How Visual Space Maps in the Optic Neuropils of a Crab

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ABSTRACT

The Decapoda is the largest order of crustaceans, some 10,000 species having been described to date. The order includes shrimps, lobsters, crayfishes, and crabs. Most of these are highly visual animals that display complex visually guided behaviors and, consequently, large areas of their nervous systems are dedicated to visual processing. However, our knowledge of the organization and functioning of the visual nervous system of these animals is still limited. Beneath the retina lie three serially arranged optic neuropils connected by two chiasmata. Here, we apply dye tracers in different areas of the retina or the optic neuropils to investigate the organization of visual space maps in the optic neuropils of the brachyuran crab *Chasmagnathus granulatus*. Our results reveal the way in which the visual space is represented in the three main optic neuropils of a decapod. We show that the crabs' optic chiasmata are oriented perpendicular to each other, an arrangement that seems to be unique among malacostracans. Crabs use retinal position in azimuth and elevation to categorize visual stimuli; for instance, stimuli moving above or below the horizon are interpreted as predators or conspecifics, respectively. The retinotopic maps revealed in the present study create the possibility of relating particular regions of the optic neuropils with distinct behavioral responses elicited by stimuli occurring in different regions of the visual field. J. Comp. Neurol. 519:1631–1639, 2011.

INDEXING TERMS: malacostracan; visual system; retinotopy; behavior

The decapod visual system is composed of a compound eye retina and three optic neuropils, all contained within the eyestalk. From the periphery to the center these neuropils are: the lamina, the medulla, and the lobula. Axons connecting the lamina with the medulla and the medulla with the lobula form successive chiasmata. The optic neuropils are organized into columnar subunits intersected by tangential strata. Columnar subunits mainly consist of columnar neurons, while tangential strata comprise lateral processes of columnar neurons, amacrine cells, and neurites from tangential cells (Strausfeld and Nässel, 1980). The lamina receives direct inputs from photoreceptors in the retina by uncrossed bundles of axons (Stowe et al., 1977). In the crab *Leptograpsus* it has been shown that the eight photoreceptor axons (R1–R8) from a single ommatidium project to a single columnar sampling unit of the lamina; hence, the outside world is projected point-by-point onto the retinotopic mosaic of the lamina (Stowe, 1977). In the crab *Chasmagnathus*, the representation of the retinotopic mosaic does not appear to be coarsened in the medulla and the lobula (Sztarker et al., 2005), suggesting that a similar degree of retinotopic representation is preserved at the level of these neuropils. However, the large-scale retinal map of the decapod lamina, medulla, and lobula is almost completely unknown. The only available description of the topographic organization in a decapod deep optic neuropil is that provided for the medulla of the crayfish. In this animal, physiological determination of receptive fields has revealed the existence of 14 light intensity sensitive neurons, the sustaining neurons, which are topographically organized across the medulla (Kirk et al., 1982).

Among crustaceans, brachyuran crabs in particular have attracted the interest of researchers because they inhabit a broad range of biotopes: from the deep sea to epiphytes high up on tropical trees, from fresh water to

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deserts (Diesel et al., 2000). They rely on visual cues for visuomotor control and navigation, conspecific and predator recognition (Woodbury, 1986; Land and Layne, 1995b), and social communication (Christy, 1988a,b; Land and Layne, 1995a; Backwell et al., 2000). Many crabs live in the intertidal zone where the landscape dramatically changes twice a day. These crabs can spend long periods out of the water, which make them very convenient for physiological experimentation (Nalbach, 1990b; Berón de Astrada et al., 2001; Frenkel et al., 2005).

Brachyuran eyes, located on vertically oriented eyestalks, contain ommatidia that spread almost all around the eyestalk, so that at some elevations the eye has a nearly 360° field of view (Sandeman, 1978). In semiterrestrial crabs there is a band of greatly increased vertical resolution around the middle of the eye that normally images the animal's horizon and delineates the dorsal and ventral visual fields of the animal (Zeil et al., 1986; Land and Layne, 1995a; Berón de Astrada, unpubl. obs.). Crabs respond differently according to the position of the stimulus on the retina (Layne, 1998). For instance, moving stimuli that appear above the horizon usually trigger escape responses, whereas stimuli moving below the horizon elicit responses such as burrow defense or courtship displays (Land and Layne, 1995a; Hemmi and Zeil, 2003). Thus, visual objects moving above or below the horizon are most likely taken as either predators or conspecifics, respectively (Layne et al., 1997). Crabs also respond 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, it first rotates and then runs sideways, maintaining the stimulus laterally (Land and Layne, 1995b). The direction of the escape response is continuously adjusted according to changes in the predator trajectory (Nalbach, 1990a). The sensory-motor transformation involved in the control of this directionality requires an internal representation of visual space.

