J. exp. Biol. 164, 227–242 (1992)
Printed in Great Britain © The Company of Biologists Limited 1992

THE QUALITY OF VISION IN THE CTENID SPIDER *CUPIENNIUS SALEI*

BY M. F. LAND

Neuroscience Research Centre, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK

AND F. G. BARTH

Institut fur Zoologie der Universitat Wien, Althanstrasse 14, A-1090 Wien, Austria

Accepted 20 November 1991

Summary

Much is known about the mechanosensory behaviour of the spider *Cupiennius salei* Keyserling, but much less about its visual capabilities. In this study the quality of the optical image, the retinal resolution and the fields of view were assessed for each of the four pairs of eyes. The image is of good quality in all eyes. The principal (antero-median) eyes lack a tapetum and have an inter-receptor angle of 2.9°. The three secondary eyes (antero-lateral, postero-median and postero-lateral) all have 'gridiron' tapeta with receptors arranged in rows. The angular separations (along rows × between rows) are 3.6° × 9.3°, 0.9° × 2.3° and 1.0° × 3.0°, respectively. Although the disposition of eyes on the head is similar to that of pisaurid spiders, all other features of the eyes, including the sizes and shapes of the fields of view, resemble those of lycosid spiders. The peripheral visual system of *Cupiennius* can thus, in principle, support a similar range of visual behaviour to that of lycosids, which includes prey capture, predator avoidance and courtship.

Introduction

Much of the behaviour of the ctenid spider *Cupiennius salei* is mediated by its mechanical senses, with both courtship and prey capture involving the detection of substratum-borne vibrations (Barth, 1985). This species is largely nocturnal and shows clear peaks of locomotor activity at night. The extent of visual involvement in the various behaviours is not known, but it has been claimed that prey capture is not impaired if the eyes are covered. In spite of this, *Cupiennius* and other ctenids appear to have eyes that are similar to those of other hunting spiders, and in their external appearance they do not seem to be either reduced or degenerate. Furthermore, the eyes connect to extensive neuropiles that again are typical of other hunting spiders (N. J. Strausfeld, P. Weltzien and F. G. Barth, in preparation). In view of the paradoxical absence of visual behaviour, we decided

Key words: spider, *Cupiennius salei*, eyes, image quality, retina, resolution, fields of view.

to examine the eyes of *Cupiennius* in detail and to assess their optical performance.

These spiders were originally classed as a separate family, the Ctenidae, but were reclassified by Homann (1961, 1971) as the Cteninae, a sub-family of the Lycosidae and sister group to the Lycosinae, or wolf spiders. This redesignation was based largely on eye morphology. However, Lachmuth *et al.* (1985) retain the family name Ctenidae in a recent revision of the genus *Cupiennius*. Whatever their exact taxonomic status, it is clear that the ctenids and lycosids are closely related. Some physiological information is available for wolf spider eyes (Homann, 1931; Land, 1985) and the new information in the present paper provides another opportunity to assess the extent of similarity between the two groups and also to make comparisons with other groups of hunting spiders such as the salticids. Many wolf spiders are known to be visual hunters, responding to moving objects with either attack or evasion. Thus, a strong resemblance between the eyes of the Cteninae and the Lycosinae would suggest that it would be worthwhile to look harder for visual behaviour in *Cupiennius* and other ctenids.

Materials and methods

Two typical adult female *Cupiennius salei* were used in this study. They came from a colony kept in Vienna, and were almost identical, with a cephalothorax length of 9.5 mm. Four kinds of measurement were made on one animal or both: anatomical measurements of the eyes and components of the retina, focal length measurements, ophthalmoscopic measurements of the retinal structures and field of view measurements.

Measurements of the external dimensions of the eyes were made from photographs of living spiders, narcotised with CO_2. The dimensions of the retinal structures were measured on 8 μm sections from standard wax-embedded preparations fixed in 5 % formaldehyde in spider saline and stained with haematoxylin and eosin. Roughly 15 % shrinkage is expected from this method, and all measurements on the sections have been increased by this amount.

Focal lengths of the lenses were measured using the 'hanging drop' method of Homann (1928; see also Land, 1985). The lenses are dissected from the head with some surrounding carapace and placed in the meniscus of a hanging drop of saline so that the outer surface is in air and the inner surface in saline, as in life (see Figs 1A, 4B). The image plane is then examined with a microscope while the spider's lens views a target, such as a pair of lines, at a known distance (u). The object and image sizes (O and I) are measured, and from these the lens–image distance (v) is determined from: $v/u=I/O$. The focal length (or posterior nodal distance, f) is then found from the lens formula: $(1/v)-(1/u)=1/f$.

The retina of the antero-lateral (AL), postero-medial (PM) and postero-lateral (PL) eyes, all of which have reflecting tapeta, can be studied directly in the living animal using an ophthalmoscope. Some detail can be seen with an ordinary medical ophthalmoscope, but in this study a special instrument was used, more

