STUDIES ON THE MYONEURAL PHYSIOLOGY OF ECHINODERMATA

IV. THE LANTERN RETRACTOR MUSCLE OF PARECHINUS: RESPONSES TO STIMULATION BY LIGHT

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The jaw apparatus of the regular echinoids is moved by a complex of muscles. Of these the largest and most accessible are the lantern retractor muscles which originate on the auricles and insert upon the pyramids which enclose the teeth. Preliminary experiments using Parechinus angulosus Mortensen showed that, while in this species these muscles could not be stimulated indirectly by way of electrical shocks applied to the radial nerves, they are photosensitive, contracting on exposure to light after a period of dark-adaptation. The existence of photosensitive nerves in echinoids is already well known from the analysis by Millott (1954) of the shadow response of Diadema. The account which follows is limited to a qualitative description of the results of photostimulation of the lantern retractor muscle, a necessary background before more detailed quantitative studies can be made.

Parechinus angulosus was collected between tide marks at Port Alfred in the eastern part of the Cape Province of South Africa. The animals are usually found in crevices beneath large stones by day, but wander freely in the rock pools at night. In laboratory aquaria they show a marked tendency to avoid bright light. After collection the animals were brought back to the laboratory where they were kept in porcelain sinks. Provided care is taken to remove all faeces and the water is violently aerated to produce a constant movement, the animals remain in good condition for a fortnight to 3 weeks.

THE LANTERN RETRACTOR MUSCLE

Each lantern retractor muscle is composed of a bundle of smooth muscle fibres which run directly from an auricle to a pyramid. The fibres are not, however, all parallel; those which lie aborally run at right angles to the oral–aboral axis, while the fibres near the oral surface of the muscle are steeply inclined towards the mouth. The details of the innervation of the lantern muscles of echinoids appear to be unknown. Cuénot (1891) describes five pairs of nerves arising from the hyponeural nervous system which latter is composed of five discrete plaques lying on the aboral surface of the circumoral nerve ring; these nerves run along the edges of the jaws. Parechinus angulosus differs from the species studied by Cuénot in so far as the hyponeural nervous system is not limited to five plaques. In this species each plaque is not isolated but connects with its neighbours by a thin layer of hyponeural cells which are clearly

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recognizable inter-radially, being separated by a very fine connective tissue sheet from the rest of the circumoral nerve ring. From each radial plaque arise two nerves as described by Cuénot. Each soon splits into two branches. Seen in transverse section a pair of pyramids is U-shaped and the tooth they enclose fits into an inter-radial groove, at the base of the U. Two pairs of nerves run to each U, one pair from each adjoining radial plaque. One nerve of each pair runs aborally at the edge of the tooth where it abuts against a pyramid, while the other lies on the inner, inter-radial face of the pyramid close to the open end of the U. These nerve branches are all very fine and it has not proved possible to trace them further.

A SINGLE RETRACTOR MUSCLE PREPARATION

In making a single muscle preparation of the lantern retractor it is convenient, for subsequent manipulation, to use the auricle attached to the test as a fixed point and to free from the rest of the jaw apparatus the pyramid which carries the insertion of the muscle. This may be done as follows. The test is cut horizontally, midway between the oral and aboral poles. The gut is immediately severed just aboral to the lantern and removed; the lantern is then rinsed in clean sea water. The compass depressor muscles are freed from the perignathal girdle and the compasses, together with their elevator muscles, removed. A rotula is now dissected away. This is done by approaching the rotula with a pair of scissor-forceps from the central axis of the lantern and making two cuts to sever the ligaments on the oral surface of the rotula which attach it to the epiphyses. The lantern protractor muscles of a neighbouring inter-radius are carefully cut away, the epiphysis of the side of the jaw remote from the selected retractor muscle is broken off and the pyramid beneath is cut downward orally immediately adjacent to the tooth. The comminator muscle adjacent to the selected muscle is also cut down to the level of the radial nerve. The auricle is weakened in its midline by scratching a deep groove, is then cut free of the perignathal girdle on the side remote from the selected muscle and is broken in the mid-line. The unwanted retractor muscle is cut away and the fragment of auricle is discarded. The test is cut along two radial lines towards the mouth, the cut being extended through the peri-oral skin to the mouth. The segment of test carrying the auricle and the jaw now comes freely away. The spines are trimmed from the outside of the test which can be inserted into a plastic clamp while the jaw may be ligatured just above the muscle and attached to a suitable lever arrangement. In the experiments described an auxotonic lever constructed of a flat watch-spring attached to a gimbal lever was used. Since prolonged exposure to white light resulted in the muscle being unresponsive for a long period after dissection, the lantern was illuminated from a microscope lamp with a red light filter during preparation.

