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REVERSAL OF THE DIRECTION OF MUCUS-FLOW ON THE CILIATED PHARYNX OF A SEA ANEMONE

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SUMMARY

1. The ciliated pharynx of the sea anemone *Calliactis parasitica* (Couch) acts as an independent selective barrier for the admission of material to the coelenteron.

2. Direct observation shows that reversal of the direction of the mucus-flow is effected by a reversal of the direction of the ciliary power-stroke.

3. Reversal of the power-stroke can only be stimulated by food juices applied directly to the pharynx and it is not propagated to unstimulated areas.

4. Reversal of the power-stroke occurs in the absence of all recordable electrical activity.

5. This is one of the few examples among the Metazoa where it has been shown that a modification of the ciliary beating pattern is unlikely to be controlled by an electrical conduction system.

INTRODUCTION

Cilia may be classified into two groups: those in which the ciliary beat pattern remains essentially constant and those in which it is modified. Neural control is common in the latter group and mediates such modifications as reversal of the direction of the power-stroke (Aiello & Guideri, 1964; Galt & Mackie, 1971; Tamm, 1982), ciliary arrest (Mackie, Singla, Sleigh & Williams, 1974; Mackie, Singla & Thiriot-Quievreux, 1976; Murakami & Takahashi, 1975; Mackie & Bone, 1978) or alteration of the beat frequency (Audesirk, 1978). An epithelial conduction system may mediate ciliary power-stroke reversal in the larvae of the echinoderm *Strongylocentrotus droebachiensis* (Mackie, Spencer & Strathmann, 1969) but there are few examples in Metazoa where ciliary beat modification occurs independently of any electrical conduction system. This paper describes observations and experiments which demonstrate that the ciliated pharynx of the sea anemone *Calliactis parasitica* (Couch) may be such a system.

Each epithelial cell of the pharynx in *C. parasitica* carries one cilium (Holley, 1982), the power-stroke of which is normally directed outward toward the mouth, causing an outward flow of mucus over the epithelium. Reversal of the direction of flow on the pharynx is an integral part of the feeding behaviour of sea anemones (see Parker, 1896). In *C. parasitica* there are at least three electrical conduction systems;

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the through-conducting nerve-net (TCNN), the ectodermal slow system (SS1) and the endodermal slow system (SS2). All three are active during feeding (McFarlane, 1975, 1982) and might, therefore, be involved in the control of the pharynx cilia. McFarlane (1975) particularly noted an increase in SS2 activity when food contacted the mouth and during ingestion. In addition to the known electrical conduction systems it is also possible that some as yet unidentified electrical conduction system could be involved.

There is conflicting evidence for the control of flow-reversal in sea anemones. Parker (1905) reported that flow-reversal in *Metridium marginatum* was probably not controlled neurally since direct food stimulation to the pharynx produced only a localized flow-reversal. Furthermore, flow-reversal was not inhibited when the anemones were anaesthetized with chloretone (Parker, 1917). Baba (1968) observed a slow (50–300 $\mu m\ s^{-1}$) unidirectional propagation of the flow-reversal on the pharynx of *Actinia equina* and concluded that this was due to electrical conduction through the ciliated epithelial cells. He also quoted unpublished observations by Yasuda who suggested that flow-reversal in *A. equina* might be neurally controlled because it was inhibited in animals anaesthetized with magnesium chloride. Shelton (1982), however, reported that when *C. parasitica* was anaesthetized with magnesium chloride there was no inhibition of flow-reversal.

Direct observations of the pharynx cilia were not reported in these studies and no recordings of activity in the electrical conduction systems were made. Direct observations of ciliary power-stroke reversal in metazoans have been made infrequently (Tamm, 1982) and it has been suggested that alternative mechanisms, such as muscular control of separate and opposing flow-channels, may mediate flow-reversal in the pharynx of sea anemones (see Aiello, 1974).

In the experiments described here the pharynx cilia of *C. parasitica* have been observed directly and activity of the electrical conduction systems has been monitored.

MATERIALS AND METHODS

Live *C. parasitica*, with pedal disc diameters of about 3·5 cm, were obtained from the Marine Biological Association, Plymouth, and were maintained in a 5000 gallon closed-circulation seawater aquarium at 12 °C. They were fed twice a week on crab, mussel or fish.

