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SPONTANEOUS ELECTRICAL ACTIVITY IN THE SEA ANEMONE *CALLIACTIS PARASITICA*

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INTRODUCTION

Behavioural activities of sea anemones can be divided into three types (Ross, 1964):

(1) *Slow movements*. Various muscles, in particular the endodermal circulars and parietals, give slow spontaneous contractions in both intact animals and isolated preparations. Most information about these activities comes from studies of *Metridium senile* (Batham & Pantin, 1950*a*, *b*, *c*, 1954) and *Calliactis parasitica* (Needler & Ross, 1958; Ewer, 1960).

(2) *Reflexes*. These may be either local or symmetrical (Pantin, 1935*a*). Light mechanical stimulation of a tentacle of *C. parasitica* will cause local withdrawal whereas strong stimulation of the column produces a rapid symmetrical contraction, mainly of the sphincter and retractor muscles.

(3) *Complex activity*. Complete behavioural sequences that may involve components from the other two categories and are normally elicited by external stimuli. For example, the normal rhythm of alternating circular and longitudinal contractions of *M. senile* changes in the presence of dissolved food substances such that circular activity predominates, leading to an extension of the column (Batham & Pantin, 1950*c*; Pantin, 1950). This is not the simple consequence of a stimulus acting upon a passive animal but represents a change in pattern of activity in an organism that is not at rest, and this activity seems inherent and not initiated by external stimuli (Pantin, 1950). A well-studied complex response is shell-climbing in *C. parasitica*, where, in an animal attached to an inert substrate, contact of the tentacles with a *Buccinum* shell initiates a behavioural sequence directed towards transfer of pedal disc attachment to the shell (Ross & Sutton, 1961).

Whereas certain fast reflex responses, such as sphincter contraction in *Calliactis polypus* (Josephson, 1966), and the initiation of certain complex responses, such a shell-climbing in *C. parasitica* (McFarlane, 1969*b*), have been related to electrical activity recorded extracellularly with suction electrodes, spontaneous activities have not been related to concomitant electrical events. This is in marked contrast to the situation in the Hydrozoa where electrical activity has been recorded from a number of spontaneous pacemaker systems (e.g. *Hydra*, Passano & McCullough, 1963; Rushforth, 1971; *Tubularia*, Josephson, 1965; *Obelia*, Morin & Cooke, 1971). As earlier work has repeatedly stressed the importance of endogenous activity in sea anemones it was considered important to look for electrical correlates of this activity. Although not previously shown in sea anemones, spontaneous electrical activity has been recorded from the pennatulid, *Veretillum* (Buisson, Tricoche & Franc, 1967).

McFarlane (1969*a*) showed the presence of electrical activity associated with three conduction systems in *Calliactis parasitica*: the rapidly conducting nerve net, and the slowly conducting SS 1 and SS 2. The present study demonstrates the feasibility of long-term monitoring of electrical activity from *C. parasitica* and indicates that at least one of the known conducting systems is spontaneously active.

MATERIALS AND METHODS

Specimens of *Calliactis parasitica*, attached to *Buccinum* shells, were obtained from the Marine Laboratory, Plymouth. They were kept in the sea-water circulation tanks of the Gatty Marine Laboratory. The water temperature was 4–14 °C. Experiments were performed under dim light and in running sea water (8–14 °C). Specimens used had an expanded oral disc diameter of 4–6 cm.

The basic recording method has been previously described (McFarlane, 1969*a*). All recordings were from tentacles as only here can all three pulse types (see Fig. 2*a*) be clearly detected. The main difficulties in recording the electrical activity are firstly that rapid movements of the animal often throw off attached suction electrodes and secondly that pulses from all three conduction systems tend to be very small. Pulse identification is facilitated by comparing activity from two recording electrodes on tentacles 1–2 cm apart. The use of two electrodes compounds the difficulty in maintaining attachment to an intact animal and so most recordings were made from half-animal preparations. Animals were removed from shells, bisected longitudinally, and were sometimes fixed endodermal side uppermost by pinning through the pedal disc. Preparations survive well and eventually seal along the cut edges and start feeding after a few weeks. Electrodes often remain attached for 4 h or more, but the time limit for monitoring is usually set by the fact that the size of recorded pulses decreases after about 2 h, possibly due to tissue damage by the electrode or to a build-up of mucus in the electrode tip. To continue monitoring the recording electrodes must then be moved to fresh sites. Pulse shape rather than pulse size is the important criterion for correct identification so pulses were observed on the storage oscilloscope at a sweep speed of 200 msec/cm. Pulse shape may vary considerably between recording sites but usually remains constant during any one period of attachment. Initial pulse identification was performed in the following way. A low-intensity shock through a stimulating electrode on the column elicits a nerve net pulse and SS 1 pulse (SP 1) only. A low-intensity shock applied to a mesentery gives only the nerve net pulse and SS 2 pulse (SP 2) (McFarlane, 1969*a*).