As a light source for stimulation a 6 V. 30 W. tungsten filament lamp was normally used. This could be run at three preset nominal lamp voltages of 5, 6 and 8 V. The muscle was at a distance of 8 cm. from the lamp. The lamp housing was fitted with a camera shutter operated by a cable release. Exposure was controlled either by the shutter mechanism or, if longer exposures were required, by an electronic timing unit which operated a solenoid acting on the head of the cable release. The exposure times provided by the shutter mechanism were determined using a photocell and an oscillog-
graph. The flash contact of the shutter was used to operate a signal marker circuit. In certain experiments where regular repetitive stimulation was required, the solenoid control of the cable release was operated by a cam fitted to the spindle of a kymograph motor.

**THE PROPERTIES OF THE RETRACTOR MUSCLE PREPARATION**

**Spontaneous activity**

When first set up these preparations are inactive or may display weak spontaneous activity; they are, further, either unresponsive or only weakly responsive to stimulation by light. Left in the dark a small proportion of the preparations showed spontaneous activity. This activity, which started from 2–12 hr. after first setting up the preparation, is expressed as a slowly increasing tension which develops over a period of at least 90 sec. to be followed by a rapid relaxation which takes 20–30 sec. (Fig. 1a). The frequency of this activity is variable; some preparations are very sluggish, a relaxation occurring only once every 30 min. or more, but more typically relaxation occurs every two or three minutes. While many preparations show a clear rhythm, others may display irregular activity (Fig. 1b). A relatively inactive preparation may sometimes be stimulated to greater activity by stretching the muscle.

**Light stimulation**

The response of the muscle to light stimulation of 20–25 sec. duration will first be considered. Typically the muscle behaves in one of two ways. It may shorten fairly rapidly and then, without any distinct break, the rate of tension development falls and the muscle contracts more slowly (Fig. 2a). The other pattern is one in which the muscle contracts rapidly at first, the tension then falls for a short while and then increases slowly (Fig. 2c). These two patterns are only quantitatively different for, in some preparations, after the initial rapid contraction, the tension is held steady for a few seconds before the second slower rise in tension starts (Fig. 2b). The two elements of this pattern are subsequently referred to as ‘quick’ and ‘delayed’ responses.

In a limited number of preparations, and typically fairly soon after they had first become responsive, the patterns were different. Thus in Fig. 2d it can be seen that no
delayed response followed the quick response although there was a transient increase in tone at the end of the period of stimulation. In Fig. 2e there is a slight fall in tone after the quick response and the preparation simply recovers its resting level at the end of stimulation. In Fig. 2f, in which the period of stimulation is far longer than in the four previous traces, there is a slight quick contraction followed by a fall in tone which then slowly recovers, but falls once again at the end of stimulation. It is noteworthy that the tension of the muscle continues to increase for 3–5 sec. after the end of stimulation. This may be clearly seen in Fig. 2b, c.

![Image](image_url)

**Fig. 2. Parechinus angulosus.** Response of lantern retractor muscles to light stimulation. Duration of stimulation is shown by upper signal marker. Time mark: 1 sec, except a and f where it is 5 sec.

