

Visually guided obstacle avoidance in the box jellyfish *Tripedalia cystophora* and *Chiropsella bronzie*

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Summary

Box jellyfish, cubomedusae, possess an impressive total of 24 eyes of four morphologically different types. Two of these eye types, called the upper and lower lens eyes, are camera-type eyes with spherical fish-like lenses. Compared with other cnidarians, cubomedusae also have an elaborate behavioral repertoire, which seems to be predominantly visually guided. Still, positive phototaxis is the only behavior described so far that is likely to be correlated with the eyes. We have explored the obstacle avoidance response of the Caribbean species *Tripedalia cystophora* and the Australian species *Chiropsella bronzie* in a flow chamber. Our results show that obstacle avoidance is visually guided. Avoidance behavior is triggered when the obstacle takes up a certain angle in the visual field. The results do not allow

conclusions on whether color vision is involved but the strength of the response had a tendency to follow the intensity contrast between the obstacle and the surroundings (chamber walls). In the flow chamber *Tripedalia cystophora* displayed a stronger obstacle avoidance response than *Chiropsella bronzie* since they had less contact with the obstacles. This seems to follow differences in their habitats.

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Introduction

Eyes in a broad sense are not uncommon among cnidarians (for a review, see Martin, 2002). Morphologically these eyes range from simple ocelli (Singla, 1974; Blumer et al., 1995) to the camera-type eyes of cubomedusae that are morphologically similar to the vertebrate and cephalopod eye (Nilsson et al., 2005).

Several cnidarians have been shown to perform light controlled behaviors. Some hydromedusae display what is known as a shadow response (Yoshida and Ohtsu, 1973; Arkett and Spencer, 1986a; Arkett and Spencer, 1986b), which may be either a predator avoidance response or a consequence of their diurnal migration (Anderson and Mackie, 1977; Arkett and Spencer, 1986a). Hydras have no eyes; however, some of their rhythmic behaviors have also been shown to be regulated by light (Taddei-Ferretti et al., 2004). This response is probably controlled by extraocular photoreceptors similar to those found in parts of the central nervous system of the hydromedusae *Polyorchis penicillatus* (Satterlie, 1985). Examples of horizontal migration guided by the solar position can be found in some Scyphomedusae, e.g. *Aurelia aurita* and those belonging to the genus *Mastigias* (Hamner and Hauri, 1981; Hamner et al., 1994).

Cubomedusae have the most elaborate visual equipment of all cnidarians. They have 24 eyes of four morphologically different types situated on sensory structures called rhopalia

(Claus, 1878; Laska and Hündgen, 1982). Eight of these 24 eyes are camera-type eyes with a spherical fish-like lens containing a graded refractive index (Nilsson et al., 2005). Cubomedusae also display a more elaborate behavioral repertoire than other cnidarians and when observed in their natural habitat the behavioral resemblance to fish is striking. They show strong directional swimming combined with rapid turns (up to 180° in two bell contractions). There are many accounts of cubomedusae displaying positive phototaxis in their natural habitat (Yatsu, 1917; Uchida, 1928; Larson, 1976; Matsumoto, 1995; Lewis and Long, 2005). In tanks they have also been shown to be attracted to light objects and avoid dark objects (Hartwick, 1991; Hamner et al., 1995). In the wild, the Caribbean species *Tripedalia cystophora* uses this positive phototaxis to forage in light shafts between the mangrove roots (Stewart, 1996; Buskey, 2003).

In view of the advanced visual equipment of cubomedusae, more elaborate visual behavior than merely positive phototaxis is to be expected. Here we explore whether two species of cubomedusae, *Tripedalia cystophora* and *Chiropsella bronzie*, display visually guided obstacle avoidance behavior. We also test which of the four eye types might be involved in this behavior and how obstacle size influences the behavior. Electrophysiological recordings have shown that at least parts of the retina of the lens eyes are color blind in the two examined species (Coates et al., 2006; Garm et al., 2007). Still, using

immunocytochemistry it has been suggested that several types of photoreceptor are present in another species, *Carybdea marsupialis* (Martin, 2004). To further investigate the possibility of color vision in cubomedusae, we performed the behavioral experiments with differently colored obstacles.

Materials and methods

Animals

Adult males and females (8–12 mm in bell diameter) of *Tripedalia cystophora* (Conant 1897) were hand collected in the mangrove swamps near La Parguera, Puerto Rico. They were kept in a 300 l concrete holding tank with running seawater at about 28°C and used for the experiments within 2 days of capture.

Adult specimens of *Chiropsella bronzie* (Gershwin 2006) were either hand collected or caught in a dragnet at Four Mile Beach, Port Douglas, Queensland, Australia. They ranged between 3 and 5 cm in bell diameter. The animals were brought back alive to James Cook University in Cairns where they were kept in a round 500 l tank with circulating seawater at 28°C. They were fed dead *Acetes* shrimps several times a day.