RESULTS

Pulse types

1. ***Nerve net pulse.*** This is a rapidly conducted pulse seen at both recording electrodes following a single shock to any part of the body (McFarlane, 1969*a*). Occasionally it appears as a short-duration (less than 10 msec) all-or-none pulse (Fig. 1*a*) possibly representing activity in the neurites of the nerve net. This is the through-conducting nerve net (Pantin, 1935*a*), as a second shock, closely following the first, produces a large muscle action potential and fast contraction of the tentacles and sphincter (Josephson, 1966; McFarlane, 1969*a*). Similar responses to single shocks

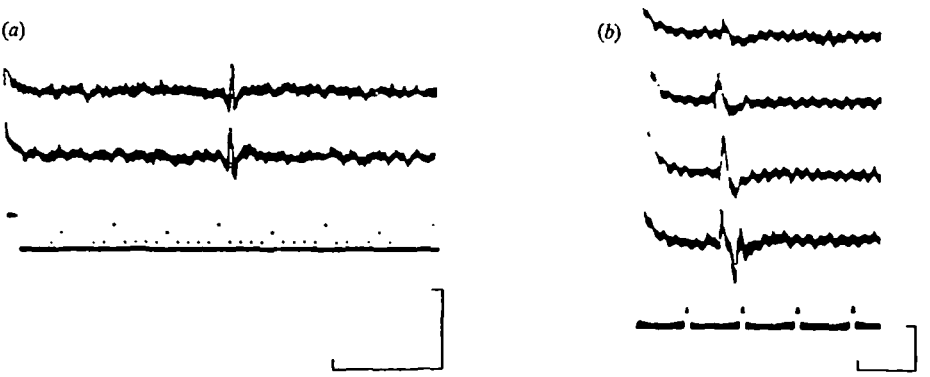

Fig. 1. Nerve net activity recorded from tentacles of *Calliactis parasitica*. (*a*) Two successive single shocks, given 30 sec apart, showing short-duration event possibly recorded from neurites of nerve net. Stimulating electrode at base of column. (*b*) Pulses from four different tentacle recording sites showing variability in pulse evoked by single shock. Initial part of pulse may represent nerve-net activity, later portion a small muscle action potential associated with tentacle twitch. Scales 100 msec, 10 μV.

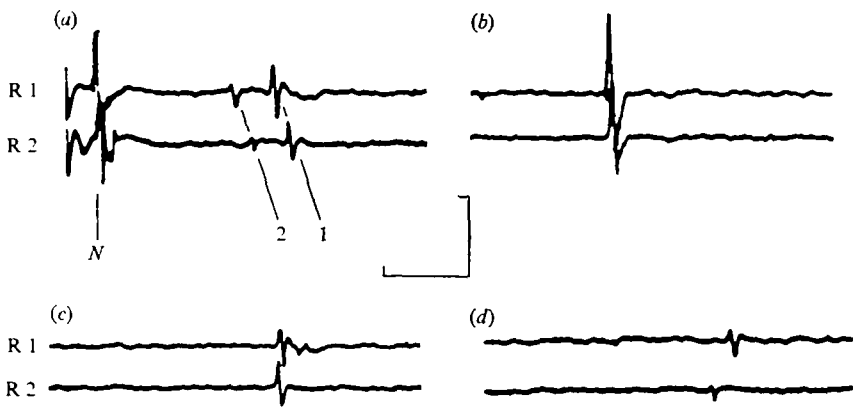

Fig. 2. Spontaneous electrical activity recorded from tentacles. Two recording electrodes (R 1, R 2) on different tentacles, 2 cm apart. (*a*) Response to single high-intensity shock to base of column showing evoked pulses in the three known conduction systems. *N*, Nerve-net pulse; 1, SP 1; 2, SP 2. (*b*) Spontaneous nerve-net pulse. (*c*) Spontaneous SP 1. (*d*) Spontaneous SP 2. Scale: 20 μV, 500 msec.

have been recorded from mesenteries of *Calamactis praelongus* (Pickens, 1969) and *Metridium senile* (Robson & Josephson, 1969). More usually, however, the pulse in *C. parasitica* is larger, more complex, and of longer duration (Fig. 1*b*). This may be summated activity in a number of neurites but could be a small muscle action potential accompanying a small twitch of the tentacles (Josephson, 1966). In one recording position the pulse remains reasonably constant in shape and duration and is easily distinguished from slow-system pulses. The conduction velocity is high and the pulse arrives almost simultaneously at the two recording electrodes, irrespective of its site of origin. The normal appearance of these pulses is shown in Fig. 2(*a*). They are smaller than the muscle action potential accompanying a large facilitated contraction

and they may be regarded as indicating the presence of a *single pulse* in the through conducting nerve net.

2. *SS* 1 *pulse* (*SP* 1). The SS 1 is thought to be ectodermal (McFarlane, 1969*a*) and a single pulse spreads over the entire ectoderm in response to a single shock to any ectodermal region. The SP 1 is usually larger than the SP 2, reaching perhaps 15–30 μV. Because of the low conduction velocity (3–14 cm/sec) pulses in the SS 1, like those in the SS 2, often show a considerable difference in time of arrival at the two recording sites.

