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THE SPECTRAL SENSITIVITY AND ABSOLUTE THRESHOLD OF *ONCHIDORIS FUSCA* (MÜLLER)

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INTRODUCTION

In general three methods have been used to determine the spectral sensitivity of invertebrates. The first is to measure the behavioural response to light over a range of wavelengths and intensities. This can be achieved by using the movement of the whole animal as an index of responsiveness, as in *Dendrocoelum* (Marriott, 1958, 1960), *Littorina* (Charles, 1961), *Calliphora* maggots (Strange, 1961) and barnacle nauplii (Siddle, 1968). Alternatively, response can be gauged from studying movement of parts of the body, such as the closing of the valves of *Pecten* (Cronly-Dillon, 1966), and the withdrawal of the siphons of *Mya* (Hecht, 1920–21) and *Pholas* (Hecht, 1927).

A second method is to record the electrical response produced by the eye after stimulation with equal intensities of light at different wavelengths. Electrophysiological responses have been measured directly from the eye in *Hermissenda* (Dennis, 1967), and from the optic nerve in *Aplysia* (Waser, 1968) and *Otala* (Gilliary & Wolbarsht, 1967).

The third method is mainly confined to studies on animals with large eyes. Here, the photolabile pigment of the eye is extracted and its absorption spectrum measured in vitro. With a pure solution of the photopigment the absorption spectrum can be read directly, but with an impure solution the absorption spectrum must be measured before and after exposure to light. A 'difference spectrum' due to the bleached photopigment is thus calculated. The spectral sensitivity of the rhodopsins of squids (Brown & Brown, 1958; Hubbard & St George, 1958; Kropf, Brown & Hubbard, 1959), octopuses (Brown & Brown, 1958; Kropf *et al.* 1959) and *Eledone* (Hamdorf, Schweimer & Taüber, 1968) have been determined by various extraction techniques.

Comparison of the three methods may provide valuable information about the biology of the species studied. Whereas the chemical method can only show the sensitivity of the isolated pigment, and the electrophysiological technique that of the eye, the behavioural studies reveal the sensitivity of the entire animal as it is in the field. The present study is concerned with the spectral responses of the intact animal. The results are then compared with those found by different methods for related animals.

MATERIALS AND METHODS

Animals

Onchidoris fusca is a dorid nudibranch with paired eyes sunk beneath thick pigmented skin. It is commonly found on sublittoral barnacle-encrusted mussels in the

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Menai Straits. Numerous specimens were collected at regular intervals during August–December 1967–8 from freshly dredged mussels at the Severnside Oyster Company (Bangor) by kind permission of Mr R. Baird.

Apparatus

The covered experimental tank measured 61 cm. long by 11·5 cm. wide by 14·5 cm. deep and was made of black Perspex. It was fitted inside a larger clear Perspex tank which served as an insulator when filled with a mixture of ice and water (Fig. 1).

The inner experimental tank was filled with fresh, clean sea water to a depth of 5 cm. before each experiment; the horizontally directed beams of light entered through two apertures of 3·8 cm. in diameter (Ci and Cii, Fig. 1) which were just covered by the seawater.

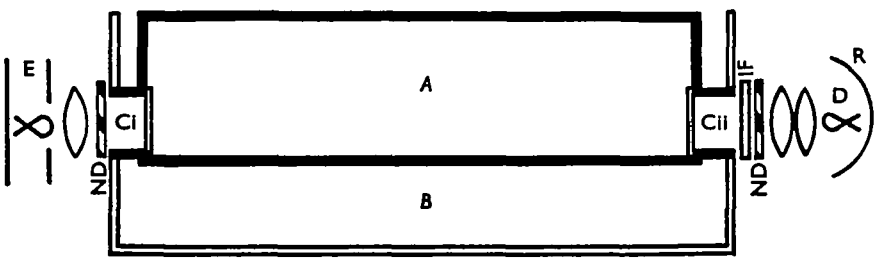

Fig. 1. A diagrammatic representation of the apparatus used for the behaviour experiments with *Onchidoris fusca*. *A*, Experimental tank; *B*, insulating tank; Ci, Cii, apertures for lights; D, projector lamp (spectral lamp); E, sodium lamp; IF, interference filter; ND, neutral density filter; R, polished metal reflector.

