A Study on the Photoreceptor of a Medusa, *Spirocodon saltatrix*[1])

By

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When the light illuminating a hydromedusa *Spirocodon saltatrix* is turned off or is suddenly dimmed, the animal responds to the decrease of light intensity by the pulsation of its bell. The red-coloured ocelli borne by the tentacles which exist in great number around the rim of the bell are responsible for this shadow reflex. This can be readily shown by the fact that the animal deprived of ocelli does not respond.

In his physiological study of this medusa, Kikuchi (1947) has revealed some relations between the pulsation of the bell and the photic stimulation of the ocellus, and made some contributions to the nature of the excitation system of this medusa. Further, the response of the tentacle which is also seen to occur as the bell pulsates seems to serve a good criterion for the function of the ocellus.

The present paper deals with some properties of the responses of the tentacles caused by the photic stimulation of the ocelli. The responses of the tentacles under various strengths of stimulation were studied, and evidence will be presented to show that the contraction of the tentacles is elicited through a conduction system connecting the ocelli with the tentacles, and that the nature of this system is not that of a muscular connection.

Experiments

1) A cut piece of bell, about one-eighth of an animal, was hung in normal sea water with a glass hook and illuminated with a 30 watt light source for microscope. The beam of light was focused on the ocellus with a condenser lens. The light intensity was regulated by a transformer for varying the applied voltage. The intensity was measured with a selenium photocell in lux (water temperature: 9.5°C).

In order to observe the response, an auxiliary light source (the light intensity at the place of preparation: 25 lux) was kept lighted during the experiment.

The cut piece of bell having intact subumbrellar muscle layer, velum, tentacles and ocelli was kept under the light of 2,000 lux for 30 minutes for the purpose of adaptation. When the light was turned off, it fully responded in a similar way to that of a whole animal, i.e. all the subumbrellar muscle, velum and ten-

1) The work was done in the Misaki Marine Biological Station, Kanagawa-ken.

tacles contracted, while the preparation having its velum removed responded only in contraction of tentacles. It is, therefore, clear that the excitation is conducted through the surface of velum from the ocelli to the muscle layer. Further, the tentacles may have a direct connection with the ocelli in the excitatory system. To make certain about this, single ocellus and tentacle preparation was dissected out removing other tentacles and ocelli together with the subumbrellar muscle layer and velum; this preparation, adapted for 30 minutes in the light of 3,000 lux, responded in the contraction of the tentacle after a short reaction time when the illumination was interrupted. In all preparations the single tentacles did not fail to contract as the ocelli they bear respectively were stimulated by the interruption of the illumination. This fact shows that the exictation of ocelli is transmitted through a conduction system to both the bell and the tentacles and that the contraction of a tentacle is not merely elicited by a mechanical stimulation which results from the pulsation of the bell.

Some attempts were made to stimulate a single ocellus in the intact animal. A point light source was prepared using a gradually tapered glass rod. Through its inside a beam of light was directed and focused on an ocellus. When an ocellus adjacent to the radial canal was chosen and the light intensity was selected, the minimum contraction of the tentacle which bears that ocellus, that is, the locally limited shortening of its distal end, was observed without provoking the activities of the bell and other tentacles, by turning off the light.

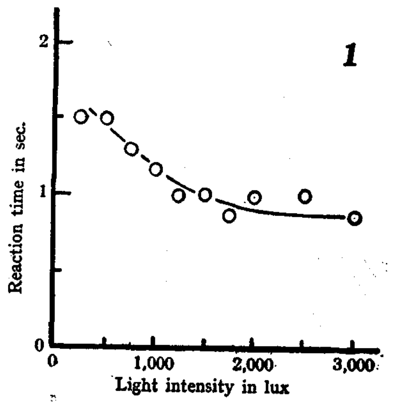
The contraction of tentacle is not simply of all-or-none nature. When the animal buoying itself in the sea water comes to rest, all the tentacles spread out rather rigidly like fishing rods projected radially from the edge of the bell and may play a role in reducing the rate of sinking. The contraction of tentacles takes place in the following manner. When the stimulation is strong enough to elicit the contraction of both the bell and the tentacles, the latter bend downward immediately at their basal parts and quickly become short. If the stimulation is comparatively weak, the tentacles respond only by shortening their distal ends. At medium strength of stimulation the lengths of the spread-out tentacles are reduced while they begin to contract from the distal ends.

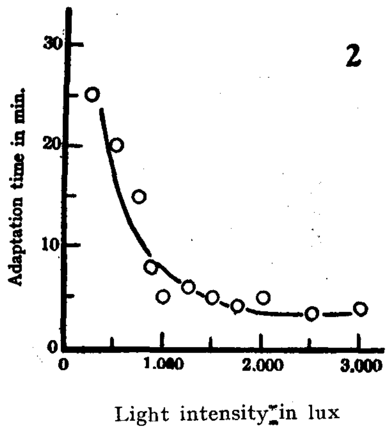
In good accordance with Kikuchi's observations on the bell pulsation, in many cases the first weak local contraction of the tentacles occurred after the reaction time of 0.6–1.5 sec. and was followed by a second but stronger contraction within 2 sec. from the stimulation. Though he has reported some cases in which a third contraction of the bell occurred later, no such case was found in the tentacle.

As described above, in the minimum response the contraction of the tentacle is definitely limited to its distal end. This indicates that there is a transmitting system which serves to conduct the excitation without causing muscular contraction along its way to the distal end of the tentacle, and that after the excitation arrives at the end, the muscular contraction is initiated to spread along the length of the tentacle from the end to the base. The conduction velocity of this system was roughly estimated, providing the latency of muscular response after the transmission is negligible. Total length of the tentacle ranges from 30 cm to 48 cm and the reaction time varies from 0.6 to 1.5 sec. Thus the conduction velocity of this system may be of the order of 20 cm/sec at 9.5°C.

