J. Exp. Biol. (1967), 46, 491–497
With 1 plate and 3 text-figures
Printed in Great Britain

SOME RESPONSES TO LIGHT IN A SPECIMEN OF *PELAGOHYDRA MIRABILIS* DENDY, 1902 (COELENTERATA: HYDROZOA)

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(*Received* 30 *November* 1966)

INTRODUCTION

The writer recently had the opportunity to carry out some experiments on a single, living, undamaged specimen of the exceptionally rare pelagic hydroid, *Pelagohydra mirabilis*. Capture of the specimen is reported elsewhere (Pilgrim, 1967), together with some remarks on the morphology of both the hydroid and the medusa phases and on its behaviour in the laboratory. This remarkable organism, known even now from only three specimens, is a pelagic hydroid *ca.* 35 mm. in extreme length including tentacles. It comprises an ovoid 'float' (terminology of Dendy, 1902) and a flexible 'proboscis', both of which carry numerous tentacles (Pl. 1 *a*, *b*). The float also bears a large number of short blastostyles from which medusae are budded. *Pelagohydra* is usually considered to form a subfamily, Pelagohydrinae, of the Margelopsidae (e.g. Rees, 1957).

In the present paper the animal is shown to exhibit a remarkable response to *reduction* in light intensity. The response constituted a sequence of reactions, each reaction comprising quite violent, concerted flexions of the tentacles. Increase in light intensity evoked no visible responses but, in appropriate circumstances, prevented the series of flexions from continuing. The experiments reported here are consequent on preliminary observations that weak, concerted movements of the tentacles, although very infrequent, occurred apparently spontaneously in bright light of constant intensity, and that the movements became vigorous and were repeated in a sequence at decreasing frequency when the light was switched off. The initial observations were made when the specimen was being examined under a stereoscopic microscope for morphological details, the microscope lamp being switched off at intervals to avoid possible overheating. Subsequent tests showed that full illumination of the experimental container, under the same conditions as those in which the animal was being examined, did not in fact raise the temperature of the contained water by more than 0·5° C. in 5 min.

METHODS

The animal was placed in a small glass vessel and subjected to overhead illumination from a 6 V, 18 W tungsten lamp. It was confined in the light path for measured periods; the light was then reduced, partly or fully, and the reactions comprising the responses were timed with a stop-clock (to half-second accuracy). Light intensity was measured with a 'Sekonic' Model L photometer substituted in position for the experimental vessel; the measurements were made in foot-candles and converted to lux.

While not regarded as of extreme accuracy the measurements may be taken as meaningful in respect of the *ratio* of intensities before and after a change in intensity. The light given by the lamp with its rheostat at maximum position is described as full illumination (= 100%); at lower values of the rheostat, the illumination quoted is calculated from the photometer measurements as percentages of the full value. Between the three groups of experiments full illumination varied slightly, and the value in lux is given below the appropriate graph. When the lamp was switched off completely there remained only a very low level (< 1%) of ambient (daylight) illumination; it is included in the photometer measurements. For convenience, this will be referred to as light 'off'.

RESULTS

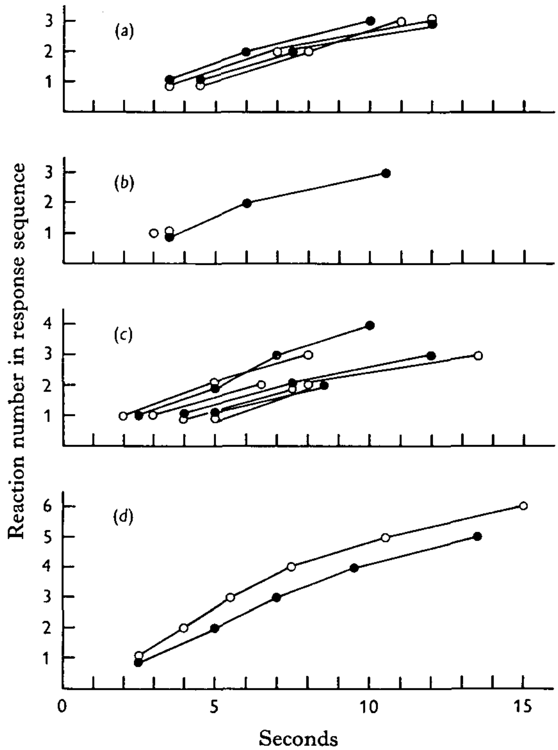
In view of the fact that this specimen is only the third captured in 65 years (Pilgrim, 1967) and the only one to survive for any length of time in the laboratory, *all* the quantitative experimental data obtained will be presented.