To very brief light pulses only the quick response is given; tension rapidly increases, is held for a few seconds and then the preparation relaxes once more. Figure 3 shows the response of a preparation to a photographic electronic flash of $10^{-5}$ sec. duration. With pulses of increasing duration it was found that the delayed response is not clearly shown until exposure time exceeds 7 sec. duration.

If the period of exposure to light is greatly prolonged another effect appears. After a variable period from about 90 to 360 sec. the preparation starts to display rhythmic movements which are strikingly similar to those shown by some spontaneously active preparations (Fig. 4).

The great variety of types of response shown by different preparations makes quantitative statements of relatively little value. This is particularly true of the delayed contraction whose time of onset cannot be critically determined. Using preparations
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in which the quick and delayed responses were well differentiated and within the limited range of light intensities available, it was found that the magnitude of the quick response increased with increasing light intensity, while its latent period, normally about 1-3 sec. duration, decreased. If the intensity of illumination was constant, the magnitude of the quick response increased with increasing durations of illumination reaching a maximum at exposure times of about one sec. The latency of the response fell with increasing exposure time, becoming constant for exposures greater than 0.3 sec.

![Fig. 3](image1.png)

![Fig. 4](image2.png)

**Repellent light stimulation**

Just as the responses to single light exposures of about 20 sec. duration display either a fairly smooth transition from one rate of tension development to another or a well-marked break between the two events, so too the responses to repetitive pulses of light fall into two categories. Where there was no differentiation of the responses to a long light exposure, the preparation responded to repeated short light pulses by a series of contractions which summed and at high frequencies of stimulation fused (Fig. 5). If, however, the preparation displayed a clear differentiation of the quick and delayed contractions to a long light pulse, then, with repetitive stimulation, the response to the first light pulse was markedly greater than that to subsequent pulses (Fig. 6). The extent of this effect varies with the frequency of stimulation and is maximal at about one light pulse every 10 sec. Figure 7 shows the results of a series of experiments in which were compared the relative amplitudes of the first and second responses to pairs of short pulses separated by different time intervals. Three different intensities of illumination were used. It can be seen that the relative depression of the second response is maximal at about 10 sec. and the effect is negligible after 30 sec. At intervals of less than 5 sec. the second response is slightly greater than the first, an effect almost certainly due to mechanical summation of the responses.

If longer intervals between light pulses are used a second depression becomes apparent. When the interval between stimuli is about 60 sec. the first and second responses are of about the same magnitude, but at longer intervals the response to the second stimulus again becomes less (Fig. 8). This second depression reaches a maximum after about 300 sec. and has disappeared when the interval between stimuli is about 20-30 min.
Superimposed light stimuli

If two light stimuli are applied in succession, the preparation will respond to the second stimulus as well as to the first. However, the response to the second stimulus may be less than that to the first owing to the effect already described and illustrated.

Fig. 5. Parechinus angulosus. Response of lantern retractor muscle to repeated light stimuli of 0.55 sec. duration. (a) 1 stim./20 sec.; (b) 1 stim./10 sec.; (c) 1 stim./5 sec.; (d) 1 stim./2.5 sec.

Fig. 6. Parechinus angulosus. Responses of lantern retractor muscle to light stimuli repeated every 10 sec. (a) stimulus duration 0.55 sec. Time mark: 10 sec. (b) stimulus duration 5.0 sec. Time mark: 5 sec.
in Fig. 6. If, however, instead of using two ‘white’ lights for such an experiment the second light is that of a mercury vapour lamp, the muscle, particularly if the experiment is made early in the life of a preparation, may relax slightly rather than contract. Tension is regained as soon as the mercury lamp is shielded (Fig. 9).

![Graph](image)

**Fig. 7.** Differences in tension between the responses to the first and second stimulus of a pair of light pulses of 0.55 sec. duration and separated by different time intervals. Data for three different light intensities (expressed as lamp voltages) are shown.

