J. exp. Biol. (1975), 63, 525–536
With 5 figures
Printed in Great Britain

AN ELECTROPHYSIOLOGICAL ANALYSIS OF CHEMORECEPTION IN THE SEA ANEMONE *TEALIA FELINA*

By I. D. LAWN*

Gatty Marine Laboratory, University of St Andrews, Scotland

(*Received* 26 *March* 1975)

SUMMARY

1. Electrophysiological techniques have been employed to examine the nature of the response observed in the ectodermal slow-conduction system (SSI) when dissolved food substances contact the column of *Tealia felina*. The response seems to consist entirely of sensory activity which may continue for periods of many minutes, provided that the stimulatory chemicals remain contacting the column.

2. The interval between each evoked pulse gradually increases as the sensory response progresses. This does not result from fatigue in the conduction system but involves a genuine process of sensory adaptation. This may occur over a period of several minutes, which is much longer than comparable adaptation in higher animals.

3. Physiological evidence suggests that the chemoreceptors involved are dispersed throughout the column ectoderm and are absent from the pedal disc, oral disc, tentacles and pharynx.

4. The basic role of the SS1 in coordinating behavioural activity in sea anemones is reviewed. It is concluded that it functions primarily as a single, diffuse-conducting unit responsible for transmitting frequency-coded sensory information from ectodermal chemoreceptors to ectodermal (and perhaps endodermal) effectors.

INTRODUCTION

In recent years much of the work on chemoreception in cnidarians has been directed towards the identification of compounds capable of eliciting feeding responses (see review by Lindstedt, 1971). In all studies on feeding responses in cnidarians, simple behavioural observations have been employed as assays for the sensory response. No attempt has been made to obtain electrophysiological data in support of these findings. It is, therefore, difficult to establish whether a true chemosensory response is being observed, or whether the response is merely due to the effects of specific chemical irritants acting directly on the muscles involved.

Although complete feeding responses may be elicited in some hydrozoans by chemical stimulation alone (Loomis, 1955; Lenhoff, 1961; Fulton, 1963), this does not seem to be true for sea anemones. Williams (1972) cites several examples in which a combination of mechanical and chemical stimuli is required to elicit a feeding response in hese animals. He concluded that this situation probably applies to most macrophagous

* Present address: Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.

anthozoans. Preparatory feeding behaviour in sea anemones, however, may be elicited by chemical stimulation alone (McFarlane, 1970) and is therefore more amenable to electrophysiological analysis. This pre-feeding response is well developed in the large macrophagous anemone *Tealia felina*. It is activated by dissolved food substances contacting the column of the animal and involves expansion of the oral disc, lowering of its margin and extension of the tentacles. Later stages in the response include lengthening and slow 'swaying' movements of the column. This behaviour would clearly increase the food-capturing range of the tentacles.

McFarlane (1970) has demonstrated that the pre-feeding response in *Tealia felina* involves excitation of a slow-conduction system located in the ectoderm (the SS1), and McFarlane & Lawn (1972) have shown that this activity has an inhibitory effect on the radial muscles of the oral disc. The work presented here has employed electrophysiological techniques to study the nature of chemoreception in *Tealia*, as seen in the pre-feeding response. This has brought to light some much-needed physiological information on the properties and location of chemoreceptors in these animals.

MATERIALS AND METHODS

Animals

Specimens of *T. felina* var. *lofotensis* were collected from the North Sea near St Andrews. Before being used in experiments they were kept in the aquarium at the Gatty Marine Laboratory for at least 2 months to allow them to recover from the effects caused by dredging. Only healthy specimens with expanded oral disc diameters of 6–12 cm were used in this study. Except where stated otherwise, experiments were carried out on unoperated, intact animals in order that the sensory response could be studied under conditions approaching those that occur naturally. To achieve uniformity between individuals, each animal was starved for 3 days before use.

Recording and stimulation

During experiments specimens were retained in running, well-oxygenated sea water at temperatures between 7–12 °C. Electrical activity was recorded by means of a polythene suction electrode attached to the mid-region of a tentacle. Signals were fed to a.c.-coupled differential pre-amplifiers (Tektronix 122) and displayed on a Tektronix 564B storage oscilloscope. Stored displays were photographed with an oscilloscope camera.

