Dear Author,

Here are the proofs of your article.

- You can submit your corrections **online**, via **e-mail** or by **fax**.

- For **online** submission please insert your corrections in the online correction form. Always indicate the line number to which the correction refers.

- You can also insert your corrections in the proof PDF and **email** the annotated PDF.

- For fax submission, please ensure that your corrections are clearly legible. Use a fine black pen and write the correction in the margin, not too close to the edge of the page.

- Remember to note the **journal title**, **article number**, and **your name** when sending your response via e-mail or fax.

- **Check** the metadata sheet to make sure that the header information, especially author names and the corresponding affiliations are correctly shown.

- **Check** the questions that may have arisen during copy editing and insert your answers/ corrections.

- **Check** that the text is complete and that all figures, tables and their legends are included. Also check the accuracy of special characters, equations, and electronic supplementary material if applicable. If necessary refer to the *Edited manuscript*.

- The publication of inaccurate data such as dosages and units can have serious consequences. Please take particular care that all such details are correct.

- Please **do not** make changes that involve only matters of style. We have generally introduced forms that follow the journal's style.
  Substantial changes in content, e.g., new results, corrected values, title and authorship are not allowed without the approval of the responsible editor. In such a case, please contact the Editorial Office and return his/her consent together with the proof.

- If we do not receive your corrections **within 48 hours**, we will send you a reminder.

- Your article will be published **Online First** approximately one week after receipt of your corrected proofs. This is the **official first publication** citable with the DOI. **Further changes are, therefore, not possible.**

- The **printed version** will follow in a forthcoming issue.

Please note

After online publication, subscribers (personal/institutional) to this journal will have access to the complete article via the DOI using the URL: http://dx.doi.org/[DOI].
If you would like to know when your article has been published online, take advantage of our free alert service. For registration and further information go to: http://www.springerlink.com.

Due to the electronic nature of the procedure, the manuscript and the original figures will only be returned to you on special request. When you return your corrections, please inform us if you would like to have these documents returned.

Metadata of the article that will be visualized in OnlineFirst

ArticleTitle	Regionalization in the eye of the grapsid crab *Neohelice granulata* (=*Chasmagnathus granulatus*): variation of resolution and facet diameters	
Article Sub-Title		
Article CopyRight	Springer-Verlag (This will be the copyright line in the final PDF)	
Journal Name	Journal of Comparative Physiology A	
Corresponding Author	Family Name	**Astrada**
	Particle	**de**
	Given Name	**Martín Berón**
	Suffix	
	Division	Laboratorio de Neurobiología de la Memoria. Depto. Fisiología, Biología Molecular y Celular, Facultad de Ciencias Exactas y Naturales
	Organization	Universidad de Buenos Aires. IFIBYNE-CONICET
	Address	Buenos Aires, 1428, Argentina
	Division	Depto. FBMC, Facultad de Ciencias Exactas y Naturales
	Organization	Pabellón 2, Ciudad Universitaria
	Address	Buenos Aires, 1428, Argentina
	Email	martin@fbmc.fcen.uba.ar
Author	Family Name	**Bengochea**
	Particle	
	Given Name	**Mercedes**
	Suffix	
	Division	Laboratorio de Neurobiología de la Memoria. Depto. Fisiología, Biología Molecular y Celular, Facultad de Ciencias Exactas y Naturales
	Organization	Universidad de Buenos Aires. IFIBYNE-CONICET
	Address	Buenos Aires, 1428, Argentina
	Email	
Author	Family Name	**Medan**
	Particle	
	Given Name	**Violeta**
	Suffix	
	Division	Laboratorio de Neurobiología de la Memoria. Depto. Fisiología, Biología Molecular y Celular, Facultad de Ciencias Exactas y Naturales
	Organization	Universidad de Buenos Aires. IFIBYNE-CONICET
	Address	Buenos Aires, 1428, Argentina
	Email	
Author	Family Name	**Tomsic**
	Particle	
	Given Name	**Daniel**
	Suffix	
	Division	Laboratorio de Neurobiología de la Memoria. Depto. Fisiología, Biología Molecular y Celular, Facultad de Ciencias Exactas y Naturales
	Organization	Universidad de Buenos Aires. IFIBYNE-CONICET

Address	Buenos Aires, 1428, Argentina
Email	

Abstract	Crabs have panoramic compound eyes, which can show marked regional specializations of visual acuity. These specializations are thought to be related to the particular features of the animal's ecological environment. Modern knowledge on the neuroanatomy and neurophysiology of the crabs' visual system mainly derives from studies performed in the grapsid crab *Neohelice granulata* (=*Chasmagnathus granulatus*). However, the organization of the visual sampling elements across the eye surface of this animal had not yet been addressed. We analyzed the sampling resolution across the eye of *Neohelice* by measuring the pseudopupil displacement with a goniometer. In addition, we measured the facet sizes in the different regions of the eye. We found that *Neohelice* possesses an acute band of high vertical resolution around the eye equator and an increase in horizontal sampling resolution and lenses diameter towards the lateral side of the eye. Therefore, the analysis of the optical apparatus indicates that this crab possesses greater visual acuity around the equator and at the lateral side of the eye. These specializations are compared with those found in different species of crabs and are discussed in connection to the particular ecological features of *Neohelice*'s habitat.

![Springer — the language of science]

Author Query Form

Please ensure you fill out your response to the queries raised below and return this form along with your corrections

Dear Author

During the process of typesetting your article, the following queries have arisen. Please check your typeset proof carefully against the queries listed below and mark the necessary changes either directly on the proof/online grid or in the 'Author's response' area provided below

Query	Details required	Author's response
1.	Reference Berón de Astrada et al. (2002) is cited in text but not provided in the reference list. Please provide reference in the list or delete this citation.	
2.	The citation Harzsch (2006) has been changed as Harzsch (2002) to match the author name/date in the reference list. Please check here and in subsequent occurrences, and correct if necessary.	
3.	References Horseman et al. (2011), Land (1997) and Wiersma et al. (1982) are given in list but not cited in text. Please cite in text or delete from list.	
4.	Please check and confirm that the authors and their respective affiliations have been correctly identified and amend if necessary.	

