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CO-ORDINATION OF PEDAL-DISK DETACHMENT IN THE SEA ANEMONE *CALLIACTIS PARASITICA*

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INTRODUCTION

Sea anemones attached to a solid substratum can be removed only by application of strong lifting forces to the basal region. However, behaviour patterns occur in which the attachment is released or loosened; for example, Portmann (1926) described detachment in *Aiptasia cornea*, followed by locomotion by means of peristaltic contractions of the column musculature. Although an active process seems to be responsible for detachment, the conduction system involved has not been described for any species.

Anemones of the genus *Calliactis* are usually found attached to molluscan shells inhabited by hermit crabs (see review by Ross, 1967). Transfer of the anemone to a shell from another substrate depends on the active participation of one or both of the partners in this symbiotic association. In the partnerships between *C. parasitica* and *Pagurus bernhardus*, and between *C. tricolor* and *Dardanus venosus*, the crab needs to play no part in the transfer; the detachment of the pedal disk and subsequent 'shell-climbing' result from a response of the anemone's tentacles to a molluscan 'shell factor' (Ross, 1960; Ross & Sutton, 1968). In the association of *C. parasitica* and *D. arrosor*, the crab can detach the anemone mechanically but successful transfer usually also depends on a 'shell response' by the anemone (Ross, 1960; Ross & Sutton, 1961*b*). The crab *D. gemmatus* seems entirely responsible for stimulating detachment of *C. polypus*, the anemone showing no 'shell response' unless the pedal disk is already free (Ross & Sutton, 1968). Once loose, the anemone is held against the shell by the crab until the pedal disk attaches.

Ross & Sutton (1961*a*) gave a full description of the shell-transfer sequence of *Calliactis parasitica* in association with *Pagurus bernhardus*. The transfer is accomplished in 10–30 min. and the following stages are clear. (1) The tentacles touch the shell and adhere, possibly by discharge of nematocysts or spirocysts. Contact must be maintained for successful completion of the subsequent stages. (2) The attachment of the pedal disk to the substratum is broken. (3) The column extends and the base swells. (4) The column bends locally, bringing the pedal disk up against the shell. (5) The pedal disk adheres on contact and moves over the shell, increasing the area of attachment. The tentacles release their hold and the column straightens.

Detachment in *Calliactis polypus* is normally effected by mechanical stimulation of the base of the column by the walking legs of the crab (Ross & Sutton, 1968). Detachment can be produced experimentally by mechanical and electrical stimulation of the column. The expected result of such stimulation is slow or fast protective closure. In

fact, although there may initially be retraction, this is followed by relaxation and pedal disk release. Ross and Sutton suggest that a basic motor mechanism is involved, producing general inhibition and then a local contraction in the pedal disk region. They also propose that the same pathway must be present in *C. parasitica*. There are two slow-conduction systems in *C. parasitica* in addition to the well-known through-conduction system (McFarlane, 1969). The experiments described here were designed to show if pedal disk release is controlled by any of the known conduction systems.

MATERIALS AND METHODS

Specimens of *Calliactis parasitica* were supplied by the Plymouth Marine Laboratory. Only animals firmly attached to *Buccinum* shells were used in the experiments. Suction electrodes were used for recording and stimulation. The recording apparatus has been previously described (McFarlane, 1969).

RESULTS

Electrical activity during shell-climbing behaviour

The slow systems will be referred to as SS1 and SS2, and associated slow pulses SP1 and SP2. The results given here show that the SS1 is excited during the 'shell response' and is most active in the stages leading up to detachment. Pedal disk detachment is an essential feature of the complex behavioural sequence whereby *Calliactis parasitica* transfers to a *Buccinum* shell. The details of this behaviour have been described (e.g. Ross & Sutton, 1961*a*) but associated electrical activity has not been recorded.

