

Strategies for retinal design in arthropod eyes of low F-number

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Summary. The superposition eyes and simple eyes of many arthropods have apertures (A) with a diameter bigger than, or about the same size as, the focal length of the eye (f). That is, these eyes have low F-numbers (f/A). Many of the light rays focussed onto a photoreceptor will not be trapped by total internal reflection in the photoreceptor and will therefore pass through and be absorbed in photoreceptors other than that for which the light was intended. This spread of light in the retina leads to a broadening of the angular-sensitivity function and a consequent degrading of the image at the retinal level. A number of solutions to this problem are found in nature, with the most effective that of isolating the photoreceptors with a sheath of either light-absorbing pigment or reflecting tapetum. A ray-tracing model was used to assess the relative merits of the tapetal and pigment sheath designs in low F-number superposition eyes, and also to investigate the effect of changing the refractive index and absorption coefficient of the rhabdom. Which sheathing solution is best depends on the quality of the image on the retina, on the spacing of the rhabdoms in the retina and on the intensity of light normally experienced by the eye. In a retina with closely packed rhabdoms, the model predicts full sheathing to be the optimal solution if the image is well-focussed, partial sheathing if poorly focussed and no sheathing if moderately well-focussed. In a retina with rhabdoms spaced apart and a well-focussed image, the model predicts partial sheathing to be optimal. A pigment sheath is predicted to be useful in eyes which experience bright light and have no need for high sensitivity. A tapetal sheath is predicted to be useful at any intensity. A survey of arthropod eyes with low F-number supports the predictions of the model.

Key words: Superposition eye – Retina – Resolution – Sensitivity – Tapetum

Introduction

A convenient way of comparing the light-gathering abilities of different eyes is to consider their F-numbers (Kirschfeld 1974; Land 1981). This useful quantity, widely used in relation to camera lenses, is the principal focal length of the lens (or posterior nodal distance, f) divided by the diameter of the aperture through which light is permitted to enter (A). The lower the F-number, the more light the eye gathers and the greater its sensitivity. As a general rule, arthropods which live in dim habitats have eyes of low F-number in order to maximise sensitivity to light, whereas those which live in bright habitats usually have eyes of much higher F-number (Table 1). Our primary interest here concerns arthropod eyes with low F-number (i.e. less than about two). Examination of Table 1 reveals two major classes of eyes which meet this criterion: the simple eyes of spiders and the superposition eyes of insects and crustaceans. A very unusual example, not included in either of these classes, is the apposition eye of the deep sea isopod *Cirolana borealis* (Nilsson and Nilsson 1981), which has an F-number 3 times smaller than its diurnal counterparts.

In eyes of low F-number, light enters the eye through a wide aperture: in superposition eyes, this aperture is a large area of corneal facets on the surface of the eye; in simple eyes the aperture is a single cuticular lens (Kunze 1979; Land 1981). Although gains are made in sensitivity, wide apertures tend to suffer from spherical aberration, leading to a spatial spread (x in Fig. 1) in the focussed spot of light (or 'blur-circle') across a number of rhabdoms. Instead of a single 'target' rhabdom detecting the light from each direction in space, several rhab-

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Table 1. F-numbers in arthropod eyes

Species	Arthropod	Eye type	F-number	Ref
<i>Anoplognathus pallidicollis</i>	beetle	NSup	0.5	1
<i>Cherax destructor</i>	crayfish	NSup	0.6	2
<i>Onitis aygulus</i>	dung beetle	NSup	0.6	3
<i>Dinopis subrufus</i> (AL)	spider	NSim	0.6	4
<i>Geolycosa godeffroyi</i> (PM)	spider	NSim	0.7	5
<i>Onitis alexis</i>	dung beetle	CSup	0.8	3
<i>Cirolana borealis</i>	isopod	DSApp	1.0	6
<i>Onitis westermanni</i>	dung beetle	CSup	1.2	3
<i>Ocybadistes walkeri</i>	butterfly	DSup	1.4	7
<i>Phalaenoides tristifica</i>	moth	DSup	1.6	8,9
<i>Phiddipus johnsoni</i> (AM)	spider	DSim	2.0	10
<i>Portia fimbriata</i> (AM)	spider	DSim	2.4	11
<i>Calliphora erythrocephala</i>	fly	DApp	2.6	12
<i>Locusta migratoria</i>	locust	DApp	3.2	13,14
<i>Apis mellifera</i>	bee	DApp	3.4	15
<i>Ciulfina</i> non-fovea	mantid	DApp	3.8	
<i>Ciulfina</i> fovea			5.1	

(Different arthropod eye types: DApp=diurnal apposition eye; DSApp=deep-sea apposition eye; NSim=nocturnal simple eye; DSim=diurnal simple eye; NSup=nocturnal superposition eye; CSup=crepuscular superposition eye; DSup=diurnal superposition eye; AL=antero-lateral eye; AM=antero-medial eye; PM=postero-medial eye. References: 1=Meyer-Rochow and Horridge 1975; 2=Bryceson and McIntyre 1983; 3=McIntyre and Caveney 1985; 4=Blest and Land 1977; 5=O'Carroll 1989; 6=Nilsson and Nilsson 1981; 7=Horridge et al. 1972; 8=Horridge et al. 1977; 9=Horridge et al. 1983a; 10=Land 1969; 11=Williams and McIntyre 1980; 12=Seitz 1968; 13=Wilson et al. 1978; 14=Williams 1982; 15=Varela and Wiitanen 1970; 16=Horridge and Duelli 1979)

doms will, resulting in a degradation of spatial resolution in the eye. Even if all the rays were perfectly coincident at one point on the target rhabdom (never the case because of diffraction by the lens), spatial resolution may still be degraded because of the inability of the rhabdom to contain (by total internal reflection) all the incident rays (de Bruin and Crisp 1957; Land 1984; O'Carroll 1989). The angular range (θ in Fig. 1) of the focussed cone of light rays is often so large in eyes of low F-number that a considerable proportion of the rays cross over into neighbouring rhabdoms where they are erroneously absorbed (Warrant and McIntyre 1990). Measurements of angular sensitivity in the superposition eye of the crepuscular dung beetle *Onitis alexis* are entirely explicable on the basis of the spatial and angular spread of rays incident on the retina (Warrant and McIntyre 1990).

How can this spread of light in the retina be prevented? Reduction in spherical aberration, as has been achieved in some euphausiids (Land et al. 1979) and several species of spiders (Blest and Land 1977; Blest 1985; O'Carroll 1989), can only lessen the spatial extent

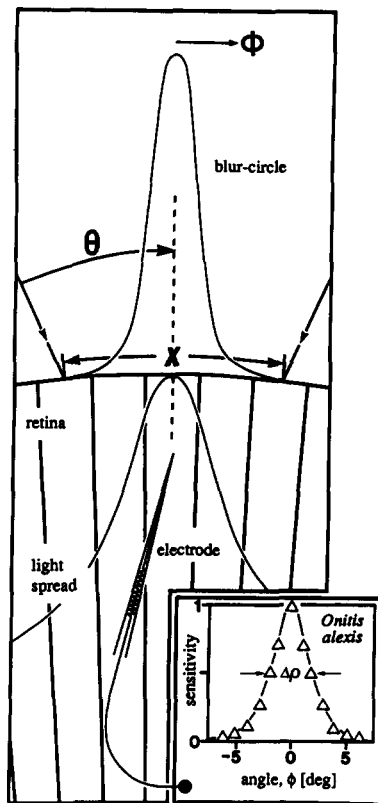


Fig. 1. Light spread in arthropod eyes of low F-number. Incident parallel light rays are focussed by the lenses to form a blur-circle of light on the retina. The rays forming the blur-circle are spread spatially over the retina (x) and are incident over a range of angles (θ) to the target rhabdom axis. As the blur-circle is moved across the retina in small angular steps (ϕ), an electrode records the response of the target rhabdom as an angular-sensitivity function whose shape is partly determined by the extent of the light spread (example shown is for the dung beetle *Onitis alexis*). The width of the angular-sensitivity function at half-height is the acceptance angle, $\Delta\phi$

of the blur-circle on the retina. There is no way of decreasing the spread of ray angles in the blur-circle because this results from a low F-number, which is after all, desirable for sensitivity. There are, however, a number of solutions to the problem of ray cross-over found in nature, as shown in Fig. 2. The simplest 'solution' is to just rely on total internal reflection (Fig. 2A). This seems to be the case in many dung beetles and in many other beetles including the water beetle *Macrogyrus striolatus* (Horridge et al. 1983b). An improvement may occur if the rhabdom is ensheathed in light-absorbing screening pigment (Fig. 2B). Oblique rays then will not degrade the neural image. This is common in the light-adapted state in many superposition eyes (e.g. the crab *Pleuroncodes*, Kampa 1963) and has also been employed by the deep sea euphausiid, *Meganycitiphanes norvegica* (Hallberg and Nilsson 1983).