Suction electrodes were also used for electrical and chemical stimulation. This technique has been previously described (McFarlane & Lawn, 1972) and basically involves filling a stimulating electrode with food extract. The electrode is then attached to the column of the animal and may be used both as a strictly localized applicator of extract and as a conventional stimulating electrode. A total of about 0·8 ml of extract could be contained within the electrode (internal diameter at tip = 1 mm), presumably ensuring that sufficient quantities of stimulatory chemicals were available. This type of electrode will be referred to as a chemical-stimulating electrode to distinguish it from a conventional stimulating electrode. Electrodes with smaller tip diameters were tested but proved unreliable. They invariably became blocked with mucus which would impair their ability to remain attached to the epithelium. Electrical stimulation

was provided by a Devices Isolated Stimulator. All electrical stimuli were of 1 ms duration.

Preparation of food extract

The mantle lobes and lamellae were dissected from living specimens of the bivalve mollusc *Mytilus edulis* and were homogenized in about 20 ml of sea water. The homogenate was then centrifuged at 10000 rpm for 20 min at a temperature of 4 °C and the resulting supernatant was used as the test extract. Extracts were stored at a temperature of 0 °C but were allowed to attain sea-water temperature before use in experiments. Freshly-prepared extracts (less than 1 day old) were used in all experiments.

RESULTS

Sensory adaptation

The placing of an electrode containing fresh food extract onto the column of *T. felina* normally evokes activity in the SS1 and expansion of the oral disc. Control experiments with electrodes containing sea water alone indicate that the pulses evoked in the SS1 are not due to the applied suction. Fig. 1 is a recording of the sensory response obtained when dissolved food substances contact the column of *Tealia*. A Servomex low-frequency waveform generator was employed to produce a series of successive sweeps, one beneath the other, on the screen of the storage oscilloscope. This was achieved by feeding a single, long-duration (about 1000 s) linear ramp into a d.c.-coupled channel of the oscilloscope's differential amplifier. The beam was thus gradually displaced from the top to the bottom of the screen and a sequence of stored sweeps over a time period of up to 16 min 40 s could be photographed in a single frame. Recording at low sweep velocities is practical only with a high signal-to-noise ratio, otherwise the pulses cannot be readily identified.

The record shows that the frequency of evoked SS1 pulses decreases during the course of the response, even though an excess of stimulatory chemicals was available. This seems to be a process of sensory adaptation (McFarlane & Lawn, 1972). In addition, the pulses are seen to decrease in amplitude as the inter-pulse interval decreases. One can clearly see the relatively large amplitude of the initial SS1 pulse and the gradual decrease in amplitude of succeeding pulses during the first stage of the response. In the later stages, when the inter-pulse interval increases, there is a corresponding increase in pulse amplitude. A similar phenomenon has been noted during repetitive electrical stimulation of the SS1 in *Tealia* (see McFarlane & Lawn, 1972). The cause of this antifacilitation of pulse amplitude has not yet been determined, but it is interesting to note that this effect can be observed both in the sensory response and during electrical stimulation of the SS1.

Occasionally, the sensory response to a single application of food extract may continue for very long periods, although there is much variation in this respect. In some instances a single application will evoke only 1 or 2 pulses, or perhaps none at all, whereas in others the application will evoke continual activity in the SS1 for periods of up to 1 h, provided that the food extract remains in contact with the column. Such long-duration firing appears to be a genuine response evoked by the food extract, for normally no spontaneous SS1 pulses are observed during 15 min monitoring periods prior to the application of the extract.

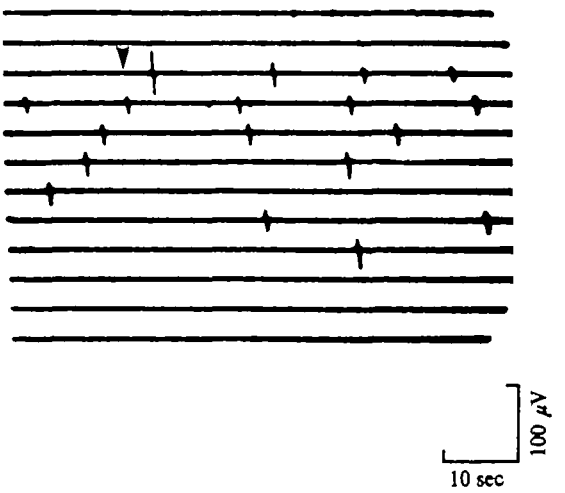

Fig. 1. Recording of electrical activity associated with the response to dissolved food substances. The arrow denotes the time of localized application of food extract to the column of the anemone. A number of pulses in the SS1 are elicited as a result of this. There is a decrease in the frequency of evoked pulses as the response progresses. Note that as the inter-pulse interval increases there is a corresponding increase in pulse amplitude. The process of sensory adaptation during this particular response seems to operate over a period of about 7 min 30 s.