The presence of electrodes on the tentacles seems to interfere with normal behaviour; an effect presumably due to mechanical stimulation. Consequently most recordings were from the sphincter region of the column. Here the SP1s are large and activity in the through-conduction system is sometimes seen as small pulses that may be activity within the nerve net (McFarlane, 1969). Fast contractions of the sphincter are seen as large muscle action potentials, easily distinguishable from SP1s. SP2s are not recorded in this position but experiments described later suggest that the SS2 is not involved in the detachment response. The presence of the electrode may affect behaviour but a number of complete and apparently normal climbing sequences have been recorded. Transfer was usually from a glass plate. A *Buccinum* shell was placed near the tentacles.

Before the tentacles contact the shell very little electrical activity is recorded; there seem to be no spontaneous SP1s and activity in the through-conduction system is rare. On contact the usual response is a fast withdrawal by tentacle and sphincter contraction. This appears on the recording as a small muscle action potential associated with the sphincter contraction. Withdrawal on contact may be repeated but in responsive animals a clear positive reaction to the shell soon appears. The tentacles touch the shell and there is no withdrawal. Some adhere and then contract; this may pull the tentacle away from the shell but usually pulls the shell and oral disk closer together. Adhesion is probably a result of nematocyst or spirocyst discharge (Ross, 1960).

It is at this stage that SP1s are recorded. Figures 1 A and 1 B show activity recorded following shell contact. All the visible pulses are SP1s. Note that when two SP1s are

close together the second is reduced in size. SS1 firing is not a remote chemosensory response but it is not clear if shell contact or nematocyst discharge excite the system. Animals already attached to shells do not give a 'shell response'; this seems to result

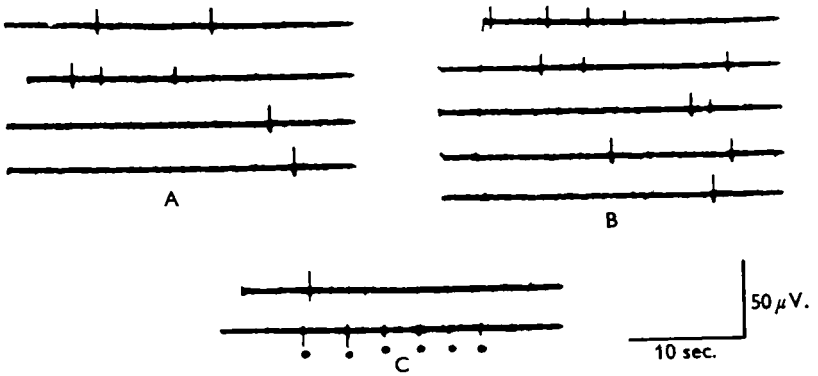

Fig. 1. Electrical activity recorded from sphincter region during response of *Calliactis* to *Buccinum* shell. Each sequence is continuous, reading from top left. A and B, activity from two animals during early stages of response. All pulses are SP1s. C, Upper recording SP1; lower recording shows small pulses (marked by dots) seen before a slow sphincter contraction.

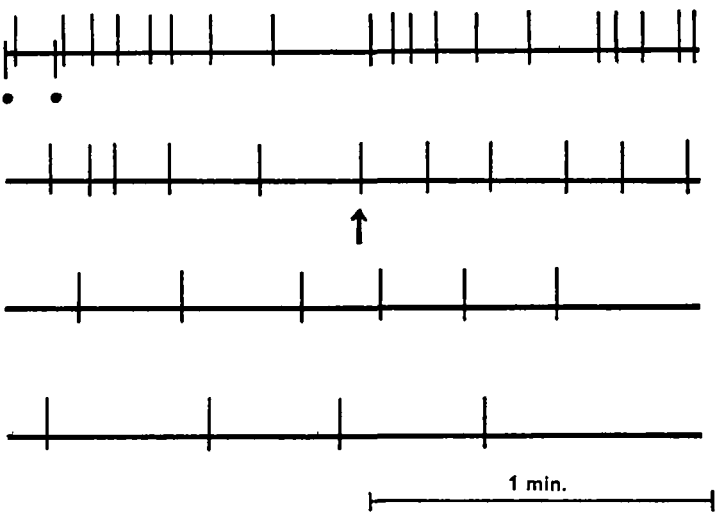

Fig. 2. Diagram showing distribution of electrical activity in one animal during period from first shell contact to first bending of the column. Recording from sphincter. Redrawn from oscilloscope records; variations in pulse size are not shown. The recording is continuous and reads from top left. First and third pulses (dots) are muscle action potentials, rest are SP1s. The pedal disk was fully detached at the time shown by the arrow.