With the aim of understanding the neural processes underlying visually guided behavior in crabs, we have systematically investigated the anatomy (Berón de Astrada and Tomsic, 2002; Sztarker et al., 2005, 2009) and physiology (e.g., Berón de Astrada et al., 2001, 2009; Berón de Astrada and Tomsic, 2002; Sztarker and Tomsic, 2004; Medan et al., 2007a) of the visual nervous system of the crab *Chasmagnathus granulatus*. We found that the escape response to visual danger stimuli can be largely accounted for by the response of a group of motion-sensitive lobula giants (LGs) neurons (Tomsic et al., 2003, 2009; Oliva et al., 2007; Starker and Tomsic, 2008). However, we do not know how the retina is represented in the optic neuropils of decapods. Here we investigate the organization of visual space maps in the crab optic neuropils by applying dye tracers in different parts of the retina or the visual system, and by following the projections into different optic regions. Our results reveal how visual space is represented in the three main optic neuropils of a decapod.

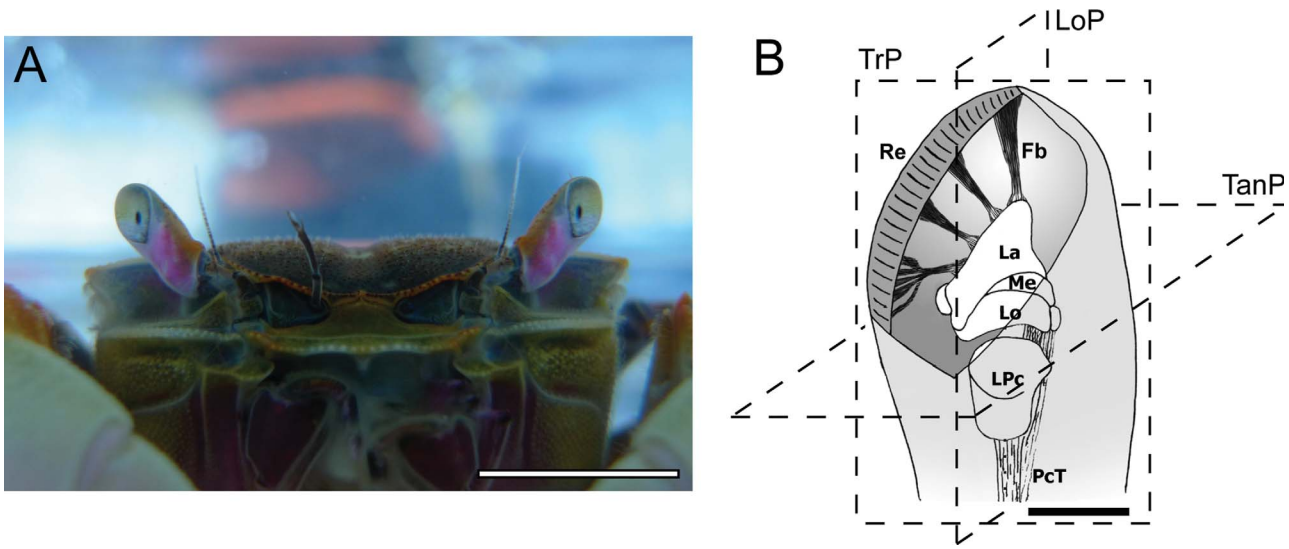

Figure 1. The crab *Chasmagnathus granulatus* and a diagram of the eyestalk containing the optic neuropils. A: Close frontal view of an adult male crab, showing the eyestalks in their normal seeing position at an angle of 50° with respect to the horizontal. B: Diagram of the right eyestalk illustrating the organization and relative dimensions of the optic neuropils (Sztarker et al., 2005). Dashed rectangles indicate the planes in which optical sections were made. Re, retina; FB, bundles of retinula cell fibers; La, lamina; Me, medulla; Lo, lobula; LPc, lateral protocerebrum; PcT, protocerebral tract; TrP, transversal plane; LoP, longitudinal plane; TanP, tangential plane. Scale bars = 1 cm in A; 500 μm in B.