Flow chamber

To maximize the number of encounters with the obstacles, the experiments were performed in a flow chamber with semi-laminar flow at 1.0–1.5 cm s⁻¹. The flow chamber was 50 cm long and 10 cm wide and had a water depth of 10 cm. The chamber had opaque white sides, and cylindrical obstacles could be mounted in the bottom 35 cm downstream (Fig. 1A,B). Plastic cylinders 10 cm high were used as obstacles and they were black, red, blue, green, transparent, or transparent with a

5 cm black top above the water. All the colored obstacles came in two widths, either 1 or 2 cm. The visual scene behind the obstacles was the opaque walls of the flow chamber under the water and above water it was white walls or the daylight lamp. In the case of *T. cystophora* three obstacles were used at a time but with the larger *C. bronzie* only two obstacles were used. Light was shone from above using a 500 W daylight lamp (MT400DL, Eyelighting International of North America Inc., Mentor, OH, USA). The spectral composition of the light reflected from the colored obstacles was measured above water with a calibrated photo-spectrometer (S2000, Ocean Optics, FL, USA) held at a right angle 1 cm away. This was weighted by the spectral sensitivity of a 500 nm opsin (Govadovskii et al., 2000), which has been shown to be present in the lens eyes (Coates et al., 2006; Garm et al., 2007), and their relative contrast with the sides of the flow chamber was calculated (Fig. 1C,D).

Experimental protocol

When running experiments with *T. cystophora*, each medusa was only used once to ensure that they did not experience fatigue during the experimental protocol. The ten different sets of obstacles were used in random order and ten medusae were confronted with each set. In the beginning of each experiment the animal was placed approximately 15 cm upstream of the obstacles and after 30 s their behavior was video recorded for 3 min using a mini-DV camcorder (only 1 min for the transparent obstacles). If a medusa passed the obstacles it was immediately picked up and put back 10–20 cm upstream in the chamber. Almost all passes included contact and were counted as such.

In the case of *C. bronzie*, each medusa was presented with the whole series of obstacles in random order. They are strong swimmers and showed no sign of fatigue throughout the approximately 40 min long protocol. The medusae were left in the flow chamber for 2 min to adjust to the experimental conditions, after which their behavior was video recorded and the obstacles were changed

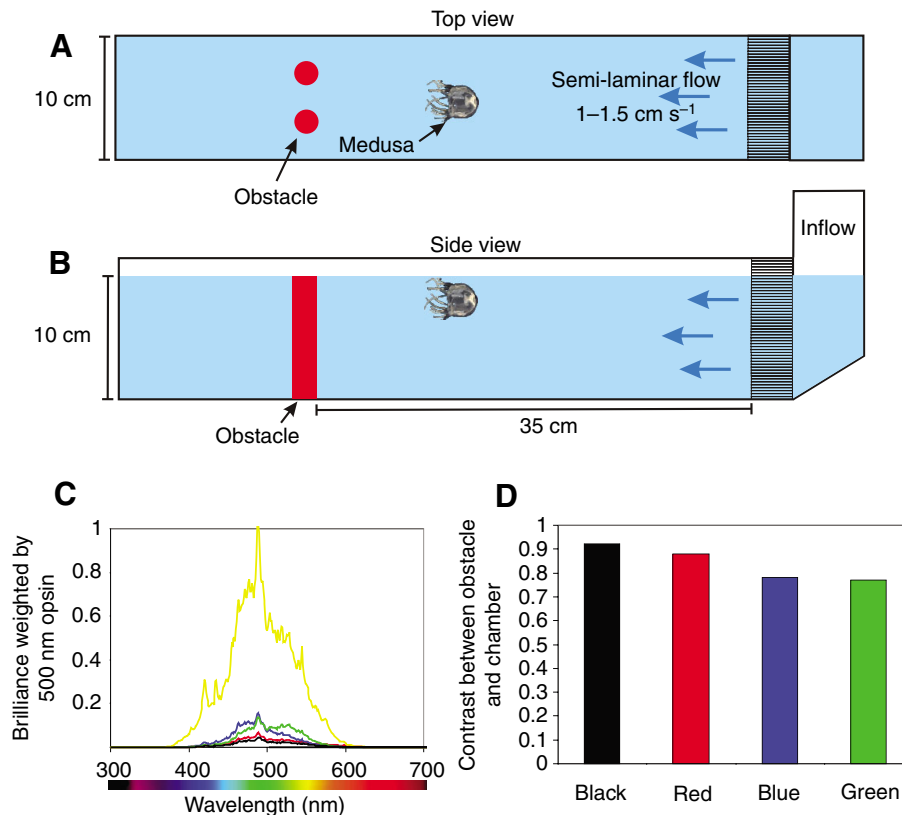


Fig. 1. Experimental set-up. The animals were forced to encounter obstacles of different color (black, red, blue, green, transparent, transparent with black top) and size (1 or 2 cm diameter) in a flow chamber (A,B). In the case of *T. cystophora*, three evenly spaced obstacles were present, and when using *C. bronzie*, two obstacles were present (A). The brilliance of the obstacle and the wall of the flow chamber was measured with a spectrophotometer and weighted by the relative sensitivity of a 500 nm opsin (C). The colors of the lines correspond to the colors of the obstacles; the yellow line represents the wall of the flow chamber. The weighted brilliance was turned into contrast between the obstacles and the wall of the chamber (D).

