye regions of the compound eye, where one principal spectral class of receptor is used for most visual tasks, while the single cones resemble the midband rows specialised for colour. Birds use colour in communication and where natural illumination is varied, such as in forests, they display in specific illumination (Endler & Thery, 1996). Such behaviour is perhaps indicative of the importance of accurate judgement in behaviour such as mate choice, and the pressure to maintain constancy will favour the evolution of narrow-band spectral tuning of single cone receptors.

Conclusion

The need to use colour vision for object identification could lead to a different eye design from that predicted by conventional information theoretic criteria (Barlow, 1982). In particular, narrow spectral tuning of receptors and small separation of peaks in a midband row of the stomatopod eye may reflect a trade-off between the demands of colour constancy and signal-to-noise ratio. Even for trichromats, the additional signal variance encoded by adding a photoreceptor class to a dichromatic eye is small in relation to receptor noise (Maloney, 1986; van Hateren, 1993), and as *Sepia* demonstrates, camouflage can be excellent, even in a monochromatic animal. This is because most natural spectra vary smoothly, and fall into a small range of types (Maloney, 1986; Osorio & Bossomaier, 1992). Perhaps then to understand spectral tuning in photoreceptors it is necessary to take account of the uses of colour, as well as spectral image statistics (Osorio & Vorobyev, 1997).

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