PRIMARY RESEARCH PAPER

Contrast and rate of light intensity decrease control directional swimming in the box jellyfish *Tripedalia cystophora* (Cnidaria, Cubomedusae)

Ronald Petie · Anders Garm · Dan-Eric Nilsson

Abstract Box jellyfish respond to visual stimuli by changing the dynamics and frequency of bell contractions. In this study, we determined how the contrast and the dimming time of a simple visual stimulus affected bell contraction dynamics in the box jellyfish *Tripedalia cystophora*. Animals were tethered in an experimental chamber where the vertical walls formed the light stimuli. Two neighbouring walls were darkened and the contraction of the bell was monitored by high-speed video. We found that (1) bell contraction frequency increased with increasing contrast and decreasing dimming time. Furthermore, (2) when increasing the contrast and decreasing the dimming time pulses with an off-centred opening had a better defined direction and (3) the number of centred pulses decreased. Only weak effects were found on the relative diameter of the contracted bell and no correlation was found for the duration of bell contraction. Our observations show that visual stimuli modulate swim speed in *T. cystophora* by changing the

swim pulse frequency. Furthermore, the direction of swimming is better defined when the animal perceives a high-contrast, or fast dimming, stimulus.

Key words Box jellyfish · Cubozoa · Visual system · Swimming

Introduction

Box jellyfish are agile swimmers and in the Caribbean species *Tripedalia cystophora* visual stimuli control swimming by setting the swim speed and direction. The direction of swimming is controlled by the shape of the opening in the velarium (Gladfelter, 1973; Petie et al., 2011). The velarium is a thin muscular sheet that functions like a nozzle during swim contractions, thereby controlling the swim direction and efficiency (Dabiri et al., 2006). The shape of the velarium is under visual control (Petie et al., 2011). A sudden darkening of a part of the visual field will cause the animal to turn away, and the orientation of the opening in the velarium is directly related to the location of the darkness (Petie, unpublished data). This is most probably the mechanism behind the obstacle avoidance behaviour described for this species (Garm et al., 2007b). In two other species of box jellyfish, *Chironex fleckeri* and *Chiropsella bronzie*, swim speed was found to be affected by bell size and the frequency of bell contraction (Shorten et al., 2005). In *T. cystophora*, which is studied here, the bell contraction

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frequency is controlled by the visual input to the animal (Stöckl et al., 2011). In addition, the swim speed of the animal could be set by the duration of bell contraction (Daniel, 1983) and the degree by which the bell volume is decreased.

The eyes of box jellyfish are grouped in four clusters, each with six eyes (Claus, 1878; Conant, 1898; Berger, 1900; Yamasu & Yoshida, 1976; Laska & Hündgen, 1982). These clusters are called rhopalia and each rhopalium has a pacemaker that together with the pacemakers from the other three rhopalia sets the bell contraction rate (Satterlie & Spencer, 1979; Satterlie & Nolen, 2001). Impulses for bell contraction originate in the rhopalia and spread through the subumbrellar swimming muscles (Satterlie, 1979). Both in recordings from isolated pacemakers (Garm & Bielecki, 2008) and whole animals (Stöckl et al., 2011) a drop in ambient light intensity will cause an increase in the pulse rate. Each rhopalium is equipped with four eye types and three of the four eye types plus the rhopalial neuropil can affect the firing rate of the pacemaker (Garm & Mori, 2009). Only two of the four eye types view the underwater scene, the lower lens eye and the slit eyes, the other eyes look up through the water surface (Nilsson et al., 2005; Garm et al., 2008, 2011). In this article, we have examined the effect of stimulus contrast and dimming time on the dynamics of bell contraction, while stimulating the eyes viewing the underwater scene.

