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RESEARCH ARTICLE

Visual control of steering in the box jellyfish *Tripedalia cystophora*

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SUMMARY

Box jellyfish carry an elaborate visual system consisting of 24 eyes, which they use for driving a number of behaviours. However, it is not known how visual input controls the swimming behaviour. In this study we exposed the Caribbean box jellyfish *Tripedalia cystophora* to simple visual stimuli and recorded changes in their swimming behaviour. Animals were tethered in a small experimental chamber, where we could control lighting conditions. The behaviour of the animals was quantified by tracking the movements of the bell, using a high-speed camera. We found that the animals respond predictably to the darkening of one quadrant of the equatorial visual world by (1) increasing pulse frequency, (2) creating an asymmetry in the structure that constricts the outflow opening of the bell, the velarium, and (3) delaying contraction at one of the four sides of the bell. This causes the animals to orient their bell in such a way that, if not tethered, they would turn and swim away from the dark area. We conclude that the visual system of *T. cystophora* has a predictable effect on swimming behaviour.

Key words: Cnidaria, box jellyfish, Cubozoa, behaviour, swimming, steering.

INTRODUCTION

Tripedalia cystophora is a remarkable cnidarian. It lives in the mangrove swamps of the Caribbean, which are rich in food but potentially dangerous for a fragile animal like a jellyfish. *Tripedalia cystophora* preys on small copepods of the species *Dioithona oculata* that swarm between the prop roots of the mangrove trees (Buskey, 2003). The copepods gather in the light shafts filtering through the overhead canopy. *Tripedalia cystophora* uses its visual system to detect the light shafts but it cannot see the copepods themselves, and would forage readily in empty light shafts (Buskey, 2003). The visual system of all box jellyfish is distributed at four sensory clusters, called rhopalia (Fig. 1A), each carrying six eyes (Claus, 1878; Conant, 1898; Berger, 1900; Laska and Hündgen, 1982; Yamasu and Yoshida, 1976). Each rhopalium contains one lens eye looking upward (upper lens eye), one lens eye looking obliquely downwards (lower lens eye), one pair of lens-less pit eyes looking upward (pit eyes) and one pair of slit-shaped lens-less eyes looking obliquely downward (slit eyes). Interestingly, the visual fields of the eyes that monitor the underwater world, the large lens eye and the slit eyes, are normally directed inward towards the centre of the bell, with the result that the animal 'looks through' its own bell. The unique visual system enables the medusae to display visually guided behaviours that appear remarkable for a 'simple' cnidarian. They can (1) navigate towards, and maintain position within, the light shafts where their prey gathers (Buskey, 2003; Garm and Bielecki, 2008), (2) avoid obstacles in the water (Garm et al., 2007b) and (3) use visual cues seen through the water surface to find their way back to the mangrove trees when washed out (Garm et al., 2011).

For any of these behaviours to work, the animal needs to be able to control its speed and direction. Box jellyfish, like other jellyfish, use periodic contractions of the bell to propel themselves through the water (Shorten et al., 2005). When observing the animals swimming, it would be logical to assume that box jellyfish use some form of jet propulsion (Daniel, 1983; Demont and Gosline, 1988a), but this has not been proven yet. The bell size, height-to-width ratio and bell contraction frequency of *T. cystophora* makes it plausible that it does not use true jet propulsion, or the rowing type of swimming described below, but another form of propulsion (Dabiri et al., 2007). Other animals that use jet propulsion to generate resistive or propulsive forces are scallops (Cheng et al., 1996), salps (Sutherland and Madin, 2010), frogfishes (Fish, 1987) and squid (Bartol et al., 2001). Jellyfish with a relatively flat disc-shaped bell, such as moon jellyfish, only move the fringes of the bell for propulsion and therefore cannot use jet propulsion. Instead, they use a rowing-type propulsion (Costello et al., 2008; Dabiri et al., 2005). In cubomedusae, swim pacemaker signals originating in the rhopalia (Satterlie and Spencer, 1979) set the rate of bell contraction and thereby control the speed of the animal. The rate of pacemaker firing is highly dependent on changes in the visual environment (Garm and Bielecki, 2008) and different eyes have different effects on the pacemaker firing frequency (Garm and Mori, 2009).

