

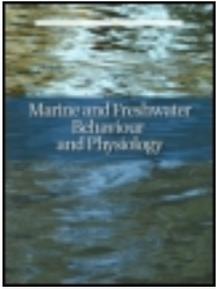
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### Visual tracking of blue bioluminescence-like light sources by hyperiid amphipods

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### Short Communication

## VISUAL TRACKING OF BLUE BIOLUMINES- CENCE-LIKE LIGHT SOURCES BY HYPERIID AMPHIPODS

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Hyperiid amphipods (*Brachyscelus*, *Phrosina*, *Phronima*) possess complex compound eyes, often split into dorsal and ventral parts. They are good swimmers and in the experiments performed here use whole body movements to track a moving LED by rotation and translation. These tracking movements attempt to keep the image of the LED in the antero-dorsal part of the field of view, which corresponds to the upper part of the retina of the ventral eye, not the specialised dorsal eye. We believe this response is normally concerned with attraction to and pursuit of luminescent gelatinous organisms upon which hyperiids are highly dependant.

**Keywords:** Amphipod; behaviour; bioluminescence; vision; tracking

Observing real behaviours in mid- and deep-water animals presents many problems. The hyperiid amphipods are one of the best groups to work with for overcoming these difficulties. In the field they are relatively common and frequently observed from submersibles and for lab work they survive capture and behave well in aquaria at the surface (Land, 1992a; Land *et al.*, 1995). A reasonable amount is known about their habits, especially their associations with gelatinous animals on which they prey or have commensal relationships (Harbison *et al.*, 1977; Madin & Harbison, 1977; Diebel, 1988). *Phronima*, for instance, is usually caught inside a tunicate barrel which it uses for shelter and to lay eggs in (Figure 1).

Most hyperiids have large compound eyes, which are often divided into a dorsal and ventral region (Figure 1). The dorsal region invariably has higher resolution and, for the animals normal swimming position, points upwards (Land, 1981, 1989; Nilsson, 1982).



FIGURE 1 *Phronima sedentaria* positioned in a tunicate barrel, often used as a home, so as to be looking out of one end with the dorsal eyes. The four black dots are retinae. The dorsal eye retinae are the inner two black dots and these make contact with the overlying facets via long light guides (Land 1981). The much smaller ventral eyes, whose retinae are the outer two black dots, have no light guides and receptors make direct contact with short ommatidial optics. Scale bar 4 mm.

Tracking behaviour was first reported by Land (1992a). It is particularly interesting because it implied some kind of social or predatory interaction and the presence, somewhere in the eye, of an acute zone. In this study (see also Land *et al.*, 1995) the techniques were refined to examine tracking behaviour using a blue light emitting diode to which the animals are readily attracted. Although a point source blue LED may seem a rather artificial stimulus, many of the gelatinous animals that hyperiids interact with are luminescent, producing blue light (Herring 1990; Widder *et al.*, 1983). Also, this is the waveband of light which best penetrates to the depths at which the hyperiids live and is therefore likely to be easily visible to their eyes (Lythgoe, 1988). Therefore the laboratory behaviours described may represent close to natural events occurring in the sea.

Amphipods were collected in the N Atlantic on the RRS Discovery and in the Caribbean during the CARDS 1991 Cruise of the RV Edwin Link. The N Atlantic amphipods were *Phrosina semilunata* and *Phronima sedentaria*, caught at depths of 200–500 m in trawls with a RMT-8 net with a closing cod end (Thurston, 1976), and kept in aquaria in a darkened room. The Caribbean animals, of which only *Brachyscelus* sp. was used, were collected by the submersible vessel 'Johnson Sea-Link II' from about 500 m off St Croix in the Virgin Island, using an illuminated cylinder with closing ends, to which the amphipods were attracted. The methods used to study the behaviour were similar to those of Land (1992a and Land *et al.*, 1995). In brief, the set-up consisted of a small aquarium, IR lighting and video camera and a movable blue LED.

