

CONTROL OF PREPARATORY FEEDING BEHAVIOUR IN THE SEA ANEMONE *TEALIA FELINA*

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INTRODUCTION

The feeding behaviour of sea anemones may show two phases:

1. Preparatory activity (pre-feeding response). Pollock (1883) observed that common sea anemones in a rock pool respond to the presence of nearby food by opening. Most descriptions of the preparatory activity refer to *Metridium senile* (Parker, 1919; Pantin, 1950), where the response to dissolved food substances involves expansion of the oral disk followed by extension and 'swaying' of the column. These movements clearly increase the chance of contacting nearby food.

2. Feeding response. Contact of tentacles or oral disk with solid food is followed by nematocyst discharge and a series of ingestive movements. Food may be moved to the mouth by ciliary action in some species or by local movements of tentacles and oral disk in others. The feeding response is normally elicited by a combination of chemical and mechanical stimulation (Pantin & Pantin, 1943). Prolonged food-deprivation may lower the threshold of the response such that nematocyst discharge and ingestive movements are elicited by mechanical stimulation alone.

There are no published accounts of the mechanism of the pre-feeding response; it is unlikely to be mediated via the through-conducting nerve net as stimulation of this system is thought to elicit only fast or slow muscle contraction (Batham & Pantin, 1954; Ross, 1957) and this cannot explain the observed expansion of the oral disk. A slow-conduction system, the SS 1, has been described in *Calliactis parasitica* (McFarlane, 1969*a*); this system seems to be ectodermal and may be non-nervous. A similar conduction system has been found in *Tealia felina* and the present study indicates that the pre-feeding response of this anemone is mediated in part at least by the SS 1.

MATERIALS AND METHODS

Although *Metridium senile* is known to give a clear response to dissolved food substances, this species was not used as it proved difficult to prevent the anemone from retracting and throwing off a recording electrode attached to a tentacle. *Tealia felina* was found to be less irritable, enabling continuous recordings to be made for an hour or more. Two varieties of *Tealia* were used: var. *coriacea*, the common shore form, and var. *lofotensis*, a deeper water form. The diameters of the expanded oral disks of the anemones used were between 5 and 10 cm. All recordings were made with suction electrodes; the recording and stimulating system has been previously described (McFarlane, 1969*a*). Observations were made at sea-water temperatures between 5 and 10° C. Test animals were deprived of food for 3 days before experimentation.

RESULTS

Recordings of electrical activity

Fast longitudinal contraction of the tentacles of *Tealia* follows two shocks, less than one second apart, applied to any part of the ectodermal surface of the anemone. A biphasic or triphasic pulse, up to $300\ \mu\text{V}$ in amplitude, is recorded from a tentacle after the second shock. Recordings from the sphincter region or from the tentacles of *Calliactis polypus* (Josephson, 1966) and of *C. parasitica* (McFarlane, 1969a) show a similar pulse preceding fast contraction; this may be a muscle action potential.

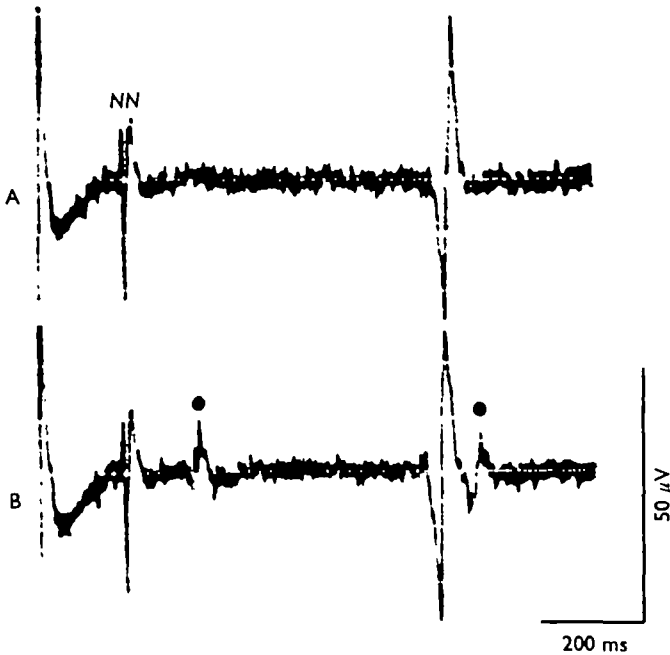


Fig. 1. Electrical activity recorded from a tentacle of *Tealia felina* var. *lofotensis* in response to a single shock to the base of the column. Inter-electrode distance approximately 6 cm. A: response showing fast pulse associated with the through-conducting nerve net (NN) and a delayed biphasic pulse from the slow conduction system (SS 1). B: as A but with two small pulses (dots) possibly representing activity in a third conduction system.

