THE VARIATION OF RESOLUTION AND OF OMMATIDIAL DIMENSIONS IN THE COMPOUND EYES OF THE FIDDLER CRAB *UCA LACTEA ANNULIPES* (OCYPODIDAE, BRACHYURA, DECAPODA)

JOCHEN ZEIL* AND MAHA M. AL-MUTAIRI

Kuwait University, Faculty of Science, Department of Zoology, PO Box 5969, Safat 13060, Kuwait

Summary

We studied variations in the optical properties of the compound eyes of *Uca lactea annulipes* using *in vivo* optical and histological techniques. The distribution of resolving power in the eyes of this fiddler crab species is typical for arthropods that inhabit flat environments: the eyes possess a panoramic equatorial acute zone for vertical resolution and a steep decrease of resolution away from the eye equator in the dorsal and ventral visual fields. The dimensions of the cellular components of the ommatidia vary accordingly: in the equatorial part of the eyes, facets are larger, and crystalline cones and rhabdoms are longer than in the dorsal and ventral parts of the eyes. Along the eye equator, horizontal resolution is low compared with vertical resolution and varies little throughout the visual field. The eyes of *Uca lactea annulipes* are unusual in that the gradient of vertical anatomical and optical resolution is steeper in the dorsal than in the ventral visual field. We interpret this difference as indicating that the information content of the world as seen by the crabs differs above and below the horizon line in specific and predictable ways.

Key words: Crustacea, *Uca lactea annulipes*, compound eyes, resolution, visual ecology.

Introduction

The distribution of optical and sensory filter properties in the compound eyes of arthropods is not uniform. For technical reasons, we know most about the distribution of resolving power and absolute sensitivity, because inter-ommatidial angles and facet diameters can be mapped in the intact eye with the aid of the pseudopupil, which is visible either as an area of dark facets in normal incident light or as an area of illuminated facets during antidromic illumination (see Stavenga, 1979). There is a bewildering variety of modifications of the sampling array in compound eyes, ranging from concentric, forward-pointing acute zones in praying mantids and some predatory flies, through large, high-resolution areas in the dorsal part of the eyes of many male insects to the equatorial acute zones in semi-terrestrial crabs and insects living in flat environments (reviewed by Land, 1989). Among the different specializations of the sampling array, these pronounced horizontally aligned acute zones for vertical resolving power are a special case. They are clearly related to the specific spatial structure of the animals' visual environment. In brachyuran crabs, the acute zones are found exclusively in semi-terrestrial species that inhabit sand and mud flats, suggesting that this particular eye design is an adaptation to spatial vision in a flat world (Horridge, 1978; Zeil *et al.* 1986, 1989; Land and Layne, 1995*a*). For an animal on a flat substratum, it is very informative to watch the horizon since anything larger than itself will disrupt the horizon line. At what distance the animal can make this discrimination depends only on the vertical resolving power of its eyes. The higher this resolution, the larger the distance at which the relative size of an object can be estimated. Using a number of behavioural tests, Land and Layne (1995*a*) have shown that *Uca pugilator* can indeed discriminate between predators and conspecifics in this way. The second kind of cue that a flat-world animal can use is the base angle of an object on the ground. The part of an object that touches the ground appears lower in the visual field the closer the object is. Again, it is vertical resolving power that determines the accuracy and the range of such size and distance judgements. Flat-world animals can thus make these discriminations, even monocularly, on the basis of the retinal position of the objects they see, provided they hold their eyes in a constant orientation relative to the substratum (Zeil, 1990). This peculiar visual situation in flat environments has influenced the design of compound eyes in very different animal groups. Equatorial acute zones for vertical resolving

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*Present address and address for correspondence: Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, PO Box 475, Canberra, ACT 2601, Australia.

power have also been found in a number of insects: in waterstriders *Gerris lacustris* that move and hunt on the water surface (Dahmen, 1991), in the backswimmer *Notonecta glauca* that hangs upside down from the water surface (Schwind, 1980) and even in empidid flies which skim the water surface to fish for drowning insect prey (Zeil *et al.* 1989).

In this paper, we relate an additional piece of evidence as to how sensory ecology has shaped the detailed structure of compound eyes. We studied the distribution of resolution and ommatidial dimensions in the eyes of the fiddler crab *Uca lactea annulipes* of Kuwait and found specific differences in these properties between the dorsal and ventral visual fields. In most other respects, our results are similar to those of a recent study of *Uca pugilator* by Land and Layne (1995*a*).

