SOME REACTIONS OF THE AMMOCOETE

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(With One Text-figure)

I. INTRODUCTION

Quite recently Young (1935) published an account of the photoreceptors of lampreys in which he showed that a photoreceptive mechanism is present in the tail of Lamproeta planeri (Bloch) and L. fluviatilis (L.) in both larval and adult stages, which serves to initiate swimming movements resulting in the ultimate withdrawal of the animal from the illuminated area. These organs are much more sensitive in this respect than are those usually regarded as light receptors (e.g. pineal or paired eyes), and which seem largely to be associated with the pituitary in maintaining a control over the melanophores of the skin. Young also showed that these caudal receptors are associated with the lateral line and that the path of the stimulus from the receptors to the brain is most probably the lateral line nerve. He further demonstrated that they act only photokinetically and that while “the reaction...does not involve any true topotaxis, its effect is to prevent the animal remaining in an illuminated area”.

The present work was undertaken in order to investigate the general taxes of larval lampreys, in an attempt to discover what part these played in the reactions of the ammocoete to its normal environment. After it had been in progress for a short time it was learned by correspondence with Dr Young that he had investigated the photokinetiс responses of the ammocoete by methods somewhat different from those adopted here. These latter have, however, yielded several new facts which are considered worthy of record.

The material used consisted of ammocoetes taken from the river Wharfe at Tadcaster, near York, and varied somewhat in size from 40 to 100 mm., but the majority ranged about 60 mm. Their species was not determined, but as the common lamprey of the Wharfe in that neighbourhood is L. fluviatilis they probably were the larvae of that species.

II. PHOTOKINESIS

The animals used in this work were kept in flat glass dishes containing about an inch of river mud at the bottom covered by slowly running tap water. Before experiment the animals to be used were transferred to clean tap water and left in darkness for a considerable time to become quiescent, each individual animal being in a separate Petri dish so that it should not be stimulated by any movement on the part of its fellows. In all cases the whole bodies and the immediate surroundings
of the animals were illuminated by an electric bulb (of varying capacity) in an ordinary shaded bench lamp, the distance from the bulb to the animals being 1 ft. unless otherwise stated. The capacities of the bulbs in candle-power, given in parenthesis, have been estimated by photometry.

Sudden illumination provoked immediate swimming movements, the threshold intensity producing this response being that of a 15-watt lamp (12 c.p.) at a distance of 2 ft. The time taken for the animals to settle is longer with prolonged or continuous illumination than when only a flash stimulus is given, and increases directly with the intensity of the illumination. But if the animals are successively illuminated for gradually increasing periods of time (e.g. 1, 2, 3 sec,…), then there tends to be a gradual decrease in the length of time taken for the animals to settle after the light has been switched off. Also, under prolonged illumination, or frequently repeated intermittent stimuli, the animals soon become sluggish and take longer to react, thus suggesting a “saturation” of the photochemical mechanism (cf. also Young, pp. 231–2).

This was also shown by submitting the animals to continuous illumination of fairly high intensity—100 watts (148 c.p.)—for an hour and recording the periods over which they were alternately still and moving. Three ammocoetes were used, each in a separate Petri dish. The experiment was repeated several times and a typical result of such observations is given graphically in Fig. 1. It should be noted that the animals were not buried in mud in these experiments, and were therefore only receiving a unilateral contact stimulus, namely, on that side of the body lying on the bottom of the dish (see below).

The most effective response is therefore obtained by a stimulus of relatively high intensity and of short duration.

The animals respond not only to illumination after darkness but also to an increase in intensity, the minimum increment being about 15 watts (12 c.p.). When they have settled under continuous illumination no reaction occurs at any decrease in intensity.

By using standard, calibrated colour filters it was found that red light—i.e. all waves longer than 0.55μ—had no activating effect whatever on the ammocoetes, and that they were most sensitive to that part of the spectrum lying between 0.55μ-

1 Experiments using a focused light-point were also carried out, but the results obtained did not differ materially from those of Young and hence need not be considered here.

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Fig. 1. Graphical representation of the movements of three ammocoetes under continuous illumination for one hour. Movement is represented by undulating, and quietude by straight lines.
and $\lambda = 4 \mu$, i.e. from green to blue. For this series of experiments light sources of very high intensity were used, up to 500 watts, so as to ensure that the light energy remaining after filtration was above threshold value, this being actually confirmed by photometric experiments.

III. THIGMOTAXIS

The following series of experiments shows an interesting relation between photokinesis and thigmotaxis. Each experiment was repeated several times, the number of animals used varying between eight and twenty. The light source varied from 60 to 120 watts (62.5–125 c.p.), nevertheless the results were substantially the same in all cases.

(i) A large glass tank (26 in. long $\times$ 11$\frac{1}{4}$ in. wide $\times$ 7$\frac{1}{2}$ in. deep) was illuminated from above and the sides surrounded with black paper. A number of small glass test-tubes ($5 \times \frac{1}{4}$ in.) were placed at one end of the tank, so as to lie indiscernibly on the bottom. The tank was about half-filled with tap water. At the end of 8 min. all the animals, which had been swimming freely in the tank at the beginning of the experiment, had collected among and in the tubes and remained there.

(ii) One-half of the tank was covered with a sheet of cardboard and the glass tubes were removed. Within 5 min. all the larvae had collected in the darkened end of the tank.