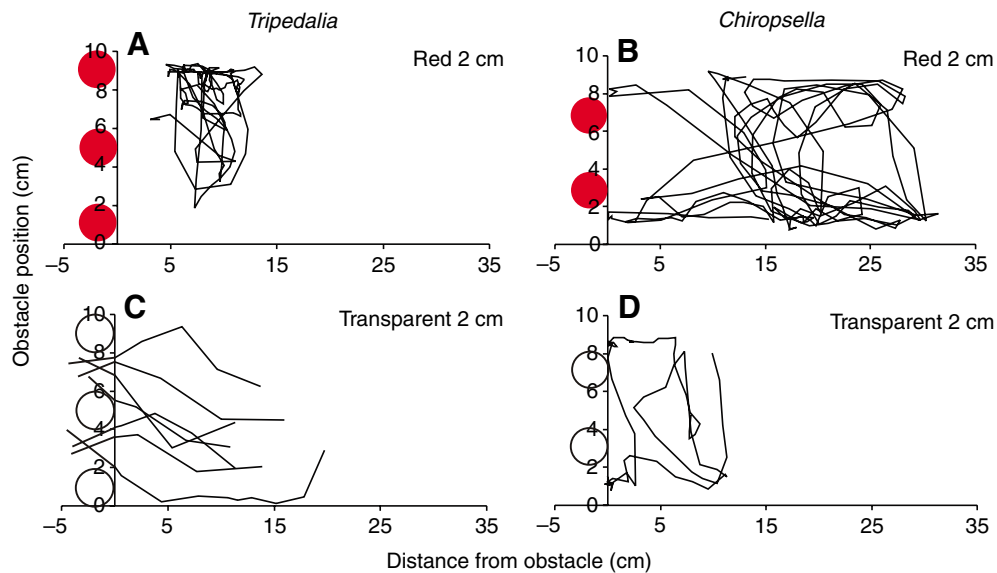


Fig. 2. Swim trajectories. During the 3 min in the flow chamber the medusae behaved differently depending on the visual appearance of the obstacle. When high contrast obstacles were present (A,B), the medusae swam against the current and in general kept at a distance from them. When transparent obstacles with or without a black top were present, the medusae did not respond to them and either bumped into them and passed them (*T. cystophora*, C) or kept swimming into them (*C. bronzie*, D). It should be noted that the tracks represent the movements of the top of the bell and therefore contacts with the obstacles by other parts of the bell can have taken place without the track showing it.

every 3 min. Six medusae of *C. bronzie* were tested with all ten different sets of obstacles and four were tested with the 2 cm wide obstacles only. Between each change of obstacles the medusae were given 30 s before their behavior was recorded.

Data analysis

The video sequences were analyzed using a program written for MatLab 7.0.1 (Mathwork, Inc., Natick, MA, USA) where the position of the medusae is turned into calibrated x/y coordinates. The swim traces were obtained with 1 s resolution and from these traces the following parameters were extracted to measure the strength of the obstacle avoidance response: mean distance of avoidances ($>120^\circ$ turn away from the obstacle within 10 cm of the obstacle without touching it), percentage of time spent in contact with obstacle (*C. bronzie*), contacts with obstacles per minute (*T. cystophora*), and number of avoidances per minute. The extracted distances were also turned into obstacle size in visual angles. The statistical analyses were single- or two-factor ANOVAs with a Fisher's PLSD or Bonferroni–Dunn *post hoc* test, respectively. For *C. bronzie*, repeated measures were included in the ANOVA tests. When comparing wide and thin obstacles, Student's *t*-test for unequal variances was used with a significance level of 0.1, since the data did not allow for a two-factor ANOVA. Except for the avoidance in visual angles, a one tailed *t*-test was used under the assumption that larger objects will create the stronger response.

Results

When placed in the flow chamber both species of medusae in general stayed at the surface and spent most of the time swimming along the sides of the flow chamber. They would swim against the current (showed positive rheotaxis) but at

regular intervals got carried towards the obstacles. *C. bronzie* is in general the stronger swimmer with observed maximum speeds of $7\text{--}8\text{ cm s}^{-1}$ against the $1\text{--}1.5\text{ cm s}^{-1}$ current. The maximum swimming speed of *T. cystophora* was $3\text{--}4\text{ cm s}^{-1}$ against the current but when calculated as body lengths per second *T. cystophora* was more than twice as fast as the much larger *C. bronzie*. The general swim pattern of the medusae varied greatly with the visual appearance of the obstacles (Fig. 2A–D). Video examples can be seen in Movies 1 and 2 in supplementary material.

T. cystophora – wide obstacles

T. cystophora only performed an obstacle avoidance response in the presence of the colored obstacles (2 cm in diameter; Fig. 3). Avoidance responses to the transparent obstacles were never seen (Fig. 2C, Fig. 3A,C), resulting in more frequent contact with transparent obstacles than with any of the colored obstacles (Fig. 3B, single-factor ANOVA, $F_{5,9}=69.9$, $P<0.0001$, followed by Fisher's PLSD, $P<0.0001$). Also, the medusae had more frequent contact with the transparent obstacles with a black top above the water than with the all-transparent obstacles (single-factor ANOVA, $F_{5,9}=69.9$, $P<0.0001$, followed by Fisher's PLSD, $P=0.02$).