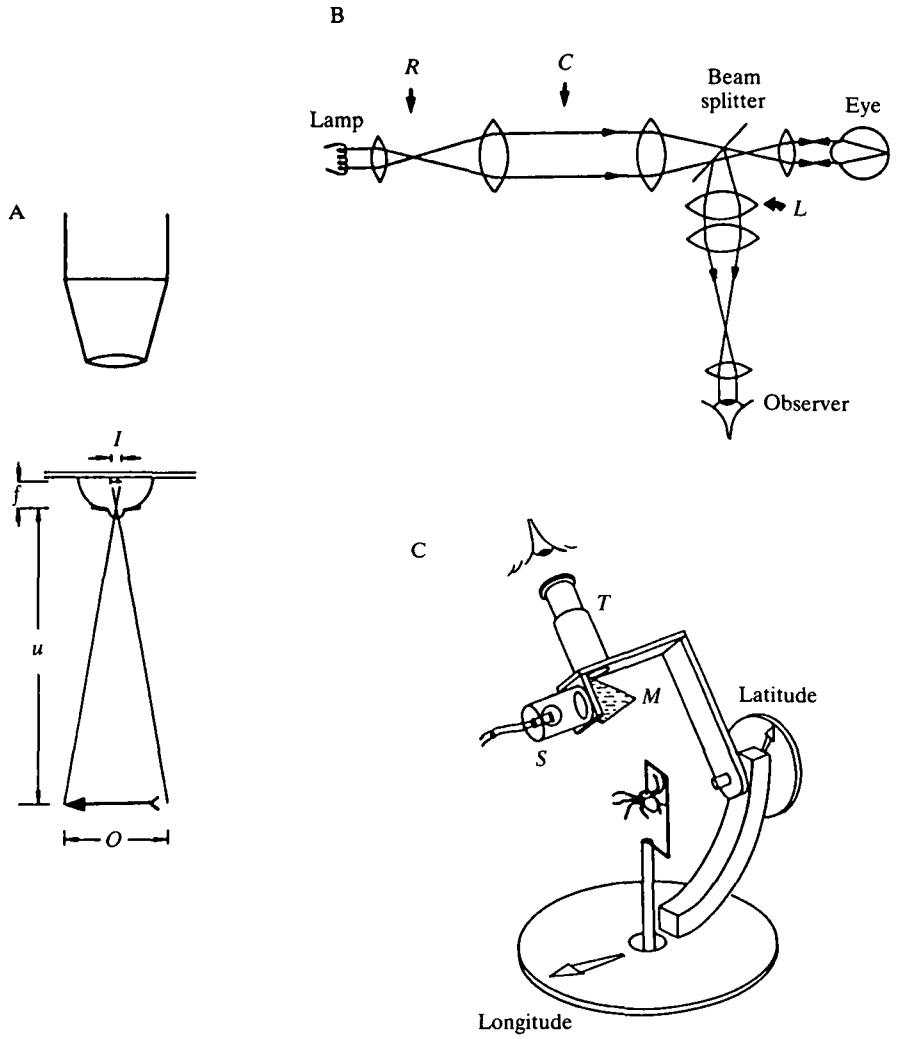


Fig. 1. Methods used in this study. (A) Hanging drop method for measuring focal length (Homann, 1928). Symbols are explained in the text. (B) Ophthalmoscope for observing living retina (see Fig. 4C) (Land, 1969). *R*, plane conjugate with infinity for objects to be imaged on retina; *C*, plane conjugate with cornea for masking illuminating beam; *L*, removable lens allowing observation of either retina or eye surface. (C) Cardan-arm goniometer for measuring fields of view (see Fig. 5) (Land, 1985). *T*, telescope; *S*, light source; *M*, mirror.

suitable for small eyes (Fig. 1B). Details of its construction are given in Land (1969, 1984). The instrument has two optical paths, for viewing and illumination, separated behind the objective lens by a beam splitter. The viewing beam can be used either as a microscope to examine the external features of the eye or, by inserting lens *L*, it can be used to view the spider's retina, which is conjugate with

infinity (Fig. 4C). When used in this way, the field of view in the eyepiece can be calibrated directly in terms of the angle subtended by structures in the spider's eye, and so can provide a direct *in vivo* measure of resolution. In the illuminating beam, objects placed in the plane *R* are imaged on the retina by the spider's own lens, and this plane can thus be used to position test objects of known angular dimensions onto the retina. The principal (AM) eyes, which lack a tapetum, do not reflect enough light for the ophthalmoscopic method to be usable.

Fields of view are measured with a small telescope mounted on a Cardan-arm goniometer (Fig. 1C). The telescope *T* has a narrow-angle light source (*S*) attached, which illuminates the viewing direction *via* a half-silvered mirror (*M*). As the telescope is rotated around the animal, each of the secondary eyes 'lights up' in turn, as green light is reflected back from the tapetum (see Land, 1985, Fig. 3c). The angular field over which a particular eye reflects light corresponds to the angle subtended by the tapetum, which we know from histological study to be co-extensive with the retina. This method can also be used to study the principal (AM) eyes, because although these lack a tapetum there is a noticeable change from a pinkish-brown reflex to a darker brown at the boundary of the retina. The fields of view in Fig. 5 are plotted on Aitoff's equal area projection, which allows the whole 360° field to be shown and preserves the relationships of the field sizes.

Results

Anatomy of the eyes

Like most other spiders, *Cupiennius* has eight eyes of two kinds. They are all superficially similar, but the antero-median, or 'principal', eyes lack a reflecting tapetum and have receptors with a quite different structure from those of the other three 'secondary' eyes (antero-lateral, postero-median and postero-lateral). The arrangement of the eyes is shown in Fig. 2. They are in two strongly curved rows, the AM and AL eyes in front of the PM and PLs. The AMs lie directly in front of the PMs, and similarly with the ALs and PLs. This disposition is very similar to that in the lycosid relative *Pisaura*, and not like that of typical lycosids, where the PL eyes are usually set much further back and the PM eyes further out, so that they lie behind the ALs rather than the AMs. The relative sizes of the eyes, however, follow the typical lycosid pattern (Table 1). The PM eyes are the largest, the PLs are slightly smaller, followed by the AMs and finally the ALs. In *Pisaura*, the ALs are larger than the AMs, and not much smaller than the other secondary eyes. In salticids the order is completely different, with the AMs much the largest, followed by the ALs, PLs and PMs.

The eyes themselves all have a similar shape, the retina forming a roughly hemispherical cup behind the lens, which is biconvex. The space between the lens and retina is filled by a cellular 'vitreous'. Both front and rear lens surfaces are near hemispheres, and they share the same centre of curvature; however, the radii are different, the smaller rear surface having a radius of curvature about 0.8 times that of the front. The focal lengths of the lenses, measured by the hanging drop