SS 1 activity is observed during the shell-climbing behaviour of *Calliactis parasitica*, and has been shown to co-ordinate detachment of the pedal disc (McFarlane, 1969*b*). This seems to be a sensory response involving the tentacles as SS 1 activity is observed only as long as the link between the tentacles and the *Buccinum* shell remain unbroken. The column of *Tealia felina* responds to contact with dissolved food substances with a series of SP 1's that seem to cause not pedal disc detachment in this case, but expansion of the oral disc (McFarlane, 1970; McFarlane & Lawn, 1972). SP 1's are also seen when *C. parasitica* is exposed to food extracts but the frequency of evoked SP 1's is too low to cause detachment of the pedal disc. The properties and actions of the SS 1 suggest that it is a neuroid (non-nervous) conduction system.

3. *SS* 2 *pulse* (*SP* 2). SP 2's rarely exceed 10 μV and have been recorded only from the tentacles. The conducting elements may be endodermal (McFarlane, 1969*a*). Neither function, location nor natural stimuli are known for this system but earlier work suggested that it was spontaneously active. This observation is extended and confirmed below.

Observations of spontaneous pulses

Spontaneous pulses may be observed in all three conduction systems. The term 'spontaneous' is used only to refer to the fact that no obvious external stimulus was applied and in no way implies genuine pacemaker activity. The spontaneous SP 1's and SP 2's shown in Fig. 2 do not originate from mechanical stimulation due to the attached stimulating electrode as the time relationships of the arrival of the SP 1's and SP 2's at the two recording sites (R 1 and R 2) show a difference between evoked and spontaneous pairs. In the example shown, evoked SP 1's and SP 2's arrive first at R 1, whereas the spontaneous pulses arrive first at R 2. The spontaneous activity associated with all three conduction systems remains when the stimulating electrode is removed. Also spontaneous SP 1's and SP 2's clearly do not originate from one or both of the recording electrodes, for in this case, as the conduction path length is finite and constant, there should always be a constant interval between members of each pulse pair and pulses should never be seen to arrive at R 1 and R 2 simultaneously. In fact, during any one recording sequence, pulses in either of the slow systems may appear simultaneously at the recording sites, or sometimes first at R 1 and at other times first at R 2. Fig. 3(*a*) shows three successive pairs of spontaneous SP 2's recorded from one animal. There is clearly no fixed site of pulse origin.

No form of natural stimulation has yet been found to elicit SP 2's and it may be proposed that the SS 2 shows genuine endogenous activity. However, both the nerve net and SS 1 are known to respond to mechanical stimulation (Passano & Pantin, 1955; McFarlane, 1969*b*) and SP 1's may also be elicited by chemical stimulation (shell

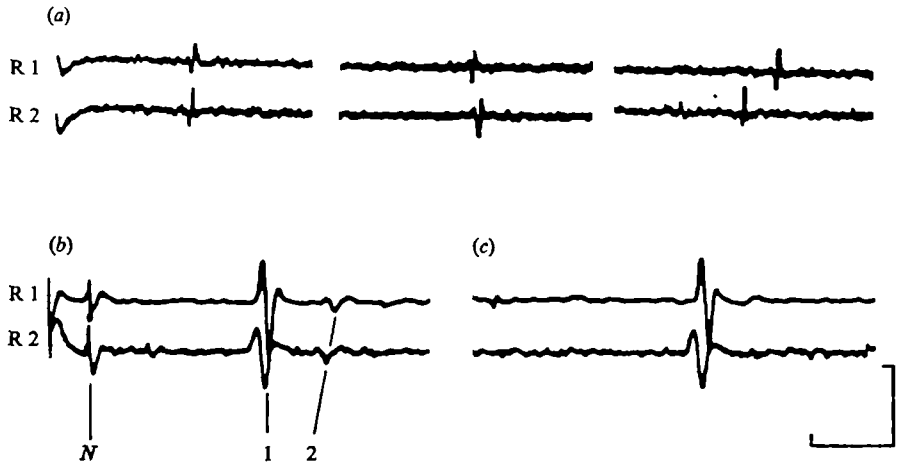

Fig. 3. (*a*) Three successive pairs of spontaneous SP 2's recorded from tentacles. The variations in arrival delay of the pulses at R 1 and R 2 show that SP 2's are originating from more than one site. (*b*) Nerve-net pulse (*N*) SP 1 (1), SP 2 (2) evoked by single shock to base of column. (*c*) Spontaneous SP 1 seen 2 min after shock. Spontaneous and evoked SP 1's in this case arrive at R 1 and R 2 with same time relationship suggesting that spontaneous pulse may result from mechanical stimulation by the stimulating electrode. Scale: 500 msec, 20 μV.

contact or dissolved food substances). As the nerve net shows bursts of activity (see below) rather than isolated events it is likely that such activity is not due to random external stimuli. However, some of the observed SP 1's may result from undetected external stimuli. Fig. 3(*b*) shows a case where the time relationship of pairs of evoked and spontaneous SP 1's is the same, implying that the spontaneous pulses arise at or close to the stimulating electrode. Here the stimulating electrode was attached to the base of the column, 2 mm from the junction with the pedal disc. The SS 1 seems particularly sensitive to mechanical stimulation in this region and a single SP 1 can be elicited by sharply tapping the electrode. Also, contraction of the preparation will pull on the pins and this may excite SP 1's, although it should be noted that spontaneous SP 1's are still present, but at a very low frequency, in the intact unstimulated animal. As the SS 1 has an established sensory input and a frequency-dependent output response (pedal disc detachment) it would be surprising if this system were truly spontaneously active.