All the 2 cm wide colored obstacles evoked obstacle avoidance responses (Fig. 3) and the medusae only touched them with an average frequency of $0.1\text{--}0.25$ contacts min^{-1} (Fig. 3B). Several individuals had zero contacts (Fig. 2A) but the few cases of contact with a colored obstacle would evoke immediate and fast escape swimming. Most often, *T. cystophora* displayed an obstacle avoidance response when approaching a colored obstacle: the medusae would approach the obstacles bell on and turn $120\text{--}180^\circ$ and swim away against the current without contacting them. There was only

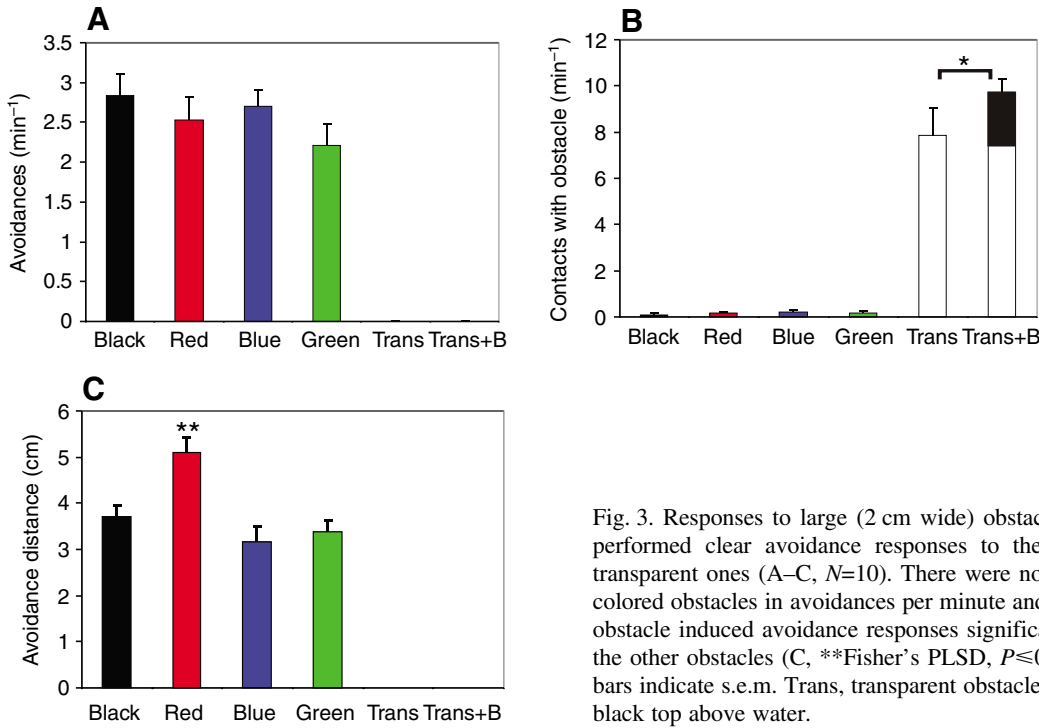


Fig. 3. Responses to large (2 cm wide) obstacles by *T. cystophora*. The medusae performed clear avoidance responses to the colored obstacles but not to the transparent ones (A–C, $N=10$). There were no significant differences between the colored obstacles in avoidances per minute and contacts per minute (A,B). The red obstacle induced avoidance responses significantly further away than from any of the other obstacles (C, **Fisher's PLSD, $P \leq 0.0001$). Values are means and error bars indicate s.e.m. Trans, transparent obstacle; Trans+B, transparent obstacle with black top above water.

a little differentiation in the strength of the response in relation to obstacle color. The medusae avoided the red obstacles, which had the second highest contrast ($c=0.88$) with the surroundings (Fig. 1D), with a greater distance than any of the other colored obstacles (Fig. 3C, single-factor ANOVA, $F_{5,9}=77.9$, $P < 0.0001$, followed by Fisher's PLSD, $P \leq 0.0001$). Other than this there were no significant differences between the responses to the differently colored

obstacles (Fig. 3, single-factor ANOVA, $F_{5,9}=77.9$, $P < 0.0001$, followed by Fisher's PLSD, $P > 0.2$).

T. cystophora – wide vs thin obstacles

When presented with colored obstacles of half the diameter (1 cm), the medusae of *T. cystophora* still displayed obstacle avoidance but the responses were weaker (Fig. 4B,C). When comparing obstacles of the same color but different diameter