The speed, efficiency (Dabiri et al., 2006) and direction (Gladfelter, 1973) of swimming by means of jet propulsion are determined by the membrane-like structure that constricts the outflow opening of the bell (see Fig. 1B,C). A similar structure exists both in Cubomedusae, where it is called a velarium, and in Hydromedusae, where it is called a velum (Gladfelter, 1973). An asymmetry in the contraction of the velum or the velarium makes medusae turn (Gladfelter, 1972) and the activity of the velum in Hydromedusae has been shown to increase swimming efficiency (Dabiri et al., 2006). In this paper we show how visual stimuli affect the shape of the velarium and the dynamics of bell contraction. We show that a sudden darkening of one quadrant of the surroundings causes a predictable asymmetry of the velarium accompanied by a lag in contraction in the side of the animal facing the dark. Together, these mechanisms make the animal swim away from the dark area.

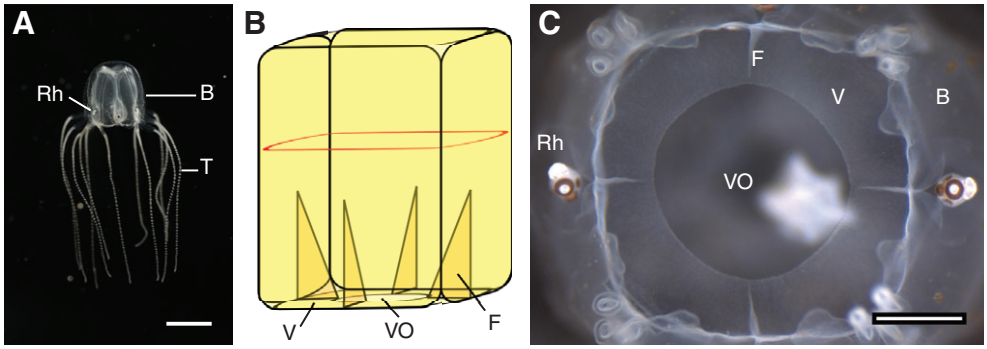

Fig. 1. The swim system of *Tripedalia cystophora*. (A) A swimming medusa. Periodic contractions of the bell propel the animal. The rhopalia bear the eyes of the animal. Scale bar, 5 mm. (B) The swim system of box jellyfish consists of circular muscles on the inside of the bell that, while contracting, empty the bell and drive propulsion. The velarium is the membrane-like structure that constricts the outflow opening of the bell. Four frenula connect the velarium to the inside of the bell. At the frenula the musculature is oriented radially. The dynamics of the velarium contributes to the animal turning and probably increases swimming efficiency too, as in some Hydromedusae. The circular muscles are indicated in red. (C) This view shows the velarium and the frenula from underneath, looking up into the bell of a preserved animal. Scale bar, 1 mm. B, bell; F, frenulum; Rh, rhopalium; T, tentacles; V, velarium; VO, velarial opening.

MATERIALS AND METHODS

Animals

Tripedalia cystophora, Conant 1897, used in the experiments were raised in cultures at Lund University (Sweden) or at the University of Copenhagen (Denmark). We used animals with a bell diameter of between 3.5 and 6 mm.

Experiments

Experiments were performed in a double-walled, transparent Perspex container with inside dimensions of 50×50×50 mm (Fig. 2A). All experiments were done in seawater of 25‰ salinity, taken from the tanks in which the animals were kept. By circulating heating water through the double walls (Fig. 2B), water inside the cube was maintained at 27°C. The animal was kept in place by attaching a small pipette to the apex of the bell using gentle suction (Fig. 2C). To facilitate placing of the pipette, the animal was anaesthetized by a 1:1 mixture of 0.37 mol l^{-1} magnesium chloride and seawater. The animals would stop moving ~30 s after anaesthesia and start pulsing again after ~1 min in pure seawater (N=5). A recovery time of 5 min was sufficient to restore the pulse rate to 81% of the untreated pulse rate (N=10). The animals were allowed to recover for at least 10 min before the experiments began.

Animals where anaesthetized outside the experimental chamber. Care was taken to transport the jellyfish to the experimental tank in the smallest possible volume of water. The experimental procedures did not have noticeable long-term negative effects on the animals. After the experiments, some of the animals were observed live on for another 4 weeks until they died of natural causes.