A novel solution is found in the barrel-shaped rhabdoms (Fig. 2C) common in crustaceans (e.g. crayfish, Bryceson and McIntyre 1983; shrimps, Ball et al. 1986; crabs, Bursley 1975; lobsters, Loew 1976) and even in

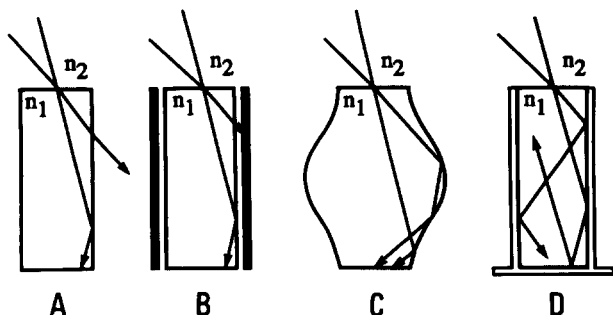


Fig. 2A–D. Solutions found by arthropod retinas to contain incident light rays within the target rhabdom. A Total internal reflection only. B The rhabdom is surrounded by a sheath of light-absorbing screening pigment. C The rhabdom is barrel shaped. D The rhabdom is encased in a sheath of tapetal reflector in addition to having a basal tapetum. n_1 and n_2 are the refractive indices of the rhabdom and external medium respectively ($n_2 < n_1$)

some insects (e.g. scarabs, Horridge and Giddings 1971a; meal moths, Fischer and Horstmann 1971; Horridge 1972). Because of the shape of the rhabdom, a much greater angle of incidence of light rays is allowable in the distal half of the rhabdom before total internal reflection no longer takes place at the rhabdom wall, thus giving rise to greater absorption. This clever trick was first noticed in crayfish (Bryceson and McIntyre 1983).

The final and most effective solution is to partially or completely encase the rhabdom in a tapetal reflector (Fig. 2D). In insects this usually takes the form of a layer of dense air-filled tracheoles, whereas in crustaceans it is usually a layer of reflecting pigment (Land 1972, 1978). A complete tapetal case will internally reflect every ray incident on a rhabdom: degradation of the neural image due to cross-over is eliminated. This solution has been employed by the day moth *Phalaenoides* (Horridge et al. 1977, 1983a), by skipper butterflies (Horridge et al. 1972; Land 1984; Shimohigashi and Tominaga 1986), beetles (*Repsimus**, Horridge and Giddings 1971a; *Anoplognathus**, Meyer-Rochow and Horridge 1975; *Anomala**, Gokan 1982a), moths (*Ephestia*, Horridge and Giddings 1971b; *Spodoptera**, Meinecke 1981; *Deilephila*, Welsch 1977; *Diatraea**, Miskimen and Rodriguez 1981), lobsters (*Nephrops**, Loew 1976), shrimps (*Penaeus**, Zyznar 1970), mysids (*Praunus*, Hallberg 1977), crayfish (*Cherax**, Bryceson and McIntyre 1983) and mayflies (*Cloeon**, Horridge 1976; *Atalophlebia*, Horridge and McLean 1978; Horridge et al. 1982). The animals marked with an asterisk do not have a complete tapetal sheath: in many cases only the proximal-most half or two-thirds of the rhabdom is surrounded.

Many animals do not even have a partial tapetal sheath, but just a single reflective layer coating the base-membrane. This layer is called the basal tapetum. Light passing through the retina is reflected at the tapetum to allow a second passage, effectively doubling the length of the rhabdom. Thus, the light-capturing ability of the entire retina (operating as a physiological unit) is considerably improved, but resolution may be reduced by the increased effects of ray cross-over. Exam-

ples of arthropods employing just a basal tapetum include the water beetle *Cybister fimbriolatus crotchi* (Meyer-Rochow 1973), the shrimp *Acetes sibogae* (Ball et al. 1986) and the rock lobster *Panulirus longipes* (Meyer-Rochow 1975).

Two other possible ways of reducing ray cross-over are to increase the refractive index of the rhabdoms or their absorption coefficient. Increasing the refractive index of the rhabdoms will allow a wider cone of rays to be captured by total internal reflection, but with realistic refractive-index values will not entirely eliminate light spread in the retina. A higher absorption coefficient will increase the absorption of all rays incident on a rhabdom and leave less light to spread into neighbouring rhabdoms.

Interestingly, many arthropod eyes of low F-number have either no tapetal or pigment sheathing, or at best only partial sheathing of the rhabdom. At first glance, this seems to be a most intriguing puzzle: why do so many arthropods throw away spatial resolution when there are (apparently) simple ways of retaining it? The aim of the present study is to attempt to answer this question by applying the computer ray tracing model of McIntyre and Caveney (1985) and Warrant and McIntyre (1990) to low F-number superposition eyes. The model allows us to simulate tapetal and pigment sheaths, and to investigate the effects of changes in rhabdom refractive index and absorption coefficient. The insights provided by the model, from the point of view of both resolution and sensitivity, indicate that there may be good reasons for the wide variety of retinal designs found in arthropod eyes of low F-number.

Experimentally, the importance of ray cross-over in the retina to resolution in superposition eyes can best be assessed by investigation of the spatial properties of higher-order visual units in the brain. It may become apparent at this level that signals from groups of ommatidia are being pooled to improve the signal-to-noise ratio at low light intensities. This has been reported in the apposition eye of the shore crab (Doujak 1985). Neural pooling always occurs at the expense of resolution, and this provides a further possible explanation why, for some animals primarily active in dim light, there may be little selection pressure for shielding structures.

Materials and methods

The ray tracing model, developed for the refracting superposition eyes of several species of nocturnal and crepuscular dung beetles (Caveney and McIntyre 1981; McIntyre and Caveney 1985), relies on an accurate knowledge of the geometry and refractive index of each component of the eye, particularly the cornea and crystalline cones. Parallel incident light rays (from a point source at infinity) are traced by the model through the cornea and crystalline cones and across the clear zone to the retina at the position of best focus. In the model, there are typically several thousand rays incident on the retina. These rays are then traced through the rhabdoms (Warrant and McIntyre 1990), with the amount of light absorbed in each rhabdom being determined. The model thus calculates the total amount of light absorbed by the target rhabdom and each of its neighbours due to a blur-circle variable in both spatial and angular

Table 2. Glossary of terms

Σ	– the percentage of light incident on the retina that is absorbed by the entire retina.
Ω	– the percentage of light incident on the retina that is absorbed by the target rhabdom.
ΔQ	– the acceptance angle (the half-width of the theoretical angular-sensitivity function) [degrees].
$\Delta\Phi$	– the interommatidial angle [degrees].
τ_{ts}	– the extent of tapetal sheathing around the rhabdom ($0 \leq \tau_{ts} \leq 1$).
τ_{ps}	– the extent of pigment sheathing around the rhabdom ($0 \leq \tau_{ps} \leq 1$).
n_{rh}	– the refractive index of the rhabdom.
k	– the absorption coefficient of the rhabdom [μm^{-1}]
σ	– the ratio of the number of rays incident on the target rhabdom to the number of rays incident on each of the six nearest-neighbour rhabdoms.

extents on the retina. From this information, the model calculates (Table 2) the percentage of the light incident on the retina that is absorbed by the *entire* retina (Σ), the percentage of the light incident on the retina that is absorbed by the *target rhabdom* (Ω), and the extent of light spread in the retina. A theoretical angular-sensitivity function is generated, the half-width of which (ΔQ : Fig. 1) indicates the severity of light spread. The model calculates $\Delta Q/\Delta\Phi$, where $\Delta\Phi$ is the interommatidial angle of the eye. The larger $\Delta Q/\Delta\Phi$, the more severe is the effect of light spread on resolution.

There are several possible criteria for best focus. The position of the retina, as set by the clear-zone width, can be such that the maximum number of rays is focussed onto the distal end of the target rhabdom (maximum signal), such that the maximum amount of light is absorbed in the target rhabdom or such that the resolution as measured by ΔQ is minimised. These positions are in general different (McIntyre and Warrant, unpublished) and the latter two positions vary with the extent of the sheathing around the rhabdom. For simplicity therefore, and because the results of this paper do not change much with the different criteria (and not at all qualitatively), we choose maximum signal as the criterion for best focus.

The approach taken in this study was to simulate 4 solutions to light spread (tapetal sheathing, pigment sheathing, vary the rhabdom refractive index, vary the rhabdom absorption coefficient) and calculate their effects on Σ , Ω and ΔQ . In the case of the tapetal and pigment sheath solutions, simulations and calculations were made for different extents of sheathing (τ_{ts} and τ_{ps} respectively: Table 2, Fig. 3) without a basal tapetum, and using a rhabdom refractive index $n_{rh} = 1.40$ and a rhabdom absorption coefficient $k = 0.0067 \mu\text{m}^{-1}$ (Bruno et al. 1977). (This refractive index is probably too high in view of the recent results of Nilsson and Howard (1989), which suggest a value in the range 1.36–1.365. However, our results are not qualitatively altered by a lower refractive index; the numbers just come out a little different in the figures.) The effects of variations in rhabdom refractive index and absorption coefficient were investigated in the absence of all forms of rhabdom sheathing. In the model, all rhabdoms were taken to be circular in cross-section.