MATERIALS AND METHODS

Animals

Animals were adult male *C. granulatus* crabs measuring 2.7–3.0 cm across the carapace and weighing about 17 g (Fig. 1A). Crabs were collected in narrow coastal inlets (rías) of San Clemente del Tuyú, Argentina. Animals were maintained in the laboratory in plastic tanks (35 × 48 × 27 cm) filled to 2 cm depth with diluted marine water (hw-Marinex, Winex, Hamburg, Germany) having a salinity of 1.0–1.4% and a pH of 7.4–7.6. They were maintained at 22–24°C on a 12-hour light/dark cycle.

Coordinates of the optic lobe and planes of optical sectioning

Most anatomical studies of crustacean visual system have been performed on species of crayfishes and shrimps whose eyestalks are oriented almost horizontally. In contrast, crab eyestalks are oriented rather vertically. In particular, *Chasmagnathus* is a broad-fronted crab whose mobile eyestalks are normally oriented at an angle of 50° from the horizontal plane (Fig. 1A). Such orientation complicates the definition of a reference system. Thus, for the sake of simplicity, we will refer to a coordinate system in which the eyestalk is oriented at 90° from the horizontal plane (Berón de Astrada and Tomsic, 2002; Sztarker et al., 2005). Longitudinal sections were obtained by performing sections along the long axis of the eyestalk and along the anteroposterior axis of the animal. Transversal sections are also along the long axis of the eyestalk but along the lateromedial axis. Tangential sections are perpendicular to the long axis of the eyestalk (Fig. 1B).

Dye staining

To trace the retinula cells projections onto the lamina and medulla we dye stained the photoreceptors with local applications of fluorescent dextrans in the retina (dextran-Alexa Fluor 488; dextran-Alexa Fluor 680; dextran-tetramethylrhodamine, 3,000 MW, Molecular Probes, Eugene, OR). The dye was applied to spots of the retina oriented toward eight different positions of the visual space: three points were in the frontal retina, three in the lateral part, and the other two were in the smaller posterior region of the eye (see Fig. 2I). These points were aligned along three longitudinal and three latitudinal lines of a normally oriented eye (i.e., at 50° from the horizontal plane; Fig. 1A), simplifying the representation of cardinal positions of the visual space in the lamina and medulla. To apply the dextran in the selected retinal points, the crab was held in an adjustable clamp and placed on ice under a dissecting microscope. The eyestalk was carefully cemented to the carapace at its normal seeing position. Dextrans were delivered through small holes made at the selected points in the cornea with a needle (Utting et al., 2000). Briefly, a fine glass micropipette with dextran crystals deposited at its tip was inserted through the cornea into the retina. The probe was gently rotated and then removed after 5–10 seconds, leaving a spot of dye in the selected area of the retina. In each eye, three sites were stained at the same time, each with a different fluorescent dextran.

To study the spatial projection pattern between medulla and lobula, the tracer was directly applied into the medulla. A small piece of cuticle was removed from the posterior side of the eyestalk and the optic neuropils were exposed. Using the methodology just described, dextrans were then applied to discrete points in the medulla. After depositing the dye, the piece of cuticle removed from the eyestalk was put back in place. Only one type of dextran was applied in each medulla preparation.

Histology

Dextran was allowed to diffuse for 3–4 hours in the living animal. Then the crab was anesthetized on ice and the optic lobe was dissected and fixed overnight (4% paraformaldehyde in phosphate buffer 0.1M, pH 7.2). After five 20-minute washes with phosphate buffer the tissue was dehydrated in ethanol series and cleared in methyl salicylate. Ganglia were imaged as whole mounts and scanned at 5-μm intervals with a confocal microscope (Olympus, Lake Success, NY, Fluoview FV 1000). Because we were interested in the identification of large-scale retinal maps, we chose to do whole-mount scanning rather than cutting serial sections, which are more difficult to align in the proper coordinates. Optic neuropils were scanned from the anterior and the posterior side, as well as from the top (tangential optical slices). Images, saved as 3D stacks, were adjusted for brightness and contrast, and illustrations were obtained by merging the individual serial sections with ImageJ 1.33U (National Institutes of Health, Bethesda, MD).