A 'standard' lamp (at Ci) was provided by an Osram sodium bulb (12 V., 100 W.) run through a Phywe universal choke from the mains supply. The sodium beam was concentrated with a collimating lens and dimmed when necessary with neutral density filters (Ilford, 5% instrument quality glass). At the opposite end of the tank (Cii) a second monochromatic light source was obtained with a fan-cooled Philips quartz-iodine projector lamp, used in conjunction with interference filters, two collimating lenses and neutral density filters. The interference filters covered the visible spectrum from 400 to 650 mμ at intervals of 10–20 mμ; filters of wavelength 409 (406), 419 (421), 442 (442) and 519 (519) mμ were obtained from Grubb Parsons; those of wavelength 461 (462), 480 (480), 491 (491), 500 (501), 540 (538), 559 (562), 579 (581), 598 (601) and 649 (649) mμ were made by Balzars. The figures in parentheses given above refer to the peak wavelengths of the interference filters measured by the spectrophotometer, and those outside parentheses are the maker's specifications. The characteristics of the interference filters and the neutral density filters were measured on a Unicam S.P. 800 automatic spectrophotometer, and the values thus obtained were used in the present calculations. The intensity of the lamps combined with the various filters was measured in μvolts in the experimental tank with a bolometer (Hilger–Schwarz thermopile No. F.T. 17·1/454) connected to an Airmec 'Galvamp' galvanometer. All measurements were taken in air, and allowance was made for the differential absorption of light by sea water (Defant, 1961). The calculated flux of the undiminished sodium bulb in the centre of the tank when filled with sea water was

29·41 μW./cm.^{2}; similarly the quartz–iodine lamp with the interference filter at 501 mμ was 85·37 μW./cm.^{2}.

No opal glass or frosted filter was used to scatter the image of the lamps (unlike Strange, 1961) because the eyes of *Onchidoris* are already covered with an opaque skin which prevents them from forming an image (Holmes, 1968).

Methods

Spectral sensitivity

Dark-adapted animals were placed in the centre of the tank and two horizontal lights of known wavelength and intensity were beamed upon them. Since *Onchidoris* has a positive response to light, the animals moved towards the end of the tank which was most brightly illuminated. In subsequent experiments the brighter lamp was dimmed in steps of 0·1–0·2 log units to a point where the majority of animals were attracted towards the opposite lamp. This procedure was repeated until the sodium lamp had been tested against all the different wavelengths provided by the interference filters, thus enabling a picture of the relative spectral sensitivity of the animal to be built up.

Between 20 and 50 animals were dark adapted for at least 1 hr., placed in the centre of the experimental tank and simultaneously illuminated by both standard and spectral lamps for 15 min. At the end of each experiment the animals which had moved more than 4 cm. away from the centre of the tank were regarded as being attracted to the lamps. The numbers of animals in each end of the tank were counted and expressed as a percentage to the total number in both ends, the ones in the centre being disregarded. The number of replicate experiments depended on the number of animals used in each, but at least 100 animals were tested at each intensity level.

For each filter the percentage response to the standard lamp was then plotted against the intensity of the spectral lamp (Fig. 2), and the intensity for each filter at which there was a 50% response to the standard lamp was used to plot a curve of relative spectral sensitivity on an equal energy basis (Fig. 3). For those wavelengths where the intensity of the standard lamp was reduced (402, 419, 442 and 649 mμ), calculations were made to bring the results to the same energy level as the other wavelengths. A graph of relative quantum sensitivity was plotted by dividing the 50% energy values (Fig. 2) for each filter (in ergs/sec./cm.^{2}) by the energy of one quantum at that wavelength. Since this calculation gave a curve of negative slope, the quantum values were then expressed as a percentage of the minimum value at 501 mμ (Figs. 4, 5) to give a curve of percentage quantum sensitivity with a positive slope. When plotted linearly the percentage quantum sensitivity curve can be considered as a first approximation to the absorption spectrum of the photopigment of the eye (Strange, 1961).