Two generalised types of low F-number eyes were simulated: (1) a poorly focussed ‘nocturnal’ superposition eye (F-number = 0.6) and (2) a well-focussed ‘diurnal’ superposition eye (F-number = 1.3). In the poorly focussed eye, the blur-circle was such that the number of rays incident on the target rhabdom was comparable to the number incident on each of its 6 neighbours. In the well-focussed eye, the number of rays incident on the target rhabdom was approximately 34 times greater than the number incident on each neighbour. In both cases, the rhabdoms were assumed contiguous (as in Fig. 9A).

The study was completed with an investigation of tapetal and

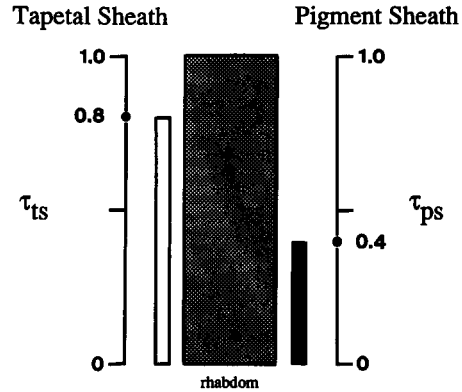


Fig. 3. Definition of the extent of tapetal sheathing (τ_{ts}) and pigment sheathing (τ_{ps}), which extend proximally to distally around the rhabdom (stippled). A tapetal sheath of $\tau_{ts} = 0.8$ is shown at left (light bar) and a pigment sheath of $\tau_{ps} = 0.4$ is shown at right (dark bar)

pigment sheathing in 4 species of dung beetles: the diurnal *Onitis belial*, the early crepuscular *Onitis westermanni*, the mid-crepuscular *Onitis alexis* and the nocturnal *Onitis aygulus*. In reality, only *O. belial* has any form of sheathing around its rhabdoms (a partial pigment sheath).

Results

The poorly focussed nocturnal eye

The blur-circle in the poorly focussed model nocturnal eye (with contiguous rhabdoms) spreads spatially over several rhabdoms (Fig. 4), with the ratio of light incident on the target rhabdom to that incident on each of its 6 neighbours $\sigma = 1.0$.

We first consider the presence of a tapetal sheath around each rhabdom; the results are shown in Fig. 5A. Both the resolution ($\Delta Q/\Delta\Phi$) and sensitivity (Ω) are optimum when a tapetal sheath surrounds the proximal-most 85% of each rhabdom. However, if this sheathing were to surround 65% or 100% of the rhabdom, the resolution of the eye would be worse than if no sheathing were present at all.

We next consider the presence of a pigment sheath around each rhabdom (Fig. 5B). The results indicate that a pigment sheath is a bad design if sensitivity is the most important requirement of the eye: the sensitivities of both the entire retina and the target rhabdom are reduced by the presence of pigment between the rhabdoms. In addition, the resolution is only modestly improved with a pigment sheath of the appropriate extent ($\tau_{ps} \approx 0.85$).

The well-focussed diurnal eye

The blur-circle of the well-focussed model diurnal eye fits neatly over a single rhabdom, with little light falling on the contiguous neighbouring rhabdoms (Fig. 6). There is negligible spherical aberration in this eye and it is prob-

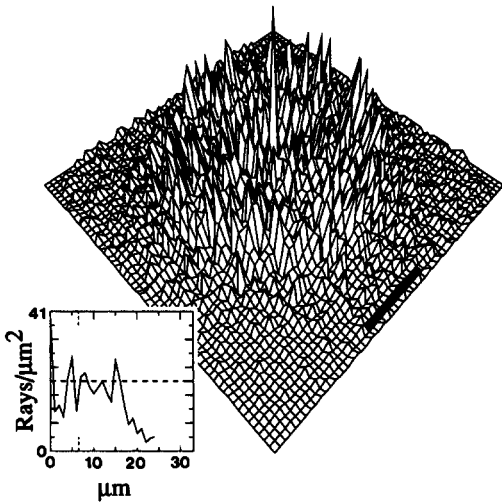


Fig. 4. The blur-circle intensity distribution on the retina in the poorly focussed model nocturnal eye, with corresponding intensity profile (inset). The dark bar in the blur-circle distribution represents the diameter of a single rhabdom. The vertical dotted line in the intensity profile is at the edge of the rhabdom (0 μm is the centre of the rhabdom)

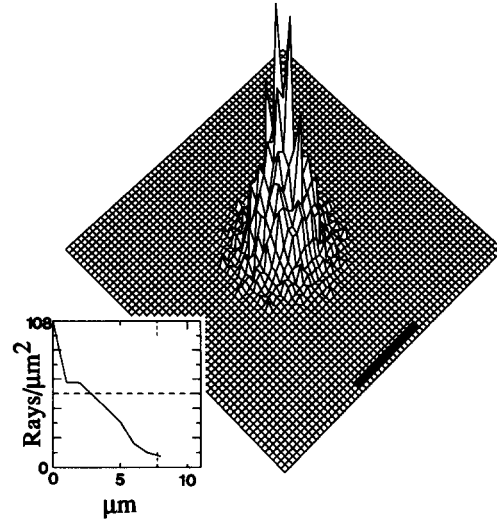


Fig. 6. The blur-circle intensity distribution on the retina in the well-focussed model diurnal eye, with corresponding intensity profile (inset). The dark bar in the blur-circle distribution represents the diameter of a single rhabdom. The vertical dotted line in the intensity profile is at the edge of the rhabdom (0 μm is the centre of the rhabdom)

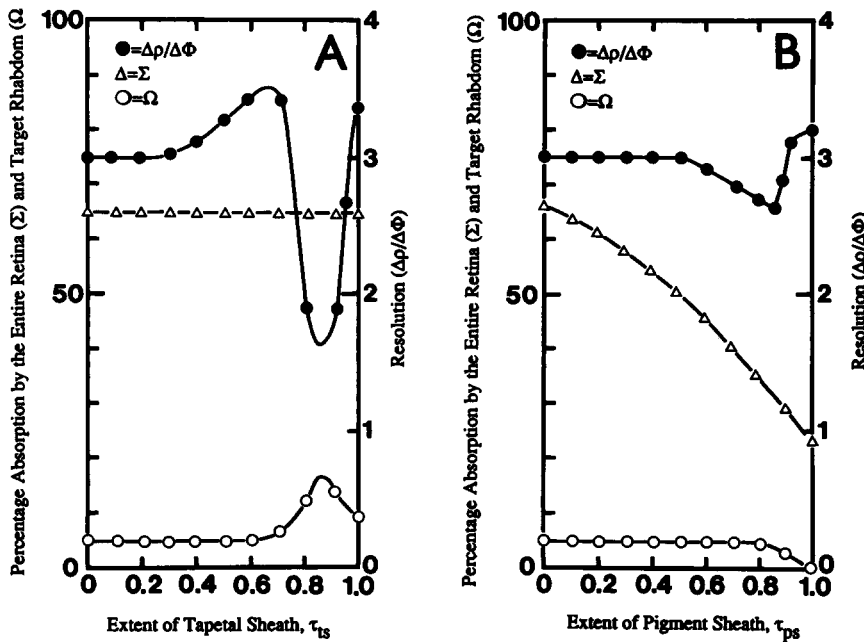


Fig. 5A, B. Resolution and sensitivity in the poorly focussed model nocturnal eye as a function of (A) the extent of tapetal sheathing (τ_{ts}) and (B) the extent of pigment sheathing (τ_{ps}). Sensitivity is defined as the percentage of light incident on the retina which is (1) absorbed by the entire retina, Σ (Δ), or (2) absorbed by the target rhabdom, Ω (\circ). Resolution (\bullet) is given by the ratio of the acceptance angle to the interommatidial angle ($\Delta\rho/\Delta\Phi$)

able that diffraction at each crystalline cone tip limits the size of the blur-circle, a situation found in the superposition eyes of diurnal moths and skipper butterflies (Horridge et al. 1977, 1983a; Land 1984) and in the simple eyes of many diurnal jumping spiders (Hardie and Duelli 1978; Williams and McIntyre 1980; O'Carroll 1989). The value for σ here is 33.8.

Figure 7A shows the effects of a tapetal sheath of different extents on the resolution and sensitivity of the well-focussed eye. Resolution and sensitivity are both optimum when a full tapetal sheath is present ($\tau_{ts} = 1.0$), and the gains made by such a design are quite substantial.