RESULTS

General structure of *Chasmagnathus eye*

Chasmagnathus granulatus is a mid-size semiterrestrial crab, up to 38 mm carapace width, whose behavior is largely driven by visual cues. Its compound eye is oval in shape and situated at the end of the eyestalk (Fig. 1A). Figure 2A–D shows a right eye from different viewpoints. The retinal surface is spread around the distal eyestalk, covering nearly the whole circumference of the eye except for a thin band of cuticle which does not bear visual cells. This band extends along the medial side of the eyestalk to end as a small round cap on the dorsal part of

the eye (Fig. 2D). The vertical extension of the eye is higher in the front than in the side and the back (Fig. 2E). These height changes occur progressively from the bottom of the eye, whereas the top part does not change. The ommatidia of *Chasmagnathus* are arranged in a hexagonal lattice with straight horizontal rows (Stavenga, 1979). The number of horizontal rows of ommatidia is 91–98 at the front of the eye and

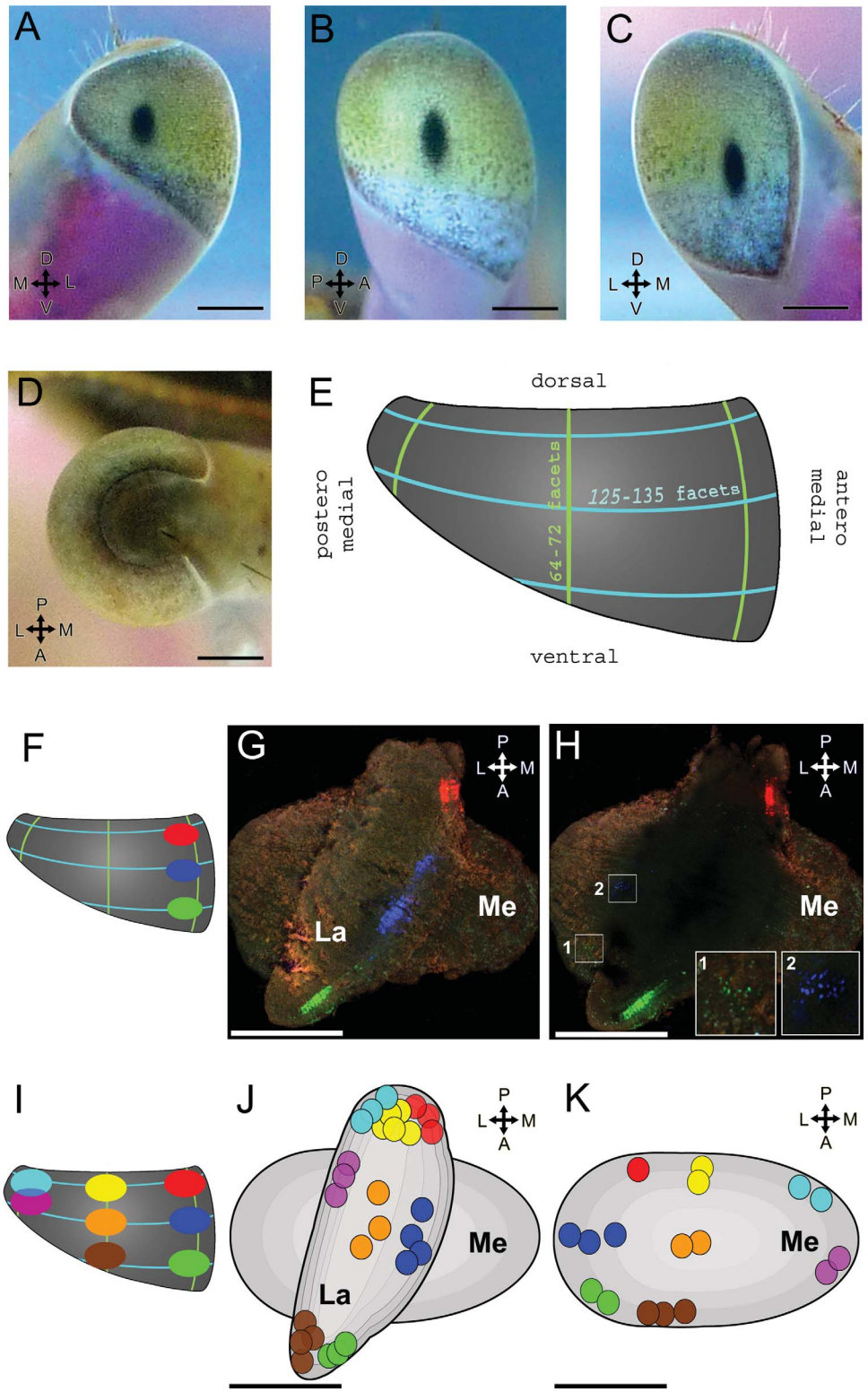

Figure 2.

decreases to 64–72 at the side and to 40–47 at the back ($n = 4$). Around the equator of the eye, the number of ommatidia on a horizontal row is between 125 and 135 ($n = 4$). The general characteristics outlined here for *Chasmagnathus* eye are consistent with previous studies in other crabs (e.g., Sandeman, 1978; Zeil and Al-Mutairi, 1996).

