NERVOUS CONTROL OF LIGHT RESPONSES IN THE SEA ANEMONE, *CALAMACTIS PRAELONGUS*

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SUMMARY

1. The burrowing sea anemone, *Calamactis praelongus*, responds to light with local, non-nervous contractions of the column. There are also more extensive responses of the column and retractor muscles co-ordinated by nerve net pulses (NNP's) under pacemaker control.

2. NNP's occur in at least two types of bursts and in sequences which sometimes indicate a rotating site of pulse initiation.

3. Light-evoked NNP sequences can be tape recorded and used later to drive a stimulator to reproduce the original sequences in the same or different anemones, evoking muscular responses which approximate the originals. This technique separates the pacemaker-directed component of the light response from the local effects of light stimulation.

4. Isolated circular and parietal muscles contract slowly when stimulated by light or excited indirectly by NNP's. Retractor muscles are insensitive to light but produce rapid contractions when excited by closely spaced light-evoked NNP's.

5. A model for light responses is proposed which incorporates the characteristics of isolated muscles and intact anemones.

INTRODUCTION

The dermal light sense has been defined by Millott (1968) as a 'widespread photic sense that is not mediated by eyes or eyespots and in which light does not act directly on an effector. Its existence is revealed by indicator reactions and in a few cases by electrophysiological evidence.' Millott suggests that this photosensitivity may be associated with nerve concentrations found in or just beneath translucent skin. Sea anemones lack eyes, eyespots or indeed any complex sense organs (Pantin, 1952) but have long been known to respond to light. Bohn (1906) demonstrated that local illumination of the column of *Metridium senile* produced parietal muscle contractions and bending in the illuminated area. Additional studies of this response were made by Parker (1916), Batham & Pantin (1954), North (1957) and North & Pantin (1958). North & Pantin noted that local illumination occasionally produced responses in *Metridium* similar to those following the initiation of pulses in the through-conducting nerve net.

Josephson (1966) devised a method for recording electrical activity from relatively

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unrestrained anemones using flexibly mounted suction electrodes. The present study using similar techniques, was undertaken to investigate possible electrical as well as behavioural responses to light in the burrowing anemone, *Calamactis praelongus*. This anemone has nerve concentrations associated with a translucent skin in its oral disc and tentacles which normally extend above the sand and are thus exposed to the ambient lighting.

MATERIALS AND METHODS

The specimens of *Calamactis* used in these experiments were collected from Cholla Bay, Sonora, Mexico. They were kept in artificial sea water at 19 °C and exposed to 12 h of fluorescent light per day. Most experiments were conducted with anemones that had burrowed in sand provided in 1000 ml beakers of sea water. In some cases, an anemone was placed in a glass tube fastened vertically in a battery jar of sea water. The bottom of the tube was connected to a syringe through a flexible hose, both filled with sea water. In this manner the anemone could be adjusted hydraulically to the desired level within the glass tube. This arrangement permitted observation and illumination of the entire animal. Tungsten filament lamps were used unless otherwise noted.

Muscular activity in intact anemones was monitored indirectly by measuring the changes in coelenteron pressure. A 1·5 mm diameter glass tube was inserted vertically into the coelenteron through the mouth and pharynx. The pharynx provided a sufficient pressure seal (the pressures encountered in this narrow burrowing anemone are higher than in most anemones). The glass tube was connected by a flexible plastic tube to a pressure transducer, the output of which was displayed on an oscilloscope. Provision was made for experimentally adjusting coelenteron pressure by adding or withdrawing sea water from the coelenteron through another connexion to the plastic tube. The anemones accepted this arrangement for long periods, contracting and expanding normally and even feeding under these conditions. This method permits the non-isobaric effects of muscular action to be monitored continuously with minimal restraint or disruption of behaviour.

Isolated circular, parietal and retractor muscles displayed characteristic differences when exposed to light and electrical stimulation. The responses of these muscle preparations were measured as isometric changes in tension using an E & M type B myograph. Careful preparation obviated the need for anaesthetics in any of the experiments. All experiments were completed within 10 h after the muscle strips were obtained. No changes in characteristics were observed during this time.

Electrical activity was monitored through flexible plastic suction electrodes that were usually attached to the tentacles. The signal was amplified by an a.c.-coupled differential preamplifier, displayed on an oscilloscope simultaneously with the pressure and event markers, and recorded photographically. Electrical stimulation in the form of 1 ms rectangular pulses was administered through another suction electrode.

