J. Exp. Biol. (1972), 57, 633–649
With 11 *text-figures*
Printed in Great Britain

EXPANSION AND CONTRACTION OF THE ORAL DISC IN THE SEA ANEMONE *TEALIA FELINA*

BY I. D. MCFARLANE AND I. D. LAWN
Gatty Marine Laboratory, University of St Andrews, Scotland

(*Received* 16 *March* 1972)

INTRODUCTION

Co-ordination of muscular action in sea anemones seems to involve a diffuse nerve net, condensed in some regions to form a rapid, through-conduction system. The properties of this system have been studied most thoroughly in *Calliactis parasitica* (Pantin, 1935*a*, *b*). Recent work (McFarlane, 1969*b*) has shown that in *C. parasitica* there are also two slow conduction systems, termed the SS 1 and SS 2. It is not yet clear whether the SS 1 and SS 2 are non-nervous (neuroid) conduction systems (see review by Mackie, 1970) or are examples of nerve nets separate from the through-conduction system.

The demonstration of the presence of multiple conduction systems requires that much of the behavioural physiology of sea anemones be re-investigated. A single electrical stimulus applied to any part of the ectoderm elicits a pulse (SP 1) in the SS 1, and this pulse is propagated over the entire ectodermal surface. The SS 1 controls detachment of the pedal disc during the behavioural response whereby *Calliactis parasitica* transfers to a *Buccinum* shell containing the hermit crab *Pagurus bernhardus* (McFarlane, 1969*c*). Maintained contact of the tentacles with a shell is accompanied by a train of pulses in the SS 1, followed by detachment. Electrical stimulation of the SS 1 can also elicit detachment. The SS 1 in *Tealia felina* is involved in the pre-feeding response (McFarlane, 1970). Dissolved food substances, contacting the column of *Tealia*, elicit activity in the SS 1, followed by expansion of the oral disc and lowering of its margin. This opening response can also be elicited by electrical stimulation of the SS 1. The pre-feeding response presumably results in a greater chance of contacting nearby food.

The present study concerns the effect of the SS 1 on activity of the radial muscles of the oral disc of *Tealia felina*. Oral disc expansion can be explained, in part at least, by an observed inhibition of the radial muscles. These muscles can be regarded as having a dual control, excitatory from the nerve net and inhibitory from the SS 1.

MATERIALS AND METHODS

Specimens of *Tealia felina* var. *lofotensis*, with expanded oral disc diameters of 6–12 cm, were used for all experiments. Observations were made at sea-water temperatures between 7 and 12 °C.

The oral disc radial muscles were chosen for this study as they appear to play a most important part in the expansion response. The only previous description of

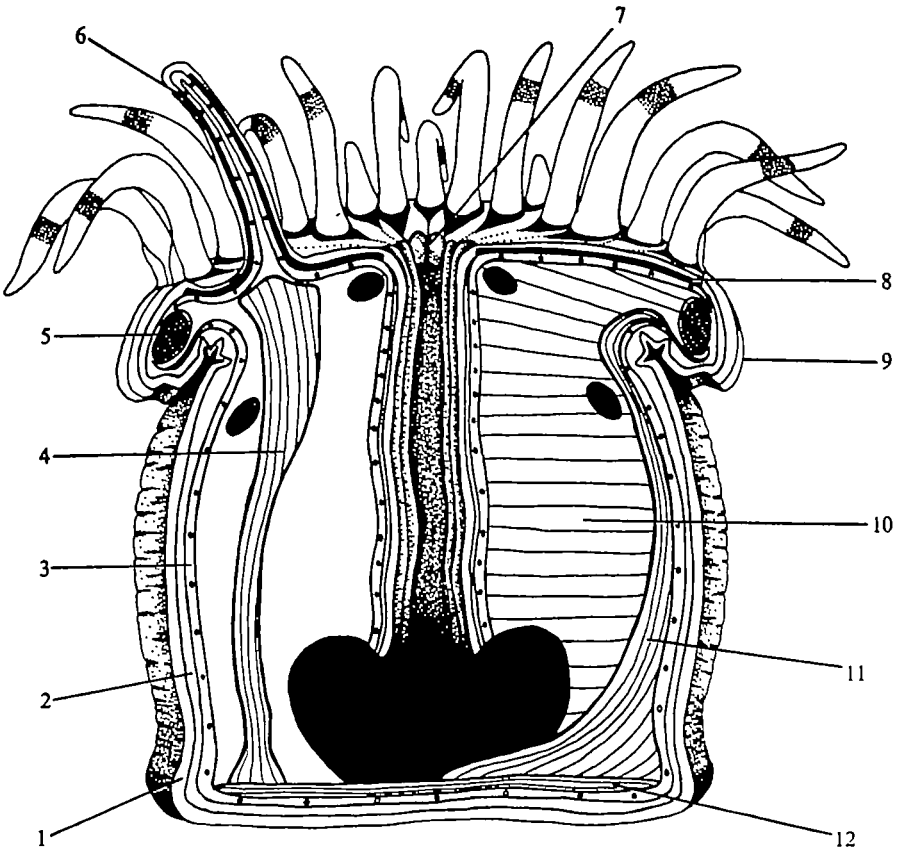

Fig. 1. Muscular anatomy of *Tealia felina* var. *lofotensis*. The diagram shows on the left the structure of the endocoelic face of a non-directive perfect mesentery, and on the right the exocoelic face. 1, Ectoderm; 2, mesogloea; 3, endoderm (includes circular muscle layer); 4, retractor muscle; 5, sphincter muscle; 6, tentacle ectodermal longitudinal muscle; 7, siphonoglyph; 8, ectodermal radial muscle of oral disc; 9, collar; 10, transverse muscles; 11, parietobasilar muscle; 12, basilar muscle. Based in part on description by Stephenson (1928).

recordings of the muscular activity of radial muscles is that of Batham & Pantin (1954), working with *Metridium*. The authors give little information concerning the preparation used. The position of the radial muscles and the general arrangement of muscles in *Tealia* are shown in Fig. 1. The radials and the tentacle longitudinals are ectodermal in origin but the latter may in some individuals lie totally or partly enclosed by mesogloea (Carlgren, 1921). The radials are strongly developed, in contrast to the sparse endodermal circular muscle of the oral disc. The other muscles referred to in this study are the transverse mesenterics, the sphincter and the retractors.