1 ORIGINAL PAPER

2 Regionalization in the eye of the grapsid crab *Neohelice granulata*
3 (=*Chasmagnathus granulatus*): variation of resolution and facet
4 diameters

5 **Martín Berón de Astrada · Mercedes Bengochea ·**
6 **Violeta Medan · Daniel Tomsic**

9 **Abstract** Crabs have panoramic compound eyes, which
10 can show marked regional specializations of visual acuity.
11 These specializations are thought to be related to the partic-
12 ular features of the animal's ecological environment. Mod-
13 ern knowledge on the neuroanatomy and neurophysiology
14 of the crabs' visual system mainly derives from studies per-
15 formed in the grapsid crab *Neohelice granulata* (=*Chas-
16 magnathus granulatus*). However, the organization of the
17 visual sampling elements across the eye surface of this ani-
18 mal had not yet been addressed. We analyzed the sampling
19 resolution across the eye of *Neohelice* by measuring the
20 pseudopupil displacement with a goniometer. In addition,
21 we measured the facet sizes in the different regions of the
22 eye. We found that *Neohelice* possesses an acute band of
23 high vertical resolution around the eye equator and an
24 increase in horizontal sampling resolution and lenses diam-
25 eter towards the lateral side of the eye. Therefore, the anal-
26 ysis of the optical apparatus indicates that this crab
27 possesses greater visual acuity around the equator and at
28 the lateral side of the eye. These specializations are com-
29 pared with those found in different species of crabs and are
30 discussed in connection to the particular ecological features
31 of *Neohelice*'s habitat.

A1 M. B. de Astrada · M. Bengochea · V. Medan · D. Tomsic
A2 Laboratorio de Neurobiología de la Memoria. Depto.
A3 Fisiología, Biología Molecular y Celular, Facultad de
A4 Ciencias Exactas y Naturales, Universidad de Buenos
A5 Aires. IFIBYNE-CONICET, Buenos Aires 1428, Argentina

A6 M. B. de Astrada (✉)
A7 Depto. FBMC, Facultad de Ciencias Exactas y Naturales,
A8 Pabellón 2, Ciudad Universitaria,
A9 Buenos Aires 1428, Argentina
A10 e-mail: martin@fbmc.fcen.uba.ar

Introduction 34

Crabs (Decapoda: Brachyura) have conquered a wide vari- 35
ety of ecological niches: from the deep sea to epiphytes 36
high up on tropical trees, from fresh water to deserts 37
(Diesel et al. 2000). Many crabs live in the intertidal zone 38
where the landscape dramatically changes twice a day. 39
Most crabs are highly visual animals that display complex 40
visual guided behaviours such as those involved in visuo- 41
motor control and navigation, conspecific and predator 42
recognition (Woodbury 1986; Land and Layne 1995b), and 43
social communication (Christy 1988a, b; Land and Layne 44
1995a; Backwell et al. 2000). 45

The compound eyes of crabs are located on cylindrical 46
mobile eye stalks. The retinal surface of each eye is spread 47
around the tip of the eye stalk. Having the eye on a raised 48
stalk helps to reduce the portion of the visual scene blocked 49
by the crab's body creating a panoramic monocular field of 50
view. The length of the eye stalks and the eye separation in 51
different species of crabs are related to the topography of 52
the biotope they inhabit: animals that live on rocky shores 53
or deep in mangrove forests, like Grapsidae and Sesarmi- 54
dae, have more spherical eyes on short eye stalks and far 55
apart at the lateral corners of their carapace (Zeil et al. 56
1986, 1989). On the other hand, species from the genus 57
Uca, *Macrophthalmus*, *Ocypode* and *Heloecius* (of the 58
family Ocypodidae) and soldier crabs (Mictyridae), all live 59
in relatively flat environments and carry almost cylindrical 60
eyes close together on long eye stalks (Zeil et al. 1986). 61
Crabs from families Ocypodidae and Mictyridae were 62
found to possess an acute horizontal band of high vertical 63

resolving power round the equator of the eye, about 30° wide (Horridge [1978](#); Land and Layne [1995a](#); Zeil and Al-Mutairi [1996](#); Smolka and Hemmi [2009](#)). Because this band imaging the horizon is most pronounced in species of crabs which inhabit flat environments, it was proposed that this eye design is an adaptation to spatial vision in a flat world where most of the relevant visual information would arrive within a narrow part of their visual field, just above or below the horizon (Zeil et al. [1986](#)).

The equator of the eye also delineates two functionally different areas, the dorsal and ventral visual fields of the animal (Zeil et al. [1986](#); Land and Layne [1995a](#)). Visual stimuli appearing in one or another visual field provoke different visually guided behaviours. Moving stimuli that appear above the horizon usually trigger escape responses, whereas stimuli moving below the horizon elicit responses such as burrow defence or courtship displays (Land and Layne [1995a](#); Hemmi and Zeil [2003](#)). Thus, visual objects moving above or below the equator of the eye are most likely taken as either predators or conspecifics, respectively (Layne et al. [1997](#); Layne [1998](#)).

Crabs also behave differently according to the position of visual stimuli in the azimuth. For example, upon a looming stimulus that appears in front or behind the animal, crabs without refuge first rotate and then run sideways maintaining the stimulus laterally (Land and Layne [1995b](#)). Such directional guided behaviour would benefit from an increased resolution in the eye lateral pole. Although a high value of vertical resolution has been observed in the lateral side of the eye (Smolka and Hemmi [2009](#)), most of the studies on crab eyes have indicated that horizontal sampling resolution is relatively constant across different horizontal viewing directions (Zeil et al. [1986](#); Land and Layne [1995a](#); Zeil and Al-Mutairi [1996](#); but see Sandeman [1978](#); Smolka and Hemmi [2009](#)).