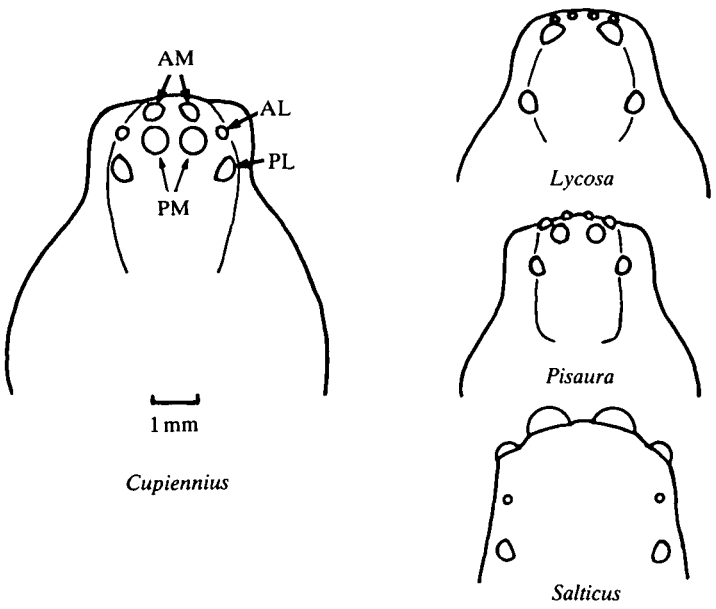


Fig. 2. Layout of the eyes of *Cupiennius*, left, and three other hunting spiders, right (not to the same scale). AM, antero-median eyes; AL, antero-lateral; PM, postero-median; PL, postero-lateral.

Table 1. *Dimensions of the eyes (μm) (spider 1)*

Eye	Diameter (D)	Radius of curvature		Focal length (f)	F-number (f/D)
		Anterior	Posterior		
AM	396	204	157	293	0.74
AL	256	147	–	148	0.58
PM	629	320	236	448	0.71
PL	625	320	–	432	0.69

AM, antero-median; AL, antero-lateral; PM, postero-median; PL, postero-lateral.

technique, are also given in Table 1. As expected, these are proportional to the eye diameters, and the F-numbers of the lenses (f/D, where f is focal length and D is diameter) are all in the range 0.58–0.74. By the standards of camera lenses, these are astonishingly low figures, implying very bright images, but they are not atypical of hunting spiders generally (Land, 1985).

The structure of the AM retina is different from that of the other three eyes. The receptors cells are about 90 μm long and 14 μm wide, with their short rhabdomeric regions adjacent to the vitreous (Fig. 3A). In cross section the cells in this region form a rather irregular lattice, with each receptor having rhabdomeres on three or