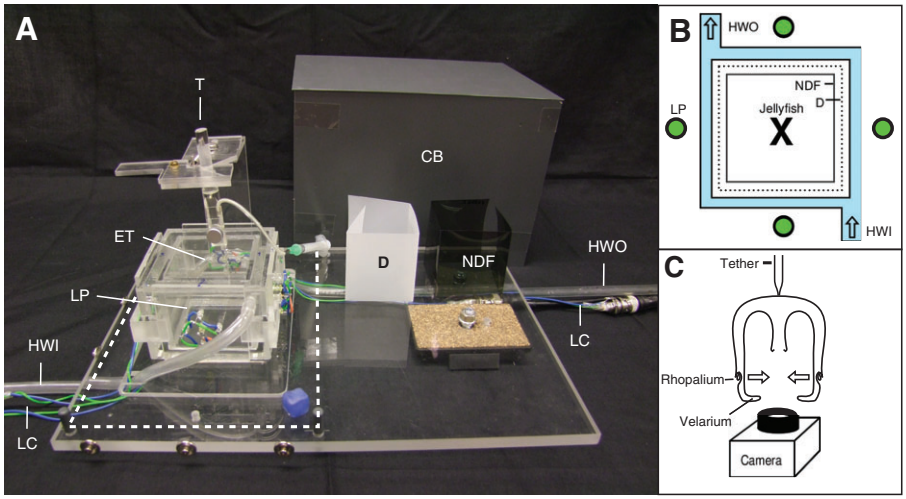

Fig. 2. The setup with its components. (A) During experiments the animal was tethered using suction in an experimental tank with inside dimensions of 50×50×50 mm. Water inside the chamber was kept at 27°C by heating water circulating between the double walls. LED panels attached to the outside of the chamber provided the light stimuli. A plastic diffuser sheet was used to create a more even illumination, while 23.5% neutral density filters enhanced contrast between lit and dark walls. Furthermore, a box was put over the experimental chamber at the location marked by the dashed line, to eliminate external interference. Recordings were made with a high-speed camera, looking up through the experimental chamber. (B) An overview of the experimental chamber. 'X' marks the position of the jellyfish. The heating water (freshwater) is indicated by the blue shading. The inside of the experimental tank contained seawater. (C) Diagram illustrating how the animal is attached at the apex of the bell, plus the location of the high-speed camera. Note that the eyes viewing the underwater scene are normally directed inward, towards the centre of the bell, as indicated by the arrows. CB, cover box; D, diffuser; ET, experiment tank; HWI, hot water in; HWO, hot water out; LC, light control; LP, light panel; NDF, neutral density filter; T, tether.

Stimulation was provided by four identical panels arranged around the animal. Each panel had four blue–green LEDs (20410-UBGC/S400-A6, Everlight Electronics Co. Ltd, Taipei, Taiwan), with a peak emission at 500 nm and spectral half-width of 25 nm, closely matching the spectral sensitivity of the lens eyes (Garm et al., 2007a; Coates et al., 2006). In the experimental container the four sides (panels) were aligned with the four sides of the squarish bell of the animal. Experiments started with all panels lit. To mimic the condition when an animal comes close to a dark object (eliciting a sharp turn), we turned off the light from a randomly chosen panel and observed the symmetry of bell contractions. To increase the contrast between the dark and the lit panels we placed a neutral density filter with a transmittance of 23.5% in front of the walls of the panels and the diffuser. Without this precaution the wall opposite a lit panel would reflect too much light and act as an additional stimulus. With the neutral density filters in place, light reflecting off the walls had to pass twice through the neutral density filter and was reduced to approximately one-eighth of the initial intensity. The diffuser was used to generate a large field illumination from the point source LEDs. In the configuration where three panels were lit and one was dark, the mean luminance over all lit panels was 144 cd m^{-2} and the luminance of the dark panel was 28.9 cd m^{-2}, providing a contrast of 0.67 between the dark panel and the lit panels. Light intensities were measured with a photometer (Universal photometer/radiometer Model S3, B. Hagner AB, Solna, Sweden). The experiments were performed with the cube covered by a light-proof box to prevent visual interference from outside the test chamber. Bell contractions were recorded by a high-speed camera (MotionBlitz EoSens Cube, Mikrotron GmbH, Unterschleißheim, Germany) operated at 150 frames s^{-1}. Additional illumination was needed because the animals were too transparent to be illuminated by the light emitted by the stimulus panels. We therefore used a high-power infrared LED (ELJ-810-228B, Roithner Lasertechnik, Vienna, Austria) with a peak wavelength of 810 nm and a half-width of 30 nm for illuminating the animal during the trials. The spectral range of the LED makes it invisible to the animal, but highly visible to the camera.