RESULTS

Column bending response

Illumination of a portion of the exposed column of a dark-adapted *Calamactis* causes the column to bend toward the illuminated area. The initial response is an
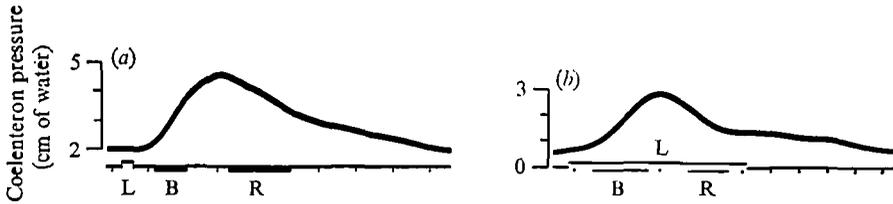
Fig. 1. Bending response to local illumination (L) of the column. (*a*) Three-second illumina-
tion followed by bending (B) and return (R) to the upright position. (*b*) Response to extended
(64 s) illumination. Scale: 10 s between markers.

increase in coelenteron pressure followed after several seconds by the onset of bend-
ing. The pressure rises to a maximum and then decreases toward the resting level as
the column returns to its original shape (Fig. 1*a*). The prompt reduction in pressure
following bending occurs even during continued illumination (Fig. 1*b*) and is consis-
tent with the responses of isolated muscles (discussed below). The bending will
follow a spot of illumination as the spot is slowly rotated around the column.

The reaction time, i.e. the interval from the onset of illumination until the be-
ginning of the response (bending), decreases from approximately 12 s at the threshold
illuminance to 7 s at 30 times threshold. Increasing the illuminance beyond this value
does not further reduce the reaction time. The reaction time for *Calamactis* and most
other animals with dermal photosensitivity consists of a sensitization period during
which the light required for a response is received, followed by a latent period when
additional stimulation is not necessary. The sensitization period for a given illumi-
nance is the minimum interval of stimulation necessary to produce the response.
Normal bending responses in *Calamactis* were evoked by stimuli ranging in time from
0·5 ms to those which extended throughout the reaction and response times. The
minimum sensitization period was not determined but is apparently less than 0·5 ms.

The column is the only region in which light will evoke the bending response.
Illumination or electrical stimulation of the oral disc or tentacles does not cause
column bending. No electrical activity related to illumination or bending of the
column could be recorded from the column or tentacles.

Column bending apparently results from local contraction of the parietal muscles
while the circular muscles are more effective in causing pressure changes (Batham &
Pantin, 1950*a*). The parietals in *Calamactis* are located along the inside of the body
wall from the oral disc to the physa. They are relatively isolated from the strong
retractors which run parallel to them down through the coelenteron. Parietal and
circular muscle preparations were obtained by excising longitudinal and circular
strips of column. These preparations were sensitive to light along their entire lengths,
responding locally with one or occasionally two contraction–relaxation cycles (Fig. 2*a*,
b). The reason for the second cycle, which may also appear in intact anemones, is
unknown. Latent periods for isolated muscles are considerably longer than those for
the bending response of an intact anemone. This may be due to the disruption of
coordinating mechanisms in the isolated muscle preparations. The shape and duration
of the tension curves in the photic responses of isolated muscles (Fig. 2) correspond
to the pressure responses during column bending (Fig. 1). The circular muscles
respond to moderate photic stimulation about three seconds faster than the parietals.
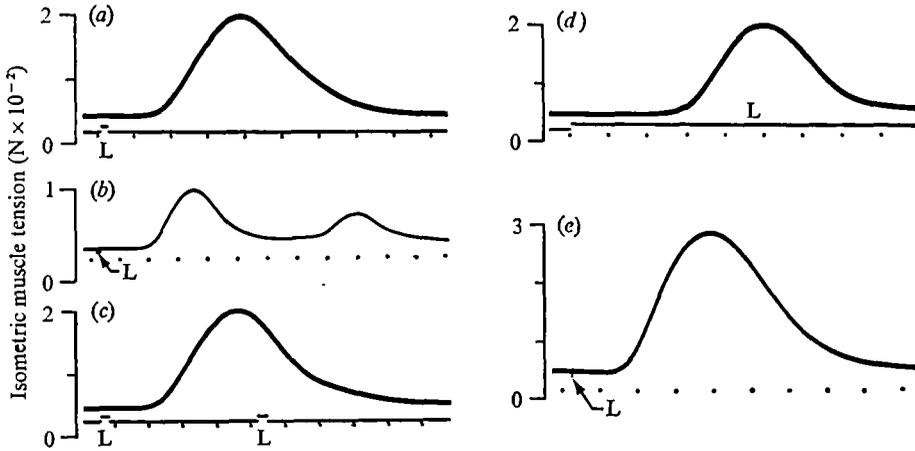
Fig. 2. Isolated muscle contractions in response to light (L). (a) Circular muscle contraction following 2 s illumination. (b) Parietal muscle response with double maxima after 2 s illumination. (c) First 3 s illumination of circular muscle creates refractory period during which second illumination is ineffective. (d) Extending illumination of circular muscle also produces refractory period. (e) Parietal muscle response to 0·5 ms electronic flash. Scale: 10 s markers.