Materials and methods

Males of *Uca lactea annulipes* (Milne-Edwards) (Ocypodidae, Brachyura, Decapoda) were collected from a sandbank at the seafront in Kuwait City, located just north of Kuwait Towers. They were kept in a flat, glass-covered plastic tray that contained rocks and small pieces of plastic tubing to provide cover for the animals. The tray was slightly inclined so that half of it was filled with sea water and the other half was dry. Crabs were fed on cat food pellets on moist tissue paper in a feeding tray.

Measurements of resolving power were carried out on isolated eye stalks. The proximal end of each stalk was sealed and glued with dental wax to a piece of soldering wire. The eyes were thus protected from desiccation and could easily be positioned and aligned on a Leitz goniometer microscope stage after fastening the soldering wire to a piece of Plasticine on the innermost goniometer ring. The goniometer was used to rotate the eye around two defined axes in order to determine the number of facets per degree across which the pseudopupil moved during the rotation of the eye. From this we calculated the local inter-ommatidial angle ($\Delta\phi$) by dividing the number of degrees through which the eye was rotated by the number of facets across which the pseudopupil moved. Resolution (ν_s in cycles degree^{-1}) is then the reciprocal of twice the inter-ommatidial angle ($\nu_s=1/2\Delta\phi$). We determined the partial inter-ommatidial angle in both the horizontal and vertical directions (following the convention introduced by Stavenga, 1979), by counting the obliquely adjacent facet rows across which the pseudopupil moved (see inset to Fig. 2A and Zeil *et al.* 1986; Land and Layne, 1995*a*). The vertical resolution was measured along vertical transects at 30° azimuth intervals from the frontal mid-sagittal plane to 60° into the medial and 270° into the posterior medial visual field. We attempted to complete these measurements throughout the visual field in a total of 15 eyes. In most cases, however, we did not succeed. For a number of reasons, the optical properties of the isolated eye stalks often deteriorated within an hour or so, which was indicated by damage to the eye surface or by unusual movements of the pseudopupil. Even in otherwise perfect preparations, it was often difficult to determine the edge of the

pseudopupil (which we used to follow its movements) partly because it has a grey tail, especially close to the eye equator, and partly because some eyes are strongly pigmented in the dorsal and ventral visual fields.

Variations in facet lens diameters were determined from photographs taken along one dorso-ventral transect in the mid-sagittal plane of one crab. The pseudopupil was photographed every 5° from the dorsal to the ventral eye border. The slides were subsequently projected together with a scale onto a large screen and the centre of each lens within the pseudopupil was marked on sheets of paper attached to the screen. The distance between two consecutive centres represents the facet diameter. We calculated the mean facet diameter from no less than 25 measurements at each position and determined the cut-off frequency (ν_{co} in cycles degree^{-1}) by dividing the facet diameter (A) by the wavelength of light ($\lambda=0.5\,\mu$m): $\nu_{co}=A/\lambda$ (see Warrant and McIntyre, 1993).

In preparation for histological measurements, isolated eye stalks were held with strong forceps, immersed in 2.5 % glutaraldehyde in phosphate buffer (pH 7.3) and an opening was cut close to the eyes with a razorblade scalpel. Eyes were left in fixative for 3–12 h at 4 °C, washed repeatedly in buffer and then post-fixed in 1 % osmium tetroxide for 1–3 h before being dehydrated in an ascending series of alcohol and embedded in Araldite. We cut 1 μm sections and stained them with Toluidine Blue. Anatomical measurements were made in mid-sagittal sections from the dorsal to the ventral eye border using the 40× objective of a light microscope equipped with a video camera. We determined the facet diameter, the crystalline cone length and the length of rhabdoms directly from the video monitor using a transparent ruler.

Results

The shape of the eye and the pseudopupil

The compound eyes of *Uca lactea annulipes* (Fig. 1) are oval in shape and are situated at the end of long eye stalks, which can be withdrawn for protection and cleaning into suborbital grooves at the fronto-dorsal carapace. The facet-bearing surface is larger at the front than at the back of the eye (compare centre left and centre right photographs in Fig. 1). There are between 70 and 120 corneal facet lenses frontally in the mid-saggital plane and 35–45 at the back. The lens surface of the eye covers nearly the whole circumference of the eye stalk except for a narrow band of cuticle that separates the frontal from the posterior part of the eye at the side facing the animal's midline (Fig. 1, bottom right). This medial cuticle ridge ends at the very top of the stalk in a flat, round, horizontal plate that forms the dorsal eye border. There are two long hairs embedded in this narrow band of cuticle. Both hairs point towards the midline and are oriented parallel to the transverse plane of the animal. They may be hair sensilla, but their function is not known.