Preparation of crab muscle extract and graphite suspension

Crab skeletal muscle (2·5 g) was homogenized in seawater (30 ml), centrifuged for 30 min at 500 ***g***, and the supernatant collected. Powdered graphite (0·1 g) was suspended in seawater (50 ml). Both preparations were stored in Polythene bottles at 12 °C and were freshly prepared on the day of each experiment.

Feeding to satiation

A *C. parasitica* was placed in an aquarium tank with the oral disc facing upward and it was then fed to satiation with 5 mm cubes of crab muscle. The animal was considered to be satiated when the tentacles failed to pass the crab muscle to the mouth.

The flow at the top of the pharynx was observed by pipetting a little of the graphite suspension onto the mouth.

Dissected preparations

A single radial cut, passing through one siphonoglyph, was made so that the pharynx and siphonoglyph epithelia were fully exposed (Fig. 1). The animal was then pinned open in a dissecting dish and placed in a water bath. The pedal disc, column, tentacles, oral disc and pharynx were stimulated while the flow on the pharynx was monitored with the graphite suspension.

Extracellular polythene suction electrodes, with tip diameters of 0·25 mm and 0·5 mm, were used for recording and stimulating electrical activity respectively. Electrical activity, recorded from the tentacles, was amplified using a differential pre-amplifier and displayed on a Tektronix Type 5111 storage oscilloscope. A Devices Isolated Stimulator Mk IV was used for electrical stimulation. Single and multiple shocks were delivered above and below the thresholds of the three known conduction systems (McFarlane, 1969). A glass rod was used to stimulate the epithelia mechanically.

Pieces of crab muscle, about 5 mm in diameter, were rinsed briefly in seawater and applied to the epithelia. When the muscle was applied to the tentacles, a glass slide was placed along the oral disc to form a barrier between the tentacles and the pharynx. This prevented direct contact between the muscle and the pharynx. The muscle extract was applied to the epithelia through a polythene suction tube with a tip diameter of 1 mm (see McFarlane & Lawn, 1972).

Anaesthetized animals

Whole animals were anaesthetized by placing them in a solution of 1:1 $MgCl_2$ (7·5 % $MgCl_2.6H_2O$ in distilled water) and seawater at 12 °C for 18 h.

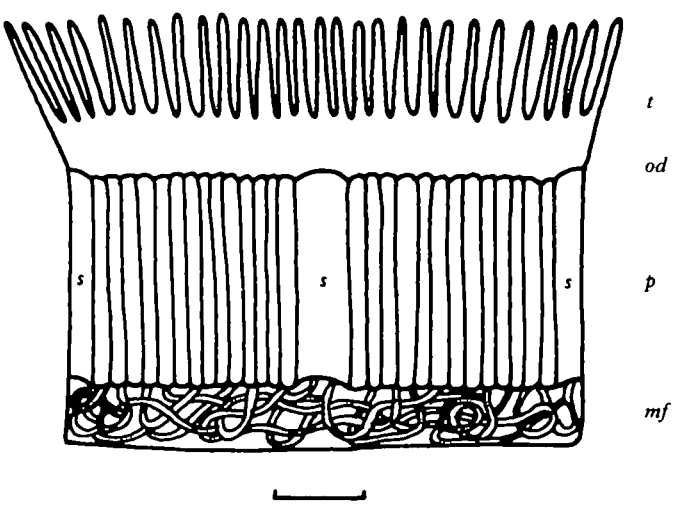

Fig. 1. Diagram of *Calliactis parasitica* opened following a single radial cut to expose the actinopharynx. *t*, tentacles; *od*, oral disc; *p*, pharynx; *mf*, mesenterial filaments; *s*, siphonoglyph. Scale bar, 1 cm.