This may explain why the pressure in intact anemones begins to rise several seconds before the bending starts.

A refractory period is present for responses to strong photic stimuli. A second light stimulus applied while the response to the first is still under way produces little or no additional effect (Fig. 2c, d). A normal second response cannot be evoked until about a minute after the first response has subsided. This refractory period may be due to the bleaching of a photosensitive pigment. As in column bending, the responses were similar for brief or extended illumination periods (Fig. 2d, e). There is no evidence for electrical activity on the surface of the circular or parietal muscles.

Tentacle extension response

Illumination of the exposed upper column and oral disc of a dark adapted *Calamactis* causes a brief increase in irregular tentacle activity after a reaction time of about 5 s. The tentacles then unfold outward toward the plane of the oral disc and a symmetrical parietal contraction causes the upper column to shorten. The tentacle activity is accompanied by a rise in coelenteron pressure, after which the tentacles remain extended and the pressure returns to its original value about 25 s after the initial response. No localized centre for initiating the response was found and if the illuminated area is significantly reduced, the response becomes sporadic. No changes in the normal electrical activity occur during this response.

Electrical activity

A variety of electrical events can be recorded from the surface of *Calamactis* as a consequence of nervous and muscular activity. Some of these are spontaneous while others are evoked by external stimuli, including photic stimuli. The photic responses to be discussed below are associated with through-conducted electrical pulses apparently occurring in the nerve net.
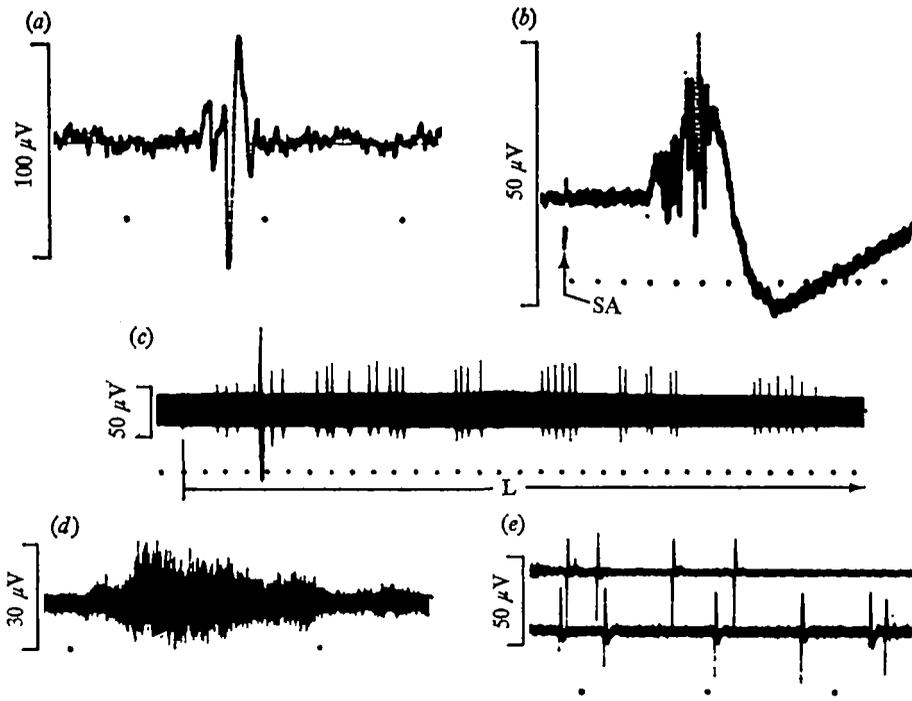
Fig. 3. Electrical activity in *Calamactis*. Recordings from retractor muscle (*a*) and tentacles (*b–e*). (*a*) Details of a nerve net pulse (NNP) from a retractor muscle. (*b*) NNP from a tentacle. SA (stimulus artifact). (*c*) Sequence of NNP's evoked by illumination (L). (*d*) Local spindle-shaped potential associated with individual tentacle movement. (*e*) Local potentials recorded from two tentacles. (*d*) and (*e*) not affected by light. Scale: (*a, b*) 10 msec markers, (*c–e*) 10 s markers.