Recordings from the tentacles of *Tealia* and *Calliactis* show a smaller pulse following a single shock (NN in Fig. 1). This pulse has the same stimulus threshold and the same conduction delay as the contraction pulse following a second stimulus; it may be a small muscle action potential associated with a small contraction of the tentacle longitudinal muscles. Fast contraction in *C. parasitica* seems due to activity in the through-conducting nerve net (Pantin, 1935). The small, fast pulse recorded from the tentacles of *Tealia* is presumably due to a single impulse in the nerve net. The conduction velocity of the nerve net in the oral disk of *Tealia* is $75\ \text{cm./sec.}$ at $10^\circ\ \text{C.}$

A single shock is also followed by a delayed biphasic pulse, up to $60\ \mu\text{V}$ in amplitude, that can be recorded from any ectodermal surface, but is largest when recorded from the tentacles (Fig. 1). The pulse follows stimulation of any ectodermal region; the stimulus threshold is approximately 50% higher than that of the nerve-net response.

Whereas stimulation of intact column surface can excite both this slow pulse and the nerve-net pulse, stimulation of a shallow flap cut in the column excites the slow system alone (Fig. 2). Stimulation of the mesogloal surface of the column under the flap excites the nerve net alone. It is concluded that the slow system is spatially separate from the nerve net.

The properties of the slow system in *Tealia* seem identical to those of the SS₁ in *Calliactis parasitica*; the *Tealia* slow system will also be called the SS₁ and the associated electrical activity, slow pulses, will be called SP₁s. As in *Calliactis*, histological

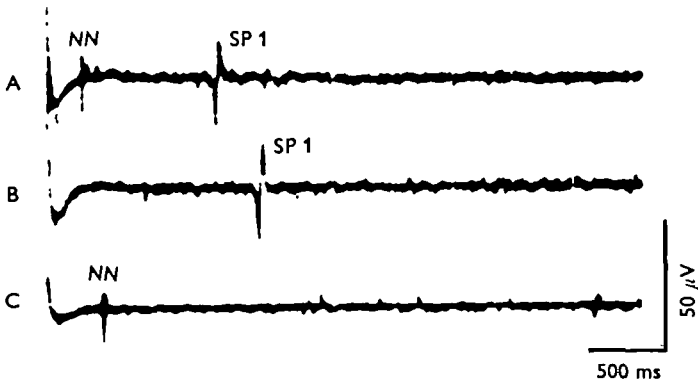


Fig. 2. Single-shock responses recorded from a tentacle of *Tealia felina* var. *lofotensis*. Stimulating electrode on A—the surface of the column, B—a mid-column ectodermal flap, and C—the mesogloal surface under the flap. NN: response associated with the nerve net. SP₁: pulse from the SS₁. This experiment suggests that the SS₁ lies in the ectoderm.

examination of flaps known to contain the SS₁ leads to the conclusion that this conduction system lies in the ectoderm or superficial mesogloea. The conduction velocity of the SS₁ in *Tealia* is 22–25 cm./sec. in the oral disk but is as low as 6 cm./sec. in the column. The SS₁ fails to conduct at stimulus frequencies greater than one shock every 3 sec.

The small pulses marked by dots in Fig. 1 B occur spontaneously (pulse following the nerve-net response) and can also be elicited by high-intensity stimulation of the column (pulse following the SP₁). These pulses have only been recorded from tentacles and they do not follow stimulation of an ectodermal flap. It is possible that they represent activity in a third conduction system equivalent to the SS₂ described in *Calliactis parasitica* (McFarlane, 1969a).

No differences were detected between the conduction systems of the two varieties of *Tealia* studied.

