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Arrangement of optical axes and spatial resolution in the compound eye of the female blowfly *Calliphora*

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Abstract We determined the optical axes of ommatidia in the wild-type female blowfly *Calliphora* by inspecting the deep pseudopupil in large parts of the compound eye. The resulting map of optical axes allowed us to evaluate the spatial resolution in different parts of the eye in terms of interommatidial angles as well as the density of optical axes, and to estimate the orientation of ommatidial rows along the hexagonal eye lattice. The optical axes are not homogeneously distributed over the eye. In the frontal visual field the spatial resolution is about two times higher than in its lateral part and about three times higher as compared to the eye's dorsal pole region. The orientation of the ommatidial rows along the eye lattice is not the same for different regions of the eye but changes in a characteristic way. The inter-individual variability in the orientation of the ommatidial rows is estimated to be smaller than 8°. The characteristic arrangement of the ommatidial lattice is discussed as an adaptation for efficient evaluation of optic flow as induced during self-motions of the animal.

Key words Compound eye · Blowfly · Visual acuity · Motion vision · Insect vision

Introduction

The compound eyes of many arthropods are highly sophisticated interfaces between the outside world and the nervous system. Since Exner (1891) described the optical properties of the compound eye many researchers have further elucidated the structure and function of different types of compound eyes in a wide range of arthropod species (reviews: Horridge 1975; Nilsson 1990; Land 1997). The astonishing variety of arthropod eyes raises the question to what degree the specific eye design can be related to certain lifestyles of the respective species, and thus to specific aspects of visual information processing. There are two aspects of eye design which may be particularly important in this context: the spatial resolution in different parts of the eye and the arrangement of optical axes in the ommatidial lattice. While much attention has been paid to the first of these, the second has only been addressed in a few studies.

Regional specializations as well as sexual dimorphisms in the spatial resolution of compound eyes were found in many species and were interpreted as functional adaptations to the specific lifestyle of the respective animal, serving behavioral tasks such as prey catching and chasing of potential mates (review: Land 1997). Arthropods such as crabs, back swimmers or water striders whose habitat is mostly confined to a flat horizontal plane are equipped with a 'visual streak', which is a narrow stripe of extremely high spatial resolution along the eye equator (e.g., crabs: Zeil and Al-Mutairi 1996; back swimmers: Schwind 1980; waterstriders: Dahmen 1991). Such a visual streak is thought to be helpful in detecting conspecifics, predators, or prey. In flying insects a common feature of the compound eye design is an 'acute zone' of high spatial resolution in the frontal visual field (e.g., Horridge 1978). This adaptation is thought to increase the resolution of fine details of the surroundings in the forward flight direction and, for instance, in robberflies and in dragonflies may thus help to detect prey (review: Land 1997). In simuliid midges, bibionid and muscoid flies the male compound eye is enlarged in the fronto-dorsal region (Beersma et al. 1975; Kirschfeld and Wenk 1976; Zeil 1983). This so-called 'love spot' has a high spatial resolution and was suggested to play a role in chasing conspecific females (Collett and Land 1975; Zeil 1979, 1983; Wagner 1986). In a similar functional context the so-called 'bright zone'

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can be seen in the male blowfly *Chrysomyia megacephala*. These blowflies have, in the dorsal parts of their eyes, facets of four times the diameter of facets in the ventral part of the eye (van Hateren et al. 1989). The resulting high photon capture in combination with an appropriate sensitivity function of the rhabdomeres is thought to enable the male flies to detect female conspecifics during dusk or dawn (van Hateren et al. 1989).

There are only a few studies that address the potential functional significance of the spatial arrangement of optical axes within the ommatidial lattice. The orientations of the ommatidial rows of the eye lattice of different fly species were found to change over the eye in a characteristic way (Beersma et al. 1975; data of Franceschini in Hausen 1981; Land and Eckert 1985). The organization of the eye's lattice has been related to the local preferred directions of motion sensitive wide-field neurons (McCann and Forster 1971) for the first time by Beersma et al. (1975) in the housefly *Musca*. For the blowfly *Calliphora* Hausen (1981, 1982b) realized that, at least in the frontal visual field, the orientation of the ommatidial rows roughly coincide with the preferred directions of the so-called tangential neurons in the third visual neuropil. The tangential neurons are thought to extract particular aspects of the optic flow as induced over the eyes during self-motion of the animal (reviews: Hausen 1981; Hausen and Egelhaaf 1989; Krapp 1999). This correspondence hinted at the possibility that the orientation of ommatidial rows might be of immediate functional significance in the context of processing of optic flow information (Hausen 1981, 1982b).

While the functional significance of an increased spatial resolution in certain parts of the visual field of compound eyes is immediately evident (see above), the spatial arrangement of the rows of the ommatidial lattice needs further quantitative analysis before any firm conclusions concerning its potential functional significance can be drawn. Firm conclusions in this regard are not even possible, so far, for the visual system of the blowfly *Calliphora*, although there are numerous studies on its eye design and the anatomical and computational properties of its visual motion pathway (e.g., Land and Eckert 1985; Hausen and Egelhaaf 1989; Laughlin 1989; Strausfeld 1989; Egelhaaf and Borst 1993a, b; Egelhaaf and Warzecha 1999; Krapp 1999). In particular, at present no published data on the arrangement of the ommatidial rows of the eye lattice of wild-type female *Calliphora* are available. This would be important for establishing quantitatively the optical properties of the eye in relation to to the underlying neuronal machinery, because most analyses of the processing of optic flow and its functional significance were done on female wild-type *Calliphora*. There is only a study by Land and Eckert (1985) on *Calliphora* and *Lucilia* of either sex using a white-eyed mutant. This mutant allows one to determine more easily than is possible in wild-type animals the orientation of the optical axes of the ommatidia, but it is not clear whether the mutation only affects the pigment of the eye. Moreover, there are no quantitative data on female *Calliphora* which allow us to compare the orientation of the ommatidial rows of the eye lattice with the preferred direction of motion of the tangential neurons. Finally, it has not been determined so far to what extent the geometrical properties of the *Calliphora* compound eye vary between individuals of this species. Again, this variability needs to be known if a potential relationship of the properties of the ommatidial lattice to the functional properties of visual interneurons is to be established quantitatively.