The reason for studying the optical system of the crab *Neohelice* (previous *Chasmagnathus granulatus;* Sakai et al. [2006](#)) is twofold. First, previous studies had been performed on crabs that were classified as either living in a complexly structured environment or in a flat environment lacking vertical structures (Zeil et al. [1986](#)). However, the grapsid crab *Neohelice granulata* inhabits mud flats that in the upper intertidal zone can be densely vegetated by cord grass up to 2 m tall, i.e. a flat but at the same time structured environment (Isacch et al. [2006](#)). The eye design of a crab inhabiting such a mixed environment cannot be predicted from previous studies (see above). A second reason is that the majority of our present knowledge on the neural organization and functioning of the visual system of crabs come from studies carried out in *Neohelice* (e.g. Berón de Astrada et al. [2001](#), 2002, [2009](#); Tomsic et al. [2003](#); Sztarker et al. [2005](#), [2009](#); Sztarker and Tomsic [2011](#); Oliva et al. [2007](#)). Knowing how the visual world is sampled by

Neohelice eye would allow to better understand how visual space is represented in the retinotopic optic neuropils of the crab (Berón de Astrada et al. [2011](#)) and to relate this to the neural circuits involved in coping with such information (e.g. Medan et al. [2007](#)). Therefore, here we investigate the distribution of resolution and facet sizes across the eye of *Neohelice*.

Materials and methods

Animals were adult male *Neohelice granulata* (=*Chasmagnathus granulatus*) crabs measuring 27–30 mm between the lateral carapace spines. They were collected from water less than 1 m deep in the rias (narrow coastal inlets) of San Clemente del Tuyú, Argentina, and transported to the laboratory where they were lodged in plastic tanks ($35 \times 48 \times 27$ cm) filled to 0.5 cm depth with water. Water used in tanks and other containers during experiments was prepared with hw-Marinex (Winex-Germany) (salinity 1.0–1.4 %, pH 7.4–7.6). To prevent deterioration in the pigmentation of the eyes, the holding room was maintained under natural sunlight illumination. Measurements were carried out between 2 and 8 p.m. from March to June within the first week after the animal's arrival to the laboratory.

To study the sampling resolution of the *Neohelice* eye, we measured the distribution of the visual axis of the ommatidia with a pseudopupil mapping method similar to that used in previous studies (Zeil et al. [1986](#); Land and Layne [1995a](#)). The eye stalk was mounted into a custom-made goniometer and rotated around the eye's vertical or horizontal axis. The proximal end of the eye stalk was sealed with vaseline to prevent desiccation and glued to a small piece of aluminium attached to the rotating axis of the goniometer. During measurements the eye was kept moist but care was taken that no water droplets were present on the eye surface. We determined the interommatidial angle in both the vertical and horizontal directions ($\Delta\varphi_v$ and $\Delta\varphi_h$, respectively) following the convention introduced by Stavenga ([1979](#)). According to this, the interommatidial angle is the angle through which the eye had to be rotated for the pseudopupil to move from one ommatidium to the next diagonal neighbouring ommatidium (Fig. [1](#)f). Following the convention used in previous studies in crabs (Zeil et al. [1986](#); Land and Layne [1995a](#), [b](#); Smolka and Hemmi [2009](#)), we considered the sampling resolution as the reciprocal of twice the interommatidial angle in vertical or horizontal direction ($v_v = 1/2\Delta\varphi_v$ and $v_h = 1/2\Delta\varphi_h$, respectively). Since facet rows in crabs are horizontally aligned (type C lattice, see Stavenga [1979](#), p 369) with regular hexagons "standing" on the horizontal axis, the ratio of vertical to horizontal interommatidial angles in the case of a symmetric eye is $\sqrt{3}$. In such a case $\Delta\varphi_v > \Delta\varphi_h$ and the ratio between vertical and horizontal sampling resolution v_v/v_h would be
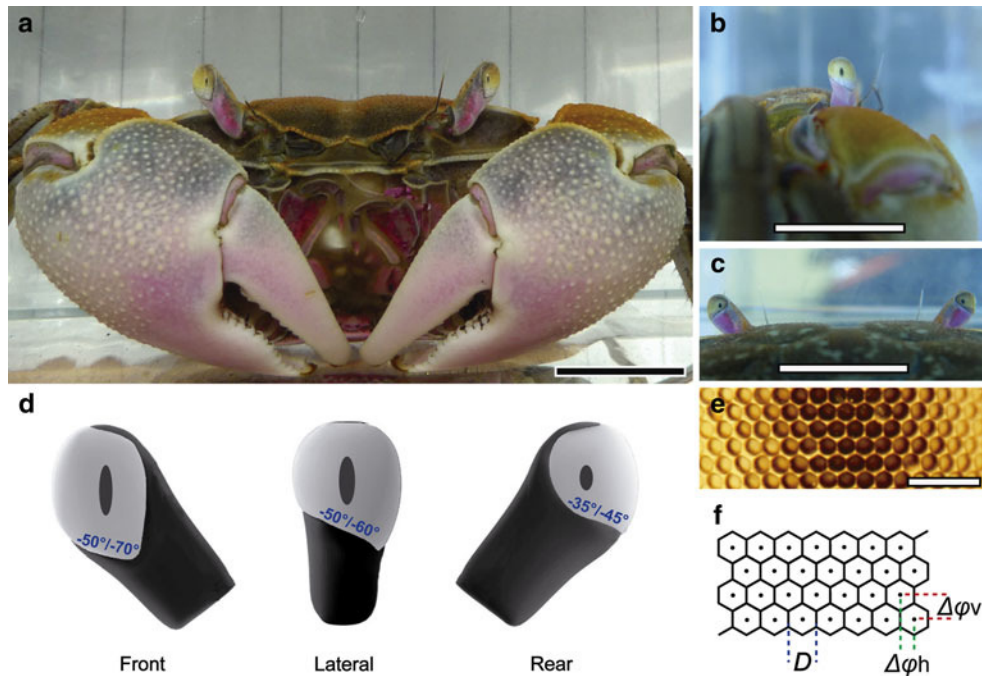
Fig. 1 The compound eyes of the grapsid crab *Neohelice granulata* (=*Chasmagnathus granulatus*). **a–c** Frontal, lateral and rear views of *Neohelice* with their eyes stalk raised at their normal seeing position. **d** Appearance of the right eye seen from the front, lateral and rear with the ommatidial surface shown in *light grey* and the pseudopupil in *darker grey*. Each eye contains about 9,000 ommatidia. Angles in *blue* indicate the edge of the ventral visual field. **e** Photograph of the facet lens array including part of the dark pseudopupil at the equator on the lateral part of the eye. **f** Facet lens pattern and interommatidial angles. Interommatidial angles $\Delta\varphi_v$ and $\Delta\varphi_h$ are determined by considering obliquely adjacent facets (Stavenga 1979). *Scale bars* in **a–c** 10 mm; in **e** 100 μm

167 0.58. In the present study, the eye was rotated so that the
168 pseudopupil crossed 5–10 ommatidia along a facet row, the
169 angle was measured, and a local average for the interommat-
170 idial angle was obtained. As the vertical interommatidial
171 angle changes steeply near the eye equator, care was taken
172 not to average more than five ommatidia in this region.
173 Throughout this paper, we use the greek letter β to denote
174 angles of elevation and θ to denote angles of azimuth.