Methods

Experimental set-up

Animals were tethered in a $5 \times 5 \times 5$ cm experimental chamber, where the light intensity of the four vertical walls could be controlled. Blue-green LEDs with a peak emission at 500 nm and a spectral half width of 25 nm were used as the visual stimuli. The colour of the LEDs was chosen to match the spectral sensitivity of the eyes (Coates et al., 2006; Garm et al., 2007a). Each wall was lit from the outside by four LEDs (20410-UBGC/S400-A6, Everlight Electronics Co. Ltd, Taipei, Taiwan) and the light intensity could be regulated up to a maximum intensity of 483 cd/m². A diffuser was used to get a more even light distribution, instead of point light sources. A light-proof box was placed over the experimental chamber

during experiments to exclude ambient light. The responses were monitored using a high-speed camera pointing up into the experimental chamber, operated at 150 frames per seconds (MotionBlitz EoSens mini1, Model MC 1370, Mikrotron GmbH, Unterschleißheim, Germany). The light intensity of the stimulus panels was measured with a photometer (Universal photometer/radiometer Model S3, B. Hagner AB, Solna, Sweden). The contrast was measured as:

$$\text{Contrast} = \frac{I_{\text{Cont}} - I_{\text{Dark}}}{I_{\text{Cont}} + I_{\text{Dark}}}, \tag{1}$$

where I stands for light intensity of the darkened (I_{Dark}) panels and the panels operated at constant light intensity (I_{Cont}). The temperature of the water was kept at 27°C. A more detailed description of the set-up can be found in (Petie et al., 2011).

Experimental procedures

First, the animal was anaesthetized by immersion in a 1:1 mixture of sea-water and magnesium-chloride (0.37 M) to facilitate attachment to the suction electrode used for tethering. Anaesthesia was done in a separate container after which the animal was moved to the experimental set-up, while taking care to transfer as little of the magnesium-chloride containing sea-water as possible. The animals were allowed to recover for at least 10 min before the first experiment was performed. This was long enough for the swim pulse frequency of the animals to return to normal values (Petie, unpublished data). Each experiment started with a period of 1 min where all four panels where lit at maximum intensity, after which two neighbouring panels where darkened, while simultaneously the high-speed camera was triggered. Switching two neighbouring panels off resulted in a very consistent response, 70% of the pulses had identical out-pocketing directions (Petie, unpublished data). In total 16 tests were performed on each animal: eight different contrasts and eight different dimming times were tested in random order. The contrasts we used were: 0.24, 0.20, 0.12, 0.10, 0.080, 0.059, 0.017 and 0.0036. We used dimming times of 0.5, 1, 3, 5, 10, 20, 30 and 60 s. For the dimming experiment, all four panels started at maximal light intensity and two panels were decreased to the minimal light intensity. The light intensity of a light panel depends both on light that it emits itself and the light it reflects from

other panels. This means that the light intensity of the panels depend on each other. In the dimming experiments light intensity was decreased over time according:

$$I_{\text{Cont}}(t) = -108.3 \cdot \log_{10}\left(\frac{t}{t_{\text{Max}}}\right) + 295.9, \qquad (2)$$

$$I_{\text{Dark}}(t) = -181.2 \cdot \log_{10}\left(\frac{t}{t_{\text{Max}}}\right) + 167.4, \qquad (3)$$

where t is time, I_{Cont} is the light intensity of the panels which are operated at a constant light intensity, I_{Dark} is the light intensity of the panels that were darkened and t_{Max} is the time in which the light is dimmed. The contrast between I_{Cont} and I_{Dark} changed over time according to:

$$\text{Contrast}(t) = 0.202 \cdot \log_{10}\left(\frac{17.27 \cdot t}{t_{\text{Max}}} + 0.667\right), \quad (4)$$

In the contrast experiments, the intensity drop to the desired contrast was instantaneous. In both experiments, the combination of neighbouring panels that were darkened was randomly selected. For the analysis, all data was rotated back to a standard orientation where the top and the right panel were darkened, illustrated by the shaded panels in Fig. 1. Based on previous experiments, we would expect the velarium to pocket out towards the centre of the dark area, which is in this case the 45° direction (Petie, unpublished data). This would make a non-attached medusa swim away from the dark area.

Animals

Ten animals were used for the experiments and their mean bell diameter was 0.77 cm (SD 0.077). The animals were grown in cultures at the University of Lund, Sweden.