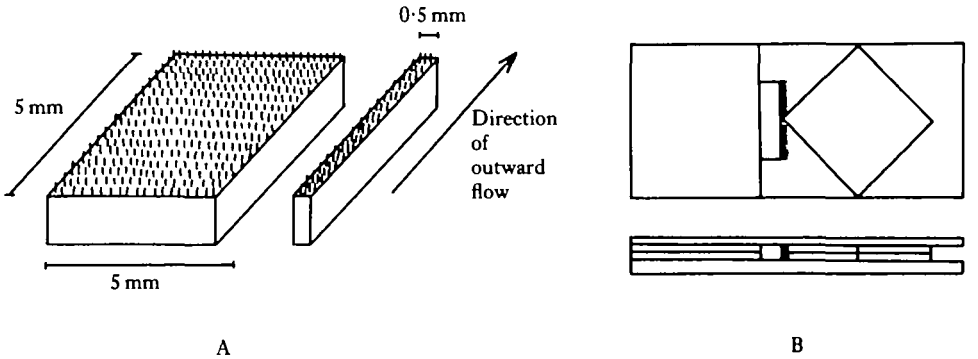

Fig. 2. Preparation of pharynx epithelial slice (A) for the direct observation of the cilia in a divided bath (B). The divided bath was constructed by securing a pair of square coverslips, one above the other, at one end of a microscope slide. A second pair was secured to the slide 2 mm from the first but rotated through 90°. Thus one corner of the second pair of coverslips was adjacent to one edge of the first pair. A slice of pharynx epithelium was placed on the slide, between the coverslip pairs, so that the ciliated surface was divided into two halves by the corner of the second pair. Another coverslip was placed over the preparation so that each half of the epithelial slice was contained in a separate bath.

Microscope preparation

The pharynx and siphonoglyph cilia were observed directly using a Nomarski interference microscope at a magnification of ×100 or ×400. A piece of epithelium was removed from a dissected animal and placed in a drop of seawater at 12 °C. A slice of epithelium, 5 mm long and 0·5 mm thick, was cut in the plane of the flow using a razor blade (Fig. 2A) and then placed on a cavity slide, bathed in seawater, and covered with a cover-slip.

The epithelia produced large quantities of mucus throughout the dissection procedure so the preparations were left at 12 °C for 20 min to allow the cilia to clear the mucus. Remaining mucus was sucked away from the epithelia by using a fine Polythene tube, 0·2 mm in diameter, attached to a 5 ml syringe. The seawater bathing the epithelial slice could be replaced using the same Polythene tube. A Dawes Strobosun stroboscope was used in the measurement of ciliary beat frequency, beat direction and metachronism.

The cilia were directly stimulated electrically, mechanically, and with the muscle extract. Two lengths of enamel coated wire (SWG 40), connected to a Devices stimulator, were used for electrical stimulation; a mounted glass needle for mechanical stimulation; and the fine Polythene tube for applying the muscle extract.

Divided bath

This was used in the examination of the pharynx cilia (Fig. 2B). The muscle extract was injected onto one side of the epithelium and then, after 5 min, onto the other side. The direction of the ciliary beat was observed on both sides during this procedure. In control experiments seawater, instead of muscle extract, was injected onto the epithelium.

RESULTS

Feeding behaviour

When a piece of crab muscle was placed on tentacles of *C. parasitica* it was immediately held by the threads of discharged nematocysts and spirocysts, the tentacles then folded around the crab and contracted so that it was pulled down onto the oral disc. Local contractions of the oral disc radial muscles and mesenteries pulled the edge of the mouth closer to the base of the contracted tentacles (Fig. 3). The pharynx was usually inflated so that it protruded from the mouth and the complete behaviour pattern ensured that the crab was placed directly onto the pharynx. It was then ingested and the mouth was closed.

When this procedure was repeated at 5-min intervals, applying the crab each time to the same tentacles, the time taken for the tentacles to place the crab on the mouth increased (Fig. 4A) but the ingestion time remained constant (Fig. 4B). In satiated animals, the tentacles, oral disc and mesenteries failed to respond to the crab which was not therefore placed onto the mouth and ingested. Crab placed directly on the mouth, however, was always ingested (Fig. 5). If feeding continued in this way the animal eventually expanded, the mouth opened, and then a rapid symmetrical contraction of the column followed which expelled all the food which was not enmeshed in the mesenterial filaments, from the coelenteron. Throughout egestion the flow on the pharynx remained inward and pieces of food placed onto the mouth immediately afterwards were readily ingested.