However, if the tapetal sheath is only slightly less than fully developed ($\tau_{ts} = 0.8$), the performance of the eye is worse than if no sheathing at all were present.

We now turn again to the pigment sheath design (Fig. 7B). As in the poorly focussed eye, the presence of a pigment sheath in the well-focussed eye reduces sensitivity, but this time only of the retina as a whole: the sensitivity of the target rhabdom is largely unaffected by a pigment sheath because, even without a sheath, few rays pass into the target rhabdom that are not incident on it. Some marginal gains are made in resolution by this design, but only if the rhabdom is fully sheathed.

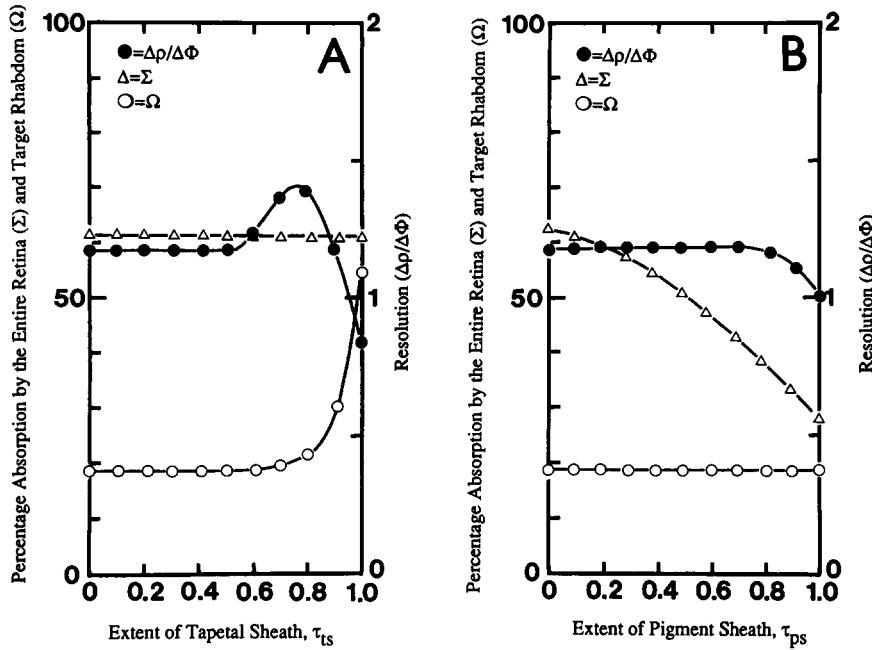


Fig. 7A, B. Resolution and sensitivity in the well-focused model diurnal eye as a function of (A) the extent of tapetal sheathing (τ_{ts}) and (B) the extent of pigment sheathing (τ_{ps}). Sensitivity is defined as the percentage of light incident on the retina which is (1) absorbed by the entire retina, Σ (Δ), or (2) absorbed by the target rhabdom, Ω (\circ). Resolution (\bullet) is given by the ratio of the acceptance angle to the interommatidial angle ($\Delta\rho/\Delta\Phi$)

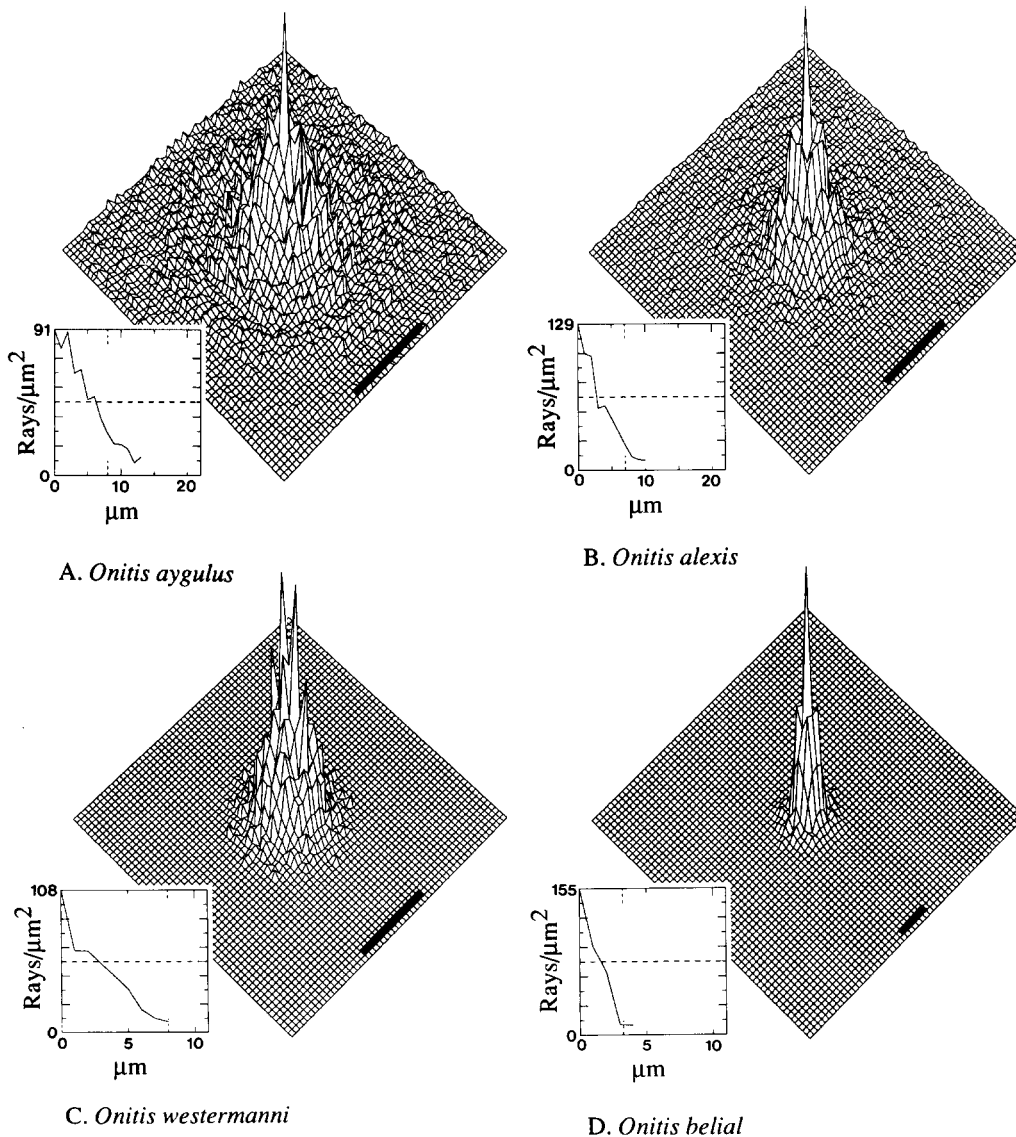


Fig. 8A–D. The blur-circle intensity distributions on the retinas of the model superposition eyes of (A) the nocturnal dung beetle *Onitis aygulus*, (B) the mid-crepuscular dung beetle *Onitis alexis*, (C) the early-crepuscular dung beetle *Onitis westermanni*, and (D) the diurnal dung beetle *Onitis belial*, with corresponding intensity profiles (insets). The dark bars in the blur-circle distributions for each species represent the diameter of a single rhabdom. The vertical dotted lines in the intensity profiles are at the edge of the rhabdom in each species (0 μm is the centre of the rhabdom). The parameters used in the ray-tracing model are given in Table 3

Table 3. Parameters used in the computer models (Fig. 8)

Parameter	<i>O. aygulus</i>	<i>O. alexis</i>	<i>O. westermanni</i>	<i>O. belial</i>
Cornea				
n_0	1.53	1.53	1.53	1.54
n_b	1.47	1.47	1.47	1.47
L_H	20.0	25.0	30.0	30.0
L_G	30.0	20.4	29.8	31.7
D	35.0	35.0	37.0	29.0
R_1	52.0	45.0	48.0	48.0
R_2	16.0	11.0	16.0	12.0
a	2.0	2.0	2.0	2.0
Cone				
n_{0c}^D	1.511	1.470	1.470	1.474
n_{0c}^W	1.501	1.470	1.470	1.460
n_{0c}^P	1.486	1.470	1.470	1.453
n_{bc}	1.35	1.35	1.35	1.35
L_H	4.8	12.4	16.6	12.0
L_G	74.4	61.2	61.2	45.8
D	24.0	21.8	22.4	17.0
W_c	8.0	7.0	7.0	5.0
x_c	18.8	18.0	20.8	15.6
a^D	3.2	2.5	2.0	3.1
a^W	2.25	2.5	2.0	2.1
a^P	2.3	2.5	2.0	1.9
Eye				
CLZ	345	264	166	195
R	899	750	600	676