from an inhibitory effect of contact between pedal disk and shell (Davenport, Ross & Sutton, 1961). SP1s were not seen when tentacles of shell-attached animals contacted shells or when tentacles adhered to food particles.

During the 'shell response' SP1 frequency seems to be correlated with the observed tentacular activity. In obviously active responses, where many tentacles are quickly brought into contact with the shell, SS1 firing frequency may approach the maximum

possible (about one pulse/3 sec. at 11° C.). Figure 2 summarizes the distribution of electrical activity during an 8-min. period of recording from one animal. Two initial retractions are both followed by SP1s. Release of pedal disk attachment occurred at the point marked by the arrow. The time between the initial response and release was about 3 min. and in this time about 25 SP1s were seen, an average frequency of one pulse/7 sec.

Differences between animals were considerable. Often there was a long initial period where activity seemed to come in bursts. Sometimes SS1 activity stopped altogether, and these animals did not detach and showed no further response. Release never occurred when there was no SS1 activity. There was no evidence of pacemaker action being responsible for SS1 firing; the intervals between pulses are always very variable. It is not clear if continued SS1 activity results from maintained tentacle contact or from contact of previously unstimulated tentacles.

After detachment, SP1 frequency declines. Typically, the intervals between the pulses increase to 20–60 sec. within 2 min. of detachment. This does not seem to be a direct response to detachment as SP1s are also recorded in the initial stages of the response to shells of animals that were already detached. SP1s still appear during column bending and initial pedal disk attachment, but stop when the tentacles loose their hold on the shell. If the shell–tentacle link is broken at any stage of the climbing sequence SS1 activity stops.

Activity in the through-conduction system can often be detected. Figure 1 C shows a series of small pulses seen just before a slow sphincter contraction. Tonic contractions of the sphincter often occur during climbing (Ross & Sutton, 1961*a*). These small pulses are easily distinguishable from SP1s. They may represent activity in the nerve net itself (McFarlane, 1969). The first two pulses are larger and may be small muscle action potentials. The firing frequency is about one pulse/2·5 sec.; this is within the range that produces slow sphincter contraction (Ross, 1957). The constancy of the frequency suggests that a pacemaker is involved.

Pedal disk release by mechanical stimulation

Calliactis polypus will detach in response to mechanical stimulation of the column by the hermit crab *Dardanus gemmatus*. *Pagurus bernhardus* does not seem to show the same behaviour with *C. parasitica* but the results given below show that the relevant sensory-motor pathway is present in the anemone and that the SS1 again seems to be involved.

The SS1 can be excited by mechanical stimulation of the column or pedal disk. The threshold is above that of the through-conduction system. The SS1 seems to be ectodermal (McFarlane, 1969) but the nature and location of the sensory structures involved in this response are not known. The SP1 response delay for mechanical stimulation is close to the delay observed following electrical stimulation in the same position. Continued poking of the column at intensities that evoke SP1s and at a frequency of about one stimulus/5 sec. produces detachment after about 30 stimuli.

It is difficult to demonstrate clearly mechanical excitation of the SS1 in the tentacles. Light touch gives local contraction of tentacle and oral disk; no SP1s are seen at a sphincter recording site. Stronger touch gives symmetrical activation of the fast musculature of the tentacles and sphincter. A single SP1 is often seen following strong

stimulation but it appears 3–6 sec. after retraction. This delay is too long to be explained as conduction delay from the tentacle to the sphincter. The SP1 may result from self-excitation caused by the fast contraction. The SP1s immediately after the contraction pulses in Fig. 2 may be part of the same phenomenon.