![Graph](image)

**Fig. 8.** As Fig. 7, but with longer intervals between the stimuli of a pair.

A few preliminary trials were made to identify the wave length responsible for this effect. Owing to insufficiencies of apparatus available these gave no positive answers. Furchgott, Ehreiclh & Greenblatt (1961) have shown that if strips of rabbit aorta are caused to contract by a variety of reagents such as adrenaline or histamine, exposure to a strong light beam will cause relaxation. The action spectrum of this effect shows a maximum in the ultra-violet at 310 m\(\mu\). If, however, with the present preparation the beam from the mercury lamp was passed through several thick sheets of glass or a photographic ultra-violet filter, the effect was not abolished. Again, working with Spisula, Kennedy (1960) has shown the presence of neurones whose spontaneous activity is abolished by light. The action spectrum of this effect shows a maximum in the yellow around 540 m\(\mu\). In the present experiments it has been possible to isolate
the yellow sodium doublet of the mercury lamp by the use of Wratten filters. This proved to be neither excitatory nor inhibitory in its action. Further experiments using these filters suggest that both the excitatory and inhibitory components of the light lie in the blue-green region of the spectrum, but more precise identification could not be made. In this connexion it is interesting to note that the photoreceptive neurones of *Procambarus* are maximally excited in the green at a wave length of 500 μm (Bruno & Kennedy, 1962), while the inhibitory action spectrum of the spine response of *Diadema* as determined by Yoshida & Millott (1960) shows a maximum in the blue between 455 and 460 μm.

**Fig. 9**

*Parechinus angulosus.* Response of lantern retractor muscle to white light followed by light from a mercury vapour lamp as indicated by the three white blocks on the upper signal. Time mark: 10 sec.

**Fig. 10**

*Parechinus angulosus.* Response of lantern retractor muscle to square-wave electrical stimuli applied directly to the muscle. Pulses of 10 msec. duration and a frequency of 2/sec. Time mark: 30 sec.

**Electrical excitation**

Only very preliminary experiments have been undertaken using direct electrical stimulation of the muscle with short square-wave pulses. These showed that the muscle contracts rapidly at first, this response being followed by a slower rise in tension. In some cases the preparation relaxed below its initial tension when the stimulation ceased and then regained its former level or sometimes a greater resting tension (Fig. 10). No attempt has yet been made to correlate the types of response shown to pulsed electrical stimulation and to light stimulation.

The effect of direct-current stimulation has also been tested. The type of response given depends upon the direction of current flow. Typically if the end of the muscle near the pyramid is cathodic the muscle relaxes, while if the current is reversed the muscle contracts slightly. This effect may be seen in Fig. 11 where the general tone of the preparation is first enhanced by a light stimulus. At higher current densities the results are complicated by twitch-like contractions at the break and sometimes at the make of the d.c. stimulus.

**Interactions between muscles**

The lantern retractor muscles work against two other sets of muscles, namely the lantern protractors and the comminator muscles which draw the jaws together. Pople & Ewer (1958) have shown that the spontaneous activity of the pharyngeal retractor muscles of *Cucumaria* may be partly or wholly inhibited by applying a stretch to the
longitudinal muscles of the body wall, their functional antagonists. Experiments were conducted with *Parechinus* in which the lantern protractors were freed from the lantern aborally and stretched to varying lengths. This in no way modified the responses of the lantern retractor muscles to light stimulation.

A further series of experiments was undertaken using the comminator muscles. To record the activity of these muscles ligatures were tied around two adjacent teeth. The recording threads ran out laterally and, passing over two pulleys, were joined again to act on an auxotonic lever. In this way the difficulty of clamping a jaw was avoided. A further recording thread was attached to the rotula above the comminator muscles, while a fragment of test distal to the auricles was clamped. In this way the action of the pair of retractor muscles on either side of the comminator muscles could be recorded as they rocked the jaws. Such recordings (Fig. 12) showed that electrical stimulation of the comminator muscles resulted in a loss of tone by the retractor muscles which was maintained after stimulation had ceased.