The preparation used for most experiments was obtained in the following way. An anemone was bisected longitudinally and a thread was sewn into one of the pair of siphonoglyphs that lie at the pharyngeal edge of the oral disc. Attachment was made here as this region was found to be less liable to tearing than the rest of the disc. However, identical results were obtained when activity was recorded from

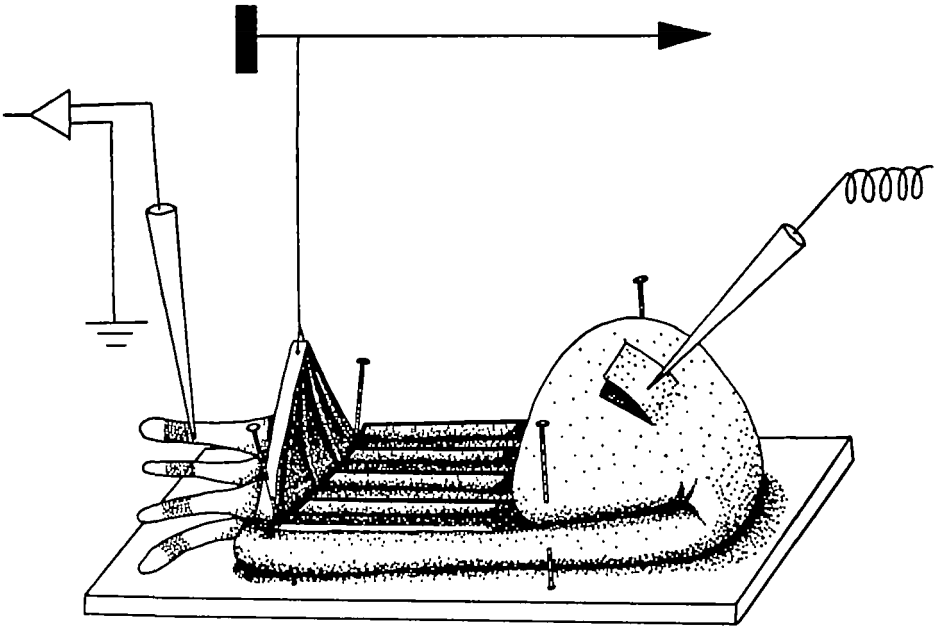

Fig. 2. The radial muscle preparation. Suction electrodes were used for recording and stimulation. The recording electrode is attached to a tentacle. The stimulating electrode is shown here attached to a flap in order to stimulate the SS 1 only. Details of other stimulus electrode positions are given in the text.

other parts of the disc. The preparation was trimmed to a sector equal to about 45° of the oral disc. The pedal disc was removed and generally the mesenteries were cut off to within a few millimetres of their attachment to the column wall and to the oral disc. It was found that this did not destroy the through-conduction system pathway. A shallow flap was cut near the base of the column; such flaps comprise ectoderm and superficial mesogloea. The basal part of the column curls over when the preparation recovers; this allows the stimulating electrode to be attached to the flap. This technique has been previously described (McFarlane, 1970) and allows stimulation of the following systems:

(1) The nerve net alone – by electrical stimulation of either the mesogloeal surface under the flap or of a mesentery. Voltage should be only just above threshold to avoid possible stimulation of the SS 2 (McFarlane, 1969*b*). The nerve net may also be stimulated with the electrode on the intact column and the stimulus voltage below SS 1 threshold. The SS 1 threshold is about 50% higher than that of the nerve net.

(2) The SS 1 alone – by electrical stimulation of the flap at voltages above SS 1 threshold.

(3) The SS 1 and the nerve net together – by stimulation of the intact column at voltages above SS 1 threshold.

The preparation was pinned with the ectodermal surface of the column down. All operations were performed without anaesthetic as preparations recovered more quickly and were generally more active than when anaesthetics were used. Preparations were left to recover in running, well-oxygenated sea water for 16–24 h. Most

studies were made between 16 and 48 h after operation. Preparations more than 72 h old were not used.

Activity of the radial muscles was recorded with a light isotonic lever writing on a kymograph. Attached preparations relaxed to about one-half their normal expanded length. Suction electrodes were used for both recording and stimulation (Josephson, 1966). Fig. 2 summarizes the experimental arrangement. The recording electrode was always attached to the mid-region of a tentacle and was used to monitor the results of electrical stimulation. This is essential with the flap-stimulation technique in order to ensure that the desired conduction system is being stimulated. In this recording position the electrode picks up activity associated with both the nerve net and the SS 1 (McFarlane, 1970). Pulses were amplified and displayed on a Tektronix 564B storage oscilloscope. All electrical stimuli were of 1 msec duration.

RESULTS

Electrical activity

Pulses recorded from preparations seem identical to those recorded from the intact animal. SS 1 activity can still be elicited by stimulation of any part of the ectoderm. Pulses in the SS 1 slowly increase in size during the first few minutes after electrode attachment but then remain at a more or less constant size. Continuous monitoring of activity can be carried out for at least 5 h. Spontaneous SS 1 pulses were not recorded from any of the preparations studied.

Evoked responses associated with the nerve net and with the SS 1 can be easily distinguished, and it is possible to state with certainty which system is being stimulated. With some attachments the nerve-net pulse is not clear, and in these cases the recording electrode was moved until a good recording position was found. This suggests that the nerve-net pulse is not a small muscle action potential associated with a small contraction of the ectodermal longitudinal muscles of the tentacle but is activity recorded from the scattered neurites themselves. Often the pulse is of very short duration (less than 5 msec) and is almost certainly recorded from the neurites; this pulse is therefore similar to the pulse recorded from the mesenteries of *Metridium* by Robson & Josephson (1969).

The only occasion when monitoring is difficult is when the SS 1 is stimulated at high frequencies (greater than 1 shock every 3 sec). Repetitive stimulation at frequencies down to about 1 shock every 15 sec results in a progressive increase in response delay and a decrease in SS 1 pulse size. Fig. 3 shows this effect at frequencies of 1 every 4 sec and 1 every 6 sec. At high frequencies the SS 1 pulse may become too small to distinguish, and it is difficult to tell whether the system has ceased to conduct or whether the pulse is too small to be visible above the noise level. Even at lower frequencies the SS 1 sometimes fails to respond to some of the shocks during a stimulus series. Repetitive stimulation has a similar effect on the SS 1 of *Calliactis parasitica* (McFarlane, 1969*b*). It is of interest that intracellular recordings of the pulse associated with myoid conduction in the siphonophore *Nanomia bijuga* show that repolarization after activity may take up to 3 sec (Spencer, 1971).

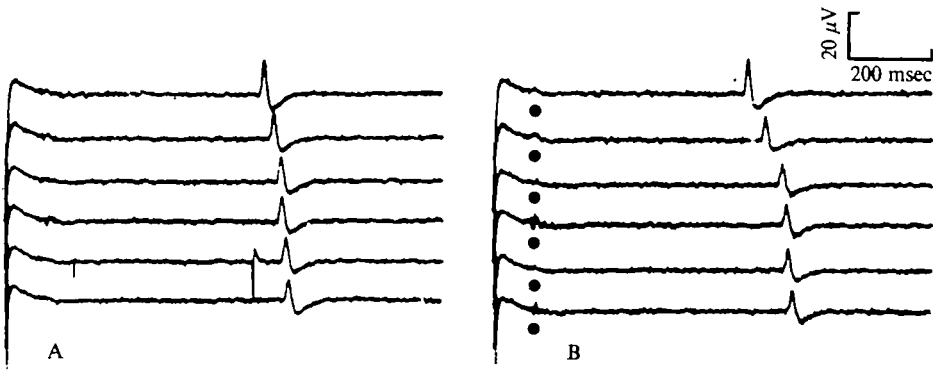

Fig. 3. The effect of repetitive stimulation of the SS 1. Recording electrode on a tentacle, stimulating electrode on intact column. Stimulus frequencies: (A) 1 shock every 6 sec, (B) 1 shock every 4 sec. Responses shown to six shocks, reading from top to bottom. Note increase in response delay of SP 1 and also decrease in pulse size, both changes being more marked at the higher stimulus frequency. Pulse associated with the nerve net is just detectable in B (position shown by dots). There is no obvious change in response delay for this pulse. Note the considerable difference in response delay between the nerve net pulse and the SS 1 pulse.