The rows of ommatidial facet lenses in the hexagonal array are aligned horizontally in the centre part of the eyes. Looking at the eyes through a dissection microscope or even with the

Fig. 1. The pseudopupil in different parts of the eye of *Uca lactea annulipes*. Left-hand column shows the frontal visual field in the dorsal part of the eye (top), the eye equator (centre) and the ventral part of the eye (bottom). Right-hand column shows the pseudopupil at the eye equator in the lateral (top), the posterior (centre) and the medial part of the eye (bottom). Scale bar, 0.5 mm.
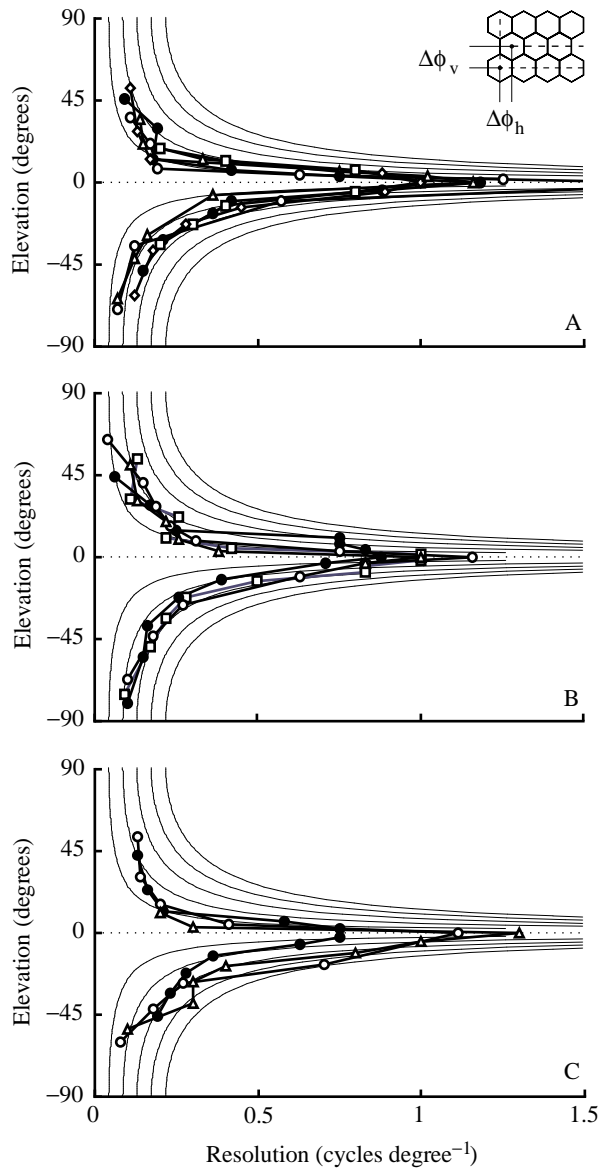
unaided eye, one always observes a dark spot on the otherwise rather bright surface of the eye (Fig. 1). This black area is called the pseudopupil. It occurs because there is no light reflected back from those ommatidia that are viewed 'head-on', that is along the direction of their optical axes. The pseudopupil thus marks those ommatidia that are aligned with the direction of the observer. It therefore moves across the facets of the compound eye when the observer moves around it or when the eye is turned.

In the compound eyes of *Uca lactea annulipes*, as in many other ocypodid species, the shape of the pseudopupil varies markedly in different parts of the eye. It has a vertically elongated shape at the equator in the cental part of the eye and becomes round and small in the dorsal and ventral eye (Fig. 1, left-hand column). Although the size of the pseudopupil depends on the aperture of the observing optics, this is normally constant, so that the observed changes in size and shape of the pseudopupil indicate that the number of ommatidia looking into a given solid angle varies in different parts of the visual field. At the equator, for instance, many more ommatidia look into the observing aperture in the dorso-ventral direction than in the horizontal direction. Hence, the pseudopupil is vertically elongated in that part of the eye. The decreasing size and the round shape in other parts of the eye show that the number of ommatidia per degree of visual space decreases and that there is no difference between horizontal and vertical resolution.

Variation in resolution across the visual field

The variation in resolution across the eye can be determined

Fig. 2. (A) Vertical resolution in the mid-sagittal plane (0° azimuth) at different elevations in the visual field of five eyes of four male *Uca lactea annulipes* (carapace width C=1.7, 1.6, 1.7 and 2.0 cm). Resolution ν_s (cycles degree^{-1}) is expressed as ν_s=1/2$\Delta\phi_v$. See inset for definition of inter-ommatidial angles. Sign convention: ventral negative. Thin continuous lines are theoretical profiles which were calculated assuming that objects of constant size are imaged onto equal numbers of ommatidia according to $\Delta\phi_v$=tan^{-1}(S/H)sinθ (with $\Delta\phi_v$ in rad), where S is the vertical object diameter, H is eye height above the ground plane and θ is retinal elevation (0° at the eye equator). The ratio S/H for the different profiles is 0.2, 0.1, 0.067, 0.05 and 0.04 (moving from inside out). (B) Similar profiles obtained from four repeated measurements in one crab (C=1.6 cm). (C) Profiles of vertical resolution at azimuth positions 30° fronto-medial of the mid-sagittal plane (open circles), 30° lateral (open triangles) and 60° lateral (filled circles) in three different crabs (C=1.7, 1.6, 1.7 cm). Conventions as above. In some measurements, the visual field does not seem to extend beyond 45° above and below the horizon. This does not reflect the real situation, however. It was simply difficult in some preparations to follow the pseudopupil further, since the ommatidia at the top of the eye can be heavily pigmented, which makes it impossible to see the pseudopupil. The visual field thus does extend further but is not represented in some of the graphs.