Lamina retinotopy

The lamina of *Chasmagnathus* has the form of an inverted canoe (Berón de Astrada and Tomsic, 2002), with its long axis extended at 30° from the anteroposterior axis (Fig. 2G). The morphology and relationship between the neural elements that compose the lamina of the decapods has been carefully studied in *Chasmagnathus* (Sztarker et al., 2005, 2009), revealing a highly ordered retinotopic organization. Nevertheless, the way in which the dorsal, ventral, frontal, and rear visual fields are organized in the lamina is still unknown. In order to study the retinal projecting map into the lamina we dye-stained the photoreceptor axons by applying different fluorescent dextrans into eight different selected sites of *Chasmagnathus* retina (Fig. 2I and Materials and Methods). Figure 2F represents the retina of an animal with the three vertically aligned frontal positions that were stained with different fluorescent dextrans. The stained photoreceptor projections can be seen from a top view of the first and second optic neuropils in Figure 2G,H. The lamina presents three stained areas corresponding to the stained retinula cells projections reaching the neuropil (Fig. 2G). Combined results from 28 successful dextran applications performed along the eight selected sites of the retina in 10 right eyes are shown in Figure 2J. A comparison between Figures 2I and 2J shows that the retinal map of the lamina consists of an uncrossed projection of the retina. In this map, azimuthal positions are represented along the shorter axis of the neuropil. The anteromedial border of the retina is represented along the medial border of the lamina, the lateral retina is represented along the midline (corresponding to the dorsal folding of the neuropil), and the posterior retina is represented along the lateral border. Elevation positions are represented along the longer axis of the lamina in such a way that visual spaces below, at the level of, and above the horizon are mapped in the anterior, central, and posterior parts of the lamina, respectively.

Medulla retinotopy

In contrast to the lamina, the medulla of *Chasmagnathus* is a dome-shaped structure elongated in the lateromedial axis that gets slightly narrower towards its medial pole. The medulla receives direct retinotopic information from the retina via the first optic chiasma by R8 receptor axons and from the lamina by monopolar and T cells (Sztarker et al., 2005, 2009). To disclose the retinal map of the medulla we tracked the R8 photoreceptor terminals in the same preparations used to study the lamina retinotopy. Figure 2H shows a deeper optical tangential section of the same optic lobe of Figure 2G, which corresponds approximately to the surface of the medulla. Because R8 axons terminate superficially in the medulla as large swellings (≈10 μm), they could be visualized as small bright dots (insets in Fig. 2H). Figure 2K represents the R8 projection sites into the medulla obtained from dye spots applied to the eight different retinal positions (Fig. 2I) in which we could observe their stained terminals ($n = 17$). A comparison of Figures 2I and 2K indicates that each horizontal row of ommatidia is mapped along the longer axis of the medulla (the lateromedial axis). This axis then contains the azimuthal representation of the visual space. The order of sampling in this axis, however, is inverted with respect to the retina and the lamina. In fact, the anteromedial border of the retina is represented in the lateral border of the ME, whereas the posterior retina

Figure 2. The compound eye and retinal projection into the lamina and medulla of *Chasmagnathus*. Pictures of the back (**A**), lateral (**B**), frontal (**C**), and dorsal (**D**) part of a right eye. Notice the vertically elongated pseudopupil (high vertical resolution) along the equatorial line of the eye (A–C). **E**: 2D representation of the retinal surface of the right eye. The number of ommatidia around the equator of the eye is between 125–135, while along the lateral meridian the number of horizontal rows is 64–72 ($n = 4$). Two additional meridians, one close to the anteromedial and the other to the posteromedial border of the retina, and two latitudinal lines, one close the dorsal and the other to the ventral border of the retina, were chosen to study the retinal projection into the lamina and medulla. **G**: Top view from a whole-mount preparation of the lamina and medulla of an animal whose retina was stained with different fluorescent dextrans in the positions indicated in **F**. The selected vertically aligned areas of the retina projected along the medial side of the major lamina axis. **H**: Optical section from the surface of the medulla of the same optic lobe in **G**. The R8 projections from two of the three stained sites, green and blue, were identified reaching the medulla. Insets show a magnification of these R8 terminals. **I**: The eight retinal positions where dyes had been applied along different experiments. Each eye was stained in three different positions only. **J**: Color code representation of combined results from 10 animals showing the sites of photoreceptor projections into the lamina. Each circle represents a single staining. **K**: Combined results from R8 projection sites into the medulla. The comparison between I,J,K reveals that the first optic chiasma produces an inversion of retinal horizontal sampling units. Scale bars = 500 μm in A–D; 100 μm in G,H,J,K.

