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Featured Article

Left–right asymmetry of the visual system in the scallop *Nodipecten nodosus* (Bivalvia: Pectinidae)

Jorge A. Audino[1], Jeanne M. Serb[2] and José E.A.R. Marian[1]

[1]*Department of Zoology, University of São Paulo, Rua do Matão, Travessa 14, n. 101, 05508-090, São Paulo, São Paulo, Brazil; and*
[2]*Department of Ecology, Evolution & Organismal Biology, Iowa State University, 2200 Osborn Dr., Ames, IA 50011, USA*

Correspondence: J.A. Audino; e-mail: jorgeaudino@ib.usp.br

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ABSTRACT

Left–right asymmetries are consistent differences between the left and right sides and represent an intriguing feature of molluscan morphology. Interestingly, external asymmetries, such as inequivalve shells, are often coupled with lateralization in the nervous system, which often includes functional and structural specializations of the left or right sides. In the case of visual asymmetries, lateralized phenotypes frequently include left–right differences in eye position, structure and use. To investigate lateralization and visual asymmetries among bivalves, we examined the visual and nervous systems of the scallop *Nodipecten nodosus*. We characterized different eye morphologies in the species and determined eye-side frequencies. We also studied the anatomy of the nervous system, focusing on the parietovisceral ganglion (PVG). Our results reveal that the visual and nervous systems of the scallop *N. nodosus* comprise consistent left–right asymmetries: (1) a greater number of eyes on the left side, (2) increased size of the left PVG lateral lobe, (3) larger glomeruli in the left PVG lateral lobe and (4) radial pallial nerves associated with the left lateral lobe spaced more widely than the more compactly arranged pallial nerves associated with the right lateral lobe. In addition, eyes with a distinctive morphology, where the optic vesicle is rotated, are more frequent on the left side. Considering the habit of this species to rest on the right valve, we hypothesize that curved eyes might contribute to expanding the overall visual field. Even though bivalves are not typically considered in the literature on lateralization, accumulating evidence for scallops, as suggested by our results, indicates their potential to reveal novel patterns of visual asymmetry in benthic invertebrates.

INTRODUCTION

Consistent differences in morphology between the left and right sides characterize directional left–right (LR) asymmetries, including striking changes in shape, size, number and position of body structures (Namigai, Kenny & Shimeld, 2014). Asymmetrical phenotypes have evolved independently across the animal tree of life many times, suggesting complex evolutionary histories of fixed and random asymmetries in species and populations (Palmer, 2009). A classic example of morphological asymmetry in molluscs is the occurrence of dextral (right-sided coiled) and sinistral (left-sided coiled) gastropods (Schilthuizen & Davison, 2005). Among bivalves, LR asymmetries represent a common feature of shell morphology, as observed in inequivalved oysters, scallops and relatives (Stanley, 1972). Interestingly, external asymmetries are often coupled with other specializations, such as brain asymmetry and behavioural bias (Frasnelli, Vallortigara & Rogers, 2012).

In many invertebrates, including molluscs, LR asymmetries indicate different functional and structural specializations of the left or right sides of the nervous system, a condition known as lateralization (Frasnelli, 2017). Many studies have demonstrated that invertebrates with relatively simple nervous systems exhibit sensory and motor asymmetries in behaviour (e.g. Hobert, 2014). Moreover, visual asymmetries are frequently associated with lateralized phenotypes, encompassing LR differences in eye position, structure and use (Frasnelli *et al.*, 2019). A dramatic case of visual asymmetry is observed in the dimorphic left and right eyes of deep-sea cockeyed squids (Histioteuthidae). The upward-oriented eye is dramatically larger than the downward-oriented eye, a unique visual strategy to capture as much dim downwelling sunlight as possible (Thomas, Robison & Johnsen, 2017). Among molluscs, visual and brain asymmetries have been characterized for some gastropod and cephalopod species, including their associated visual ecologies and behaviours (e.g. Byrne *et al.*, 2006). For example, side-turning preference is correlated with the asymmetrical size of the left and right optic lobes in cuttlefish (Jozet-Alves *et al.*, 2012).

Despite the growing knowledge of brain asymmetries in invertebrates, one open question is whether visual asymmetries are correlated with brain asymmetries in the context of distinct taxonomic groups and visual systems. In contrast to vertebrates and insects, lateralization is still poorly understood in other animals, such as bivalves, which bear multiple, noncephalic eyes distributed across their mantle margins. A better understanding of these so-called 'distributed visual systems' (Chappell, Horan & Speiser, 2021) and associated neurobiological patterns should provide novel opportunities to investigate the function and evolution of asymmetrical phenotypes.

Scallops (Bivalvia: Pectinidae) can help elucidate patterns of lateralization given that morphological asymmetries are documented for many species, especially for hard parts. For example, directional asymmetry in shell shape is a crucial aspect of scallop macroevolution and is associated with different life habits (Sherratt, Serb & Adams, 2017). The scallop visual system comprises dozens to hundreds of mirror-based eyes along the mantle margins, which have been extensively characterized for their anatomy (Dakin, 1910a; Speiser & Johnsen, 2008) and optical properties (Land, 1965; Speiser, Loew & Johnsen, 2011). Interestingly, LR asymmetries in the visual system have been reported for *Pecten* species (Dakin, 1910a), *Euvola ziczac* (Linnaeus, 1758) (Wilkens & Ache, 1977) and *Placopecten magellanicus* (Gmelin, 1791) (Whoriskey, Whoriskey & Whoriskey, 2014), including left-side eyes outnumbering the right-side ones. In the scallop nervous system, the lateral lobes of the parietovisceral ganglion (PVG) are likely responsible for processing visual information (Speiser & Wilkens, 2016), and a relatively larger left lateral lobe is present in *Pecten* (Dakin, 1910a). However, ganglionic and visual asymmetries remain largely unknown for the family. Consequently, the lack of comparative data hampers the identification of lateralized patterns and the inference of evolutionary hypotheses.

