RESPONSES OF *BRANCHIOMMA VESICU-LOSUM* (MONTAGU) TO PHOTIC STIMULATION

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(Text-figs. 1–6)

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INTRODUCTION

The light sensitivity of sabellid and serpulid polychaetes has been investigated on a number of occasions, but this subject is still poorly understood. Early workers commented on the extreme sensitivity of certain species to various stimuli, including changes in illumination. These animals are tubicolous, and normally they protrude their branchial crowns from the mouths of their tubes. When disturbed the animal usually jerks back into its tube. This quick withdrawal is the result of synergistic contraction of the longitudinal muscles, and it is intermediated through a giant axon system (review by Nicol, 1948 a).

Many, perhaps all, species of the Serpulimorpha retreat into their tubes on interruption of the light or during the passage of shadows. This response is reported for: *Sabella spallanzanii* (Viviani), *S. microphthalma* Verrill, *Bispira volutacornis* (Montagu), *Potamilla reniformis* (O. F. Müller), *Branchiomma vesiculosum* (Montagu), *B. vigilans* Claparède, *Dasychone bombyx* (Dalyell), *Myxicola infundibulum* (Montagu), *Eudistylia polymorpha* (Johnson), *Hydroides dianthus* (Verrill), *H. uncinata* (Philippi), *Serpula vermicularis* L., *Pomatoceros*

triqueter L., *Protula intestinum* (Lamarck) (Dalyell, 1858; Gosse, 1863, 1877; Claparède, 1868, 1870; Soulier, 1891; Andrews, 1891; Hesse, 1899; Hargitt, 1906, 1909 *a*, *b*, 1912; Buddenbrock, 1913, 1928; Hess, 1914; Loeb, 1918; Ricketts & Calvin, 1939; Nicol, 1948 *b*; *et al.*). Observers have noted that animals react to sudden decreases in light intensity, to moving shadows, and to slight movements of the observer within view of the animal. These are largely qualitative impressions. A response certainly occurs to a sudden decrease, but not to a sudden increase, in light intensity, for example in *Hydroides dianthus* (Hargitt, 1906) and *Serpula vermicularis* (Hess, 1914).

Evidence from ocular structure is ambiguous. *Branchiomma vesiculosum*, which possesses ocular spots near the tips of its branchial filaments, withdraws into its tube when the light dims; it still gives this response when the ocular spots are removed (Hesse, 1899). In *Hydroides dianthus*, which possesses no such special branchial receptors, the withdrawal reflex is equally well developed. Photo-sensitivity is greatest in the distal quarter of the filaments; total ablation of the filaments abolishes the reflex (Andrews, 1891; Hargitt, 1906). Consequently, it would appear that the specialized ocular organs on the branchial filaments are not necessary for this response (cf. Hesse, 1899).

Constant illumination also acts as a stimulus for other behavioural activities in some of these sedentary polychaetes. Loeb (1906, 1918) claimed that *Sabella spallanzanii* and *Hydroides uncinata* turn their branchial crowns and the anterior portion of their tubes towards the source of the light. This behaviour would constitute a kind of photo-tropism. Hargitt (1909 *a*, *b*, 1912), who repeated Loeb's experiments, found no evidence for orientation towards the light, but Fox (1938) considered that *Sabella spallanzanii* is positively photo-tropic. No conclusion seems possible without reinvestigating the subject.

Again, Fox (1938) found that *S. spallanzanii* is usually retracted within its tube during the day, and emerges at night; other observers also indicate that *S. pavonina* protrudes its crown mainly at night. This is a negative postural response to light intensity.

The following account presents the results of experiments carried out on photo-sensitivity in the sabellid worm, *Branchiomma vesiculosum*. This species was chosen because it is available in quantity, it is large, hardy in the laboratory, and because it displays a well-marked light reflex when compared with *Sabella* and *Myxicola*, the two other large species which are common locally. The photo-receptors and the physiological mechanisms involved will be described in a further paper.

METHODS

Animals were kept in dishes under circulation in the laboratory, and specimens were chosen at random for any particular experiment. The experiments were carried out in a cellar where the temperature remained fairly constant for long periods; the seasonal variation over 6 months was 6° C.

Intensity measurements were made with a selenium rectifier photocell ('Electrocell', German make) which was calibrated for absolute photo-sensitivity against a substandard lamp. The sensitivity of this cell ceased to be linear above 25μA., with a high resistance galvanometer, and a correction was applied to readings at higher intensities. Readings were made on a Gambrell Bros. Onwood patent galvanometer ($557\cdot3\Omega$ at $17\cdot75°$ C.) and on a Cambridge unipivot galvanometer (9.99Ω at $17\cdot75°$ C.). These were calibrated in terms of each other and against a potentiometer and accurate resistances. Their sensi-tivities, respectively, were $0\cdot27$ and $1\cdot92\,\mu$A. per scale division, and they were read to a $0\cdot2$ scale division. Reduction of intensity was achieved on occasion by the use of a Chance ON 31 neutral filter $3\cdot5$ mm. in thickness. This filter, according to the manufacturer, gives nearly uniform transmission from 4000 to 7000 A. Its overall transmission measured in the visible spectrum was $8\cdot2$ %.