2) The reaction time of the contraction of the tentacle elicited by stimulating the ocellus was measured. It varied in relation to the light intensity, when the adaptation was fixed at 30 minutes (Fig. 1). The time lapse was measured whithin an error of 10% as the distance of two points inscribed on a kymographic record by a pen connected to a hand key at the time of turning off the light and at that of initiation of the minimal response.

If the time of adaptation was reduced, the tentacle showed a shortening of





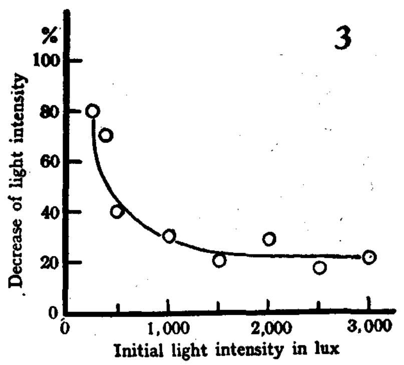


Fig. 1. Reaction time of the contraction of tentacle, when the ocellus was stimulated by turning off the light of various intensities. The light intensity was measured with a photocell in lux. Average from 4 experiments.

Fig. 2. Adaptation time necessary to elicit the minimal response of the tentacle when the intensity of adaptation light was varied. Average from 4 experiments.

Fig. 3. Intensity decreased in per cent of the initial intensity of adaptation light sufficient to evoke the minimal response of the tentacle at various initial intensities of illumination. Average from 3 experiments.

less magnitude. By choosing proper combinations of the light intensity and the adaptation time, the author was able to make the response just perceptible at the end of the tentacle. The relation between the light intensity and adaptation time which is sufficient to elicit this minimum response is given in Figure 2. Though the response was largely dependent on the individual difference, if the light-adaptation was shorter than 3.5 minutes the preparation failed to respond even with the strongest light available, while with the lower intensity of illumination a longer adaptation was required.

It is not necessary for the excitation of an ocellus to turn off the light completely, but a relative decrease in intensity is sufficient for the excitation.

Using two light sources, which were separately controlled by two transformers, the preparations were stimulated by turning off one light and thus reducing the light intensity.

The intensity decrease sufficient to evoke the minimum response is plotted in Figure 3 in per cent of initial intensity. While the light intensity is comparatively strong, the threshold decrease of light intensity on per cent stays constant, and the weaker light requires a further reduction of intensity.

Discussion

In medusae three different conduction systems have been hitherto described: first, the system in which the excitation is tarnsmitted between muscle fibers coinciding with their contraction, second, the system in which the excitation is conducted through a nervous continuity to elicit the muscular contraction concomitantly along its route (Horridge, 1954) and, third, the conduction system which does not call forth simultaneous muscular contraction while the impulse travels along (Romanes, 1876; Bethe, 1903; Mayer, 1906; Pantin, 1935; Bullock, 1943). The observed fact proves that the conduction system connecting the ocellus with the tentacle as described above may have the property of the last system. So the transmission may be of the same nature as that which Romanes (1876) demonstrated in tentacle retraction in *Aurellia* and in the initiation of a beat from a tentaculocyst following stimulation at a distant point.

Horridge (1954) succeeded in recording an electrical activity similar to that of nerve impulses in higher animal from a single large bipolar nerve cell in the subumbrellar epithelium of *Aurellia*; he has suggested the existence of another pathway for other transmitted excitation and that this system may be the nerve net. It must be necessary and quite interesting to locate the system anatomically and to try to record the electrical activity which may occur along the system while the impulse of excitation is being conducted.

When the bell of the hydromedusa used in these experiments pulsates, the contraction of tentacle is invariably observed to some degree. The question whether the tentacle contracted as a result of mechanical agitation or if it was stimulated by the excitation of the ocellus remains open to doubt. In fact, the tentacle contracts whether the bell moves or not. The observations show that the response of a tentacle is quite similar to that of bell muscle in regard to the stimulation (cf. Kikuchi, 1947). Then it seems safe to assume that the ocellus sends out the impulses both to the subumbrellar muscle layer and to the muscle of the tentacles at the same time ; the former results in the pulsation of the bell and serves to lift the animal in the sea water while the latter results in shortening of tentacles, which in turn contributes to the activity of bell in facilitating the movement upward.

The decrease in light intensity necessary to elicit the response of the tentacle relative to the initial intensity (i.e. the threshold of difference) stayed constant while the intensity was relatively high (cf. Fig. 3). This relation seems to follow Weber-Fechner's law. On the other hand, at lower intensity the threshold of difference increased. Whether this increase is attributable to the nature of the ocellus or is caused by the change of the quality of the illumination is not decided, because the quality of the light used in stimulation inevitably changed as its intensity was varied and no care was taken to eliminate this defect, though a rough check of the results was made with neutral tint filters (Matsuda : absorption rate, one-tenth and one-hundredth).

Summary

1) It has been shown that the contraction of the tentacles of a hydromedusa, *Spirocodon saltatrix*, is elicitable by the photic stimulation of the ocelli independent of the contraction of subumbrellar muscle.

2) Evidence was presented on the existence of a conducting system which carries the excitation prior to the muscular contraction along its route.

3) The relations between the light intensity and the response of the tentacles were measured.

4) The possible nature of the transmission of the impulse was discussed.

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