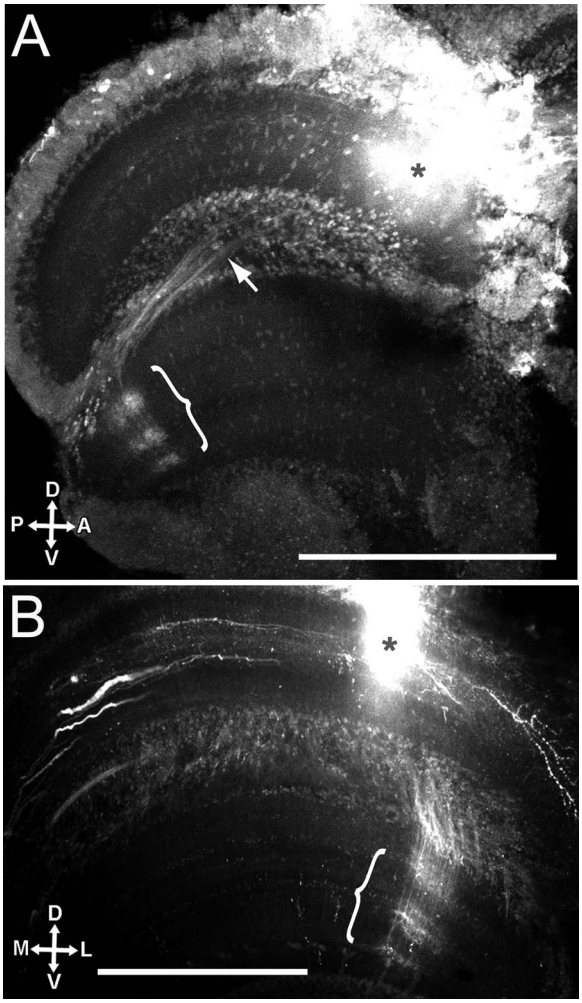

Figure 3. Projection of neural fibers through the second optic chiasma of *Chasmagnathus*. Fluorescent dextran crystals were locally applied into the medulla (asterisks). **A**: Longitudinal optical section showing that transmedullar neurons from the anterior side of the medulla project to the posterior side of the lobula, where they arborize at different tangential strata (bracket). **B**: Transversal optical section showing that transmedullar neurons do not decussate in the lateromedial axis. Arrow: crossing fibers. Scale bars = 200 μm.

is represented in the medial border. Thus, the optic chiasma between lamina and medulla inverts the anteroposterior representation of the horizontal visual map. Elevation, on the other hand, is mapped across the shorter axis of the medulla, with the lower and upper visual fields represented in the anterior and posterior part of the medulla, respectively.

It is worth mentioning that in all cases where dextran applications in the medulla (see below) stained neurons projecting to or from the lamina, the projecting pattern for the first optic chiasma was entirely confirmed. In addition, we counted the number of aligned columns at the midline of the long and short medulla axes and found that the lateromedial axis contains between 126–137 columns, while the anteroposterior axis has between 62–66. This closely matches the number of ommatidia found along the corresponding horizontal and vertical axes of the eye (Fig. 2E).

Lobula retinotopy

Like the medulla, the lobula of *Chasmagnathus* is a dome-shaped structure also elongated in the lateromedial axis. Because the medulla and the lobula are nested retinotopic neuropils, the mapping of visual space in the lobula can be discerned by determining the orientation of the chiasma connecting the two neuropils (the second optic chiasma). To this end, we locally applied crystals of a fluorescent dextran in the medulla and then followed the stained neural projections into the lobula (see Materials and Methods). Figure 3A shows a lateral view of the medulla and the lobula of such stainings. The white spots in the medulla correspond to the sites of dye application (asterisks). The axons of the stained columnar elements decussate (arrow), projecting to the contralateral side of the lobula (brackets). Thus, the second optic chiasma produces an inversion of the neuronal projections in the anteroposterior axis. Conversely, posterior views of the neuropils (as illustrated in Fig. 3B) show that columnar elements stained in a particular lateromedial region of the medulla project their axons to a similar lateromedial region of the lobula. Therefore, the second chiasma produces no inversion in the lateromedial axis.