The nerve net pulses and SP 1's are always clear and easy to recognize, but the small size of the SP 2's requires some confirmation that the observed spontaneous pulses are actually identical with SP 2's elicited by electrical stimulation. Both slow systems show an increased response delay with repeated stimulation, and the SS 1 shows evidence of fatigue even when stimuli are 20 sec apart (McFarlane, 1969*a*). Conduction in the SS 2 is even more likely to fail with repeated stimulation (although this may be due in part to the high level of spontaneous activity in this system). Fig. 4 shows the effect of stimulating the SS 1 and SS 2 at a frequency of one shock every 4 sec. At stimulus frequencies higher than one shock every 3 sec both systems also show a progressive decrease in pulse size. The small size of the SP 2 makes it difficult to determine the refractory period but it seems to be in the region of 1 sec. Fig. 5(*a*) shows the nerve net pulse, SP 2 and SP 1 following a single shock. In Fig. 5(*b*) a shock

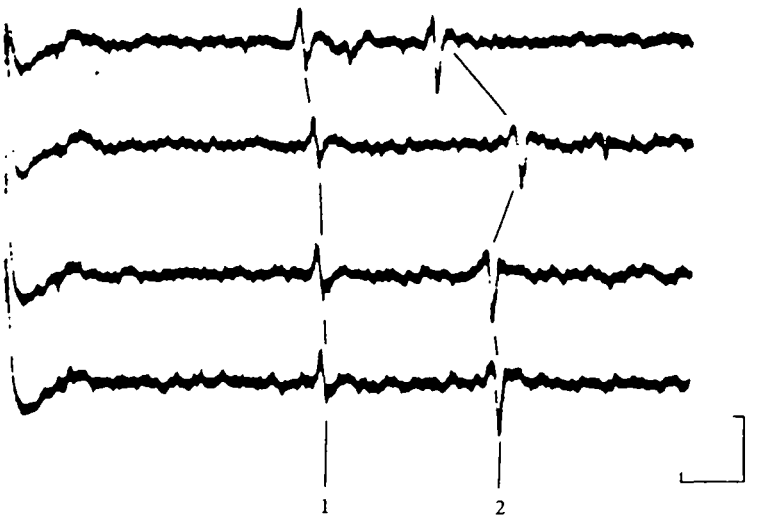

Fig. 4. Effect of repetitive stimulation on SS 1 and SS 2. Single recording electrode on a tentacle. Four successive stimuli at one shock every 4 sec. Records read from top. Note progressive increase in response delay, 1, SP 1; 2, SP 2. Scale: 200 msec, 10 μV.

of the same intensity was applied to the same site but this time about 500 msec after the appearance of a spontaneous SP 2. A nerve net pulse and SP 1 follow stimulation but an SP 2 was not elicited, implying that the SS 2 was still refractory following the passage of the spontaneous pulse. If the interval between the spontaneous pulse and the test shock is increased to 2 sec, stimulation elicits a small SP 2. When the interval is about 3 sec the evoked SP 2 is normal-sized but still shows an increased conduction delay. The same technique can be used to confirm the identity of the other spontaneous pulses. With the nerve net pulse, an evoked pulse inserted into the system shortly after a spontaneous pulse elicits a fast contraction and associated muscle action potential.

Long-term monitoring of spontaneous activity

Fig. 6 shows activity in the three known conduction systems, monitored for 130 min, The graph shows the time of occurrence of each individual pulse plotted against instantaneous frequency (the reciprocal of the interval between that pulse and the preceding pulse).

Both the nerve net and the SS 1 show long quiet periods. However, nerve net activity often occurs in short bursts whereas SS 1 activity is arrhythmic, supporting the suggestion made above that many of the observed SP 1's result from external stimuli. The SS 2, on the other hand, shows considerable activity, and for at least the first 60 min of this sequence shows rhythmic activity. In this instance SS 2 frequency varies between 7·5 pulses/min and 0·2 pulses/min. The mean firing frequency over this monitoring period was 1·5 pulses/min. Peaks of activity here occur every 20–25 min. Occasionally no clear rhythmicity was evident and in some cases SS 2 frequency remained consistently low for up to 60 min. Observed mean firing frequencies ranged from 1·2/min (50 min monitoring) to 2·5/min (60 min monitoring).