The thick dorsal skin of *Onchidoris* was measured on the S.P. 800 for its relative spectral absorption, and the figures produced were used to calculate the sensitivity curve for the naked eye.

Absolute threshold

To investigate the absolute threshold of *Onchidoris*, one lamp of wavelength 501 mμ was used to stimulate the animals, and the opposite aperture (Ci) was blocked. The intensity of the beam was successively reduced in steps of 0·1–0·5 log units. About 100 animals were tested in a series of 30-min. experiments at each light level. After the experiments at each light intensity had been completed, the number of animals which had reacted positively to the light was expressed as a percentage of the number of animals which moved during the experiments (Fig. 6). When the intensity of the beam fell below the sensitivity of the bolometer, the flux was calculated by extrapolation from a graph of percentage transmission of the neutral density

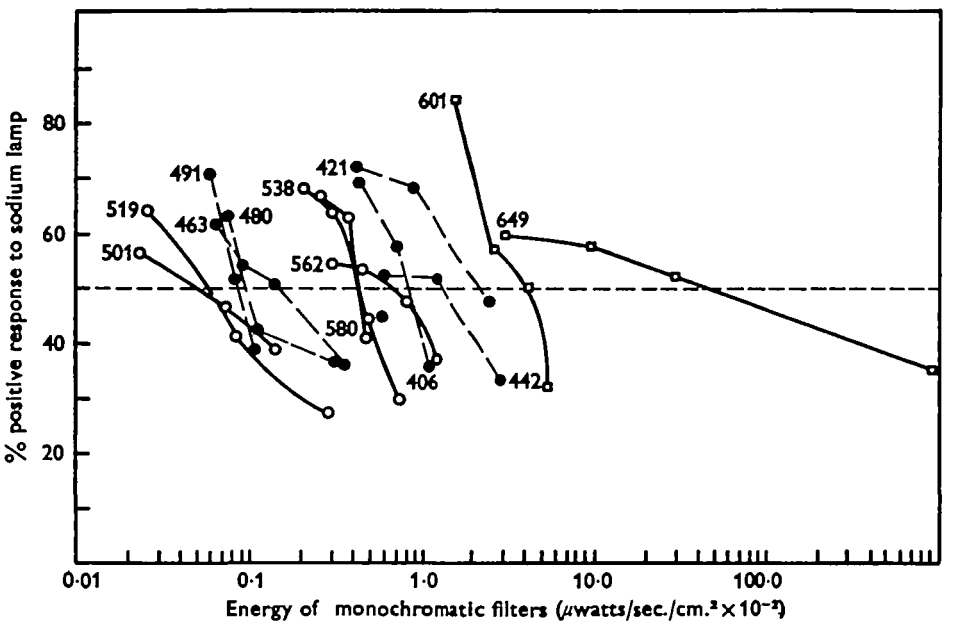

Fig. 2. The relationship between the percentage response to the standard lamp (intensity = 29·41 μW./cm.²) and the log energy of the spectral lamp with various interference filters.

filter against optical density. Quanta/sec./cm.^{2} at the threshold intensity were calculated from the threshold energy measured in ergs/sec/cm^2, divided by the energy of one quantum at 501 mμ (hc/λ, where h = Planck's constant; c = velocity of light; λ = wavelength in cm.). The effective threshold energy of the *Onchidoris* eye was then found by multiplying the threshold quantum value by the area of the aperture of the eye (diameter 100 μ). The absolute threshold of the 'naked' *Onchidoris* eye was then found after allowance had been made for the percentage transmission of the dorsal skin (9·23%; Holmes, 1968).