It was noted in earlier work (McFarlane & Lawn, 1972) that the decrease in frequency of evoked SS1 pulses during the sensory response may involve genuine sensory adaptation near the point of chemical stimulation, or may in fact involve fatigue in the conduction system. In order to investigate this problem, a conventional stimulating electrode was attached to the column of an intact *Tealia* and its ability to elicit an SS1 pulse was tested by delivering a single shock at an intensity above SS1 threshold. Once this had been confirmed, spontaneous electrical activity in the animal was monitored for 15 min. During this time no SS1 pulses were observed. The chemical-stimulating electrode containing fresh food extract was then applied to the column, about 1 cm from the attached conventional electrode, and a typical sensory response was evoked. As the interval between successive pulses increased, during the later stages of the response, single shocks were delivered through the conventional electrode. Each intercalated shock evoked a single pulse in the SS1 distinguishable from those induced chemically owing to its characteristic response delay. This indicated that the conduction system was in a non-refractory state during the long inter-pulse intervals of the later stages of the response. SS1 pulses could also be evoked by similar shocks delivered through the chemical-stimulating electrode. This would indicate that the conducting elements near the chemoreceptive region were also in a non-refractory state. These observations suggest that the decrease in pulse frequency during the pre-feeding response is due to sensory adaptation in the chemoreceptors involved. This adaptive process is remarkable in that it functions over a much longer time-scale than the comparable phenomenon in higher animals: the adaptation shown in Fig. 1 lasts for 7 min 30 s, and the mean inter-pulse interval is 25 s.

Source of evoked electrical activity

McFarlane (1970) has shown that the SS1 in *Tealia* can also be excited by mechanical stimulation of the column, sensitivity being greatest near the base. If the column is prodded with a needle, a pulse in the through-conducting nerve-net is usually recorded together with a pulse in the SS1. A light touch with a clean paintbrush, however, often evokes one or two SS1 pulses in the absence of nerve-net activity. Since, under certain conditions, mechanical stimulation is capable of evoking SS1 activity, it remains possible that the food extract acts as an irritant, eliciting localized muscular contractions which pull against any points of attachment. In the intact animal these points would be along the pedal disc margin when attached to the substrate, whereas in a preparation the pins themselves would act in this way. It was, therefore, necessary to estimate the source of the pulses evoked during the pre-feeding response. For this purpose two recording electrodes were used.

A specimen of *Tealia* was bisected longitudinally without use of anaesthetic (see Lawn, 1975), and one half was placed pharynx-downwards onto a piece of cork. Four pins were used to hold the half animal in position. Such preparations were usually left to recover for at least 24 h and invariably appeared to be in good condition. The two recording electrodes (R_1 and R_2) were attached to diametrically opposed tentacles, as shown in Fig. 2. For reference purposes, the pin through the lower column region on the same side as R_1 was designated P_1, and that on the opposite side, P_2. A stimulating electrode is shown attached to the lower column adjacent to P_1. The electrical events shown in Fig. 2 are simultaneous recordings from R_1 and R_2 and were evoked from a single shock applied through the stimulating electrode in the position shown. The dots denote the pulse evoked in the through-conducting nerve-net. The large biphasic event that follows this is the pulse associated with the SS1. Note that the SS1 pulse arrives later at R_2 than at R_1 because of the longer conduction pathway between the point of stimulation and R_2. This difference in arrival time at the two electrodes is less noticeable with the nerve-net pulse owing to its higher conduction velocity (see McFarlane, 1970). This technique may consequently be used to estimate the source of the evoked SS1 pulse simply by comparing the simultaneous recordings from R_1 and R_2.