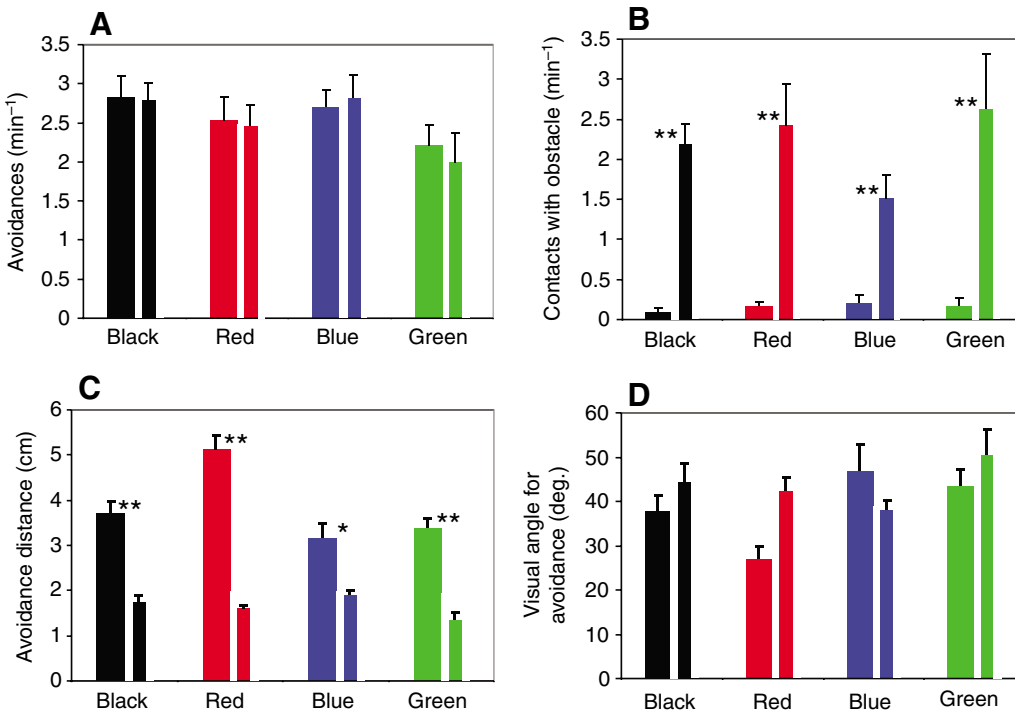


Fig. 4. Responses to differently sized colored obstacles by *T. cystophora*. The thickness of the histogram bars follows the width of the obstacles. The medusae responded more strongly to the wide obstacles than to the thin ones. When comparing obstacles of the same color (e.g. red 2 cm vs red 1 cm), medusae had fewer contacts with (B) and performed avoidances further away from (C) the wide obstacles. The rate of avoidance did not differ with obstacle size (A). When converting the distances of avoidance into visual angles none of the pairs differed significantly (D). $N=10$ except for the thin green obstacle where $N=6$. Values are means and error bars indicate s.e.m. * P values between 0.05 and 0.0001 from ANOVA with Bonferroni–Dunn *post hoc* test. ** P values < 0.0001 .

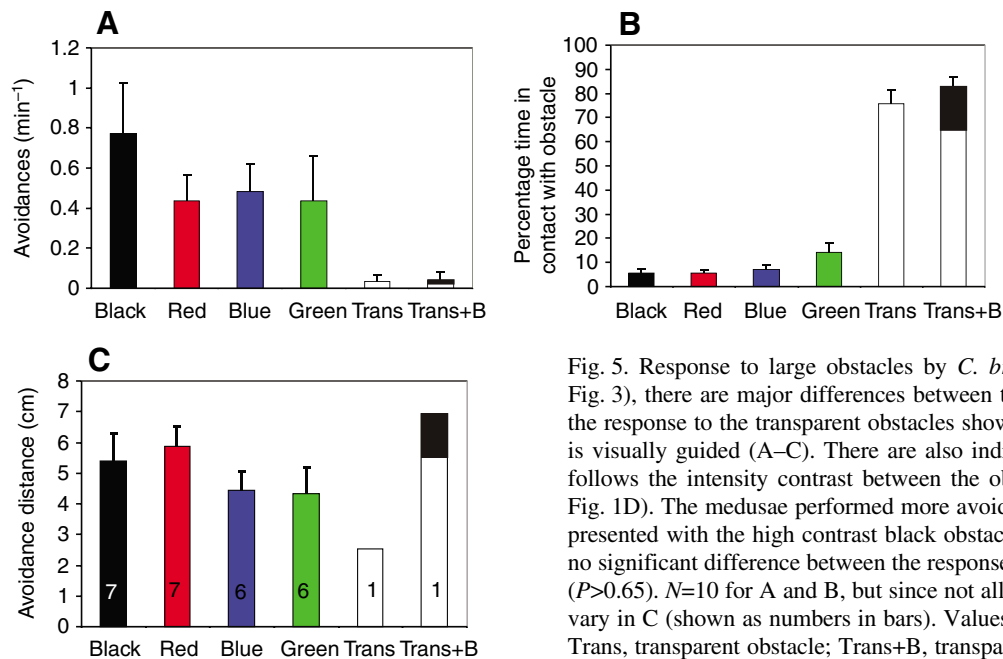


Fig. 5. Response to large obstacles by *C. bronzie*. As found for *T. cystophora* (see Fig. 3), there are major differences between the response to the colored obstacles and the response to the transparent obstacles showing that the obstacle avoidance response is visually guided (A–C). There are also indications that the strength of the response follows the intensity contrast between the obstacle and the chamber wall (A–C; see Fig. 1D). The medusae performed more avoidances (A) and had less contact (B) when presented with the high contrast black obstacles (for statistics see Results). There was no significant difference between the responses to the two types of transparent obstacle ($P>0.65$). $N=10$ for A and B, but since not all medusae displayed avoidances, N values vary in C (shown as numbers in bars). Values are means and error bars indicate s.e.m. Trans, transparent obstacle; Trans+B, transparent obstacle with black top above water.