Response to dissolved food substances

Fig. 3 shows a typical response of *Tealia felina* var. *lofotensis* at 0, 5, 15 and 25 min. after addition to the water of 10 parts per million by dry weight of molluscan (*Mytilus*) tissue. The response shows three main features:

1. An increase in the area of the oral disk, possibly due to relaxation of the sphincter muscle at the top of the column and of the radial muscles of the oral disk.
2. Lowering of the margin of the oral disk, again possibly resulting from relaxation of oral disk radials.

3. Mouth opening and protrusion of the pharynx. Mouth opening may be caused by contraction of the transverse muscles of the mesenteries. Protrusion of the pharynx was not always seen and seems to require a high concentration of dissolved food substances.

Movements of the oral disk and tentacles increase during exposure to food. In the expanded state the tentacles will readily seize any object they contact, but the same response is shown to a lesser extent in an anemone not exposed to food substances. After a long interval the column may extend and become very sensitive to touch,

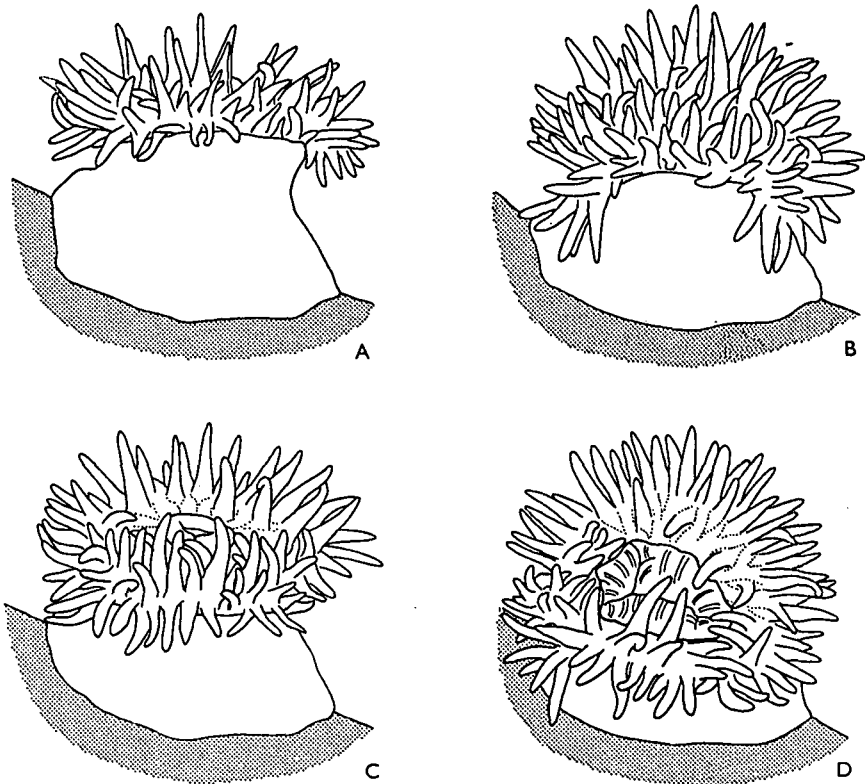


Fig. 3. Drawings from photographs of *Tealia felina* var. *lofotensis* at 0(A), 5 (B), 15 (C) and 25 (D) minutes after addition of food extract to the water. The opening response involves expansion of the oral disc, lowering of the oral disc margin, mouth opening and pharynx protrusion. This pre-feeding response clearly increases the 'food-catching' area of the anemone.

giving a rapid bending towards the point of stimulation. The anemone may remain in an expanded state for up to an hour after removal of dissolved food substances from the medium. Not all anemones showed a clear response to food; the reason for the failure of some to react is not known. Var. *lofotensis* showed a greater and more consistent response to dissolved food substances than did var. *coriacea*.

The stages of the pre-feeding response are easily recognized and the question can be asked: Can any part of this behaviour be elicited by electrical stimulation of any known conduction system?

Responses to electrical stimulation

Pantin (1950) was unable to elicit preparatory feeding activity in *Metridium senile* by electrical stimulation; the stimulation technique possibly excited more than one conduction system. Using the flap technique described above it is possible to stimulate the nerve net and SS I separately or together. A recording electrode on a tentacle serves as a check that the required system is being stimulated.