Analysis

High-speed videos were analysed using ImageJ version 1.45j (http://imagej.nih.gov/ij/). The animals were oriented with the sides of the bell parallel to the walls of the experimental chamber (Fig. 1). For each bell contraction a number of parameters were measured. The time at which a swim pulse occurred was defined as the time at which the bell was maximally contracted. At the same point in time the diameter of
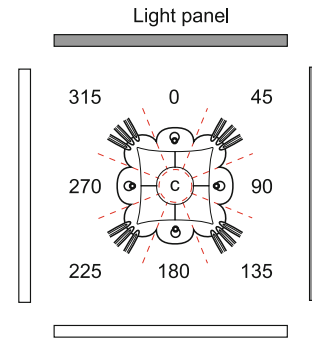
Fig. 1 Schematic representation of the experiments. The jellyfish was viewed from underneath. Two neighbouring panels were darkened, illustrated by the *grey shading*. During a swim pulse the opening in the bell could be centred, as is drawn here and marked by a *c*. Alternatively, the opening in the bell could be off-centred and pocket out towards one of the four rhopalia or one of the four pedalia (Petie, unpublished data). The direction of out-pocketing was categorised in sectors with 45° separation. Three other parameters of bell contraction were determined: the bell contraction frequency, the diameter of the contracted bell and the duration of the contraction phase of the swim pulse

the bell was measured as the distance between the left and right rhopalium in the image. The contraction duration was defined as the time that elapsed from the moment the bell started contracting until the moment water started flowing back into the bell, indicated by the velarium starting to pocket inwards. Under the present experimental conditions, the off-centred pulses can pocket out towards one of the four rhopalia, or one of the four pedalia (Petie, unpublished data). Based on this observation, we divided the bell margin into eight 45° sectors, as illustrated in Fig. 1. For the off-centred pulses, the direction of the opening in the velarium was visually determined for each swim pulse and scored according to the eight sectors. Pulses with a centred opening in the velarium were also counted. After the onset of the change in light intensity six pulses were measured, or as many pulses as occurred within the 22 s of recording time of the high-speed camera.

The data were analysed using *R* (R Development Core Team, 2012) and the R packages *circular* (Agostinelli & Lund, 2011), *CirStats* (S-plus original by Ulric Lund and R port by Claudio Agostinelli, 2009), *Hmisc* (Frank E Harrell Jr and with contributions from many other users 2012), *nortest* (Gross, 2012) and *mvoutlier* (Filzmoser & Gschwandtner, 2012). For the linear models and the circular statistics animal means were used. For the linear regression on

the relative diameter against contrast, three outliers were removed. We tested the residuals of the regressions for normality using the Lilliefors (Kolmogorov–Smirnov) test, homogeneity of variances was tested for by the Barlett test. The P values under the circular plots were obtained by the Rayleigh test, which tested whether the observed directions were randomly distributed. Confidence intervals were only given when the pulses were non-randomly distributed.

Results

Dynamics of bell contraction

To determine the dynamics of bell contraction we measured three parameters: (1) the pulse frequency, (2) the degree of bell contraction and (3) the duration of the contraction phase of the swim pulse. We found highly significant correlations for the pulse frequency for both the dimming time (Fig. 2a, $F[1,78] = 32.12$, $P < 0.0001$, $r = -0.54$) and the contrast of the stimulus (Fig. 2b, $F[1,74] = 23.49$, $P < 0.0001$, $r = 0.49$). Over the range of stimulation pulse frequency decreased 46%, from 2.3 to 1.3 Hz, for the dimming experiment and it increased 71%, from 1.4 to 2.3 Hz, for the contrast experiment. We found that the contracted bell diameter had a weak, but significant, relationship to the dimming time of the stimulus (Fig. 2c, $F[1,78] = 5.08$, $P = 0.027$, $r = 0.25$). Here, the relative bell diameter increased with 8.2% over the stimulus range, from 0.58 to 0.63. A similar, but non-significant, relationship to the contrast of the stimulus existed (Fig. 2d, $F[1,75] = 3.93$, $P = 0.051$, $r = -0.22$). Now, the bell diameter decreased with 5.7% over range of stimulation, from 0.62 to 0.59. The duration of the contraction phase did not change with the dimming time of the stimulus (Fig. 2e, $F[1,78] = 2.66$, $P = 0.107$, $r = 0.18$) or the contrast of the stimulus (Fig. 2f, $F[1,78] = 2.42$, $P = 0.124$, $r = -0.17$). This means that the contraction duration was consistent, with an average of 0.12 s (SD 0.012).