A chemical-stimulating electrode was filled with food extract and applied to the column at a selected site. An electric shock was delivered through this electrode in order to determine from the recordings the appropriate differential delay for this particular placement. The SS1 pulses evoked during the sensory response to the food extract were also monitored for this placement. Fig. 3 shows recordings obtained for three different placements of the chemical-stimulating electrode. The electrode was placed on the column adjacent to P_1 in Fig. 3A, adjacent to P_2 in Fig. 3B, and mid-way between P_1 and P_2 in Fig. 3C. In each case the difference in arrival time of the SS1 pulse evoked by electrical stimulation (E) is identical to that of the SS1 pulses evoked during the sensory response to food extract (S). This indicates that the SS1 pulses associated with the sensory response originate from the site of the applied chemical stimulus and are not evoked at a region remote from this site by some other form of stimulation.

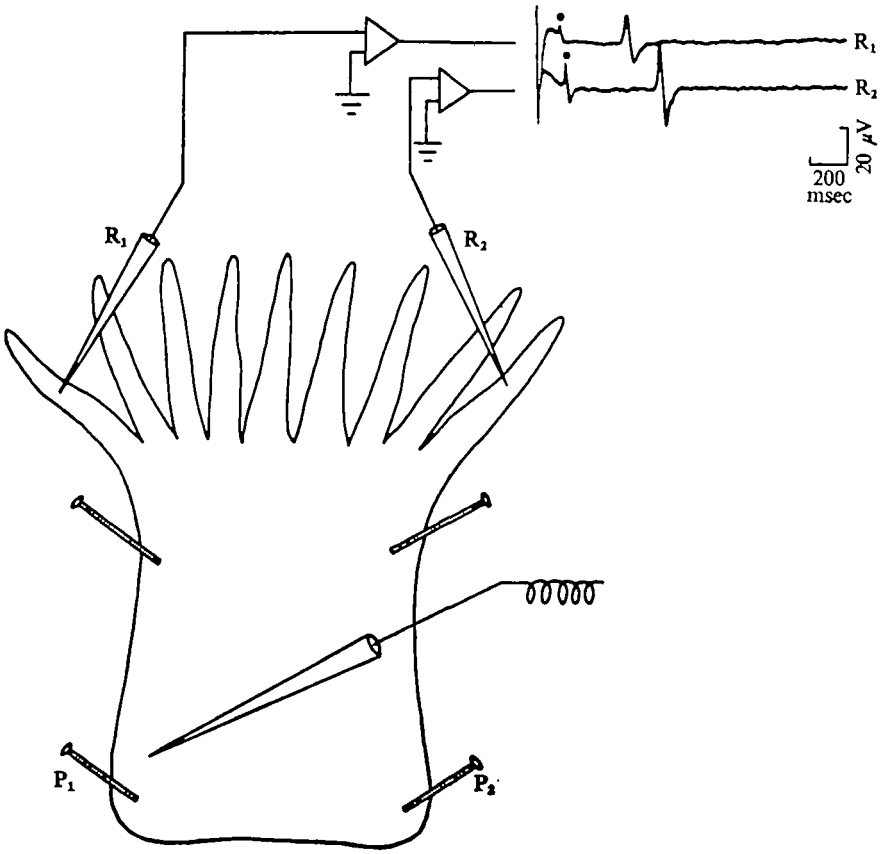

Fig. 2. Experimental arrangement to detect source of evoked electrical activity. The stimulating electrode was placed on the column close to the pin P_1, as shown. The response to a single shock from this electrode is shown in the simultaneous records obtained from the two recording electrodes (R_1 and R_2) attached to diametrically opposed tentacles. Note that the nerve-net pulse (denoted by the dot) and the pulse in the SS1 arrive later at R_2 than at R_1. This is because the stimulating electrode is further from R_2 than R_1.

Location of receptor sites

Once it had been definitely confirmed that the sensory response originated from a chemoreceptive region in contact with the locally-applied food extract, it was possible to use the chemical-stimulating electrode to delineate the extent of the chemoreceptors involved in the pre-feeding response. The food extract was applied locally to various regions of the column, pedal disc and pharynx in order to define those regions capable of eliciting the chemosensory response. Suitable controls, employing sea water in place of food extract, were used throughout these experiments.