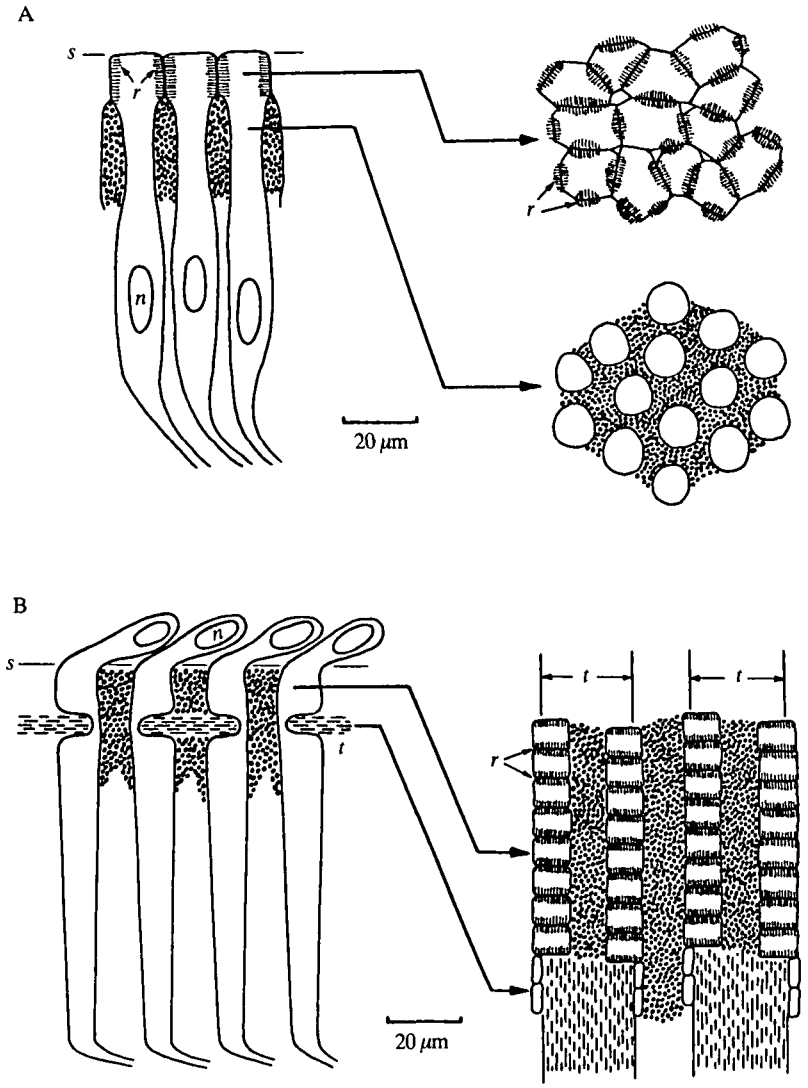


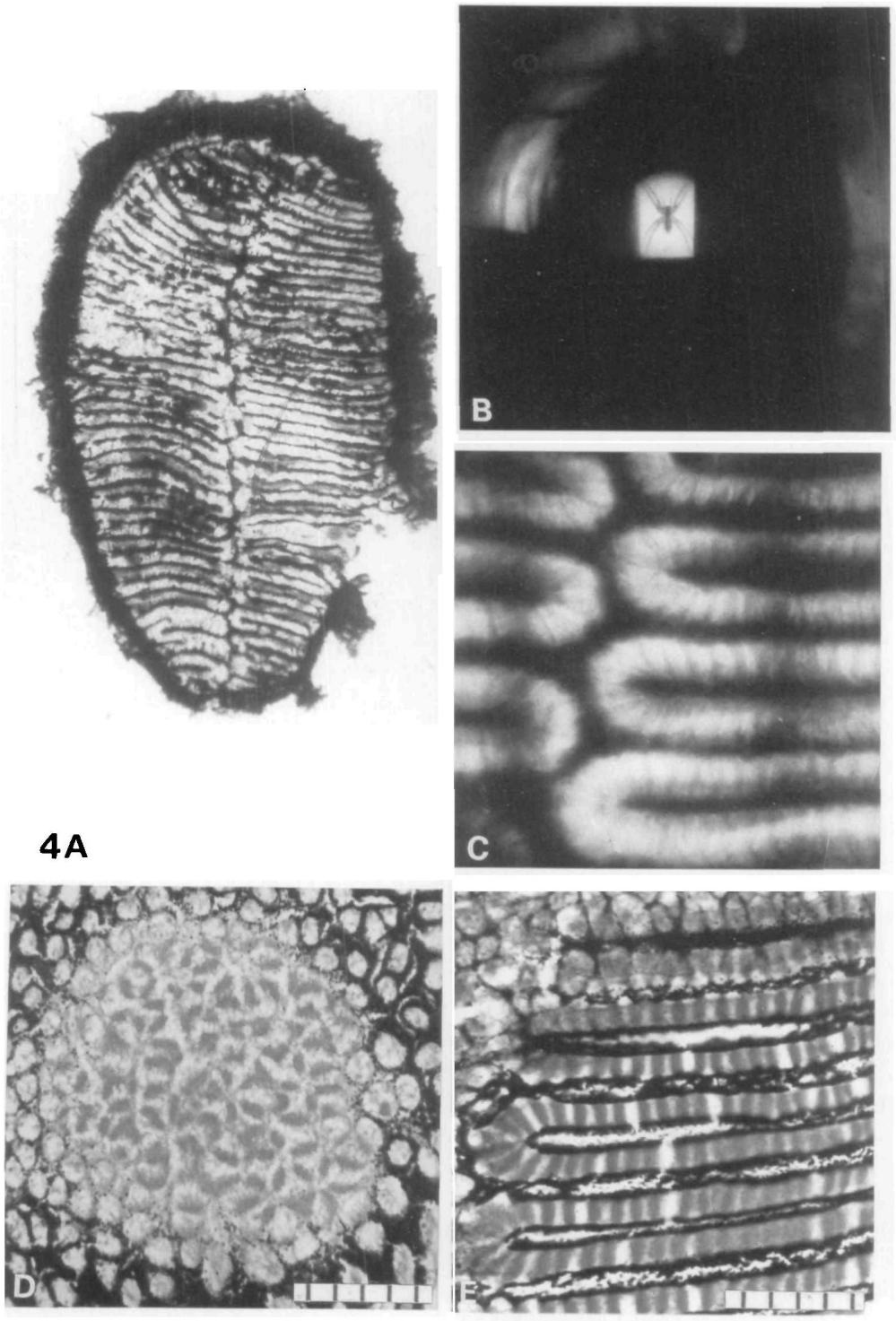
Fig. 3. Histology of the retinae of a principal eye (A) and a secondary (PM) eye (B). Semi-diagrammatic, but to scale. *n*, receptor nuclei; *r*, rhabdomeres; *s*, surface of retina; *t*, location of tapetal strip.

four sides (Figs 3A, 4D); their appearance is very similar to that described for the lycosid *Arctosa* by Baccetti and Bedini (1964). It seems that the rhabdomere in one cell is always paired with a rhabdomere in the adjacent cell, and the rhabdomeres occupy about 40% of the cross section in this region. The rhabdomeric region is surprisingly short, 12.5 μm, for an eye whose other features suggest low-light use (see Discussion). Beneath this region the receptor runs through a 25 μm thick layer of dark pigment and then widens into a long region containing the nucleus. This

then tapers to form an axon of the optic nerve which runs to the first optic neuropile. There are no other neurones in the eye. The retina occupies most of the back of the eyecup and appears to be uniform. There is no suggestion that this retina has any of the characteristics of salticid retinae, namely multiple receptor types arranged in tiers, with large differences in packing density in different regions (Land, 1969). Blest and O'Carroll (1989) have found evidence of two-layer tiering in the AM eyes of the wolf spider *Geolycosa godeffroyi*, although not in the type genus *Lycosa*. *Cupiennius* does not show tiering and appears to have an AM retina typical of those described previously for lycosids (Homann, 1931; Baccetti and Bedini, 1964).

The secondary eyes all have a similar structure, except that the AL eyes are much smaller than the PMs and PLs and are less precisely ordered. They are all built around a 'gridiron' tapetum, which consists of a series of parallel strips of reflecting material forming a double ladder-like array (Fig. 4A). In the PM and PL eyes the strips run roughly horizontally (parallel to the animal's longitudinal plane). Each tapetal strip supports two rows of receptors as indicated in Fig. 3B. These receptors differ from those of the AM eyes in a number of ways. First, the nucleus is in the part of the cell nearest the lens, and the nuclei form a thin layer between the vitreous and the retina proper. Second, the rhabdomeres are on two sides of the receptors only, the cells being rectangular in cross section in the region above the tapetum and organised into linear arrays (Fig. 4E). As in the AM eyes, the rhabdomere of one receptor abuts the corresponding one from the next receptor, to form what appears to be a single rhabdom. Again, about 40 % of the cross section in this region is occupied by the rhabdomeres. Third, the rhabdomeric part of the cell 'sits' on the tapetal strip, with a narrow isthmus passing around it before expanding again. The receptor then extends inwards without rhabdomeres for about 85 μm before tapering to form an optic nerve fibre. This structure means that nearly all of the rhabdomeric region is backed by tapetum, and so receives light twice, once before and once after reflection; this doubles the effective length of the rhabdom for the purposes of light absorption. The gridiron structure of the secondary eyes results in retinae which sample the image in a very different way from the AM retina. Not only are the receptors arranged strictly in rows, but the spacing of their centres differs considerably, depending on the direction. The receptor spacing between the receptor rows is greater than that along the rows by more than a factor of two (see Table 2), and this must mean that the horizontal resolution of the eyes is much better than the vertical resolution.

This description of the secondary eye structure is once again very similar to that given by Baccetti and Bedini (1964) for *Arctosa*. One small difference is that in *Arctosa* there is dark pigment between receptors within a row, rather than just between the rows themselves as in *Cupiennius*. Amongst lycosids, *Pardosa* is similar to *Arctosa*, but *Geolycosa* and *Trochosa* are like *Cupiennius*. Presumably these differences in the optical isolation of one receptor from another, as well as the asymmetries in sampling, must have functional meanings; but our ignorance of the behavioural role of these eyes is too profound to provide any clues.