175 A feature of compound eye acute zones is that the facets
176 are usually bigger than elsewhere in the eye (Land 1989).
177 We determined the facet lens diameter from photographs
178 taken with a camera (Olympus DP71, 12.5 megapixels)
179 attached to the dissecting microscope (Olympus SZX10).
180 Photographs were taken every 5° along the dorso-ventral
181 transect in the mid-sagittal plane of the eye ($\theta = 0°$, i.e. the
182 vertical transect imaging the frontal visual field); and every
183 10° along the equator of the eye ($\beta = 0°$, i.e. the horizontal
184 transect imaging the horizon).

185 **Results**

186 Eye morphology

187 The following description is based on nine male crabs. The
188 eyes of *Neohelice* are ellipsoidal in the front and more
189 spherical in the rear (Fig. 1a–c). The retina wraps around
190 the tip of mobile eyes stalk leaving only a narrow cuticular
191 ridge free from ommatidia at the median surface of the eye
192 stalk. This band extends along the medial side of the eye
193 stalk to end as a small round cap on the dorsal part of the
194 eye (Fig. 1d). On a flat horizontal substrate, the eye stalks
195 of *Neohelice* make an angle of 50° with the horizontal in
196 the transverse plane while changes in the substrate slope
197 and crab's own movement provoke compensatory eye
198 stalks movements that keep the long axis of the eye almost
199 perfectly vertical (Neil 1982; Nalbach 1990). In a crab of
200 28.5 mm carapace width, the eye stalks are 4.6 mm long
201 and the eye is 2.4 mm high and 1.6 mm wide in the front.
202 When the crab is walking normally, the eyes are held 30
203 mm above the ground and the center of both eyes are placed
204 22 mm apart from each other.

205 Eye visual field

206 The dark pseudopupil marks those ommatidia that are
207 aligned with the direction of the observer (Stavenga 1979);
208 therefore, the extension of the visual field can be inferred
209 from the direction of observation of the pseudopupil at the
210 borders of the eye. When looking at the equator of the eye
211 and rotating the eye through its vertical axis, the pseudopu-
212 pil moves continuously from the antero-medial to the

postero-medial surface of the eye. This indicates that the two ends of the facet-bearing surface that border the sides of the medial cuticular ridge sample the same region of visual space. The sampling array at the equator covers monocularly the full 360° horizontal panorama.

A similar continuous movement of the pseudopupil is observed dorsally along anterior and posterior ommatidia meeting at the dorsal round cap of exoskeleton, indicating that the dorsal visual field is also fully covered monocularly. Although the optical axes of the ommatidia along the outer-most ventral border of the sampling array are difficult to define due to a dark pigmentation that appears in many eyes, we were able to assess the ventral visual field extension from the last 2–3 ventral rows of ommatidia. The visual field reaches ventrally −50° to −70° of elevation in the front, −50° to −60° in the lateral and −35° to −45° in the rear of the eye (Fig. 1d). This reduction of the ventral field of view from the front to the rear of the eye occurs mainly by the loss of the ventral area of ommatidia imaging the lower part of the field, which would sample the space occupied by the dorsal carapace (Fig. 1b, c). The total number of ommatidia in a vertical row is 93–101 at the front of the eye, it decreases to 65–72 at the side and to 44–49 at the rear ($n = 4$).

Vertical sampling resolution and lens diameters in elevation

Previous studies in crabs found that the distribution of vertical resolution across their panoramic eyes is quite heterogeneous. In particular, species of the families Ocypodidae and Mictyridae possess a narrow horizontal band of greatly increased vertical resolution in the middle of the eye (Zeil et al. 1986). The size and shape of the pseudopupil indicate the number of ommatidia looking into a given solid angle. At the equator of the eye of *Neohelice*, the pseudopupil appears elongated while dorsally and ventrally it becomes round and smaller (Fig. 2a–c). Consequently, at the equator there would be more vertically aligned ommatidia looking into the same solid angle than dorsally and ventrally. The sampling resolution (expressed in cycles/degree) is related to the finest grating resolvable by the ommatidial lattice (e.g. see Land and Layne 1995a). Figure 2d shows the distribution of vertical sampling resolution v_v in the mid-sagittal plane ($\theta = 0°$, i.e. front) of three eyes. Elevation from the ventral to the dorsal visual field is plotted against the vertical sampling resolution v_v. *Neohelice* has a sharp peak in vertical resolution around 0° elevation which corresponds to the equator of the eye ($\beta = 0°$). This maximum in vertical resolution decreases sharply towards more dorsal and more ventral directions of view. In the different eyes, the peaks of vertical resolution v_v reached values between 0.83 and 1.2 cycles/deg (interommatidial angles φ_v between 0.6° and

0.4°, respectively). The vertical angular span (i.e. height) of the region around equator where the vertical resolution reached half the maximal vertical resolution, was between 22° and 34°. Using the eye of another crab, we measured the profile of vertical resolution v_v along vertical transects in the front, lateral and rear of the eye (θ: 0°, 90° and 180°, respectively). We found a similar profile of vertical resolution around the eye but with a reduction (with respect to the front) in the peak of resolution of 25% at lateral and 50% at rear azimuthal positions (Fig. 2f). Figure 2e shows the diameter of the facet lenses in the mid-sagittal plane ($\theta = 0°$) of three eyes. The diameter of the lenses reaches a maximum of 34–36 μm in the region of the eye that images the horizon and decreases towards dorsal and ventral directions of view.

Behavioural and anatomical studies on crabs of the genus *Uca* reveal that the information content of the world as seen by the crabs may differ above and below the horizon (Zeil and Al-Mutairi 1996; Layne et al. 1997). The inset of Fig. 2d shows a histogram in which the vertical sampling resolution v_v was averaged for 10° bins while the inset of Fig. 2e shows a histogram in which the diameter of facet lenses was averaged. Even when this procedure smoothens and widens the distribution of the variables, the histograms clearly indicate that in *Neohelice* both sampling and lenses diameter are higher for ventral than for dorsal equidistant elevations from the horizon. This result suggests that, as for some species of the genus *Uca*, for *Neohelice*, there is differential information content on the ventral and dorsal visual field.