Out-pocketing shape

In Fig. 3, we can see a decreasing linear trend in the percentage of centred out-pocketings for the dimming experiment (Fig. 3a, $F[1,6] = 4.92$, $P = 0.068$,

$r = 0.67$). The trend has a strong correlation, but is not significant. A linear trend was also observed in the contrast experiment, also non-significant (Fig. 3b, $F[1,6] = 5.21$, $P = 0.062$, $r = -0.68$). The height of the linear functions at zero contrast, or the longest dimming time represent the predicted proportion of centred out-pocketings at constant light. In both cases, this value is 29%, which is in the range of the observed 37% centred pulses under constant light (Petie, unpublished data).

For analysis of the directional component of the response, we disregarded the swim pulses with a centred opening and performed circular statistics on the mean direction of the off-centred pulses for each animal. For the different dimming times (Fig. 4a–h), we found that the pulses have a non-random direction up to a dimming time of 30 s, while also the expected 45° out-pocketing direction was included in the 95% confidence intervals. For the contrast experiment (Fig. 5a–h), we saw that the response lost directionality after a contrast of 0.20, or arguably 0.12.

Using the strongest stimulation, the first pulse in the expected direction was found after 0.93 s (SD = 0.68, $N = 10$) for the dimming experiment and 0.82 s (SD = 0.55, $N = 10$) for the contrast experiment.

Discussion

We have examined the response to a directional light-off stimulus in the box jellyfish *T. cystophora*, and found the response is graded with faster dimming and higher contrast resulting in stronger responses. From our data, we conclude that changing the dimming time or contrast of a stimulus mainly influenced the speed of swimming through the swim pulse frequency. Furthermore, when presented with a high-contrast or fast dimming stimulus, the animals produce less centred pulses and the off-centred pulses have a better defined direction.