The nerve net pulses (NNP's) are transmitted without decrement throughout the nerve net of the tentacles, oral disc, upper column epidermis and retractor muscles (Pickens, 1969). These pulses have compound wave-forms characteristic of the region from which they are recorded. NNP's recorded from a retractor muscle and a tentacle are shown in Fig. 3 (*a*), (*b*) respectively. The tentacle pulse appears to be composed of the action potentials from neurones within the suction electrode superimposed on the initial portion of a slower muscle potential. The slower component is absent in the retractor muscle pulse presumably because facilitation of neuromuscular junctions by a second NNP is required (Josephson, 1966). NNP's may arise spontaneously or be evoked by photic or other stimulation.

Other prominent types of electrical activity observed in intact, buried *Calamactis* are illustrated in Fig. 3 (*c–e*). The sequence of NNP's in Fig. 3 (*c*) resulted from light stimulation. The local spindle-shaped potentials of Fig. 3 (*d*) are associated with individual tentacle movement and occur every few minutes even in severed tentacles. The local pulses in Fig. 3 (*e*) were recorded simultaneously from two tentacles. They appear to be muscle potentials and occur occasionally after mechanical stimulation. Light has little if any effect on these local potentials.
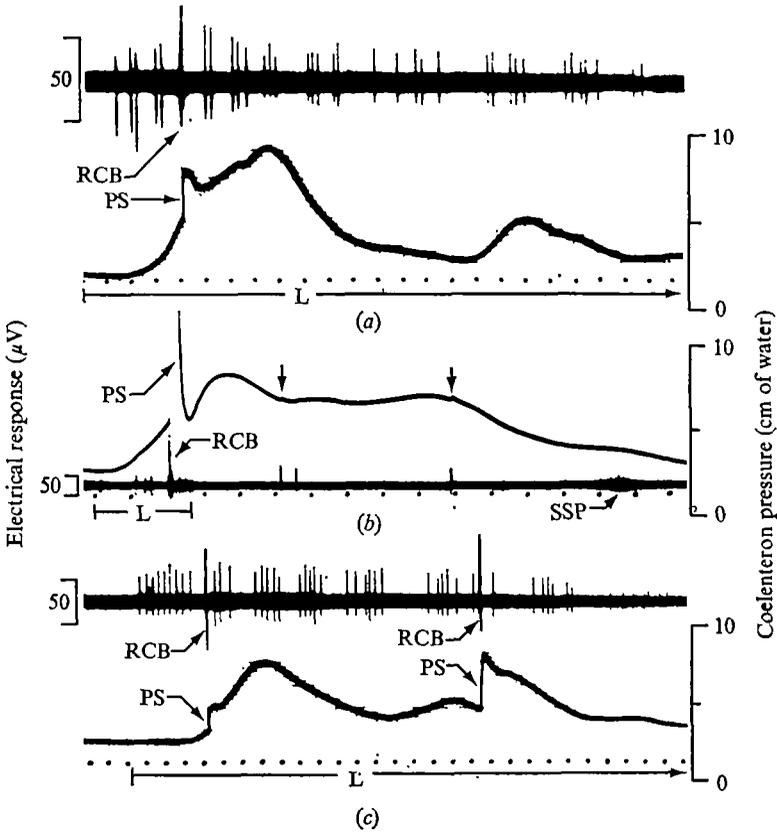
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Fig. 4. Nerve net responses. (a) Response containing single NNP's, slow contraction bursts (2–4 s pulse separation) and a single rapid contraction burst (RCB) with its accompanying pressure spike (PS). (b) Response with two small pressure spikes (arrows) caused by tentacles contracting with individual NNP's. Spindle shaped-potential (SSP). (c) Response with single NNP's, slow contraction bursts and two RCB/PS pairs. The powerful incandescent illumination used in (b) evoked a tentacle extension response which preceded the NNP's. The weaker fluorescent lighting of (a) and (c) triggered the pacemakers but was insufficient to produce initial tentacle extension responses. Scale: 10 s markers.

