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Unique horizontal gaze control in the box jellyfish, *Tripedalia cystophora*

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**ABSTRACT**

All known cubozoans, box jellyfish, have a similar visual system. They possess four sensory structures called rhopalia, which carry six eyes each. Two of these six eyes are true image-forming camera type eyes in several ways similar to vertebrate eyes. The rhopalia hang by a thin flexible stalk and in the distal end, there is a high-density crystal. In an earlier study of the Caribbean species *Tripedalia cystophora*, we showed that the crystals act as weights ensuring that the rhopalia are always upright no matter the orientation of the medusa and the vertical part of the visual field of the eyes thus kept relatively constant. Here we have examined the horizontal part of the visual field under different experimental conditions including different visual environments. We find that the horizontal gaze direction is largely controlled by the anatomy of the rhopalium and rhopalian stalk, similar to what has previously been shown for the vertical gaze direction. In a vertically oriented medusa, the rhopalia are kept with a 90° angle between them with the lower lens eyes (LLE) pointing inwards. This 90° shift is kept in horizontally swimming medusa, resulting in the left LLE gazing right, the right gazing left, the bottom gazing aborally (backwards compared to swimming direction), and the top LLE gazing aborally (forwards compared to swimming direction). The light environment was manipulated to test if the visual input influences this seemingly strict horizontal gaze direction but even in complete darkness there is tight mechanistic control.

**1. Introduction**

Gaze control differs substantially throughout the animal kingdom. In most animals, the eyes are embedded in the head or other parts of the body and the orientation of the head and body thus sets the gaze direction, which is true for animals like most insects and annelids (e.g. Nilsson, Land & Howard, 1988, Purschke, 2010). In other animals, gaze direction is highly dynamic with a number of special muscles moving the eyes, as exemplified by vertebrate and cephalopod eyes (Land, 2015, Martinez-Conde, Otero-Millan & Macknik, 2013). Having such a highly dynamic gaze control has the obvious advantage that the animal is able to focus its visual attention on areas of special interest in its surroundings, as well as stabilize its gaze to compensate for self-motion or motion of the object being viewed (Land, 2015, Land, 2019). A dynamic gaze control has a high neural and computational demand in order to precisely control the eye movement while also keeping track of where in the surroundings the visual information comes from. This demand is clearly seen in primates where a high number of individual neuronal circuits are involved in controlling eye movements (Fraser, 2016). Interestingly, some animals possessing image-forming eyes have rather simple nervous systems, and thus may not have the processing power needed for such controlled eye movements. This calls for alternative strategies in gaze control and a unique system seems to be found within a small group of cnidarians, the cubozoans or box jellyfish.

Light sensing organs are found in a number of cnidarian clades and are putatively the result of several independent evolutionary events (Picciotti et al., 2018). The majority are simple pigment cup eyes, or ocelli, as seen in the hydromedusa *Bougainvillia principis* (Singla, 1974) or the scyphomedusa *Aurelia aurita* (Yamasu & Yoshida, 1973). Cnidarian ocelli were first described more than a century ago (Hertwig & Hertwig, 1878, Romanes, 1877), and they are believed to act as non-image forming light meters (Nilsson, 2013). Proper image-forming eyes are also found within Cnidaria, but only in the small group Cubozoa, or box jellyfish, which comprises about 60 species (Bentlage et al., 2009). The eyes of box jellyfish are situated along the bell margin on sensory structures called rhopalia and all known species have four rhopalia each holding six eyes (Bentlage et al., 2009, Claus, 1878, Conant, 1898, Larson, 1976, Nilsson, Gislén, Coates, Skogh & Garm, 2005). The six eyes are of four different morphological types: Two pairs of lesser eyes, the pit- and slit eyes, and two camera-type eyes, called the upper- and lower lens eyes (ULE and LLE respectively) (Claus, 1878, Conant, 1898, Lewis & Long, 2005, Pearse & Pearse, 1978, Yamasu & Yoshida, 1976).
This surprisingly complex visual system is best understood in the small species *Tripedalia cystophora*, which is found in mangrove areas of the Caribbean (Werner, 1971). It has been shown for this species that the two lens eyes are camera-type eyes in several ways structurally similar to vertebrate eyes and that they form proper images, although of low spatial resolution (Nilsson et al., 2005).