Horizontal sampling resolution and lens diameters in azimuth

Around the equator of the eye of *Neohelice* the pseudopupil looks wider in the lateral than in the frontal and posterior parts of the eye, indicating that horizontal resolution is not homogeneous (Fig. 3a–c). On an equatorial horizontal row, the number of ommatidia is between 125 and 135 ($n = 4$). The distribution of horizontal sampling resolution v_h around the equator of three eyes is shown on Fig. 3d. In each of the measured eyes, there is a gradual and marked increase in the horizontal sampling resolution towards the lateral side of the eye. Laterally, the horizontal sampling resolution v_h reaches peak values between 0.5 and 0.65 cycles/deg (interommatidial angles φ_h between 1° and 0.75°, respectively). However, in the front ($\theta = 0°$) horizontal resolution v_h is between 0.31 and 0.38 cycles/deg; while fronto-medially ($\theta = -45°$) it is between 0.22 and 0.28 cycles/deg. This distribution of horizontal sampling resolution implies that laterally the eye of *Neohelice* has approximately 60% higher resolution than frontally and 120% higher resolution than fronto-medially.
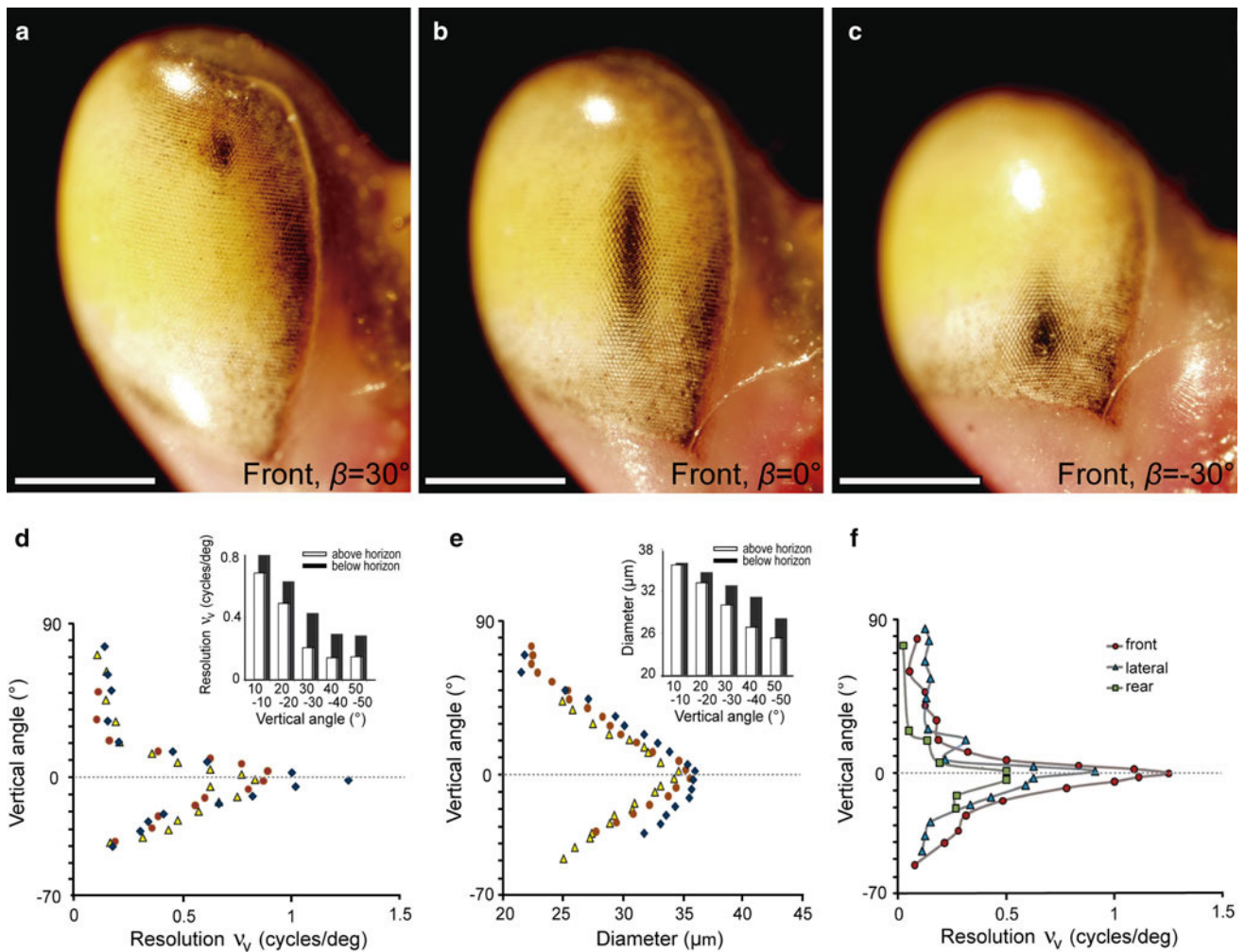
Fig. 2 Anatomical and optical properties along vertical transects in the eye of *Neohelice*. **a–c** The pseudopupil along a dorso-ventral transect in the mid-sagittal plane ($\theta = 0°$, frontal visual field) of a right eye. Photograph in **a** shows the pseudopupil in the dorsal part of the eye ($\beta = 30°$); **b** in the eye equator ($\beta = 0°$); and **c** in the ventral part of the eye ($\beta = -30°$). Note the vertical enlargement of the pseudopupil at the equator of the eye. **d** Profile of vertical resolution v_v in the mid-sagittal plane of three crabs (carapace width $C = 28$, 29 and 30 mm). The ordinate represents the elevation in degrees with respect to the horizon ($\beta = 0°$). Even when there are slight differences in the measured peak resolution v_v for the different eyes, all of them showed an acute band of high vertical resolution looking at the horizon. **e** Diameter of facet lenses along the same vertical transect of the same three crabs. The larger facet diameters correspond to the higher vertical resolution. **f** Profile of vertical resolution in vertical transects of another crab ($C = 28$ mm) at the frontal, lateral and rear visual field (θ: 0°, 90°, 180°, respectively). Note the marked reduction in vertical resolution in the rear of the eye. *Insets* in **d** and **e** are averaged histograms for 10° bins in the dorsal (positive angles, *white bars*) and ventral visual fields (negative angles, *black bars*) ($n = 3$). Both vertical sampling resolution v_v and facet diameters appear to be higher in the ventral visual field. *Scale bars* in **a–c** 1 mm

The diameter of the facet lenses along the equator of the eye is shown in Fig. 3e. The largest lenses (38–40 μm) are found rearwards from lateral direction, at around azimuth $\theta = 120°$. Even though we have measured the lenses diameter only along one vertical and one horizontal transect, the inspection of the surface of the eye confirmed that the largest ommatidia of *Neohelice* are those looking laterally at the equator of the eye.