Analysis

For quantitative analysis of behaviour we tracked the movements of the animal. Because the rhopalia are such conspicuous structures, these made a natural choice of tracking markers. The spatial coordinates of the rhopalia were obtained using the Mtrack2 plugin for ImageJ (http://rsb.info.nih.gov/ij/) written by Nico Stuurman (http://valelab.ucsf.edu/~nico/IJplugins/). The midpoint of the animal was determined as the mean position between all four rhopalia:

$$X_m = \frac{X_1 + X_2 + X_3 + X_4}{4}, Y_m = \frac{Y_1 + Y_2 + Y_3 + Y_4}{4}, \quad (1)$$

where X_m and Y_m are the coordinates of the midpoint and X_1 to X_4 and Y_1 to Y_4 and are the coordinates of the individual rhopalia. The speed and direction of travel of this midpoint are indicative of the movement of the entire animal and the speed of the rhopalia indicate the contraction speed of the sides of the animal. The contraction speed of the individual sides of the animal was used for determining differences in the contraction timing of each of the four sides.

During experiments, each animal was tested by switching off each of the stimulus panels once, providing us with four repeats for each animal. We recorded the behaviour 7 s prior to and 7 s after switching off the stimulus panel and calculated the contraction speeds for each of the four sides of the animal. We applied a three-point running average to the speed data before further analysis. Differences in contraction timing were best observed by looking at the timing of the onset of movement. We considered a side to be moving when its speed reached 25% of the speed of the fastest moving side during that contraction. This gave us contraction timing data for each pulse, for four repeats, which was combined to obtain the animal mean.

Analysis was done in MATLAB (MathWorks, Natick, MA, USA). For the circular statistics we used the 2009 Toolbox (Berens and Velasco, 2009).

RESULTS

The experiments revealed different bell contraction rates for different light stimuli. In an environment with a constant light level the animals pulsed at 1.54±0.77 Hz (mean ± s.d., N=4). Decreases in light intensity increased contraction rates. After switching off one panel, contraction rates were 2.33±0.63 Hz (N=4). A typical recording is shown in Fig. 3. Swim pulses were followed by a free damped oscillation caused by the elasticity of the bell, as observed before in hydromedusae (Demont and Gosline, 1988b).

Fig. 4 shows a time series of a single swim pulse. Swim pulses took 190±29 ms (N=24, 6 pulses per animal). The contraction of the bell took 92±15 ms (N=24, 6 pulses per animal), while relaxation took 98±17 ms (N=24, 6 pulses per animal). During the contraction shown in Fig. 4, the area of the opening of the bell decreased to as little as 17% of the resting area. In some contractions, elasticity caused the bell to rebound to as much as 110% of the resting bell opening area. During the contraction, the animal expelled water from

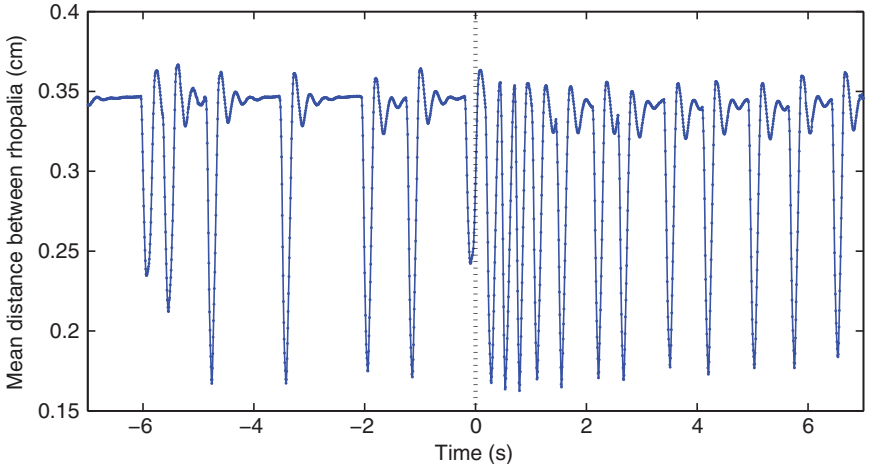

Fig. 3. A drop in light intensity increases swim pulse frequency. Box jellyfish have four visual groups, called rhopalia, situated on four sides of the bell. As the animal contracts, the sides close in towards each other and the distance between neighbouring rhopalia decreases. In this figure, the mean distance between neighbouring rhopalia is plotted as a measure of contraction strength and frequency. The figure shows 14 s of recording. During the first 7 s all panels are lit. At 0 s one of the panels is switched off. After switching off the panel, swim pulse frequency increased, and the degree of contraction was kept more constant and closer to maximum. Some of the swim pulses showed a free damped oscillation caused by the elasticity of the bell.