Responses to electrical stimulation

The majority of preparations showed spontaneous activity but the frequency of contractions was often very irregular. Batham & Pantin (1954) do not mention spontaneous activity in their preparations of the oral disc of *Metridium*. There is no information available to indicate whether the oral disc shows spontaneous activity in the intact animal, and it is possible that the contractions are induced by stretching. However, one observation, of uncertain significance, is that preparations that showed little or no activity could be made to start spontaneous contractions by applying a small number of shocks to the SS 1. The initial results refer to preparations that were spontaneously active.

The general result of stimulation of the SS 1 alone is a reduction in the size of the spontaneous contractions and an increase in the length of the radials. Fig. 4A shows the response to 35 shocks at a frequency of 1 every 5 sec. A clear response is visible within 1 min of the start of stimulation. A consistent aspect is the prolonged recovery phase; the inhibitory effect persists beyond the end of stimulation and the recovery process involves a gradual increase in activity and decrease in length. Contractions occurring late in the recovery period are often larger than normal spontaneous contractions. The minimum frequency of SS 1 stimulation found to give a clear relaxation was 1 shock every 30 sec (Fig. 4B). The maximum frequency observed to cause relaxation was 1 shock every 2 sec. The minimum number of shocks that need be applied to produce a clear effect was found to be 5 (at 1 every 5 sec). Insufficient results are available for us to be able to state the optimum frequency of stimulation. Rarely, relaxation was not obvious during stimulation but became obvious shortly afterwards. Fig. 4C shows this following 20 shocks at 1 every 6·3 sec.

Stimulation of quiescent preparations also elicited an increase in length (Fig. 5A), and the recovery process invariably involved an increase in spontaneous activity, this effect often being long-lasting. Sometimes a very large recovery contraction was evident (Fig. 5B).

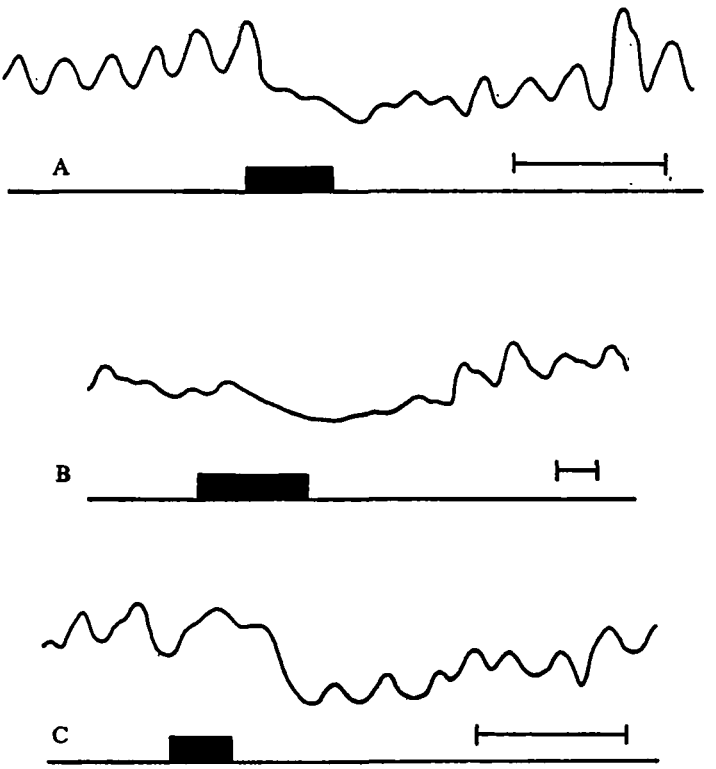

Fig. 4. Action of SS 1 stimulation on spontaneously active preparations. Stimulating electrode on a flap so that only the SS 1 is stimulated. (A) Response to 35 shocks at 1 every 5 sec, (B) 30 shocks at 1 every 30 sec, (C) 20 shocks at 1 every 6·3 sec. In this and all subsequent kymograph records contraction is upwards. Note reduction in spontaneous activity, increase in length and the prolonged recovery phase. There is a delayed onset of relaxation in C. Time scale = 5 min.

In contrast, low-frequency stimulation of the nerve net alone produces slow contraction of the preparation (Fig. 6A). Such slow contractions have been previously described (Batham & Pantin, 1954) for *Metridium* radials, where they occur at stimulus frequencies between 1 shock every 5 sec and 1 shock every 20 sec. Batham and Pantin point out that the slow contraction might result from action of the endodermal muscles, the transverse mesenterics, but that this is unlikely as these are attached only where the mesenteries insert into the oral disc and buckling is not seen to accompany contraction. Another similarity between *Tealia* and *Metridium* is that in both the radials show small but clear fast contractions to every shock after the first of a series at high frequency (greater than 1 shock every 2 sec). Electrical recordings from the oral disc of *Tealia* show that muscle action potentials are not recorded after the first (facilitating) shock but are observed following all subsequent shocks.

Since the above results indicate that low-frequency stimulation of the SS 1 causes inhibition whereas low-frequency stimulation of the nerve net causes slow contraction, it is interesting to consider the interactions of the nerve net and SS 1 effects. Stimulation of the two systems together should result in a conflict between the two

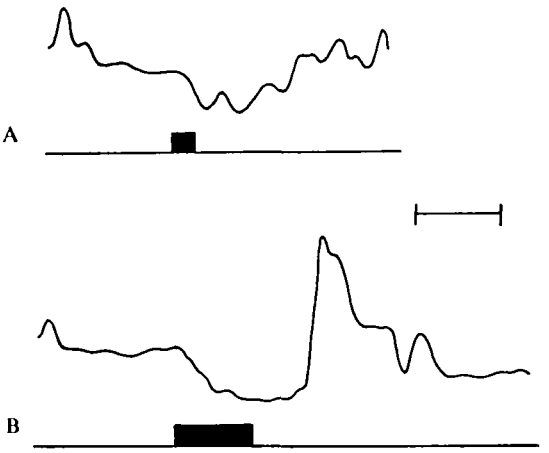

Fig. 5. Effect of SS 1 stimulation during periods of reduced spontaneous activity. (A) 25 shocks at 1 every 5 sec (SS 1 pulses recorded following first 15 shocks only), (B) 30 shocks at 1 every 10 sec. Note the very large recovery contraction in B. Time scale = 5 min.