These results, in conjunction with those of the previous sections, reveal that the second optic chiasma inverts the retinotopic arrangement in elevation but not in the horizontal plane. In the retinal map of the lobula, lower and upper portions of the animal visual field are respectively represented in the posterior and anterior areas of the neuropil, whereas the frontal, the lateral, and the rear visual fields are represented respectively in the lateral, central, and medial parts of the lobula (Fig. 4).

DISCUSSION

Crabs and other decapods are visual animals that offer excellent opportunities for neuroethological studies (Yeh et al., 1996; Hemmi and Zeil, 2003b; Tomsic et al., 2003). Because their behavior is largely determined by the position of stimuli in space, the purpose of this study was to disclose the way in which the coordinates of visual space are represented in the visual nervous system of a representative of the group, the semiterrestrial grapsid crab *C. granulatus*. The outcome of our findings is depicted in Figure 4. The retinal surface projects uncrossed into the lamina. As indicated by the line color code of Figure 4, positions in azimuth and in elevation are correspondingly represented along the minor and major axes of the lamina. The frontal, lateral, and rear visual fields are mapped

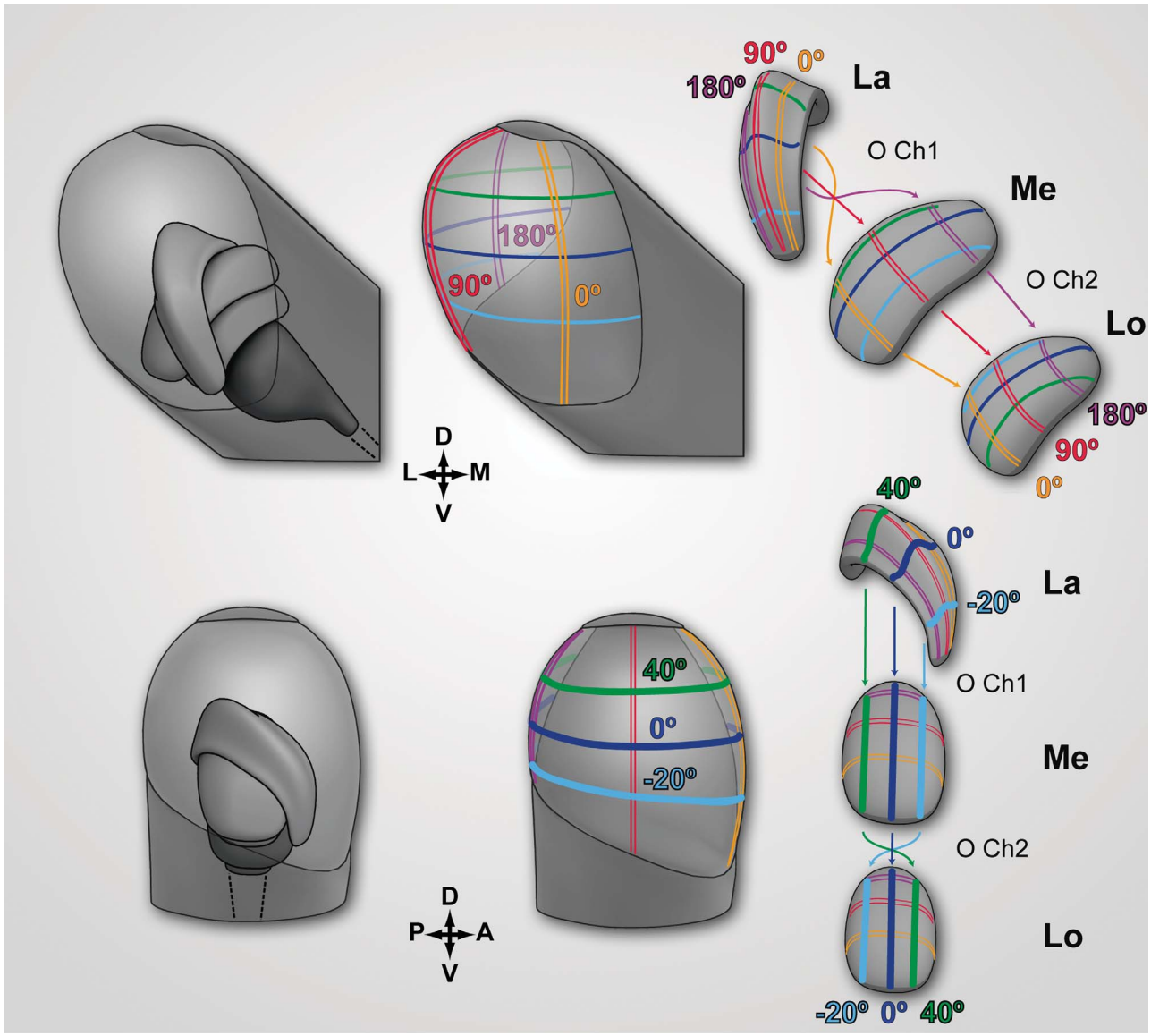

Figure 4. Visual space maps of the optic neuropils of the crab. Upper and lower panels represent frontal and lateral views (from a slightly dorsal perspective) of the right eye and its optic neuropils. Vertical color lines represent meridian positions across the retina at 0 (yellow), 90 (red), and 180 (violet) degrees, while horizontal lines represent positions in elevation at the eye equator (blue), and at 40° above (green) and 20° below the equator (light blue). The color code is preserved across the three optic neuropils and the chiasmata. In the crab the first optic chiasma inverts the order of representation corresponding to the horizontal plane (upper panel), while the second optic chiasma inverts the order corresponding to the vertical plane (lower panel). Functional implications of the retinal maps of the optic neuropils are discussed in the text. La, lamina; Me, medulla; Lo, lobula; O Ch1, first optic chiasma; O Ch2, second optic chiasma.

respectively in the medial, central, and lateral areas of the lamina. Visual fields below, at the level of, or above the eye equator are mapped in the anterior, central, and posterior parts of the neuropil, respectively. The relative positions in the vertical plane are preserved along the anteroposterior axis of the medulla, in which lower and upper visual fields continue being represented in the anterior and posterior part of the neuropil. However, the map of azimuthal positions is inverted along the medulla lateromedial axis. In fact, the frontal, lateral, and rear visual fields are correspondingly