Stimulation of the nerve net of *Tealia* produces contraction; as in *Metridium* (Batham & Pantin, 1954), different muscles respond maximally at different stimulus frequencies. Simultaneous stimulation of the nerve net and the SS I often gave contraction but the results showed considerable variation. Stimulation of the SS I alone gave expansion of the oral disk. In the anemone shown in Fig. 4 a mid-column flap was stimulated at one shock every 10 sec. The drawings show the appearance of the anemone after 0, 1, 2, 4, 6 and 8 min. Stimulation was stopped after 7 min., so a total of 42 shocks was given. SP 1s followed every stimulus. A response is obvious after only 6 shocks (Fig. 4B). Continued stimulation gave continued expansion of the oral disk and lowering of the oral disk margin. Slight mouth opening was evident after 4 min. This experiment was repeated at different stimulus frequencies and the results can be summarized as follows:

1. Stimulation of an ectodermal flap at frequencies between one shock every 5 sec. and one shock every 30 sec. gave detectable expansion of the oral disk.
 2. The expansion response and the SS I have the same stimulus threshold.
 3. Continued stimulation is necessary to give maintained relaxation but recovery of the initial state is slow after cessation of stimulation.
 4. Opening was faster at higher frequencies of stimulation than at lower and was also faster than the opening response seen to dissolved food substances.
 5. Open anemones can always be made to open further by stimulation but closed anemones often fail to open.
 6. Slight opening of the mouth is often seen but never pharynx protrusion.
- It seems then that at least part of the normal pre-feeding response can be elicited by stimulation of the SS I.

In *Calliactis parasitica* stimulation of the SS I at frequencies between one shock every 3 sec. and one shock every 10 sec. gave detachment of the pedal disk (McFarlane, 1969*b*). Detachment forms an important part of the behavioural response whereby *Calliactis* detaches from the substratum and climbs on to a *Buccinum* shell. In only two cases out of twenty was detachment seen during stimulation of the SS I in *Tealia*; the anemones in both cases were var. *lofotensis* and the stimulus frequency used was one shock every 5 sec. However, in four other cases (also var. *lofotensis*) local loosening of pedal disk attachment was obvious. Stephenson (1928) records that *lofotensis* is less inclined than *coriacea* to adhere very firmly.

As in the response to dissolved food substances an anemone expanded by electrical stimulation will readily seize any object touching the tentacles. This in practice meant that the recording electrode was often actually ingested. An unstimulated animal was never observed to ingest a recording electrode attached to a tentacle. This implies that SS I stimulation can also lower the feeding-response threshold so that an inert object touching the tentacles elicits a normal feeding response. Unstimulated *Tealia*

often seize inert objects but rarely ingest them, seizing being rapidly followed by rejection.

Mechanical and chemical stimulation

Mechanical stimulation of the column of *Calliactis parasitica* excites the nerve net; the receptive region appears to be endodermal and to be excited by column deformation