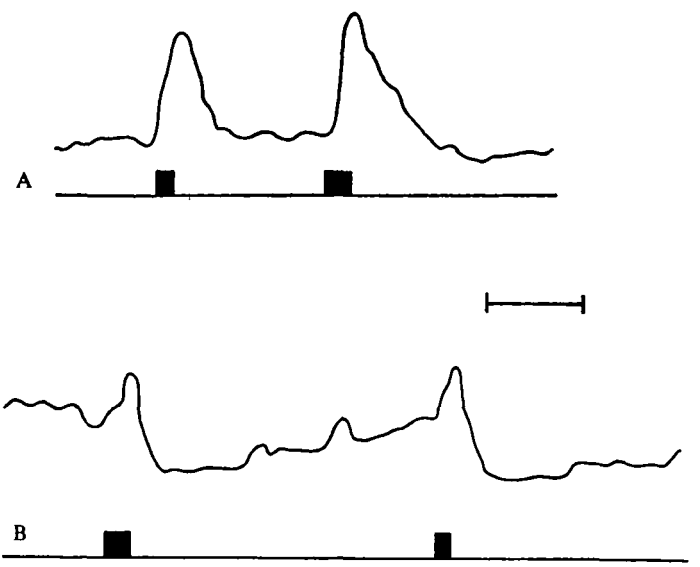

Fig. 6. Showing interaction of effects of nerve net and SS 1 stimulation. (A) Electrical stimulation of nerve net only (stimulating electrode on mesentery); firstly 10 shocks at 1 every 5 sec and secondly 10 shocks at 1 every 10 sec. The radials respond with slow contractions. (B) Stimulation of intact column (nerve net and SS 1 together); firstly 10 shocks at 1 every 10 sec and secondly 10 shocks at 1 every 5 sec. Note reduced slow contraction followed by increase in length and reduction of spontaneous activity. All results from the same preparation. Time scale = 5 min.

opposing actions of excitation and inhibition. Fig. 6B shows the result of stimulation of the intact column of the same preparation as in Fig. 6A. A slow contraction is the first obvious response, but this is smaller than that seen following stimulation of the nerve net alone. Relaxation then leads to a marked increase in the length of the radials and a slight reduction in spontaneous activity, followed by a slow recovery to the resting length. This may be interpreted as showing that the inhibitory action

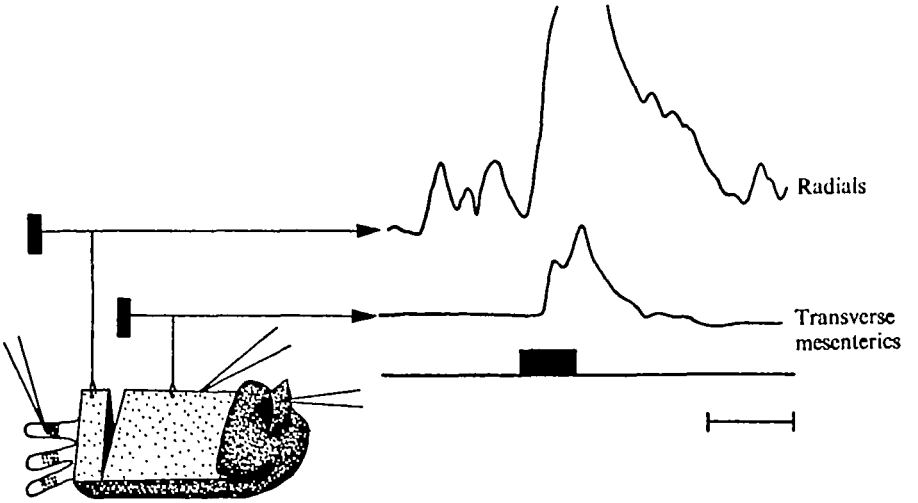

Fig. 7. Response of double preparation to nerve-net stimulation. The preparation is shown with a stimulating electrode on a mesentery (to excite the nerve net) and on a flap (to excite the SS 1). Thirty shocks to the mesentery at 1 every 15 sec elicit a slow contraction from both the oral disc radials and the transverse muscles of the mesentery. Time scale = 10 min.

of the SS 1 has a slower onset than the excitatory action of the nerve net. This result also shows that in addition to affecting spontaneous activity, SS 1 activity can reduce the size of slow contractions elicited by nerve net activity.

As Batham & Pantin (1954) point out, results obtained with radial muscle preparations may be liable to misinterpretation as the strip of oral disc also inevitably contains some endodermal muscle. The activity of the oral disc circulars is at 90° to that of the radials and is unlikely to affect the mechanical recordings. However, the transverse muscles run parallel to the ectodermal radials and clearly could produce some of the observed actions. To test this a double preparation was used (Fig. 7). The mesenteries were not excised and an additional thread was attached to a mesentery, close to the oral disc. The transverse muscles were found to show little or no spontaneous activity; the radials must be responsible for the spontaneous activity recorded from the strip of oral disc. Nerve-net excitation by electrical stimulation of either a mesentery or of the column under a flap results in a slow contraction of both muscle groups (Fig. 7). The contraction of the transverse muscles appears comparatively weak. Fig. 8 shows the effect of stimulating a flap, firstly just below and secondly just above SS 1 threshold. In the absence of SS 1 pulses there is no response, confirming that the relaxation action is not due to stimulation of a conduction system in the ectoderm with a threshold lower than that of the SS 1. Inhibition of the radial muscles but not of the transverse muscles follows the second stimulus series. This implies that relaxation to SS 1 stimulation is truly a response of the radials. The recovery phase in Fig. 8 shows a large contraction that was, surprisingly, observed in both parts of the preparation. The pathway for this excitation of the transverse muscles is not known.

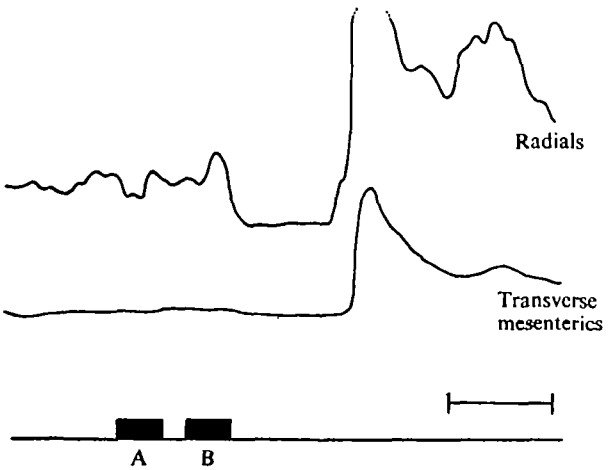

Fig. 8. Response of double preparation to SS 1 stimulation. Firstly the flap was stimulated below SS 1 threshold (A) and no response was elicited. Then stimulation was applied above SS 1 threshold (B), causing inhibition of radial activity but showing no clear action on the transverse muscles. However, both muscle groups showed a recovery contraction. In both cases 30 shocks at 1 every 15 sec were applied. Time scale = 10 min.

Action of food extract

Dissolved food substances, contacting the column of *Tealia*, elicit SS 1 activity and expansion of the intact animal (McFarlane, 1970). The results of the electrical stimulation experiments suggest that addition of food extract to a preparation should cause inhibition of spontaneous activity of the radial muscles.