For full details of the computer model and parameters, see McIntyre and Caveney, 1985. L is a length; H denotes homogeneous region; G denotes a graded-refractive-index region; D is diameter; R_1 , R_2 , R are the radii of curvature of the outer and inner surfaces of the corneal lens and of the whole eye respectively; n_0 , n_b are the refractive indexes of the cornea on its axis and in the homogeneous region and at its edge, respectively; a is the exponent in the refractive-index profile; n_{0c} is the refractive index of the cone on its axis, with superscripts D , W , P denoting distal, waist and proximal regions, respectively, and n_{bc} is the refractive index at the edge of the cone; a with the same superscripts is the refractive-index profile exponent in the cone; W_c is the width of the curved part of the distal end of the cone; x_c is the length of the elliptical tip of the cone; CLZ is the clear-zone width for best focus. All length in microns

Examples: nocturnal, crepuscular and diurnal dung beetles

We next model the effects of tapetal and pigment sheathing in the refracting superposition eyes of 4 species of dung beetles: the diurnal *Onitis belial*, the early-crepuscular *Onitis westermanni*, the mid-crepuscular *Onitis alexis* and the nocturnal *Onitis aygulus* (McIntyre and Caveney 1985). The blur-circles formed on the retinas in the 4 species are shown in Fig. 8. As the species becomes more nocturnal, the aperture of the eye increases (McIntyre and Caveney 1985) and the blur-circle becomes broader, with more light rays striking the retina away from the target rhabdom (as indicated by the increasingly 'bumpy' background of the blur-circle). The calculated values of σ reflect this trend (infinite in *O. belial*; 75.4 in *O. westermanni*; 9.6 in *O. alexis*; 4.3 in *O. aygulus*).

In reality, only *O. belial* has any sheathing (a pigment sheath extending distally to about 85% of the rhabdom length); the other 3 species lack sheathing entirely. *O. belial* also differs from the other 3 species by having much smaller rhabdoms (diameter 6.5 μm , rather than 13–15 μm), separated by a much larger relative distance (Fig. 9), than the rhabdoms of *O. aygulus*, *O. alexis* and *O. westermanni* which are more or less contiguous. The retinal arrangement in *O. belial* is common in day-flying dung beetles with superposition eyes.

Contiguous rhabdoms: nocturnal and crepuscular species

The nocturnal or crepuscular species *O. aygulus*, *O. alexis* and *O. westermanni* all show similar trends in resolution and sensitivity (Fig. 10 A–C) to those found for the well-focussed diurnal eye (Fig. 7) when a tapetal or pigment sheath is extended around the rhabdom. As the extent of tapetal sheathing (τ_{ts}) is increased, the percentage of light absorbed by the entire retina (Σ) remains constant and the percentage of light absorbed by the target rhabdom (Ω) initially remains constant but then

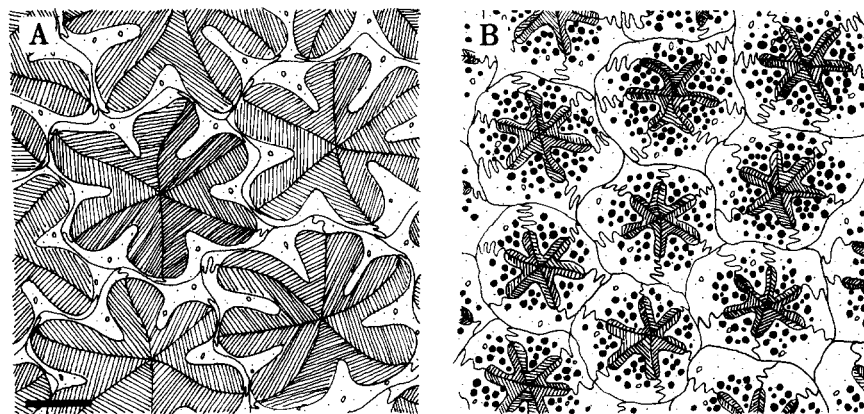


Fig. 9A, B. Schematic transverse cross-sections through the retinas of two dung beetle species. **A** *Onitis aygulus*, a nocturnal species with rhabdoms (hatched flower-shaped objects) which are large and closely apposed (i.e. contiguous). The retinas of *O. alexis* and *O. westermanni* are similar. **B** *Onitis belial*, a diurnal species with rhabdoms which are small and separated by a large relative distance (i.e. non-contiguous). Note that in this species the rhabdoms are surrounded by a sheath of screening pigment granules. Scale bar for both parts: 5 μm

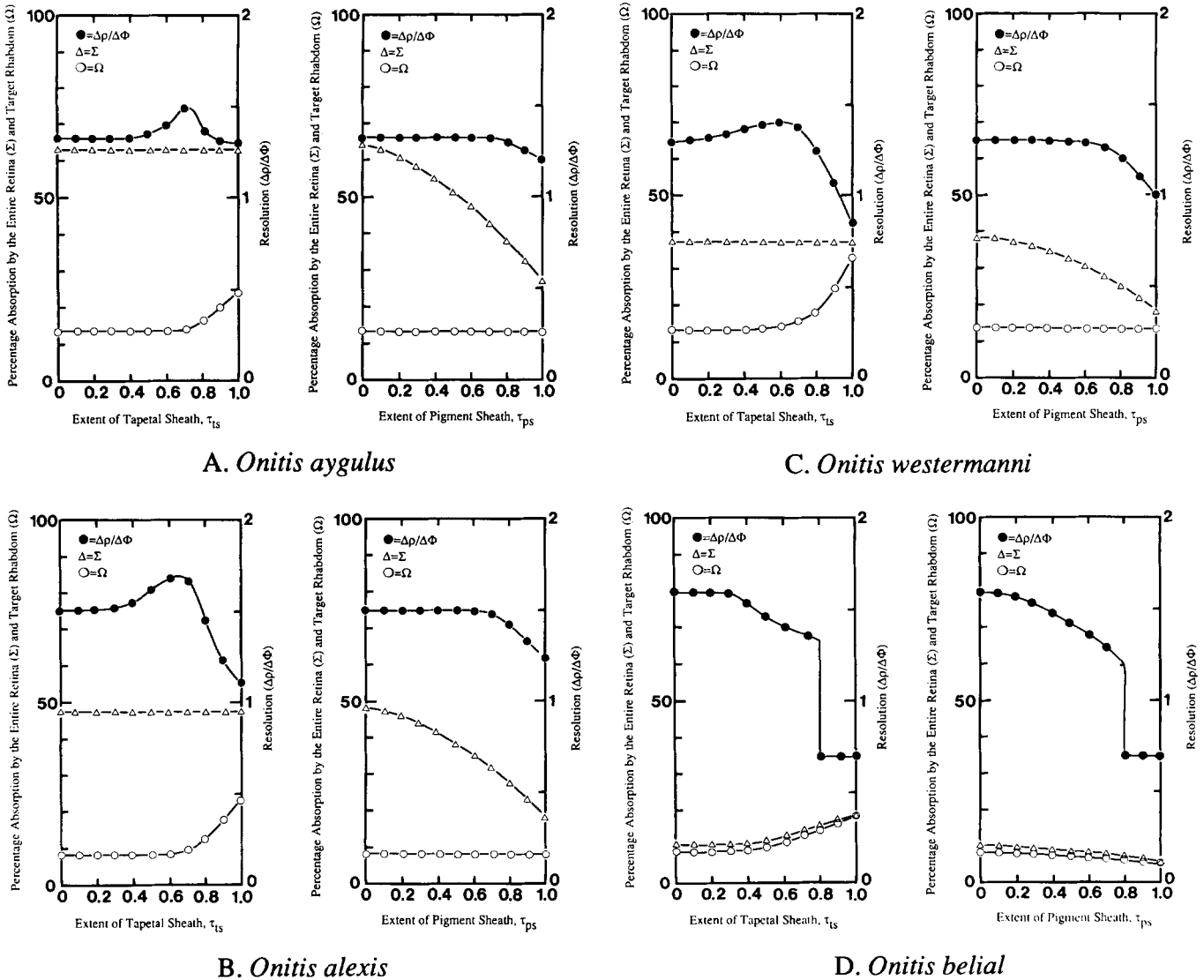


Fig. 10A–D. Resolution and sensitivity in the model superposition eyes of the dung beetles (A) *Onitis aygulus*, (B) *Onitis alexis*, (C) *Onitis westermanni* and (D) *Onitis belial* as a function of the extent of tapetal sheathing, τ_{ts} (left), and the extent of pigment sheathing, τ_{ps} (right). Sensitivity is defined as the percentage of light incident on

the retina which is (1) absorbed by the entire retina, Σ (Δ), or (2) absorbed by the target rhabdom, Ω (\circ). Resolution (\bullet) is given by the ratio of the acceptance angle to the interommatidial angle ($\Delta\rho/\Delta\Phi$)

increases to a maximum for full sheathing. The resolution of the eye ($\Delta\rho/\Delta\Phi$), initially constant, deteriorates to its worst value at an intermediate value of τ_{ts} but then improves to its best value when the rhabdom is fully sheathed (except in *O. aygulus*, which regains its original unshathed resolution). As the extent of pigment sheathing (τ_{ps}) is increased, the percentage of light absorbed by the entire retina (Σ) declines steadily, the percentage of light absorbed by the target rhabdom (Ω) remains roughly constant and the resolution of the eye ($\Delta\rho/\Delta\Phi$) initially remains constant, but then improves, reaching its best value when the rhabdom is fully sheathed.