mapped in the lateral, central, and medial parts of the medulla. Therefore, the first optic chiasma inverts the azimuthal retinotopic representation. By tracking neural fibers stained in the medulla until the lobula, we found that the second optic chiasma inverts the map of visual positions in elevation. Consequently, the lower visual field is represented in the posterior part of the lobula, whereas the upper field is represented in the anterior part.

A number of studies in malacostracan species indicate that the first and second optic chiasmata are oriented in the same plane, such that the first reverses and the

second re-reverses the anteroposterior order of the retinotopic mosaic (Elofsson and Dahl, 1970; Strausfeld, 2005). However, Waterman (1961) and Elofsson and Dahl (1970) have mentioned that in brachyurans, chiasmata may be oriented perpendicular to each other. Our results with *Chasmagnathus* support the latter observation.

The results we present here receive additional support from recent experiments on a particular class of lobula neurons, the MLG1, which is composed of 14 parallel elements serially arranged throughout the entire proximal layer of the lobula. Each of these 14 cells has an exceptionally wide-diameter primary branch (8–10 μm in diameter) oriented along the anteroposterior axis (see Sztarker et al., 2005; Medan et al., 2007a). By using in vivo intracellular recording and staining techniques, we were able to determine the correspondence between the receptive field and the location in the lobula of several MLG1 neurons. MLG1 neurons which have a receptive field oriented towards the medial side of the animal are located in the lateral part of the lobula, whereas those having their receptive field oriented towards the side of the animal are located in the medial side of the neuropil (Medan et al., 2007b). These data are in agreement with the results of the present study. Therefore, our studies confirm that in brachyurans the optic chiasmata are perpendicularly oriented. This feature can now be considered in studies using brain characters to infer phylogeny in arthropods (e.g., Strausfeld, 1998, 2009; Harzsch, 2002).

Very few physiological or anatomical studies have been performed on decapods that can be directly related to their visual behavior. This is quite remarkable given the advantages offered by these animals for neuroethological research. Our studies in *Chasmagnathus* allowed us to identify several classes of giant lobula neurons that play central roles in the animals visually guided behaviors (Tomsic et al., 2003; Oliva et al., 2007). In crabs, visual behaviors are highly determined by the retinal position of the eliciting stimuli. Thus, the retinal maps disclosed in the present article now make it possible to relate activity occurring in distinct regions of the medulla and lobula with visual behavior.

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