Behavioural experiments have confirmed that the image information from the lens eyes of *T. cystophora* is used to control several of their visually guided behaviours (Garm, Hedal, islin & Gurska, 2013; Garm, Oskarsson & Nilsson, 2011). Perhaps the most advanced visually guided behaviour documented in box jellyfish described so far is habitat navigation. *T. cystophora* hunts between mangrove prop roots exclusively during daytime hours and rests at night anchored to vegetation in the mangrove lagoon (Garm, Bielecki, Petie & Nilsson, 2012). At dawn, they navigate back to the feeding grounds between the prop roots and this is done visually using the ULEs. These eyes gaze out through Snell’s Window into the terrestrial environment and use the contrast between the dark mangrove canopies and the bright sky to set the direction to the nearest mangrove trees (Garm et al., 2011). The visual field of the ULE has a tight match with Snell’s Window and in order not to mistake the high contrast edge of Snell’s Window for the canopies, the medusae also need to keep tight control of their gaze direction. This is achieved by the special morphological arrangement of the eye-carrying rhopalia. The rhopalia attach to the bell by a thin flexible rhopalial stalk and they hold a heavy crystal in their distal end, often referred to as to a statoloth in the literature (e.g. Martin, 2004; Sötje et al., 2011). It has been shown, though, that at least in *T. cystophora* and *Copula sivickisi* this crystal is not a statoloth but rather acts as a weight, and along with the flexible rhopalial stalk it keeps the rhopalia upright independent of the orientation of the medusa (Berg, 1900). As a consequence of this ingenious arrangement, the vertical part of the visual fields is kept constant and the ULEs are always gazing straight upwards centered in Snell’s Window (Garm et al., 2011). This unique arrangement is a clear example of a ULEs are always gazing straight upwards centered in Snell’s Window for the canopies, the medusae also need to keep tight control of their gaze direction. This is achieved by the special morphological arrangement of the eye-carrying rhopalia. The rhopalia attach to the bell by a thin flexible rhopalial stalk and they hold a heavy crystal in their distal end, often referred to as to a statoloth in the literature (e.g. Martin, 2004; Sötje et al., 2011). It has been shown, though, that at least in *T. cystophora* and *Copula sivickisi* this crystal is not a statoloth but rather acts as a weight, and along with the flexible rhopalial stalk it keeps the rhopalia upright independent of the orientation of the medusa (Berg, 1900). As a consequence of this ingenious arrangement, the vertical part of the visual fields is kept constant and the ULEs are always gazing straight upwards centered in Snell’s Window (Garm et al., 2011). This unique arrangement is a clear example of a matched filter in the spatial domain. Matched filters are typically narrow bandpass filters allowing only the most essential information to pass and thereby lessen the need for processing power (Barth, 2004, Wehner, 1987). Such filters are essential for animals like cnidarians which only possess a sparse central nervous system (CNS) (Koizumi, 2007, Laska & Hündgen, 1983, Mackie, 2004).

It is not only the vertical orientation of the rhopalia, which is important for the visual input in box jellyfish - the horizontal orientation is equally important. This is true for visually guided behaviours like obstacle avoidance where the LLEs need to tell the direction to the mangrove prop roots, which are to be avoided (Garm, O’Connor, Parkefelt & Nilsson, 2007). Thus, we hypothesize that the horizontal orientation of the rhopalia (and thereby the eyes) in *T. cystophora* is also under tight control putatively involving the anatomy and mechanical properties of the rhopalia and rhopalial stalk. To test the hypothesis we did macro-video recordings of tethered live medusae held horizontally while spinning slowly around their oral-aboral axis, mimicking directional horizontal swimming in their natural habitat. To test whether the visual input has any influence on the rhophalial orientation, we did the experiments under different light regimes including infrared recordings in otherwise darkness.