Therefore, we investigated in female wild-type *Calliphora* the spatial resolution along the ommatidial rows and the orientation of the ommatidial rows within the eye lattice. We determined the deep pseudopupil (Franceschini 1975) at many measuring positions over large parts of the eye. Furthermore, we investigated the reliability of our measuring and data analysis procedure by repeating measurements at two selected positions in the same specimen. Finally, the orientations of the ommatidial rows of the eye lattice were determined in different animals to estimate the inter-individual variability of this parameter.

Material and methods

Preparation of the animals

Female blowflies (*Calliphora*) were taken from the stock of the Max-Planck-Institut für Biologische Kybernetik, Tübingen, Germany. We analyzed only 1- to 2-week-old specimens. Animals of such age have a completely hardened cuticle and could be easily prepared for the experiments without any distortions of the eye shape.

After briefly anesthetizing the flies with CO_2 wings and legs were removed. We used wax to close the resulting wounds and to fix the head to the thorax, the thorax to the abdomen and the entire fly to a holder. Light reflections caused by the orthodromic illumination (see below) close to the eye margins render the inspection of the deep pseudopupil more difficult than in the other parts of the eye. We reduced these reflections covering the respective regions with a mixture of black pigments and nontoxic fast glue.

Optical apparatus and adjustment of the flies

The measurements were performed on an optical apparatus which was specially developed to investigate the arrangement of optical axes of compound eyes (Dahmen 1991). The apparatus consisted of a goniometer carrying a microscope. The orientation of the microscope could be adjusted to different angles of azimuth and elevation by rotating the microscope around a vertical and a horizontal axis. The angular position of measurements were determined from angular scales arranged around the respective rotation axes.

The holder carrying the fly was placed into the goniometer such that the fly's head was in the center of the goniometer and the lateral part of the right and of the left eye pointed upwards and downwards, respectively. By adjusting in the frontal eye region the symmetrical deep pseudopupil (Franceschini 1975) and by taking into account anatomical markers, i.e., the ocelli and the basis of the antennae, the animal's sagittal plane was aligned with the goniometer's horizontal plane.

The fly's deep pseudopupil was observed by the microscope of the goniometer. The working distance of the objective used for adjusting the animal (4×, Leitz combined with 10× eyepieces, Spindler and Hoyer, including a reticule) and the one used for the

actual measurements (10×, Leitz, with integrated diaphragm combined with 4× eyepieces) amounted to 20 mm. For orthodromic illumination of the investigated eye we used a controllable light source (Fiberoptic, Heim). The light was transmitted through a fiber-optic light guide and reflected by a semi-translucent mirror onto the eye. To control the diameter of the light bundle and the intensity of illumination we used a diaphragm (Spindler and Hoyer) and a condenser lens. The light bundle and the optical axis of the microscope were co-linearly arranged.

Measurements and reconstruction of the map of optical axes

When positioned at the pole of the goniometer the microscope looked at the lateral part of the eye in its equatorial region. We started our measurements at the pole of the goniometer apparatus. Consecutive measurements were taken in 5° steps along meridians and in 10° steps along the azimuth of the goniometer's spherical coordinates. A black-and-white video camera (CF 7A, Kappa) was mounted on the microscope. The camera was connected to a monitor and a video recorder. At each measuring direction we took photographs at two different focus levels: The first was taken at the level of the cornea and the second at the level of the deep pseudopupil. The photographs were digitized by a frame grabber and were stored in bitmap format on the hard-disc of a PC.

For each orientation of the microscope's optical axis we determined in the corresponding photograph taken at the deep focus level the pixel coordinates of the center of the deep pseudopupil. These coordinates were used to identify in the photograph taken from the same direction, this time at the corneal level, the ommatidium which most closely coincided with the center of the pseudopupil. Thus, the optical axis of this ommatidium corresponded to the orientation of the optical axis of the microscope. To reconstruct the entire map of optical axes the photographs taken from different orientations – and thus containing different but overlapping parts of the eye – had to be aligned with each other. This was achieved with chalk dust markers which were distributed over the eye immediately prior to the measurements and could be identified individually in the photographs taken from adjacent orientations. The ommatidia with the optical axes of four neighboring measuring directions were then identified in one of the photographs. Thus, for these four ommatidia both the pixel coordinates and the orientation of the optical axes in spherical coordinates were known. The orientation of the optical axes of all ommatidia surrounded by these four ommatidia were estimated by two-dimensional linear interpolation.

After transforming the pixel coordinates into the spherical coordinates of the corresponding optical axes the measured and interpolated optical axes were plotted in a Mercator map of part of the visual field. In the map the direction of each optical axis is given by two angles: the azimuth (φ) and the elevation (θ), where $\varphi > 0°$ denote the right and $\varphi < 0°$ the left visual field. Elevations of $\theta > 0°$ indicate the dorsal and $\theta < 0°$ the ventral visual field, respectively. Towards the dorsal and ventral pole the area within a Mercator map is increasingly over-emphasized by a factor of $1/\cos(\theta)$.

For customizing the photographs on a PC we used Global Lab Image (Data Translation). The software for further data analysis was written in Matlab 5.3 (The MathWorks).