(e.g. red 2 cm vs red 1 cm) the medusae had fewer contacts with (Fig. 4B, two-factor ANOVA, $F_{1,9}=88.6$, $P<0.0001$, followed by Bonferroni–Dunn, $P<0.0002$, where $P<0.008$ is significant), and displayed the avoidance responses at greater distances from wide than from thin objects (Fig. 4C, two-factor ANOVA, $F_{1,9}=179$, $P<0.0001$, followed by Bonferroni–Dunn, $P<0.0001$, where $P<0.0018$ is significant). The obstacle size had no effect on the rate of avoidance (Fig. 4D, two-factor ANOVA, $F_{1,9}=0.071$, $P=0.79$, followed by Bonferroni–Dunn, $P=0.98$). When the distances for avoidances were converted into the size of obstacles in visual angles, none of the differences between pairs of the same color were significant (Fig. 4D, two-factor ANOVA, $F_{1,9}=3.1$, $P=0.08$, followed by Bonferroni–Dunn, $P>0.06$, where $P<0.0018$ is significant). The smallest visual angle that provoked an obstacle avoidance response was approximately 12° . There was no significant difference in the response to the differently colored thin obstacles for any of the parameters.

C. bronzie – wide obstacles

Similar to the results from *T. cystophora*, both types of transparent obstacle evoked very little response in *C. bronzie* (Fig. 5). A total of only one avoidance-like behavior was seen for each of the transparent obstacles. When using the colored obstacles, the medusae displayed an obstacle avoidance response, but less efficiently than *T. cystophora*. They came in contact with the obstacles more often and when this happened they did not turn and swim away immediately but could stay in contact with the obstacles for several seconds. This is why the analyzed parameter is ‘percentage time in contact’ instead of ‘contacts per minute’. When presented with either of the transparent obstacles the medusae spent most of the time swimming against them (Fig. 2D, Fig. 5B), which resulted in significantly fewer avoidances per minute (Fig. 5A, single-factor ANOVA, $F_{5,9}=5.3$, $P=0.03$, followed by Fisher’s PLSD, $P<0.003$) and more time spent in contact with the obstacles

(Fig. 5B, single-factor ANOVA, $F_{5,9}=2.1$, $P=0.01$, followed by Fisher’s PLSD, $P<0.001$). There was no significant difference in the responses to the transparent obstacles and the transparent obstacles with a black top above water for these two parameters (Fisher’s PLSD, $P>0.65$). The differences in mean distance for avoidances cannot be tested statistically, since $N=1$ for the transparent obstacles (Fig. 5C).

There was no significant difference between the responses to the differently colored obstacles. Still, the differently colored obstacles evoked avoidance responses with varying strength, which had a tendency to follow the intensity contrast weighted by the sensitivity of a 500 nm opsin (see Fig. 1D). The black high contrast obstacles ($c=0.92$) provoked the largest number of avoidances per minute (Fig. 5A) and the *C. bronzie* medusae spent the least time in contact with the black obstacles (Fig. 5B). The green obstacles with the lowest contrast ($c=0.76$) evoked the weakest response and the medusae avoided them the fewest times (Fig. 5A), spent more time in contact with them (Fig. 5B), and came closer before avoiding them (Fig. 5C).

C. bronzie – wide vs thin obstacles

The medusae of *C. bronzie* responded more strongly to the wide (2 cm) than to the thin (1 cm) obstacles and a total of only eight avoidances were seen in response to the thin obstacles (Fig. 6). In general they avoided the wide obstacles more often and spent less time in contact with them than with the thin obstacles even though this was only significant at the 0.10 level (one tailed t -test for uneven variance) in some cases (Fig. 6A,B). In the case of the black pair, the medusae also came closer to the thin obstacles before avoiding them (Fig. 6C, $P=0.02$, one tailed t -test for uneven variance). The low N values for the thin obstacles should be noted for this parameter. When distance for avoidance is converted into obstacle size in visual angles (Fig. 6D) the results are not as clear as for *T. cystophora*. The difference in response to the differently sized obstacles decreases for the black and red pairs but for the blue and green pairs it increases. None