4A

Fig. 4. (A) Whole PM retina, showing the gridiron pattern of tapetal strips. (B) The image of a lycosid spider photographed at the focus of the lens of a PM eye, using the hanging-drop method (Fig. 1A). The image size is approximately that of another *Cupiennius* at 25 cm. The magnifications in A and B are approximately the same, so that the optical and retinal resolution can be compared directly. (C) Ophthalmoscopic image of part of the PM retina, near the midline, photographed through the eye's own lens using the instrument pictured in Fig. 1B. The boundaries between the receptors are clearly visible (compare Figs 3 and 4E). The two blurred vertical lines are the images of lines 10° apart in the field of view and act as a direct angular calibration. (D) Tangential histological section of the centre of the AM retina (cf. Fig. 3A), showing the irregular arrangement of the rhabdoms. (E) Similar section of the PM retina (cf. Figs 3B and 4C), showing the linear arrangement of the rhabdoms. Scale bars, 5×10 μm.

Resolution

The capacity of an eye to resolve detail in the environment is limited by two factors: the ability of the eye to produce a sharp image and the fineness of the retinal mosaic (see Land, 1981). In the human eye both factors are approximately matched, with the cone mosaic just able to resolve the finest pattern the optics can provide – a grating with a period of 1 min of arc. In some spiders, such as the salticid *Portia*, the resolution of the AM eyes is perhaps only a factor of 5 lower than that in humans (Williams and McIntyre, 1980), but in *Cupiennius* the eyes' performance is not comparable with this. The relatively coarse receptor mosaic in both the principal and secondary eyes means that the finest resolvable grating will have a spatial period (the angular subtense of a line pair at the eye) of 2° or more.

It is clear that the *potential* resolution of the eyes' optics is much better than this. The ultimate limit to resolution, which cannot be improved upon, is set by the amount of blur that results from diffraction at the aperture. Expressed as the angular spatial period of the finest grating that can be resolved, this limit is given by w/D rad, or $57.3w/D$ degrees, where D is the eye diameter and w the wavelength of light. Notice that the bigger D is, the finer the resolution. Eye diameters range from 256 μm (AL) up to 629 μm (PM) and, taking w as 0.5 μm, this gives grating periods between 0.11 and 0.05°. These values are smaller by more than an order of magnitude than the angular receptor spacing, so diffraction certainly does not limit resolution in any of these eyes. It is also possible that the quality of the image is affected by defects other than diffraction, the most important being spherical aberration, which is potentially very serious in a lens with an F-number as low as 0.6. However, there are good reasons for thinking that spider lenses are at least partially corrected for this by having an optically inhomogeneous structure (Blest and Land, 1977).

Two kinds of direct evidence suggest that the image is as good as or better than the sampling ability of the retina. (The finest grating the retina can resolve will have a period equal to twice the receptor spacing, since one receptor is required for each dark and each light stripe; see Land, 1981.) Direct inspection of the image produced by an excised lens (Fig. 4B) shows that it is indeed of good quality and

considerably finer than the retinal mosaic, which is also shown on the same scale. The images of the spider's palps, for example, have a diameter only about one-tenth of the width of a receptor. This demonstration is not entirely convincing, however, because the 10× objective (N.A. 0.25) used to take the photograph does not accept the whole of the 72° cone of light that the spider's lens uses to produce the image. This means that the image seen in Fig. 4B is likely to be of somewhat better quality than that in the eye itself, unless the lens is entirely free from defects, which is perhaps unlikely. The second method avoids this problem. The ophthalmoscope (Fig. 1B) views the retina, and any image upon it, through the whole pupil of the eye, and so the view of the retina seen through this instrument is degraded by the eye's optics in the same way as the image seen by the spider itself. An important corollary of this, explained by Land and Snyder (1985), is the following: if the pattern of retinal receptors is clearly visible ophthalmoscopically, using the eye's natural pupil, then the optical resolution must be at least twice as good as the resolution of the retinal mosaic. Fig. 4C shows that this is the case. Not only are the receptor rows clearly visible, but so too are the divisions between receptors along the rows. We can conclude confidently that the optics of these eyes is more than adequate for the resolution of the receptor mosaic.

The retinal resolution can be obtained in two ways. If the receptor spacing (s) and focal length (f) are known, then the inter-receptor angle is s/f rad, or $57.3s/f$ degrees. This calculation was made for the AM, AL and PM eyes, where the receptor spacing was determined histologically (Fig. 4D,E and Table 2). The second method is direct ophthalmoscopic observation (Fig. 4C). When the instrument (Fig. 1B) views the spider's retina it is actually focused on infinity, because light reflected from the retina emerges from the eye as a parallel beam, and if the spider is removed the instrument simply becomes a telescope. This can be calibrated in angular units by observing a scale at a known large distance (e.g. 1 cm scale at 57.3 cm provides units of 1°); this calibration, transferred to an eyepiece graticule, can then be used to provide an angular scale for the structures that are visible in the eye. This method is very direct, it can be used on the living eye, and it should be very accurate. Its only drawback is that it cannot be used with the AM eyes, which lack a tapetum. In Table 2 the results of the methods are compared. In the PM eyes, for which both kinds of data are available, the methods agree to within 20%. The discrepancy may be due to measurement errors or to differences in the part of the retina chosen. In any case, it is not large and indicates that either method can be used to give a reliable result.

The results in Table 2 show that the PM and PL eyes have the highest resolution, with inter-receptor angles close to 1° along the rows (approximately horizontal) and 2–3° in the orthogonal direction. The AL eyes have very much poorer resolution, which is only partly explained by the shorter focal length. In the ophthalmoscope they also seem to be poorly focused. Poor AL resolution is also found in lycosids, but interestingly not in pisaurids, where the three secondary eyes (AL, PM, PL) seem to be functionally similar. The principal (AM) eyes have inter-receptor angles of about 3°, larger than in the PM and PL eyes, but by no

Table 2. *Resolution of the retinae (spider 2)*

Eye	Receptor spacing measured histologically, allowing 15% shrinkage (μm)		Angular separation (degrees) from histology ophthalmoscopy			
	Along rows (a)	Between rows (b)	$57.3a/f$	$57.3b/f$	Direct measurement	
AM	14.9	14.9	2.9	2.9	–	
AL	9.2	23.9	3.6	9.3	–	
PM	7.5	20.3	1.0	2.6	0.9	2.3
PL	–	–	–	–	1.0	3.0

AM, antero-median; AL, antero-lateral; PM, postero-median; PL, postero-lateral; f, focal length.

means poor by spider standards generally. They do not compare, however, with the AM eyes of salticids, where the resolution is at least an order of magnitude finer (Land, 1969; Williams and McIntyre, 1980).