Results

The map of optical axes

The optical axes of 108 ommatidia were directly determined and are marked in the Mercator map of the visual field shown in Fig. 1a by crosses. Interpolated directions are represented by dots. The total number of reconstructed optical axes amounts to 2386. Since the observation of the deep pseudopupil in wild-type flies is difficult close to the eye margin, the map only comprises directions of optical axes which could reliably be reconstructed. Therefore, the region of binocular overlap in the frontal visual field is not appreciated in its complete extent (cf. Beersma et al. 1977; Land and Eckert 1985). Nevertheless, optical axes of ommatidia residing in the frontal to dorsofrontal part of the eye are clearly directed towards the contralateral left visual field. This is particularly obvious for the ommatidium at the very dorsal margin of the eye (Fig. 1a). It is shown in the following that the distribution of optical axes is not isotropic, but that both the spatial resolution of the eye and the orientation of the rows of the ommatidial lattice change systematically within the visual field.

Spatial resolution and axis density

A commonly used measure to quantify the spatial resolution of compound eyes is the interommatidial angle. In the fly the interommatidial angle approximately corresponds to the angular difference between the photoreceptors sampling light at neighboring points in the visual field (e.g., Land 1997). Because of the hexagonal organization of the ommatidial lattice which can be observed over most parts of the eye (but see Stavenga 1979) there are three rows along which directly adjacent ommatidia can be connected. In the equatorial region of the eye, two of these rows, termed *x*- and *y*-row, are diagonal (Braitenberg 1967), the third one, the *v*-row, is oriented vertically. An additional row, the *h*-row, can be defined which connects next but adjacent ommatidia along an axis oriented exactly between the *x*- and *y*-rows (see inset of Fig. 1a, bottom right). To quantify the regional differences in spatial resolution we evaluated along the *x*-, *y*-, and *v*-rows the mean interommatidial angle within circular areas of 10° in diameter at equally spaced locations along the azimuth at an elevation of 0° (Fig. 1b) and along a frontal meridian at an azimuth of 5° (Fig. 1c). Along the *x*-, *y*- and *v*-rows the minimum interommatidial angle of about 1.2° and thus the highest spatial resolution was found in the frontal visual field (Fig. 1b, c). From here the spatial resolution decreases toward the dorsal, ventral and lateral visual field. The spatial resolution is almost identical for the *x*- and *y*-rows along both azimuth and elevation. The interommatidial angle along the *v*-row is slightly smaller over the azimuth (Fig. 1b) and assumes higher values along the elevation towards the dorsal pole of the eye (Fig. 1c). Along the *h*-row we found a similar dependence of the interommatidial angles on azimuth and elevation as was obtained for the *x*- and *y*-rows. However, for geometrical reasons the angle along the *h*-row is somewhat larger than the interommatidial angles along the other ommatidial rows (data not shown).

Since the spatial resolution is frequently assessed in terms of the density of optical axes of ommatidia per area (e.g., Land and Eckert 1985), this measure is also

