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Recordings from *Distaplia* colonies show large electrical signals correlated with siphon contractions and arrest of the branchial cilia. These pulses occur rhythmically at 2- to 4-s intervals during sustained ciliary arrest. There is no coordination of the ciliary control pacemakers of adjacent zooids.

Strong stimulation of one zooid leads to contractions and ciliary arrest in adjacent zooids. The response is transmitted slowly (<1 cm/s) and the latency is very variable. Interaction between zooids may be mechanical.

Distaplia shows no photic sensitivity.

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Chez des colonies de *Distaplia*, on enregistre des signaux électriques importants reliés aux contractions du syphon et à l'arrêt des cils branchiaux. Ces ondes sont rythmiques et se produisent à intervalles de 2 à 4 s durant un arrêt ciliaire prolongé. Il n'y a pas de coordination des centres d'automatisme du mouvement ciliaire des zoïdes voisins.

Une forte stimulation d'un zoïde entraîne la contraction et l'arrêt ciliaire chez les zoïdes adjacents. La transmission du stimulus est lente (<1 cm/s) et la période de latence, très variable. Il se peut que l'interaction entre les différents zoïdes soit de nature mécanique.

Distaplia ne manifeste pas de sensibilité à la lumière.   [Traduit par le journal]

While much has been written on the responses of solitary ascidians, the behaviour of colonies is scarcely mentioned in the main reference works (Berrill 1950; Brien 1966; Bullock and Horridge 1965; Huus 1937–1940; Seeliger 1893–1907). In particular, these works give no clue whether responses can be spread from one zooid to another across the colony, as in most coelenterate and some bryozoan colonies. The present study represents an attempt to clarify the picture so far as ascidian colonies are concerned.

Materials and Methods

Specimens of *Distaplia* were dredged from 33 m between Helby and Wizard Islands of the Deer Group, in Barkley Sound near Bamfield. The specimens resembled *D. occidentalis*, which is common in the inner coastal waters of British Columbia, but the zooids were larger and had about 20 stigmata in each row, as against 12–14 in *D. occidentalis*. Huntsman (1911) found two species of *Holozoa* (*Distaplia*) near Ucluelet in 1909. His species A, found intertidally, is probably *D. occidentalis* according to Van Name (1945). No details are given of species B, which was dredged from 5–10 fathoms. As there may be two species of *Distaplia* in this locality, and as the present specimens did not exactly conform to *D. occidentalis*, it seems best to refer to them as *Distaplia* sp., pending determination by a specialist.

The specimens were kept in the seawater system at the Bamfield Marine Station.

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For stimulating and recording, seawater-filled polyethylene tubes drawn to a tip of about 30 microns (u), inside diameter, were used as electrodes. They were held to the preparation by suction applied from a syringe. Signals were fed push–pull into Grass 7P511 EEG amplifiers with output from a J6 to a Tektronix 5103 N dualbeam storage oscilloscope. Paper records were made on a Grass 79C polygraph. Electrical stimuli were delivered at 1-ms duration, the voltage normally being held to a value near the response threshold.

Results

Undisturbed colonies in clean water opened their siphons and drew in a feeding current (Fig. 1). In younger zooids where the tunic was transparent, particles could be seen passing through the pharynx and being collected in the mucus sheet, as described for *Clavelina* (Werner and Werner 1954). The heart could be seen beating at about 80–100 beats per minute, with reversals about every 2 min.

Ciliary Arrests

The flow of water and particles through the pharynx is subject to intermittent interruptions, apparently set off by impact of large particles. With a water-immersion lens, it was possible to relate these interruptions to cessation of beating in the stigmatal cilia.

Ciliary arrests were often accompanied by siphonal contractions, so that a squirt of water was emitted through the branchial siphon at the

same time. MacGinitie (1939) first noted the correlation of squirting with ciliary arrest in ascidians. The duration of the response appeared to depend on the strength of the irritant stimulus.
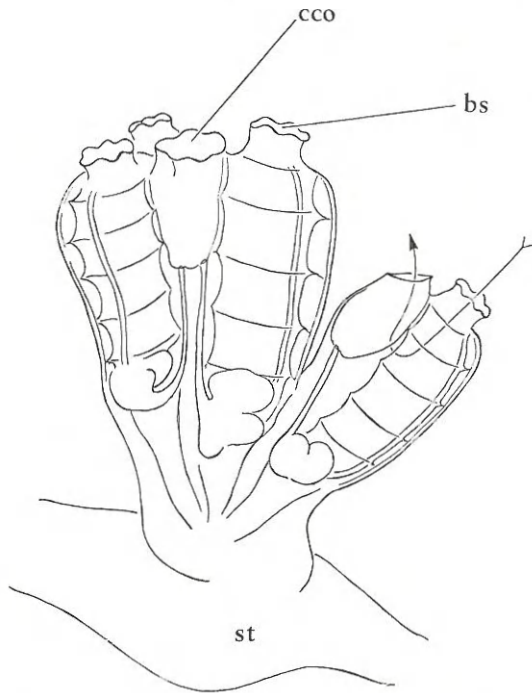