Nerve net response

Illumination of the upper portion of an anemone can produce a second response in addition to the more consistently evoked tentacle extension response. This is the nerve net response (Fig. 4), which includes NNP's and an extended period of muscular activity that may be preceded by a tentacle extension response. This activity produces a more complex pressure curve than the curves of one or two maxima that accompany the previous responses. It seemed possible that the NNP's could be initiated by stretch or pressure receptors and thus be the result of muscular activity rather than a photochemical event in the nerve net. This possibility was investigated by artificially raising the coelenteron pressure to 15 cm of water above the ambient pressure for periods of several minutes. The increases in pressure caused slight distensions in the column but evoked no NNP's. Moderate mechanical stimulation of the tentacles, oral disc and column with a glass rod produced only occasional NNP's.

Nerve net responses are evoked by illuminating the entire upper portion of the
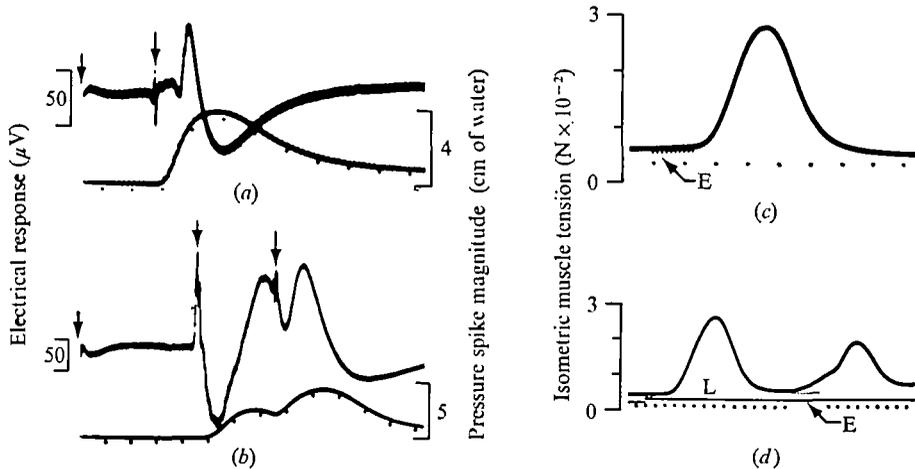
Fig. 5. Details of rapid contraction bursts containing (*a*) two NNP's (arrows) and (*b*) three NNP's (arrows) with their accompanying pressure spikes. Sweeps triggered by first NNP in both cases. (*c*) Circular muscle contraction in response to electrically evoked NNP's (E) in attached strip of tissue. (*d*) Parietal muscle response to electrically evoked NNP's (E) during refractory period for light stimulation. Scale: (*a*, *b*) 100 ms markers, (*c*) 10 s markers, (*d*) 5 s markers.

anemone. The NNP's occur singly, in slow contraction bursts with 2–4 s pulse separation (Fig. 4*a*, *c*) and in rapid contraction bursts with 250–500 ms pulse separation (Fig. 4*a–c*). In order to locate the sites of pulse initiation with greater precision, a light source focused to a 1 mm diameter spot was used to stimulate the anemone. With this light, occasional NNP's could be evoked from the outer margin of the oral disc, but from no other area on the anemone. These pulses were obtained with less reliability and after considerably longer exposure times than with illumination of the entire oral disc. The NNP's, then, appear to originate from pacemaker systems distributed around the margin of the oral disc. This distribution of photosensitivity is suggestive of that encountered for photoreceptors in medusae.

