

SHORT COMMUNICATION

THE SPECTRAL SENSITIVITY OF *NAUTILUS POMPILIUS*

By W. R. A. MUNTZ

Faculty of Science, Monash University, Clayton, Victoria, 3168, Australia

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Recent studies (Muntz & Raj, 1984; Muntz, 1986) have measured the visual acuity and sensitivity of *Nautilus pompilius*, using two behavioural responses (the optomotor response and the positive phototactic response) which are well developed in this species. In both cases, as might be expected for an animal that has a pin-hole camera eye, vision was poor compared to that of animals that have camera eyes with lenses. Thus for visual acuity it was found that the minimum separable angle lay between 1.25° and 5.5° , compared with values between $4.9'$ and $10.8'$ for various species of fish (Muntz, 1974), and a value of $17'$ or better for *Octopus vulgaris* (Sutherland, 1963), and the absolute sensitivity was estimated to be around 2 log units worse than for a typical deep-sea fish.

In the present study the spectral sensitivity of *Nautilus* was measured using the positive phototactic response. No behavioural studies on spectral sensitivity appear to have been published for any cephalopod, nor indeed for any deep-sea animal. The absorption spectra for the visual pigments of a variety of cephalopods are known (e.g. Messenger, 1981), and visual pigment extracts from *Nautilus* absorb maximally at around 467 nm, which is typical for a deep-sea animal (Muntz, 1986). However, the metabolism of cephalopod visual pigments differs markedly from that of both vertebrates and other invertebrates (e.g. Goldsmith, 1972; Hara & Hara, 1972) and spectral sensitivity, measured behaviourally, need bear no straightforward relationship to the absorption spectrum of an animal's visual pigments (Muntz, 1974). A knowledge of spectral sensitivity of *Nautilus* might also help to explain the role of positive phototaxis in the animal's natural life.

Animals with dorsoventral shell diameters between 11 and 14 cm were trapped off the main reef at Suva, Fiji, and kept as described previously (Muntz & Raj, 1984; Muntz, 1986). Spectral sensitivity was determined by means of their positive phototactic behaviour using the Y-maze shown in Fig. 1. On any trial the animal was placed in the starting chamber, S, and swam to one or other of the illuminated windows, W. One window was illuminated by a standard light of fixed intensity and spectral composition, while the other was illuminated at various intensities with a different wavelength for which the threshold relative to the standard light was being determined. Four thresholds were measured relative to a standard stimulus of 608 nm, and two relative to 650 nm. Stimulus wavelength was controlled by Balzars

Key words: *Nautilus pompilius*, spectral sensitivity, phototaxis.

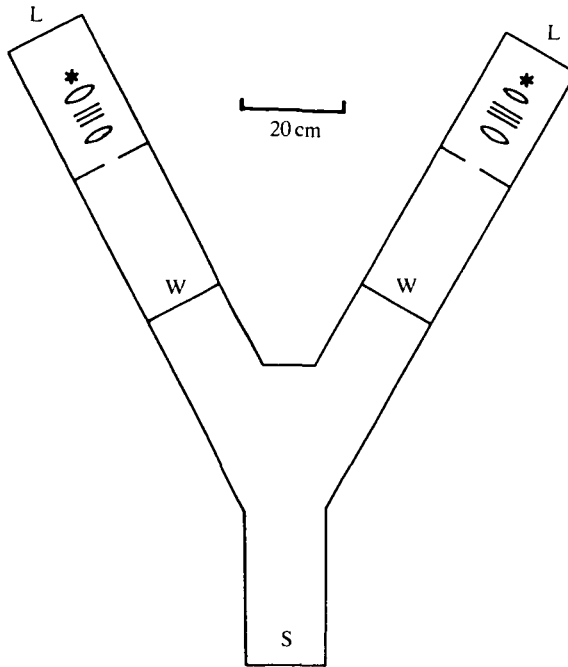


Fig. 1. Y-maze used in present experiments. L, light boxes containing 15 W, 24 V tungsten filament lamps run from a stabilized power supply, interference and neutral density filters, and collimating and projecting lenses; W, opal Perspex windows; S, starting chamber. The maze was painted matt black and filled with water to a depth of 13 cm between the starting chamber and the opal Perspex windows.