The extract was prepared by grinding mollusc (*Mytilus*) tissue in a ground-glass homogenizer, centrifuging at 10000 rev/min for 20 min and drawing off the clear portion of the extract. The technique used was to monitor evoked SS 1 activity and contractions using the preparation previously described. No spontaneous SS 1 activity is detected in a normal preparation. However, following addition of food extract to the bath a series of SS 1 pulses was recorded. The occurrence of each SS 1 pulse was marked directly on the kymograph drum with an event marker. Fig. 9A shows the results of such an experiment.

Inhibition of spontaneous activity is not clear in this type of preparation; instead, a large slow contraction often follows addition of food extract (except once where a very low concentration was used, resulting in relaxation, but this was short-lived and was followed by slow contraction). This action may result from the fact that the food extract has access to all parts of the preparation and may elicit true feeding responses, involving contraction of the tentacles and oral disc.

A new technique of applying the extract was used to overcome this problem. A suction electrode was filled with food extract and was then attached to the column in the normal way. This electrode could be used both as a normal stimulating electrode and also as a strictly localized applicator of extract. The best results were obtained with electrodes of approximately 1 mm diameter at the tip. A total of about 0·8 ml of extract could be contained in the electrode, presumably ensuring that adequate amounts of stimulatory chemical were available. The basic extract was very con-

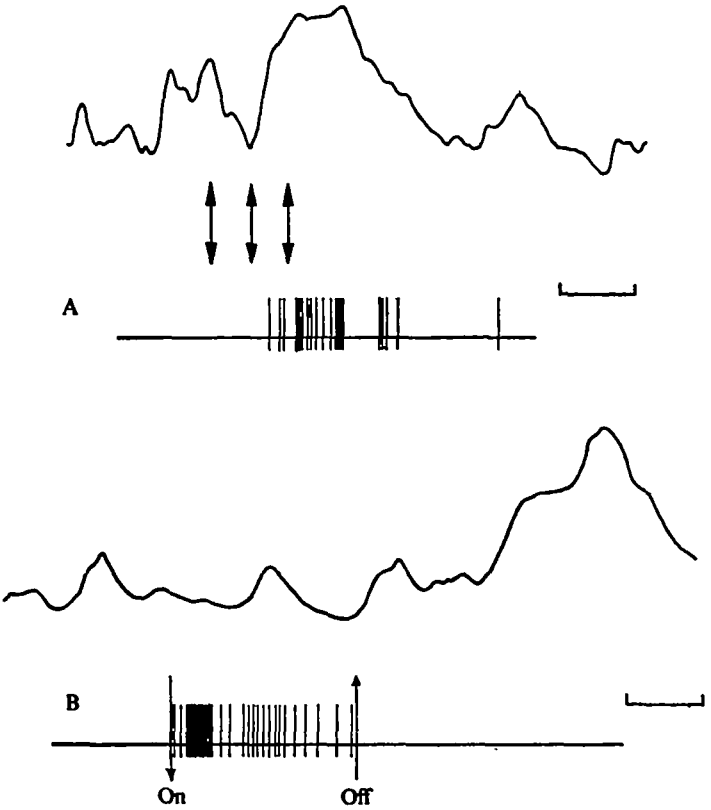

Fig. 9. The response to dissolved food substances. In each case the upper line shows the activity of the radial muscles and the lower line shows SS 1 activity (the length of this line indicates the period of SS 1 monitoring and the vertical lines show the position of SS 1 pulses. In A *Mytilus* extract was simply placed in the bath (the arrows show three successive applications of equal quantities of extract). No SS 1 pulses were seen before application of extract. The radials contracted, possibly due to stimulation of other systems by the extract. In B the extract was applied to a small part of the column only (see text for description of technique). The arrows show the time of application and removal of the stimulus. SS 1 pulses were seen only during the period of stimulation. The radials show a slight relaxation followed by a delayed recovery contraction. Time scale = 10 min.

centrated, usually being diluted with an equal volume of sea water; this was in order to ensure an active SS 1 response. In all experiments the electrode was attached a few millimetres from the base of the column.

Fig. 9B shows the results obtained. Again no SS 1 pulses were observed during the monitoring period prior to electrode attachment. The first SS 1 pulse was seen 40 sec after electrode attachment. To prevent leakage of extract during application sea water was slowly sucked into the electrode and this 40 sec delay may result from the fact that the stimulatory substances must diffuse a short distance to the column. During stimulation considerable suction was applied to the electrode so it is unlikely that extract could escape into the bath as a tight seal was formed between the column ectoderm and the wall of the electrode. Control experiments with electrodes containing sea water only showed that evoked SS 1 pulses are not a result of the applied suction. During the 24 min of stimulation 30 SS 1 pulses were seen. No further SS 1 pulses were seen once the electrode was removed. The kymograph results are

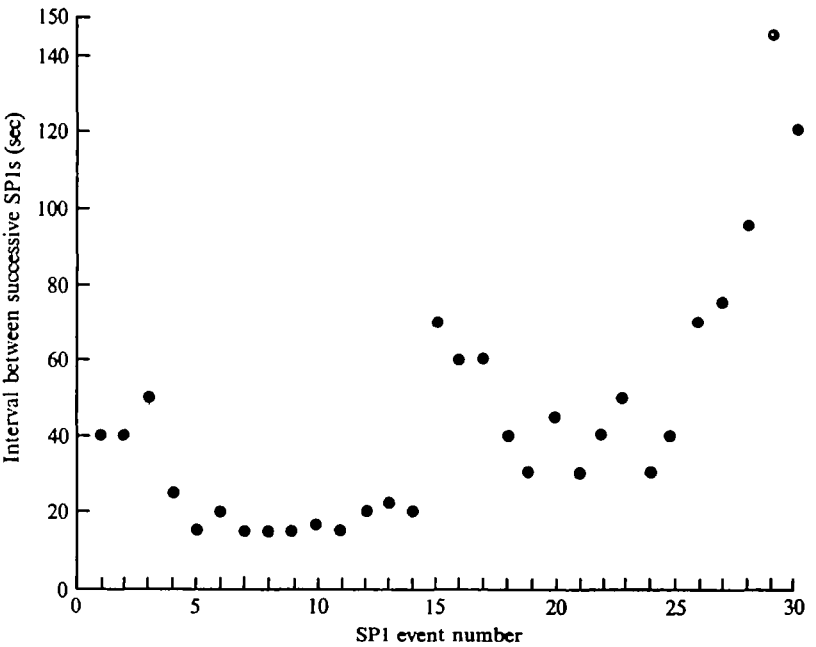

Fig. 10. Showing possible sensory adaptation in the response to dissolved food substances. These results are taken from Fig. 9B and show the gradual increase in pulse interval of the 30 SS 1 pulses elicited during the 24 min of stimulation. Application of extract was restricted to a small area of the column, and although stimulation was continuous the frequency of evoked SS 1 pulses fell considerably during the response.

not as clear as those obtained with electrical stimulation but there does appear to be a slight relaxation and loss of spontaneous activity. The contraction that did occur during the period of SS 1 activity in fact came after a period when firing frequency fell below 1 SS 1 pulse/min; perhaps this enabled excitation to overcome inhibition. The large contraction that followed removal of the electrode may represent the recovery phenomenon described earlier, though it is possible that some food extract may have escaped into the bath when the electrode was removed.