FIG. 1. Sketch of a small group of zooids of *Distaplia* growing from a stolon. Three zooids share a common cloacal opening; one grows independently from the side. CCO, common cloacal opening; *bs*, branchial siphon; *st*, stolon. Arrow shows direction of feeding current.

The state of ciliary arrest sometimes continued after the siphons had opened. Conversely, small siphonal contractions sometimes occurred without ciliary arrest. Normally the two went together. The response consists basically of a series of discrete events, shown initially as muscular twitches in the siphons and flicks in ciliated epithelium, but in sustained responses the contraction appeared tonic and the cilia were held motionless in the arrested state.

Recording electrodes were inserted into the pharynx and attached to the ciliated epithelium. Each time the cilia stopped beating a large electrical potential was picked up. Sustained arrests were represented by a rhythmical series of potentials at 2- to 4-s intervals (Fig. 2). Introduction of electrodes caused persistent tactile stimulation of the branchial tentacles and led to persistent ciliary arrest.

It was found that the signals could be picked up almost as well by placing the electrodes outside on the tunic, in a thin region near the base of the branchial siphon, and in this position the irritation was only momentary. The siphons opened and a feeding current was set up. The ability to pick up electrical correlates of ciliary arrest from the outer body wall was noted by Galt and Mackie (1971) in *Oikopleura*.

Not only did electrodes, attached externally, pick up ciliary arrest potentials (CAP's) from the zooid they were attached to, but they also recorded attenuated CAP's from nearby zooids (Fig. 3). Evidently the CAP record, like an
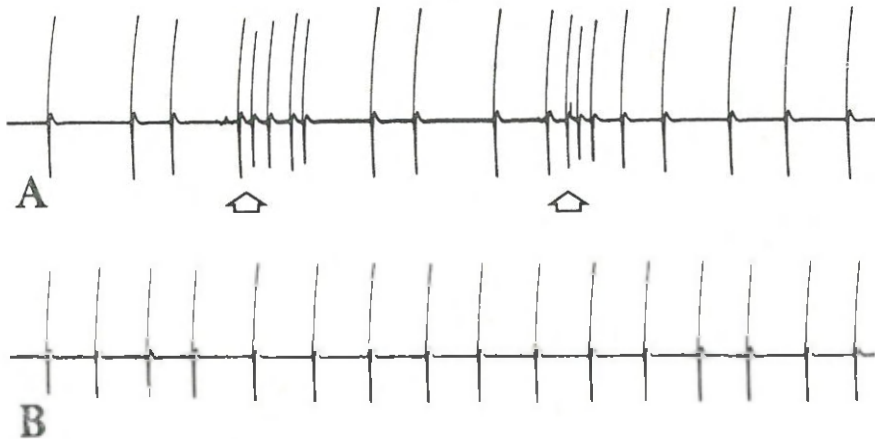

FIG. 2. Ciliary arrest potentials. (A) During a sustained period of ciliary arrest the branchial siphon was touched twice (arrows), giving an increase in the frequency of the potentials. (B) Steady rhythm seen in a specimen which had a piece of filamentous alga lodged in the branchial siphon. Scale, 10 s.

electrocardiogram, registers a rhythmically oc-curring series of bioelectric disturbances of sufficient magnitude to cause current flow through all connected tissues in the preparation.

Recordings from the common cloacal open-ings showed CAP's from all or most of the associated zooids; though depending on the recording site, pulses from one zooid always predominated. The common cloacal opening is not a physiological entity, behaving rather as the sum of the participating atrial languets.

No coordination or correlation whatsoever was detected between the CAP rhythms of inter-connected zooids. Clearly each zooid has a strictly local pacemaker system. This state of affairs contrasts markedly with the situation in the colonial hydroid *Tubularia*, where coupling is observed between the pacemakers of connected polyps (Josephson and Mackie 1965).