Swim speed

To find out how *T. cystophora* controls its swim speed we measured three bell contraction parameters: swim pulse frequency, the degree of contraction and the duration of contraction (Fig. 2). The strongest, and highly significant, correlations with the stimulation were found for the swim pulse frequency. Weak
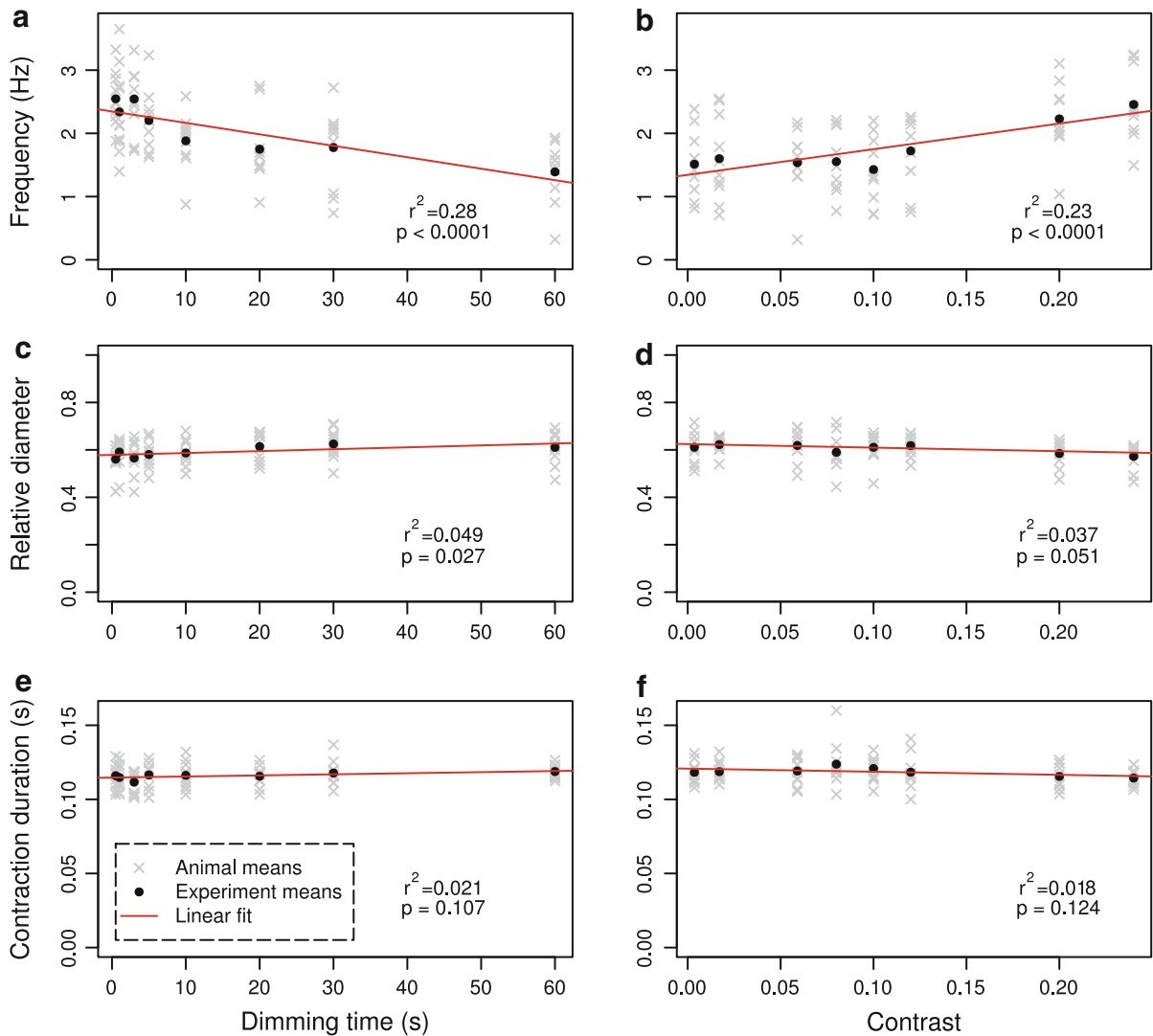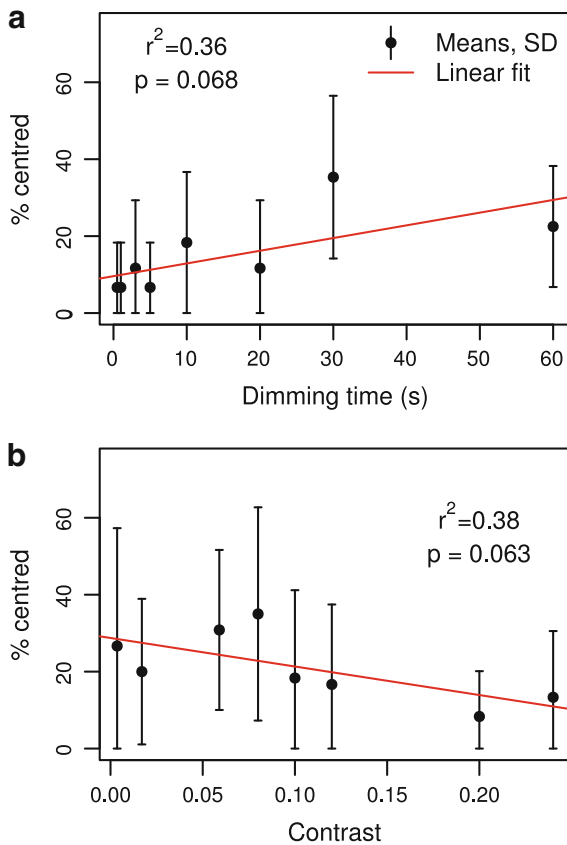
Fig. 2 The relationship between the dimming time and contrast of the stimulus and **a**, **b** the frequency of bell contraction, **c**, **d** the relative diameter of the contracted bell and **e**, **f** the duration of the contraction phase of the swim pulse. The contrast or the dimming time affected the swim pulse frequency most. Significant but weak correlations were found for bell diameter and no significant relationship was found for the duration of bell contractions