The experimentally unstimulated animal, whether floating at or beneath the surface or resting on the floor of the vessel, usually maintained its tentacles at approximately right angles to the body surface (Pl. 1*a*). The tentacles were capable of independent bending and writhing movements which were slow and apparently spontaneous. No significant translatory motion was produced by these movements, or by the more vigorous, concerted activities described below.

Even after the first few (unintentional) stimuli, a pattern of behavioural responses was very soon detected, and this was not deviated from qualitatively in the remaining experiments: a few seconds after the illumination was reduced the tentacles as a whole, on both float and proboscis, bent markedly and rapidly to make a small angle with their respective body surfaces (Pl. 1*b*). Since this bending was always directed towards the mouth, it will be referred to as 'oro-flexion'. After the reaction the tentacles reverted to their normal orientation, the recovery movement being very much slower. A few seconds later, a second oro-flexion occurred, to be followed by slow recovery. The reaction was repeated at increasing intervals throughout each experimental 'run' of about 1 min. The second and subsequent reactions, however, were much more violent than the first and the tentacles came to be closely applied to the body surface. Recovery movements also became slower so that in some instances recovery had not been completed before the next oro-flexion occurred and the latter became superimposed on the still partly flexed condition of the tentacles.

In the first group of experiments (Text-fig. 1) the animal was subjected to illumination for short periods (10–15 sec.) between 1 min. runs. Illumination was initially full (100% = 20,600 lux) in those of Text-fig. 1*a* and reduced to 'off' (0·8%) at zero time; four reaction sequences were recorded, each sequence consisting of three reactions during the time allowed for the experimental run.

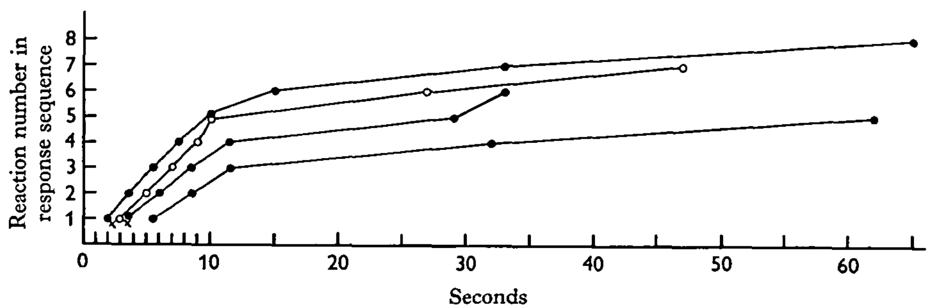
In the experiments (Text-fig. 1*b*) which followed shortly after those of Text-fig. 1*a*, the animal was subjected to light at intermediate intensities of 28% or of 8% before switching off. After 28% illumination there were again three reactions forming a sequence with approximately the same intervals as before. After illumination at 8% intensity, however, only a single reaction occurred within each 1 min. run (open circles). To ascertain whether the animal was becoming unresponsive, further experiments immediately followed (Text-fig. 1*c*) in which the animal was again first subjected to 100% illumination. Clearly the animal was still as responsive as before, in that definite sequences of reactions were given in the minute following 'light off'. In two instances (Text-fig. 1*d*) the animal gave more than three reactions within the observation period—in these cases the animal had been left for approximately 5 min. before switching the light off, instead of the usual 10–15 sec.



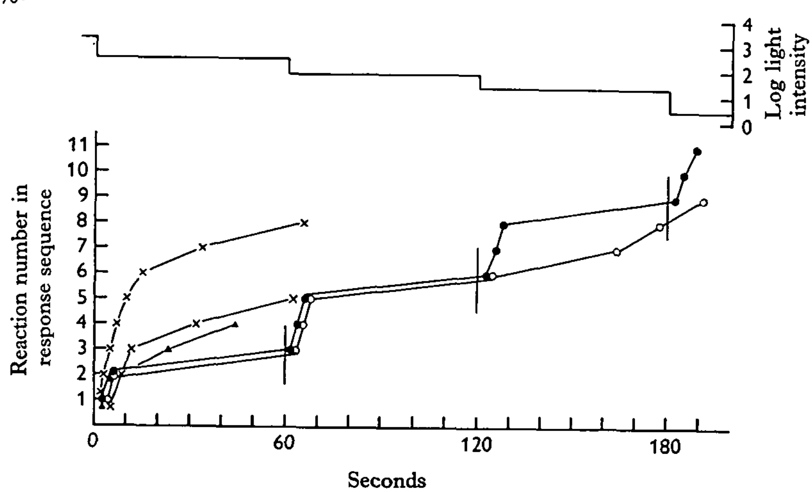
Text-fig. 1. Responses of *Pelagohydra mirabilis* to 'light off' stimulus (at zero time). First, second, etc., reactions in the response sequence are plotted on the ordinate. Points joined by a line represent a separate experimental run. In (*a*), (*c*) and (*d*) the stimulus is reduction of light from 100% (20,600 lux) to 0·8%; in (*b*) the stimulus is reduction of light from 28% to 0·8% (solid circles), or from 8% to 0·8% (open circles).