their distance from the observing animal, with a constant number of ommatidia (see Zeil *et al.* 1986; Dahmen, 1991). The inter-ommatidial angle $\Delta\phi_v$ (rad) in this case would need to vary with elevation in the visual field according to:

$$\Delta\phi_v = \tan^{-1}[(S/H)\sin\theta] ,$$

where S (cm) is vertical object diameter, H (cm) is eye height above the ground plane and θ (degrees) is retinal elevation (which equals 0° at the eye equator).

The dorso-ventral asymmetry in the gradient of vertical resolution is a robust phenomenon. Fig. 2B shows repeated measurements of the mid-sagittal profile in one crab to give an indication of the accuracy which which resolution can be determined. The asymmetry is also present at medial and lateral azimuth positions (Fig. 2C). The overall dorso-ventral distribution of ν_s is otherwise similar in different parts of the visual field, with a maximum at the equator and a steep decrease in the dorsal and ventral parts of the eye. The acute zone extends right around the equator of the eye, whereby the maximal vertical resolution at the eye equator is large in the fronto-medial and fronto-lateral parts of the eye and decreases in the posterior and posterior-medial parts of the eye. This can also be verified in the photographs in Fig. 1 (right-hand column): the frontal part of the eye surface is much larger than the posterior one and exhibits a vertically more elongated pseudopupil. In the medial visual field, interestingly, one can observe two pseudopupils, one on each side of the cuticular ridge. The anterior and the posterior parts of the eye thus share an overlapping visual field on both sides of the ridge.

In contrast to the large variations in vertical resolution, horizontal resolution does not change much across the eye, as is evident from the rather constant width of the pseudopupil in different parts of the eye. Along the eye equator, horizontal

quantitatively by turning the eye and observing the motion of the pseudopupil across the facet lens array. Fig. 2A shows the results of such an analysis for the vertical resolution (ν_s=1/2$\Delta\phi_v$) in the mid-sagittal plane of five crabs. Elevation is plotted against the resolution from the ventral (negative values) to the dorsal visual field (positive values). Resolution reaches a pronounced maximum at the horizon and decreases sharply towards more dorsal and more ventral directions of view. However, there is a distinct difference between the gradient of resolution in the ventral and the dorsal visual fields: the change in resolution with elevation is shallower when one follows the gradient into the ventral visual field, while resolution drops quite rapidly with elevation just dorsal of the eye equator. To facilitate comparison, the figure includes five theoretical profiles which model the gradient of vertical resolution away from the eye equator under the assumption that the eye is designed to image objects on the ground or those moving above and parallel to the ground plane, irrespective of

resolution is much lower than vertical resolution [ν_s=0.39±0.096 cycles degree^{-1}; $\Delta\phi_h$=1.33±0.32°; means ± S.D., N=12). We did not measure horizontal resolution at different elevations, but the rather constant width of the pseudopupil in the dorsal and ventral visual fields indicates that horizontal resolution never exceeds vertical resolution. There is one observation that suggests that the sampling array differs in one other respect between the ventral and dorsal visual fields. If one views a crab from the front, the vertically elongated pseudopupil is not perpendicular to the horizontal facet rows. It is inclined by approximately 13° relative to the rows in a dorso-medial to ventro-lateral direction (see Fig. 1, centre left). The ventral part of the pseudopupil is not noticeably broader than the dorsal part, which rules out the possibility that horizontal resolution is markedly different. The slanted pseudopupil may indicate that eye shape changes gradually from the dorsal to the ventral eye or that ommatidia are skewed relative to the surface of the eye in the fronto-ventral visual field. Interestingly, the pseudopupil is most strongly slanted in the frontal visual field. It is nearly perpendicular to the horizontal facet rows at the equator in the lateral and posterior parts of the eye (Fig. 1, top and centre right).