Inhibition may be less clear here than in response to electrical stimulation because the average SP 1 frequency was only 1 every 45 sec, although the maximum frequency in the early stages of the response was one every 15 sec. With electrical stimulation of the SS 1, inhibition could not be detected at stimulus frequencies below 1 shock every 30 sec, although the effective frequency for the intact animal may be lower. The sensory response seems little different from that of the intact animal (McFarlane, 1970). The SP 1 intervals for this particular response are shown in Fig. 10. This graph is interesting as it is the first information relating to activity frequency in a chemosensory response of a sea anemone. One important feature is that although an excess of stimulatory chemicals was provided, the response showed apparent sensory adaptation, though of course on a much extended time-scale compared with sensory responses of higher animals. Experiments with two stimulating electrodes should reveal whether this adaptation is local to the point of stimulation or in fact involves fatigue in the SS 1.

DISCUSSION

The only ectodermal muscles in *Tealia* are the oral disc radials and the tentacle longitudinals. In a few sea anemones – for example, *Gonactinia prolifera* – there are muscles and an associated nerve net in the column ectoderm (Robson, 1971). However, in the majority of species there is no evidence of muscles in the column and pedal disc ectoderm. Although there is clearly a nerve net in the ectoderm of the tentacles and oral disc, the presence of a nerve net in the column and pedal disc ectoderm is uncertain. The Hertwigs (1879–80) state that in these regions the nerve net is extremely sparse compared with the oral disc and tentacles. Most modern authorities have failed to detect nervous elements; for example, Batham (1965) could not find any in the column ectoderm of *Mimetridium cryptum*. However, Leghissa (1965) describes a sparse net in the column ectoderm of *Actinia equina* and also notes the presence of receptors, especially in the region of the sphincter. Clearly the anatomical evidence does not yet enable us to decide whether the SS 1 is a nervous or non-nervous conduction system.

The connexion between the ectodermal nerve net and the endodermal through-conduction system may occur at the oral disc. In *Mimetridium* (Batham, 1965) neurites pass from the mesenteries to the oral disc and then to the tentacles. This nerve net seems to link the muscles involved in the protective withdrawal response. Strong mechanical stimulation causes the retractors and the sphincter to show fast contractions that pull the oral disc down and constrict the upper part of the column. This is a symmetrical contraction in which the ectodermal muscles also play a part by causing shortening of the tentacles and reduction in oral disc diameter. The nature of this fast contraction has been described by Pantin (1935*a*) and typically a single pulse in the nerve net does not result in contraction but facilitates the response in some way such that subsequent pulses, arriving before the decay of facilitation, will elicit fast contractions. Muscle action potentials have been recorded from muscles showing fast contractions (Josephson, 1966; Robson & Josephson, 1969; McFarlane, 1969*b*). Electrical responses to single shocks have been recorded from tentacles of *Calliactis polypus* (Josephson, 1966), tentacles and sphincter of *Calliactis parasitica* (McFarlane, 1969*b*) and from mesenteries of *Metridium* (Robson & Josephson, 1969). In some cases these are clearly recordings from the nerve net itself, in others they may be small muscle action potentials associated with a small contraction.

Probably all muscles show another type of symmetrical response, a slow contraction, that apparently can be elicited by stimulation of the same nerve net (Batham & Pantin, 1954; Ross, 1957), at low frequencies. The ability to give both fast and slow contractions may be due to muscle properties and not to the presence of dual innervation or two muscle types. Extracellular suction electrodes do not record activity associated with slow contractions.

In addition to these symmetrical responses, most muscle groups seem capable of showing asymmetrical contractions. Such responses are very important during feeding, where they are seen in such events as local tentacle shortening, tentacle bending and local raising of the oral disc margin. These particular responses may involve just ectodermal muscles and they enable a restricted part of the disc and tentacles to transfer food to the mouth while the rest of the crown stays expanded in

readiness for further food capture. Pantin (1935*a*) explained such actions on the basis of interneural facilitation, implying that lateral spread in the oral disc is dependent upon facilitation of neural elements. However, although *Anemonia sulcata* is said to show almost total local activity as opposed to symmetrical responses (Pantin, 1935*b*), a single shock to a tentacle produces a nerve-net pulse that can be recorded from a tentacle on the opposite side of the disc, even though the observed response to stimulation is a strictly local contraction of the stimulated tentacle and a small number of neighbouring tentacles (McFarlane, 1969*a*). The results of Josephson (1966) for *Calliactis polypus* and of Horridge (1958) for *Cerianthus* also suggest that local disc contraction involves a conduction system separate from the through-conduction system. Until direct evidence can be obtained, we consider it simplest to assume that this activity is the result of mechanical or myoid conduction between fibres in the ectodermal muscle sheet and that restrictions on spread are imposed in some way by the radial orientation of fibres. Suction electrodes record complex electrical activity associated with these local contractions (McFarlane, 1969*a*).

Most muscles also appear to be spontaneously active. The site of origin of this activity is not known but in some cases groups of multipolar nerve cells in the endoderm have been proposed as pacemakers (Robson, 1961). In the case of the radials we consider it more likely that the rhythm is intrinsic and that it is this that is modified by SS 1 activity. Suction electrodes do not record electrical activity associated with this spontaneity.

Considering then just the ectodermal radial muscles, it appears that they show the following responses:

(1) Local activity; myoid or mechanical conduction?
(2) Spontaneous activity; possibly intrinsic.
(3) Fast contractions; symmetrical and co-ordinated by the nerve net.
(4) Slow contractions; symmetrical and co-ordinated by the nerve net.
(5) Induced relaxation; probably symmetrical and co-ordinated by the SS 1.

All the ectodermal muscles should perhaps be regarded as being a single muscle field; certainly the activity of the tentacle longitudinals is similar to that of the radials. Parker (1917*a*) showed that addition of *Mytilus* extract to isolated tentacles of *Condylactis* gave active writhings often accompanied by elongation. Davenport (1962) showed that tentacle preparations of *Radianthus*, *Anemonia* and *Tealia* were often quiescent but sometimes spontaneously active. The frequency of contractions was about 1 every 5 min. These contractions were more evident in *Radianthus* than in the other species studied. He found that 12 shocks at 7/sec caused a very dramatic relaxation and cessation of spontaneous activity of a *Radianthus* tentacle. Following this relaxation the tentacle remained inactive for some time. These were isolated tentacles and clearly more than one conduction system was being stimulated. These experiments were carried out at 23–24 °C, so that although a high stimulus frequency was used it is possible that this relaxation is equivalent to that shown by the radials of *Tealia*. The tentacle preparations also showed fast and slow contractions. Although direct recordings have not been made, our observations of the relaxation response of intact animals suggests that there is also extension of the tentacles. This clearly would play an important part in the pre-feeding response by further increasing the food-capture range of the tentacles.