To investigate lateralization and visual asymmetries in pectinid bivalves, we examined the visual and nervous systems of the scallop *Nodipecten nodosus* (Linnaeus, 1758). First, we characterized different eye morphologies in the species and compared eye abundance among individuals. Then, we determined eye-side frequencies to investigate left–right asymmetries. Finally, we studied the nervous system, focusing on the anatomy of the PVG.

MATERIAL AND METHODS

We obtained 23 specimens of *Nodipecten nodosus* from the scallop farm of the Institute of Eco-Development from Baía de Ilha Grande (IED-BIG), Rio de Janeiro (RJ), Brazil. The species has inequivalve shells, with the left valve bearing numerous knobs on the ridges, and rests preferably on the right valve. Based on shell asymmetry and body position, we expected some asymmetry in eye distribution. All individuals (3–8 cm width) were anaesthetized for 2 h by adding 7.5% $MgCl_2$ in seawater prior to fixation in 10% formalin in seawater. After 24 h, all individuals were transferred to 70% ethanol. To expand the study, we examined nine additional specimens (10–18 cm width) preserved in ethanol from the Museum of Zoology of the University of São Paulo (MZSP, catalogue numbers 70493, 86853, 85106, 84991, 23128, 35667, 23130 and 82724; specimens from the southeastern Brazilian coastal waters). In total, 32 adult individuals were observed under a stereomicroscope for general morphology and eye count, and six individuals had their PVG dissected.

Eye-side frequencies were determined and tested for LR asymmetry using resampling methods in order to avoid distribution assumptions of parametric tests (Manly, 1991). Under the null hypothesis describing the same abundance on both sides, there should be no difference between left–right means. Thus, the mean difference under H_0 should be close to zero ($\mu_{\text{left}} - \mu_{\text{right}} = 0$). We generated a permutation-based empirical sampling distribution after 100,000 iterations to assess statistical significance. Data analysis was performed in the R environment (R Core Team, 2020). Raw data and code are available as Supplementary Material.

We selected five individuals of *N. nodosus* to investigate eye and nervous system anatomy by means of histological techniques. They were anaesthetized for 2 h under refrigeration by adding 7.5% $MgCl_2$ in seawater and then dissected. The PVG and mantle tissue containing eyes were removed and fixed for 5 h at 4 °C in a 4% paraformaldehyde solution of a phosphate-buffered saline modified for marine organisms (3% NaCl). Samples were completely dehydrated in graded ethanol series, and then embedded in glycolmethacrylate resin (Leica Historesin Kit, Germany). Serial sections of 3 μm were obtained using a Leica RM2255 microtome and stained with haematoxylin and eosin (HE) or toluidine blue and basic fuchsin (TB). Histological sections were mounted on slides, covered with coverslips and analysed under a light microscope.

General terms and definitions used here for invertebrate neuroanatomy follow Richter *et al.* (2010), bivalve terminology is in accordance with Carter *et al.* (2012), and scallop-specific terminology follows Speiser & Wilkens (2016).

RESULTS

Eye anatomy and curved eyes

Concave mirror eyes in *Nodipecten nodosus* (Fig. 1A) are distributed along the middle mantle fold on both left and right sides of the animal body. The eyestalk is typically brownish, while the distal region is light blue (Fig. 1A). In contrast to the more cuboidal and less pigmented cells from the eyestalk, the blue band consists of a simple columnar epithelium with a high density of granules (Fig. 1B). The pupil aperture in the centre is shaped by unpigmented epithelial cells forming the cornea (Fig. 1A, B). Internally, the optic vesicle includes a lens, a double retina formed by distal and proximal layers, a reflector mirror layer (also referred to as 'tapetum') and a pigmented layer (Fig. 1B).

In most cases, the mirror eyes of *N. nodosus* have the eyestalk axis nearly aligned with the optic vesicle axis, which is the axis that passes through all inner components (Fig. 1C). Nevertheless, a less common eye morphology was consistently observed among all individuals, in which the optic vesicle axis is at an oblique angle with the eyestalk axis, resulting in a curved appearance of those eyes on both valves (Fig. 1D–F). Eye morphology has been investigated in live specimens under a stereomicroscope before preservation to ensure that the curved aspect was not an artefact produced by fixation. Therefore, the curved appearance of these eyes is not artificial and corresponds to a natural morphology. The curved eyes, as named henceforward, occur in lower frequencies, representing around 12% of the total eyes examined. Except for the oblique angle of the optic vesicle, all the inner components of the curved eyes are arranged precisely as described above but slightly rotated (Fig. 1E, F).