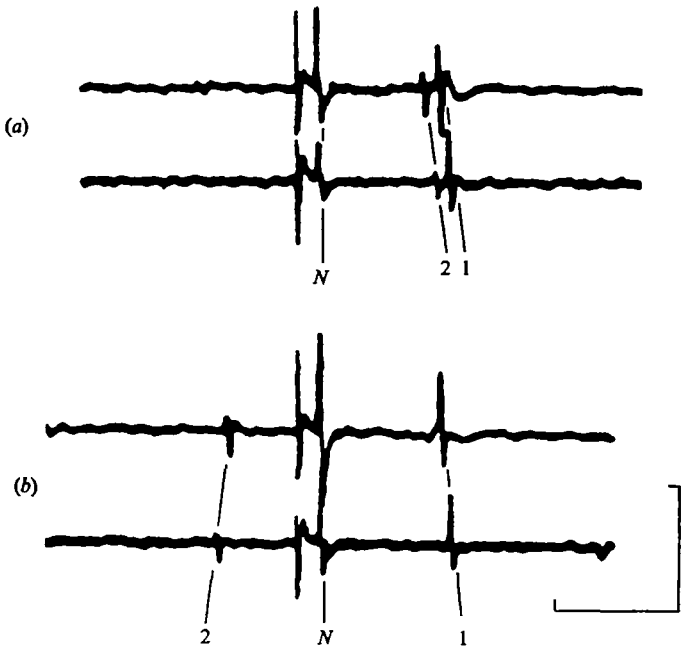

Fig. 5. Confirmation of identity of spontaneous SP 2's. (*a*) Single high-intensity shock to base of column gives nerve-net pulse (*N*), SP 2 (2), SP 1, (1). (*b*) Single shock of same intensity at same site given 500 msec after spontaneous SP 2 elicits nerve-net pulse and SP 1 only. SS 2 failure must be related to fatigue due to the passage of the spontaneous pulse. Scale: 1 sec, 20 μV.

There seems to be a relationship between SS 2 and nerve net activity. Figs. 6 and 7 show that nerve net bursts tend to occur when SS 2 activity is at its minimum. A burst consists of a small number of nerve net pulses (maximum number seen was 10) occurring at a high frequency (up to 15/min). Immediately after a burst the SS 2 frequency rapidly rises to its maximum point, from which it slowly falls. Once the frequency falls below a certain level (usually less than 0·5 pulses/min) another burst of nerve net activity appears.

When nerve-net firing frequency was high, a slow sphincter contraction was often evident in the preparation. Ross (1957) showed that the isolated sphincter of *Calliactis parasitica* contracts slowly in response to electrical stimulation over the frequency range of 1 shock every 2 sec to 1 shock every 15 sec. The slow contraction has the same threshold as fast contraction and is presumably also mediated via the through-conducting nerve net. The observed burst frequencies and numbers of pulses per burst fall within the range known to elicit slow sphincter contraction. A similar burst of nerve-net activity and slow sphincter contraction was observed during monitoring of electrical activity accompanying shell-climbing (McFarlane, 1969*b*), underlining the concept that complex behaviour patterns often involve components observed during normal spontaneous activity.

It is not known whether the nerve net and SS 2 have independent pacemakers that are in some way linked or whether only one system has a pacemaker and this indirectly drives the other. During long periods of low-frequency SS 2 activity, or

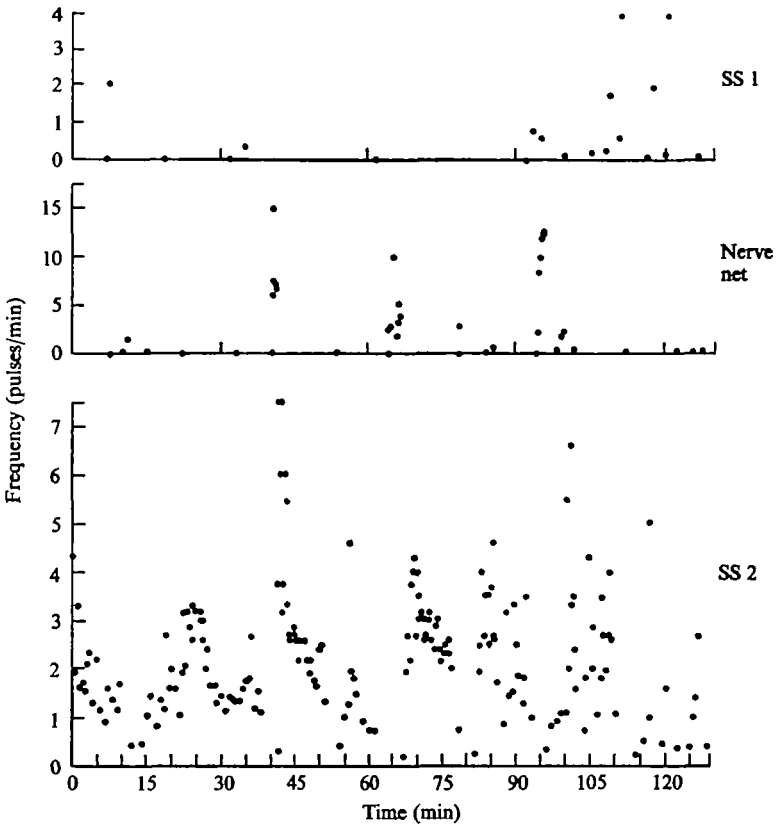

Fig. 6. Frequency of activity in the three conduction systems during a 130 min monitoring period. Pulse frequency plotted against time. Note the slow rhythmic changes in SS 2 frequency and the fact that bursts of nerve-net activity occur when SS 2 frequency is low and are almost immediately followed by a sudden increase in SS 2 frequency.