A prominent feature of most nerve net responses is the occurrence of one or more rapid contractions which cause the column to shorten and partially or totally enfold the oral disc and tentacles. The rapid contractions appear as abrupt increases in recorded pressure, coinciding with distinctive bursts of NNP's. These are the rapid contraction bursts of either two or three NNP's which produce rapid contractions of the retractor muscles (Fig. 5*a*, *b*). The first NNP in the burst precedes the second by about 300 ms. This second pulse is followed by a positive pressure spike that rises to its maximum of approximately 5 cm of water within 200 ms. When three pulses occur (Fig. 5*b*), the third follows the second by about 300 ms and enhances the pressure spike initiated by the second. The second and third pulses are accompanied by large muscle potentials which make rapid contraction bursts easily recognizable among the NNP's of the nerve net response (Fig. 3*c*, 4). The intervals between NNP's in a nerve net response are greater than 2 s except during rapid contraction bursts. The distinctively shorter inter-pulse intervals in rapid contraction bursts suggest that they are produced as separate groups, apparently to initiate rapid contractions in the retractor muscles. Rapid contractions are produced only by the retractor muscles responding to NNP's
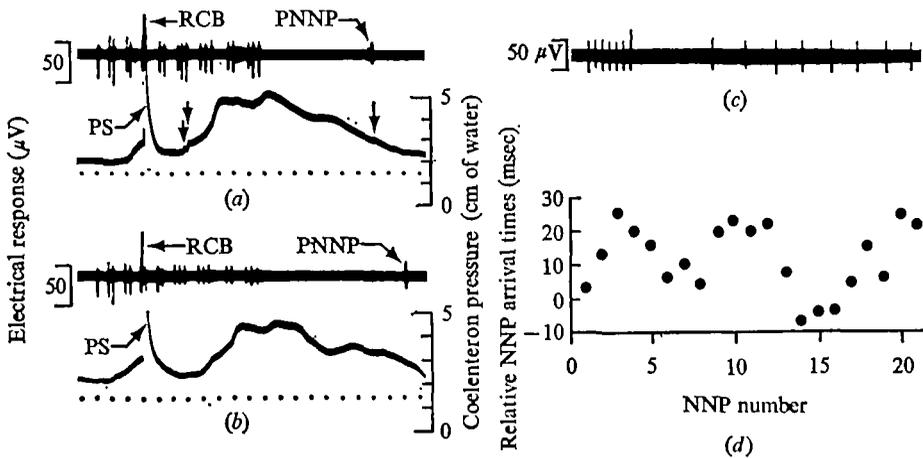
Fig. 6. (a, b) Responses to consecutive stimulations (23 min apart) with a sequence of NNP's previously recorded during a nerve net response. Stimulation administered in the dark. Arrows indicate small pressure spikes caused by tentacle contractions. PNNP (poststimulation NNP), RCB (rapid contraction burst), PS (pressure spike). (c) Group of seven NNP's electrically evoked at 15 s intervals followed by a slow withdrawal and a poststimulation sequence (first eight NNP's shown) which continued for more than an hour. Light stimulation is also effective. (d) Relative arrival times of NNP's recorded from opposite tentacles during a light-evoked poststimulation response similar to the one in (c). Scale: (a, b) 10 s markers.

separated by less than about 1·5 s (the retractors themselves are not sensitive to light). Circular or parietal muscles have not been observed to produce rapid contractions under any conditions.

The slow component of the pressure response may also be due in large part to the action of NNP's. These NNP's occur in slow contraction bursts (Fig. 4a, c), which are only produced as a result of light stimulation, and as individual pulses (Fig. 4b). Isolated circular and parietal muscles contract slowly when NNP's are evoked in a tentacle connected to the muscle preparation by a thin strip of tissue (Fig. 5c). These contractions indicate an effective conduction system in the circular and parietal muscles although no electrical activity has been detected. It will be recalled that a strong light stimulus evokes a brief period of increased pressure or tension followed by a refractory period during which light is ineffective as a stimulus. For electrical stimulation, however, there is no refractory period. Repeated electrical stimulation results in a sustained contraction even during the refractory period for light (Fig. 5d). Simultaneous light stimulation and initiation of NNP's by electrical stimulation produces a greater initial pressure or tension response than when either stimulation is applied alone. It is therefore suggested that the initial pressure rise in a nerve net response is due to the combined effects of local light reactions and light-evoked NNP's while the remaining pressure pattern is maintained, at least in part, by nerve net pulses.

The nerve net response, then, seems to consist of initial local light-evoked reactions combined with more sustained activity directed by light stimulated pacemakers acting through the nerve net and the column conducting system of the circulars and parietals. The portion of the response governed by pacemakers can be determined by recording

the NNP sequence from a nerve net response on magnetic tape and using this record-ing to trigger a stimulator to duplicate the original NNP sequence in the same or other anemones. Pulses from the stimulator are applied to a tentacle with a suction electrode and the resulting NNP's are monitored from another tentacle to ensure that the recorded pulse pattern is accurately reproduced in the nerve net. The coelenteron pressure is recorded as usual and used to compare the responses. Since the recorded NNP sequences can be administered in the dark, this technique effectively isolates the responses produced by pacemaker generated NNP's from the local light responses. Consecutive responses (23 min apart) to a sequence of NNP's originally recorded from a different anemone are shown in Fig. 6(a), (b). Both responses in Fig. 6 were recorded in the dark and show pressure drops after the rapid contractions. In the three light-stimulated nerve net responses of Fig. 4 the pressure continued to increase during this time, presumably because of the local light responses. The details of a response are influenced by the physiological state of the anemone at the time of stimulation and may show considerable variation from one trial to another. Closely spaced stimulations are more likely to produce similar responses than widely spaced ones or stimulations of different animals. Preliminary results of the effects of experimental modifications of the stimulating sequence were obtained but are not reported here.