The spatial resolution of compound eyes is limited not only by the inter-ommatidial angle, which determines the sampling frequency ν_s or anatomical resolution, but also by the diameter A of the individual facet lenses (see Land, 1981; Warrant and McIntyre, 1993). The effect of lens diameter on resolution can be expressed as the cut-off frequency ν_{co}=A/λ (where ν_{co} is measured in cycles degree^{-1}), the highest spatial frequency at which there is just no contrast left in the image. We determined the lens diameter at different elevations in the compound eyes of *Uca lactea annulipes* in order to determine whether optical resolution, which is constrained by the facet lens diameter, matches the variations in anatomical resolution ν_s=$1/2\Delta\phi$, which is basically constrained by the local radius of the eye. For a direct comparison between anatomical and optical resolution, we plotted the cut-off frequency ν_{co}, calculated from the data on lens diameters in a male crab (C=1.7 cm), together with the anatomical resolution ν_s, based on the angular separation $\Delta\phi_v$ of obliquely alternating rows, of another male of comparable size (C=1.6 cm) against elevation (Fig. 3). Both optical and anatomical resolution have their maximum at the eye equator and decrease towards more dorsal and ventral directions of view. The notable difference between the dorsal and the ventral gradients of lens diameters, and consequently of the cut-off frequency, is an independent confirmation of the difference we found in the distribution of inter-ommatidial angles. Optical and anatomical resolution are only matched at the eye equator. In the dorsal and ventral eye regions, anatomical resolution is much worse than optical resolution.

Histological measurements

The pronounced acute zone for vertical resolution at the eye equator leads us to expect that there are also regional variations in the dimensions of relevant cellular components of the
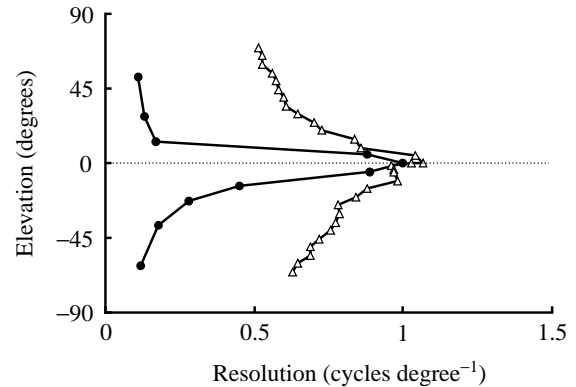

Fig. 3. Optical and anatomical resolution of *Uca lactea annulipes* compared. Resolution is expressed as spatial cut-off frequency (ν_{co}, open triangles), which was determined from lens diameters (optical resolution) and as sampling frequency (ν_s, filled circles) which was determined from inter-ommatidial angles (anatomical resolution). Measurements were taken in the mid-sagittal plane. Filled circles, ν_{co} for a male crab (C=1.7 cm); open triangles, ν_s of another male of comparable size (C=1.6 cm).