An important question that so far remains unanswered is this: are the endodermal muscles also affected by SS 1 activity? It would seem at first sight that if the sphincter or retractor muscles did not relax the anemone would not open even if the radials relaxed. However, observations of the structure of *Tealia* suggest to us that for an anemone going from an open state to a more open state, relaxation of the radials will produce spreading of the oral disc and lowering of the margin, without involvement of any other muscle group. This is summarized in Fig. 11. A sea anemone can be regarded as a closed box with an internal hydrostatic pressure slightly positive with respect to the surrounding sea water (Chapman, 1949). In some anemones (e.g. *Tealia*, *Metridium* and *Actinia*) there lies below the margin a clear circular fold of the body wall (the parapet or collar). This encloses on its upper side a circular groove (fosse). The sphincter lies in the collar region, and between it and the bases of the tentacles lies a delicate upper part of the column (capitulum). As an open anemone relaxes (Figs. 11 B to C) there is initially folding at the fosse such that the outer tentacles point more and more towards the base of the anemone. Then there is a folding around an area of thin mesogloea at the junction of the collar and the main part of the column (Fig. 1). The collar region and attached sphincter thus twist round and downwards, involving little or no change in the resting length of the sphincter. The retractors become bent outwards, and again little change in length need be postulated. When the anemone closes (Fig. 11 B to A) the retractors contract, pulling the upper part of the column up and altering the angle at the two hinges (one on either side of the collar). The sphincter is circumscript; that is, it is a sharply marked cord of muscle, projecting into the body cavity and attached only along a narrow line to the body wall. The arrows in Fig. 11 indicate this point of attachment. In the open positions (Fig. 11 B and C) contraction of the sphincter will pull against this attachment. However, once the collar has rolled over due to retractor contraction (Fig. 11 A) the sphincter will act in the direction of the attachment.

For a closed animal to open, some relaxation of retractors and sphincter must be necessary. A relevant observation is that electrical stimulation of the SS 1 of open *Tealia* always causes further relaxation whereas closed anemones often fail to respond (McFarlane, 1970). Pantin (1950) says that food extracts often but not invariably cause closed *Metridium* to open. This suggests that the failure to respond lies not at the receptor level (as electrical stimulation of the SS 1 also is sometimes unsuccessful) but that failure to open is due to maintained contraction of sphincter and retractors. We have often observed that closed anemones open slowly during SS 1 stimulation but close again immediately stimulation ceases. There is as yet no evidence for an endodermal inhibitory action by the SS 1. Stimulation of the endoderm does not excite the SS 1 but does excite the SS 2 (McFarlane, 1969*b*) in *Calliactis parasitica*. It is not known whether SS 1 and SS 2 are interconnected.

The presence of an SS 1 has been detected in a number of other species of sea anemone: *Anemonia sulcata*, *Actinia equina* (McFarlane, 1969*a*), *Metridium senile*, *Condylactis aurantiaca* (McFarlane, unpublished). The behavioural output of the SS 1 has not been determined for these species but control of expansion seems likely. There are many references in the literature to expansion in response to food substances, for example for the 'common' sea anemone (Pollock, 1883), *Metridium* (Allabach, 1905) and *Actinia* (Piéron, 1906). *Calliactis parasitica* also responds to

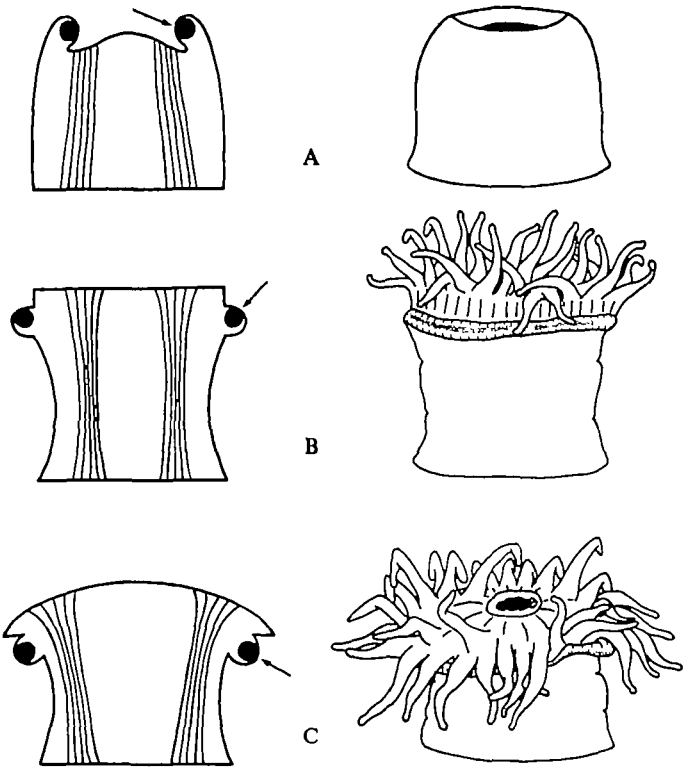

Fig. 11. Showing relationships of radial muscles, sphincter, and retractors in open and closed *Tealia*. Diagrams on left show model of relative positions of the muscles and those on right show external appearance. In the model the line at the top represents the radials, the black circle the sphincter and the parallel lines the retractors. The arrow shows the position of attachment of the sphincter to the body wall. (A) closed anemone, (B) open anemone, (C) expanded anemone. Note change in position of collar region. For expansion from B to C (during the pre-feeding response) there need be no change in the length of the sphincter or retractors, but for opening of a closed anemone (A to B) relaxation of these muscles seems necessary. Relaxation of the radial muscles seems the main cause of expansion (B to C).

dissolved food substances with SS 1 pulses and associated relaxation (McFarlane, unpublished). This is surprising as the SS 1 has been shown to co-ordinate pedal disc detachment in *C. parasitica* (McFarlane, 1969*c*) and SS 1 activity during a pre-feeding response might be expected to lead to detachment. However, SS 1 frequency during response to food substances rarely exceeds 1 SP 1 every 30 sec whereas the frequency leading to detachment must lie in the range 1 every 3 sec to 1 every 10 sec. Relaxation is also observed when the hermit crab *Dardanus gemmatus* detaches *C. polypus* by mechanical stimulation (Ross & Sutton, 1968). Mechanical stimulation of the column of *C. parasitica* can cause SS 1 pulses (McFarlane, 1969*c*). Expansion and detachment also play an important part in the swimming response of *Stomphia coccinea* and SS 1 involvement is likely here, especially as Ross & Sutton (1964) have shown that the swimming response has a higher threshold to electrical stimulation than the retraction response.

The important features of the demonstrated SS 1 action on the radials may be summarized as follows:

(1) The evoked SS 1 activity seems due to the presence of nearby food, although it is possible that other stimuli, such as water currents, may elicit the response (Parker, 1917*b*).

(2) The response represents part of a long-term change in behaviour. Normal fast contractions will still occur, however, so that the defensive reaction is more or less unaffected.

(3) Completely closed anemones can be made to open. In this situation only the column ectoderm is available as the chemosensitive surface. Localized application of food extract shows that SS 1 activity can be elicited by stimulation of a small area of the column. It is not yet known whether there are specialized receptors or whether the ectodermal surface is generally responsive.