Both intact animals and half-animal preparations were tested. More than 30 different individuals were examined to help overcome the problem of variation between animals. The various regions tested are depicted in Fig. 4. For the purposes of this study the column (more specifically, the scapus) has been sub-divided into several regions. The collar region is that portion of the column enclosing the marginal sphincter. Immediately below the collar is the upper column, and below this a more extensive mid-column

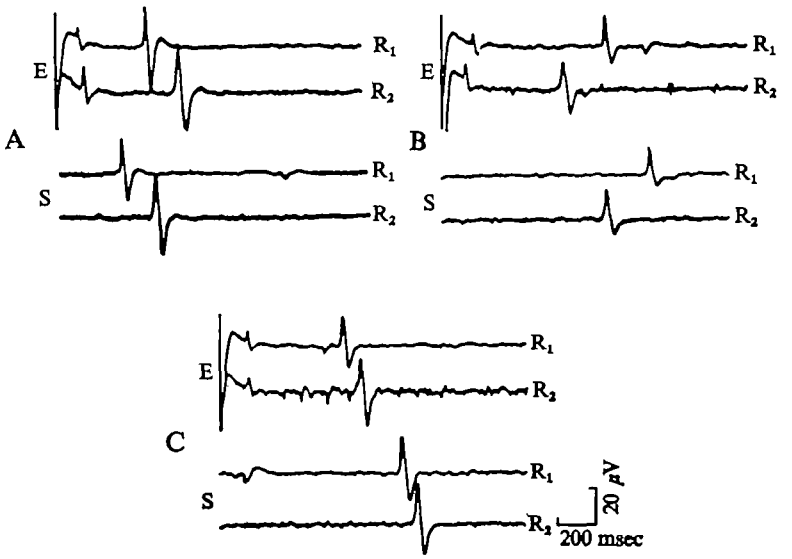

Fig. 3. Source of SS1 pulses evoked during the sensory response to dissolved food substances. A chemical-stimulating electrode containing food extract was applied to different sites on the column. In each case a single electric shock was administered through the electrode to determine from the recordings obtained in R_1 and R_2 the difference in arrival time of the SS1 pulse for a particular placement (E). The SS1 pulses evoked during the accompanying sensory response to the food extract were also monitored (S) to compare their differences in arrival time with those of the electrically-evoked SS1 pulse. Position of chemical-stimulating electrode: (A) adjacent to P_1, (B) adjacent to P_2, (C) mid-way between P_1 and P_2. These recordings confirm that the SS1 pulses evoked during the sensory response originate from the site of the applied chemical stimulus.

region in which the majority of the 'warts' (verrucae) are concentrated. The region below this contains a lower density of verrucae and is termed the lower column, and below this is a region of column that eventually connects with the margin of the pedal disc. This is termed the column base and the complete absence of verrucae in this region distinguishes it from the lower column. It should be stressed that such a subdivision of the column for the purpose of this investigation does not necessarily imply that significant structural or functional differences exist between these regions.

Fig. 5 shows that a sensory response may be obtained from all parts of the column, although it was consistently found that the column base, lower column and mid-column regions were more responsive than the upper column and collar regions. No point on the column was found to elicit a negative response consistently. The pedal disc and pharynx, however, seemed to give no consistent sensory response to food extract. Occasionally, one or two SS1 pulses were evoked when the chemical-stimulating electrode was placed on the pedal disc, but these could also be obtained when a control electrode was placed in the same region. The detached pedal disc was unusual in this respect as none of the other regions tested showed this degree of sensitivity to mechanical stimulation.

The ability of the pharynx to conduct SS1 activity was confirmed by administering a single electric shock through the chemical-stimulating electrode whilst attached to the pharyngeal epithelium. It remained possible that mucus secreted by the pharynx