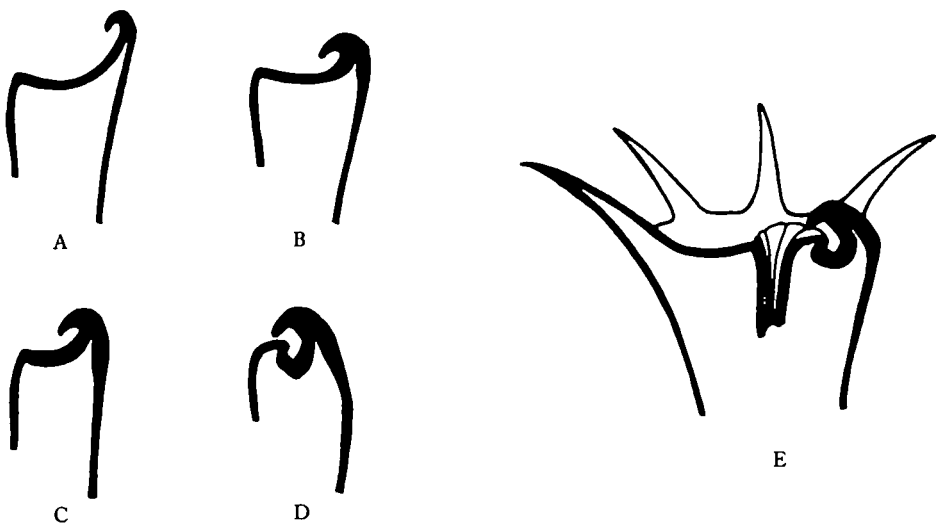

Fig. 3. When food touched a tentacle, it was held by the discharged threads of nematocysts and spirocysts. The tentacle folded towards the mouth (A) and then shortened (B). These movements were due to the contraction of the tentacle longitudinal muscles. Local contraction of the oral disc radial muscles (C) and mesenteries (D) caused the mouth to protrude towards the food if the animal was well expanded (E). The food was thus placed into direct contact with the top of the pharynx and then drawn into the coelenteron by the action of the cilia.

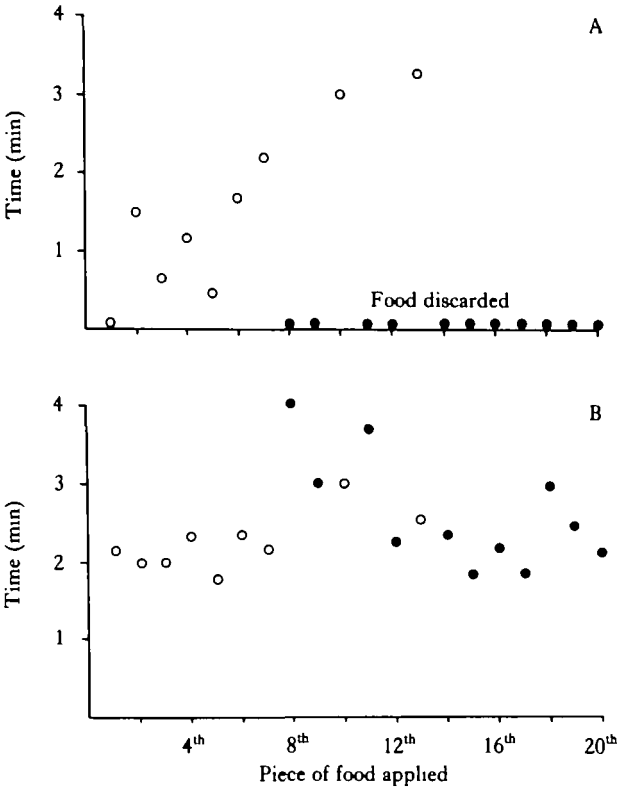

Fig. 4. Graph showing the time for successive pieces of crab muscle to be passed from the tentacles to the mouth (A), and from the mouth to the bottom of the pharynx (B). 5-mm cubes of crab were placed on selected tentacles at 5-min intervals. Closed circles indicate that the food was discarded by the tentacles and so had to be placed on the mouth directly. The two graphs illustrate results from the same animal during one experiment. The animal was satiated after consuming 13 pieces of crab.

Anaesthetized animals

In *C. parasitica* anaesthetized with excess magnesium an outward flow on the pharynx was readily reversed by the direct application of crab muscle extract but no electrical activity could be detected. Following these observations, the recording electrodes were left on the tentacles while the magnesium seawater was replaced with fresh seawater. Electrical activity of the three conduction systems gradually re-appeared (Fig. 6) thus confirming that its absence was not due to a malfunction in the recording apparatus.