For obtaining light from restricted spectral regions, a set of four Corning coloured filters was used. These same filters have been described and their characteristics presented by Atkins & Poole (1931). These were: C. dark blue (H. lantern blue) with 20 % transmission of visible light, 50 % cut-off at 4800 A., and very slight transmission in the red; C. sextant green, with a transmission of $2\cdot2$ % of visible light, and 50 % cut-offs at 5000 and 5700 A.; C.H.R. yellow, green shade, with 50 % cut-off at 5500 A., and 67 % trans-mission of visible light; C. selenium red G. 24, with 50 % cut-off at 6400 A., and 66 % transmission of visible light.

Unless otherwise specified, the following additional experimental conditions obtained. The light source was a 100 W., gas-filled tungsten 'daylight' lamp (Crompton), maintained at 200 V. by a variable transformer (Variac). The animals, in their tubes, were placed in an aquarium with a glass front. The transmission of this glass, measured with the selenium rectifier photocell and coloured filters specified above, was: $88\cdot7$ % in unfiltered ('white' light); $88\cdot3$ % in blue light; $89\cdot7$ % in green light; $88\cdot9$ % in orange light; 83 % in red light. These figures were used to correct the intensity measurements made in front of the aquarium glass. No allowance was made for absorption by sea water; the animals lay $1-5$ cm. behind the glass; usually some part of the crown was within 2 cm. of the glass. The inside of the tank was dark brown; a piece of matt-black paper covered the rear wall. At very low intensities, when it was difficult for the partially dark-adapted eye to distinguish the animals, a piece of white paper was placed at the back of the tank. Under these conditions, reflectance was not measurable with the photocell. The arena in front of the

tank contained a movable lamp housing; this area was enclosed and was painted matt-black.

Branchiomma is extremely sensitive to mechanical stimuli, and reacts promptly to vibrations of low intensity. The aquarium was mounted on a brick column topped with a slate slab, and the column rested on a concrete floor founded on solid rock. Even with this rigid arrangement, and with two inches of felt between the slate and the bottom of the aquarium, it was not possible to damp all vibrations to below the threshold of sensitivity of the animals.

OBSERVATIONS
Photic stimulation and the withdrawal reflex
Effect of sudden alteration in intensity

Specimens of *Branchiomma vesiculosum* frequently withdraw into their tubes when the light is suddenly extinguished. In several thousand trials no specimen ever withdrew in response to sudden increase in intensity of illumination. Response to intensity change, therefore, is to decrease, not increase, in intensity. This agrees with results obtained for *Hydroides dianthus* and *Serpula vermicularis* (Hargitt, 1906; Hess, 1914; cf. also Buddenbrock, 1928).

Adaptation to photo-stimulation

When the light is suddenly diminished, the animals respond to the first stimulation or first few photic stimuli by a withdrawal, but thereafter cease to react. In Fig. 1 are shown the results of subjecting the worms to repeated
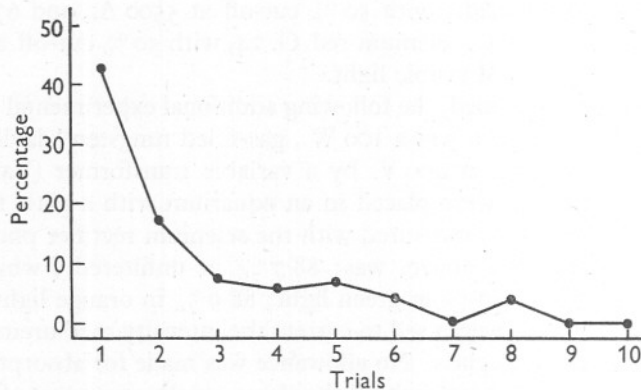

Fig. 1. Course of adaptation to photic stimulation (sudden decrease in intensity). Ordinates, proportion of animals responding; abscissae, successive trials.

stimulation. The animals were placed in white bowls underneath a white (pearl) tungsten lamp (100 W., 200–230 V. input). The measured intensity at the level of the containers was about 419 lux. Successive stimuli were delivered

usually at intervals of 1–10 min. It was not possible to standardize the interval because of great variability in times of emergence in different animals. About half the animals responded to the first stimulus; thereafter the number responding rapidly decreased to zero at the ninth trial. Adaptation or habituation to photic stimulation has been reported for other Serpulimorpha, namely, *Hydroides dianthus*, *Serpula vermicularis* and *Bispira volutacornis* (Bohn, 1902; Hargitt, 1906; Hess, 1914).

Minimal effective intensity change

The limen for decrease in light intensity at different initial intensities was determined as follows. Two daylight lamps were used at empirically dermined distances so as to give a certain initial intensity and a certain decrease in

TABLE I. LIMEN FOR DECREASE IN PHOTIC INTENSITY AT EIGHT DIFFERENT INITIAL INTENSITIES

Further explanation in text.