2. Materials and methods

2.1. Animals

Adult-sized specimens of *Tripedalia cystophora* (bell diameters of 6–9 mm) came from cultures kept at the Marine Biological Section, University of Copenhagen. The cultures were kept at a temperature of 28–29 °C and salinity of 35–37 psu. They were kept in a 10:14 light–dark cycle and fed SELCO enriched *Artemia* nauplii daily. One of the experimental animals was a sexually mature male but for the others, the sex was not determined. After use, animals were discarded to make sure they were not reused in the experiments.

2.2. Macro images

Adult medusae were transferred to a small photo aquarium (2.5 cm × 10 cm × 15 cm, D:H:W) where light was provided from two 100 W spotlights. When medusae were oriented vertically macro images were taken using a Nikon D300 camera equipped with a Micro Nikkor 105 mm lens (Nikon Corporation, Tokyo, Japan).

2.3. Setup for rotating horizontally orientated medusa

The experiments were conducted in a glass tank measuring 10 W × 15 D × 48 L cm (Fig. 1), which included a custom-made device where medusae tethered by the aboral end of the bell could be held horizontally and rotated in the vertical plane. The device was made from a set of LEGO Mindstorm NXT (LEGO, Billund, Denmark) and a plastic (PVC) stand holding a standard plastic pipette. The tip of the pipette was modified to have a diameter of approx. 1 mm, to better hold the medusae of *T. cystophora* without adding too much stress to the bell (Fig. 1). Proper attachment resulted in the medusae producing symmetric swim pulses throughout the experiment with a frequency of 0.5 – 1 Hz matching natural conditions (Stewart, 1996). A computer-controlled step motor was used to rotate the pipette with the desired direction and angular speed. All experiments were captured with a USB 3 uEye® CP Rev. 2 camera (IDS Imaging Development Systems GmbH, Obersulm, Germany) equipped with a Nikon 105 mm Micro Nikkor lens (Nikon Corporation, Tokyo, Japan) (Fig. 1).

2.4. Light environment

To test how the light environment and thus the visual input potentially influences the gaze control three different light settings were used. The first experimental series mimicked the light environment in the natural habitat of *T. cystophora*. Here almost all light comes from the water surface and Snell’s Window thus has high contrast edges (Fig. 2A). To accomplish this the sides and the bottom of the tank were darkened using black cardboard and light came from directly above using a P5R.2 flashlight (LED LENSER, Portland, OR, USA, see fig. S1 for light spectrum) position-wise mimicking the sun in zenith (Fig. 2B). Still, some internal reflections could not be avoided. A hole measuring 1.1 × 1.4 cm was cut in the front shading to allow video recordings. The second series ran with a low contrast Snell’s Window using the same light source but without the blackened sides and bottom (Fig. 2C). A last series was done in darkness under infrared (IR) light (peak emission at 940 nm). The IR-light source was placed on the side of the tank, which gave the highest contrast in the video recordings. The number of test animals was 10, 9, and 9 in the three experiments respectively.

2.5. Experimental protocol

A specimen of *T. cystophora* was caught in the culture tank using a large pipette and transferred to the experimental chamber via a small petri dish. Caution was taken to not damage the animal and the experimental tank was filled with water from the culture tanks to make sure no osmotic or chemical stress occurred. In the experimental tank, the medusa was held horizontally using a pipette and then attached to the pipette of the setup at the apex of the bell with a slight suction (Fig. 1). Proper attachment resulted in the medusae producing symmetric swim pulses throughout the experiment with a frequency of 0.5 – 1 Hz matching natural conditions (Stewart, 1996). A computer-controlled step motor was used to rotate the pipette with the desired direction and angular speed. All experiments were captured with a USB 3 uEye® CP Rev. 2 camera (IDS Imaging Development Systems GmbH, Obersulm, Germany) equipped with a Nikon 105 mm Micro Nikkor lens (Nikon Corporation, Tokyo, Japan) (Fig. 1).
subsequent analysis showed that rotational speed and direction did not affect rhopalial orientation, the medusa tested with low contrast Snell’s Window and in darkness were only rotated clockwise and only at mid-speed, $13^\circ /s$.