correlations were found with the bell diameter. Interestingly, we did not find any significant relationship for the duration of the contraction phase. In a theoretical study (Daniel, 1983), the duration of contraction has been shown to be a factor in determining the average velocity during constant swimming for a medusa with approximately the same size and shape as *T. cystophora*, but it appears not to be a factor the animals change in response to visual stimulation. Only very weak correlations were found to the relative contracted diameter of the bell. We used

this parameter as an indication of the volume of water expelled during each swim pulse and it implies that the animal contracts slightly more when presented with a high-contrast, or fast dimming, stimulus. Over the entire range of stimulation the change in contracted bell diameter for the dimming experiment was 8.2 and 5.7% for the contrast experiment. Pulses vary in all of the three parameters measured but only pulse frequency was strongly correlated to the stimulation. Pulse frequency decreased 46% for the dimming experiment and increased 71% for the contrast

Fig. 3 The relationship between the dimming time and contrast of the stimulus and the percentage of centred swim pulses. **a** The percentage of centred pulses increased with increasing dimming time. **b** The percentage of centred pulses decreased with increasing contrast

experiment. Based on our bell diameter measurements, we can assume that the volume of water expelled from the bell is close to constant, if we now make the reasonable assumption that swim speed is directly correlated with pulse frequency, we can conclude that swim pulse frequency is the main way *T. cystophora* controls swim speed upon visual stimulation. In order to swim faster the animal produces more pulses per unit time. From a neurobiological stand point this also makes sense. In an animal with a nervous system as simple as *T. cystophora* you would not expect swim speed to be controlled by several mechanisms. The seemingly pre-set degree and speed of contraction might have a neurobiological explanation. It is possible that *T. cystophora* has a similar control mechanism as found in the hydrozoan jellyfish *Polyorchis penicillatus*, where a clever

system ensures bell contraction synchronicity (Spencer, 1982). As a spike travels around the motor neuron in the nerve ring its duration decreases. Here, the duration of the spike is a measure for the distance travelled. For shorter spikes the latency of the swim muscle action potential decreases, this way the time travelled via the nerve ring is compensated. If a similar mechanism exists in *T. cystophora,* this leaves probably not a lot of possibility to vary other parameters of bell contraction than swim pulse frequency.

Swim direction

From our previous study (Petie et al., 2011), we know that for *T. cystophora* the direction of off-centred pulses correlates with the direction the animal swings to on a tether. Free swimming animals would make a turn away from the direction of out-pocketing. Since centred pulses will normally result in straight swimming this is a system where the animal can control straight swimming, or turning, by producing pulses with a centred or off-centred opening in the bell. We observed that the percentage of centred pulses increased with increasing dimming time and decreasing contrast. For the off-centred pulses, we saw that the opening in the velarium had a well-defined direction throughout almost the entire dimming experiment (Fig. 4), while directionality was quickly lost when the contrast decreased (Fig. 5). Combining the observations of the centred and off-centred pulses we can conclude that at low contrasts and long dimming times the animals perform more straight swimming and turn in random directions, while having a low swim pulse frequency. With increasing contrast and decreasing dimming time the percentage of centred pulses decreases and the off-centred pulses have a much better defined direction, while swim pulse frequency is increased.