We next measured the horizontal sampling resolution v_h in the front ($\theta = 0°$), lateral ($\theta = 90°$) and rear ($\theta = 180°$) of one eye at different elevations (β: −20°, −10°, 0°, 10°, 20°, 40° and 60°). The results are shown in Fig. 3f. We found that horizontal sampling resolution v_h is fairly uniform at different elevations within the front (0.35–0.47 cycles/deg), the lateral (0.51–0.63 cycles/deg) and the rear part of the eye (0.36–0.42 cycles/deg). The results show that the increase in horizontal sampling resolution in the lateral side of the eye is preserved for the different elevations. These results highlight the importance of the lateral visual field in the functional representation that the panoramic eye of this grapsid crab builds from the visual world.
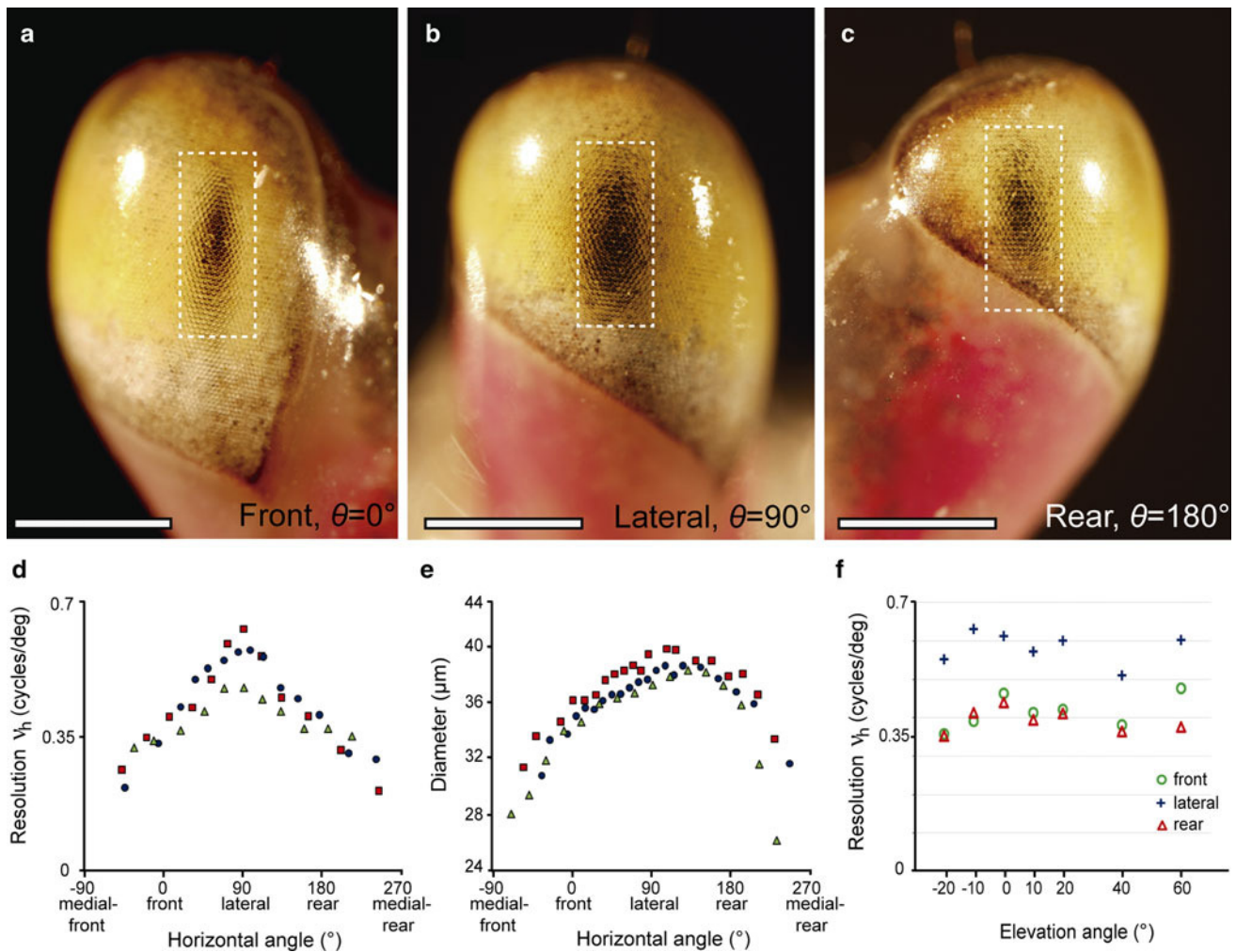
Fig. 3 Anatomical and optical properties along horizontal transects in the eye of *Neohelice*. **a–c** The pseudopupil at the equator of the eye on the front, lateral and rear of the eye (θ: 0°, 90°, 180°, respectively). At the lateral side the pseudopupil looks wider than in the front and rear of the eye (*white dashed rectangles* have the same size in the three pictures). **d** Profile of horizontal sampling resolution v_h along the equator of the eye of three crabs (carapace width C = 27, 28 and 30 mm). Here, the ordinate represents the horizontal resolution v_h and the ab-scissa the azimuth in degrees. Horizontal resolution shows a gradual increase towards the lateral visual field. **e** The diameter of facet lenses also shows a gradual increase in the lateral of the eye but a few degrees rearwards. **f** Measurements of horizontal resolution v_h in another crab (C = 28 mm) in the front, lateral and rear of the eye at different elevations, β: −20°, −10°, 0°, 10°, 20°, 40° and 60°. The increase in horizontal resolution at the lateral visual field is conserved at different elevations. *Scale bars* in **a–c** 1 mm

Discussion

Many vertebrate and artrophod species inhabiting flat environments possess a steep horizontal band of high vertical resolution imaging the horizon (Hughes 1977; Horridge 1978; Schwind 1980; Zeil et al. 1989; Dahmen 1991). This has been interpreted as an adaptation to vision in a two-dimensional habitat. Previous studies in crabs found that this acute band was more pronounced in crabs with closely set elongated eyes mounted on top of long stalks that inhabit mud or sand flats areas (families Ocypodidae and Mictyridae), but less so in species that have their eyes relatively apart and inhabit more complex environments (e.g. families Grapsidae and Sesarmidae) (Zeil et al. 1986).