Initial intensity i (lux)	Lowest effective decrease in intensity tested δi_e (lux)	Highest ineffective decrease in intensity tested δi_i (lux)	$\delta i_e/i$	$\delta i_i/i$
407·2	17·2	12·9	0·0423	0·0317
308·1	12·9	8·6	0·0406	0·0279
185·3	12·9	8·6	0·0698	0·0465
64·6	4·3	2·2	0·0666	0·0334
34·7	2·9	2·2	0·0870	0·0620
17·9	2·9	2·5	0·1600	0·1400
5·3	1·2	1·1	0·2300	0·2030
2·3	0·5	0·4	0·2240	0·1550

intensity when one lamp was extinguished. At each initial intensity animals were tested to determine the minimal intensity change necessary to evoke a response, and the maximal intensity change that failed to evoke a response. All samples used in these tests were drawn from one laboratory group.

The results have been plotted in Fig. 2 as $\delta i/i$, where δi is the minimal intensity change that evoked a response. The vertical lines represent the interval between this effective value and the maximal non-effective intensity change that was determined. Absolute values are presented in Table I. The procedure was very slow and tedious, and to obtain these figures many more observations were required than those shown and utilized. The variability of this biological material will be discussed in a later section. Here it is noted that these results are not interpreted as representing the absolute photosensitivity limits of this species under manifold conditions. The stimulus-response method as here employed does give an indication of what these animals can do under these particular conditions but not necessarily of their ultimate discriminatory powers. These observations were all obtained on a given lot of worms in which all animals were kept under similar conditions,

and were tested in one period of time. It is therefore submitted that the observations are of value as relative and comparative data.

The curve in Fig. 2 shows that a relatively greater intensity change is required to effect a response at low intensities than at high intensities over the range explored (2·32–407·19 lux.).

These results obviously do not conform to the Fechner-Weber law for intensity discrimination. Comparable results are not available for other polychaete species. Hess (1914) sought the minimal decrease in intensity that would evoke a response in *Serpula vermicularis*. He found that moving a lamp from 60 to 61·5 cm. called forth retraction of the crown. The relevant
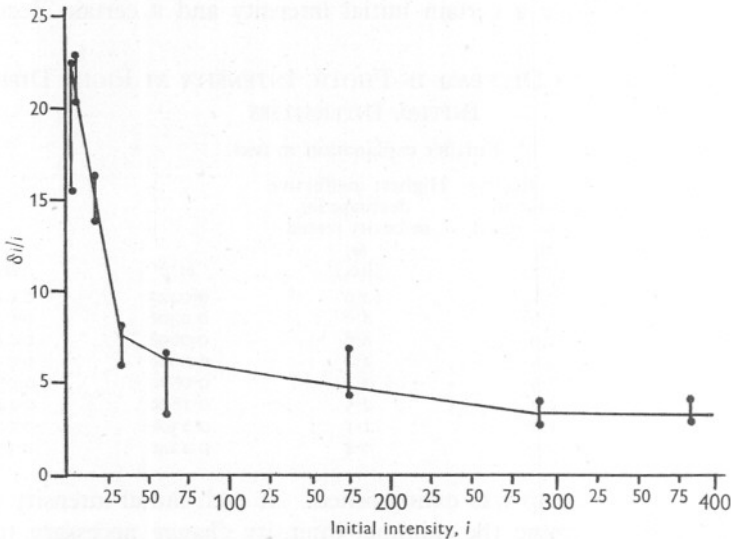

Fig. 2. Relation of minimal decrease in intensity necessary to evoke a response to initial intensity. Ordinates, $\delta i/i \times 100$; abscissae, intensity i, in lux. The data are grouped in pairs for a given value of i. The upper point of each pair represents the minimal value at which a response occurred; the lower point the maximal value at which no response occurred; vertical lines represent the unexplored range. Each point is based on trials of at least 10 specimens.

intensities were as 1:0·95; this gives a value for $\delta i/i$ of 0·05. This is within the range determined for *Branchiomma*. Hecht (1924) has studied an analogous situation in *Mya arenaria*. He utilized retraction of the siphons as an indicator of discrimination, and he tested for sensitivity to increases in light intensity. Hecht also found that the ratio $\delta i/i$ is not constant for this species at different initial intensities; the ratio decreases as intensity is increased up to a certain point, beyond which the ratio increases. However, the Fechner-Weber law for visual discrimination does not hold even in man, the subject for which it was erected. 'For visual intensity discrimination $\Delta I/I$ is approximately constant over the range from medium to very high light intensities, and below these

increases very markedly' (Rawdon-Smith, 1938, p. 18). Since *Mya* is responding to an increase in intensity, and *Branchiomma* to a decrease, it is suggested that the underlying photochemical reactions are similar, but that differences exist in the nature of the central correlatory mechanisms.

Sensitivity in lights of different spectral composition

The following experiments were designed to obtain information for sensitivity to lights of different spectral composition. The lowest initial intensities of light at which a response could be obtained by reduction of intensity were sought. Animals were tested in white and coloured lights of different initial intensities by cutting off the light (reduction to zero intensity). 'White' light from a daylight bulb, blue, green, orange and red lights were used (spectral composition described above under methods). Experiments were carried out on a single sample of worms kept under similar conditions.

White light. The minimal light intensity at which a response occurred to complete extinction of illumination was 2·5 lux. Only one animal in ten contracted at this intensity. At higher initial intensities a greater proportion of animals responded amounting to 80 % at 175 lux (Fig. 3).