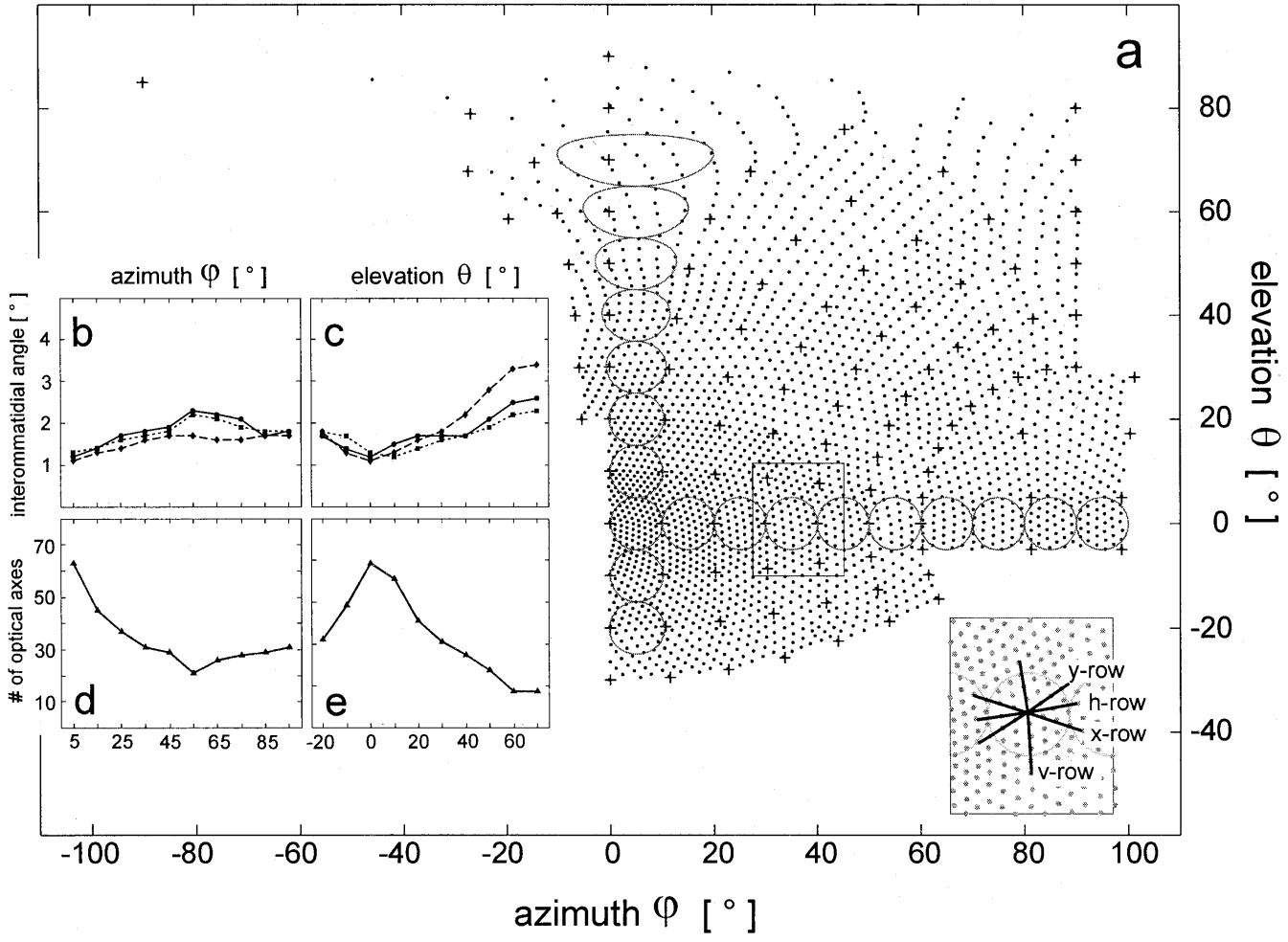


Fig. 1 Mercator map of optical axes (**a**), the interommatidial angles (**b, c**), and the density of optical axes (**d, e**) determined for part of the female compound eye of *Calliphora*. **a** The orientation of optical axes within the spherical visual field is described by its angular coordinates along azimuth φ and elevation θ; where $\varphi = 0 = \theta$ indicates the frontal eye equator. $\varphi < 0$ indicates positions in the right, $\varphi < 0$ in the left visual field; positive elevations define dorsal and negative elevations ventral angular positions. The *crosses* denote the angular coordinates of measured optical axes, *dots between the crosses* indicate the orientation of optical axes determined by interpolation. If neighboring optical axes are connected in the equatorial region of the eye the three major ommatidial rows of the regular hexagonal pattern can be visualized: there are two diagonal rows called *x*- and *y*-rows as well as a vertical *v*-row (cf. *inset* bottom right). Towards the dorsal and ventral pole the regular pattern is increasingly tilted which is only partly due to the Mercator map which over-emphasizes the area by a factor of $1/\cos(\theta)$ (note that also the circular areas plotted in the eye's dorsal pole region comprise the same visual angles as the once plotted in the equatorial region). **b, c** To estimate the eyes spatial resolution along azimuth and elevation within the circular areas plotted in **a**, the mean interommatidial angle was estimated for the three ommatidial rows. It is plotted over the azimuth (**b**) and the elevation (**c**). Interommatidial angles are indicated for the *x*-row by *solid*, for the *y*-row by *dotted*, and for the *v*-row by *dashed* lines, respectively. **d, e** The density of optical axes. As a measure of density the number of optical axes was determined independently on the ommatidial rows within the 10° circular areas shown in **a**. This measure is plotted over the azimuth in **d** and over the elevation in **e**. The smallest interommatidial angles, and thus the highest density of optical axes, are found for the fronto-equatorial region of the eye which defines an 'acute zone' in the direction of straight forward locomotion

used here. The density of optical axes was determined by counting ommatidia within the same circular areas of 10° in diameter used for the estimation of the interommatidial angles (cf. Fig. 1a). In eye regions where the mean interommatidial angles ($\Delta\phi$) along the different ommatidial rows are of approximately the same size the density of optical axes and the spatial resolution are related by the expression $2/\sqrt{3}\Delta\phi^2$). Thus, the regions of minimum interommatidial angles result in maximum ommatidial densities (cf. Fig. 1d, e with Fig. 1b, c). More pronounced regional differences between minimum and maximum density compared to the differences in the interommatidial angles are due to the fact that the density is related to an area.

Orientation of the ommatidial rows in the eye lattice

In earlier studies on different fly species it was found that the orientations of the ommatidial *x*-, *y*-, *v*-, and *h*-rows within the eye lattice are not the same over the entire eye but change in the dorso- and ventro-frontal part of the eye (Hausen 1981; Land and Eckert 1985). For *Musca* the same also holds true with respect to the caudal part of the eye (Beersma et al. 1975). Here we determine for large parts of the eye of a wild-type female *Calliphora*

the orientation of the ommatidial lattice. The orientation of the ommatidial rows was obtained by connecting in the map of optical axes neighboring ommatidia along the different ommatidial rows. Figure 2a shows a map of every single *x*- and *y*-row. The *h*- and *v*-rows are presented in Fig. 2b. In both maps orientation changes of the ommatidial rows are most pronounced toward the dorso-frontal part of the visual field. The deviations from the diagonals, horizontal, and vertical are less dramatic in the equatorial region of the eye and are absent close to the eye equator in the lateral visual field (azimuth = 90°, elevation = 0°; Fig. 2a, b).

Two aspects concerning the course of ommatidial rows need to be mentioned here. First, at certain locations of the eye irregularities of the ommatidial lattice are obvious. Such irregularities can be seen in Fig. 2a, b in the lateral part of the visual field. Two examples are illustrated in Fig. 3a in a magnified map of a small part of the eye. In the upper half of the enlargement two rows of ommatidia fuse. In the bottom half two rows seem to cross each other. Second, since the linear interpolation of optical axes of ommatidia surrounded by optical axes of ommatidia actually measured is performed patch-wise (see Material and methods), along the boundaries of adjacent patches abrupt changes of ommatidial rows may occur (Fig. 3b). Such abrupt changes are mostly confined to regions the eye curvature of which increasingly changes. Irrespective of these orientation changes of the ommatidial rows their overall course can still be reliably reconstructed.