ommatidia (see Horridge and Duelli, 1979). Since the largest differences in anatomical and optical resolution are between the dorsal, the ventral and the equatorial parts of the eye, we sectioned resin-embedded eye stalks in the sagittal plane. In mid-sagittal sections, one can recognize many of the features of the *Uca lactea annulipes* compound eye which we have documented above for the intact eye (see Fig. 4): the surface of the eye is larger at the front than at the back, and its curvature is small at the centre and increases away from the centre, especially in the dorsal part of the eye. The radius of the eye is thus large at the equator and small in the dorsal and ventral visual fields. This reduction is more pronounced in the dorsal eye and barely visible in the ventral part. The dimensions of the optic and receptive components of ommatidia vary accordingly: the central part of the eye, which corresponds to the eye equator, occupies a much larger space in the eye stalk than the parts close to the dorsal or ventral eye border. In Fig. 5A–C, the facet lens diameter, the length of the crystalline cone and the length of the rhabdom are plotted as a function of their facet row position in the dorso-ventral plane. The dimensions of all three anatomical parameters co-vary: the crystalline cone length, the length of the rhabdoms and the facet lens diameter all reach their largest dimensions in the centre part of the eye. Towards the dorsal and ventral eye borders, ommatidia become shorter and decrease in diameter. In Fig. 5D, the inter-ommatidial angle and the sampling frequency ν_s, which we had determined in the intact eye of another crab, are replotted so that they can be directly compared with the histological parameters. The change in $\Delta\phi_v$ with facet row number can be modelled approximately by fitting a parabola to the data (continuous line in Fig. 5D) and this, in turn, can be used to reconstruct the sampling array of the compound eye in visual space (see Dahmen, 1991; Land and Layne, 1995a). For *Uca lactea annulipes*, the parabola that
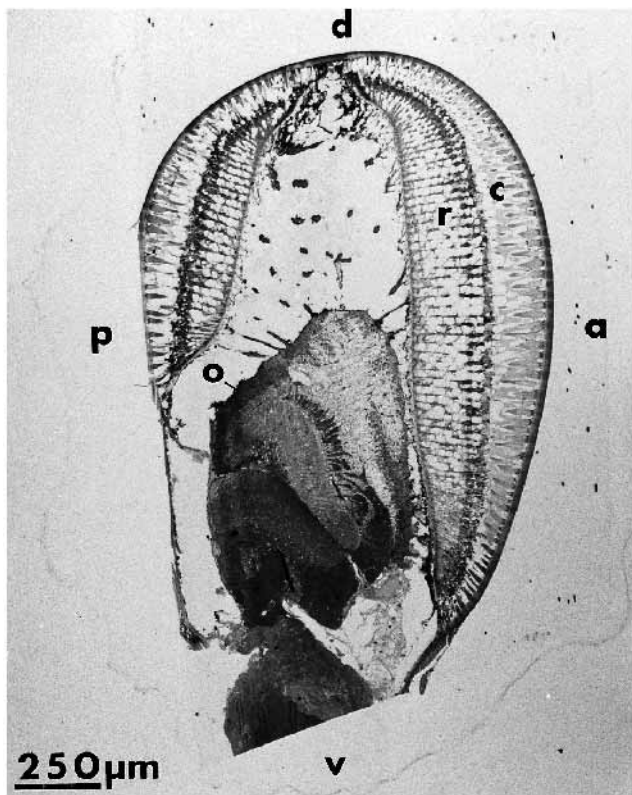
Fig. 4. Light micrograph of a semi-thin longitudinal section through the dorsal part of an eye stalk of *Uca lactea annulipes* (carapace width *C*=1.5 cm). a, anterior; d, dorsal; v, ventral; p, posterior. The section lies close to the mid-sagittal plane and shows both the compound eye and the optic lobes (o). The surface of the eye is formed by a layer of facet lenses, below which is a wide crystalline cone layer (c) and then the layer of retinula cells and rhabdoms (r). Scale bar, 250 μm.

best fits the data has the equation $\Delta\phi_v=0.0025(n-41)^2+0.25$, where *n* is the facet row number.

Discussion

Uca lactea annulipes has a horizontally aligned acute zone for vertical resolution at the eye equator where facet lenses are larger and the crystalline cones and rhabdoms are longer than in the rest of the eye. Vertical resolution decreases away from the eye equator in the dorsal and ventral visual fields and this gradient is steeper in the dorsal eye. Within the acute zone, vertical resolution is maximal at the front of the eye and decreases towards both the medial and the posterior parts of the visual field. Horizontal resolution at the eye equator varies only slightly around the eye and is generally much worse than vertical resolution. Anatomical resolution, depending on the facet lens diameter and the local radius of the eye, and optical resolution, depending on the facet lens diameter alone, are matched only in the acute zone. In the dorsal and ventral visual fields, optical resolution is much better than anatomical resolution.

Equatorial acute zones in crabs

It is only very recently that a detailed study similar to ours
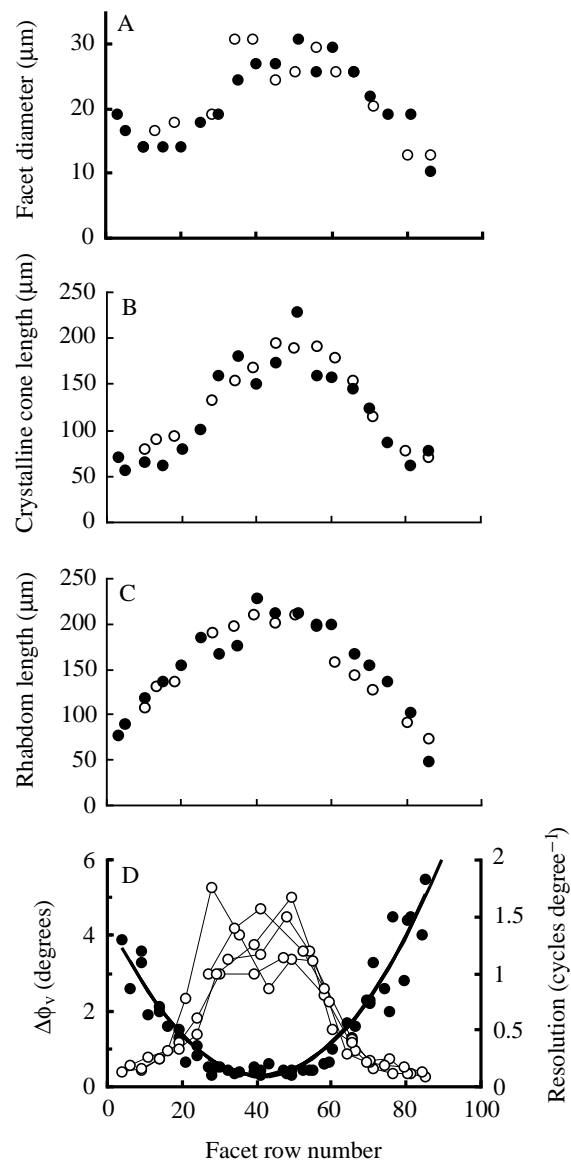