**DISCUSSION**

Millott and Yoshida in a series of papers (Millott, 1954; Yoshida, 1962; Millott & Yoshida, 1957, 1959, 1960a, b; Yoshida & Millott, 1959, 1960) have shown that the spine responses of *Diadema* to shadows are due to a double action of light. Exposure to light is excitatory, but this activity is normally inhibited and is only expressed when the light intensity falls. After light stimulation ceases rhythmical beating of the spines may persist for as long as 90 sec. The present preliminary results strongly suggest that light stimulation also has a double effect upon the lantern retractor muscle of *Parechinus*. Its stimulatory action is normally dominant and persists for only a few seconds after light stimulation ceases (Fig. 2). Its inhibitory action is shown by the action of the light of a mercury lamp upon the preparation (Fig. 9) and is also expressed
in the diminution of the amplitude of response in certain preparations when exposed to repetitive light pulses (Fig. 6). That this latter effect is an inhibition and not an adaptation phenomenon is demonstrated by an experiment with superimposed lights shown in Fig. 13. Following initial illumination a short light pulse was given at A. The preparation contracted and then relaxed below its previous tension to regain its former value in about 20 sec. The similarity of time relations with those shown in Fig. 7 is striking. At B a series of five brief light pulses were given, spaced at 10 sec. intervals. The response of the preparation is similar to that shown in Fig. 6 and can be attributed to the fact that each stimulus after the first will fall in the period of inhibition due to the preceding light pulse. There is a further effect which might be regarded as an inhibition, namely that shown in Fig. 8. It seems more probable, however, that this prolonged depression of response is due to some type of adaptation phenomenon and that the results shown in this graph are really the product of two separate events. One is the brief post-stimulatory inhibition shown also in Fig. 7. The other is a far longer effect (Fig. 8), whose real character is suggested by the broken curve at short time intervals. The physico-chemical basis of an event which reaches a maximum about 5 min. after stimulation is obscure.

Yoshida & Millott (1959) have shown convincingly that the responses of Diadema to photostimulation arise from the direct action of light upon the nerves. In Parechinus this has not been shown. From experiments with narrow beams of light it is clear that the photosensitive structures are limited to the retractor muscle itself, illumination of other regions of the lantern or test are not followed by responses from the retractor muscle. Such results might imply that the light responses arise directly from the muscle cells: this possibility cannot be excluded but the complexity of the results obtained, and especially the varying balance of excitation and inhibition, strongly suggest that the light is acting, in part at least, upon some co-ordinatory system within the lantern retractor muscle akin to the motor complex of the pharyngeal retractor muscle of Cucumaria (Pople & Ewer, 1954). This conclusion receives some support from the form of response shown by the lantern retractor muscle to pulsed electrical stimulation (Fig. 10). This closely resembles the response to light stimulation, suggesting that the latter is also of nervous origin. Further, the variation of response of the preparation to d.c. stimulation with change in polarity and especially the fall in tension when the pyramid is cathodic (Fig. 10) suggest the presence of inhibitory neural elements.

The response of the lantern retractor preparation to light pulses of about 20 sec. duration (Fig. 2) is typically a quick contraction followed by a slower rise in tension.
This closely resembles the quick and delayed responses shown by the pharyngeal retractor muscle of *Cucumaria* to indirect electrical stimulation of the radial nerve (Pople & Ewer, 1954, fig. 7) and we have therefore adopted the same terminology for *Parechinus*. The present preparation also shares with the retractor muscle of *Cucumaria* the property of spontaneous activity, albeit the pattern of this activity is very different. In *Cucumaria* it is typically a slow rise in tension followed by a very prolonged relaxation while in *Parechinus* there is a prolonged rise in tension followed by a more rapid fall. In *Cucumaria* this spontaneous activity has been regarded as neurogenic in origin, arising from events within the motor complex of the retractor muscle (Pople & Ewer, 1958). It appears necessary to postulate a similar type of ganglionic complex to explain the events observed with the lantern retractor muscle of *Parechinus*.