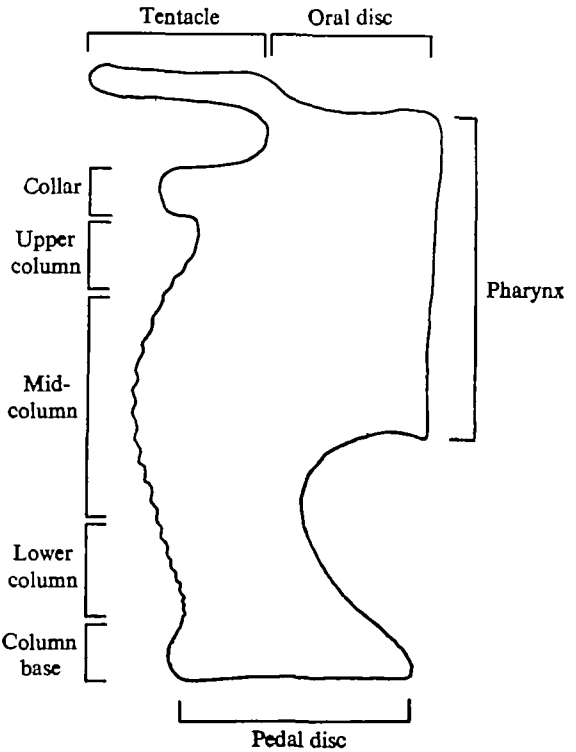

Fig. 4. Regions tested to determine the location of chemoreceptor sites involved in pre-feeding activity. The diagram represents one side of a bisected *Tealia*. The column was sub-divided into the regions shown to facilitate the analysis procedure.

might be blocking the electrode tip, thereby preventing the food extract from contacting the epithelium. To test this, the chemical-stimulating electrode was applied to the pharynx and left attached for 5 min. No SS1 pulses were evoked during this period. The electrode was then carefully detached from the pharynx and immediately placed on the mid-column region of the animal. Within the first 2 min of placement 5 SS1 pulses were evoked. This confirmed that the mucus at the tip of the electrode was not preventing contact of food extract with the chemoreceptors.

The oral disc and tentacles produced a negative pre-feeding response owing to the fact that true feeding responses were elicited as soon as the food extract contacted these regions. This involved local contractions of the underlying muscles, which usually led to the suction electrodes becoming detached. Such activity is obviously essential in macrophagous anemones for the transfer of food material across the oral disc to the mouth. In cases where the recording electrodes managed to remain attached to the tentacles, no SS1 pulses were recorded. This is consistent with the observation that true feeding responses are not elicited by electrical stimulation of the SS1 (McFarlane, 1970; McFarlane & Lawn, 1972). It was noted during the course of these experiments that some placements of the chemical-stimulating electrode on those regions of the column that were normally responsive produced a negative pre-feeding response. This may indicate that the chemoreceptors concerned are not generally

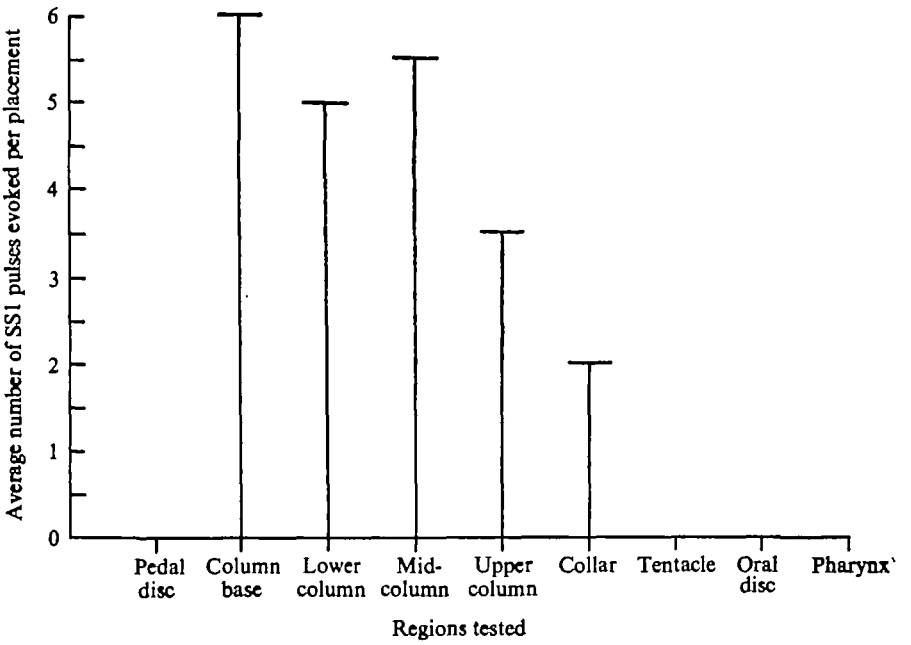

Fig. 5. The responsiveness of different regions of *Tealia* to dissolved food substances. Food extract was applied locally via a chemical-stimulating electrode to each of the regions depicted in Fig. 4. The results plotted here were taken from typical experiments in which each region was tested with four separate placements. The average number of SS1 pulses recorded from each region was then calculated to provide quantitative data on the responsiveness of each region to food extract.

dispersed but concentrated locally in the responsive regions. On the other hand, such an observation may merely reflect differences in sensory threshold between separate populations of chemoreceptors. At this stage, however, it is impossible to decide between these alternatives until more refined techniques have been developed for use on sea anemones.