Coloured lights. The minimal intensities at which a response could be elicited, and the maximal intensities at which no response occurred to diminution of intensity were determined for blue, green, yellow and red light. The coloured filters used have been described above under methods. The values obtained were weighted for the spectral composition of light from the source, and the spectral sensitivity of the photocell. The results are presented in relative units as the reciprocals of the intensities determined. This gives some indication of relative sensitivity to different spectral regions. The values obtained are green 6–18, blue 3–8, yellow 7–10, red 1·6–2·4 (units of relative sensitivity). The wide spread between the values in green and in blue light is due to the fact that the photoelectric cell has maximal sensitivity in green light (5700 A.) and sensitivity falls off much more rapidly in long than in short wavelengths (Lange, 1940). The difference between the two figures for green light actually represented only 0·1 μA. in photoelectric current.

The data show that *Branchiomma* is sensitive to the whole visual spectrum from 4000–7000 A. Owing to the spread of the data it is not possible to make a firm statement for relative sensitivities in different spectral regions. Sensitivity is least in the red, increases for shorter wave-lengths, and probably has a maximum between 5000–6000 A. These conclusions require confirmation.

Responses of specimens kept in light and darkness

The effect of retention in total darkness on the withdrawal response of *Branchiomma* was investigated as follows. Specimens were kept in an aerated container in the dark for 5 and 10 days. Sensitivity in weak illumination was thereafter determined by permitting the animals to expand at some given

intensity, and then turning off the light. As a control, an equal number of specimens was kept in constant illumination (257·5 lux) for 5 and 10 days.

Specimens retained in darkness:
(i) For 5 days. Tested at 1·97 lux. Proportion of animals responding: 60 %.
(ii) For 10 days. Tested at 0·36 lux. Proportion of animals responding: 70 %.

Specimens retained in constant illumination (257 lux):
(i) For 5–8 days. Tested at 0·72 lux. Proportion of animals responding: 30 %.
(ii) For 9–10 days. Tested at 0·36 lux. Proportion of animals responding: 27 %.

The data show that animals kept for periods up to 10 days in either constant light or darkness are sensitive to light of intensity at least as low as 0·36 lux. It is probable that the animals are sensitive to weaker intensities, but 0·36 lux was about the lowest intensity at which it was possible to observe the animals. There is slight evidence for greater responsiveness of animals maintained in darkness than in light, but not for greater sensitivity to weak light. Owing to voltage variation in the power mains the light occasionally flickered. Illumination of specimens kept in the light was therefore constant, but light intensity occasionally dropped momentarily. These sudden decreases in light intensity were sufficient to cause the animals to react. If these results are compared with the figure for minimal intensity of white light given on p. 309 it will be seen that the minimal intensity at which the animals responded is only one-seventh as great in the present experiments. Corresponding observations on other tubicolous polychaetes are conflicting. Hargitt (1905) found that in *Hydroides dianthus* specimens obtained from deep water (20 fathoms), or kept in a dimly lighted basement over winter, failed to respond to shadows. Bohn (1902), however, noted that in *Hermella ascolata* prolonged exposure to sunlight tended to weaken the sensitivity of the worm to reduction in photic intensity. He explained the reaction to shadows as a learnt response, based on mechanical factors as the unconditioned stimuli. Copeland (1930) has demonstrated the possibility of establishing a conditioned response in a specimen of *Neanthes virens* by associating feeding with light diminution and increase. Yerkes (1906) selected two specimens of *Hydroides dianthus* that failed to respond to shadows, and she repeatedly subjected them to reduction of photic intensity, followed by weak tactile stimuli. After a training period the animals became conditioned to react negatively to shadows.

Interspecific variation may explain some of the differences listed above. But apart from this factor it is clear that the previous history of the animal has considerable influence upon its responsiveness to decrease in light intensity, and upon the threshold of light intensity at which a response can be elicited. The operating factor in *Branchiomma* seems to be not the level of light intensity to which it was generally exposed, but the frequency or infrequency of stimulating decreases in intensity. When animals are kept for some time in either light or darkness and are undisturbed, more react to decrease in light

intensity, and at much lower initial intensities, than when kept under other laboratory conditions where they are frequently subject to variations in light intensity. Repetitive photo-stimulation leads to a lasting state of apparent habituation in which the energy change required to evoke a response is also raised.

Variability in response

It has already been intimated that different animals show considerable variability in their response to photic stimulation. For this reason, when determining critical values, a sample of at least ten specimens was tested (occasionally increased to eleven or twelve specimens). In Fig. 1, which illustrates the course of adaptation to repeated photic stimulation, two aspects of variability are depicted. This graph is based on examination of fifty-six specimens, of which only twenty-four (43 %) responded to the first photic stimulation (intensity 419·13 lux, p. 306). Considerable variation thus exists in the responsiveness of different animals within a population to intensity diminution as a stimulus-signal. The second aspect lies in different rates of adaptation in different animals, some ceasing to respond after the first stimulus, others continuing to respond for nine or more stimuli. Fig. 3 shows still another aspect of individual variation, namely, differences in the number of animals that respond to diminution of illumination at different intensities. In these experiments samples of ten animals were tested at different initial intensities by turning off the lamp. The observations form a fairly regular series from the lowest intensity tested, 2·51 lux, at which 10 % of the animals responded, to 174·6 lux, at which 80 % of the animals responded. In the previous section it has been noted that animals kept under conditions of minimal disturbance have greatly enhanced sensitivity at low intensities. Presumably the behaviour of these animals approaches that of animals living under natural conditions.