Indeed, many grapsid species known as rock crabs (e.g. purple rock crab = *Leptograpsus variegatus*; the marbled rock crab = *Pachygrapsus marmoratus*), live on rock shores or promontories where they find refuge in crevices. These animals then live in a structured complex world that forces them to walk, climb and rest in tilted surfaces and vertical walls, a condition where there are no apparent advantages for a specialization of the region around the eye equator. However, some grapsid species, like *Neohelice*, inhabit mud flat areas, which can be fairly open or densely vegetated by cord grass (mainly *Spartina densiflora,* Isacch et al. 2006). Despite the fact that vegetated areas contain a great deal of vertical and even overhead structures, *Neohelice* still lives, moves, and interacts with other crabs in a

well defined horizontal plane, which means they can take advantage of having a band of high vertical resolution at the eye equator (for a comparison of *Neohelice* eye design with that of other crabs, see Fig. 6 in Zeil et al. 1986: in the front *Neohelice* vertical/horizontal resolution = 2.8 and eye separation/carapace width = 0.75).

Previous studies found that horizontal sampling resolution is fairly uniform in crab eyes (Zeil et al. 1986; Land and Layne 1995a; Zeil and Al-Mutairi 1996). Therefore, our finding that in *Neohelice*, the horizontal sampling resolution and the size of facets significantly increase towards the lateral side of the eye was unexpected. When looking the study of Zeil et al. (1986) in more detail we noticed that *Pachygrapsus* (a grapsid crab like *Neohelice*) also shows a similar increase in horizontal sampling resolution at the lateral side of its eye (Fig. 5, Zeil et al. 1986). Both *Neohelice* and *Pachygrapsus* have their eyes relatively far apart and present the greatest increase in horizontal sampling resolution in the lateral visual field found in any crab (60 and 100%, respectively). Crabs which have their eyes relatively far apart were proposed to take advantage of binocular integration (Zeil et al. 1986). In fact, in the third optic neuropil of *Neohelice*, we have found binocular neurons (Sztarker and Tomsic 2004). The increase in lateral resolution may then serve to compensate the lack of binocular sampling present in the frontal and rear visual fields.

When challenged by a visual danger stimulus (e.g. a predator appearing above the horizon) crabs either flee down their burrow or, if caught in the open without a refuge, run directly away in opposite direction to the threat. While running the escape direction is adjusted in order to keep the stimulus centered in the lateral visual field, which allows the animal to continue running in its faster way, i.e. sideways (Land and Layne 1995b). Therefore, the increase in resolution at the lateral side of the eye could help the animal to accurately control its visually guided escape in the lateral direction away from the predator (see also Smolka and Hemmi 2009).

Recently, we have described the large-scale retinal map of the optic neuropils of the crab (Berón de Astrada et al. 2011). Results of the present study will allow a refinement of such a map as well as to relate this information with previous knowledge on neuronal movement detector circuits found in *Neohelice* (e.g. Medan et al. 2007). Comparative studies on the development and structure of the optic neuropils in malacostracan crustaceans and insects suggest a homology of the optic neuropils in these two groups (e.g. Harzsch and Waloszek 2002; Harzsch 2002; Strausfeld 2005, 2009). Beneath the retina lie three serially arranged retinotopic optic neuropils that in crabs are connected by two orthogonal chiasmata. From the periphery to the center these neuropils are: the lamina, the medulla, and the lobula. In *Neohelice*, the retinal representation is preserved at the level of these three neuropils (Sztarker et al. 2005). Results from the present account make now possible to investigate the correspondence between the sampling specialization found in the retinal mosaic and the sampling properties of the columnar arrangement in the retinotopic optic neuropils.

References

Backwell PR, Christy JH, Telford SR, Jennions MD, Passmore NI (2000) Dishonest signalling in a fiddler crab. Proc R Soc Lond B Biol Sci 267:719–724

Berón de Astrada M, Sztarker J, Tomsic D (2001) Visual interneurons of the crab *Chasmagnathus* studied by intracellular recordings in vivo. J Comp Physiol A 187:37–44

Berón de Astrada M, Tuthill JC, Tomsic D (2009) Physiology and morphology of sustaining and dimming neurons of the crab *Chasmagnathus granulatus* (Brachyura: Grapsidae). J Comp Physiol A 195:791–798

Berón de Astrada M, Medan V, Tomsic D (2011) How visual space maps in the optic neuropils of a crab. J Comp Neurol 519:1631–1639

Christy JH (1988a) Pillar function in the fiddler crab *Uca Beebi*. (I). Effects on male spacing and aggression. Ethology 78:53–71

Christy JH (1988b) Pillar function in the fiddler crab *Uca Beebi*. (II). Competitive courtship signaling. Ethology 78:113–128

Dahmen HJ (1991) Eye specialisation in waterstriders: an adaptation to life in a flat world. J Comp Physiol A 169:623–632

Diesel R, Schubart CD, Schuh M (2000) A reconstruction of the invasion of land by Jamaican crabs (Grapsidae: Sesarminae). J Zool 250:141–160

Harzsch S (2002) The phylogenetic significance of crustacean optic neuropils and chiasmata: a re-examination. J Comp Neurol 453:10–21

Harzsch S, Waloszek D (2002) Serotonin-immunoreactive neurons in the ventral nerve cord of Crustacea: a character to study aspects of arthropod phylogeny. Arthropod Struct Dev 29:307–322