RESULTS AND DISCUSSION

Spectral sensitivity

For the interference filters used in this work the curves of percentage response to the standard lamp plotted against the intensity of the spectral lamp (Fig. 2) are generally sigmoid in shape, although the slopes vary. The wavelengths closest to 500 mμ require the smallest amounts of energy to complement the flux of the standard lamp. When the 50% response values are plotted against wavelength (Fig. 3) it becomes apparent that *Onchidoris* is particularly sensitive to blue-green light of 500–505 mμ, and that this sensitivity drops off quickly on either side of the peak, but

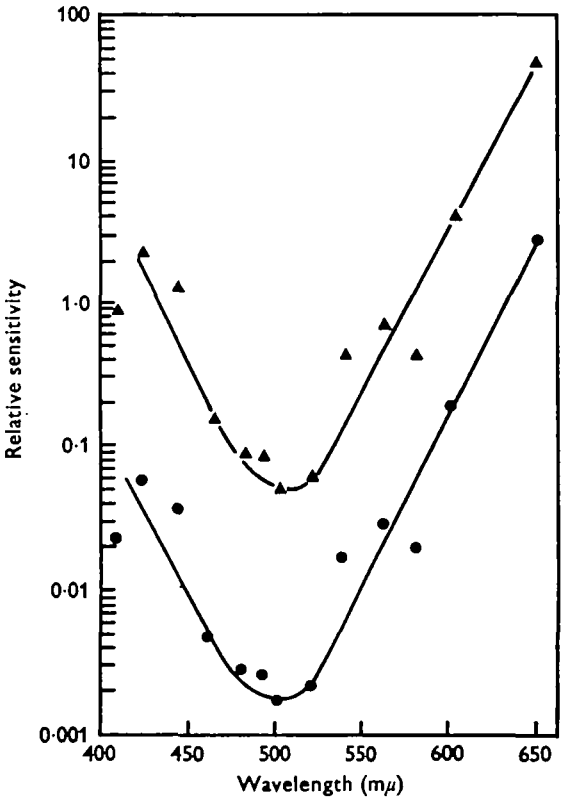

Fig. 3. The relative quantum sensitivity as a function of the wavelength. ▲ refers to the observed values for *Onchidoris*; and ● to the calculated values for the naked eye.

declines more steeply towards the red end of the spectrum than towards the ultraviolet. The lower curve in Fig. 3 corresponds to the calculated 50% response values of the naked eye of *Onchidoris*. The brown skin of *Onchidoris* transmits more red light than blue (Holmes, 1968), and consequently the observed and calculated curves diverge more towards the shorter wavelengths. However, when expressed as percentages of the peak wavelength (501 mμ) the shapes of the two curves differ very little.

The percentage sensitivity curve plotted on a linear scale (Fig. 4) gives a bell-shaped

curve, which according to Strange (1961), is typical of a photopigment of the rhodopsin group. If this curve is compared with that of a hypothetical 'normal' curve having a $\lambda_{max.}$ at 500 mμ (Dartnell, 1953) it appears too steep and narrow (Fig. 4). However, Dartnell's 'Nomogram' is the curve expected for a pure solution of extracted pigment and does not take pre-retinal absorption into account. It has been shown in man (Ludvigh & McCarthy, 1938), other vertebrates (Kennedy & Milkman, 1956) and

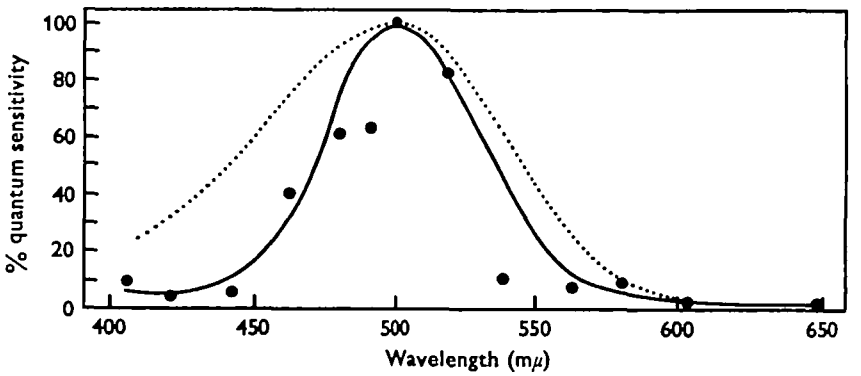

Fig. 4. The percentage quantum sensitivity of the naked eye of *Onchidoris* as a function of the wavelength (solid line). The dotted line refers to Dartnell's 'Nomogram' of $\lambda_{max.}$ 500 mμ.