Reliability of the method and inter-individual variability of lattice orientation

Next we addressed the question of how reliably the map of optical axes can be determined by our method. Therefore, in a single animal we repeated five times all steps of the procedure from the adjustment of the fly within the optical apparatus, the measurements, up to the data analysis. In this experiment two restricted areas were considered: a 10° × 10° area centered at an azimuth of 10° and an elevation of 5°. The second area was sized 18° × 10° and centered at an azimuth of 90° and an elevation of 0°. Two quantities were evaluated to assess the reliability of the method: (1) the reliability in assigning the known optical axes to an individual ommatidium, and (2) the variability with respect to the orientation of the *x*-, *y*-, and *v*-rows. For both areas we found the assignment of a known optical axis to be possible with a precision of ±1 ommatidium (results not shown). To determine the variability of the lattice orientation we approximated at the two areas the local

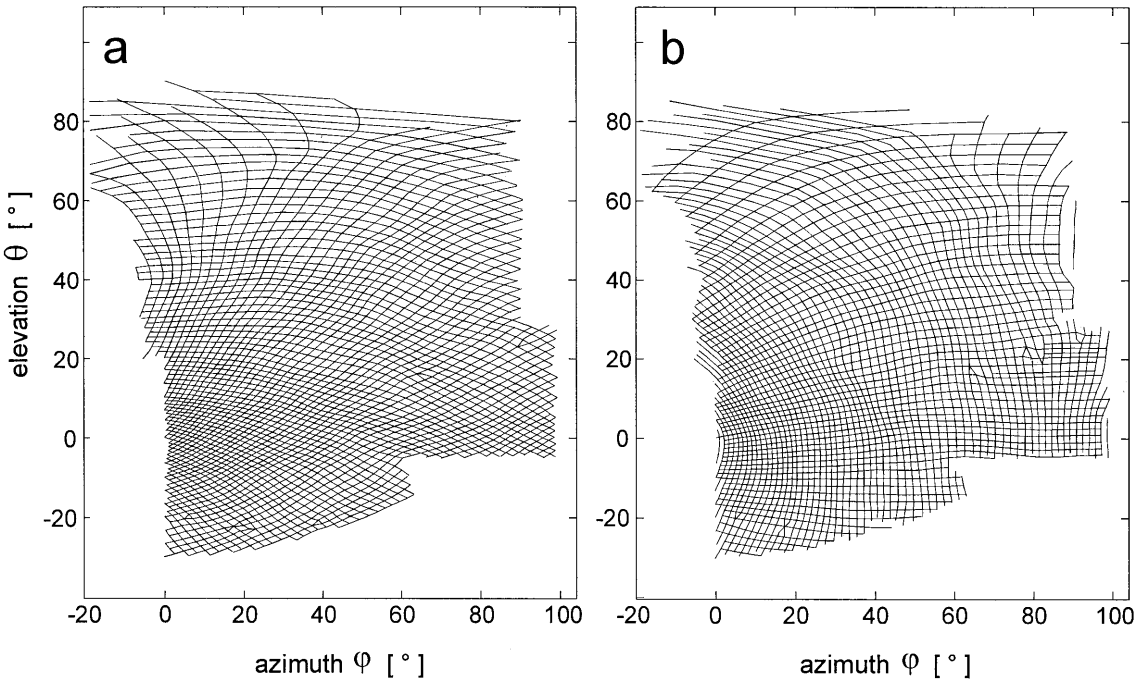


Fig. 2a, b Orientation of ommatidial rows along the eye lattice in a female *Calliphora* plotted in a Mercator map. By connecting adjacent optical axes within the hexagonal arrangement of the compound eye the ommatidial rows can be visualized. **a** All the ommatidial *x*- and *y*-rows – which are diagonally oriented in the equatorial region of the eye – are shown for the analyzed part of the eye. Note that the diagonal orientation within the equatorial region of the eye is increasingly tilted towards the dorsal aspect of the frontal eye. The *y*-rows become vertically oriented and than, close to the dorsal pole they partly flip their orientation by up to 90° or become about horizontally aligned in the dorsolateral eye. The *x*-rows change into a horizontal orientation in the dorsofrontal eye region. **b** All ommatidial *v*- and *h*-rows of the analyzed part of the compound eye lattice; *v*-rows are oriented about vertically in the equatorial and lateral eye region. Towards the dorsofrontal region of the eye the *v*-rows become horizontally oriented. The *h*-rows which indicate next, but neighboring, connections of optical axes are oriented about horizontally in the equatorial and lateral region of the eye. In the dorsofrontal part they are tilted downwards