(4) The response is shown over a wide frequency range of SS 1 activity – from about 1 every 2 sec to 1 every 30 sec in radial preparations and perhaps even lower in intact animals.

(5) Mechanical stimulation can excite both the nerve net and the SS 1. Strong mechanical stimulation of *Calliactis parasitica* seems to produce a burst of nerve-net pulses that result in fast contraction (Passano & Pantin, 1955). Low-frequency mechanical stimulation may eventually lead to relaxation of the radials.

What is the mechanism of this inhibitory action? The ectodermal supporting cells may be the site of the SS 1, and as these lie in close proximity to the radial muscles some interaction is clearly possible. If the SS 1 is a neuroid conduction system like that found in the siphonophore *Hippopodius* (Mackie & Mackie, 1967) where calcium seems in some way involved in the propagated response, then removal of external calcium from the vicinity of the muscles might result in a reduction of spontaneous activity. It is to be hoped that a study of the mechanism of this inhibitory process will shed some light on the question of whether the SS 1 is a nervous or a non-nervous conduction system.

SUMMARY

1. Electrical stimulation of the SS 1 of *Tealia felina* causes inhibition of spontaneous activity and increase in length of oral disc radial muscle preparations. This response is elicited over a wide stimulus frequency range (1 every 2 sec to 1 every 30 sec). The response shows a slow onset and a long recovery period.

2. Stimulation of the nerve net at frequencies between 1 shock every 5 sec and 1 shock every 20 sec produces slow contraction. The radials also show fast contractions to shocks less than 2 sec apart.

3. Dissolved food substances excite the SS 1 in the column. The sensory response to application of food extract to a small area of the column shows evidence of sensory adaptation.

4. These observations are related to the pre-feeding response of *Tealia* and a model for oral disc expansion is described.

I. D. L. gratefully acknowledges the support of a Science Research Council Research Studentship grant.

REFERENCES

ALLABACH, L. F. (1905). Some points regarding the behaviour of *Metridium*. *Biol. Bull. mar. biol. Lab., Woods Hole* **10**, 35–43.

BATHAM, E. J. (1965). The neural architecture of the sea anemone *Mimetridium cryptum*. *Am. Zool.* **5**, 395–402.

BATHAM, E. J. & PANTIN, C. F. A. (1954). Slow contraction and its relation to spontaneous activity in the sea-anemone *Metridium senile* (L.). *J. exp. Biol.* **31**, 84–103.

CARLGREN, O. (1921). Actiniaria. Pt. I. *Dan. Ingolf-Exped.* **5** (9).

CHAPMAN, G. (1949). The mechanism of opening and closing of *Calliactis parasitica*. *J. mar. biol. Ass. U.K.* **28**, 641–50.

DAVENPORT, D. (1962). The responses of tentacles of actinians to electrical stimulation. *Bull. Inst. Océanogr. Monaco.* no. 1236, 1–24.

HERTWIG, O. & HERTWIG, R. (1879–80). Die Actinien anatomisch und histologisch mit besonderer Berücksichtigung des Nervenmuskelsystems untersucht. *Jena Z. Naturw.* **13**, 457–640; **14**, 39–89.

HORRIDGE, G. A. (1958). The co-ordination of the responses of *Cerianthus* (Coelenterata). *J. exp. Biol.* **35**, 369–82.

JOSEPHSON, R. K. (1966). Neuromuscular transmission in a sea anemone. *J. exp. Biol.* **45**, 305–19.

LEGHISSA, S. (1965). Nervous organization and the problem of the synapse in *Actinia equina*. *Am. Zool.* **5**, 411–24.

MCFARLANE, I. D. (1969*a*). Ph.D. Thesis, University of Bristol.

MCFARLANE, I. D. (1969*b*). Two slow conduction systems in the sea anemone *Calliactis parasitica*. *J. exp. Biol.* **51**, 377–85.

MCFARLANE, I. D. (1969*c*). Co-ordination of pedal-disk detachment in the sea anemone *Calliactis parasitica*. *J. exp. Biol.* **51**, 387–96.

MCFARLANE, I. D. (1970). Control of preparatory feeding behaviour in the sea anemone *Tealia felina*. *J. exp. Biol.* **53**, 211–20.

MACKIE, G. O. (1970). Neuroid conduction and the evolution of conducting tissues. *Q. Rev. Biol.* **45**, 319–32.

MACKIE, G. O. & MACKIE, G. V. (1967). Mesogloeal ultrastructure and reversible opacity in a transparent siphonophore. *Vie Milieu* **18**, 47–72.

PANTIN, C. F. A. (1935*a*). The nerve net of the Actinozoa. I. Facilitation. *J. exp. Biol.* **12**, 119–38.

PANTIN, C. F. A. (1935*b*). The nerve net of the Actinozoa. II. Plan of the nerve net. *J. exp. Biol.* **12**, 139–55.

PANTIN, C. F. A. (1950). Behaviour patterns in lower invertebrates. *Symp. Soc. exp. Biol.* **4**, 175–95.

PARKER, G. H. (1917*a*). The movements of the tentacles in actinians. *J. exp. Zool.* **22**, 95–110.

PARKER, G. H. (1917*b*). Actinian behavior. *J. exp. Zool.* **22**, 193–229.

PASSANO, L. M. & PANTIN, C. F. A. (1955). Mechanical stimulation in the sea-anemone *Calliactis parasitica*. *Proc. R. Soc.* B **143**, 226–38.

PIÉRON, H. (1906). Contribution à la psychologie des actinies. *Bull. Inst. Gén. Psychol.* **6**, 40–59.

POLLOCK, W. H. (1883). On indications of the sense of smell in Actiniae. With an addendum by G. J. Romanes. *J. Linn. Soc. Zool.* **16**, 474–6.

ROBSON, E. A. (1961). The swimming response and its pacemaker system in the anemone *Stomphia coccinea*. *J. exp. Biol.* **38**, 685–94.

ROBSON, E. A. (1971). The behaviour and neuromuscular system of *Gonactinia prolifera*, a swimming sea-anemone. *J. exp. Biol.* **55**, 611–40.

ROBSON, E. A. & JOSEPHSON, R. K. (1969). Neuromuscular properties of mesenteries from the sea-anemone *Metridium*. *J. exp. Biol.* **50**, 151–68.

ROSS, D. M. (1957). Quick and slow contractions in the isolated sphincter of the sea anemone, *Calliactis parasitica*. *J. exp. Biol.* **34**, 11–28.

ROSS, D. M. & SUTTON, L. (1964). The swimming response of the sea anemone *Stomphia coccinea* to electrical stimulation. *J. exp. Biol.* **41**, 735–49.

ROSS, D. M. & SUTTON, L. (1968). Detachment of sea anemones by commensal hermit crabs and by mechanical and electrical stimuli. *Nature, Lond.* **217**, 380–1.

SPENCER, A. N. (1971). Myoid conduction in the siphonophore *Nanomia bijuga*. *Nature, Lond.* **233**, 490–1.

STEPHENSON, T. A. (1928). *The British Sea Anemones*, vol. I. London: Ray Society.