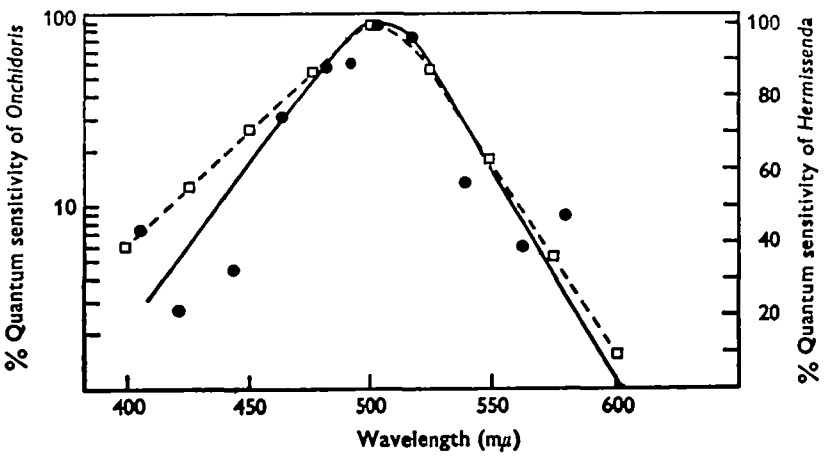

Fig. 5. The percentage quantum sensitivity as a function of wavelength. The curve for *Onchidoris* (●) is plotted logarithmically, and the curve for *Hermissenda* (modified from Dennis, 1967) is plotted arithmetically. (□). Since the electrical response of the eye has been shown to increase arithmetically for a logarithmic increase in light intensity (Hartline, 1938; Denton & Pirenne, 1954*a*; Waser, 1968) the comparison in this graph is considered to be valid.

cephalopods (Denton, 1960) that the cornea, lens and humour absorb a significant proportion of the light entering the eye, and that the lens in particular may differentially absorb light at the blue end of the spectrum. It is at the blue end of the spectrum that the *Onchidoris* action spectrum differs most widely from Dartnell's 'Nomogram' (Fig. 4). In addition to pre-retinal absorption within the eye, there is the possible differential absorption of light by the pigmented connective tissue which covers the

eyes and brain of many dorids (Holmes, 1968). This possibility has not been taken into account in these calculations. Such extra-optic absorption may account for the differences between the curves of *Onchidoris* and *Hermissenda* (Fig. 5); but the fact that the spectral sensitivity curves of the two species are essentially the same, and that they differ from the 'Nomogram' to a similar degree, suggests that it is something within nudibranch eyes which is masking the photopigment and causing this disparity (Figs. 4, 5). Hamdorf *et al.* (1968) measured the spectral sensitivity of *Eledone* by extraction techniques and by electrophysiology. The differences between the findings of the two methods were attributed to the masking of the deeper tubuli of the retina by rhodopsin and its intermediates situated on the more distal villi.

In contrast to these observations on the eyes of molluscs, the spectral sensitivity curve of *Calliphora* maggots (Strange, 1961), determined from behaviour experiments, agrees well with the 'Nomogram' of the same peak wavelength (Dartnell, 1953). *Calliphora* maggots have simple eyes with no lens and are covered by thin, opaque, white skin. It is probable that only such simple eyes will give close agreement between the experimental and the hypothetical spectral sensitivity curves.

It may be the case that in species such as *Calliphora* the retina does receive an uninterrupted spectrum of light. In other animals the situation is not as clear. The retinal characteristics of *Aplysia californica* (Waser, 1968), for example, appear to be different from those of other simple eyes. This difference may be due to the experimental method used with *Aplysia*. The parameter measured was the frequency of spikes in the optic nerve in response to different wavelengths of the same energy content. A plateau of peak sensitivity from 400 to 600 mμ was found by this method, but the curve does not fit any known or hypothetical pigment (Dartnell, 1953). The plateau of *Aplysia* would therefore seem to be masking the true peak, or peaks, of sensitivity.