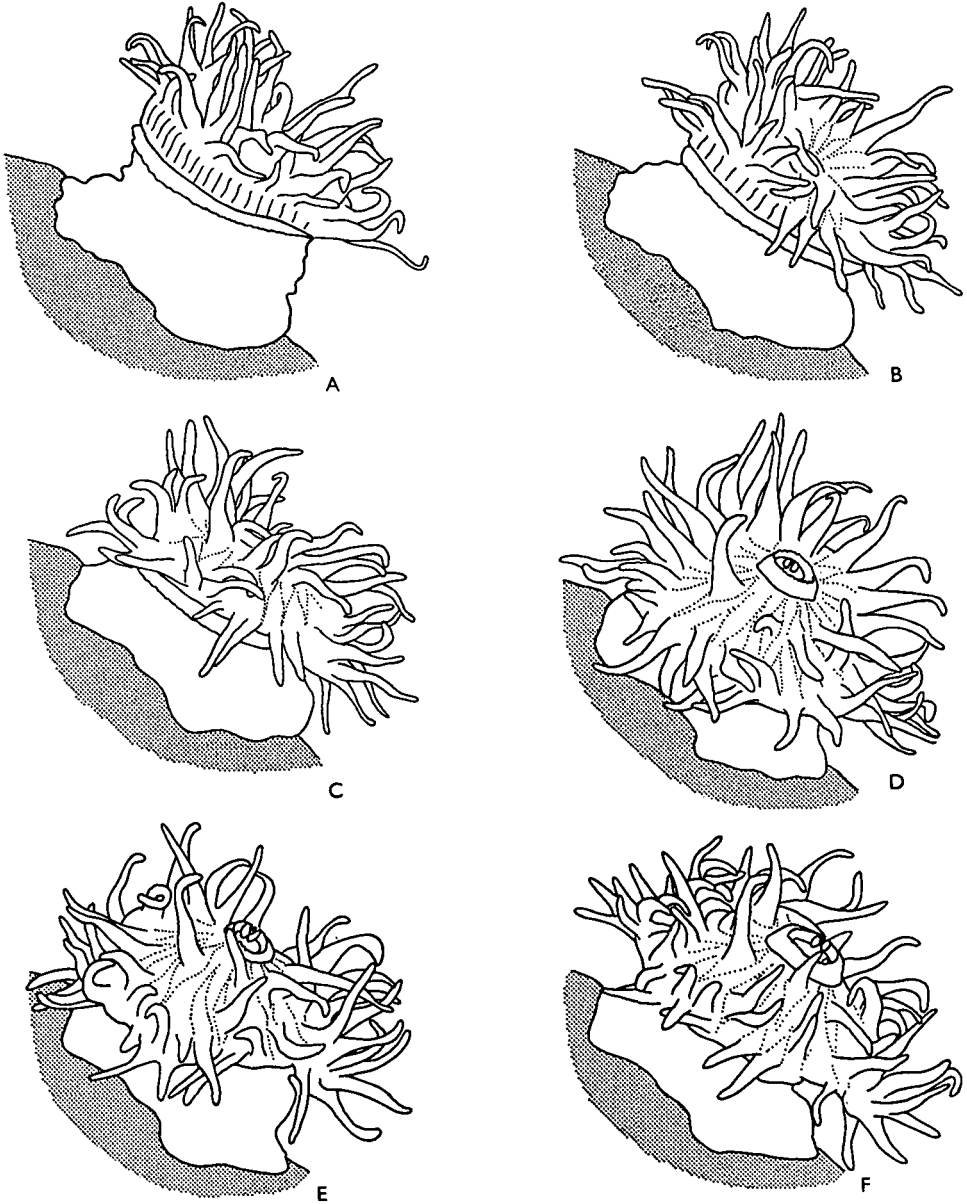


Fig. 4. Response of *Tealia felina* var. *lofotensis* to electrical stimulation of the SS 1 at one shock every 10 sec. Drawings show appearance at 0 (A), 1 (B), 2 (C), 4 (D), 6 (E) and 8 (F) min. after start of stimulation. The main features of the response are expansion of the oral disc and lowering of the oral disc margin.

(Passano & Pantin, 1955). The SS I in *C. parasitica* is excited by contact of the tentacles with a *Buccinum* shell or by mechanical stimulation of the column (McFarlane, 1969*b*).

Prodding the column of *Tealia* excites both the SS I and the nerve net, the latter having the lower threshold. By lightly stroking the column with a small brush it is possible to stimulate the SS I alone. Very light touch with a brush fails to excite either system. If the brush is dipped in crushed *Mytilus* tissue, light touch gives one or occasionally two SP I's. Continued, low-frequency firing of the SS I results from placing a small piece of *Mytilus* tissue in contact with the column. Inert material of similar size and weight gives either no response or just a single SP I as the material is placed on the column. SP I's are not clearly seen following chemical or mechanical stimulation of the tentacles but the electrical recording in these cases is confused by the presence of activity due to tentacle contractions associated with a feeding response or with a protective withdrawal.