2.6. Analysis and statistics

All recorded videos were analyzed manually in the software TrouplePix (NorPix Inc., Montreal, CA). Since the eyes are unable to move on the rhopalia the horizontal gaze direction of all eyes can be determined by mapping the horizontal orientation of the largest eye, the LLE. Watching the videos it was obvious that the horizontal orientation of the rhopalia was to a high degree connected to the position in the rotational cycle of the medusa. To quantify this connection three standard orientations of the rhopalia were chosen and then it was mapped where in the rotational circle of the medusa these standard orientations occurred. The standard orientations were 1) LLE gazing backwards (orally), 2) LLE gazing perpendicular to the oral-aboral axis to the left, and 3) LLE gazing perpendicular to the oral-aboral axis to the right. These three directions were chosen since they could be determined with the highest accuracy and repeated analyses of the same video sequences determined this accuracy to be $+/-2^\circ$. A fourth standard position could have been the LLE gazing forwards (aborally) but since the eyes are not seen in the videos when in this orientation it was not possible to maintain a high accuracy and this position was thus skipped.

When analyzing the video recordings, each of the four rhopalia was followed separately for two full rotations, and when in one of the standard orientations its angular position in the rotational movement was measured. This was done using the program ImageJ ver. 1.8.0_172 (Schneider, Rasband & Eliceiri, 2012). First, the multipoint tool was used to mark all four rhopalia, after which a circle was fitted to these points. The top of this circle was set to $0^\circ /360^\circ$ and the angular position of the rhopalium of interest was measured using the angle tool. Two rotations resulted in each of the four rhopalia being measured twice in each of the three standard orientations and this total of eight measurements was averaged and used for the statistical analysis. See supplementary Fig. 2 for variation in the rhopalial orientation during the two rotations of individual medusa.

The angular data was tested with circular statistics in Oriana (Ver. 4.02, Kovach Computing Services, UK) where circular plots were made, the direction and length of the mean vector were calculated, and a Rayleigh test was used to check for random distribution with a critical p-value of 0.05. Lastly, the 95 % confidence interval of the angular direction of the mean vector was calculated.

3. Results

3.1. Horizontal gaze direction in vertically oriented medusae

When the medusae of *T. cystophora* are oriented vertically (oral end downwards) in the water column all four rhopalia are upright and oriented in a similar way (Fig. 3). The ULEs point straight upwards and the LLEs are all directed inwards towards the center of the animal. This arrangement results in the horizontal part of LLE visual fields covering the complete 360 with a shift of approx. 90 between neighboring LLEs.
When changing the direction of rotation to CCW there is still a tight control of the horizontal gaze control judged by when the rhopalia are in the standard orientations (Fig. 6). Interestingly, when setting the positions in the rotation relative to the orientation of the medusa (right side of medusa = 90°, left side of medusa = 270°) the positions of the standard orientations differed from CW rotation (mean vector direction +/− 95% confidence interval: 311° ± 20°, 167° ± 14°, and 115° ± 4.5° for left, bottom, and right standard orientation, respectively, n = 3, Fig. 6A). When this is mirrored, though, such that the position in the rotation is set relative to the direction of rotation instead, this difference disappears (mean vector direction +/− 95% confidence interval: 245° ± 4.5°, 193° ± 14°, and 49° ± 20° for left, bottom, and right standard orientation, respectively, n = 3, Fig. 6B). The 95% confidence intervals overlap for all 3 standard orientations between mirrored CCW at 13°/s and CW at 13°/s.