The spectral sensitivity of two other gastropod eyes, *Hermissenda* (Dennis, 1967) and *Otala* (Gilliary & Wolbarsht, 1967), found electrophysiologically by measuring spike height rather than spike frequency, show broad peaks of sensitivity around 490 mμ, which is in general agreement with the peak at 500–505 mμ of *Onchidoris*. This suggests that gastropods may have a single photopigment with peak efficiency at 490–510 mμ, which may also be the pigment present in cephalopods. The variations in $\lambda_{max.}$ of 485–500 mμ found in cephalopods may be due to differences in the protein 'opsin' part of the rhodopsin molecule (Brown & Brown, 1958). A similar argument could also apply to gastropods. However, the broad peak in gastropods may be due to experimental error, in which case the true maximum could only be resolved by extraction of the photopigment.

Pelecypods, on the other hand, may prove to have two or more photopigments, since *Mya* (Hecht, 1920–1) and *Pecten* (Cronly-Dillon, 1966) show two unequal peaks of sensitivity. In comparison *Pholas* (Hecht, 1927) has only a single peak of spectral efficiency. A further step in the study of the spectral sensitivity of the pigments of molluscs (not including cephalopods) would be the devising of a practicable method of measuring the absorption spectrum of very small quantities of photopigment. With present methods it is estimated (H. J. A. Dartnell, personal communication) that at least 500–1000 animals with eyes of about 100 μ in diameter would have to be dissected in order to provide a sufficient quantity of pigment.

Absolute threshold

The movements of *Onchidoris* within the experimental tank remained significantly different from random at the 5% level after the addition of neutral density filters of value 6·9 log units, which is equivalent to an intensity of $5{\cdot}83 \times 10^{-5}$ ergs/sec./cm.^{2} (Fig. 6), but became random at an intensity of $4{\cdot}47 \times 10^{-5}$ ergs/sec./cm.^{2} (7·0 log units). After taking into account the transmission of the dorsal skin and the diameter of the aperture of the eye, the smallest number of quanta/sec. necessary to stimulate the eyes of *Onchidoris* was found to lie between 81 and 106. If 10% of the incident light at 501 mμ is absorbed by the lens and cornea, a conservative estimate in comparison with the eyes of other animals (Pirenne, 1956; Ludvigh & McCarthy, 1938), then only 72–90 quanta/sec. are available to the receptors at threshold intensities. Assuming that there are five receptor cells in each *Onchidoris* eye (Holmes, 1968; Hughes, 1970), then each cell could respond to as few as 12–18 quanta/sec.

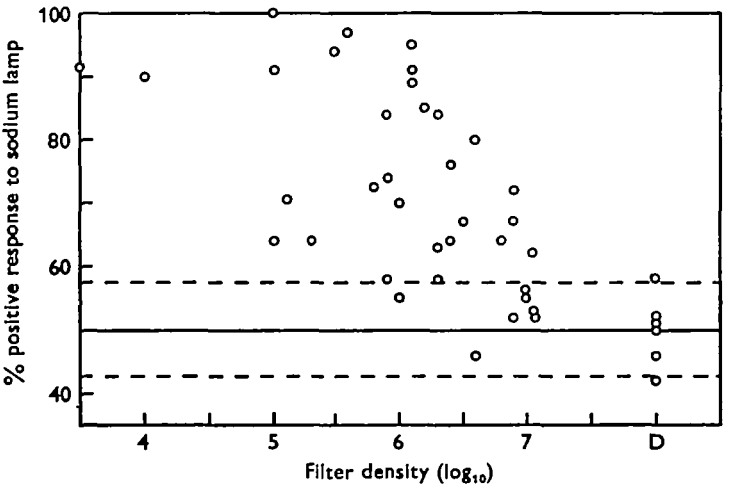

Fig. 6. Determination of the absolute threshold of *Onchidoris* at 501 mμ. The percentage response to the lamp is measured against its intensity (regulated by the neutral density filters). Each point (O) represents a single experiment. Level (D) indicates the control experiments which were carried out in darkness. Points between the dotted lines at 42% and 58% are not significantly different (at the 5% level) from a value of 50%.