during periods when firing is very irregular, nerve net activity still occurs but in the form of scattered pulses rather than bursts. This implies that there is a very close relationship between the two systems but does not help identify the pacemaker.

The location of possible pacemakers is not known. The variations in arrival times at the two recording electrodes suggest that spontaneous SP 2's can come from more than one site (Fig. 3*a*). Robson (1961*a*, 1965) describes multipolar nerve cells in the column endoderm of *Calliactis parasitica*. These are situated above the circular muscles and connect with sense cells and bipolar neurites. A layer of much larger multipolar cells in *Stomphia coccinea* has been proposed as the pacemakers during the swimming response of that anemone (Robson, 1963). SP 2's may represent activity in an endodermal nerve net in the tentacles but Batham (1965) was unable to detect such a net in *Mimetridium cryptum*. If the pacemaker is within this multipolar nerve net it is more likely that it feeds into the through-conduction system. The observed spontaneous nerve net pulses may in fact only represent the occasional pulse that 'leaks out' into the through-conduction system and they will thus bear little or no relationship to the actual pacemaker activity. Alternatively the bursts of nerve net activity may be reflexly excited by stretch of sensitive elements within the net. The endodermal musculo-

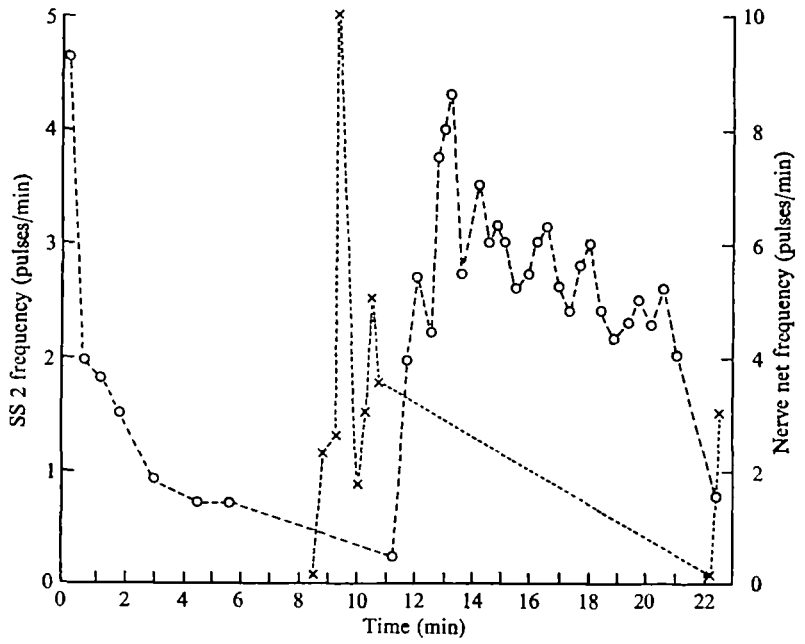

Fig. 7. Expanded portion of Fig. 6, showing the relationship between SS 2 and nerve-net activity. Note the very short delay between the end of the nerve-net burst and the sudden increase in SS 2 frequency. O, SS2 pulses; ×, nerve-net pulses.

epithelium could be the site of the SS 2, conduction being in either the muscular or non-muscular part of the cells. Pacemaker activity may be inherent within these cells or the cells may be excited via the multipolar nerve net. The main barrier to locating the SS 2 has been the difficulty in recording SP 2's from mesenteries. This seems in part at least to arise from the fact that the cells are fragile and quickly broken-up by a suction electrode. However, the cells may be large enough for microelectrode penetration, being greater than 10 μm in diameter in stretched mesenteries of *Metridium senile* (Robson, 1957).

There may also be a link between SS 1 activity and spontaneous SP 2's and nerve net pulses. On the rare occasions when SS 1 activity is high (for example towards the end of the monitoring period shown in Fig. 6) there seems to be a decrease in activity in the other two conduction systems. However, as the SP 1's may result from undetected external stimuli (see above), the same stimuli may be directly affecting activity in the SS 2 and nerve net.