Individual differences in the responses of different worms to light have been noted by Andrews (1891) and Hargitt (1906) for *Potamilla* and *Hydroides*. In practice one would expect to find a normal variability in behaviour such as one encounters in investigating any species of animal. The data for *Branchiomma*, however, also suggest a process of adaptation akin to learning, which can modify the withdrawal reflex. Adaptation leads to cessation of the withdrawal response on repeated stimulation, and it raises the limen for photic stimulation.

Following withdrawal there is great variation in the time taken to re-emerge in different animals. The length of time during which the animals remained within their tubes following repetitive photic stimulation was recorded for 35 specimens. In the first three trials, the average periods of withdrawal were 3·9, 3·8, 3·9 min. The means of the differences between the periods of withdrawal in the first and second, and second and third trials, were 0·19 and −0·06 min. respectively. Thereafter, as the number of observations greatly

declined, the mean figures became very variable, without any apparent trend. The observations from the first three trials would indicate that, on the average, animals tend to remain the same length of time in their tubes before expanding their branchial crowns again.
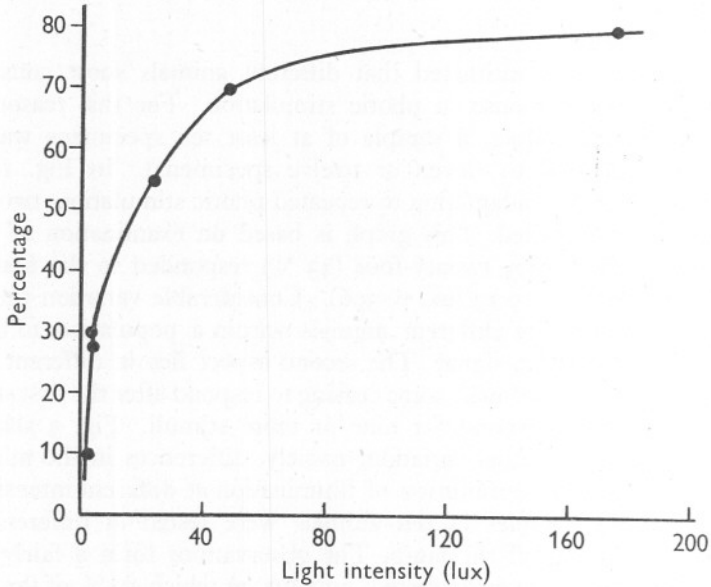

Fig. 3. Proportion of animals that respond to decrease in illumination at several initial light intensities. Ordinates, proportions of animals responding at selected initial intensities; abscissae, light intensities in lux.

Differential responsiveness to intensity change and movement

Two lots of animals were repeatedly stimulated by turning off the light for ten successive trials. Immediately following the last (tenth) trial with this stimulus, a black card was moved across the field between the lamp and the animal for another ten trials. The source of light was a white (pearl) 100 W. tungsten lamp. The intensity at the level of the animals was 419 lux. When the lamp was turned off, the intensity fell to zero. When the card was removed in front of the lamp the intensity fell to about 29 lux. The results are depicted graphically in Fig. 4.

The results show that after the animals have become adapted to a sudden decrease in intensity, they are still sensitive to a moving shadow or moving intensity change of nearly the same magnitude. Slightly less than half the animals responded to a sudden decrease in intensity and to a moving shadow (38·1 and 42·9 % respectively). There is a distinct difference, on the other hand, in the course of adaptation which takes place more slowly to a moving shadow, than to sudden decrease in light intensity. To both events the response

is the same, and the effective stimuli involve diminution in photic intensity, slightly less in movement of the card than in sudden extinction of the illumination. The different adaptation curves show that two distinct sensory processes are involved. This difference arises ultimately from the fact that the one stimulus (the moving shadow) includes a varying temporal and spatial component, as well as an intensity change. Further experiments to elucidate the processes and the photo-receptors involved will be described in a later paper.
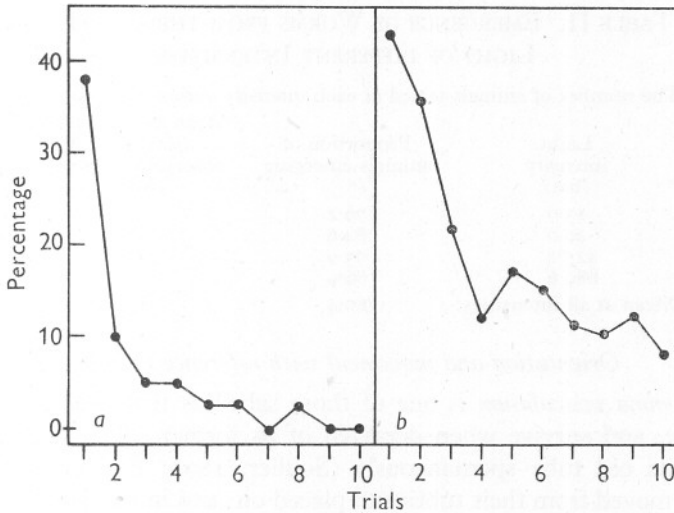

Fig. 4. Course of adaptation to photic stimulation: (*a*) sudden decrease in intensity; (*b*) moving shadow. Observations of 42 specimens. Initial intensity 419 lux. Ordinates, proportions of animals responding; abscissae, successive trials. Trial *b* 1 followed immediately after *a* 10.