Eye abundance

Mirror eyes of *N. nodosus* are more abundant on the left mantle lobe (mean ± SD = 43.21 ± 4.4) than on the right mantle lobe (27.09 ± 2.8) (Fig. 2A). The hypothesis of LR asymmetry is significant ($P < 0.001$) when the mean difference between eyes (16.12) is compared to the empirical sampling distribution produced under the null hypothesis of symmetry (Fig. 2B). A similar result was observed when considering the distribution of curved eyes only. They are more common on the left mantle lobe (6.71 ± 3.1) than on the right side (1.63 ± 1.84) (Fig. 2C). The LR asymmetry is also significant ($P < 0.001$) for curved eyes (Fig. 2D). Interestingly, curved eyes on the left mantle are oriented with their pupils facing upwards (left side; Fig. 3), and those on the right mantle are oriented with their pupils facing downwards (right side).

Nervous system anatomy

The nervous system of *N. nodosus* includes one pair of cerebral ganglia, one pair of partially fused pedal ganglia and a fused PVG

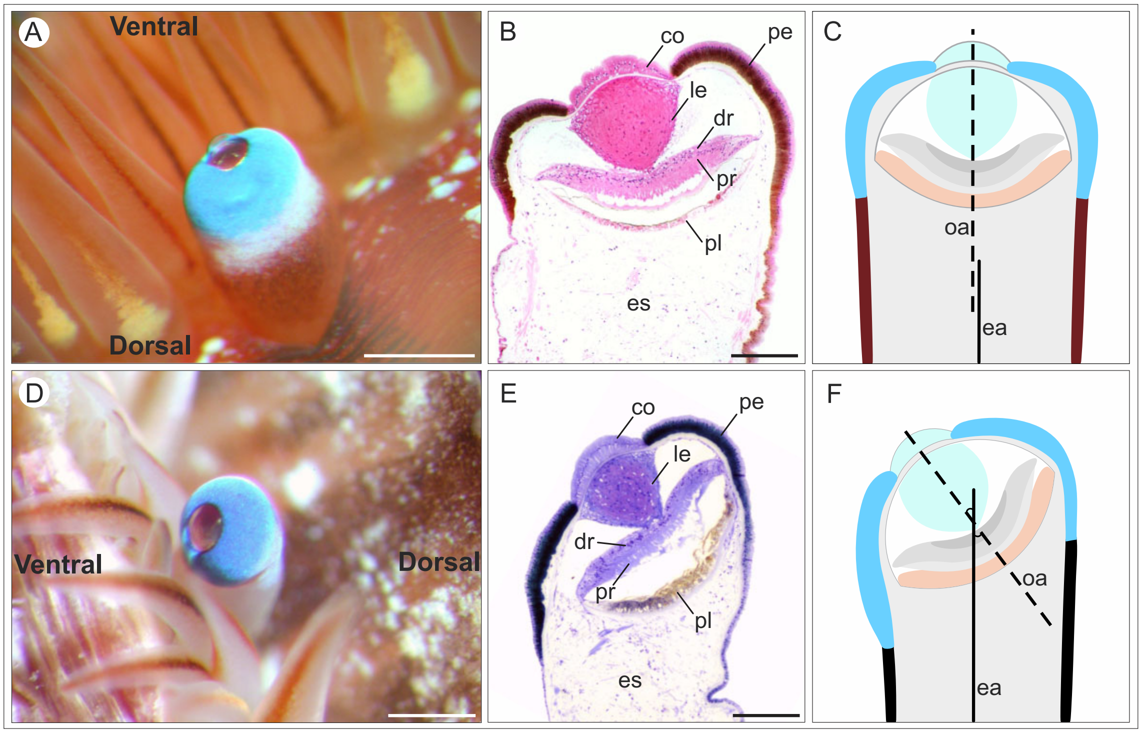

Figure 1. Mirror eyes of the scallop *Nodipecten nodosus*. **A.** Detail of the most frequent eye morphology, with the pupil on top. **B.** Histological section of a mirror eye showing the inner components of the optic vesicle. **C.** Schematic representation of an eye showing the eyestalk axis nearly aligned with the optic vesicle axis, which is the axis that passes through all inner components. **D.** Mirror eye with a curved appearance and pupil oriented to the left. **E.** Histological section of a curved eye showing the optic vesicle rotated. **F.** Schematic representation of a curved eye, in which the optic vesicle axis is at an oblique angle with the eyestalk axis, resulting in a rotated appearance and a more lateral pupil. Abbreviations: co, cornea; dr, distal retina; ea, eyestalk axis; es, eyestalk; le, lens; oa, optic vesicle axis; pe, pigmented epithelium; pl, pigmented layer; and pr, proximal retina. Scale bars: **A** = 1 mm; **B** = 200 μm; **D** = 1 mm; and **E** = 200 μm.

(Fig. 4A). Cerebral and pedal ganglia comprise minute organs in the anterior region, close to the mouth and embedded in the digestive mass (Fig. 4B). The cerebral ganglia consist of a pair of bilobed structures (fused cerebral and pleural ganglia) connected to each other by a commissure around the oesophagus (Fig. 4A). A pair of statocysts is connected to the cerebral ganglia by a pair of delicate nerves (Fig. 4A). The cerebral ganglia are responsible for the innervation of the labial palps and the anterior dorsal mantle (Fig. 4A). Each cerebral ganglion is connected to the partially fused pedal ganglia, from where a pair of nerves runs through the foot. No LR asymmetry was observed in the cerebral or pedal ganglia. Cerebro-visceral connectives exit each cerebral ganglion and run ventrally to reach the PVG (Fig. 4A). The PVG consists of fused lobes in a single, large ganglion located on the ventral surface of the adductor muscle and embedded in multiple layers of connective tissue (Fig. 4C). Most of the mantle is innervated by radial pallial nerves from the PVG (Fig. 4D), which is also the ganglion that innervates the gills via branchial nerves (Fig. 4A). The circumpallial nerve runs parallel to the mantle margin (Fig. 4A).