![Fig. 14. Hypothetical motor unit. For further explanation see text.](image)

It is possible to construct a hypothetical model (Fig. 14) of a controlling motor unit which will display the properties shown by the lantern retractor preparations. A grouping of such units in a motor complex controlling the complete muscle is assumed. The value of such a model lies in the fact that it reflects the minimal number of distinct events which appear to be necessary to account for the phenomena observed. Whether these events occur in anatomically distinct structures and precisely how these structures may be interrelated can only be determined by further study. The model serves simply to indicate the types of event whose loci have to be identified.

It is assumed initially that there are, in the motor unit, two types of motor cyton, *Q* and *D*. These are sensitive to both electrical and photo-stimulation. The *Q* cytons are stimulated by brief light flashes and respond by a brief discharge (Fig. 3). The *D* cytons are stimulated only by longer exposure to light and discharge for several seconds after the end of stimulation (Fig. 3b, c). The *Q* cyton adapts rapidly to light stimulation; the *D* cyton does not.

The presence of an inhibitory cyton, an *I* cyton, must also be postulated. When briefly stimulated this responds with a discharge lasting about 20 sec. (Fig. 7). We have seen how this offers an explanation of the type of response to repetitive stimulation shown in Fig. 6. It has also been emphasized that such effects are only displayed by preparations which exhibit a well-marked differentiation between the quick and delayed responses. This suggests an interpretation of the various types of response shown in Fig. 2. If the *I* cyton is unresponsive to light stimulation, there is a smooth transition from quick to delayed response. If, however, the *I* cyton is excitable the delayed response is somewhat depressed and its latency prolonged; this results in a
clear differentiation of the quick and delayed responses (Fig. 2c). At higher levels of excitability of the I cyton the delayed response may be completely suppressed and the quick response depressed (Fig. 2d, e). In the most extreme conditions the tone of the preparation may fall during illumination (Fig. 2f). There are, furthermore, results which suggest that when the I cyton is exposed to prolonged illumination it may respond with an 'off' discharge. In a number of preparations stimulated until after the onset of rhythmic activity, the rate of relaxation at the end of stimulation was very high. Such an effect would also explain the fall in tension below the resting level shown at 'off' in fig. 2f, while the curious stepped relaxation which is to be seen in Fig. 5d may be due to a combination of excitatory and inhibitory after-discharge, the I cyton of the preparation being only very weakly responsive.

Prolonged light stimulation results in the development of rhythmic activity (Fig. 4) which is closely similar to the type of spontaneous activity displayed in the dark by certain preparations. This suggests that the action of prolonged light stimulation is to raise the excitatory level of a preparation until it shows activity. The simplest assumption is that the rhythm depends upon some negative feed-back arrangement, impulses passing to the muscle generating a partial inhibition of its activity. The obvious candidate for such a role is the I cyton. It is postulated that a collateral fibre runs from the D axon to the I cyton and gradually depolarizes this cell until, at a critical level, it discharges to inhibit the D cyton. We have already postulated that the I cyton may respond to photo-stimulation by a discharge of about 30 sec. duration. It is striking that the relaxation phase in spontaneous activity is of about the same duration. Clearly to obtain rhythmical activity a considerable number of the motor units here postulated must be capable of acting together, some one possibly taking the role of pacemaker for a while. A rhythmic spontaneous activity as seen in Fig. 1b may be due to failure of one motor unit to establish complete dominance.