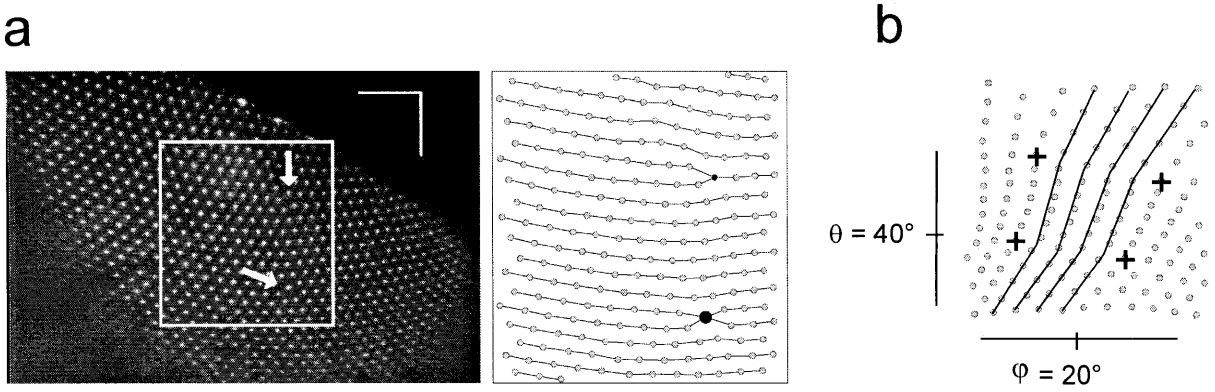
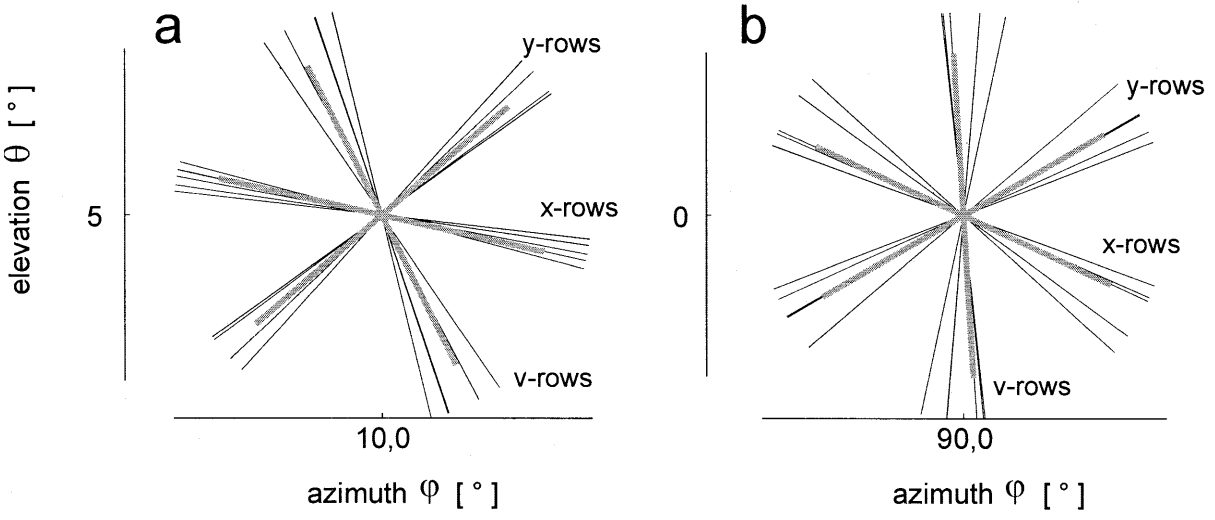


Fig. 3 Anatomical irregularities of the compound eye lattice (**a**) and abrupt changes in the course of the ommatidial rows due to patch-wise interpolation of optical axes (**b**). **a** The left hand side shows a photograph of part of the frontoventral eye taken at the corneal focus level. Scaling bar corresponds to 1 mm. The *white arrows* indicate two sorts of anatomical irregularities which disturb the regular pattern of ommatidial rows. (In the *left hand* part of the figure the framed region is enlarged and shows the consequences of the two irregularities for the map of the corresponding optical axes.) The upper one is due to the fusion of two parallel rows which merge into a single one. The lower irregularity is caused by the replacement of two ommatidia belonging to two parallel rows by a single ommatidium of enlarged diameter. **b** Along the boundaries of adjacent patches due to differences in the eye curvature the patch-wise interpolation between actually determined optical axes causes abrupt changes along the ommatidial rows within the map of the optical axes shown in Fig. 2a, b. Nevertheless, the general course – and thus the orientation – of the ommatidial rows can still be traced reliably

arrangement of optical axes along the *x*-, *y*-, and *v*-rows by straight lines. Subsequently for each row the mean orientation as well as the mean angular deviation (which, for small deviations of the angles, is equivalent to the linear standard deviation) was calculated. The mean angular deviation was in all cases smaller than 6° in the frontal area of the eye and smaller than 9° in the lateral area.

In the next step we estimated the inter-individual variability in the orientation of the ommatidial lattice. We used in these experiments five female flies of about equal age and size. We determined the variability of the lattice orientation in a small area centered around an ommatidium which had the same optical axis in the different specimens. Otherwise, measurements were carried out and were analyzed in the same way as described above. In our sample of different flies we found for the three ommatidial rows of the eye lattice which are defined by connecting the optical axes of directly adjacent ommatidia angular deviations of less than 7° in the frontal and less than 8° in the lateral area of the eye. Figure 4a, b shows the results obtained in the five different flies (thin lines), as well as the orientation of the respective ommatidial rows of the animal whose optical axes were mapped in a more extended region of the eye (short thick lines). From the good correspondence of the data in two distant areas of the eye we conclude that the maps showing the orientation of the ommatidial lattice

Fig. 4a, b Inter-individual variability with respect to the orientation of the ommatidial rows along the eye lattice obtained in five female *Calliphora*. **a** The orientations of the ommatidial rows at a fronto-equatorial position given by the angular coordinates within regions of 10° × 10° were approximated by straight regression lines fitting the respective rows. The variability observed is for all ommatidial rows <7°. **b** Same procedure at a position slightly above the equator in the lateral part of the eye within a region of 18° × 10°. Here the variability was found for all rows to be <8°. *Thick gray lines* indicate the row orientations determined for the animal whose eye was investigated in more extended parts (cf. Fig. 1). Note that the ommatidial orientations of this individual fit very well into the distributions of respective ommatidial rows obtained in the five locally analyzed flies



shown in Fig. 2a, b are representative of the compound eye organization in *Calliphora* females.

Discussion

We presented a map of the optical axes determined for large parts of the compound eye of the wild-type female *Calliphora*. Based on this map the spatial resolution of the eye was analyzed along the equatorial region of the eye and along a vertical section of the frontal part of the eye. By connecting the optical axis of neighboring ommatidia along the *x*-, *y*-, *v*-, and *h*-rows of the map of optical axes we reconstructed the orientation of the ommatidial lattice.