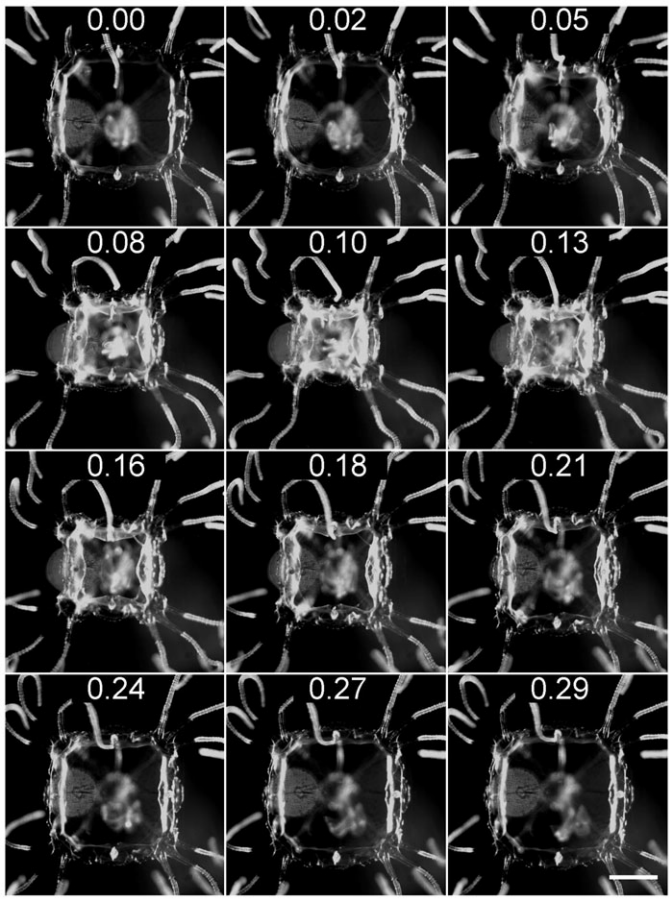

Fig. 4. A single swim pulse. The swim pulse starts at the first frame and ends at the last frame. Maximum contraction is reached at 0.10 s, after which relaxation draws water back into the bell. Scale bar, 2 mm.

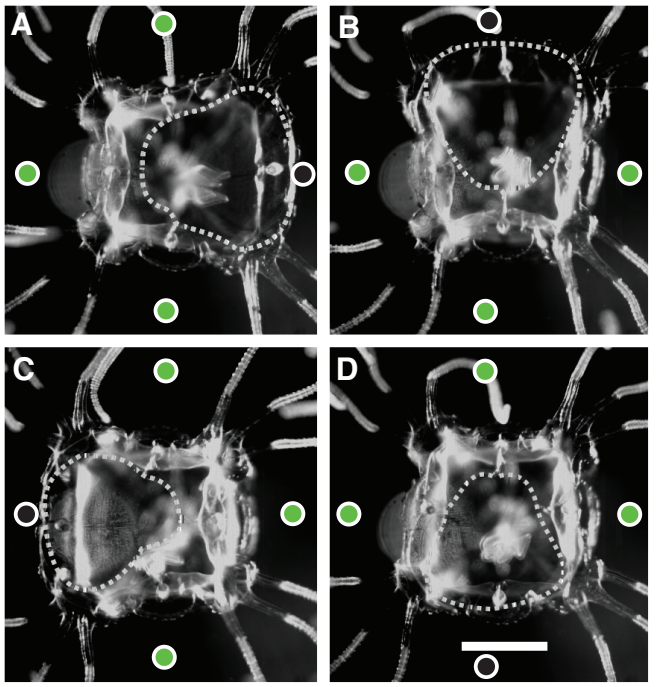

Fig. 5. A decrease in light intensity in one part of the visual environment causes a predictable change in the shape of the velarial opening. This figure shows the velarium of the same animal during four swim pulses, using four different lighting conditions. The pictures are taken out of an image sequence shot by the high-speed camera after one of the panels had been switched off, and show the shape of the velarial opening about 55 ms after the start of a swim pulse. The dark panel is indicated by a black circle and lit panels by green circles. The outline of the velarial opening is indicated by the broken line. The shape of the velarium is roughly the same in all images, but the orientation depends on the location of the dark panel. Scale bar, 2 mm.

the bell until maximum contraction was reached at ~0.10 s, after which an inflow of water started and the bell returned to its resting state.