Evidently the duration of exposure to light affects the number of reactions in the sequence. A second group of experiments was therefore carried out. In these, the initial illumination of 100% was maintained for precisely 1 min. in each instance. The first three runs (Text-fig. 2, solid circles) showed a very marked and consistent phenomenon: although the early reactions followed a time course similar to that illustrated in the short runs in Text-fig. 1, after about a quarter of a minute the interval between successive reactions became very much prolonged. Immediately after carrying out these three runs the experiments were repeated but, as soon as the first reaction was recorded (crosses), the light was switched on to full once more; no further reaction was observed during the remainder of the minute, the normal sequence of reactions being inhibited by the return to 100% light. Finally, the experiment was repeated in its original form and a sequence of reactions was once more obtained (open circles). Clearly the animal had not suffered from the rapid return to light in the two preceding runs.

In all cases in which a sequence of reactions was obtained the first reaction was weak, the succeeding ones strong. In addition to these two observations the fact must be mentioned that after each experiment the animal was, of course, re-subjected to full illumination preparatory to the next run; in no case was any oro-flexion or other activity observed following this increase in light intensity.



Text-fig. 2. As for Text-fig. 1, but experimental runs longer. Stimulus is reduction of light from 100% (22,600 lux) to 0·14%. At ×, single reactions from two separate runs in which remainder of sequence of reactions was inhibited by immediate increase of illumination to 100%.



Text-fig. 3. As for Text-fig. 1, but illumination reduced stepwise (circles, open and solid). Light intensity, in lux, is plotted logarithmically above the curves. Final run in which stimulus was 'light off' (100% to 0·15%) shown with triangles. For comparison with previous experiments, the two extreme curves from Text-fig. 2 are superimposed (crosses).

In the final group of experiments an attempt was made to determine whether smaller reductions in light intensity would have the same (or any) effect on the responses of the animal. In these experiments the animal was exposed to full illumination for 1 min., then the light intensity was reduced in four steps at 1 min. intervals. The results (Text-fig. 3) show that the animal responds with a sequence of reactions following *each* reduction in light. During each minute of constant but reduced light intensity, the pattern of response resembled that obtained in the experiments of Text-fig. 2, but the smaller the reduction of light intensity the fewer reactions were evoked. The next stepwise reduction appears to bring about a fresh sequence of reactions in similarly rapid succession. The curves of the two experiments (circles, open and solid) are, nevertheless, clearly lower on the graph than are the curves of the experiments in Text-fig. 2 (for convenience in comparison on the different time scale the two extreme curves from Text-fig. 2 are reproduced in Text-fig. 3 (crosses)). Clearly, the extent by which the light is reduced affects the rate at which successive reactions occur. Finally, in this group of experiments the animal was subjected to one run under conditions similar to those obtaining in the experiments shown in Text-fig. 2. The results are shown in Text-fig. 3 (triangles). The animal clearly exhibited a sequence of reactions comparable with those in Text-fig. 2, i.e. the full reduction in light intensity is accompanied by a more rapid sequence of reactions. As in the previous groups of experiments the first reaction was comparatively weak, the succeeding reactions very strong and the recovery movements correspondingly greatly extended.

DISCUSSION

The animal survived in the laboratory for 7 days before shedding almost all of its medusae and becoming moribund, at which time it was preserved. The experiments described here were carried out on the third day after capture when the animal appeared to be healthy and active. There is no reason, therefore, to doubt that the reactions are those of a normal animal. The reactions comprising the oro-flexion response are strong, in that if the signal arrives at the effectors (tentacle muscles) while the tentacles are still only partly relaxed, oro-flexion will still occur, overriding the recovery phase of the previous reaction. Since the reactions involve all the tentacles of the float and proboscis and, within these two categories, involves them apparently equally, it is probable that a fast, through-conducting system is involved. Local responses, which diminish in effect from a stimulated point, are not evident here, but are presumably responsible for the responses to localized mechanical stimuli in this animal (Pilgrim, 1967).