DISCUSSION

The results presented here have shown that a genuine sensory response in the SS1 is elicited by dissolved food substances contacting the column of *Tealia*. This response usually persists for several minutes and may even, on occasions, continue for periods of up to 1 h, provided that the stimulatory chemicals remain in contact with the column. A process of sensory adaptation also occurs during the course of the response, and it may also operate over time periods of several minutes. These observations indicate that if the pre-feeding response is to be regarded as typical, then chemosensory mechanisms in sea anemones work over much longer time-scales than similar mechanisms encountered in higher animals.

Physiological evidence suggests that the chemoreceptors involved in the pre-feeding response are dispersed throughout the column ectoderm, although they appear to be less densely concentrated on the collar and upper column regions. None of these pre-feeding chemoreceptors seem to be located on the pedal disc, oral disc, tentacles or pharynx, even though these regions are potentially capable of conducting SS1

activity. In contrast, the chemoreceptors concerned with true feeding responses seem to be located on the tentacles and oral disc, since local application of food extract to these regions elicits contractions in the underlying muscles. In this respect it is interesting to note that feeding chemoreceptors have been identified on the tentacles and oral disc of the zoanthid *Palythoa psammophilia* (Reimer, 1971). Behavioural observations suggested that these receptors were more densely concentrated on the borders of the mouth and peristome. No visible feeding response could be elicited by contact of feeding activator with the column of the polyp.

To date, practically all studies on feeding responses in cnidarians (Lindstedt, 1971) have employed behavioural observations as the measured output of the response. The advantage of using electrophysiological data for a bioassay is that the sensory response elicited by the chemical activator can be measured in precise quantitative terms, simply by counting the number of sensory pulses evoked. An attempt has been made to correlate some electrophysiological observations with feeding behaviour in *Hydra* (Rushforth & Hofman, 1972). It was found that 10^{-5} M reduced glutathione (GSH) had an inhibitory effect on pulses associated with column and tentacle contractions, but the Rhythmic Potential Pacemaker System was unaffected. Unfortunately, nothing that could be described as sensory activity was detected.

The well-defined sensory response evoked during pre-feeding behaviour in *Tealia* affords a useful bioassay for testing various compounds in order to determine the chemical activator involved in this response. Preliminary work on the identification of the pre-feeding activator (Lawn, 1973) has shown that this is a heat-stable, acetone-soluble compound with a molecular weight of less than 1000. Although many identified compounds (including several amino acids, vitamins, carbohydrates, bactopeptone and casamino acid mixtures, and a non-ionic surfactant) have been assayed, the pre-feeding activator has not yet been determined. A certain amount of confusion concerning pre-feeding activators in sea anemones seems to have arisen. Williams (1972) refers to any chemical which, in the absence of mechanical stimulation, is capable of evoking behavioural responses as a pre-feeding activator. This has led to the erroneous designation of chemicals which evoke contraction rather than extension of the tentacles as pre-feeding activators. A similar misunderstanding occurs in a study on the sea anemone *Calliactis polypus* (Reimer, 1973) in which pre-feeding behaviour is described as 'tentacle writhing and twitching'. Such activity would involve local asymmetric contractions of the tentacle longitudinal muscles and therefore cannot be related to the behavioural and physiological activity associated with the pre-feeding response (McFarlane, 1970; McFarlane & Lawn, 1972). Contraction, twitching and writhing of tentacles would be better described as components of true feeding behaviour. The 'pre-feeding activators' described by these authors, therefore, ought to be considered as feeding activators capable of evoking certain stages of the true feeding response. A pre-feeding activator for a sea anemone will be defined here as a soluble substance capable of eliciting expansion of the oral disc and extension of the tentacles by evoking activity in the SS1. To date, therefore, no pre-feeding activator has been identified.