Reliability of the results

In one experimental set we assessed the reliability of our procedure to determine the map of optical axes of ommatidia by several independent measurements performed in the same animal. Potential methodological shortcomings are misalignments of the optical apparatus, erroneous adjustment of the animal, inaccuracies in reading the positions from the angular scales of the optical apparatus and errors in evaluating the photographs taken from the different directions. The optical axes of individual ommatidia could be determined with a precision of ± 1 ommatidium. The mean angular deviation of the orientations of the different rows of the ommatidial lattice due to methodological errors was less than 9°. The angular deviation of the orientation of ommatidial rows between the eyes of different animals did not exceed 8°. Hence, the inter-individual variability is smaller than the methodologically caused inaccuracies. This finding suggests that, at least with respect to the lattice orientation, differences between individuals seem to be rather small. The inter-individual variability was determined in animals of approximately the same size. Although it is conceivable that the lattice orientation is independent of the size of the eyes, this needs not necessarily to be true for other eye parameters like the interommatidial angle. During the larval stage a shortage of food leads to adult flies of markedly reduced size. It is not known, yet, whether the total number of ommatidia in these small-sized specimens is reduced which would presumably result in greater interommatidial angles. Alternatively, the diameter of ommatidia could decrease and their total number kept constant resulting in the same interommatidial angles as observed in normal sized flies.

Comparison of the results with data obtained in earlier studies

The spatial resolution of the *Calliphora* eye was already characterized to some extent in previous studies (Burkhard et al. 1966; Land and Eckert 1985). In addition, the region of binocular overlap was mapped (Beersma et al. 1977). Only two studies were concerned with the orientation of the rows of the hexagonal ommatidial lattice in *Calliphora* (data of Franceschini shown in Hausen 1981; Land and Eckert 1985). With respect to the spatial resolution serious discrepancies exist between our results and the data of Burkhard et al. (1966) who found interommatidial angles of at least twice the values we observed. The reasons for these discrepancies remain obscure because neither the exact method used nor the sex of the investigated animals were mentioned in the report by Burkhard et al. (1966).

Land and Eckert (1985) investigated the compound eye of the white-eyed *Calliphora* mutant *chalky* with respect to the spatial resolution, the density of optical axes and the orientation of the ommatidial rows of the eye lattice. Despite the fact that they investigated white-eyed mutant flies there is, in general, a good agreement between the results of Land and Eckert (1985) and our findings. The minimum interommatidial angle in the white-eyed female was 1.28°; in our wild-type female it was 1.20°. Differences between interommatidial angles obtained in the two studies at comparable positions were always smaller than 8%. In addition, the ommatidial density distribution between the frontal and lateral region of the equatorial to dorsal part of the eye was very similar in white-eyed and wild-type flies. The maximum density, and thus the minimum interommatidial angle, was found in either case around the frontal eye equator. Thus, the acute zones of white-eyed and wild-type *Calliphora* females coincide very well. Moreover, there is no observable difference between white-eyed mutants and wild-types with respect to the extent of the binocular overlap and the distribution of facet diameters (cf. Kuiper 1966; Beersma et al. 1977; Land and Eckert 1985). Thus, the loss of the eye pigment in the white-eyed mutant does not seem to affect the position of the acute zone and the regionalization of the eye's spatial resolution.

Since Land and Eckert (1985) plotted the orientation of the ommatidial lattice of the female white-eyed mutant on a sphere rather than in a Mercator map, the orientation of the ommatidial rows of the eye lattice cannot be inferred quantitatively and thus cannot be compared in detail with our data. A Mercator map of the *v*- and *h*-rows comprising a comparable part of the visual field is only available for a white-eyed male *Calliphora* (Land and Eckert 1985, their Fig. 3) which shows a remarkable similarity to the corresponding map of female wild-type flies for all but the fronto-dorsal eye region. The latter part of the eye exactly coincides with the region of marked sex-specific differences known to exist between the male and female eyes of *Calliphora* (Beersma et al. 1977; Land and Eckert 1985). The same conclusion can be drawn by comparing our data on the orientation of the ommatidial lattice with the second available, more fragmentary, Mercator map of the wild-type *Calliphora* male (see data of Franceschini shown in

Hausen 1981; see also Land and Eckert 1985, their Fig. 3). Hence, the orientation of the ommatidial lattice in male and female *Calliphora* is quite similar – at least outside the dorso-frontal eye region.

Functional significance of eye regions with different spatial resolution

In the compound eye of female wild-type *Calliphora* the ommatidial density and thus the interommatidial angles change over the eye. This is true for most compound eyes which were analyzed in this regard. Acute zones, i.e., regions of the eye with a particularly high angular resolution, were discussed to be functionally relevant in different behavioral contexts. Many flying insects are equipped with an acute zone aligned with the forward direction of locomotion which makes the frontal eye region well suited to resolve fine details (for a general discussion see Land 1997 for example). The animals may utilize the higher resolution for obstacle avoidance, for identifying and approaching attractive sites as well as for guiding landing maneuvers. Prominent acute zones may also facilitate finding a mate, catching prey, or detecting potential predators. Acute zones are not necessarily confined to the fronto-equatorial eye region but can also consist of a visual streak which is oriented to the external horizon, especially in animals whose habitat is confined to a flat world (e.g., Schwind 1980; Dahmen 1991; Zeil and Al-Mutairi 1996). In male flies the position as well as the maximum spatial resolution of the acute zone is different from that in its female conspecifics. Whereas the female acute zone is confined to the direct forward direction, the male acute zone is extended towards the fronto-dorsal part of the eye. This anatomical difference at the level of the eye is accompanied by a sexual dimorphism at the neuronal level. The region of highest spatial resolution is most likely sampled by visual small-field elements converging on male specific interneurons (Hausen and Strausfeld 1980). These male specific interneurons are thought to be involved in the known chasing behavior of the male (Land and Collett 1974; Wehrhahn 1979; Wagner 1986).