Pedal disk release by electrical stimulation

Ross and Sutton (1968) made *Calliactis polypus* detach by stimulating the column electrically at 1 shock/sec.; this frequency was too low to excite fast sphincter contractions. At the environmental temperature of *C. polypus* (26–30° C.) the withdrawal reflex was elicited at frequencies above 3 shocks/sec. At 11° C. *C. parasitica* gives fast contractions when the interval between stimuli is less than two seconds. A stimulus frequency of 1 shock/5 sec. was used in the initial detachment experiments.

Detachment follows column stimulation at 1 shock/5 sec. at an intensity 100% higher than the through-conduction system threshold. Reactive animals give fast sphincter contractions to the first few stimuli but this is usually succeeded by relaxation and spreading of the oral disk, due mainly to a relaxation of the sphincter muscle. This effect is maintained for as long as stimuli are given, but a slow sphincter contraction often occurs after cessation of stimulation. The first signs of pedal disk detachment are obvious after 10–20 stimuli, the usual indication being a slight loosening and lifting of the pedal disk margin. After about 30 stimuli the anemone is completely detached and falls away from the shell. Sometimes the stimulating electrode held the animal in place and release could only be detected by moving the shell. If the pedal disk is left touching the shell and stimulation stopped, re-attachment takes place immediately. However, the attachment is loose and the animal can be pulled off the shell easily; it is several hours before a firm bond is established. The initial loose attachment may involve nematocyst discharge while the firm bond requires the secretion and hardening of cementing substances (Ross, 1965). In cases where stimulation was continued for up to 15 min. there was no re-attachment before the stimulus series was stopped. Whatever the mechanism of re-attachment it is clearly blocked by low-frequency stimulation.

Sphincter loop preparations give fast or slow contractions depending on the frequency of stimulation (Ross, 1957). The situation in the whole animal is different, as low-frequency stimulation usually fails to give slow sphincter contraction; this phenomenon has already been noted by Ross & Sutton (1968) in *Calliactis polypus*. However, a few animals did give a slow closure and remained contracted for as long as stimulation was maintained. This did not affect detachment and there was no obvious difference between relaxed and retracted animals with regard to the number of stimuli required. It is clear that relaxation of the crown is not an essential part of pedal disk release.

The stimulus intensity necessary to cause release was compared with the thresholds of the known conduction systems in an attempt to locate the system mediating detachment; this showed that the SS1 and detachment are excited at the same threshold. Evoked activity was monitored from the tentacles or sphincter. For mid-column stimulation the threshold of the SS1 is 50–100% higher than that of the through-conduction system and in this position the SS2 is excited only at considerably higher intensities. Disk detachment occurred at stimulus intensities well below those that

excite the SS2 so this system is clearly not involved in the response. When activity is present only in the through-conduction system the effects of stimulation are variable and depend largely on stimulus frequency. Whereas slow sphincter contraction is elicited by stimulation of a fresh animal at frequencies between about one shock/2 sec. and one shock/7 sec., the same stimuli applied to the same animal a few minutes later may fail to give contraction. Slow sphincter contraction is rarely seen when stimuli are above SS1 threshold, but because of the variability of sphincter response described above it cannot be concluded that SS1 excitation produces the observed sphincter inhibition. Only slow sphincter contractions are inhibited, as double shocks given during low-frequency stimulation will give fast contraction. Detachment of the pedal disk never occurs in the absence of SS1 activity. This suggests that the SS1 is the pathway co-ordinating detachment but does not deny through-conduction system involvement as this system is also active at the stimulus intensities which give release. Activity in the through-conduction system alone will not produce detachment.