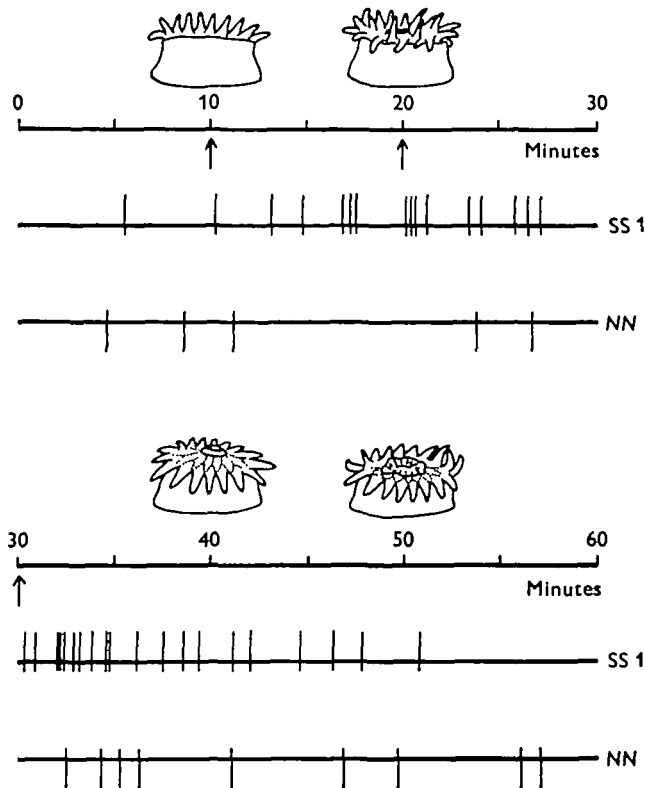


Fig. 5. Nerve net (NN) and SS I activity during exposure of *Tealia felina* var. *lofotensis* to food extract. Recording electrode on a tentacle. Pulses redrawn from oscilloscope records. Equal quantities of food extract added at 10, 20 and 30 min. (arrows) after start of recording. The appearance of the anemone is shown after 10, 20, 40 and 50 min. The pre-feeding response to dissolved food substances is clearly associated with an increase in SS I activity. The extract was washed away at 45 min.

Electrical activity during opening

Part of the response of *Tealia* to dissolved food substances can be evoked by electrical stimulation of the SS I. SS I activity can be elicited by touching the column with food material. Further to confirm the action of the SS I, electrical activity was recorded

from tentacles during the response to dissolved food substances. SP 1s and nerve-net pulses are sufficiently different to be distinguished during monitoring. In the resting animal pulses are on occasion recorded from both systems in the absence of any obvious stimulus. Following addition of food extract there is little or no alteration in nerve-net activity but there is a considerable increase in the rate of SS 1 firing and this is abolished when the extract is washed away. Active responses to dissolved food substances were accompanied by a large number of SP 1s, the minimum interval between pulses being 5 sec.; no SP 1s, or only a few, were seen if the animal showed no expansion response.

Fig. 5 shows a typical recording sequence. In the 10 min. before addition of food extract only one SP 1 was recorded. Following addition of ten parts per million by dry weight of *Mytilus* extract SP 1 activity increased to six pulses in 10 min. Further additions of food extract were followed by further increases in SS 1 activity. SS 1 firing declined to the resting level within 10 min. of removal of dissolved food substances. There seems in this particular case to be a slight increase in nerve-net firing during the most active period of SS 1 firing, but this was not always seen.

DISCUSSION

The above results indicate that dissolved food substances, contacting the column of *Tealia felina*, excite SS 1 activity. The SS 1 seems to be ectodermal, and impulses in this system are conducted throughout the ectoderm. The behavioural output associated with continued low-frequency firing of the SS 1 is expansion of the oral disk and lowering of the oral disk margin, due perhaps to relaxation of the sphincter muscle at the top of the column and of the radial muscles in the ectoderm of the oral disk. This relaxation response has the appearance of being preparatory feeding behaviour, increasing the chances of contacting nearby food, and has been termed the pre-feeding response to distinguish it from the true feeding response, which involves co-ordinated movements of the tentacles, oral disk and mouth, associated with the ingestion of solid food. The two responses may be separated on the basis that the pre-feeding response is elicited by chemical stimulation alone whereas the feeding response in sea anemones seems to require mechanical stimulation in addition.