Poststimulation responses

Occasionally light or some other stimulus triggers a series of low frequency NNP's which begin after the stimulation has ended. The prerecorded electrical stimulation applied in Fig. 6(a), (b) initiated a series of these pulses in both instances. The first pulse (PNNP) of each series is indicated in the figure. The initiation of another series is shown in Fig. 6(c) where the first seven NNP's were evoked electrically at 15 s inter-vals giving rise to the second series (first eight shown) which continued for more than an hour and was accompanied by a slow withdrawal of the oral disc beneath the sand. These pulse sequences may occur with or without accompanying movement.

Further analysis of the NNP's in these sequences is possible by observing the shifts in the sites of NNP initiation. These shifts can be observed by comparing the pulse arrival times from tentacles on opposite sides of the oral disc. This technique reveals that the relative arrival times vary irregularly in the absence of visible movement. However, sustained muscular activity (such as slow column withdrawal or burrowing) is accompanied by periodic organization of the relative pulse arrival times. In well developed cases such as is shown in Fig. 6(d) (recorded during light-stimulated slow column withdrawal) the periodicity is distinctly sinusoidal. This sinusoidal shape suggests a possible rotating site for NNP initiation, probably in the oral disc or upper column.

Effects of $MgCl_2$

Excess magnesium ions have a paralysing effect on both intact *Calamactis* and iso-lated muscles. Magnesium is commonly used to block nerve net conduction, ap-parently acting at synapses as well as the neuromuscular junctions. A solution of ½ sea water and ½ $MgCl_2$ isosmotic with sea water causes the spindle activity such as that shown in Fig. 3(d) to stop immediately in an intact buried anemone. Spontaneous pressure changes and electrical activity cease in about an hour. NNP's can be evoked

by electrical stimulation for several hours but the number of individual nerve impulses is sharply reduced as is the magnitude of the accompanying muscle potential. In contrast, Mackie & Passano (1968) found that conduction in non-nervous tissues of hydromedusae is not affected by magnesium ion concentrations that suppress presumed nervous activity.

Slowly increasing the magnesium concentration in the sea water bathing a preparation of circular or parietal muscles by adding isosmotic $MgCl_2$ causes the magnitudes of contractions in response to both light and electrical stimuli to decrease and the reaction times to increase. The responses to electrical stimuli are depressed more readily than the responses to light. The reaction times can be extended by 100% (due to increased latent periods) before the responses cease at a magnesium ion concentration of about 80 mM. The responses return to normal as the magnesium solution is gradually replaced with sea water. Ross (1960) also found that excess magnesium ions depress the size and increase the latency of the response to electrical stimulation in *Metridium* before the preparation becomes inexcitable.

Microscopic examination by North & Pantin (1958) revealed that isolated mesenteries of *Metridium* contract when illuminated, even after sufficient anesthetization with magnesium chloride to prevent reflex responses. This led them to suggest a possible photosensitivity in the muscular system itself.

DISCUSSION

Dermal photosensitivity has been observed to occur widely throughout the animal kingdom. Although this dermal light sense is found in every major phylum, electrophysiological evidence has been obtained in relatively few instances. This study establishes the presence of complex light-evoked nervous and muscular responses in the actinian, *Calamactis*.