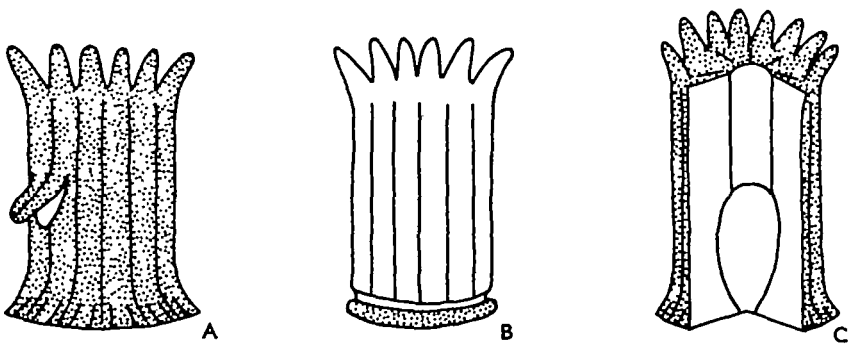

Fig. 3. Showing the operations performed to determine the location of the conducting system controlling detachment. (A) Superficial flap cut in column. (B) Pedal disk margin removed. (C) Animal bisected longitudinally. Stippling shows areas where stimulation will elicit detachment.

The action of the SS1 was further confirmed by placing the stimulating electrode in other positions to find the extent of the system controlling detachment. The SS1 seems to be ectodermal and can be excited by stimulation of all ectodermal surfaces (McFarlane, 1969). Detachment can be produced by low-frequency stimulation of any part of the ectoderm (pedal disk, column, tentacles and oral disk) providing the stimulus intensity is above the SS1 threshold. Correlation between SS1 and detachment was also shown by experiments on operated animals. Five animals were used for each experiment; the results are summarized in Fig. 3.

Stimulation of a superficial flap cut in the column (Fig. 3A) will excite only the SS1 (McFarlane, 1969). Such flaps consist of ectoderm and superficial mesogloea only. Low-frequency stimulation below SS1 threshold does not cause detachment, but if the intensity is increased so that the SS1 is excited the pedal disk is freed after about 30 shocks. Stimulation of the mesogloea under the flap excites the through-conduction system but not the SS1, and does not result in detachment. Figure 3B shows an animal with the margin of the pedal disk removed. This operation destroys all ectodermal connexions between the pedal disk and the rest of the animal but leaves intact

all communication via the mesenteries, that is the cut is a barrier to the SS1 but not to the through-conduction system. Stimulation of any region oral to the cut has no effect on the pedal disk but detachment follows stimulation of the ectoderm pedal to the cut. Stimulation of the pharynx or mesenteries of a longitudinally bisected animal (Fig. 3C) excites the SS2 and through-conduction system only (McFarlane, 1969) and does not cause detachment.

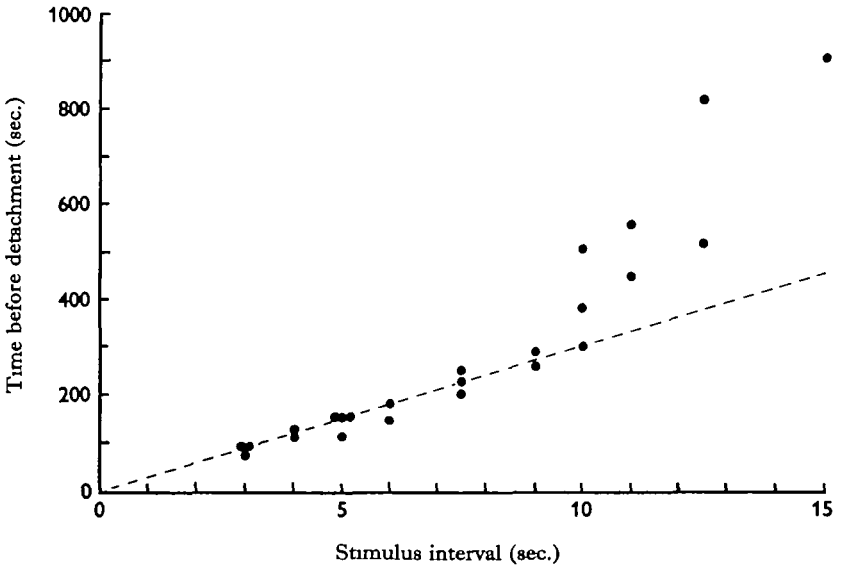

Fig. 4. The effect of stimulus frequency on detachment. Frequency shown as the interval between successive stimuli. Time measured from the start of stimulation to the completion of detachment. Dashed line shows the time for 30 stimuli at all intervals.