The PVG includes a pair of lateral lobes (also known as optic lobes), a ventro-central lobe and a pair of dorso-central lobes (Fig. 5A). In addition, one accessory ganglion is present above each cerebrovisceral connective (Fig. 5A). The radial pallial nerves exit the lateral portion of the lateral lobes and run towards the expanded ventral region of the mantle, while the posterior pallial nerves connect the ventral region of the lateral lobes to the posterior mantle (Fig. 5A). Two ganglionic asymmetries are notable. First, the left lateral lobe is consistently longer (1.14 ± 0.12 mm) and wider (0.31 ± 0.01 mm) than the right lateral lobe (1.01 ± 0.07 and 0.22 ± 0.1 mm, respectively), as observed in six dissected individuals, with a mean difference of 0.13 ± 0.01 mm for length and 0.09 ± 0.02 mm for width. Second, the radial pallial nerves associated with the left lateral lobe are spaced more widely than the more compactly arranged pallial nerves associated with the right lateral lobe (Fig. 5A).

Histological sections from the lateral lobes provide additional information on mantle innervation. The lateral lobes, just like the remaining ganglion, are organized in cortical and neuropil regions. The cortex is more external and formed by neuronal somata and glial cells (Fig. 5B). The neuropil is formed by neurites occupying the central space of the lobe (Fig. 5B, C). Axons from the pallial nerves can be observed reaching the lateral lobe and passing through the neuropil (Fig. 5C). Curiously, the neuropil in the lateral lobes forms spherical arrangements of neurites, named glomeruli (Fig. 5D). Based on the analysis of serial histological sections of two visceral ganglia, including six glomeruli from each lateral lobe, the left lateral lobe has larger glomeruli (168.5 ± 9.5 μm wide) than the right lobe (136.93 ± 12.27 μm).

DISCUSSION

Scallop eyes have proved to be a fascinating system for physiological, anatomical and evolutionary research. Detailed descriptions of ocular components have been extensively reviewed for many species (e.g. Dakin, 1910a; Land, 1965; Speiser & Johnsen, 2008; Malkowsky & Götze, 2014), including for the focal species *Nodipecten nodosus* (Audino *et al.*, 2015a), and therefore will not be discussed further. Here, we focus on eye distribution and nervous system anatomy of *N. nodosus* to investigate visual asymmetries and lateralization in bivalve molluscs.