3.3. Influence by light conditions on the horizontal gaze control

Overall the firm control of horizontal orientation of the rhopalia did not change with changing light environment. In the case with unnatural low contrast in Snell’s Window there was an overlap in the 95% confidence intervals of the mean vector direction with all three speeds and natural high contrast Snell’s Window (mean vector direction +/− 95% confidence interval: 240° ± 5.8°, 188° ± 10°, and 47° ± 7.9° for left, bottom, and right standard orientation, respectively, n = 9, Fig. 7A). The same was seen for medusa rotated in darkness (mean vector direction +/− 95% confidence interval: 232° ± 5.7°, 186° ± 7.4°, and 46° ± 9.0° for left, bottom, and right standard orientation, respectively, n = 9, Fig. 7B). In the experiments with unnatural low contrast Snell’s Window and darkness (n = 9 in both cases) the 95% confidence intervals are in both cases slightly broader than with natural high contrast Snell’s Window (n = 7) for all three standard orientations (Figs. 5 and 7).

4. Discussion

4.1. Mechanistic control of gaze direction

Gaze control is of capital importance to all visual systems because it helps them maintain high-quality directional information typically needed for visual tasks. Here we have investigated gaze control in the unique visual system of the box jellyfish T. cystophora carrying 24 eyes on four sensory structures, the rhopalia. We show that alongside the previously shown control of the vertical part of the visual field (Garm et al., 2011) there is a similar control of the horizontal gaze direction in both vertically and horizontally oriented medusae. This is putatively governed by the mechanical properties of the system, such that when the medusae rotate in the vertical plane the rotation is transferred mechanically to the rhopalia via the stalk. Interestingly, the rhopalial rotation is not completely smooth, since the medusa has to rotate a certain threshold, the tension will swing the crystal around making the rhopalia to the side are rotated 180° relative to each other and 90° to the rhopalium in the back (lower insert). Note that the rhopalium in the back is photographed through two times body wall of the animals testifying to the optical transparency of the tissue. Modified after Bielecki, Hoeg & Garm, 2013.

Fig. 3. Free swimming T. cystophora. When swimming upright all rhopalia are upright with the upper lens eyes (ULE) pointing upwards and the lower lens eyes (LLE) pointing towards the center of the animal. This means that the horizontal visual fields of the LLE shift by approximately 90° between neighboring rhopalia. Inserts show a close up of the three visible rhopalia – the two rhopalia to the side are rotated 180° relative to each other and 90° to the rhopalium in the back (lower insert). Note that the rhopalium in the back is photographed through two times body wall of the animals testifying to the optical transparency of the tissue. Modified after Bielecki, Hoeg & Garm, 2013.
Fig. 4. Rhoparial orientation during horizontal rotation. The pictures illustrate the three orientations of interest of the rhopalia – where the lower lens eye (LLE) gazes either straight to the left (A), straight backward (orally) (B), or straight to the right (C). The row of close-up images below shows the gradual rotation of the rhopalia during the approx. 180-degree turn of the medusa shown in A-C. Note that the medusa has to rotate approx. 130° to rotate the rhopalia from the right to the bottom standard position, but only approx. 55° to shift the 90° from the bottom to the left standard position. In (D) a rhopadium is in the top position where the LLE gazes forwards (aborally). The insert is a close-up of this rhopadium. Note that since the lens eyes are not visible it is not possible to accurately determine the orientation of the rhopadium. Also note that the upper lens eye (ULE) points straight upwards in all pictures. The center arrow in A indicates the direction of rotation.