Light intensity and emergence from the tube

The following experiments were designed to seek whether the intensity of illumination governs protrusion of the branchial crown from the mouth of the tube. It was not practicable to secure the necessary observations from animals in their natural habitat; consequently, laboratory study had to suffice. Animals were chosen that had recently been collected from their natural habitat, and they were tested within 48 hr. of reaching the laboratory. Twenty-three animals were used. These were placed in the aquarium, which was successively illuminated at four different intensities. Each lot of animals was kept under observation for 30 min.; time of emergence and number of animals that emerged were recorded for each group. The data obtained are presented in Table II. The intensities used were 13·93, 20·04, 125·22, and 689·56 lux. The mean proportion of animals that emerged at all intensities in 30 min. was 80·4 %, and the average time to emerge at all intensities was 10·05 min. There is no apparent trend in the numbers of animals that emerged at different

intensities. The mean times of emergence might be taken to indicate that the animals tend to protrude their branchial crowns sooner in strong than in weak light. However, the length of time which different animals spend in their tubes is very variable; on this basis a difference of 5·3 min. is not significant. In any event, there is no evidence, from these observations, that *B. vesiculosum* is principally a nocturnal form and that it tends to withdraw or remain in its tube when illuminated, as does *Sabella* (cf. Fox, 1938).

TABLE II. EMERGENCE OF WORMS FROM THEIR TUBES IN
LIGHT OF DIFFERENT INTENSITIES

The number of animals tested at each intensity varied from 19 to 23.

Light intensity (lux)	Proportion of animals emerging (%)	Mean time to emerge (total time of observation, 30 min.) (min.)
13·9	76·2	12·5
20·0	84·6	10·3
125·2	73·9	10·2
689·6	86·9	7·2
Mean at all intensities:	80·4	10·05

Orientation and movement with reference to light

Branchiomma vesiculosum is one of those sabellids that can burrow, build a new tube, and survive when deprived of its former tube. On occasion it abandons its old tube spontaneously (Soulier, 1891; Buddenbrock, 1913). Animals removed from their tubes and placed on sand immediately commence to burrow; they are positively geotropic (Buddenbrock, 1913). When placed on a hard surface, such as a glass dish in which burrowing is impossible, they

TABLE III. ORIENTED LOCOMOTION AWAY FROM THE LIGHT

Time (hr.)	No. of animals in		Proportion of animals in shade (%)
	Light	Shade	
1417 (start)	6	5	45·5
1517	3	8	72·7
1618	1·5	9·5	86·4
1715	0	11	100·0

usually glide along backwards by slow undulatory waves. Since the animals are capable of free locomotory movement, it is necessary to consider whether light acts as a token stimulus by which they can orientate themselves.

To test orientation to light, groups of 10–11 animals were placed in a white enamel pan, 24 × 33 cm., with overhead illumination. The light source was a white (pearl) tungsten lamp. One half of the dish was covered by a black card. The intensity in the illuminated half of the dish was about 145 lux. A protocol of an experiment is given in Table III, and the data are plotted in Fig. 5.

In these experiments all the animals moved into the shaded half of the container in 4 hr. Consequently, they display negative orientation to light. Orientation under these conditions could be to an intensity difference, or to direction of the light (lateral reflectance from the walls of the dish; cf. Ullyott, 1936). Further experiments are in progress to determine the mechanism of orientation in this species.
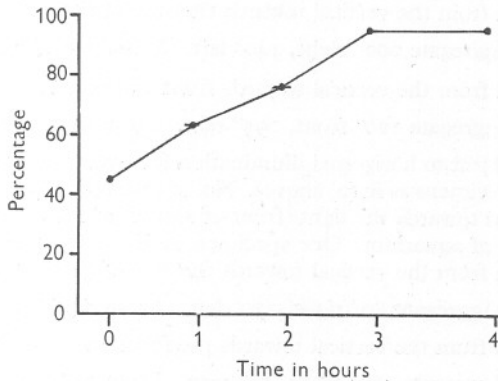

Fig. 5. Oriented movements away from light into shaded region. Ordinates, proportion of animals in shaded portion of container; abscissae, time in hours. Data obtained from two experiments and twenty-two animals. One animal apparently was injured; this would account for the leveling off of the curve slightly below 100 %. Further explanation in the text.

Orientation of tubes to direction of the light (*photo-tropism*)

The possible influence of the direction of incident illumination on the orientation of the animals' tubes was investigated as follows. Specimens were removed from their tubes, and placed on the surface of clean sand in the bottom of an aerated aquarium. Black matt paper was used to cut off unwanted illumination. Diffuse light was obtained from a 100 W. white (pearl) tungsten lamp. Animals were subjected to total darkness, and to lateral illumination.