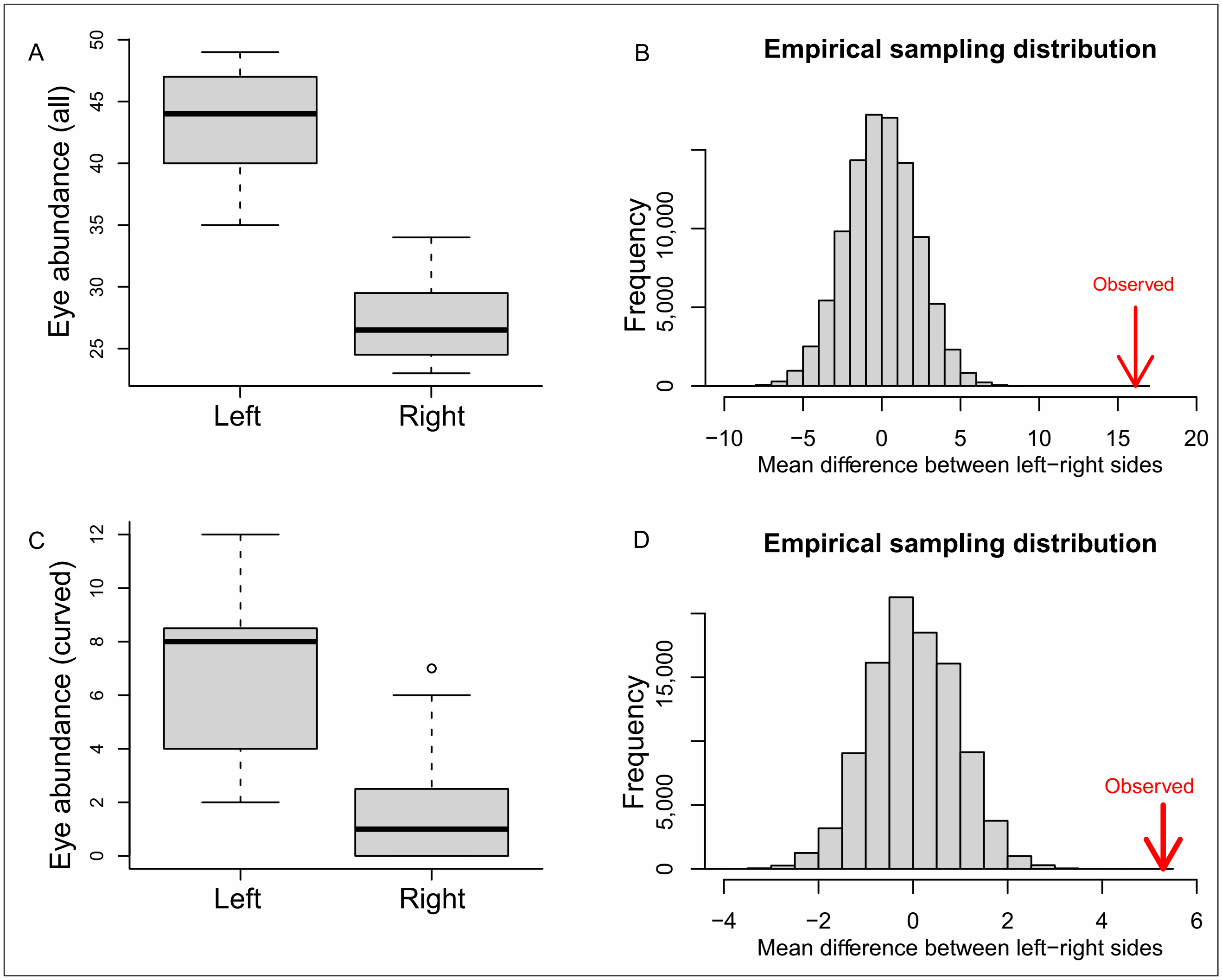

Figure 2. Left–right distribution of eyes in the scallop *Nodipecten nodosus*. **A.** Boxplot of the total number of eyes on each side. **B.** Empirical sampling distribution generated to test left–right asymmetry of the total eye number. Under the null hypothesis, the mean difference between sides approaches zero (symmetrical abundance). Observed value is indicated by a red arrow ($P < 0.001$). **C.** Boxplot of the total number of curved eyes on each side. **D.** Empirical sampling distribution generated to test left–right asymmetry of the curved eye number. Under the null hypothesis, the mean difference between sides approaches zero (symmetrical abundance). Observed value is indicated by a red arrow ($P < 0.001$).

Interocular variation of scallop eyes

The presence of eyes with different orientations has received no attention since its first description in a comprehensive treatment on eye development and anatomy by Küpfer (1916). In that study, the author described eyes with different orientations, mainly based on *Palliolum incomparabile* (Risso, 1826) (= *Pecten testae* Bivona in Philippi, 1836). In this species, most eyes are typically arranged with the optic vesicle axis aligned to the eyestalk axis. However, a small number of eyes deviate from that condition and exhibit a rotated appearance. Similar to our observations on *N. nodosus*, curved eyes have the optic vesicle axis forming an oblique angle with the eyestalk axis. In addition, Küpfer (1916) also described an extreme condition with the optic vesicle axis nearly perpendicular to the eyestalk axis, resulting in a lateral pupil. Such a level of optic vesicle rotation was not observed in *N. nodosus*.

The scallop visual system represents a unique visual strategy that combines intraocular and interocular vision. Each eye has a field of view of *c.* 100°, and total eye distribution provides at least 270° of panoramic vision (Chappell, Horan & Speiser, 2021). Different orientations of the optic vesicle might help explain how scallops use a distributed visual system to sample visual information from different directions. Curved eyes were originally thought to be associated with the growth of the mantle and the body position on the substrate (Küpfer, 1916). We hypothesize that different eye orientations, produced by variations of the angle formed by the optic vesicle and eyestalk axis, can be advantageous for widening the overall visual field viewed by the array of eyes. In addition, curved eyes on the left mantle lobe are curved to the left (facing upwards; Fig. 3), and the (less frequent) curved eyes on the right mantle lobe are curved to the right (facing downwards). Considering the preference for resting on the right valve, we hypothesize that individuals of *N. nodosus* with curved eyes on the left should be able to provide a better field of view above the animal (Fig. 3). The double-layered retina may enable the scallop eye to discriminate distinct fields of view and consequently sample multiple types of information, although there is still no evidence that scallops integrate information gathered separately by their different retinas (Wilkens & Ache, 1977). The presence of dozens of curved eyes might contribute to the distributed visual system sampling the visual field from different directions, allowing scallops to view moving objects from below and resulting in an improved upper visual field.

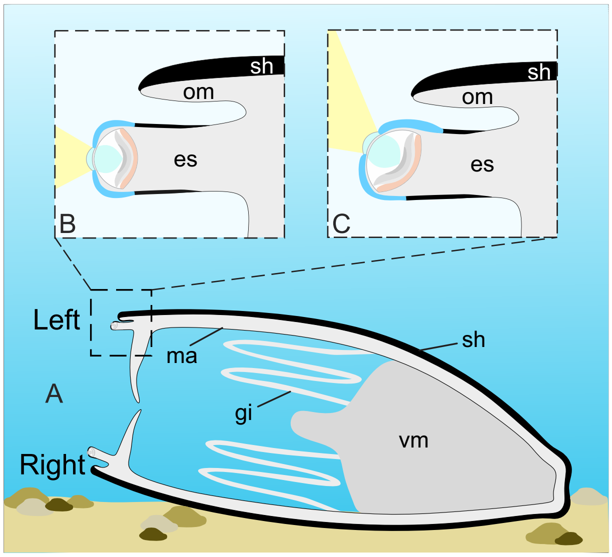

Figure 3. A. Schematic representation of the scallop *Nodipecten nodosus* reclining upon the right valve on the seafloor. **B.** Detail of a mirror eye on the left (upper) side. **C.** Detail of a curved eye with a more lateral pupil. Note that the field of view (in yellow) has rotated in (**B**), likely expanding the field of vision upwards. Abbreviations: es, eyestalk; gi, gill; ma, mantle; om, outer mantle fold; sh, shell; and vm, visceral mass.