Fig. 5. Control of the horizontal visual field with high contrast Snell’s Window. The diagrams are circular plots of where in the rotation of the medusa the rhopalia are in the orientations of interest (shown by schematic drawings at the top). Rotations were done clockwise (CW) at three different speeds, 9°/s, 13°/s, and 17°/s (A-C). It is seen that there is very little variation in the horizontal orientation of the rhopalia between individuals and that it is independent of rotational speed. The arrow in each circular plot is the mean vector and the inner ring indicates the 0.05 p-value from the Rayleigh test. The broken lines on the sides of the vector indicate the 95% confidence intervals of the vector also given below the plots along with the angular direction of the vector. The green arrows indicate the direction of rotation and the blue dots represent the individual medusa. n = 7, 7, and 6 for the three speeds respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Fig. 6. Control of the horizontal visual field with high contrast Snell's Window. The diagrams are circular plots of where in the rotation of the medusa the rhopalia are in the orientations of interest (shown by schematic drawings at the top). Rotations were done counter-clockwise (CCW) at a speed of 13°/s (A). As for the clockwise rotations, there is tight control of the rhopalial orientation during the rotation. The orientations of interests are reached at physically different positions in the rotational circle compared to the CW rotation (compare with Fig. 5), but interestingly these differences disappear when the results are mirrored (B). The arrow in each circular plot is the mean vector and the inner ring indicates the 0.05p-value from the Rayleigh test. The broken lines on the sides of the vector indicate the 95% confidence intervals of the vector also given below the plots along with the angular direction of the vector. The green arrows indicate the direction of rotation and the blue dots represent the individual medusa. n = 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 7. Control of the horizontal visual field in two unnatural light environments. The diagrams are circular plots of where in the rotation of the medusa the rhopalia are in the orientations of interest (shown by schematic drawings at the top). Rotations were done clockwise (CW) at a speed of 9°/s. (A) With an unnatural low contrast at the edge of Snell's Window the rhopalial orientations of interest are still seen in the same part of the rotational circle as in the high contrast experiments (compare with Fig. 5). Note, though, that the 95% confidence intervals (broken lines on the sides of the vector) are broader than with the high contrast. (B) In darkness, the horizontal visual field of the eyes is still following the rotational circle, as in the other light environments, but again with relatively broad 95% confidence intervals. The arrow in each circular plot is the mean vector and the inner ring indicates the 0.05p-value from the Rayleigh test. The 95% confidence intervals of the vector are given below the plots along with the angular direction of the vector. The green arrows indicate the direction of rotation and the blue dots represent the individual medusa. n = 9 in both A and B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
the orientation of the medusae the four LLEs will gaze in different directions with an approx. shift of 90° between neighboring rhopalia covering the complete 360° underwater visual scene outside Snell’s Window (Nilsson et al., 2005). Importantly, it also ensures that the gaze direction of each LLE, and thereby knowledge about the direction to visual objects, is predictable from its position in the rotational cycle. The directional obstacle avoidance shows that such information is available and vital to the medusae (Garm, O’Connor, Parkefelt & Nilsson, 2007). How this positional information is conveyed to the CNS is still unknown but we find a striking functional correlation with the suggested proprioceptive nerve found in the rhopalian stalk (Garm, Ekstrom, Boudes & Nilsson, 2006). If this nerve registers both the degree and direction of bending it could relay the information about rhopalian orientation along with orientation of the medusa. Furthermore, we see no alternative pathway for acquiring this vital information.

The experiments with unnatural low contrast in Snell’s Window and in darkness also support that both the vertical and the horizontal gaze directions in *T. cystophora* are at least to a large degree controlled by the anatomy of the rhopalian system. Even though the 95% confidence intervals are slightly broader than for the experiments with natural high contrast there is no significant difference in the standard orientations of the rhopalia between the three experiments. This shows that at least the tested light environments have little, if any, influence on the horizontal gaze direction.