Switching off one of the panels in the setup caused the outflow opening of the bell, the velarium, to change shape predictably. Fig. 5 illustrates how the shape of the velarial opening changed after the light in one of the panels was turned off. The wide side of the opening always coincided with the side where the light panel has just been switched off. The animal was not reoriented during the trial and changes in velarial symmetry were caused solely by visual stimulation.

The asymmetry in the velarium was accompanied by a lag in contraction in one of the sides of the animal, as shown in Fig. 6B. Not all pulses showed such a pronounced delay in the 'time to peak' and such a high contraction speed as shown in the figure. Instead, the delay in the onset of contraction, shown in Fig. 6C, was found to be a more constant factor. Throughout our trials, the side closest to the dark panel was found to be lagging in contraction, while all sides contracted synchronously under continuous illumination. This shows that medusae contracted asymmetrically, in both the velarium and the swim musculature, when a panel was turned off.

Animals can alternate between symmetric and asymmetric contractions. Fig. 7 shows that animals can change between symmetric and asymmetric contractions for every pulse, although a preference appears to exist for asymmetric contractions.

In free-swimming animals an asymmetric contraction would make the animal turn (Gladfelter, 1973); in our experiments the animal swung around on the tether. The midpoint of the animal was used to indicate movement of the whole animal. The midpoint of the animal was calculated, and determined as the position centred between the four rhopalia. The turning direction depended on visual stimulation. Fig. 8A shows the directions the medusae swung to in response to one of the LED panels being switched off. While tethered, the midpoint of the animal swung towards the darkened panel, which when free swimming would make them swim in the opposite direction, away from the dark panel. This turning behaviour was not seen at constant light, which is shown in Fig. 8B.

DISCUSSION

To control their swimming, animals need to be able to regulate their swim speed and direction. Our data shows that light has a direct effect on the swimming behaviour of the box jellyfish *T. cystophora*. The findings presented in Fig. 3 confirm studies performed on both isolated pacemakers and whole animals (Garm and Bielecki, 2008) and show that swim pulse frequency increases after a drop in light intensity. By regulating its swim pulse frequency the animal regulates its swim speed. From earlier observations (Gladfelter, 1973), it was already known that box jellyfish can make turns by creating an asymmetry in the velarium. But, exactly how this is controlled, and which stimuli are relevant, was not known. In this