When needed the animals can respond swiftly to a change in light intensity. On average, the animals responded within a second with a swim pulse in the expected direction for both stimulus types, when we applied the strongest stimulation possible. For the dimming experiment, the first pulse in the expected direction was on average found after 0.93 s, while this was 0.82 s for the contrast experiment. This implies that the total integration time for the directional response is less than a second. The maximum flicker frequency resolved by the eyes is only known for one

Fig. 4 The direction of the off-centred pulses for different dimming times. The *arrows* show the direction and magnitude of the mean vector for each experiment. The radius of the circle represents a magnitude of 1. The *shaded rectangles* in **a** illustrate the panels that were switched off and based on previous experiments we would expect the direction of out-pocketing to be 45°. The Rayleigh test was used to test whether the pulses were randomly distributed. Mean directions and *P* values from the Rayleigh test are given beneath the *circular plots*. The *dashed lines* visualize the borders of the 95% confidence intervals for the experiments that had a non-random distribution. Up to a dimming time of 30 s, 45° falls within the 95% confidence intervals
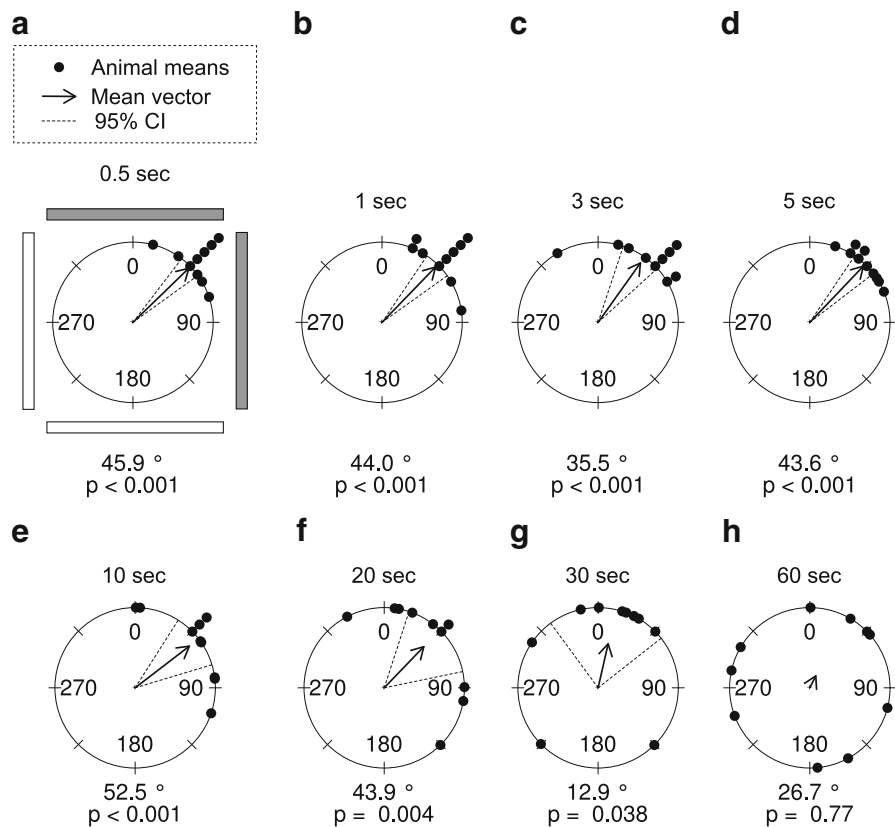
of the eyes viewing the underwater scene. The flicker fusion frequency of the lower lens eye is 8 Hz (O'Connor et al., 2010), which sets the minimal time for integrating visual information to $1/8 = 0.125$ s. Contraction of the bell took on average 0.12 s, which leaves another 0.58–0.68 s for processing of visual information by the nervous system.

Bell contraction

In *T. cystophora* an off-centred opening in the bell is accompanied by an asymmetric contraction of the bell (Petie et al., 2011). The scyphozoan jellyfish *Aurelia* sp. uses a 'rowing' form of propulsion (Colin & Costello, 2002; Dabiri et al., 2005). Interestingly, it has asymmetric contractions of the bell too, but now in response to shear flow (Rakow & Graham, 2006). The authors propose a delay mechanism to be the cause of the asymmetric contraction of the bell and similar mechanisms could exist in *T. cystophora*. Local delays in contraction could very well cause the asymmetry needed in the contraction of the bell and the velarium to enable the animal to turn. Another parameter that

can affect bell contraction kinematics in scyphome-dusae is the presence of prey (Matanoski et al., 2001).