This hypothesis is clearly formal. Not only is it unsupported by histological evidence, but the interrelations between the various elements are arbitrary within certain limits. Thus it is possible to replace the I cyton by a photosensitive inhibitory axon, making the seat of interaction of inhibitory and excitatory events at the muscle fibres rather than within a motor complex. Again the two types of response attributed to Q and D cytons might well be the expression of two distinct types of response to light stimulation by a single cell. Another alternative is that the motor axons are photosensitive, responding rapidly and adapting quickly so as to produce a quick response, while their cell bodies have a longer sensitization period and the potential of continuous discharge; such an hypothesis implies that the site of the inhibitory action is at the muscle cells.

It can be seen that there are marked similarities between the behaviour of the lantern retractor muscle of Parechinus and the pharyngeal retractor muscle of Cucumaria. The pharyngeal retractor shows three distinct rates of contraction (Pople & Ewer, 1958), the lantern retractor only two; the presence of a 'slow' contraction has not been shown. Functionally this is not surprising as it seems likely that the slow contraction shown by the holothurian retractor muscle is part of a pattern specifically associated with tentacular feeding. Both systems also show an inhibition. In Cucumaria this is readily demonstrated upon the slow response and no such effect has been shown decisively with the quick and delayed components. In Parechinus its action
is most striking upon the delayed response. It seems unlikely that it is coincidence that the inhibitory action is closely associated in each case with the contraction type shown when the muscle is spontaneously and rhythmically active.

The two systems differ in so far as the pharyngeal retractor can be stimulated to activity by way of the radial nerves. This can again be understood in functional terms. The tentacle complex of a holothurian is liable to damage and must be rapidly withdrawn if need arise. It is therefore to be expected that sensory nerves from the skin will run, by way of the radial nerves, to the motor complexes of the retractor muscles. Sensory information must not only be able to release rapid retraction of the tentacles, but also maintain tone in the retractor muscles to prevent tentacular extrusion if the coelomic pressure is high. These needs are met by the quick and delayed responses. In an echinoid, however, the jaw apparatus is not in special danger and need therefore not receive sensory information from the test. The functional significance of the two modes of contraction of the lantern retractor muscles has yet to be elucidated.

Both the lantern retractor muscle of *Parechinus* and the pharyngeal retractor muscle of *Cucumaria* are photosensitive (Pople & Ewer, 1958). It seems unlikely that in either case this has any biological significance. More probably it reflects some metabolic characteristic frequently, but not invariably, found in echinoderm nerve and exploited both in the shadow response of *Diadema* and the covering response of *Lytechinus*. This discovery of photosensitive myoneural systems deep in the body of both echinoids and holothurians supports Millott’s (1957) suggestion that the dermal light sense of many echinoids is not primitive, but a secondary specialization.

**SUMMARY**

1. The lantern retractor muscle of *Parechinus angulosus* responds to light stimulation by a rapid contraction which is followed by a slower increase in tension. The details of these contractions vary from preparation to preparation.

2. With very brief light exposures only the quick response is shown, while with prolonged light stimulation rhythmical activity develops after a minute or more.

3. Exposure of a contracting preparation to the light of a mercury vapour lamp causes a slight fall in tone. This is not due to the ultra-violet component of this light.

4. Responses to repeated light pulses may result in simple summation or the response to the first pulse may be markedly greater than those which follow. In preparations which show this latter effect, there is evidence for an inhibitory phenomenon which persists for about 30 sec.

5. With paired stimuli the response to the second stimulus may show an initial depression which reaches a maximum at an interval of about 10 sec., then a recovery and finally a second depression of response which is maximal when the interval between stimuli is about 5 min.

6. There is evidence that stimulation of the comminator muscles may result in loss of tone of the lantern retractor muscles.

7. A provisional hypothesis to explain these effects is presented.
During the course of these investigations, one of us (R.E.B) was in receipt of a bursary from the South African Council for Scientific and Industrial Research, while much of the work was made possible by the loan of certain equipment by the Council. We wish to express our thanks for this assistance.

REFERENCES