When food was placed on the tentacles or oral disc of anaesthetized animals, it was not passed to the mouth but if placed directly on the mouth it was ingested. The lips of the pharynx slowly crawled around the food so that the mouth was forced open (Fig. 5) and then ingestion occurred at a rate similar to that in normal feeding (see Fig. 4B).

Dissected preparations

Crab muscle extract or pieces of muscle, applied directly to the pharynx, caused an outward to inward flow-reversal. If the flow was already inward then it remained s[illegible] The pharynx epithelium did not respond as a single coordinated unit and small area[illegible]

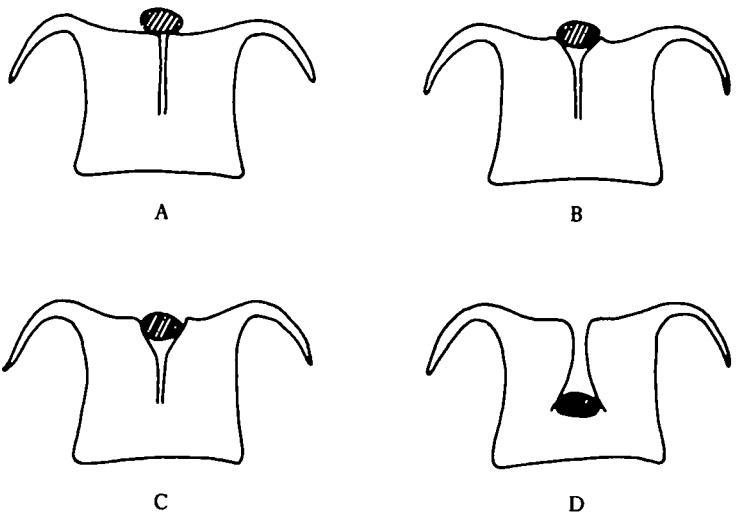

Fig. 5. When *Calliactis parasitica* was anaesthetized with magnesium, food placed on the mouth was ingested. An inward ciliary flow on the pharynx forced the mouth open (A–C). Once in the mouth, the food passed down the pharynx in the normal way (C–D). During this process, no muscular movements were observed and no electrical activity was recorded from the tentacles. Similar behaviour was observed in satiated animals although the conduction systems were not artificially anaesthetized.

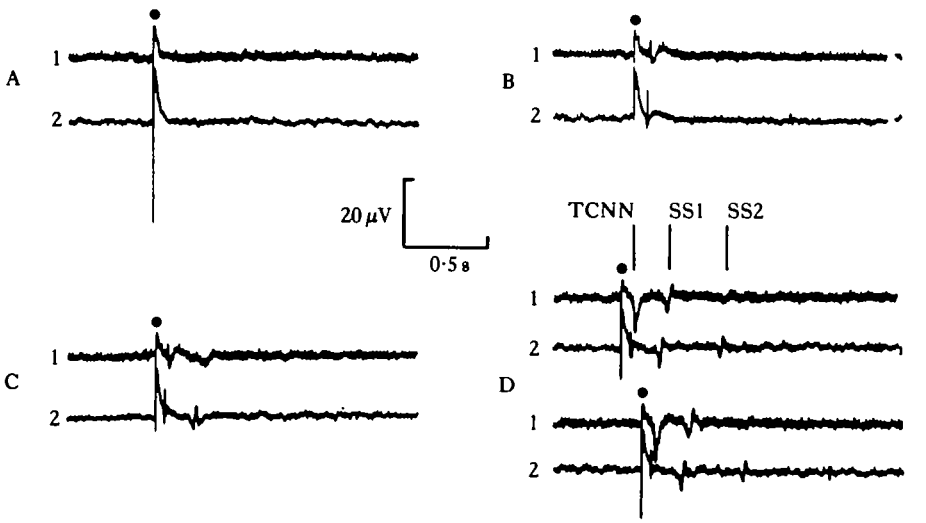

Fig. 6. Response of the nerve net, SS1 and SS2 to electrical stimuli (20 V, 1 ms) in an animal recovering from anaesthesia. The animal was placed in excess magnesium chloride until recordable electrical activity in the conduction systems had ceased. Reversal of the direction of an outward flow of mucus on the pharynx was successfully stimulated by crab muscle extract. No electrical activity was recorded during flow-reversal. The anaesthetic solution was then replaced with normal seawater (Time 0 min). After 30 min (A) all conduction systems were inactive and only the stimulus artifact was recorded (spot). The nerve net (TCNN) had recovered after 55 min (B), the SS1 after 70 min (C) and the SS2 after 100 min (D). The two recording electrodes (1 and 2) remained attached to the same tentacles throughout the experiment. Two separate traces are shown in (D).