Even though the rowing form of propulsion is biomechanically different to the jetting propulsion used in *T. cystophora* similar mechanisms could control swimming. One indication is the fact that some jellyfish change from a jetting form when they are small, to a rowing form when mature (Weston et al., 2009); the same nervous system controls both propulsive modes. Not all jellyfish change form to cope with the changing flow regimes, changing bell contraction kinematics can serve the same purpose (Blough et al., 2011).

Concluding remarks

Tripedalia cystophora is found in the mangrove swamps in the Caribbean. This is a food-rich environment, but the animals, and specifically their tentacles, are fragile and need to avoid contact with the roots of the mangrove trees. This behaviour is called the obstacle avoidance response (Garm et al., 2007b). With the slow and low-resolution visual

Fig. 5 The direction of the off-centred pulses for different contrasts. The figure reads as Fig. 4. Only in the two highest contrasts, 45° falls within the 95% confidence intervals. The off-centred pulses loose their orientation after the second (**b**), or arguably, the third (**c**) contrast level
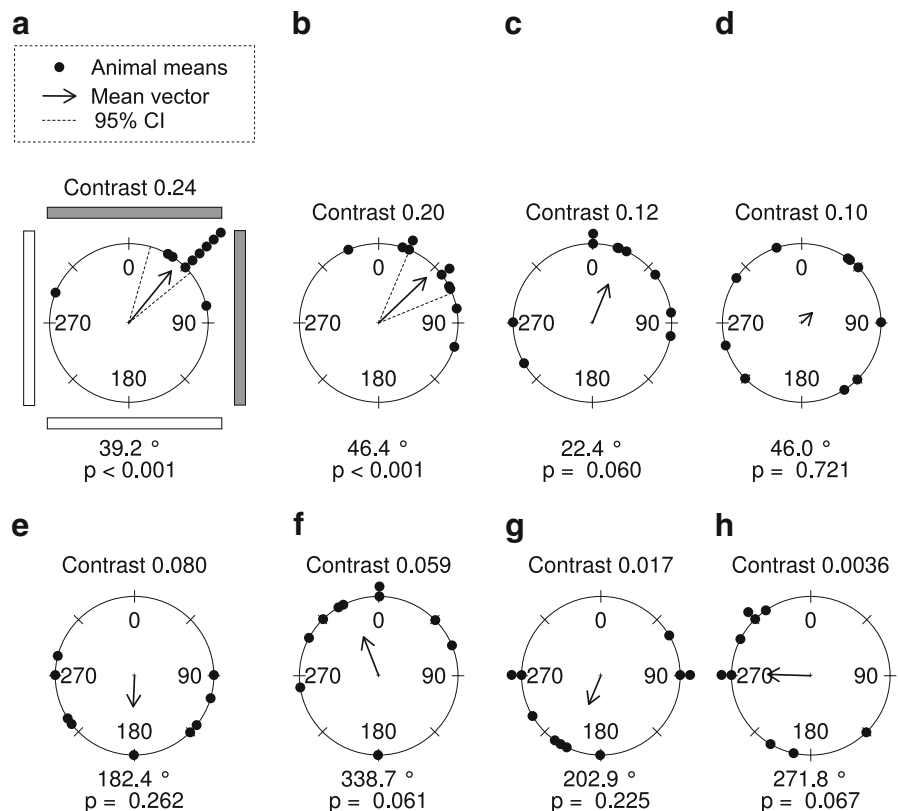
system of these animals (Nilsson et al., 2005; Garm et al., 2007a) the roots of the mangrove trees will present contrast rich features that will slowly move in and out of the visual field of the animal. The stimuli we used in our experiments resemble the stimuli the animals could encounter in the wild. We found that the animals are especially well equipped to respond to slowly dimming stimuli. Over the contrast range we used the animals quickly lost their directional response but retained the increase in swim pulse frequency. This suggests that when using contrast as a stimulus, swim speed is regulated by a system with a different threshold than the system regulating directional swimming. In the dimming experiments, both the directional response and the increase in swim pulse frequency were retained over the entire range of dimming times. We conclude that contrast and dimming time both affect the swim behaviour by changing the swim pulse frequency and the direction of the opening in the bell.

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