While the presence of curved eyes raises intriguing functional hypotheses, as described above, many other questions arise. For example, how common is the presence of different eye orientations among scallop species? Symmetric muscular contraction has been observed to cause eyestalk retraction (Audino *et al.*, 2015b), but we still do not know if asymmetric contractions could adjust an eye's curvature. Based on observations of anaesthetized animals before and after fixation, the curved morphology is likely a fixed condition since relaxed eyestalk muscles do not change the curvature in curved eyes. Interestingly, previous work has shown that scallops track moving objects with their sensory tentacles (Chappell *et al.*, 2021), which raises the question of whether scallops can track moving objects with their eyes. Future studies are necessary to elucidate the interocular variation of scallop eyes and determine its impact on visual performance.

Scallop nervous system

Scallop nervous systems typically comprise: (1) one pair of cerebral ganglia, (2) one fused pedal ganglion and (3) one fused PVG (Speiser & Wilkens, 2016). The cerebral ganglia are usually reduced, and the size of the pedal ganglion varies with the size and use of the foot and byssal gland. The PVG is greatly enlarged due to the fusion of several nervous elements, including lobes responsible for processing nervous information from most of the animal's body (Dakin, 1910b, 1928a). The nervous system of *N. nodosus* resembles that of *Pecten maximus* (Linnaeus, 1758) (Duvernoy, 1853; Dakin, 1910b),

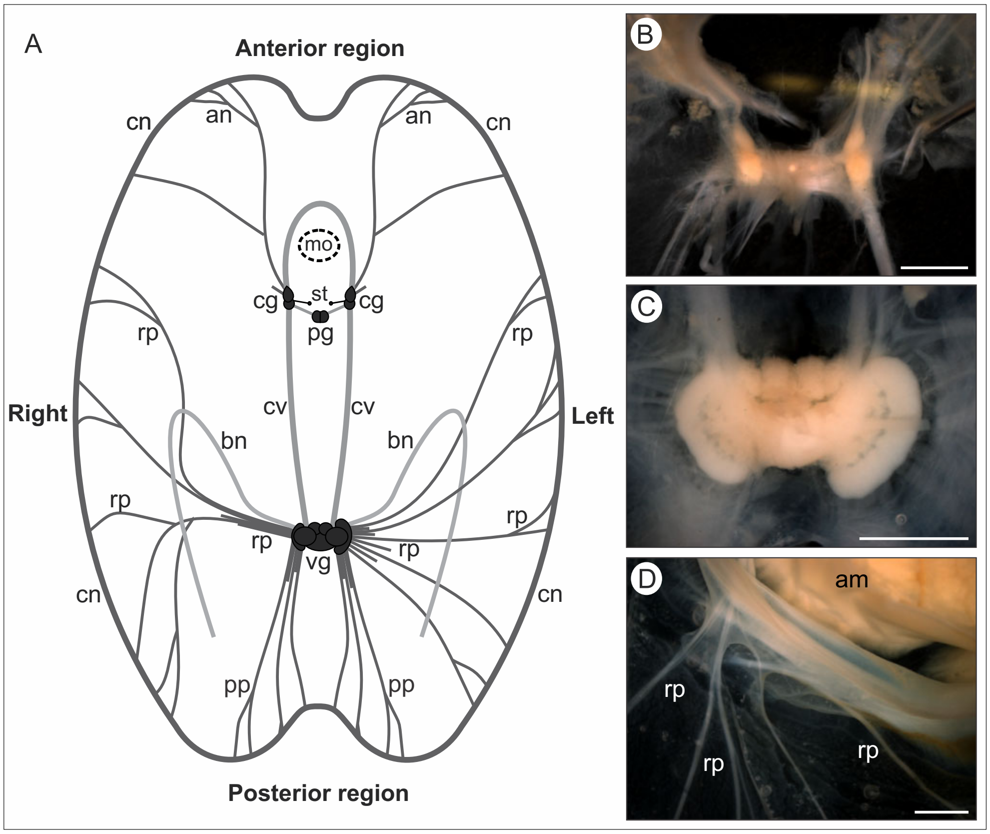

Figure 4. The nervous system of the scallop *Nodipecten nodosus*. **A.** Schematic representation of the nervous system, including main ganglia (black) and nerves (shades of grey). **B.** Pair of cerebral ganglia. **C.** PVG; note the left lobe (on the right) is larger. **D.** Left radial pallial nerves. Abbreviations: am, adductor muscle; an, anterior pallial nerves; bn, branchial nerve; cg, cerebral ganglia; cn, circumpallial nerve; cv, cerebro-visceral connective; mo, mouth; pg, pedal ganglion; pp, posterior pallial nerves; rp, radial pallial nerves; st, statocysts; and vg, parietovisceral ganglion. Scale bars: **B** = 2 mm; **C** = 2 mm; and **D** = 1 cm.