Hemmi JM, Zeil J (2003) Burrow surveillance in fiddler crabs. I. Description of behaviour. J Exp Biol 206:3935–3950

Horridge GA (1978) The separation of visual axes in apposition compound eyes. Philos Trans R Soc Lond B 285:1–59

Horseman BG, Macauley MW, Barnes WJ (2011) Neuronal processing of translational optic flow in the visual system of the shore crab *Carcinus maenas*. J Exp Biol 214:1586–1598

Hughes A (1977) The topography of vision in mammals of contrasting life style: Comparative optics and retinal organization. In: Crescitelli F (ed) Handbook of sensory physiology, vol VII/5. Springer, Berlin, pp 613–756

Isacch JP, Costa CSB, Rodríguez-Gallego L, Conde D, Escapa M, Gagliardini DA, Iribarne O (2006) Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. J Biogeogr 33:888–900

476 Land MF (1989) Variations in the structure and design of compound
477 eyes. In: Stavenga DG, Hardie RC (eds) Facets of vision. Spring-
478 er, Berlin, pp 90–111
479 Land MF (1997) Visual acuity in insects. Annu Rev Entomol 42:147–
480 177
481 Land M, Layne J (1995a) The visual control of behavior in fiddler
482 crabs. I. Resolution, threshold and the role of the horizon. J Comp
483 Physiol A 177:81–90
484 Land M, Layne J (1995b) The visual control of behavior in fiddler
485 crabs. II. Tracking control systems in courtship and defense.
486 J Comp Physiol A 177:91–103
487 Layne JE (1998) Retinal location is the key to identifying predators in
488 fiddler crabs (*Uca pugilator*). J Exp Biol 201:2253–2261
489 Layne J, Land M, Zeil J (1997) Fiddler crabs use the visual horizon to
490 distinguish predators from conspecifics: a review of the evidence.
491 J Mar Biol Assoc UK 77:43–54
492 Medan V, Oliva D, Tomsic D (2007) Characterization of lobula giant
493 neurons responsive to visual stimuli that elicit escape behaviors in
494 the crab *Chasmagnathus*. J Neurophysiol 98:2414–2428
495 Nalbach HO (1990) Visually elicited escape in crabs. In: Wiese K,
496 Krent WD, Tautz J, Reichert H, Mulloney B (eds) Frontiers in
497 crustacean neurobiology. Birkhauser Verlag, Basel, pp 165–172
498 Neil DM (1982) Compensatory eye movements. In: Sandeman DC,
499 Atwood HL (eds) The biology of Crustacea, vol 4: neural integra-
500 tion and behavior. Academic, New York, pp 133–163
501 Oliva D, Medan V, Tomsic D (2007) Escape behavior and neuronal
502 responses to looming stimuli in the crab *Chasmagnathus granul-
503 atus* (Decapoda: Grapsidae). J Exp Biol 210:865–880
504 Sakai K, Turkay M, Yang SL (2006) Revision of the *Helice/Chasmag-
505 nathus* complex (Crustacea: Decapoda: Brachyura). Abh Senc-
506 kenberg Naturforsch Ges 565:1–76
507 Sandeman DC (1978) Regionalization in the eye of the crab
508 *Leptograpsus variegatus*: eye movements evoked by a target
509 moving in different parts of the visual field. Comp Physiol
510 123:299–306
511 Schwind R (1980) Geometrical optics of the *Notonecta* eye: adapta-
512 tions to optical environment and way of life. J Comp Physiol
513 140:59–68
514 Smolka J, Hemmi JM (2009) Topography of vision and behaviour.
515 J Exp Biol 212:3522–3532
516 Stavenga DG (1979) Pseudopupils of compound eyes. In: Autrum H
517 (ed) Handbook of sensory physiology, vol VII/6A. Springer,
518 Berlin, pp 357–439
519 Strausfeld NJ (2005) The evolution of crustacean and insect optic lobes
520 and the origins of chiasmata. Arthropod Struct Dev 34:235–256
521 Strausfeld NJ (2009) Brain organization and the origin of insects: an
522 assessment. Proc Biol Sci 276:1929–1937
523 Sztarker J, Tomsic D (2004) Binocular visual integration in the crusta-
524 cean nervous system. J Comp Physiol A 190:951–962
525 Sztarker J, Strausfeld NJ, Tomsic D (2005) Organization of the optic
526 lobes that support motion detection in a semi-terrestrial crab.
527 J Comp Neurol 493:396–412
528 Sztarker J, Strausfeld N, Andrew D, Tomsic D (2009) Neural organi-
529 zation of first optic neuropils in the littoral crab *Hemigrapsus
530 oregonensis* and the semiterrestrial species *Chasmagnathus gran-
531 ulatus*. J Comp Neurol 513:129–150
532 Sztarker J, Tomsic D (2011) Brain modularity in arthropods: individ-
533 ual neurons that support "what" but not "where" memories.
534 J Neurosci 22:8175–8180
535 Tomsic D, Berón de Astrada M, Sztarker J (2003) Identification of
536 individual neurons reflecting short- and long-term visual memory
537 in an arthropod. J Neurosci 23:8539–8546
538 Wiersma CAG, Roach JLM, Glantz RM (1982) Neural integration in
539 the optic system. In: Sandeman DC, Atwood HL (eds) The
540 biology of the crustacea, vol 4. Neural integration and behavior.
541 Academic Press, New York, pp 1–31
542 Woodbury PB (1986) The geometry of predator avoidance by the blue
543 crab, *Callinectes sapidus* Rathbun. Anim Behav 34:28–37
544 Zeil J, Al-Mutairi M (1996) The variation of resolution and of omma-
545 tidial dimensions in the compound eyes of the fiddler crab *Uca
546 lactea annulipes* (Ocypodidae, Brachyura, Decapoda). J Exp Biol
547 199:1569–1577
548 Zeil J, Nalbach G, Nalbach HO (1986) Eyes, eyes stalks and the visual
549 world of semi-terrestrial crabs. J Comp Physiol A 159:801–811
550 Zeil J, Nalbach G, Nalbach H-O (1989) Spatial vision in a flat world:
551 optical and neural adaptations in arthropods. In: Singh RN,
552 Strausfeld NJ (eds) Neurobiology of sensory systems. Plenum,
553 New York, pp 123–137