The conducting elements of the SS1 are believed to be the epithelial cells of the ectoderm (McFarlane, 1969*a*) and the system as a whole seems to function as a single conducting unit. The lack of both intracellular and ultrastructural data does no

allow one to determine whether the chemoreceptors are part of the outer-facing membrane of these epithelial cells, or whether they are individual cells that form chemical or electrical synapses with the cells of the SS1. In the sea anemone *C. parasitica* the SS1 is involved in coordinating pedal-disc detachment during the behavioural response in which the anemone detaches from the substrate and attaches to a molluscan shell (McFarlane, 1969*b*). Soon after the tentacles contact the shell, repetitive firing in the SS1 is observed. Detachment of the pedal disc typically occurs after about 3 min from the initial contact, during which time 25 SS1 pulses may be evoked (a mean inter-pulse interval of 7 s). Later in the response (usually within 2 min of detachment) the inter-pulse intervals increase to 20–60 s, and if the shell-tentacle contact is broken at any stage the SS1 activity ceases. It seems, therefore, that chemoreceptors on the tentacles of *Calliactis* recognize a specific chemical in the molluscan shell and somehow evoke frequency-coded sensory activity in the SS1. This activity is propagated throughout the SS1 and eventually brings about a response in the effector system. In the case of the detachment response this may involve secretion of some sort of 'solvent' from ectodermal 'detachment' cells.

Similar processes seem to occur in the pre-feeding response of *Tealia*. Chemoreceptors on the column recognize a specific chemical in the food extract and evoke frequency-coded sensory activity in the SS1. The effector system activated in response to this is also ectodermal; in this case the radial muscles of the oral disc (McFarlane & Lawn, 1972). In the swimming sea anemone *Stomphia coccinea* the SS1 also seems to play an important role in transmitting sensory information to ectodermal effectors (Lawn, unpublished observations). The picture that is now beginning to emerge concerning the primary role of the SS1 in sea anemones is one in which it acts as a single, diffuse-conducting unit responsible for transmitting frequency-coded sensory information from ectodermal chemoreceptors to ectodermal effectors. Whether it also conveys sensory information directly to endodermal effectors has not yet been conclusively established. Much work still remains to be done before its role in coordinating behavioural activity in sea anemones can be described completely.

I am grateful to Dr I. D. McFarlane for his helpful suggestions and advice throughout the course of this work, and to Professor D. M. Ross for reading the manuscript of this paper. This work was supported by a Science Research Council Research Studentship grant.

REFERENCES

FULTON, C. (1963). Proline control of the feeding reaction of *Cordylophora*. *J. gen. Physiol.* **46**, 823–37.

LAWN, I. D. (1973). Behavioural physiology of sea anemones. Ph.D. Thesis, University of St Andrews, Scotland.

LAWN, I. D. (1975). The marginal sphincter of the sea anemone *Calliactis parasitica*. I. Responses of intact animals and preparations. *J. comp. Physiol.* (in the Press).

LENHOFF, H. M. (1961). Activation of the feeding reflex in *Hydra littoralis*. I. Role played by reduced glutathione, and quantitative assay of the feeding reflex. *J. gen. Physiol.* **45**, 331–44.

LINDSTEDT, K. J. (1971). Chemical control of feeding behaviour. *Comp. Biochem. Physiol.* **39**A, 553–81.

LOOMIS, W. F. (1955). Glutathione control of specific feeding reactions of hydra. *Ann. N.Y. Acad. Sci.* **62**, 209–28.

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

MCFARLANE, I. D. (1969*b*). 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.

McFARLANE, I. D. & LAWN, I. D. (1972). Expansion and contraction of the oral disc in the sea anemone *Tealia felina*. *J. exp. Biol.* **57**, 633–49.

REIMER, A. A. (1971). Specificity of feeding chemoreceptors in *Palythoa psammophilia* (Zoanthidea, Coelenterata). *Comp. gen. Pharmac.* **2**, 383–96.

REIMER, A. A. (1973). Feeding behaviour in the sea anemone *Calliactis polypus* (Forskål, 1775). *Comp. Biochem. Physiol.* **44**A, 1289–301.

RUSHFORTH, N. B. & HOFMAN, F. (1972). Behavioral and electrophysiological studies of *Hydra*. III. Components of feeding behavior. *Biol. Bull.* **142**, 110–31.

WILLIAMS, R. B. (1972). Chemical control of feeding behaviour in the sea anemone *Diadumene luciae* (Verrill). *Comp. Biochem. Physiol.* **41**A, 361–71.