The following experiment determined the number and frequency of stimuli effective in producing detachment. A large number of firmly attached animals were used. Five animals were used twice but at least 3 days were allowed between trials for re-attachment. The temperature of the sea water was maintained close to 11° C. for all the trials. All stimuli were applied to the mid-column and were twice SS1 threshold. Evoked activity was monitored by an electrode on the sphincter. The number of shocks producing release at known frequencies was recorded. Figure 4 is plotted as the time taken for detachment against the interval between stimuli. The dashed line shows the time for 30 stimuli at each stimulus interval. For stimulus intervals between about 3 and 9 sec., most of the points lie close to the 30 stimuli line. Thus, over a wide frequency range there is little variation in the number of effective stimuli. When shocks are separated by less than 3 sec. or by more than 15 sec. there is no detachment. At intervals between about 10 and 15 sec. the points show a wide scatter. In five cases at 15-sec. intervals and two at 12·5 sec. intervals no detachment occurred within 30 min.

The failure to produce pedal disk release at stimulus frequencies greater than 1 shock/3 sec. provides further evidence that the SS1 is concerned with detachment. Stimulation of an attached animal at frequencies higher than about one shock/3 sec. gives fast sphincter contractions; the animal stays closed for as long as stimulation is

maintained and does not detach. The recording electrode is always thrown off during closure so it is impossible to be certain of the electrical activity present during stimulation, but failure to elicit detachment may be due to failure of SS1 conduction. Both slow systems show a marked increase in conduction delay on repetitive stimulation (McFarlane, 1969). At 11° C. the SS1 fails to conduct at frequencies above 1 shock/3 sec. At higher temperatures the SS1 and pedal disk release follow stimulation at higher frequencies. At 15° C. the SS1 fails to conduct, and detachment is not seen, at frequencies higher than 1 shock/2 sec. Ross & Sutton (1968) used stimulation at 1 shock/sec. to detach *Calliactis polypus* at 26–30° C.; detachment rarely took longer than 1 min.

The mechanism of detachment

Detachment may result from muscular or chemical action or a combination of both. Release by muscular action would involve mechanical breakage of the pedal disk–shell bond, and chemical action would presumably break this bond by a cellular secretion. The phenomenon of detachment in *Calliactis parasitica* has been outlined by Ross (1968), who describes the muscular movements apparently involved and also suggests that there may be weakening of cementing substances by secretions from the pedal disk.

Although muscle movements are seen during low-frequency stimulation these do not seem to be primarily responsible for release as they also occur when stimulation is below the detachment threshold. The muscles most likely to be concerned with release are the parietals, parietobasilars, circular muscles of the column and the basilars of the pedal disk. However, it is generally agreed (e.g. Batham & Pantin, 1954; Ross, 1957) that every muscle system is excited at the same threshold, that of the through-conduction system. Each muscle group has a different optimum frequency for activation. Some muscles are capable of giving both fast and slow contractions, but these too appear to have identical thresholds. The fact that the threshold of the detachment response is higher than that of the through-conduction system implies that muscle action is not the primary cause of release, or perhaps that the muscles can also be activated by the SS1.

Chemical destruction of cementing bonds can be put forward as a possible explanation for detachment but the physiological evidence is equivocal. The shape of Fig. 4 could be interpreted on the basis of chemical action. Each SP1 seems to produce a certain amount of loosening, and successive pulses can summate until detachment is effected. The loosening effect from a single pulse seems to last for about 9 sec. but decays rapidly after this. If SP1s arrive at intervals greater than 9 sec. there is either no detachment or else a larger number of pulses is required. This may mean that broken links between the shell and pedal disk are re-made within about 9–15 sec. but an alternative explanation is that a certain amount of muscular action is needed to complete detachment and this may be absent at very low stimulus frequencies.