The reactions are not due to a change in the temperature of the water (see p. 491). Since the reactions of the animal following switching the light off (initial observations) were entirely unexpected and so spectacular, it was thought that they might be due to vibration accompanying the operation of the tumbler switch on the lamp transformer. However, no reactions resulted from similar vibrations occurring when the lamp was switched on; furthermore, hand-holding of the transformer while switching did not affect the responses in any way, nor did much more severe jolting of the bench bearing the experimental preparation. Mechanical stimulation was therefore eliminated as a possible cause of the response.

The responses described must thus be considered as being due to the effects of light; briefly, it is postulated that there is evidence for the following three statements:

(i) Decrease in light intensity is the immediate stimulus calling forth the active response of oro-flexion (see Text-figs. 1 *a–d*, 2, 3). Comparison of the results in Text figs. 2 and 3 shows that the *magnitude* of the response (number and frequency of reactions) is related to the *extent* by which the light intensity is reduced. This result is not unlike that found in the case of the shock effect occurring after changes in concentration of the bathing media of isolated gill filaments and the cilia thereon (Pilgrim, 1953). There, the magnitude of the effect was found to be related to the *ratio* of the nitial and final concentrations, rather than to the absolute value of either concentration.

(ii) Light of constant intensity does not constitute a stimulus for oro-flexion; it does, however, act indirectly as a sensitizing mechanism. From Text-figs. 1 *c*, *d* and 2 it is clear that the number of reactions in the response sequence depends partly on the duration of this sensitizing illumination. From Text-fig. 3 it is clear that constant levels of illumination below 100% are similarly capable of sensitizing action, and that succeeding reductions in illumination are followed by further responses.

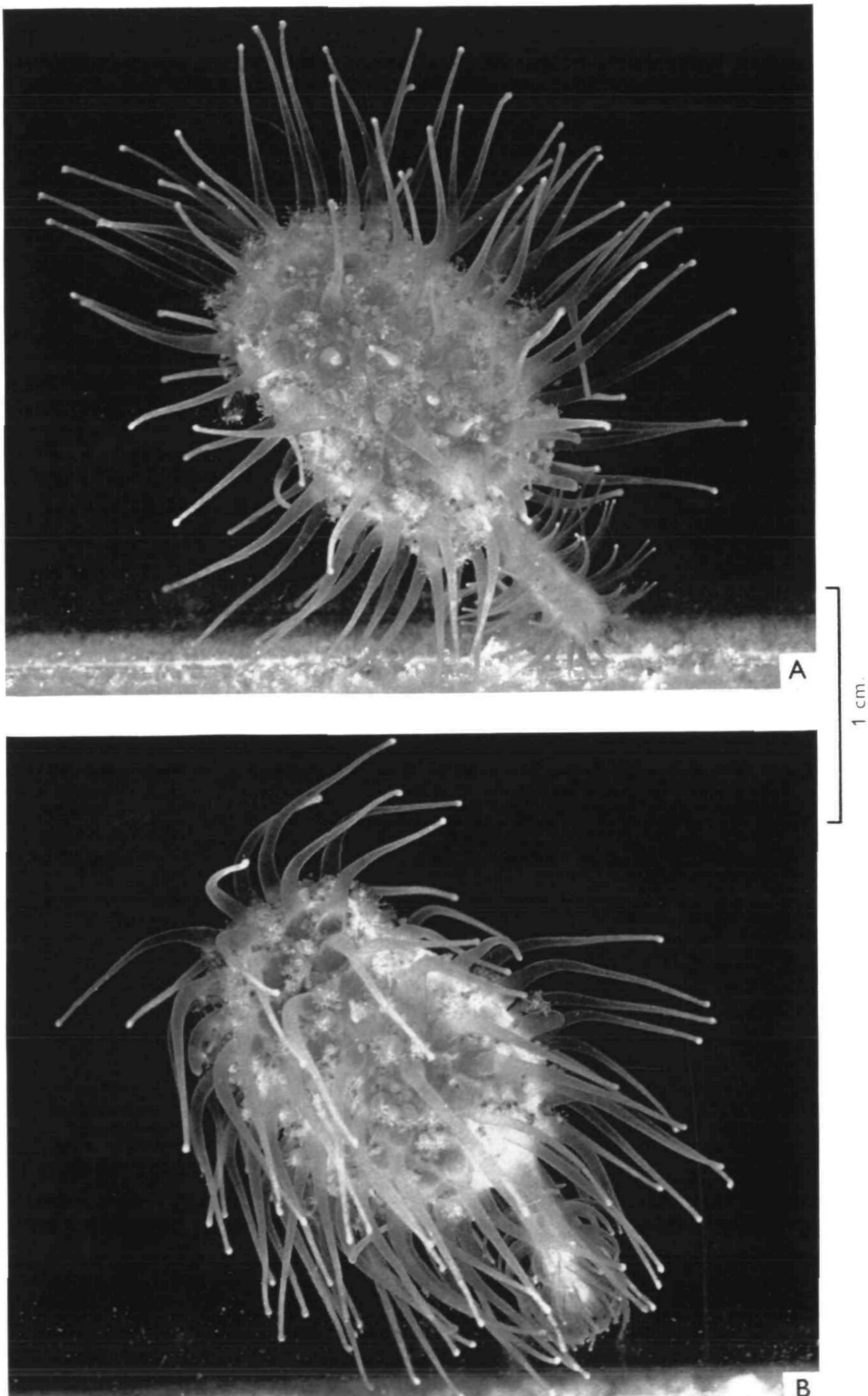
(iii) Increase in light intensity does not produce any active response, but acts in an inhibitory fashion, preventing the oro-flexion response (see Text-fig. 2). Examples of inhibitory stimuli among coelenterates are not numerous (Horridge, 1955) and the photic responses following increase in light, which have been described in these animals, mostly refer to a *positive* reaction. Passano & McCullough (1962), however, reported that light interrupted the rhythmical potential changes associated with pacemakers in *Hydra* and that their resumption after 20 sec. was at a more frequent rate. In *Metridium* Batham & Pantin (1950) found that strong localized light initiated locomotory activity, while general illumination tended to inhibit it.