B-20 interference filters, and stimulus intensity by neutral density filters. The spectral transmissions of the different filters were measured individually, and in the various combinations that were used, by a Varian Superscan recording spectrophotometer. Relative energies were calculated from these data, assuming that the stimulus lamps had a colour temperature of 2500 K. While this method of calibration is indirect, an error of, for example, 400 K in the estimate of the colour temperature will cause a relative error of only about 0.1 log units in the estimates of energy at 450 nm and 650 nm, which is small in relation to changes in the animals' sensitivity with wavelength. Absolute energies were estimated from a knowledge of the absolute luminosities of different wavelengths (Weaver, 1949), after measuring the luminance of the stimulus when no filters were in the beam with a Macbeth illuminometer.

Sixteen animals were used, individually marked with a waterproof felt-tipped pen for identification. Four combinations of wavelength and intensity were used in the morning and four in the evening of each day. If, on any given combination, the first seven animals tested all chose the same stimulus no further animals were tested on that combination; similarly if, out of the first ten animals, nine chose the same stimulus. These criteria, which are significant at the 1% level on the sign test (Siegel, 1956), were used to reduce the amount of testing needed. If neither criterion was met, testing was continued for all 16 animals. A trial was discontinued if an animal failed to reach the end of either arm of the maze within 20 s.

For each wavelength tested against the 608 nm stimulus, linear regression lines were fitted to plots of the logarithm of the intensity of the variable stimulus against the percentage choice of this stimulus (the frequency of seeing curve). The intensity at which the variable and standard stimuli were chosen equally often (the relative threshold) was taken from these regressions. Fig. 2 shows all the frequency of seeing curves obtained during this part of the experiment, adjusted to a common relative threshold of one. While individual curves have few points, the overall agreement is good and shows that an intensity change of 2 log units is enough to reverse the animal's choice of stimulus completely. This was considerably less than the range of over 4 log units which was needed in the apparatus used in Muntz (1986), and presumably reflects the difference between the previous T-maze and the present Y-maze, with the latter requiring a much smaller change of direction when the animals make a choice. When the 650 nm standard stimulus was used the behaviour was less precise, the animals frequently failing to complete a trial within 20 s. This suggests that the 650 nm stimulus was close to the animals' absolute threshold. Only two relative thresholds were obtained under these conditions. Spectral sensitivity relative to both standard stimuli is shown in Fig. 3, which also shows Dartnall's (1953) nomogram for a visual pigment based on vitamin A₁ and absorbing maximally at 467 nm.

Although no behavioural spectral sensitivity curves have hitherto been reported for any cephalopod, electroretinogram determinations of spectral sensitivity have