Responses to light in *Calamactis* are composite events involving the coordination of several muscle groups with inputs from pacemakers and areas of local photosensitivity. Fig. 7 illustrates a model of the photoresponsive mechanisms described above. The circular and parietal muscles both possess local sensitivity to light. Illumination of a small area on the column causes the circulars to contract, producing a modest rise in pressure, followed in several seconds by the parietal contraction and column bending in that direction. If the entire upper column is illuminated, all of the parietals and upper circulars contract, the pressure rise is greater than for bending and a tentacle extension response occurs. With sufficient stimulation, pacemakers located around the margin of the oral disc are activated to trigger NNP's. Widely spaced NNP's and slow contraction bursts prolong the response by activating the circulars and parietals, causing additional contractions and the maintenance of an elevated pressure. Single NNP's sometimes evoke tentacle contractions which are registered as small pressure spikes on the overall pressure response. The rapid contraction bursts of two or three closely spaced NNP's are responsible for evoking rapid contractions in the retractors. The column conducting system which seems to coordinate circular and parietal activity apparently interacts with the nerve net and is probably involved with local photic responses. It may eventually be identified with slow conduction systems similar to those described by McFarlane (1969, 1973, 1974a, b).
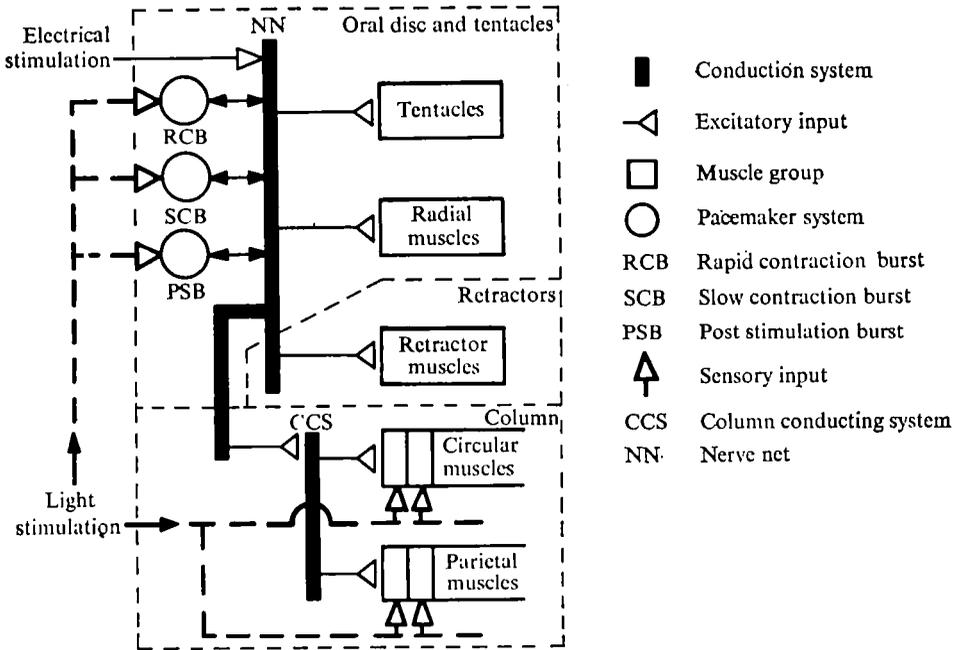
Fig. 7. Photoresponsive mechanisms in *Calamactis*.

Bending is a local response in which the mechanisms involved are probably not very different from the contraction response in isolated muscles. Both of these responses can be consistently evoked by light stimulation. This is not the case for the more complex nerve net response. Often this response cannot be evoked at any illuminance. At other times it can be evoked repeatedly with only moderate illumination. The threshold of the pacemakers to photic stimulation apparently depends on the prevailing physiological state of the anemone. Batham & Pantin (1950c) described a hierarchy of activity patterns (phases) and their initiating stimuli in *Metridium*. A stimulus could be prevented from triggering its respective phase if, for example, a conflicting phase was in progress at the time. A similar situation apparently exists in *Calamactis*.

Reaction times for the bending response in *Calamactis* are similar to those in *Metridium* except for two significant differences concerning variability and latent period. In *Calamactis* the reaction times for stimuli of a particular illuminance rarely vary by more than 25 % of the mean time for that illuminance. North (1957) found up to a sevenfold fluctuation in reaction times for *Metridium*. North also found that illumination must be continued for the entire reaction time; consequently, *Metridium* does not have a latent period for the bending response. This is the only known case for which a latent period is absent (Steven, 1963). A definite latent period exists for *Calamactis* and, in fact, is the major part of the reaction time.

Substantial reaction times of from 3 to 25 s precede the photic responses in *Calamactis*. This is consistent with Steven's (1963) observation that reaction times of dermal photoreceptors are generally much longer than those of eyes. There are numerous examples of reaction times equal to or even longer than those for *Calamactis*. Slow conduction systems such as those described by McFarlane (1969), with conduc-

tion velocities of 3–15 cm/s, have not yet been found in *Calamactis*. Even if such systems were present, however, their conduction velocities are much too fast to account for the length of the reaction times observed in *Calamactis*. Alternative, non-nervous conduction systems occur in other coelenterates. Mackie (1965) described a nerve-free epithelial conduction in siphonophores and epithelial conduction was also found in hydromedusae (Mackie & Passano, 1968). However, the conduction velocities are even greater than for McFarlane's slow conducting systems. Batham & Pantin (1950b) concluded that the long delays in coordinating inherent contractions in *Metridium* were due to local effects and not to slow conduction. This appears to be the case in *Calamactis* as well.

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