DISCUSSION

Significance of spontaneous nerve net pulses

In his study of fast contraction of the sphincter in *Calliactis parasitica*, Pantin (1935*b*) noted that about 30% of animals studied often gave abnormal responses to paired stimuli. Instead of a single fast contraction they showed one or more supernumerary contractions, at an interval after the primary response to the stimulus which was often far too long to be due to conduction delays. Fig. 8(*a*) shows such

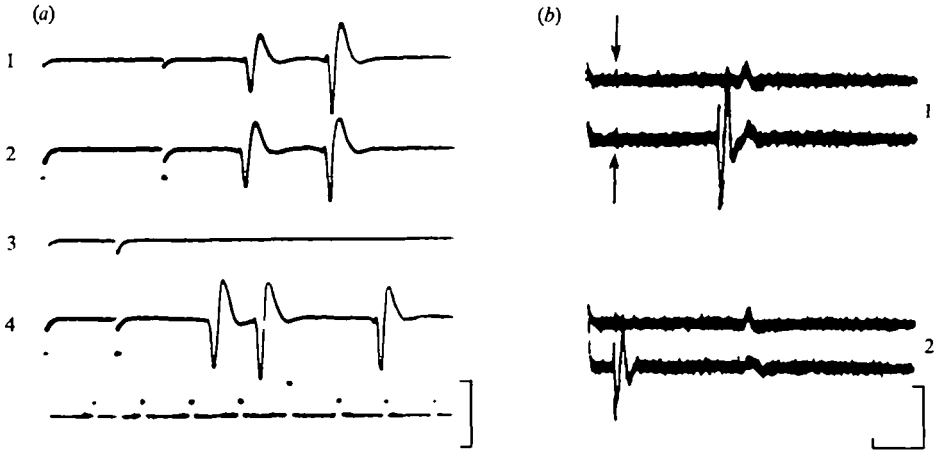

Fig. 8. (*a*) After-discharges. Muscle action potentials recorded from a tentacle of a specimen of *C. parasitica* that gave consistent after-discharge. The normal fast contraction is followed by an additional contraction, 1, 2. Two successive responses to a pair of shocks 250 msec apart. When shocks are 150 msec apart, contraction is sometimes not elicited (3) but the following pair of shocks gave two additional contractions. The regularity in occurrence and delay show that after-discharge cannot be associated with spontaneous events in the nerve net. Scale: 100 μV, time scale divisions 100 msec.

(*b*) Fast contractions in response to single shocks, recorded from a different specimen of *C. parasitica*. The upper record in each pair shows the normal response – a single shock to base of column is followed by nerve-net pulse (arrow) and SP 1 (SS 2 not excited at this stimulus intensity). Lower trace shows (1) a delayed fast contraction, (2) a fast contraction at the same delay as the nerve-net pulse. See text for interpretation. Scale: 200 msec., 20 μV.

'after-discharges' recorded from an intact *C. parasitica*. This particular animal gave supernumerary responses following every applied pair of stimuli. This fact and the very regular delay of the additional contraction leads to the same conclusion as reached by Pantin – that the extra contractions cannot be related to spontaneous pulses in the nerve net as these would give additional contractions occurring at widely different delays after stimulation.

The observed spontaneous nerve-net pulses can, however, explain the phenomenon of fast responses to single shocks. Monitoring has shown that although spontaneous fast contractions are rare, single events in the through-conducting nerve net are common but occur in widely separated bursts. It is accepted as a general property of fast musculature in sea anemones that a single pulse in the nerve net will not cause a fast contraction but will have a facilitatory effect such that a second pulse, arriving before the decay of facilitation, is followed by a fast contraction (Pantin, 1935*a*). Batham & Pantin (1954) concluded that in *Metridium senile* close impulses do occasionally occur in the through-conduction system of unstimulated animals as these sometimes show a spontaneous fast contraction of the mesenteric retractors and this must mean that two impulses have arisen in the system within about 2 sec of each other. However, single electrical shocks will on occasion give a fast contraction in *M. senile*. Ross (1952) and Batham & Pantin (1954) suggested that these responses occur because the evoked pulse acts in conjunction with a spontaneous pulse to produce a facilitated fast contraction. By applying low-frequency single shocks and

pbserving the percentage that elicited a fast contraction it was possible (as the duration of the facilitatory effect of a single pulse was known) to calculate the frequency of spontaneous nervous events. Batham and Pantin give figures of 1 pulse every 2 min to 1 pulse every 12 min and calculate from Ross's results a range of 1 pulse every 7 min to 1 pulse every 70 min. The results of the present study given an approximate figure of 1 pulse every 3 min for *Calliactis parasitica* (though it should be remembered that these pulses occur in bursts of much higher frequency), and both confirm the suggestion that spontaneous nerve-net events occur in sea anemones and support the indirect estimates of frequency made by Batham and Pantin for *M. senile*.