Another method of detachment has been suggested by Robson (1961*a*) for *Stomphia coccinea*. This anemone detaches and swims in response to contact with certain species of starfish and nudibranchs. A histological study of the pedal disk showed thin strands running between the cementing layer and the mesogloea. Robson proposed that if these were contractile the cementing layer could be shed during detachment. There seem to be similar structures in *Metridium* (Batham & Pantin, 1951) but it is not known if they are present in *Calliactis*.

DISCUSSION

The 'shell response' of *Calliactis parasitica* involves excitation of the SS1. Evidence has been given that the SS1 activity is associated with pedal disk detachment. 'Shell climbing' also involves complex muscular movements aiding detachment and bringing the pedal disk against the shell. The SS1 seems to have no muscular outlet so the 'shell response' must also include excitation of the co-ordinating system supplying the muscles active in the climbing sequence. Pacemaker activity may be important in controlling the relevant muscles.

Detachment of the pedal disk may be important in other species. Although normally found firmly attached, many sea anemones can detach and move around in various ways. Some swim, others move by slow creeping movements of the pedal disk, and some are moved passively by water currents. It is possible that all these examples have a common basis and that the release mechanism is co-ordinated by a slow-conduction system like the SS1 in *Calliactis parasitica.*

Detachment is an important part of the swimming response of *Stomphia coccinea* and is some fifty times faster than in *Calliactis parasitica* (Ross, 1965). This increased speed seems in part at least attributable to a greater muscular contribution to release, but again a chemical process may be involved. Ross & Sutton (1964) have shown that retraction and swimming in *Stomphia* have different thresholds and so are presumably controlled by separate conduction systems. An ectodermal system such as the SS1 cannot control swimming, as this is a manifestation of activity of the endodermal parietal muscles. Robson (1961*b*) described an endodermal nerve net that may be the site of the swimming pacemaker. However, there is no evidence that swimming and detachment are excited by a single conduction system. Electrical activity has not been recorded from *Stomphia* but there may be a slow conduction system controlling detachment.

Stomphia also shows a 'shell response' (Ross & Sutton, 1967) whereby it can transfer to certain mollusc shells after swimming or from another substrate providing it has not been attached for more than a few hours. In the latter instance pedal disk detachment is involved. It is interesting that there is no tentacle adhesion in this response; as pointed out above, in *Calliactis parasitica* it is not clear whether shell contact or the adhesion stimulate activity in the SS1.

The different methods of shell transfer found in different species of *Calliactis* have been outlined in the Introduction. The common features in all methods seem to be detachment and re-attachment of the pedal disk, these probably being the most primitive features of the behaviour sequence and derived directly from the detachment mechanism common to many anemone species. This primitive stage may be represented by the 'shell response' of *Stomphia* where the transfer involves slow creeping movements similar to locomotory movements in other anemones. Transfer in *Calliactis* differs from this because the target shell contains a hermit crab. When the crab is not directly aiding transfer special methods are developed to ensure successful climbing on to a moving shell; the obvious examples are the initial tentacle adhesion and the complex sequence of muscular contractions that brings the pedal disk into contact with the shell.

SUMMARY

1. Electrical activity has been recorded from the sphincter region of *Calliactis parasitica* during the behavioural sequence in which the anemone detaches from the substrate and attaches to a *Buccinum* shell. The ectodermal slow-conduction system (SS1) fires repetitively, the majority of observed pulses occurring in the period prior to detachment (a typical example is 25 SS1 pulses at an average frequency of 1 pulse/7 sec.). Shell–tentacle contact is essential for stimulation of SS1 activity.

2. Mechanical stimulation of the column excites the SS1, and 30 stimuli at a frequency of about one shock/5 sec. give pedal disk detachment.

3. Electrical stimulation of the ectoderm excites the SS1 and about 30 stimuli at frequencies between one shock/3 sec. and one shock/9 sec. produce detachment. Detachment and the SS1 have an identical stimulus threshold. It is concluded that detachment is co-ordinated by the SS1.

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