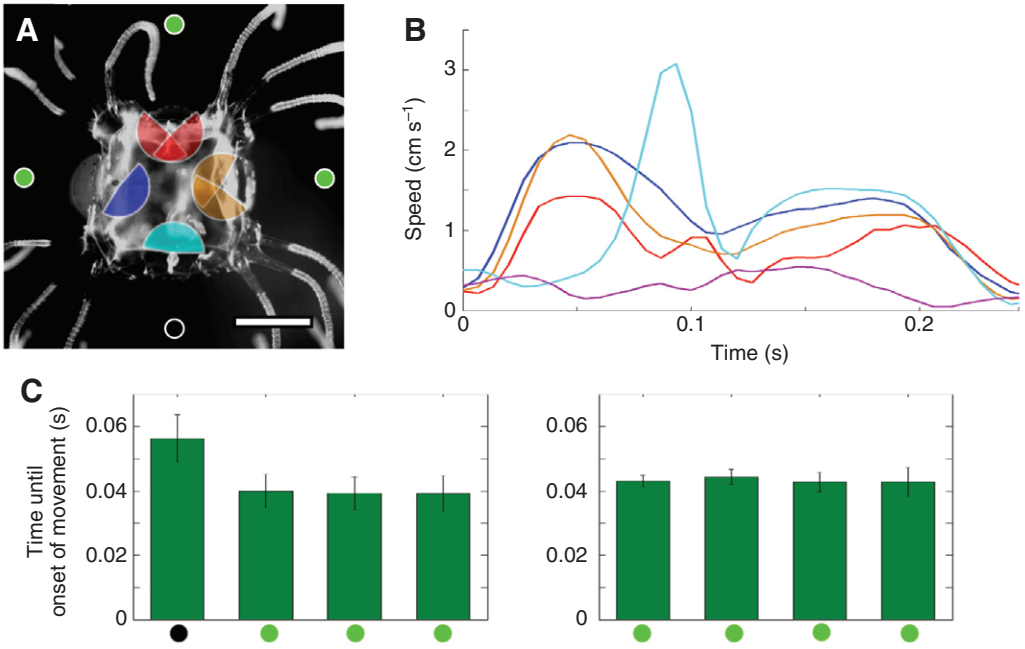

Fig. 6. The symmetry of bell contraction is correlated with visual stimulation. (A) A single frame from a recording where one of the panels has just been switched off. Lit panels are indicated by green circles and the dark panel by a black circle. Approximations of the visual fields of the large lens eyes of two rhopalia are drawn using dark blue and light blue, and the visual fields of the paired slit eyes are drawn for the other two rhopalia in orange and red. Note that the visual fields of both eye types are directed away from the closest panel. Scale bar, 2 mm. (B) Contraction speeds of the four sides of the animal plotted for a single contraction. Colour coding matches that of A. The purple line indicates the speed with which the entire animal moves. Note that the light blue line, which corresponds to the side of the animal closest to the dark panel, contracts later than the other three sides. Interestingly, the large lens eye and the slit eyes on this side of the animal do not see the dark panel directly. (C) The left figure shows that, after switching off one of the panels, there is a clear latency in contraction in the side of the animal closest to the dark panel. (One-way ANOVA, N=4, F=8.0, P=0.034, followed by Tukey–Kramer. The side marked with the black circle differed significantly from the three other sides, P<0.05, marked with green circles. No difference existed between the three sides marked in green P>0.05.) With all panels lit, as shown in the right figure (all green circles), all sides of the animal contracted simultaneously, and the animal performed a symmetric contraction. (One-way ANOVA, N=4, F=0.27, P=0.85, followed by Tukey–Kramer. No significant difference was found between sides. P>0.05.)

study we show that *T. cystophora* responds to a sudden darkening of one part of its visual environment by: (1) increasing the swim pulse rate, (2) creating an asymmetry in the velarial opening and (3) delaying contraction in the side facing the direction where light intensity decreased. The last two changes serve to reorient the bell in such a way that the animal would swim away from the decrease in light intensity.

In the setup, we provided the animal with a controlled visual environment, and were able to evoke predictable responses. We believe that tethering had no or a minimal effect on the behaviour of the jellyfish. We observed that animals had a normal contraction frequency including occasional long pauses, and they had their tentacles extended. Stressed animals usually display continuous swimming with retracted tentacles. We also observed that tethered animals reduced their swim pulse rate in continuous darkness, which would be unlikely to happen in stressed animals. Finally, animals were transferred back to the culture tanks after the experiments and some individuals were observed to live for another 4 weeks before they died of natural causes.

The asymmetry in the velarial opening is most probably caused by a local contraction of the frenula and the velarium. Contraction of the velarium and contraction of the frenula are likely to be coupled, as the frenula are a part of the velarium and the ring musculature that runs through the velarium also runs through the frenula (Satterlie et al., 2005). The asymmetry in the velarial opening could be caused by a weak contraction in the frenulum at the side of the animal facing the dark panel. Strong contractions of the frenula at the other three sides locally restricts the range of movement of the velarium and causes the outflow opening to become asymmetric. Alternatively, contraction of the muscles in the velarium itself could

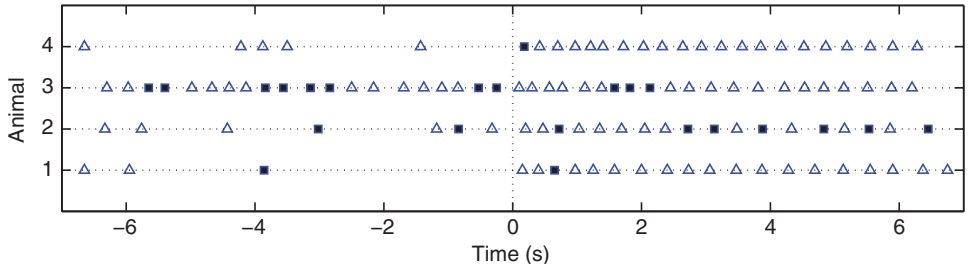

Fig. 7. Animals alternate between symmetric and asymmetric contractions. For each animal (1–4), one trial is plotted, showing 7 s before and after switching off one panel. Squares mark symmetric contractions while triangles mark asymmetric contractions.