About twenty specimens were placed in the aquarium for each test. Most of the animals immediately started to burrow downwards into the sand. A few animals failed to burrow and these were discarded after 2–3 days. The remaining animals were examined. The general direction in which the branchial crowns pointed was noted, and two measurements were made for the protruding section of each tube, namely, the angular deviation from the vertical towards either side of the aquarium, and towards the front or rear of the aquarium. The data obtained are shown below and in Fig. 6.

Specimens building new tubes and subject to horizontal illumination (from front of aquarium). Two days.

(1) No. of specimens—19 (two failed to burrow). Fourteen specimens directed their crowns towards the light. Four specimens directed their crown laterally and towards the light.

Angular deviation from the vertical towards the sides of the aquarium:

Aggregate 190° right, 190° left. Mean 0°

Angular deviation from the vertical towards the front and rear of the aquarium:

Aggregate 630° front, 0° rear. Mean 37° front

(2) Specimens building new tubes in total darkness. 3 days. No. of specimens—19 (1 failed to burrow). Branchial crowns pointed randomly in all directions.
Angular deviation from the vertical towards the side of the aquarium:

Aggregate 200° right, 140° left. Mean 3·3° right

Angular deviation from the vertical towards front and rear of the aquarium:

Aggregate 120° front, 295° rear. Mean 9·7° rear

(3) Specimens subject to horizontal illumination for five days after previous sojourn in darkness (same specimens as in (2) above). No. of specimens—17. Eleven specimens directed their crowns towards the light (front of aquarium). Four specimens directed their crowns to rear of aquarium. One specimen directed its crown to one side.
Angular deviation from the vertical towards the side of the aquarium:

Aggregate 80° right, 230° left. Mean 8·3° left

Angular deviation from the vertical towards the front and rear of the aquarium:

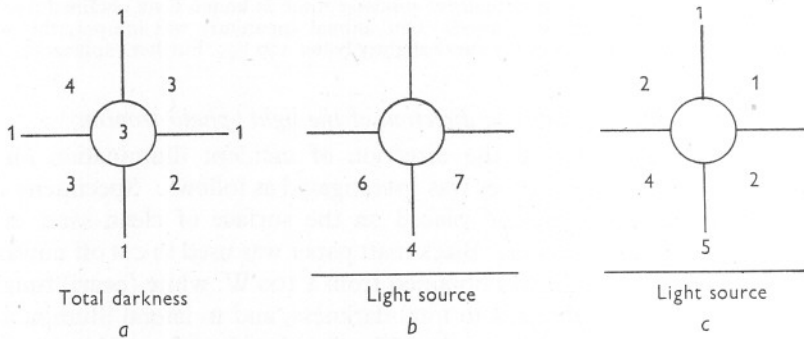Aggregate 460° front, 90° rear. Mean 22° front

Fig. 6. Diagrammatic representation of the effect of light on direction in which tubes point. The figure in the central circle represents the numbers of animals that directed their tubes and branchial crowns vertically upwards. The figures opposite each radius represent the numbers that directed their crowns and tubes towards the left, right, front or rear of the aquarium. The figures in each quadrant represent the numbers of animals that inclined their tubes and crowns in that direction. It is to be noted that rarely is a tube bent so that it is parallel to the ground; the mean angular deviation from the vertical is given above. A horizontal line beneath the diagram represents the relative position of the light source. (a) Total darkness for 3 days. (b) Horizontal unilateral illumination for 2 days. (c) Horizontal unilateral illumination for 5 days after previously being in the dark for 3 days.

There is definite evidence from these experiments that *Branchiomma* directs the distal portion of its tube and, in consequence, its branchial crown towards the light. Specimens kept for 3 days in total darkness built new tubes which inclined randomly in all directions, but predominantly upwards (Fig. 6a). Specimens kept for 2 days in an aquarium illuminated from one side built

new tubes, all of which inclined towards the light. The mean deviation from the vertical towards the light source ($90°$ to the vertical) was $37°$ (Fig. 6*b*). Finally, specimens which had been in the dark for 3 days, were subjected to unilateral illumination for 5 days. At the end of this period 69 % of the specimens were pointing towards the light, and the mean deviation from the vertical towards the light source was $22°$, an increase of 37 % and $31.7°$ for unilateral deviation over corresponding values for previous sojourn in darkness (Fig. 6*c*). It is concluded that *Branchiomma* tends to direct the exposed extremity of its tube towards the light when building a new tube, and can alter the direction in which the tube points, to conform to a change in the direction of incident illumination.