The chemical identity of a number of feeding response activators is known for many coelenterates (Lenhoff, 1968). In *Hydra littoralis* reduced glutathione causes mouth opening and contraction of the tentacles towards the mouth. As this involves tentacle shortening it must lessen the chance of contacting prey and can be interpreted as a true feeding response. Other Hydrozoa show similar responses to solutions of reduced glutathione or certain amino acids. Valine causes the sea anemone *Bolocerooides* sp. to ingest inert material (Lindstedt *et al.* 1968); mechanical and chemical stimuli are required to elicit the feeding response. Except for slight mouth opening, no expansion or pre-feeding response was described for *Bolocerooides* in the presence of valine solution. Glutamine seems to be the feeding activator in an unidentified acontiate sea anemone (Lindstedt *et al.* 1968); again the feeding response also required mechanical stimulation. The chemical that elicits preparatory, pre-feeding behaviour has not been identified for any sea anemone. There is as yet no evidence to suggest that the pre-feeding response and the feeding response are elicited by the same compound.

It is generally supposed that the feeding-response activator for Hydrozoa is released from the prey when it is pierced by nematocysts, so that actual contact is required to elicit a feeding response. The pre-feeding response of sea anemones seems to involve distant chemoreception, perhaps of chemicals diffusing from prey that escapes from tentacle contact but remains, wounded, in the vicinity of the anemone. In a well-expanded anemone the tentacles touch the substratum and could pick up food lying near or against the base of the column. In later stages of the response the column extends and becomes very sensitive to touch, bending rapidly towards the point of stimulation; this too can be interpreted as improving the chances of food capture. In addition, marine zooplankton seem to release dissolved free amino acids (Johannes & Webb, 1965) and the anemone may be able to respond to the presence of large numbers of suitable food animals. Further speculation must wait until the pre-feeding activator of *Tealia* has been identified.

The nature of the SS₁ is still unknown and the way in which this system causes relaxation is not clear. Three possible modes of action are: inhibition of spontaneous nervous impulses maintaining muscular tone, direct relaxation of muscles, or a reversible change in the properties of the mesogloea giving a decrease in elastic restraining force. Direct recording suggests that there is no decrease in the number of nervous impulses reaching the muscles. It is of interest that Rushforth (1965) has shown that in *Hydra* reduced glutathione inhibits body contractions induced by light or by mechanical agitation.

Nervous elements have not been clearly demonstrated in the ectoderm of the column of sea anemones, and it may be proposed that the only possible site for the SS₁ is the ectodermal supporting cells. Non-nervous conduction between epithelial cells has been demonstrated in hydromedusae and siphonophores (Mackie & Passano, 1968; Mackie, 1965). The ectodermal radial muscles of the oral disk presumably lie close to the ectodermal cells and a functional connexion is clearly possible. However, relaxation of the sphincter muscle is difficult to explain as this muscle lies some way from the ectoderm.

Relaxation responses in sea anemones are not always associated with feeding. When the hermit crab *Dardanus arrosor* moves to a new shell it will often detach the anemones (*Calliactis parasitica*) attached to the old shell and transfer them to its new home. The crab strokes and pokes the column of the anemone with its walking legs until the anemone detaches (Ross & Sutton, 1961). The crab *Dardanus gemmatus* shows similar behaviour towards *Calliactis polypus* (Ross & Sutton, 1968). The mechanical stimulation may initially result in a retraction response on the part of the anemone but this is soon followed by relaxation and detachment of the pedal disk from the substratum or from the old shell. Detachment in *C. parasitica* has been shown to be mediated by the SS₁ (McFarlane, 1969*b*) and it seems likely that this system is also involved in the relaxation response.

This work has provided the first evidence for a conduction system involved in the feeding behaviour of sea anemones and emphasizes that many aspects of actinian behaviour need to be re-investigated in the light of the demonstration of multiple conduction systems.

SUMMARY

1. Dissolved food substances elicit preparatory feeding behaviour in the sea anemone *Tealia felina*. This behaviour takes the form of expansion of the oral disk and lowering of the margin of the disk. Food may also cause mouth opening and pharynx protrusion. This pre-feeding response may increase the chance of food capture.
2. The expansion and lowering of the oral disk can also be elicited by electrical stimulation of a slow conduction system, the SS₁, thought to be located in the ectoderm.
3. SS₁ activity is seen when the anemone is exposed to dissolved food substances.
4. It is concluded that preparatory feeding behaviour in *Tealia* is mediated in part by the SS₁.

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