(iii) One-half of the tank remained shaded as before, but the glass tubes were replaced at the illuminated end. The ammocoetes gradually collected in the light, in contact with the tubes. The result of one particular experiment, in which twenty animals were used and half the tank illuminated by two 60-watt bulbs (totaling 125 c.p.), is given in Table I. Occasional excursions into the dark were made by the animals which were among the tubes but they soon returned. It was noticed that movement ceased when the sides of the body were in contact with the tubes, the head and the tail being less important in this respect and frequently free from contact. There was no preference shown for the interior of the tubes, the animals choosing rather to lie between adjacent ones. Thus they were not mechanically

<table>
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<th>Time p.m.</th>
<th>No. of larvae in light in contact with tubes</th>
<th>No. of animals in dark</th>
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<td>17</td>
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hindered from making further swimming movements since the tubes were very light and easily moved.

It is thus shown that though ammocoetes normally collect in the dark rather than in an illuminated area, their strong positive thigmotaxis will overcome and mask their negative photokinesis when the alternatives presented are, darkness, or illumination together with the possibility of contact.

IV. RHEOTAXIS

In order to study the reactions of the ammocoete to water currents a wooden trough was employed which was modelled on that described by Beauchamp (1933), and used by him in his experiments on the rheotaxes of *Planaria alpina*. The principle of this device is that the water shall flow from a reservoir into the trough over a sill and leave in a similar manner. In this way it was possible to arrange a steady stream of water 6 ft. 6 in. long, 4½ in. wide and 1 in. deep, without eddies. About four ammocoetes at a time were introduced into the stream and their movements watched both in ordinary daylight and in a dark room with a red light, thus, in the latter case, obviating any possible disturbance due to their photokinesis. No definite orientation to the stream could be detected, the animals swimming vigorously in all directions, or lying passively on the bottom of the trough, allowing themselves to be rolled over and moved about by the flowing water.

V. DISCUSSION

It has been shown above that light stimulus below a certain fairly well-defined threshold of intensity will not cause movement on the part of the ammocoete. It would be interesting to know how this threshold value compares with the light intensity at the bottom of a river, i.e. with the stimulus to which the animal would be exposed when the mud was disturbed. No measurement of this has been attempted.

The relation between photokinesis and thigmotaxis is perhaps the most interesting result of the present series. When an ammocoete buries itself in the mud, it does so with great rapidity until its head and the major portion of its body are covered. The tail, with its light-sensitive organs, is finally withdrawn much more slowly, or may even be left exposed for a time. In fact, it usually is left exposed if the animal is burying itself in the dark or in a very subdued light. This paradoxical state of affairs is easily understood if thigmotaxis is more important than the absence of light. The desire for contact having been satisfied by the submergence of the body, the photokinetic impulse acts more slowly in causing the tail also to be withdrawn. The photokinetic response thus produces two effects of importance to the burrowing animal: (i) it initiates swimming movements—and burrowing reactions, in the initial stages, are largely modified swimming movements; (ii) it causes the ultimate withdrawal of the tail into the burrow. It is tentatively suggested that the photoreceptors of the tail may further serve in nature to make the animal aware of the diurnal rhythm. It was found that the ammocoetes which were being kept in the laboratory for these experiments were very persistent in utilising
the hours of darkness to escape from the glass dishes in which they were con-

fined. It by no means follows that nocturnal movement is normal on the part of the

ammocoete living under natural conditions, nevertheless it is quite possible that the
diurnal rhythm is of some importance to it.

We have not found it practicable to devise an experiment which will separate

satisfactorily geotaxis from thigmotaxis, but it was noticed that while the larvae
were lying among the glass tubes in the thigmotaxis experiments they frequently
made "shovelling" movements with their oral hoods similar to those employed in
burrowing. Now these movements were directed equally against the floor of the
tank, the sides of the tubes, or even upwards against the overlying tubes; in other
words their action was suggestive of "tunnelling" rather than "burrowing". Their
action in their native mud is also to make an almost horizontal tunnel rather than a
deep burrow. They normally commence operations with their bodies at a very
acute angle to the surface of the mud, while their wriggles may be followed for some
distance, even after they have become submerged. The water from the glass dishes
containing the stock of ammocoetes which were being used for these experiments,
was allowed to run into a larger tank, which thus acted as a trap to prevent the
escape of the larvae. The water from this larger tank was led away periodically by
U-shaped glass siphon tubes, which reached right to the bottom of the tank. On
several occasions animals which had escaped into the larger tank were found in
these tubes perfectly content to remain vertically upright on the tips of their tails,
while on one occasion an individual was found in a similar posture wedged in
between two siphon tubes and the side of the tank—a position which gave it the
maximum area of contact. These facts taken together would seem to suggest that
geotaxis—although it may be present—can play only a minor part in their burrowing
reactions, which are very probably controlled to a large extent by their sensitivity
to touch and to the relative firmness of the material composing the walls of the
tunnel.

The absence of rheotaxis is rather surprising. In the metamorphosed Lampera
fluviatilis there is a downstream migration to the sea and a corresponding upstream
migration of the adult for spawning, which presumably are controlled by rheotaxis.
It would be interesting to know when this response first appears and whether its
direction is affected by the development of the gonad, as in Planaria alpina (Beau-
champ), but experiments to elucidate these matters would need to be conducted
on a much larger scale and with a greater volume of water than is possible in the
laboratory.

VI. SUMMARY

1. Experiments are described which show that the threshold value for the
light energy, which will initiate swimming movements in the ammocoete, is in the
region of 3 foot-candles.

2. The part of the spectrum which is most active is in the green-blue region
(0.55μ-0.4μ).
3. Ammocoetes are very strongly thigmotactic, the most sensitive region being the sides of the trunk.
4. Ammocoetes between 40 and 70 mm. long are not rheotactic.
5. The relation of these responses to one another and their relative importance to the ammocoete in its natural environment are discussed.

REFERENCES