4.2. Gaze control outside Tripedalia cystophora

The gaze control in the box jellyfish discovered here seems unique. We know of no other visual system where the gaze direction, both vertically and horizontally, is kept steady no matter the orientation of the animal. Outside Cubozoaa there are in general two alternatives when it comes to control of gaze direction. The most common is that the eyes are embedded somewhere in the body of the animal, normally the head, and not able to move independently, which is seen for most polychaete worms (Hermans & Eakin, 1974, Purschke, 2010), flatworms (Shettigar, Joshi, Gopalkrishna, Chakravarthy & Patnaik, 2017), chitons (Li et al., 2015), velvet worms (Kirwan, Graf, Smolka, Mayer, Henze & Nilsson, 2018), spiders (except for their anterior medial eyes with movable retinas) (Norregård, Nilsson, Henschel, Garm & Wehner, 2008), and many insects and other crustaceans (Fergus, Johnsen & Osborn, 2015, Nilsson et al., 1988). The other and more advanced systems allow the eyes to move freely independent of the rest of the body. This is typically combined with high-quality image formation as seen for vertebrates, cephalopods and some malacostracan crustaceans (Land, 2019; Marshall, Land & Cronin, 2014). The ability to freely move the eyes undoubtedly requires an advanced CNS in order to control the normally fast and precisely coordinated eye movements. Such an advanced CNS is not present in box jellyfish and we suggest that the most obvious evolutionary driver for the morphologically automated gaze control in box jellyfish has been the need to significantly lessen information processing (Barth, 2004, Wehner, 1987). A visual system in some ways comparable to that of *T. cystophora* and other box jellyfish is found in starfish. Here an eye is found at the tip of each arm also potentially providing the animal with a constant 360° horizontal view of the world (Garm & Nilsson, 2014, Pettie, Garm & Hall, 2016, Yoshida, 1966). Furthermore, starfish are also radially symmetric putatively lacking a single centralized brain for vision-related processing. Interestingly, the starfish eyes are situated on the flexible distalmost tube foot and display a dynamic gaze control (Beer, Wentzel, Pettie & Garm, 2016), in many ways similar to what is seen in vertebrates, cephalopods and malacostracans. This indicates that the starfish CNS and information processing are surprisingly complex as also indicated by the diversity of neurotransmitters (García-Arrarás, Rojas-Soto, Jimenez & Diaz-Miranda, 2001).

It should be noted, though, that so far this unique morphologically determined gaze control has only been shown for two species of box jellyfish, *T. cystophora* and *Copula sivickisi*, and in *C. sivickisi* only the vertical gaze direction has been tested (Garm et al., 2016). There are indications that it is not universal for all species of box jellyfish. There seems to be a difference in the relative thickness of the rhopalial stalk where especially the large members of the family chirodropidæae (*Bentlage et al., 2009*) have a thicker and putatively less flexible stalk. This is seen for *Chironex yumaguchii* (Lewis & Bentlage, 2009), *Chiro- psalmus quadramanus* (Herandez, Couch-Concha, Loman-Ramos & Leon-Deniz, 2019), and *Chiropsella bronzei* (O’Connor, Garm & Nilsson, 2009). Little is known about the visual systems in *C. yumaguchii* and *C. quadramanus* but there are notable differences in the optics of the ULE between *C. bronzei* and the two species *T. cystophora* and *C. sivickisi* (Garm, Bielecki, Pettie & Nilsson, 2016, O’Connor et al., 2009). In *C. bronzei* the optical power of the ULE lens-like structure is very weak and probably doesn’ t support image formation, instead it is suggested that the eye is optimized for navigation by point sources of light like celestial objects (O’Connor et al., 2009). If true, this would still require control/knowledge of gaze direction, though, and macro footage of the rhopalia in live medusae is needed to examine whether they have the same kind of control of the rhopalial orientation despite the apparently less flexible stalk.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Author contributions

AG conceptualized the study, wrote the initial version of the manuscript incl. first version of the figures and financed the study. SHW performed the experiments and the data analysis. Both authors contributed to the final version of the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.visres.2022.108159.

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