The tracking behaviour shown in all cases was controlled and clearly involved feedback control, rather than being random swimming round an attractive light source. Figure 2 shows tracking behaviour by *Phronima* and *Phrosina* in response to a moving stimulus. Due to the constraint faced by *Phronima* of swimming inside its open ended barrel, the styles are rather different. *Phronima* tends to track the moving LED by adjusting the angle of its body, and of the barrel around it, relative to the vertical. One open end of the barrel is thus kept pointing at the LED and tracking is therefore mainly by rotation. Despite the handicap of the barrel, tracking can be very exact (Figure 3). *Phrosina* and *Brachyscelus* usually track the LED by translation, treading water in one position and moving bodily as the stimulus moves. Tracking is achieved with the animal in a head up tail down forward or backward locomotion. In all species the tracking behaviour tends to keep the animals pointing at the LED with antero-dorsal part of the lower eye, rather than the specialised dorsal region. Suggested mechanisms behind this are detailed in Land *et al.* (1995).

## THE BIOLOGICAL SIGNIFICANCE OF TRACKING

Hyperiid are among the commonest animals attracted to the lights on submersibles and the findings described here may be related to this behaviour. Many Hyperiid are found living in close association with gelatinous organisms either as a food source or as protection for themselves, eggs and young (Madin and Harbison, 1977; Harbison, Biggs and Madin, 1977). Gelatinous mid-water animals such as these are usually bioluminescent and, although relatively common, could be hard to locate for a small amphipod. None of the species of hyperiid used here luminesce themselves, so intra-species attraction is improbable. Medusae, ctenophores, siphonophores and other gelatinous mid-water animals luminesce when disturbed (Herring, 1990). The patterns of light produced

may be quite complex, lasting for several seconds and are often bright enough to be easily visible in room lighting. The behaviour seen here in response to a blue photodiode may be normally directed towards potential gelatinous prey animals. Paradoxically, such displays of bioluminescence are probably to deter predators. Attraction to these animals, made visible by their luminescence, may be the evolutionary driving factor behind some of the complexity of Hyperiid compound eye design.

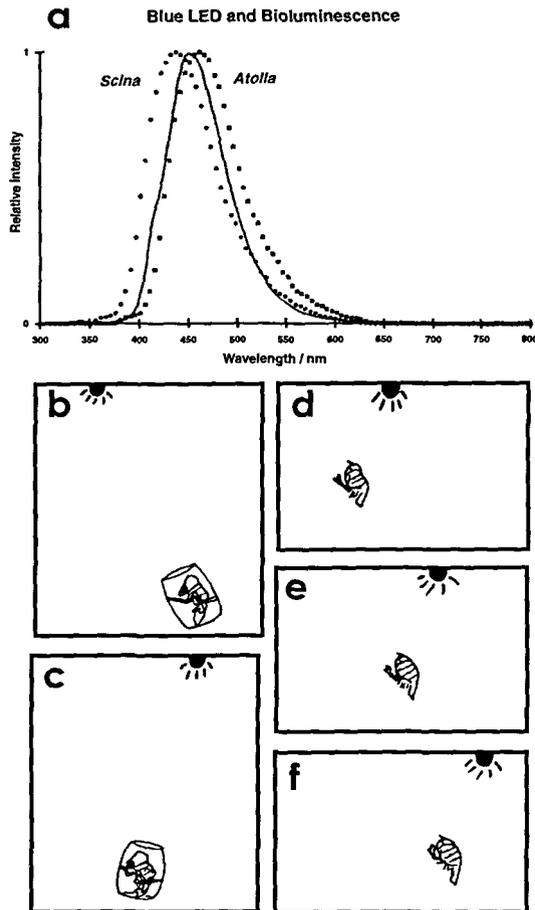


FIGURE 2 a) Relative emission spectra of the blue LED, solid line, used for tracking experiments compared with the bioluminescent jellyfish *Atolla wyvillei* and the crustacean *Scina rattrayi* (Widder *et al.* 1983). b & c) Two traced video frames of *Phronima* rotating its barrel in the pitch plane to track a moving overhead blue LED. d, e & f) Three traced video frames of *Phrosina* tracking blue LED, in this case by posterodorsal translation.