Significance of oro-flexion in nature.

Dendy (1902, p. 3) wrote: 'The...tentacular processes of the float occasionally exhibited spasmodic movements of flexion, like gigantic flagella, many of them simultaneously, or nearly so; and from this I am led to conclude that the animal has the power of rowing itself through the water by means of those organs.' Dendy was evidently, and not unnaturally, convinced that his specimen was not in a normally healthy state when in the laboratory and implied that the movements observed *might* be more effective in a healthy animal. Garstang (1946) was, however, not so cautious in transcribing from Dendy's paper; on page 147 he states that '...the cauline "float" of *Pelagohydra*...carries an equipment of locomotive tentacles...the theoretical predecessors of paddling bracts...' and on page 181 he again refers to the tentacles as 'locomotive', although there is no evidence that the animal can make effective progress through the water.

In the present investigation it was found that there was very little effective result from the oro-flexions described; even the most vigorous served to translate the animal no more than *ca.* 1 cm. through the water, in an aboral direction. *Pelagohydra* is thus (macro) planktonic rather than nektonic. It is difficult to see, therefore, what functional significance the response could have for the animal in its natural habitat. If it normally lives in the photic zone of the sea, occlusion of daylight by a large superposed predator would stimulate the animal to move only an insignificant distance; further, the response is so delayed as to render it of no obvious survival value in this context. There was, moreover, no indication that the animal moved in any particular direction—the tentacles appeared to flex equally on all sides under experimental conditions.

Although only one specimen was available, the results of the experiments are offered for consideration now. The three known specimens were discovered in 1901, 1929 and 1966 respectively; it seems unwarranted to wait for further specimens before


A
1 cm.
B

attempting to obtain more data for publication. The present experiments point to some interesting aspects of behaviour which could perhaps be elucidated if more material is collected on oceanographic expeditions.

SUMMARY

1. A single specimen of *P. mirabilis* was subjected to varying degrees of illumination.

2. In constant light occasional spontaneous reactions occurred, the tentacles flexing in an oral direction and moving the animal aborally a very insignificant distance each time.

3. When the level of illumination was reduced suddenly and almost completely there occurred a sequence of such reactions; successive reactions in the sequence occurred with increasing vigour and at diminishing frequency.

4. Readmission of light was shown to act as an inhibitory condition, since it interrupted the reaction sequence.

5. When the illumination was reduced in a series of steps, each step was followed by a sequence of reactions, the sequences showing increase in vigour and decrease in frequency. Each such sequence appeared to be freshly initiated by the stepwise reduction in light.

I wish to acknowledge the assistance of my daughter Jennifer in conducting the experiments and of Mr J. Darby for taking the photographs. I am grateful for criticism and comment from Dr E. J. Batham, Dr V. L. Benzie and Dr P. M. Ralph.

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EXPLANATION OF PLATE

Fig. (*a*). *Pelagohydra mirabilis* in an aquarium. The animal had been subjected to strong light prior to the photograph. Some float tentacles show independent writhing movements.

Fig. (*b*). The same animal photographed during the *first* oro-flexion reaction following a 'light off' stimulus. Succeeding reactions within the same response sequence were even more pronounced.