The same data allow us to estimate the eyes' depth of focus, which is a function of the size of the eye and the separation of the receptors. The animal's nearest distance of clear vision (U) is given approximately by $U=fD/2s$ (Land, 1981, p. 499). For the AM eyes, U is about 4 mm, which is so close that everything the animal might need to see is effectively in focus. For the larger PM eyes, U is larger, between 7 and 19 mm depending on whether the value for the separation is taken along or between rows. Both figures are less than the length of a leg, so again there is no degradation of vision at any distance at which behavioural interactions might take place. No accommodation mechanisms are known in spider eyes, and in this case it is clear that none is needed.

Fields of view

The fields of view of the eyes of both living *Cupiennius* specimens were measured with the telescope goniometer (Fig. 1C). They are shown in Fig. 5, plotted onto an Aitoff equal area projection which represents a globe at infinity with the spider at the centre. The right fields of view of the secondary eyes are shown for both animals and the left principal (AM) eye is shown for one only. Fields of view for representatives of three other families are also given for comparison.

The main features are that the PM and PL eyes between them cover nearly the whole upper hemisphere, and down to 40° below the horizontal plane. The anterior edge of the PM field just reaches the sagittal midline, where the eye on the other side takes over. Similarly, above the animal the PM and PL fields on the two sides just meet in the sagittal plane. In both specimens there is a gap 5–20° wide between the fields of the PM and PL eyes: this does not seem to be an artefact of the method, because no such gap is seen between the PM fields at the front. Presumably there really is a gap in the animal's visual coverage in this region.

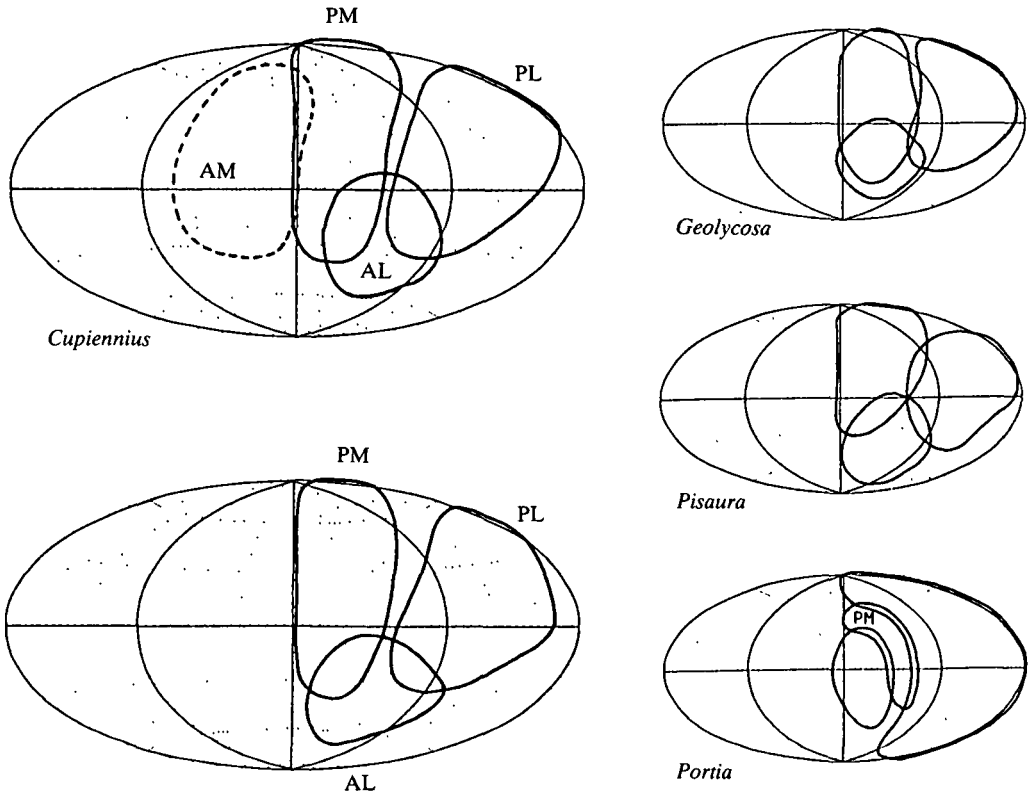


Fig. 5. Fields of view of the eyes of two female *Cupiennius* (left) and three other hunting spiders (right) measured with the goniometer depicted in Fig. 1C. The fields are plotted onto a globe with the spider at the centre, and the projection used depicts the whole of that globe, marked off at 90°, 30° and 5° intervals. The projection gives equal areas for equal solid angles, but does distort shapes especially in the posterior hemisphere. The projection is centred on the spider's vertical plane of symmetry and a plane level with the ventral rim of the carapace of the cephalothorax. The lycosid and pisaurid (right) are closely related but the salticid (*Portia*) is not. *Portia* was chosen because its PM eyes do have a distinct field of view, whereas in most salticids they do not. Fields of view of other spiders are given in Land (1985).

There is also a small gap at the rear of the animal, where the abdomen would in any case obscure the view. The PM eye has a distinctly elongate field, as one would expect from the shape of the retina (Fig. 4A), whereas the PL eye's field is not far from circular, although this appears rather distorted on the projection used here. The field of the AL eye is small and downward-pointing, looking at the region just in front of the spider's chelicerae. It overlaps the bottom of the fields of view of both the PM and PL eyes. This overlap, and the poor resolution of the AL eye, are characteristics of lycosids, but not, for example, of pisaurids (Fig. 5).