The density of ommatidial axes may have another consequence. Under the assumption that visual information is analyzed and projected retinotopically up to the input layers of downstream processing stages the density distribution may affect the sensitivity profiles of, for instance, integrating motion sensitive wide-field neurons. The wide-field tangential neurons in the third visual neuropil of the fly are not equally sensitive to motion within their entire receptive field. Rather, the sensitivity usually decreases towards the edges of the receptive fields, although not necessarily symmetrically around the receptive field center (see Hausen 1982b; Krapp et al. 1998). Are these sensitivity distributions correlated with the distribution of the ommatidial density? At first sight, this might well be the case for part of the tangential neurons. For instance, the so-called HS-cells are most sensitive in the frontal region of the visual field where the ommatidial density is highest (Hausen 1982b). The so-called VS-neurons are most sensitive in the equatorial region of the visual field where the ommatidial density is higher than in the dorsal and ventral part. Nonetheless, it seems doubtful that the distribution of ommatidial density is the major determinant of the spatial sensitivity distribution of the fly tangential neurons. First, there are neurons which are most sensitive in a more lateral region of the visual field, although they receive input also from its frontal part (e.g., Egelhaaf 1985). Second, the different HS-neurons and VS-neurons, respectively, receive their input from different, only partly overlapping regions of the visual field, and thus from areas with clearly different ommatidial densities (Hausen 1982b; Krapp et al. 1998). Nonetheless, all HS-neurons and all VS-neurons have similar properties with respect to their response amplitude and sensitivity to motion. It should be noted that Hausen (1982a, b) tentatively attributed the characteristic spatial sensitivity distribution of HS-neurons to the gradients in their dendritic densities, rather than to gradients in ommatidial density. In a few cases the ommatidial density can be compared to the animal's behavioral sensitivity to motion stimuli presented at different positions in the visual field. Although there is no evidence in flies available in this regard, it has been shown for the hummingbird hawkmoth that the compensatory optomotor responses to translatory motion are strongest in the frontal part of the visual field, while the response to rotational motion is particularly high in the lateral part (Kern and Varjú 1998). This finding is paralleled at the neuronal level by the sensitivity distribution of neurons most sensitive to translational and rotational optic flow (Kern 1998). Since the ommatidial density of this animal is highest in the frontal part of the visual field (Warrant et al. 1999) there is a clear spatial dissociation between behavioral sensitivity for rotational motion and the spatial acuity of the eye. Similarly, the highest density of optical axes in the compound eye of the water strider is confined to an equatorial visual streak (Dahmen 1991). However, in behavioral experiments the animal's highest sensitivity to rotational stimuli was found around elevations of about $+45°$, where the density of optical axes is clearly reduced relative to the visual streak (H. Dahmen, personal observation).

In this context it is important to note that the fly tangential neurons as well as the above-mentioned neurons found in the hawkmoth are likely to be involved in estimating self-motions of the animal. The performance of this task is clearly increased if global aspects of the optic flow pattern induced over the eyes are taken into account. This is achieved by the neurons by pooling motion information from large parts of the visual field. There is both experimental and theoretical evidence that the time-course of pattern velocity can be estimated best if the high spatial frequencies of the stimulus pattern are smoothed out in the input of the movement detection system (Egelhaaf and Reichardt 1987; Egelhaaf and

Borst 1993a). Hence, there is no computational need for a detection of spatial details and thus for a high spatial acuity in a visual motion pathway which is primarily devoted to estimating self-motion of the animal.

Potential functional significance of the orientation of ommatidial rows of the eye lattice

The above-mentioned tangential neurons are thought to provide information about the fly's self-motion, such as its direction of motion or the axis around which the animal rotates. These cells are likely to be involved in controlling optomotor turning responses of the animal as well as gaze stabilization by compensatory head movements (Hausen 1981; Hausen and Egelhaaf 1989; Egelhaaf and Borst 1993a; Hengstenberg 1993). It is a general feature of these neurons that the preferred directions of motion are not constant across their large receptive fields but change in a way characteristic of each individual neuron (Krapp and Hengstenberg 1996; Krapp et al. 1998). The distributions of local preferred directions have been concluded to partly reflect retinal image shifts induced during particular flight maneuvers (Krapp 1999). For a small sample of tangential neurons Hausen (1981, 1982b) compared within a restricted area of the frontal visual field the orientation of local preferred directions with the orientation of the ommatidial lattice. Although the local preferred directions were measured in female blowflies and the ommatidial lattice was obtained in a male (data of Franceschini shown in Hausen 1981, 1982b), Hausen found qualitative similarities between the orientation of both the orientation of the local preferred directions and the orientation of the ommatidial lattice. Based on the data obtained in our study for a more extended area of the female *Calliphora* eye, we can now compare the local orientations of the ommatidial rows of the eye lattice with the local preferred directions determined at many positions within the receptive fields of tangential neurons obtained in flies of the same genus and sex. This comparison, which is the goal of a current project, may further elucidate the logic behind the wiring which maps local motion information onto the retinotopically organized input layers of higher processing stages in the fly visual system thought to be concerned with visual self-motion estimation. Preliminary results indicate that, for at least part of the tangential neurons, the local preferred directions of motion are matched quite well by the local orientations of the ommatidial rows of the eye lattice (Krapp and Egelhaaf 1999). Hence, it is conceivable that the geometry of the fly's compound eye might be of immediate functional significance for the processing of optic flow, and thus serve visually guided behavioral tasks like flight and gaze stabilization.

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