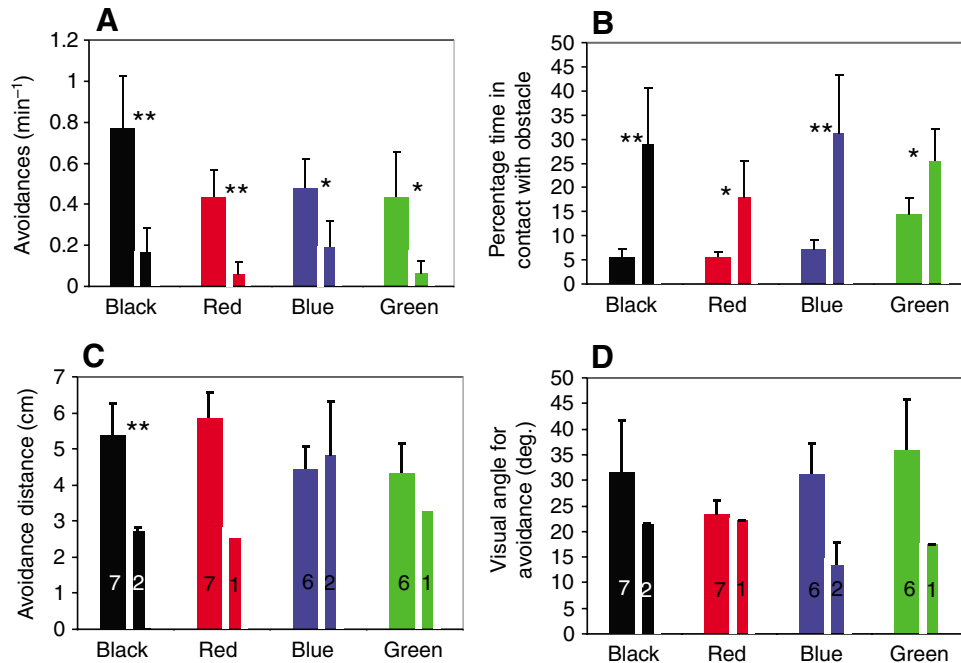


Fig. 6. Response to differently sized colored obstacles by *C. bronzie*. The thickness of the histogram bars follows the width of the obstacles. Again, the wide obstacles provoked the strongest responses (A–C). Only a weak response was seen when the medusae were presented with thin obstacles and the medusae spent up to 31% of the time in contact with them (blue bar in B). The thin obstacles evoked a total of only eight avoidances (C). When mean distance for avoidance is transformed into visual angles similar values are seen across obstacle size (D). There is some more variation in the visual angles but this is probably due to the very low value for N (1 or 3) for the thin obstacles. $N=10$ for wide obstacles and 6 for thin obstacles, unless shown otherwise in the bars (repeats in A and B; recorded events in C and D). Values are means and error bars indicate s.e.m. *Significant difference at the 0.10 level from t -test, **significant differences at the 0.05 level.

of the differences is significant at the 0.10 level, though (Fig. 6D). There is no significant difference between the four differently colored thin obstacles for any of the examined parameters.

Discussion

Cubomedusae are found in habitats where very few other jellyfish are found, such as between the roots of mangrove trees, on coral reefs and on shallow water beaches (Coates, 2003). Having a delicate body in such habitats is demanding, since they contain hard and sharp obstacles which must be avoided. Here we have explored the obstacle avoidance response in two species of cubomedusae, *Tripedalia cystophora* and *Chiropsella bronzie*, found in different habitats. *T. cystophora* is found in mangrove swamps in the Caribbean where it lives at the surface in between the prop roots (Buskey, 2003; Coates, 2003) whereas *C. bronzie* is found in shallow water off sandy beaches in northern Queensland, Australia (Gordon and Seymour, 2004). The beaches of *C. bronzie* contain the occasional large stone, and trees and branches washed out after heavy rainfalls (A.G., personal observation).

Visually guided obstacle avoidance

The visual system of cubomedusae comprising 24 eyes is intriguing and very little data are available on its functional significance. Here we provide the first experimental data documenting visually guided behavior in these fascinating jellyfish. Theoretically the obstacles could also have been detected by chemoreceptors, mechanoreceptors or

electroreceptors. Electroreceptors are not known from cnidarians but mechano- and chemoreceptors are found scattered across the epithelium of many cnidarians including cubozoans (Mariscal and Bigger, 1976; Golz and Thurm, 1993; Thurm et al., 2004; Watson and Mire, 2004; Skogh et al., 2006). Still, all obstacles were made of the same material and had the same shape and therefore none of these three sensory modalities would be able to tell them apart. It must therefore be concluded that the obstacle avoidance in the cubomedusae is visually guided. Mechanoreceptors may amplify the response for *T. cystophora*, since direct contact with the colored obstacles resulted in very strong escape responses.

Most moving animals are able to avoid the obstacles in their surroundings, and in general fast moving animals use vision as the sensory base for this behavior (Robertson and Johnson, 1993; Errigo et al., 2001; Griffin, 2001; Schindler et al., 2004). Slow moving animals often employ other senses such as touch (Migita et al., 2005). This generalized picture fits well with the obstacle avoidance in cubomedusae being visually guided, since these animals are agile swimmers (Shorten et al., 2005).

The results indicate that *T. cystophora* avoids obstacles more effectively than *C. bronzie* and this may follow differences in their habitats. *T. cystophora* lives between prop roots of which many are about 2 cm in diameter (A.G., personal observations) and it is therefore essential for this species to be able to respond efficiently to obstacles of this size. *C. bronzie*, on the other hand, lives off sandy beaches with fewer and in general large obstacles

(large stones, branches and fallen trees; A.G., personal observations). This means that the obstacles can be detected further away, and a weaker obstacle avoidance response would be sufficient.

Which eyes mediate the response?