Despite these similarities, the 3 species do show differences:

1. the improvements in resolution and sensitivity made by increasing the extent of tapetal sheathing (τ_{ts}) towards maximum are most marked in *O. westermanni*, which has

the highest F-number and the best blur-circle focus ($\sigma = 75.4$). The most nocturnal species, *O. aygulus* (with lowest F-number and worst focus), makes no improvement in resolution ($\Delta\rho/\Delta\Phi$) by having a tapetal sheath and makes only moderate improvements in target rhabdom absorption (Ω). In fact, with a partial tapetal sheath of $\tau_{ts} = 0.7$, the eye of *O. aygulus* would perform worse than if no sheathing at all were present. The improvements made in *O. alexis* lie between these two extremes;

2. a pigment sheath provides most benefit and least disadvantage to the eye of *O. westermanni*. As the extent of pigment sheathing (τ_{ps}) is increased, this species shows the greatest improvements in resolution ($\Delta\rho/\Delta\Phi$) and the least decline of retinal sensitivity (Σ). *O. aygulus* shows the least improvement in resolution and the greatest decline in retinal sensitivity.

Non-contiguous rhabdoms: diurnal species

The effects of rhabdom sheathing in the day-flying species *O. belial* (Fig. 10D) show many similarities to the effects observed in the nocturnal and crepuscular species. For instance, the inclusion of either a pigment or tapetal sheath results in improved resolution ($\Delta_Q/\Delta\Phi$). However, the improvement in *O. belial* ceases when the extent of sheathing (τ_{is} and τ_{ps}) exceeds about 0.8. For sheath extents greater than 0.8, none of the incident light is absorbed by other than the target rhabdom: no rays are incident on the neighbouring rhabdoms because the image is well-focused, and any rays outside the target rhabdom do not pass through other rhabdoms because they are spaced well away. Thus there is no spreading of light between rhabdoms and Δ_Q remains constant with increasing sheath extent. This constant value of Δ_Q is set by the convolution of the blur-circle with the angular cross-section of the rhabdom (Warrant and McIntyre 1990), giving $\Delta_Q/\Delta\Phi = 0.7$ ($\Delta\Phi = 2.0^\circ$). Any value of the sheath extent greater than 0.8 would give the same resolution, and so a partial-to-full sheath is predicted. Interestingly, the rhabdoms of *O. belial* are surrounded by a partial pigment sheath with $\tau_{ps} = 0.85$ (McIntyre and Caveney, unpublished). A closely related day-flying dung beetle *Onitis ion* similarly has small, non-contiguous rhabdoms sheathed by pigment (McIntyre and Caveney, unpublished), but in this species the sheath extends all the way to the distal tips of the rhabdom ($\tau_{ps} = 1.0$). As with the nocturnal and crepuscular species, *O. belial* shows an increase in sensitivity (Σ and Ω) with a tapetal sheath, but a decrease with a pigment sheath.

Discussion

What is an optimal retinal design?

Before discussing the details of retinal design, we first address the issue of what determines an 'optimal' design for a particular arthropod. There are essentially 4 constraints on the evolution of a design, not only of the retina, but of the eye as a whole (Dumont and Robertson 1986): (1) adaptive influences (i.e. the visual requirements of the animal); (2) developmental constraints, which restrict the final form of the design; (3) historical influences (i.e. the influence of the ancestral design on that of the present-day); and (4) certain architectural features imposed by the materials and design of the organism. In other words, the design of the retina is not simply the result of the visual requirements of the animal: if two design strategies similarly satisfy the requirements of a particular eye, whichever is manifested will reflect the remaining 3 constraints.

What exactly constitutes an arthropod's visual requirements? The simplest reduction would be to those of resolution and sensitivity. These two parameters generally trade off against one another (review Land 1981): when resolution is high in an eye, its sensitivity is usually low, and vice versa. For example, in an effort to maximise sensitivity, the eye of a nocturnal or deep-sea arthropod

generally sacrifices resolution (because of aberrations and light spread associated with a wide aperture and low F-number). Conversely, an arthropod living in bright sunlight can afford to have an eye that sacrifices sensitivity but maximises resolution.

Of course, there is no point in having a retinal design that is evolutionarily expensive (having to overcome constraints 2 to 4 above) and/or endows an arthropod with a visual performance beyond its basic survival requirements. Even though a particular design may allow much greater visual performance in a given arthropod, if this design is expensive or unnecessary for normal activity, then it is unlikely to evolve; a simpler design is likely to appear instead. Thus, there is a kind of 'cost-benefit analysis' that must take place during the evolution of a particular 'optimal' retinal design. We are in no position to say what is an optimal design for a particular arthropod, but rather we must try to explain why the solution adopted by an arthropod is optimal for its lifestyle and habitat. Having done this, we may gain valuable insights into the trade-off a particular arthropod has made between the competing benefits of good resolution and high sensitivity.

The tapetal sheath design

The effect of a full tapetal sheath ($\tau_{is} = 1$) is to reflect internally every ray of light incident on the rhabdom, regardless of its angle of incidence. Unfortunately, no distinction is made between rays which are intended for absorption in that rhabdom and rays which are not. Hence, if most rays intended for absorption in the target rhabdom (i.e. those incident from the direction in space in which the rhabdom is looking) are also incident on that rhabdom (as they are in a well-focussed eye), and if some of these rays are not trapped by total internal reflection, then a full tapetal sheath is beneficial: light spread is eliminated, maximising both resolution and sensitivity. In retinas in which the rhabdoms are non-contiguous, a partial tapetal sheath achieves the same result, as in the diurnal dung beetle *O. belial* (see Results). On the other hand, if many rays intended for absorption in the target rhabdom are not incident on that rhabdom but are instead incident on its surrounding neighbours (as in a poorly focussed eye), then a full tapetal sheath is quite deleterious. In this situation, rays intended for the target rhabdom have no chance of ever arriving there because they are retained by reflection within the neighbouring rhabdoms upon which they are incident. This leads to fewer rays absorbed by the target rhabdom and more rays erroneously absorbed by its neighbours, degrading both resolution and sensitivity.

These qualities of the tapetal sheath design are clearly seen in our model calculations. In the well-focussed diurnal eye (Figs. 6 and 7), the blur-circle has $\sigma = 33.8$, and a full tapetal sheath is predicted as the best design for retinas with contiguous rhabdoms, both from the point of view of resolution ($\Delta_Q/\Delta\Phi$) and sensitivity (Ω). This is also the prediction in the dung beetles *Onitis westermanni* ($\sigma = 75.4$) and *Onitis alexis* ($\sigma = 9.6$) (Figs. 8 and

10), both of which have contiguous rhabdoms. In *Onitis belial* (σ infinite), with non-contiguous rhabdoms, a partial-to-full tapetal sheath is predicted.

In the poorly focussed nocturnal eye (Figs. 4 and 5), the blur-circle has $\sigma = 1.0$, which means that a considerable amount of light falls on neighbouring rhabdoms. In this eye a partial tapetal sheath ($\tau_{is} = 0.85$) is predicted to be the optimal retinal design: sensitivity ($\Delta Q/\Delta \Phi$) and resolution (Ω) both become maximal. It is this degree of sheathing that provides the best balance between the retention of rays striking the target rhabdom and the acceptance of rays initially striking neighbouring rhabdoms, but crossing over into the target rhabdom. If the extent of sheathing is less than 0.85, more light escapes from the target rhabdom (following incidence there) than enters it via neighbouring rhabdoms. This causes the amount of light absorbed by the nearest-neighbour rhabdoms to become larger relative to that absorbed by the target rhabdom, resulting in a degradation of resolution and of the sensitivity of the target rhabdom. If, on the other hand, the extent of sheathing becomes greater than 0.85, many of the rays incident on the nearest-neighbour rhabdoms are prevented from entering the target rhabdom by the tapetal sheath. These rays remain trapped in the neighbouring rhabdoms where they increase the light absorbed relative to that absorbed by the target rhabdom. Again, resolution and the sensitivity of the target rhabdom are degraded. The optimum value of τ_{is} a poorly focussed eye depends on the spatial and angular distribution of rays in the blur-circle. If these distributions are altered, the predicted optimum value of τ_{is} will almost certainly change.