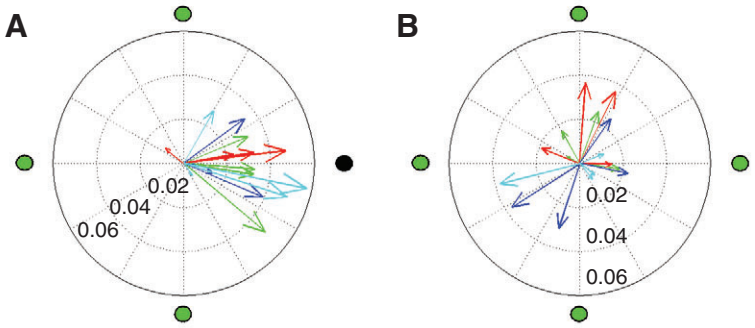

Fig. 8. A sudden darkening of one part of the visual world makes the animal try to swim in the opposite direction. Asymmetry in velarium and bell contraction makes the animal turn. In our setup the animal swings on the tether. Swing direction vectors from all swim pulses in one trial were averaged to obtain the mean swing direction vector for each side of four individuals. Each individual is indicated by a different colour. (A) Responses to turning off one LED panel. (B) Behavioural responses under constant illumination. The numbers on the radial axis show the length of the swing vectors in mm. Lit panels are indicated by green circles and the dark panel by a black circle. Switching off one panel makes the underside of the bell orient towards the dark panel (N=4, P=0.0026, V-test), while this effect is absent under constant light (N=4, P=0.56, V-test).

cause the asymmetry. But the observed asymmetry is probably caused by contractions in both the frenula and the velarium. In addition to the muscles in the bell and the velarium, a radial strip of smooth muscle runs from just above each rhopalium to the top of the bell (Satterlie et al., 2005). Contraction of this muscle could induce an asymmetry in both the bell and the velarium. However, it is probably not involved in creating the asymmetry observed in our experiments because contraction of the smooth muscle strip would be slow and long lasting, whereas our results show that animals can alternate between symmetric and asymmetric pulses for every pulse. It would be interesting to confirm the functional connection of bell and frenula by morphological and electrophysiological investigations.

Fig. 8 demonstrates that the animal turns the underside of the bell towards the panel that has just been switched off. The animal does so by a combination of an asymmetric contraction of the velarium and an asymmetric contraction of the bell. The reorientation would make the animal swim away from the newly formed dark area in the visual environment. Therefore, we argue that we are looking at the mechanics behind the obstacle-avoidance behaviour (Garm et al., 2007b) that has been investigated in free-swimming animals.

The effects we found are probably coupled to the large lens eye, the slit eyes or a combination of both. In our experiments these eyes viewed the equatorial world where the stimulus panels were located. The upper lens eye and the pit eyes looked up through the water surface and did not have a direct view of the stimulus panels. Previously it has been shown by single eye stimulation that the large lens eye reacts to the offset of light by increasing the pulse frequency of the pacemaker system, while the effect of the slit eyes is unclear (Garm and Mori, 2009). In our experiments a decrease in light intensity resulted in an increase in swim pulse frequency, which argues that the lower lens eye is at least involved in controlling the swim pulse rate in our experiments. Whether the large lens eye also controls the shape of the velarium is unknown. Two systems could operate in parallel, one for setting the swim speed by means of controlling bell contraction rates and one for controlling swimming direction by affecting the shape of the velarium.

The stimulus we present here is very coarse. A simple light meter with a broad visual field would be sufficient to control this behaviour, which leaves us with the question of how box jellyfish use the relatively high spatial resolution (Nilsson et al., 2005) found in the lower lens eye. What role the paired slit eyes with their peculiar horizontally flattened visual fields play (Garm et al., 2008) is also unknown. For future experiments it would be worthwhile to test the effect of dimming smaller sections of the environment and also to ablate specific types of eyes.

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