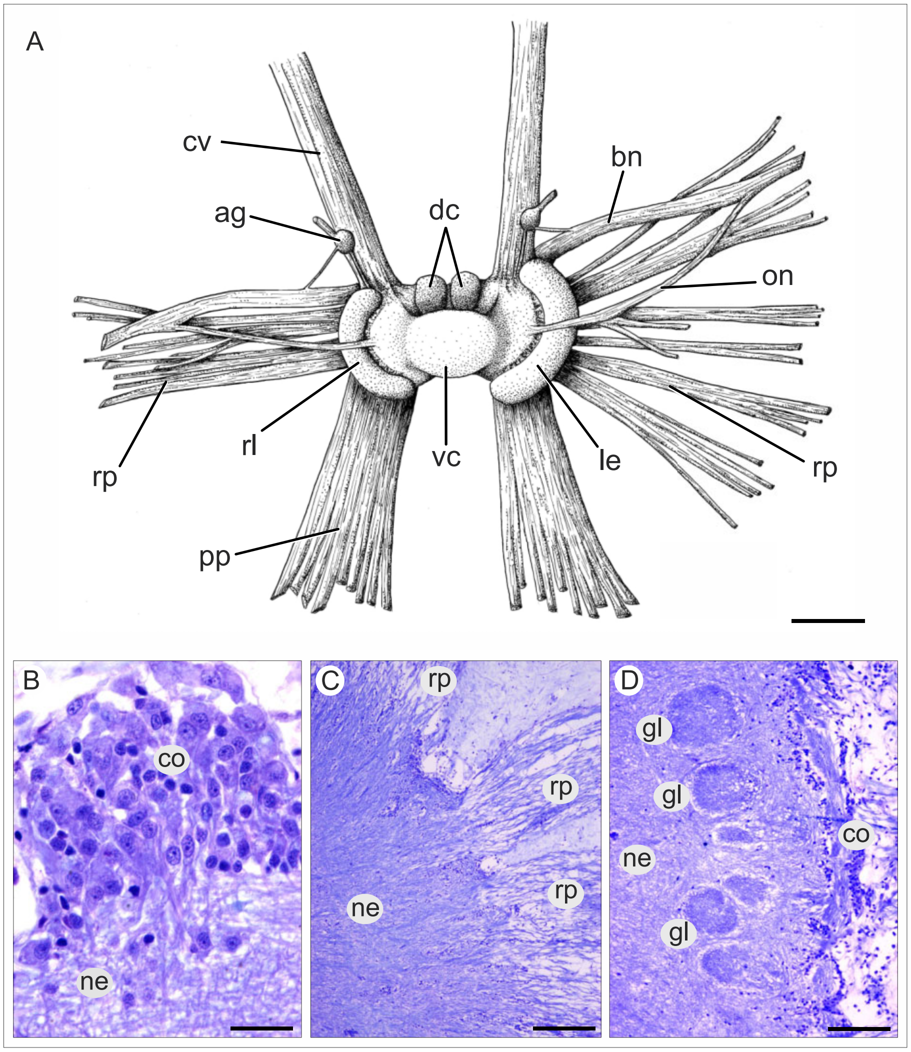

Figure 5. Details of the PVG in the scallop *Nodipecten nodosus*. **A.** Illustration of the PVG, showing the left–right asymmetry of the lateral lobes and the organization of the radial pallial nerves. **B**–**D.** Frontal sections of the PVG stained with toluidine blue and basic fuchsin. **B.** Detail of the lateral lobe evidencing the cortex (cellular bodies) and neuropil (cellular projections). **C.** Left radial pallial nerves connecting to the left lateral lobe. **D.** Presence of numerous glomeruli in the neuropil of the left lateral lobe. Abbreviations: ag, accessory ganglion; bn, branchial nerve; co, cortex; cv, cerebro-visceral connective; dc, dorso-central lobes; gl, glomerulus; le, left lateral lobe; ne, neuropil; on, osphradia-branchial nerve; pp, posterior pallial nerves; rl, right lateral lobe; rp, radial pallial nerves; and vc, ventro-central lobe. Scale bars: **A** = 1 mm; **B** = 20 μm; **C** = 100 μm; and **D** = 100 μm.

including the organization of ganglia, connectives and nerves. As in *P. maximus* (Dakin, 1910b, 1928a), *Aequipecten tehuelchus* (d'Orbigny, 1842) (Ciocco, 1998) and *Placopecten magellanicus* (Drew, 1906), the cerebral ganglia and the pedal ganglia in *N. nodosus* are separate organs connected by connectives. Except for differences in lobe asymmetry, which are discussed below, the observations on the PVG of *N. nodosus* are consistent with descriptions for *Argopecten irradians* (Lamarck, 1819) (Gutsell, 1931), *A. tehuelchus* (Ciocco, 1998) and *Placopecten magellanicus* (Drew, 1906).

Histological organization of PVG with cortex and neuropil is in accordance with previous studies with *P. maximus* (Dakin, 1910b), including the presence of glomeruli in the neuropil of the lateral lobes, representing packed neurites from the first-order interneurons that form the cortex (Dakin, 1910b; Spagnolia & Wilkens, 1983). Glomerular structures in the neuropil suggest high-level sensory integration (Speiser & Wilkens, 2016). In fact, anatomical data and physiological experiments support the lateral lobes of the PVG as 'optic lobes' for processing visual information from the circumpalial and optic nerves (Dakin, 1910b; Wilkens & Ache, 1977; Spagnolia & Wilkens, 1983; Speiser & Wilkens, 2016).