The dung beetle *Onitis aygulus* has a moderately well-focussed eye with $\sigma = 5.4$ (Figs. 8 and 10). This eye shows few benefits in having a tapetal sheath. The percentage of light absorbed by the target rhabdom (Ω) improves marginally by having a full tapetal sheath, but no gains in resolution ($\Delta Q/\Delta \Phi$) are made. Why bother therefore to have a complicated, evolutionarily expensive solution that provides no significant benefits to visual performance? Not surprisingly, *O. aygulus* lacks tapetal sheathing.

From these examples, one can see basic design principles emerging: (1) if an eye is well-focussed (i.e. $\sigma \gg 1$), a full tapetal sheath is probably optimal when the rhabdoms are contiguous and a partial-to-full sheath when they are non-contiguous; (2) if the eye is moderately well-focussed (i.e. $\sigma \approx 5$), no sheathing is optimal (although slight gains may be made with a tapetal sheath); and (3) if the eye is poorly focussed (i.e. $\sigma \leq 1$), a partial tapetal sheath is optimal. Example of all these designs are common in nature.

Full tapetal sheaths are very commonly found in diurnal insects with superposition eyes. Examples include the agaristid moth *Phalaenoides tristifica* (Horridge et al. 1977; Horridge et al. 1983a), skipper butterflies (Horridge et al. 1972) and the dorsal eyes of the mayflies *Cloeon* (Horridge 1976) and *Atalophlebia* (Horridge and McLean 1978; Horridge et al. 1982). A full tapetal sheath is also found in the nocturnal superposition eye of the hawk moth *Deilephila elpenor* (Welsch 1977). Diurnal

moths and skippers are known to have very well-focussed eyes, with small superposition apertures and diffraction-limited optics (Land 1984). It is quite possible that mayflies, which also have very small superposition apertures (D.-E. Nilsson, personal communication), are similarly well-focussed. The fabulous visual behaviour of hawk moths indicates that these insects also have good vision. Thus, the model predicts that full tapetal sheaths are the optimal design in insects with well-focussed eyes, and this indeed seems to be the case.

The complete absence of tapetal (and pigment) sheathing is a common feature in the superposition eyes of many beetles, including the nocturnal and crepuscular dung beetles modelled in this study (McIntyre and Cavey 1985) and many other dung beetles, especially nocturnal species, but also including some diurnal species (Meyer-Rochow 1978; Gokan 1989). Other examples of sheath-free eyes include the superposition eyes of euphausiids (Land et al. 1979) and the simple eye of the nocturnal spider *Dinopis* (Blest and Land 1977; O'Carroll 1989). Even though the model predicts that the dung beetles *O. westermanni* and *O. alexis* would benefit from a full tapetal sheath, such benefits may be quite unnecessary for their normal activities. Even without sheathing of any kind, *O. alexis* was found to have quite adequate resolution and sensitivity during its normal dusk activity (Warrant and McIntyre 1990). The model also predicts that a tapetal sheath is probably an expensive and useless addition to the eye of *O. aygulus*. Thus, one must conclude that in many arthropods the benefits provided by a tapetal sheath are simply not sufficient to warrant its inclusion in the retina, and this is possibly why it is absent in so many species.

A partial tapetal sheath is also a common design in arthropod eyes, as discussed in the Introduction. The extent to which the sheath envelops the rhabdom varies from species to species, and, until now, it has not been entirely obvious why. The model provides two possible explanations. The nocturnal animals probably have eyes of low F-number and therefore could suffer badly from spherical aberration (giving a blur-circle of low σ) and light spread in the retina. According to the model, the optimal retinal design in such an eye includes a partial tapetal sheath (Fig. 5), with the extent of the sheath reflecting the quality of the blur-circle. In animals with non-contiguous rhabdoms, a partial tapetal sheath performs the same function as a full sheath, as shown above for *O. belial*. A full sheath, while not degrading resolution or sensitivity as it would in a poorly focussed eye, is therefore not necessary.

Our measure of resolution ($\Delta Q/\Delta \Phi$) only accounts for two-point discrimination by the eye. A more informative indicator of the resolution is the modulation transfer function (MTF) of the eye, which is the Fourier transform of the angular-sensitivity function (Dubs 1982; Warrant and McIntyre 1990). The MTF takes account of the entire shape of the angular-sensitivity function (not just its half-width ΔQ), an important consideration in arthropod eyes of low F-number in which aberrations and light spread give rise to an angular-sensitivity function with large off-axis flanks (Warrant and McIntyre

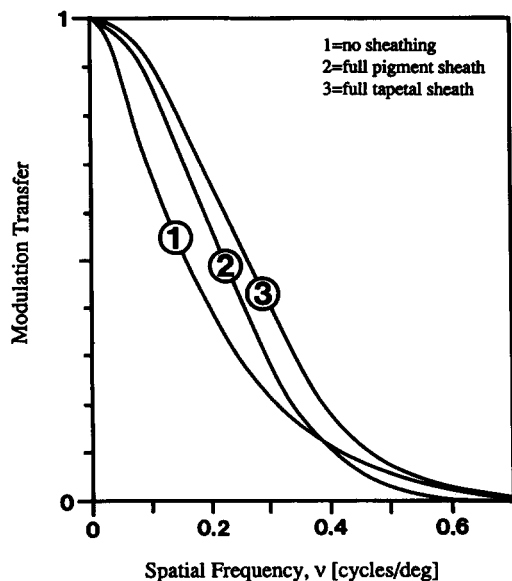


Fig. 11. Modulation transfer functions (MTFs) for the well-focussed diurnal eye assuming no sheathing of the rhabdoms (curve 1), full pigment sheathing of the rhabdoms (curve 2) and full tapetal sheathing of the rhabdoms (curve 3). MTFs were calculated by Fourier transforming the theoretical angular-sensitivity functions generated by the model

1990). The MTF quantifies how well a particular eye is able to detect different spatial frequencies: the more prominent the flanks in the angular-sensitivity function, the lower the discriminability of spatial information.

The effects of sheathing on the MTF of the well-focussed diurnal eye are illustrated in Fig. 11. If the retina has a full tapetal sheath, light spread is almost eliminated, thus greatly reducing the flanks of the angular-sensitivity function. The corresponding MTF (curve 3) indicates a greater discrimination of low to medium spatial frequencies than if tapetal sheathing was absent from the retina (curve 1).

The pigment sheath design

A tapetal sheath removes light spread by redistributing the light rays in the retina without itself depleting their number. A pigment sheath removes light spread by absorbing rays. The net effect of this difference is that a tapetal sheath actually enhances the sensitivity of the eye by increasing the path lengths of rays, whereas a pigment sheath reduces the sensitivity by the removal of rays. Despite this drawback, a pigment sheath may actually be the preferable solution to light spread in some arthropod eyes: structurally it is much simpler than a tapetal sheath and therefore may be less expensive to evolve.

The deleterious effects of a pigment sheath are evident in all the eyes modelled. The sensitivity of the entire retina (Σ), and in some cases of the target rhabdom (Ω), is reduced as the extent of pigment sheathing (τ_{ps}) is increased (Figs. 5B, 7B and 10). In most cases the resolu-

tion ($\Delta\Omega/\Delta\Phi$) is improved when a full pigment sheath is present, but the gains made are quite modest. In the poorly focussed nocturnal eye (Fig. 5B), the loss of sensitivity (both Σ and Ω) is quite dramatic, with Σ falling from 65% in the absence of a pigment sheath to 23% when a full sheath is present. In addition, in this eye a full sheath actually worsens resolution. Resolution is best when a partial pigment sheath ($\tau_{ps} = 0.85$) is present. The reasons for this are identical to those which explain why a partial tapetal sheath is also preferable (see above). The losses in sensitivity are least, and the gains in resolution greatest, in the well-focussed eye of *O. belial* (Fig. 10D). The situation is exactly opposite in *O. aygulus* (Fig. 10A): there is a large loss in sensitivity with negligible gain in resolution.

As with the tapetal sheath, some basic design principles for pigment sheathing are evident. If an eye has no requirement for high sensitivity, then: (1) if an eye is well-focussed ($\sigma \gg 1$), a full pigment sheath is probably optimal when the rhabdoms are contiguous and a partial-to-full sheath when they are non-contiguous; (2) if the eye is moderately well-focussed ($\sigma \approx 5$) no sheathing is optimal; and (3) if the eye is poorly focussed ($\sigma \leq 1$) a partial pigment sheath is optimal. Again, all these examples are common in nature.