frequently supported a flow in the opposite direction whether the general flow was inward or outward. Sometimes, particularly in the first 24 h after feeding to satiation, opposing flows existed between the top and bottom halves of the pharynx. When the flows were convergent, graphite was accumulated in the middle of the pharynx, and when they were divergent, the graphite was simultaneously expelled from the top and bottom edges. Regardless of the flow beforehand a coordinated inward flow was always produced if the entire pharynx was immersed in crab muscle extract.

When the muscle extract was applied to the pharynx *via* the Polythene suction tube, no flow reversal was observed outside the area stimulated. When a piece of muscle was transported down the epithelium, a band of inward flow was left in its wake but in neighbouring areas of pharynx the flow remained outward. Application of muscle or muscle extract to any other part of the animal, including the tentacles, oral disc and column, did not influence the ciliary flow on the pharynx. Electrical or mechanical stimulation applied to any part of *C. parasitica*, including the pharynx, did not induce a flow-reversal. Inward to outward flow-reversal occurred slowly and usually developed first on the top margin of the pharynx. When dissected preparations were left in fresh seawater a coordinated outward flow was nearly always found in animals observed after 24 h.

Microscope preparation

The pharynx cilia were about 10 μm long and beat at a frequency of 18–21 Hz. No obvious metachronism was observed although similar preparations of the siphonoglyph cilia (20 μm long) revealed a well developed laeoplectic metachronal wave very similar to that of the lateral cilia in the mussel *Mytilus edulis* (Aiello & Sleigh, 1972). The siphonoglyph cilia normally beat inward and propelled water currents into the coelenteron. They were never observed to beat outward.

When outward beating cilia from any part of the pharynx were stimulated with the crab muscle extract the direction of the ciliary power-stroke, and of the fluid-flow, was reversed. Reversal was initiated 5–20 s after the stimulus but it did not occur synchronously along the epithelial fragment. The cilia first became uncoordinated, each apparently disrupting the beat of its neighbours, and then an inward flow gradually developed along the entire stimulated area. The beat frequency of pharynx cilia beating inward or outward was the same. Direct electrical stimulation of the epithelia caused a discharge of nematocysts and release of mucus which, until cleared by the cilia, impeded the flow but a sustained reversal of the ciliary beat was not observed. The cilia were tickled mechanically with a glass microneedle without stimulating mucus or nematocyst discharge but this also did not induce a ciliary beat reversal.

In the divided bath, an outward ciliary beat was reversed only if the cilia were stimulated directly with the crab muscle extract. Reversal, initiated either on the upper or lower half of the epithelial fragment, was not propagated across the mechanical barrier to the unstimulated half.

DISCUSSION

Inward flow along the pharynx of *C. parasitica* is essential for the ingestion of food and if the flow is outward before feeding then the food stimulates a flow-reversal. The

Results of this study have shown that flow-reversal is achieved by a reversal of the direction of the ciliary power-stroke. It is unlikely that this reversal is controlled by any known or unknown electrical conduction system because:

(i) the pharynx did not behave as a single coordinated unit,

(ii) reversal of the power-strokes of cilia on adjacent cells was not synchronized,

(iii) the reversal was not propagated past a mechanical barrier placed on the epithelial surface,

(iv) the reversal was observed in anaesthetized animals from which no electrical activity could be recorded.

Neural control is important for rapid synchronized responses such as arrest of the stigmatal cilia in the pelagic tunicate *Pyrosoma*, which is coordinated with activity of the siphon and the luminescent organ (Mackie & Bone, 1978). Feeding in *C. parasitica*, however, is relatively slow and the pharynx cilia are not closely co-ordinated with any other specific type of behaviour.