Visual asymmetry and lateralization in scallops

A crucial goal in understanding lateralization is to characterize asymmetrical patterns and determine their association with evolutionary ecology and behaviour (Frasnelli, 2017). Here, we provide evidence that the visual and nervous systems of the scallop *N. nodosus* comprise consistent morphological asymmetries: (1) the greater number of eyes on the left side (including a greater number of curved eyes), (2) the increased size of the left PVG lateral lobe, (3) the larger glomeruli in the left PVG lateral lobe and (4) the left radial pallial nerves spaced more widely than the more compactly arranged right radial pallial nerves.

Asymmetry in scallop eye distribution, with more units on the left side, has been reported for *P. maximus* and *Pecten jacobaeus* (Linnaeus, 1758) (Dakin, 1910a), *Placopecten magellanicus* (Whoriskey, Whoriskey & Whoriskey, 2014) and *Euvola ziczac* (Wilkens, 1981). Similarly, our results reveal significant visual asymmetry in *N. nodosus*. In contrast, *A. tehuelchus* has equally distributed eyes on the left and right sides (Ciocco, 1998). Detailed information on the left–right distribution of eyes for more scallop species would be beneficial in identifying major patterns of visual asymmetry.

While the visceral ganglia are symmetrical in most bivalves (Duvernoy, 1853), the lateral lobes of the scallop PVG vary in size according to the number of eyes along the left mantle margin (Dakin, 1910b). For example, the lateral lobes are nearly identical in size in *A. tehuelchus*, which displays a similar number of eyes on both sides (Ciocco, 1998). In the case of *Placopecten magellanicus*, the lateral lobes are similar in size (Drew, 1906), but more eyes (*c.* 32%) are distributed on the left side (Whoriskey, Whoriskey & Whoriskey, 2014). Similarly, *Aequipecten opercularis* (Linnaeus, 1758) has a few more (*c.* 28%) eyes on the left (Dakin, 1910a) and alike lateral lobes (Dakin, 1910b). In contrast, the scallops *P. maximus* and *P. jacobaeus* exhibit larger left lateral lobes and a greater number of eyes (*c.* 300%) along the left side (Dakin, 1910b). The same pattern was observed here in *Nodipecten*, with *c.* 160% more eyes on the left side, expanding our knowledge of visual asymmetries in Pectinidae. The PVG asymmetry observed in these species correlates with the increased number of eyes on the left side, thus supporting a functional and evolutionary correlation between the visual system and information processing in that ganglion (Speiser & Wilkens, 2016).

The LR asymmetry extends broadly into the nervous system. Our data show that *N. nodosus* has larger glomeruli in the left lateral lobe. A similar pattern was also recovered in a histological investigation of *P. maximus*, where more glomeruli are present on the left lateral lobe than on the right one (Dakin, 1910b). Following these observations, studies with live PVG tissue of *Argopecten irradians* revealed that the number of glomeruli per lateral lobe is proportional to the number of eyes on the corresponding side of the mantle (Spagnolia & Wilkens, 1983). The difference in organization between left and right radial pallial nerves, as observed in *N. nodosus*, seems to be another feature evolving asymmetrically. In *P. maximus*, the left radial pallial nerves are spaced more distantly, while the right radial pallial nerves leave the ganglion in a broad trunk, remaining closely grouped until reaching the mantle (Dakin 1928). In contrast, left and right pallial radial nerves are similarly organized in *Argopecten irradians* (Spagnolia & Wilkens, 1983), which exhibits symmetrical lateral lobes and equal distribution of eyes. Overall, our results with *N. nodosus* add another piece of evidence to characterize lateralization in molluscs and support the correlation between visual and neural asymmetries.

The evolution of morphological asymmetries is often associated with biased behaviours and particular ecological conditions. In the case of Pectinidae, rates of shell evolution reveal a highly variable magnitude of shell asymmetry in response to different life habits (Sherratt, Serb & Adams, 2017). On the one hand, scallops with equivalve shells seem to bear a similar distribution of eyes on both sides, as observed in *A. opercularis* and *A. tehuelchus* (Ciocco, 1998). On the other hand, scallops with inequivalve shells, typical of more sedentary species, exhibit an asymmetrical distribution of eyes, as noted in *P. maximus*, *P. jacobaeus* and *E. ziczac* (Dakin, 1928b). In the case of *N. nodosus*, valves are convex and slightly inequivalve because the left valve bears nodules. Also, in *N. nodosus*, animals are byssally attached to a hard substrate by the right valve, and swimming is restricted to short-range movements. This species shares with *Pecten* and *Euvola* the visual asymmetry. Interestingly, the three genera are nested in a monophyletic clade (Sherratt *et al.*, 2016), suggesting a shared similarity due to common ancestry. However, whether lateralization and visual asymmetries have convergently evolved in other scallop clades is still unknown. In this context, systematic data on eye distribution and PVG anatomy are crucial to estimate the evolutionary history of scallop visual asymmetries and possible ecological drivers.

The results presented here for *N. nodosus*, combined with data for other asymmetrical scallops, provide important evidence to discuss patterns of visual asymmetries in molluscs. The distributed visual system of scallops is not only a promising model for a multitude of visual studies but also for exploring the evolution of asymmetrical phenotypes. Even though bivalves are not typically considered in the literature on nervous system lateralization, accumulating evidence for scallops, as suggested by our results, indicates their potential to reveal novel patterns of lateralization and visual asymmetry in benthic invertebrates.

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SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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