The AM field of view is harder to determine precisely because there is no tapetum, but there is just sufficient difference in the reflected colour of the parts of

the back of the eye where retina is present and absent for an approximate map to be made (dotted line in Fig. 5). The field covers a similar frontal region of space to that viewed by the PM eye, although the field is slightly less elongate, and it has a small contralateral region. It is quite unlike the boomerang-shaped AM field of a salticid, which is very much smaller and narrower. Salticid retinae can move over tens of degrees in any direction, however, and this ability to scan makes up for their small size. *Cupiennius* eyes also move, but only over a few degrees and probably only in one plane. The impression one has is that this is more of a jitter, possibly to keep the image 'refreshed', rather than systematic scanning.

Comparing the fields of view of *Cupiennius* with those of all the other hunting spiders for which data are available, it seems that the best 'match' is with the Lycosidae.

Discussion

The quality of vision

Nothing in this study has given any reason to suppose that ctenid vision is in any way defective compared with lycosid vision. Fig. 4B,C demonstrates that the images provided by the lenses are good and certainly of as high a quality as the retinal mosaic can exploit. Comparing the retinal resolution of the different eyes of *Cupiennius* with those of *Lycosa*, worked out by Homann (1931) by methods similar to those used here, we find that *Cupiennius* has slightly better resolution in all cases. The inter-receptor angles are: AM eyes, 2.9° (4–7°); AL, 3.6°×9.2° (7°); PM, 0.9°×2.3° (1.8–2.3°); PL, 1.0°×3.0° (1.8°) (numbers in brackets are for *Lycosa*). The *Lycosa* studied by Homann was considerably smaller than *Cupiennius*, but in fact that makes rather little difference. Quite small *Pardosa* species have better resolution still, and it seems to be true that retinal resolution is more or less independent of eye (and body) size within the lycosids and their near relatives. This will occur naturally if the dimensions of the receptors increase in direct proportion to the focal length, so that the whole eye scales up together. Such a strategy will result in larger animals having greater sensitivity because their lenses are larger, but with no change in resolution.

We can conclude that *Cupiennius* should be capable of much the same visual performance as a wolf spider. Certainly, there is nothing in the peripheral visual system to prevent this. It has to be said, however, that lycosid vision generally is nothing like as acute as that of the most impressive visual hunters, the salticids. Comparable inter-receptor angles to those just given, for *Phidippus johnsoni*, are: AM, 0.15°; AL, 0.5–1.5°; PM, >10°; PL, 1° (Land, 1969). Interestingly, the PM eyes are the 'best' in lycosids, but are almost functionless in most salticids (*Portia* in Fig. 5 is an exception).

Affinities of the ctenid spiders

The present study gives strong support to Homann's view that ctenids and lycosids are closely related. Apart from the external layout of the eyes (Fig. 2),

which is possibly more pisaurid-like than lycosid-like, all other features are indistinguishable from those of lycosid eyes. Perhaps the most telling are the small size, small field of view and low resolution of the AL eyes, which suggest that they are no longer part of the same system as the PM and PL eyes. The wolf spiders (*Lycosinae*) are the only other group where this occurs. It is not found in *Pisaura*, where the AL resolution is similar to that of the other two secondary eyes (M. F. Land, unpublished observations) and where the three fields of view are contiguous rather than overlapping.

Problematic aspects of eye design

The secondary eyes of *Cupiennius*, and lycosids generally, have a very odd design, not found elsewhere in the animal kingdom. The lens is fairly conventional, although of an extremely low *F*-number, suggesting use in low light levels. The gridiron tapetum is certainly unusual, although it is a perfectly good solution to the problem of providing the receptors with a reflector behind each rhabdom, whilst at the same time allowing the cell bodies to pass through and beyond the tapetum (in vertebrates the problem is solved by the retina's inverted structure). The strangest feature, however, is the extremely short length of the rhabdoms, only about 10 μm, compared with 50 μm for a fish rod outer segment and 200 μm for a squid or octopus rhabdom. Rhabdoms of insects and crustaceans absorb about 1 % of the incident light per micrometre, at the wavelength of maximum absorption, meaning that a 10 μm rhabdom absorbs less than 10 %, whereas a squid rhabdom, 20 times longer, will absorb nearly all light reaching it. Since vision in dim conditions requires the highest photon signal that can be obtained, because of the 'noisiness' of small photon numbers (see Land, 1981), an absorption of only 10 % seems to mean that the spider is throwing away the advantage gained by the high light-gathering power of the lenses.

The reason for this problem is that the retinal design makes it impossible to have both good resolution and high photon capture; the receptors cannot be made very long because light will cross between them and thereby wreck the quality of the received image. Fig. 6 illustrates this. A lens with an *F*-number of 0.7 produces an imaging cone of light 71° wide {2arctan[1/(2×*F*-number)]}. However, an arthropod rhabdom with a refractive index of not more than 1.37, surrounded by fluid of refractive index 1.335, will only contain within itself an incident cone smaller than the angle of total internal reflection, approximately 26° {2[90−arcsin(1.335/1.37)]}. Only within this angle will the rhabdom act as a light guide, and clearly it is much too small to take in all the light from the lens. The excess will spill through into neighbouring receptors, unless these are so short that the whole of the geometrical image of a point source can be contained within them. Fig. 6 shows some of the conditions that allow this. For a rhabdom 8 μm wide, a 71° beam will be contained only if the receptor is less than 11.2 μm long (Fig. 6A) and, if there is a flat tapetum behind the receptor, the acceptable length will be only half this (Fig. 6B), although a concave tapetum will help matters slightly (Fig. 6C). Thus, in spiders where the individual receptors are not optically isolated, as is the case