Fig. 5. Anatomical parameters in the eye of a male *Uca lactea annulipes* (*C*=1.5 cm) as determined from semi-thin mid-sagittal sections. Open and filled circles show the data from two different sections of the same eye. (A) Diameter of facet lenses as a function of facet row number from the dorsal edge of the eye (facet row 0) to the ventral edge (facet row 100). (B) The length of crystalline cones as a function of facet row number. (C) The length of rhabdoms as a function of facet row number. (D) Inter-ommatidial angle $\Delta\phi_v$ (filled circles) and sampling frequency or anatomical resolution v_s (open circles) over facet row in the mid-sagittal plane of another crab (*C*=1.6 cm). Repeated measurements on one crab. The thick line is a parabola fitted to the distribution of inter-ommatidial angles. The broad minimum at the eye equator corresponds to the maxima of the anatomical parameters shown in A–C.

has been published on the compound eyes of *Uca pugilator* (Land and Layne, 1995*a*). In all major aspects, the organisation of the compound eye in *Uca pugilator* and *Uca lactea annulipes* is quite similar and both share their specialisations with a number of other ocypodid, and also mictyrid, crab

species (Zeil *et al.* 1986). The results of our histological analysis agree well with the available *in vivo* optical measurements. The increased facet diameter at the centre of the eye decreases diffraction and increases the cut-off frequency. The long rhabdoms increase the sensitivity of the eye in the equatorial zone, and the long crystalline cones increase the focal length, decrease the angular capture cross section of the rhabdom and help to narrow the angular sensitivity function (see Warrant and McIntyre, 1993). The observation that optical and anatomical resolution are not matched outside the equatorial acute zone is a consistent feature of the eyes in both *Uca* and *Gerris* species (Dahmen, 1991; Land and Layne, 1995*a*). This apparent undersampling and also the potential variations in sensitivity throughout the visual field call for a detailed analysis of the distribution of rhabdom diameters and of angular sensitivity functions.

Our study of *Uca lactea annulipes* has revealed two novel aspects that have either been overlooked in previous studies or may be specific to this particular species. In this fiddler crab, the elongated pseudopupil at the eye equator in the frontal visual field is not oriented perpendicular to the horizontal rows of facet lenses, as is the case in the lateral and posterior parts of the eye. Provided that the crabs do not naturally hold their facet rows skewed relative to the line of the horizon, one consequence of slanted pseudopupils is that the ommatidia in the two eyes, which look in the same direction in space, are further apart in the ventral than in the dorsal visual field. The effective eye separation is therefore larger, possibly indicating an increased range and acuity for binocular stereopsis in the fronto-ventral visual field. Whether the improvement is significant, however, needs to be studied in more detail by mapping horizontal resolution at different elevations in the frontal visual field and by accurately measuring, in unrestrained crabs with normal orientation of their eye stalks, the horizontal distance between the frontal pseudopupils in the two eyes. The second novel observation that we made is that the dorsal and ventral gradients of vertical resolution differ in *Uca lactea annulipes*. Vertical resolution decreases rapidly in the dorsal visual field, while the gradient in the ventral part of the eye is much more shallow. The difference between the dorsal and the ventral eye is also confirmed by the histological data. The curvature of the eye surface is shallower in the ventral visual field, as is the decrease in facet lens diameter and cone length. We will discuss the possible significance of this observation below.

The functional significance of equatorial acute zones

The non-uniform distribution of optical properties in compound eyes reflects what one might call the statistics, i.e. the probability structure or the information content, of the visual world (see also Hughes, 1977). The extent to which the probability structure of the world can shape the visual system of animals is most clearly seen in the type of equatorial acute zones we describe here for *Uca lactea annulipes*. As in many other crabs and in insects that live in a flat world, a large part of the eye is devoted to the very narrow strip of the visual field