The model predicts that the pigment sheath design is completely useless in an eye which requires high sensitivity. However, this is precisely why most arthropod eyes of low F-number evolved (Nilsson 1989). A much better design, from the point of view of sensitivity, would be a tapetal sheath, and if sensitivity is an important requirement, it would in fact be better to have no sheath at all than to have an absorbing pigment sheath. One would therefore not expect to find a pigment sheath in the eyes of nocturnal or deep-sea arthropods, and indeed one rarely does. Any screening pigment is usually located very close to the basement membrane, and it remains there regardless of the state of adaptation. According to Tuurala (1954), pigment sheaths are universally absent in the superposition eyes of nocturnal moths. Instead they often have partial or complete tapetal sheaths. Nocturnal spiders also typically lack both tapetal and pigment sheaths (Blest and Land 1977; Blest 1985; O'Carroll 1989). In these spiders, the rhabdoms are often distributed in rows, and at most, pigment exists between the rows. Most crepuscular and nocturnal dung beetles (including those species modelled here) are also devoid of any form of sheathing. One must assume therefore (as we did earlier) that visual performance in nocturnal spiders and dung beetles is quite sufficient without sheathing.

According to the model, the pigment sheath design is only useful to an eye that can afford to throw away sensitivity. The only candidates for such eyes would be those which experience bright daylight and are reasonably well-focussed. This prediction of the model is supported by the design strategies found in real eyes: the presence of a pigment sheath is common in the low F-number eyes of diurnal arthropods. This is the situation for the day-flying dung beetle *O. belial* which the model predicts should have pigment sheaths developed at least 80% distally (Fig. 10D): in actual fact this species has

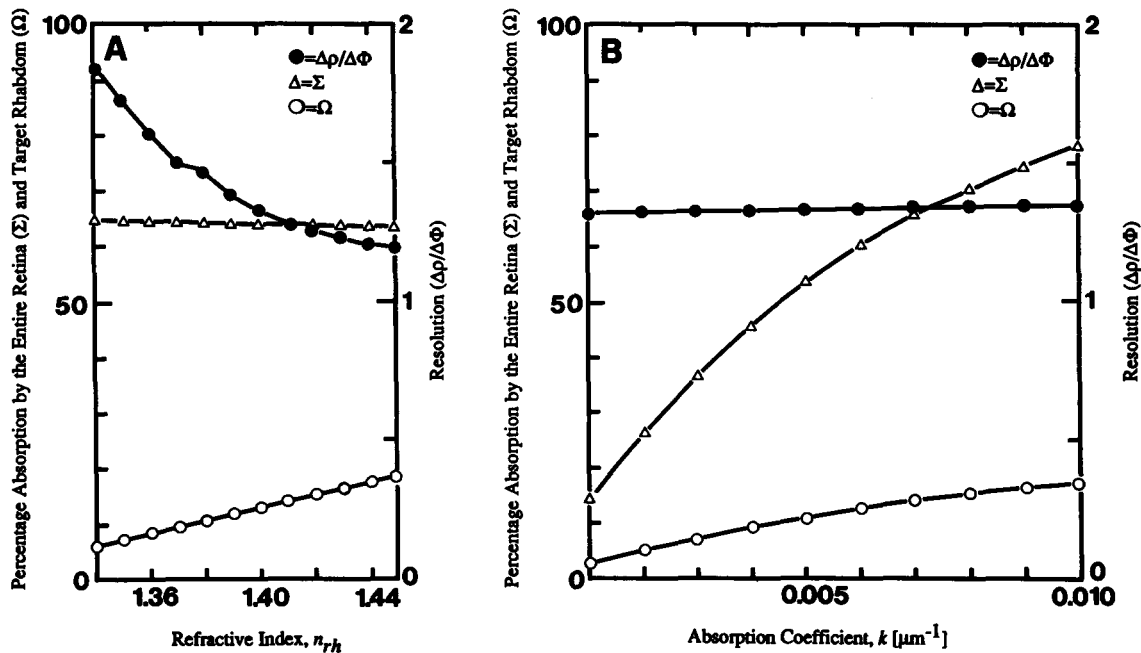


Fig. 12A, B. Resolution and sensitivity in the model superposition eye of the dung beetle *Onitis aygulus* (in the absence of both pigment and tapetal sheathing) for (A) variable refractive index, n_{rh} (k held constant at $0.0067 \mu\text{m}^{-1}$), and (B) variable absorption coefficient, k (n_{rh} held constant at 1.40). The refractive index of the medium

surrounding the rhabdoms is 1.34 in both cases. Sensitivity is defined as the percentage of light incident on the retina which is (1) absorbed by the entire retina, Σ (Δ) or (2) absorbed by the target rhabdom, Ω (○). Resolution (●) is given by the ratio of the acceptance angle to the interommatidial angle ($\Delta\Omega/\Delta\Phi$)

sheaths extended distally to about 85%. Other examples of pigment sheathing include the secondary simple eyes of day-active lycosid, salticid and thomisid spiders (Blest 1985; O'Carroll 1989), the superposition eyes of diurnal agaristid and thyridid moths (Horridge et al. 1977, 1983a; Yagi and Koyama 1963), the superposition eyes of diurnal skipper butterflies (Horridge et al. 1972; Shimohigashi and Tominaga 1986) and the superposition eyes of some diurnal beetles (Gokan 1982b, 1989; Gokan et al. 1987). Diurnal moths and skippers usually also have a tapetal sheath.

Interestingly, many arthropods, especially crustaceans, have a pigment sheath which moves up and down the rhabdoms. Examples include the superposition eyes of the crayfish *Cherax destructor* (Bryceson and McIntyre 1983), and the shrimps *Acetes sibogae* (Ball et al. 1986) and *Penaeus setiferus* (Zyznar 1970). Many of these arthropods have both nocturnal and diurnal activity: during the darkness of night, the pigment sheath is retracted proximally to a location slightly above or below the basement membrane ($\tau_{ps} = 0$), whereas during the day the pigment sheath is extended distally to surround the rhabdom completely ($\tau_{ps} = 1$). This supports the predictions of the model: at night there is no pigment sheath because of the need for greater sensitivity; during the day sensitivity is not required and an extended tapetal sheath is used to cut down light spread and improve resolution. However, a full sheath can only benefit resolution if the blur-circle is reasonably well-focussed (Fig. 7B). This condition may well be satisfied in many arthropods active both during the day and at night, because proximal migration of the distal screening pig-

ments into the clear zone during the day causes the removal of aberrated rays, greatly improving the quality of the blur-circle (Bryceson and McIntyre 1983; Warrant and McIntyre, unpublished). In the crayfish *Cherax* (Bryceson and McIntyre 1983) and also in day-active moths (Horridge et al. 1977), the pigment sheath migrates over the distal tip of the rhabdom during the day, thus reducing the rhabdom diameter and improving resolution even further.

Finally, we turn to the MTF to quantify the improvements to resolution afforded by a full pigment sheath (Fig. 11). Provided that sensitivity can be sacrificed, an eye having a full pigment sheath (curve 2) has greater potential to discriminate low to medium spatial frequencies than an eye having no sheath at all (curve 1).

Alternatives to sheathing: modifying the optical properties of the rhabdom

So far we have only dealt with solutions to light spread which involve sheathing the rhabdom in pigment or tapeta. Two other possibilities also exist: (1) increase the refractive index of the rhabdom (n_{rh}) and thereby capture a wider cone of rays by total internal reflection, or (2) increase the absorption coefficient of the rhabdom (k) and thereby allow less light to spread into neighbouring rhabdoms. Here, because many rays pass obliquely through the rhabdoms, it is the absorption coefficient (absorption per unit length) that is important, and not the optical density of the whole rhabdom (absorption coefficient \times rhabdom length).

The effect of increasing n_{rh} in the model eye is three-fold (Fig. 12A): (1) the percentage of light absorbed by the entire retina (Σ) marginally decreases; (2) the percentage of light absorbed by the target rhabdom (Ω) increases steadily; and (3) the resolution of the eye ($\Delta\theta/\Delta\Phi$) steadily improves. Nevertheless, these improvements are only relatively modest, especially over a realistic range of refractive index. The available evidence suggests that arthropod rhabdoms have refractive indices in the range 1.35–1.40 (Land 1981; Nilsson and Howard 1989).

An equivalent alternative to increasing the refractive index of the rhabdom is to decrease the refractive index of the medium surrounding the rhabdom. This solution would likewise allow a wider cone of rays to be captured. A low refractive-index surround or 'refractive index barrier' (Blest 1985) is not just restricted to arthropod eyes of low F-number (such as diurnal salticid spiders: Blest 1985; O'Carroll 1989), but may also be found in diurnal apposition eyes of much higher F-number (e.g. locusts and dragonflies: Horridge 1969; Williams 1983). The barrier is usually formed by non-pigmented glial cells or even by enlargements of the extra-cellular space around the rhabdom (Meyer-Rochow 1974).

If the absorption coefficient (k) of the rhabdom is increased, the sensitivities of both the entire retina (Σ) and the target rhabdom (Ω) increase, but there is no change in resolution ($\Delta\theta/\Delta\Phi$). Vertebrates typically have an absorption coefficient 5 times larger than that of arthropods (Denton and Nicol 1964), and it would appear from the model that the only advantage conferred by this strategy is improved sensitivity.

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