The 24 eyes of cubomedusae are of four morphologically different types [for morphological description of the eye bearing rhopalia, see Nilsson et al. (Nilsson et al., 2005)]. This suggests that the eyes are special-purpose eyes with a division of labor. When trying to determine which eyes mediate the obstacle avoidance response the orientation of the rhopalia needs to be taken into account. A crystal is found in the distal part of each rhopalium and is often referred to as a statolith (Claus, 1878; Pearse and Pearse, 1978; Laska and Hündgen, 1982). It is also a weight and since the rhopalium hangs by a flexible stalk the crystal ensures that the rhopalium, and thereby the eyes, is always orientated in the same way in relation to the field of gravity (Berger, 1898; Coates, 2005). As a result, two of the eye types, the upper lens eye and the pit eyes, always look upwards through Snell's window and into the terrestrial world. The two other types, the lower lens eye and the slit eyes, look obliquely downwards and observe the underwater world. In the natural habitat of *T. cystophora* the obstacles (the prop roots) enter the water from above and could therefore be detected both below water and above water through Snell's window. The obstacles in our study with the black top above water (visible through Snell's window) elicited no responses while the colored obstacles (only visible under water) resulted in many avoidance responses. This shows that the obstacles need to be seen under water to be avoided. As in their natural habitat, the medusae swam at the very surface in the flow chamber, hence the colored obstacles would not have entered the visual fields of the upper lens eye and the pit eyes of *T. cystophora* before they were within 1–2 cm. These eyes therefore cannot have triggered the majority of avoidances.

The ability to see the obstacles demands some degree of spatial resolution, which is probably present in the lower lens eye of *T. cystophora* (Nilsson et al., 2005). The minimum size of the obstacle in visual angles that provoked an avoidance response was $\sim 12^\circ$, which fits nicely with the calculated half-widths of the receptive fields in the lower lens eye of *T. cystophora*, which are $10\text{--}20^\circ$ (Nilsson et al., 2005). The slit eyes do not have image forming optics and their spatial resolution must be very coarse. Taken together the data suggest that the lower lens eye mediates the obstacle avoidance response. This hypothesis will be tested by selective ablation experiments in the future.

Color vision or intensity contrast?

Our earlier results have shown that the lens eyes of both *T. cystophora* and *C. bronzie* are probably color blind, having a single receptor population containing a 500 nm opsin (Coates et al., 2006; Garm et al., 2007). Color blindness is also suggested from the few other examined cnidarian eyes (Weber, 1982a; Weber, 1982b). When the brilliance of the obstacles is weighted by the spectral sensitivity of the 500 nm opsin it is seen that the black obstacles have the highest contrast with the wall of the flow chamber ($c=0.92$), slightly higher than the red obstacles

($c=0.88$), followed by the blue ($c=0.78$) and the green obstacles ($c=0.77$) (Fig. 1C,D). This contrast span is rather small, which may explain why the response differences to the differently colored obstacles remained small (see Results for the detailed statistics). Although not significant, the results from *C. bronzie* suggest that the strength of the obstacle avoidance response in this species is influenced by the intensity contrast between the obstacle and the surroundings. They display the strongest response to the black obstacles (Fig. 5): when confronted with the black obstacles the medusae had less contact with them, they performed avoidances further away from them and also displayed more avoidances. The low contrast green obstacles evoked the weakest responses in *C. bronzie*: the medusae had the most contact with them, and came closest to them before performing avoidance responses.

For *T. cystophora* there was very little difference in the response to the differently colored obstacles but, interestingly, they performed avoidances significantly further away from the red obstacles than from any of the other obstacles. This suggests that *T. cystophora* respond most strongly to objects with intermediate contrast. However, it could also imply that obstacle avoidance behavior involves color vision, despite our electrophysiological data to the contrary (Coates et al., 2006; Garm et al., 2007). Color vision has been indicated in another cubozoan species, *Carybdea marsupialis* (Martin, 2004). More experiments using gray scale objects and colored obstacles with a wider contrast span are needed to resolve which explanation is the right one.

Response triggered by angular size of obstacles

An interesting question when analyzing the obstacle avoidance behavior is what parameters are involved in triggering the response. This question may at least in part be answered by comparing the response to obstacles of two different sizes, 1 or 2 cm in diameter. In both species the medusae responded much more strongly to the 2 cm wide obstacles. When the mean distances for avoidances are transformed into obstacle size in visual angles it is seen that across obstacle size this parameter is fairly constant, especially for *T. cystophora* (Figs 4, 6). This suggests that at least for *T. cystophora* the angular size of the obstacle on the retina triggers the response. The mean visual angle that triggered a response ($30\text{--}45^\circ$) provides a measure of the minimum spatial resolution of the visual system involved, but the actual resolution is probably higher. There is a lag period between detection of the obstacle and turning, during which the medusa comes closer to the obstacle. This is especially true for the slow turning *C. bronzie*. The threshold size triggering the response could of course also be larger than the minimum detection size. The minimum angular size that triggered an avoidance, about 12° , is in good agreement with the calculated half-widths of the receptive fields of the lower lens eye of *T. cystophora* (Nilsson et al., 2005).

The 1 cm wide obstacles seem to be close to the minimum obstacle size that *C. bronzie* will respond to since they evoked very little response in this species. In total, only eight avoidances were seen. *T. cystophora* displayed the same rate of avoidances to the slim obstacles as to the wide ones and this species difference again follows the observation that the habitat of *T. cystophora* has the smallest obstacles.

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