that views the horizon. In the Introduction, we have argued that this particular distribution of resolving power reflects the high information content of that part of the world. Most importantly, the horizon can be used to distinguish predators from conspecifics (Land and Layne, 1995*a*). Many of the social signals in semi-terrestrial crabs seem to have tapped into this reliable aspect of the sensory world (Christy and Salmon, 1991; Land and Layne, 1995*a*; Christy, 1995) and have certainly been shaped by the predictable geometry of vision in a flat environment. Although a large variety of signals is used, they have one feature in common: seen from the point of view of a crab, they extend above the horizon line. Ghost crab males of *Ocypode ceratophthalmus* and *O. saratan* build sand pyramids to attract females (Linsenmair, 1967), some ocypodid crabs grow long, dark styli extending vertically upwards from their eyes (von Hagen, 1970; Haley, 1973), males of some fiddler crab species (e.g. *Uca lactea* and *Uca beebei*) build hoods of sand to advertise their burrows (Christy, 1988) and the males signal their presence, size and intention in both territorial and mating interactions by raising and waving their massively enlarged claw (Crane, 1975; Salmon and Hyatt, 1983). Significant events in the life of crabs therefore occur within a narrow horizontal strip of the visual world, approximately $10°$ above and below the horizon. The information content includes differences between the visual signs generated by predators and conspecifics, the relative sizes and the sex of conspecifics, and their mating motivation. By penetrating the visual horizon of females, the sand pyramids built by males from the excavate of specially constructed mating burrows indicate the size and burrow location of males even during their absence. Correlated with this high density of relevant information in the equatorial slice of the visual world is the vertically condensed sampling array in the compound eyes with which semi-terrestrial crabs view the horizon. The correlation is specific because only vertical resolution is enhanced, while horizontal resolution is rather uniform and comparatively low throughout the visual field.

The predictable structure of the visual world also extends below the horizon of animals living on flat ground. The substratum is mapped onto the retina of a flat-world animal in such a way that objects on the ground are seen lower in the visual field the closer they are. Retinal position relative to the horizon is thus a reliable, monocular cue to the distance of an object, irrespective of its azimuthal direction. Animals can exploit retinal elevation as a cue to depth and the information content close to the horizon line provided that the substratum is reasonably flat and provided that the equatorial acute zone is aligned with the local visual horizon and not perpendicular to gravity. For a few flat-world crabs, it has indeed been shown that they align their eye stalks visually so that the acute zone views the local horizon (Nalbach *et al.* 1989; Zeil, 1990). Fig. 6 shows that this is also the case in *Uca lactea annulipes*: animals that have their burrows on inclined sections of the beach do hold their eye stalks perpendicular to the local substratum and not to the true, remote horizon line.

Looking at the world below the horizon is a ventral gradient

Fig. 6. A male *Uca lactea annulipes* on an inclined part of the beach. Beach slope is approximately 30° to the horizontal. Note that the eye stalks are held perpendicular to the local substratum. The equatorial acute zone is consequently aligned with the local horizon of the crab and not with the true horizon, which can be seen as the sea–sky boundary in the background on the upper right of the photograph.

of vertical resolving power in semi-terrestrial crabs, waterstriders and the backswimmer *Notonecta glauca* which can be modelled quite accurately assuming that an object at different distances along the substratum is seen by a constant number of ommatidia (Schwind, 1978, 1980; Zeil *et al.* 1986, 1989; Dahmen, 1991). The particular construction of the *Uca lactea annulipes* eye now gives more weight to the hypothesis that this size-constant gradient is a specific adaptation to visual ecology. The gradient is different in the ventral part of the eye, which views the substratum where the sizes and distances of conspecifics need to be discriminated, and the dorsal part, which may only need to tell the animal that something larger than itself is approaching. Note that a fiddler crab, with its eyes approximately 2.5 cm above the substratum, will see objects on the ground that are 2.5–12.5 cm away at retinal positions between 45 and 11° below the horizon. It is in this part of the visual field that fiddler crabs discriminate between males and females (Land and Layne, 1995a), and in *Uca lactea annulipes* it is particularly in this range of elevations that resolution is slightly better in the ventral eye compared with the equivalent retinal positions in the dorsal visual field (Fig. 2). Although clearly improving distance and size judgements, the survival value of the shallower ventral gradient must be rather subtle. To demonstrate in what respect it is adaptive will require both a careful study of visually guided behaviour, like the one carried out by Land and Layne (1995b) with *Uca pugilator*, and an analysis of the outcome and the reproductive effect of social interactions (see Christy and Schober, 1994). In comparison, the selective advantage of the acute zone for vertical resolution that looks at the horizon seems to be much more straightforward. Maximal vertical resolution translates directly into the distance at which a predator can be detected and into the time available to escape into the safety of the burrow. Some predators do indeed need to work hard against the crabs' early warning system: crab plovers (*Dromas ardeola*) take straight short runs across mudflats inhabited by *Uca* species and other ocypodid crabs. During these dashes, they continuously lower their heads and crouch as if trying to stay below the crabs' visual horizon for as long as possible and to minimize vertical looming (J. Zeil, unpublished observation).

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