Baba (1968) suggested that in *Actinia equina*, flow-reversal was propagated by the pharynx epithelial cells but he did not report direct observation of the cilia. Our observations indicate that mucus-flow on the pharynx is dictated by the activity of the majority of the cilia; in some cases the mucus was observed to flow in the opposite direction to that of the ciliary power-strokes beneath it. If the mucus was removed from such an area the surrounding seawater was propelled in the same direction as the power-strokes. Our results with *C. parasitica* do not agree with Yasuda's observations from *A. equina* that flow-reversal is inhibited by magnesium chloride anaesthesia (see Baba, 1968). Yasuda used the amino acid creatine to stimulate flow-reversal but although we found some amino acids to be effective, they were never as effective as the crab muscle extract.

Elmhirst (1925) and Aiello (1974) suggested that muscular movement might bring oppositely directed adjacent tracts of cilia into position in different situations. Horridge (1957) described centripetal conduction of the reversal of mucus-flow, affecting both the cilia and the muscles, on the oral disc of the coral *Fungia fungites*. All muscular activity was apparently inhibited in *C. parasitica* when it was anaesthetized, which implies that muscular action is normally unnecessary for effecting flow-reversal or ingestion.

The independence of the pharynx cilia was apparent in the feeding experiments. To ensure an inward flow on the pharynx the food had to be placed into direct contact with it. This clearly occurs in *C. parasitica* and in several other anthozoans during normal feeding (Pantin & Pantin, 1943; Reimer, 1971, 1973; Bursey & Gunciale, 1977). This study showed that although the musculature of anaesthetized and satiated *C. parasitica* was inactive, food placed onto the mouth was readily ingested. Furthermore, flow-reversal was not effected by electrical, mechanical or food stimulation to the column, tentacles or oral disc. It is unlikely, therefore, that any part of the feeding sequence prior to food or food juices contacting the pharynx plays any role in mediating flow-reversal.

Flow-reversal was observed on epithelial fragments removed from any part of the pharynx and it was not propagated past the mechanical barrier in the divided bath. If discrete chemoreceptors mediate flow-reversal then they must be widely and evenly distributed. It is possible that the pharynx cilia of *C. parasitica* respond directly to

food stimuli *via* chemoreceptors on the ciliary or the cell membrane. In the *Paramecium* cell membrane, receptors control voltage-sensitive ion-channels which, by regulating the internal free calcium concentration, control the direction of the ciliary power-stroke (see Eckert, Naitoh & Machemer, 1976; Naitoh, 1982). Calcium ions may also mediate reversal of the ciliary beat direction in sea anemones (Gentleman & Mansour, 1974).

Sea anemones have an open hydrostatic skeleton and the pharynx cilia facilitate ingestion, a function which cannot be undertaken easily by a simple musculature. Egestion, however, can be controlled by the musculature. With the mouth open, a symmetrical contraction of the column causes expulsion of the free content of the coelenteron. During this type of behaviour, inward flow on the pharynx is not reversed. This capability for rapid egestion may explain why the reversal of an inward flow on the pharynx is less specific than the reversal of an outward flow. An outward flow is probably useful for the continual expulsion of debris from the coelenteron without strong muscular contractions, but it has another function. The pharynx acts as an independent, selective gateway to the coelenteron. Mechanical stimuli may initiate a feeding response, but food juices are required to reverse the pharynx cilia. If material placed on the mouth has the capacity to reverse the cilia then it is ingested. There is a delay before the cilia beat outward again and during this period material which lacks the capacity to reverse the cilia will be ingested. The muscles do exert some control over ingestion, however, since the food must be placed directly onto the mouth by the tentacles; in satiated animals this does not happen.

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Note added in proof

Baba found that local electrical stimulation of the pharynx of *Actinia equina* induced a unidirectional spread of ciliary reversal at a velocity of 50–300 $\mu m\ s^{-1}$. This was based on direct observation of the cilia using a phase contrast microscope (personal communication). No such effect was observed by us in *Calliactis parasitica*. Mucus flow-rates, however, are usually 200–450 $\mu m\ s^{-1}$ (Holley, 1983). It is possible that a very slow electrical conduction system propagates the ciliary reversal response or that food progressively stimulates ciliary reversal as it is propelled down the pharynx. Our experiments with divided baths, using both dissected animals and small strips of excised pharynx, support the latter hypothesis.

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