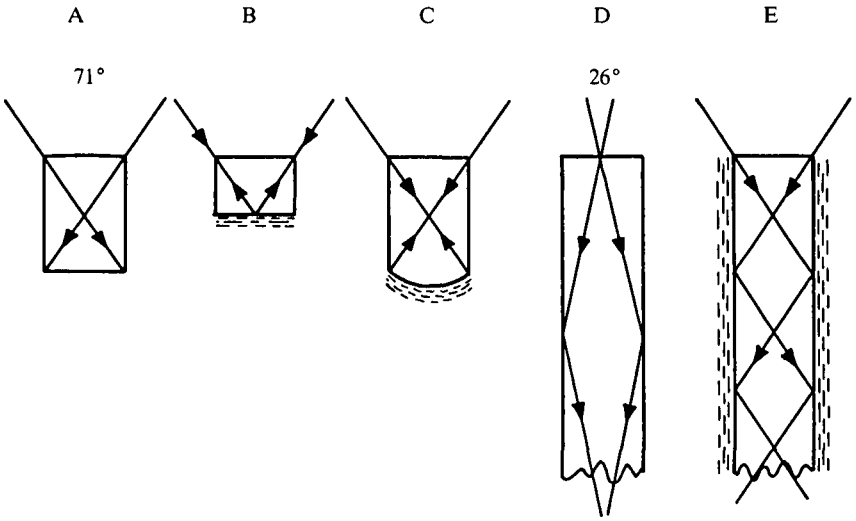


Fig. 6. Constraints on the length of receptors of different types such that they do not lose light to their neighbours. Explanation in the text.

along tapetal rows in *Cupiennius*, a short rhabdom is mandatory if resolution is not to be compromised. The alternative is to have an eye with a high *F*-number, as in the AM eyes of salticids. A lens that provides the 26° cone of light that will just be retained in a receptor by total internal reflection (Fig. 6D) will have an *F*-number of 2.2, and this provides an image that is dimmer than that of a lens with an *F*-number of 0.7 by a factor of 9.9. This is almost the same as the difference in photon absorption by a 10 μm rhabdom (about 10 %) and one several hundred micrometres long. Low *F*-number, short-rhabdom eyes and high *F*-number, long-rhabdom eyes are thus alternative solutions to the same problem. As Warrant and McIntyre (1991) have recently pointed out, a better solution, which some moths and many crustaceans use, is to have reflecting material isolating each receptor from its neighbours. Putting each receptor in a 'tin can' will permit a low *F*-number without receptor crosstalk (Land, 1984) and without light loss (Fig. 6E). No spider seems to have found this solution.

A dual visual system

The AM eyes differ from the others in retinal structure (Fig. 3) and also in being moveable. In *Cupiennius* each has two muscles joining the back of the eye to the carapace above and below the eye. The extent of movement, judged by looking for shifts of the edge of the field of view (Fig. 5), is not great, perhaps a few degrees, and it is not comparable with the large scanning movements seen in salticids. However, these small movements occur frequently and if they do nothing else they will prevent the neural image in the AM eyes from adapting. We presume that the neural image in the fixed secondary eyes *does* adapt, and that they are thereby only able to detect changes induced by the movement of external objects.

We anticipate that, as in salticids (see Land, 1972), the function of the secondary eyes is to detect motion and that of the principal eyes is to analyse stationary objects. The observation that the AM and PM eyes have essentially the same field of view (Fig. 5) argues strongly in favour of them having different and complementary roles. As we have seen, *Cupiennius* has potentially impressive visual capabilities. It is time to seek some visual behaviour to go with them.

References

BACCETTI, B. AND BEDINI, C. (1964). Research on the structure and physiology of the eyes of a lycosid spider. I. Microscopic and ultramicroscopic structure. *Archs ital. Biol.* **102**, 97–122.

BARTH, F. G. (1985). Slit sensilla and the measurement of cuticular strains. In *Neurobiology of Arachnids* (ed. F. G. Barth), pp. 162–188. Berlin: Springer.

BLEST, A. D. AND LAND, M. F. (1977). The physiological optics of *Dinopis subrufus* L. Koch: a fish lens in a spider. *Proc. R. Soc. Lond.* B **196**, 198–222.

BLEST, A. D. AND O'CARROLL, D. (1989). The evolution of the tiered principal retinae of jumping spiders. In *Neurobiology of Sensory Systems* (ed. R. N. Singh and N. J. Strausfeld), pp. 155–170. New York: Plenum.

HOMANN, H. (1928). Beiträge zur Physiologie der Spinnenaugen. I. Untersuchungsmethoden. II. Das Sehvermögen der Salticiden. *Z. vergl. Physiol.* **7**, 201–269.

HOMANN, H. (1931). Beiträge zur Physiologie der Spinnenaugen. III. Das Sehvermögen der Lycosiden. *Z. vergl. Physiol.* **14**, 40–67.

HOMANN, H. (1961). Die Stellung der Ctenidae, Textricinae und Rhoicininae im System der Araneae. *Senck. Biol.* **42**, 397–408.

HOMANN, H. (1971). Die Augen der Araneae. Anatomie, Ontogenie und Bedeutung für die Systematik (*Chelicerata, Arachnida*). *Z. Morph. Tiere.* **69**, 201–272.

LACHMUTH, U., GRASSHOFF, M. AND BARTH, F. G. (1985). Taxonomische Revision der Gattung *Cupiennius* Simon 1891. *Senkenbergiana biol.* **65**, 329–372.

LAND, M. F. (1969). Structure of the principal eyes of jumping spiders (*Salticidae: Dendryphantinae*) in relation to visual optics. *J. exp. Biol.* **51**, 443–470.

LAND, M. F. (1972). Mechanisms of orientation and pattern recognition in jumping spiders (*Salticidae*). In *Information Processing in the Visual Systems of Arthropods* (ed. R. Wehner), pp. 231–247. Berlin: Springer.

LAND, M. F. (1981). Optics and vision in invertebrates. In *Handbook of Sensory Physiology*, vol. VIII/6B (ed. H. Autrum), pp. 471–592. Berlin: Springer.

LAND, M. F. (1984). The resolving power of diurnal superposition eyes measured with an ophthalmoscope. *J. comp. Physiol.* **154**, 515–533.

LAND, M. F. (1985). Morphology and optics of spider eyes. In *Neurobiology of Arachnids* (ed. F. G. Barth), pp. 53–78. Berlin: Springer.

LAND, M. F. AND SNYDER, A. (1985). Cone mosaic observed directly through natural pupil of live vertebrate. *Vision Res.* **25**, 1519–1523.

WARRANT, E. J. AND MCINTYRE, P. D. (1991). Strategies for retinal design in arthropod eyes of low F-number. *J. comp. Physiol.* A **168**, 499–512.

WILLIAMS, D. S. AND MCINTYRE, P. (1980). The principal eyes of a jumping spider have a telephoto component. *Nature* **288**, 578–580.