Parietal contractions in *M. senile* occur both spontaneously and in response to electrical stimulation, and Batham & Pantin (1954) suggested that the larger observed spontaneous contractions coincide with bursts of several nerve net pulses at a frequency of 1 pulse every 5 sec to 1 pulse every 10 sec. The parietals of *C. parasitica* are activated by electrical stimulation over approximately the same frequency range and so the observed bursts of nerve-net pulses may be correlated with spontaneous parietal contractions. Slow sphincter contractions were seen during bursts and it is of interest that Ross (1957) says that isolated sphincter preparations of *C. parasitica* do not show spontaneous activity, although Needler & Ross (1958) describe slow sphincter contractions in the unstimulated intact animal. Assuming that sphincter contraction is not here being confused with contraction of the circular muscles of the upper part of the column, this apparent contradiction implies that the nerve-net bursts are either inhibited or the pacemaker sites are destroyed in the isolated preparations (but clearly not in half-animal preparations) and leads to the possibility of locating the site of origin of spontaneous nerve-net activity.

An apparent anomaly in the responses to single shocks in *Metridium senile* was pointed out by Ross (1952). He argued that if the fast contractions were caused by the evoked pulse acting in conjunction with a spontaneous pulse then they should occur equally often on the stimulus as after a short delay (determined by the decay time of the facilitatory effect of the evoked pulse). In other words the spontaneous pulse is equally likely to precede as to follow the test shock. In fact only about 3% of fast responses to single shocks were delayed, implying that the spontaneous pulse can facilitate the response but that it is not often capable of causing contraction following facilitation by the evoked pulse. As the occurrence of spontaneous nerve-net pulses in *Calliactis parasitica* is difficult to predict it has not proven possible to test this by stimulating just before the arrival of a spontaneous pulse to see whether fast contraction ensues. However, delayed contractions seem more common in *C. parasitica*. Fig. 8(*b*) shows two examples of fast contractions to single shocks – one occurring at the point of arrival of the nerve-net pulse and the other after a short delay. The interpretation is that in the first case a spontaneous pulse occurred just before the shock was given and in the second case a spontaneous pulse arrived just after the evoked pulse. It is possible that unknown factors may influence the state of the neuromuscular junctions so that a single pulse is capable of directly eliciting a fast contraction, but this does not explain the delayed contractions. There is no evidence that the SS 1 or SS 2 are involved in these fast contractions to single shocks.

Significance of spontaneous slow-system pulses

The behavioural output of the observed SP 1's is not known. Their frequency is too low to cause detachment of the pedal disc (this occurs over a frequency range of 1 pulse every 3–10 sec). Although there is some doubt as to whether the SS 1 shows genuine endogenous activity, this is of minor importance compared with the question of whether the SS 1 is capable of affecting activity of the other systems. The reduction in nerve-net and SS 2 activity during periods when the SS 1 is active may represent pacemaker inhibition. In *Tubularia* inhibition of the NP pacemaker system may result from stimulation of the distal opener system (DOS) (Josephson & Ulrich, 1969). Such a possible interaction is of interest in the shell-climbing behaviour of *Calliactis parasitica* because it appears that the primary sensory response involves excitation of activity in the SS 1. The SS 1 may be an ectodermal system and the initial result of its activity (pedal disc detachment) may be restricted to the ectoderm (McFarlane, 1969*b*). However, the later stages of the response involve endodermal elements that produce column extension and bending (Ross & Sutton, 1961). Either there is an additional sensory response involving endodermal components or there is some connexion between the ectodermal SS 1 and the endoderm. The same problem – that of the location of a connection between the ectoderm and the endoderm – exists in the swimming response of *Stomphia coccinea* (Robson, 1961*b*). However, there is as yet no evidence that an SS 1 exists in *S. coccinea* or that it is involved in the swimming response.

Metridium senile shows reciprocal inhibition between the circular and parietal muscles (Batham & Pantin, 1954). It is not clear to what extent the same phenomenon exists in *Calliactis parasitica*, but if the nerve net bursts elicit parietal contraction then perhaps the SS 2 is in some way involved in circular contraction. The rhythmic potential system in *Hydra* (Passano & McCullough, 1965) is in many ways similar to the SS 2; the pulses are small, conducted at 4 cm/sec and the system shows spontaneous activity at a frequency of 1–10 pulses/min. The pulses trigger contraction of endodermal circular muscles, producing column elongation (Shibley, 1969).

Calliactis parasitica has been much studied in the past, with attention focused on the fast protective withdrawal contraction of the sphincter, slow spontaneous contractions, and the shell-climbing response. Whilst it has been generally realized that studies of sea-anemone behaviour were conducted against a background of inherent activity (see, for example, Pantin, 1950), the present study is the first demonstration of spontaneous electrical events. This, combined with the knowledge that there are multiple conduction systems, should allow fresh advances in our understanding of actinian behaviour.

SUMMARY

1. Activity in the three known conduction systems in *Calliactis parasitica* (nerve net, SS 1, SS 2) has been monitored for periods up to 2 h.

2. The ectodermal slow system (SS 1) shows irregular activity and many of the observed spontaneous pulses may in fact result from undetected external stimuli.

3. The SS 2 shows rhythmic changes in frequency (approximate range 0·2–7·5 pulses/min.)

4. During periods of low-frequency SS 2 activity a short (up to 10 pulses), high-frequency (up to 15/min) burst of activity in the through-conducting nerve net is seen. A slow contraction of the sphincter muscle is often seen after a nerve net burst.

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