The eye of *Onchidoris* has a similar order of sensitivity to the eye of *Xenopus* (Denton & Pirenne, 1954*b*), *Dendrocoelum* (Marriott, 1958, 1960) and barnacle nauplii (Siddle, 1968). These animals have eyes which are about 20 times less sensitive than the human eye (Denton & Pirenne, 1954*a*; Marriott, 1960) which can respond to 5–15 quanta/sec. on the retina (Hecht, Shlaer & Pirenne, 1942; Pirenne, 1956). Waser (1968) found that *Aplysia californica* gave a measurable electrical response down to an illumination of 0·01 μW./cm.^{2}. Calculations based on his data give a threshold value of approximately $7{\cdot}8 \times 10^6$ quanta/sec./eye. Jacklett (1969) estimates that there are approximately 7000 receptors in the eye of *Aplysia californica*, so that each cell could react to $11{\cdot}14 \times 10^2$ quanta/sec. Assuming the threshold energy to be applicable to the $\lambda_{max.}$ of the eye, then the absolute sensitivity of the eye of *Aplysia californica* would be 10^5 lower than the eye of *Onchidoris*, and that of the individual cell 100 times lower.

Two other nudibranchs tested in the present series of experiments were found to have much higher effective thresholds than *Onchidoris*. *Coryphella verrusosa*, a thin-skinned aeolid, became unresponsive at $4{\cdot}2$–$6{\cdot}1 \times 10^{-1}$ ergs/sec./cm.^{2}, and *Goniodoris nodosa*, a thin-skinned dorid, at $7{\cdot}3$–$12{\cdot}4 \times 10^{-1}$ ergs/sec./cm.^{2}. These values would bring them closer to the threshold energy of *Aplysia californica*. However, because of the much lower threshold of *Onchidoris* (a thick-skinned dorid), and of the common difficulty experienced when animals became unresponsive to light of any intensity while in breeding condition or at the end of their life cycle (Holmes, 1968), it is considered that the true threshold of *Coryphella* and *Goniodoris* was not discovered.

If the threshold sensitivity of *Onchidoris* is representative of the nudibranchs in general then the dense skin, the sunken position and the paucity of sensory cells in their eyes (Willem, 1892; Dennis, 1967; Eakin, Westfall & Dennis, 1967; Holmes, 1968; Hughes, 1970) does not necessarily indicate diminished sensitivity. However, an opaque skin does mean that the *effective* sensitivity of the eye is reduced. Thus the effective threshold of the *Onchidoris* eye at 501 mμ is 881–1148 quanta/sec./eye. The lowering of the effective sensitivity of the nudibranch eye by the covering of opaque skin would be of little importance to animals which live intertidally or in the upper regions of the sublittoral zone, where the purpose of photoreceptors would be to detect changes in light intensity well above the effective threshold. Positive phototaxis (Holmes, 1968) would ensure that the animals seldom find themselves in areas where the diurnal light intensity is below their effective threshold.

SUMMARY

1. The response of *Onchidoris fusca* to monochromatic light in the range 400–650 mμ was measured in behaviour experiments with two opposing lights.

2. The peak sensitivity was found to lie at 500–505 mμ. The thick, brown, dorsal skin of *Onchidoris* has the effect of reducing the sensitivity of the eye to ultraviolet and blue light.

3. After allowing for a 90% absorption of light by the dorsal skin, the absolute threshold of the naked eye of *Onchidoris* (at 501 mμ) was found to lie between 81 and 106 quanta/sec./eye.

4. If the lens and cornea absorb a further 10% of the available light, then each of five receptor cells in the eye of *Onchidoris* may be capable of responding to 12–18 quanta/sec. However, the effective threshold of the eye of *Onchidoris* is much higher, lying at 881–1148 quanta/sec.

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