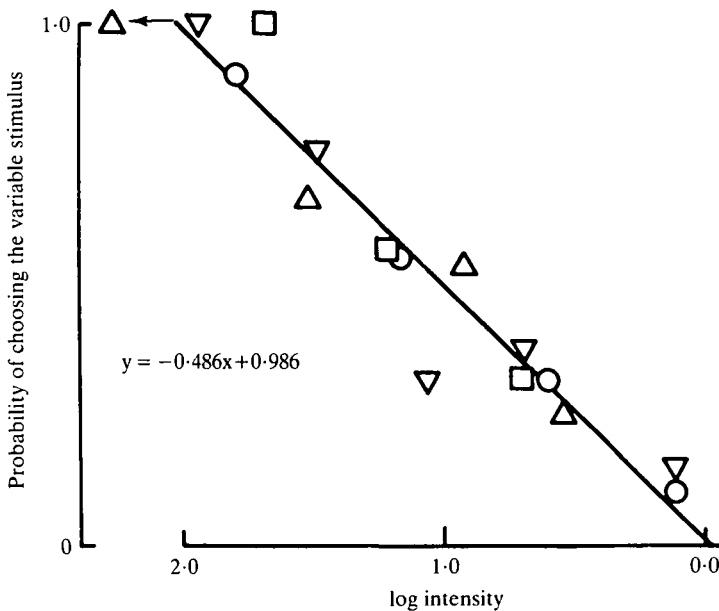


Fig. 2. Probability of choosing the variable stimulus against the logarithm of its intensity, with the thresholds relative to 608 nm in all cases made equal to unity. The wavelengths used were 391 nm (O), 452 nm (Δ), 513 nm (□) and 550 nm (▽). The data point for 452 nm marked with the arrow has a log intensity value of 3.7.

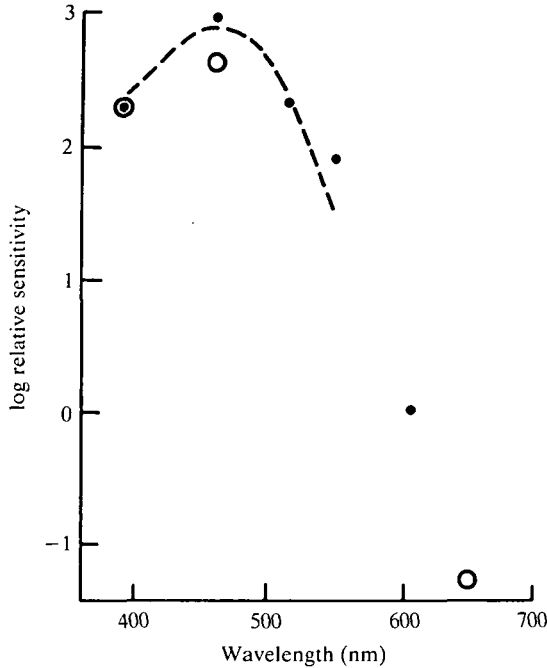


Fig. 3. Spectral sensitivity for *Nautilus pompilius*. The dots show the thresholds relative to a standard stimulus of 608 nm and energy approximately $3.24 \mu\text{W cm}^{-2}$. The open circles show results using a standard stimulus of 650 nm and $5.33 \mu\text{W cm}^{-2}$. The second set of results have been adjusted vertically so that the two sets of data coincide at 391 nm. The dashed line shows the absorption of a vitamin A₁-based visual pigment with its maximum at 467 nm (from Dartnall, 1953).

been undertaken on *Eledone moschata* (Hamdorf, Schwerner & Tauber, 1968), *Octopus vulgaris* (Hamasaki, 1968), *Todarodes pacificus* (Ito, Karita, Tsukahara & Tasaki, 1973) and *Loligo peali* (Daw & Pearlman, 1974). In all cases the sensitivity maximum agreed with the absorption maximum of the extractable visual pigment, and the results were interpreted as being due to a single pigment. The fact that cephalopods are probably colour blind (Messenger, Wilson & Hedge, 1973; Flores, Igarashi & Mikami, 1978) also suggests the presence of only a single visual pigment. The present behavioural results with *Nautilus* are also in agreement with expectations based on the absorption curve of its visual pigment (Muntz, 1986).

The role of positive phototaxis in the natural life of *Nautilus* is unclear. Possibilities that have been suggested (Muntz, 1986) are that it contributes to vertical migration, and that it takes the animals towards areas of bioluminescent activity, since the animals are commonly found in association with bioluminescent shrimps (Saunders, 1984). The animals' spectral sensitivity would be well adapted to either of these functions, since it matches well both the light that penetrates clear oceanic water and the bioluminescent output of most deep-sea organisms (e.g. Lythgoe, 1972).

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