Tracking responses are not common in the crustacea, other examples being the Cladocera (Consi *et al.*, 1990) and Stomatopoda (Cronin *et al.*, 1988) but are relatively frequent in the insects (see Land, 1992b for a review). Optomotor eye movements are found in all animal groups but are distinguished from tracking by the visual inputs involved (Land, 1992b). Optomotor responses are responsible for visual stabilisation and the input is large field sources (like a striped drum) whose angular velocity drives the system (Horridge, 1966). In tracking, on the other hand, the input is usually the position of a small stimulus, relative to a forward-directed fixation point on the animal's retina. There is a preferred position on the retina, usually an area of high resolution (acute zone or fovea), to which the system tends to return the stimulus. For *Phrosina* and *Phronima* and *Brachyscelus* there is such a position in the ventral eye. The exact position of this fixation point in *Phrosina* is almost certainly the ventral eye's acute zone, also a region of binocular overlap (Land, 1989). Where it is in *Phronima* is not obvious, however it is clear that when tracking they view the object through the end of barrel with the ventral eye. Although salp barrels can be very transparent, female *Phronima* lay eggs around the inner surface of their barrels making the only clear view out of the ends.

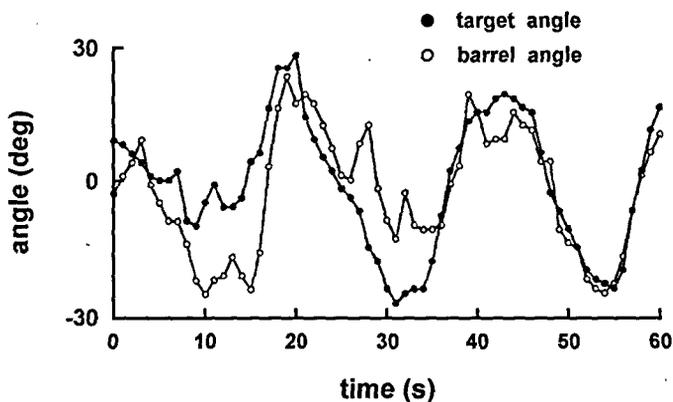


FIGURE 3 Record of *Phronima* tracking over a 1 minute period. The two traces show the target angle *i.e.*, the angle between a line joining the LED to the animal's head and the vertical and the response angle between the axis of the barrel and the vertical. The discrepancy between the traces in the first two cycles is explained by the fact that the axes of the barrel and the head do not quite coincide in the pitch plane. In the 3rd cycle the animal tracks in the yaw plane and there is coincidence.

## DORSAL AND VENTRAL EYES

*Phronima* is very mobile within its barrel home and was occasionally observed looking out of the end with the dorsal eyes (Figure 1). Most hyperiids have

double eyes, the dorsal part having higher resolution than the ventral, but a much more restricted field of view (Land, 1981, 1989; Nilsson, 1982). It was argued in an earlier paper (Land, 1989) that various features of the dorsal eye, notably the small inter-ommatidial angles and large facets, could be explained if the eye was used to detect small dark objects against the residual down-welling daylight. In ventral eyes, inter-ommatidial angles are typically many times larger, and the facets smaller, implying a different and less demanding function. The detection of self luminous objects is such a task. What we now need is a clear demonstration of function for the dorsal eye.

### THE BLUE LED AS A SOURCE OF BIOLUMINESCENCE?

Spectrally the blue LED is a very good substitute for natural bioluminescence (Figure 3a) and is easily visible to hyperiids. It is possible that, if seen by their eyes, they would also track a red (or other colour) LED equally as well. However most marine animals living below a few hundred meters in the sea have spectral sensitivities narrowed by the light available at such depths to a peak around 475 nm (Lythgoe, 1988). As a result, for whatever functional reason, blue LEDs are a good controllable stimulus for deep-sea organisms. For future work we are developing an *in situ* blue LED probe to be placed on mid-water platforms to examine such behaviour in more natural conditions.

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