DISCUSSION

There is no lack of explanation for the value of the withdrawal reflex to tubicolous polychaetes. Jenkins (1940, p. 479) summarizes the prevalent concept when he says: 'It is a common observation that various species of flatworms, annelids and nematodes respond in characteristic fashion to sudden changes of intensity....For instance, the tubicolous annelids, such as *Hermella ascolata* [Sabellariidae] usually retract the tentacles into their tubes with the onset of shadows. This is probably a type of anticipatory response, as if to shadows cast by carnivorous swimming animals.' (cf. Buddenbrock, 1928, p. 12). Known enemies of tubicolous polychaetes are certain species of flatfish, notably the lemon dab (*Pleuronectes microcephalus*) and the sole (*Solea vulgaris*) (Steven, 1930; Wilson, 1935). The evidence is presumptive that they would feed upon *Branchiomma vesiculosum* when available. All stimuli to which *Branchiomma* responds by a withdrawal reflex, namely touch, mechanical vibrations, and decrease in photic intensity, could be token signals of the approach of a predator. In this regard the animal's sensitivity to a moving shadow or intensity change is of particular interest. To a sudden decrease in intensity the animal soon adapts itself, but adaptation to a moving shadow, in general, is considerably slower. Predation involves movement, and it is of advantage to the animal to maintain considerable sensitivity to a token stimulus of a predator's approach. On the other hand, tidal movements and currents in the lower littoral and sublittoral zone can create conditions in which there are regular and repetitive changes of light intensity and, accordingly, photic stimuli without biological significance to the animal. Presumably, adaptation represents a compromise between two conflicting needs of the organism, withdrawal to escape from enemies, and maintained expansion for feeding and respiration. Adaptation also occurs to certain qualities of mechanical stimuli, namely water currents and vibrations; the proportion of animals that respond is greater, and the course of adaptation is slower, than to photic stimulation. Adaptation, apparently, does not occur to tactile stimuli (above the levels of muscular and nervous fatigue). These mechanical

stimuli have greater biological significance and urgency to the animal, in terms of survival value.

For the animal, normally living in its tube, the steady or slowly varying intensity of illumination is apparently without significance in daily behaviour. *Branchiomma* expands its branchial crown in light or darkness in contrast to *Sabella* which is nocturnal (Fox, 1938). This may explain why the light reflex is more highly developed in *Branchiomma* than in *Sabella*, two closely related species living side by side in practically the same niche. The light reflex has greater biological value to *Branchiomma*, which feeds in the daytime, than to *Sabella*, which tends to stay withdrawn during the day. Moreover, the reflex is more efficacious in strong light: a greater proportion of animals respond and a smaller intensity change produces a response at greater light intensities (in these experiments, intensities above about 80 lux were most effective).

It is not certain to what depths in the sublittoral zone *Branchiomma* descends. Locally, in the Salcombe estuary (South Devon), it is found on the lower shore at low spring tide level, and slightly above. The tidal range in this estuary is 17·3 ft. (Evans, 1947). Absolute values for submarine light intensities are not available for the Salcombe estuary, but Atkins (1945) has summarized information for coastal and inshore waters near Plymouth. At a depth of 5 m., transmission of light would be reduced to about 10 % of subsurface illumination. This would permit bottom illuminations of about 5400 and 1800 lux at high-water springs on clear days in June and December respectively. Higher intensities would be encountered of course as the animals approached emergence during low water. In somewhat turbid water maximal transmission occurs in green light, and transmission decreases somewhat in the blue, and markedly in the red (Atkins, 1939, 1945; Atkins & Poole, 1940). In conjunction with this information we may observe that *Branchiomma* is sensitive to light in all parts of the visual spectrum (blue to red, 4000–7000 A.), but is more sensitive to light of short and medium wave-lengths, than to red light.

Most workers on the behaviour of tubicolous polychaetes have considered only the withdrawal or giant axon reflex. This reflex must have considerable survival value in terms of predation-pressure. Light can be one sensory modality eliciting this response, but for various sabellids and serpulids, light influences the character of other responses as well. Protrusion of the branchial crown in light and darkness has already been considered; the influence of light on this activity varies in two species of sabellids (*Branchiomma* and *Sabella*). The orientation of the branchial crown and anterior end of the tube towards the light would ensure that the feeding organs were directed towards the open, when the animals were in confined surroundings. This response is of particular interest since the effectors concerned in orientation of the tube appear to be glands in the body wall (Loeb, 1906; Fox, 1938). Finally, *Branchiomma*, divested of its tube, executes locomotory movements in which light has a directive value, and which lead it into darker regions.

SUMMARY

In *Branchiomma vesiculosum* decrease in light intensity causes the animal to contract and withdraw into its tube. A decrease, never an increase, in illumination is the effective stimulus. When repeatedly stimulated the animals quickly become adapted to intensity changes and no longer respond.

The minimal effective intensity change has been determined for a range of intensities. $\Delta I/I$ is found to increase in low light intensities, and to be fairly constant in intensities over 50 lux. The animals are least sensitive to red light; sensitivity increases in shorter wave-lengths.

Animals show considerable sensitivity in weak light. They respond to intensity changes in illumination at least as low as one-third of a lux. Animals kept under undisturbed conditions show enhanced sensitivity and responsiveness. Frequent stimulation raises the stimulation-threshold and establishes a lasting state of habituation.

Animals respond both to a sudden diminution of illumination and to a moving intensity change. Adaptation to the former does not necessarily abolish response to the latter, which shows an independent course of adaptation.

Branchiomma protrudes its branchial crown in light and darkness.

Tubes and branchial crowns are directed towards the light (positive phototropism).

Branchiomma, removed from its tube, shows negative orientation to light in its locomotory movements (retrograde creeping). Animals congregate in dark places.

The sensitivity and responses to light are discussed in terms of the life habits of the animal.

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