Spread of Excitation between Zooids
Purely local contractions were evoked in branchial siphons with gentle tactile or electrical stimulation. With slightly stronger stimulation the contraction spread to the atrial languet,

deforming the common cloacal opening. Stronger stimuli caused a more powerful response, includ-ing a shortening of the whole zooid accompanied by degrees of contraction in adjacent zooids. The stronger the stimulus, the more extensive, com-plete, and sustained was the response of neigh-bouring zooids. Contractions did not always spread to all members of the group. Some stayed open and continued to feed while their neigh-bours contracted. The contraction sometimes appeared to be virtually simultaneous in the neighbours of a stimulated zooid, but at other times it spread sequentially from one to another.

Electrical recordings showed the response latency, of one zooid after a shock to a remote zooid, to be highly variable. In one experiment, latencies of 400–1400 ms were observed in responses transmitted over a distance of 4 mm. In another, where the two zooids were adjacent, latencies ranged from 50 to 600 ms. Velocities of spread measured over the most direct route were generally in the range 0.3 to 1.0 cm/s.

The electrical record of a zooid's response to direct tactile stimulation (Fig. 4) typically showed two potentials in rapid succession followed by
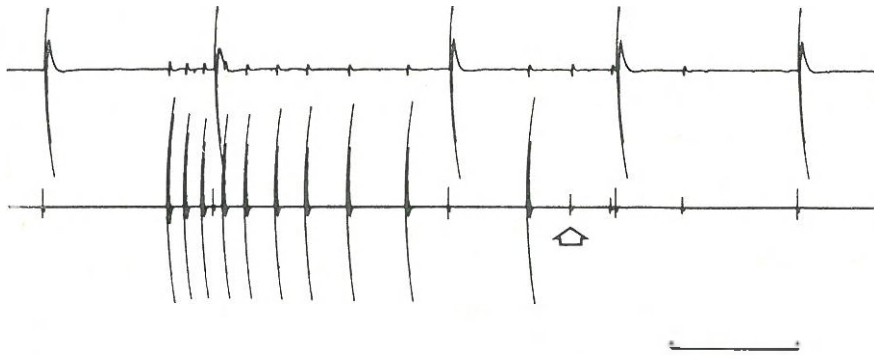

FIG. 3. Simultaneous recordings at high amplification from two of three zooids sharing a common cloaca. The lack of correlation between the CAP's of the two zooids will be noted. Small deflections represent CAP's picked up electrotonically from adjacent zooids. Three of these, of which the first is marked with an arrow, are from the zooid which had no electrode attached to it. Scale, 5 s.
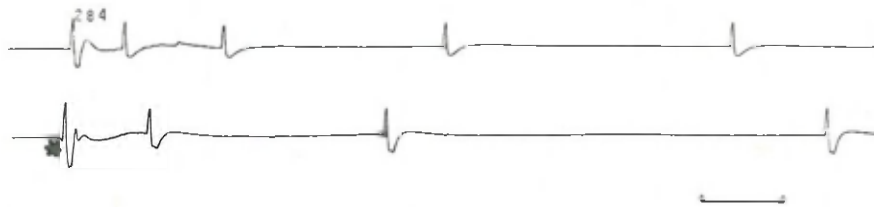

FIG. 4. Simultaneous recordings from two adjacent zooids after tactile stimulation (asterisk) to the siphon of the one whose record is shown on the bottom. The other zooid (upper line) started to contract 50 ms after the first. Scale, 500 ms.

further potentials at lengthening intervals. These events represented siphon contractions and accompanying ciliary arrests. Simultaneous records from an adjacent zooid showed a similar pattern. Apart from the initial events in each series, which are causally related, the pulse patterns from the two zooids show no coordination.

Effects of Light

Dark-adapted colonies were suddenly illuminated and light-adapted colonies were suddenly plunged in darkness. Neither treatment caused zooid contraction or ciliary arrest, nor were established pulse patterns altered. In *Ciona,* by contrast, photic stimulation causes muscle contractions (Hecht 1918).

Discussion

The responses of *Distaplia* zooids to electrical and tactile stimuli closely resemble those of solitary ascidians and no differences worth stressing have emerged from this study.

So far as coordination within the colony goes, the complete lack of coupling between the ciliary control pacemakers of adjacent zooids is rather striking. When a strong local stimulus is given, a wave of siphon contraction plus ciliary arrest spreads through the colony, and the condition may persist for a considerable period, but the electrical records show that there is no coordination after the initial spreading event.

The mechanism whereby the initial response is spread cannot be identified from the present evidence. Nerves run in the tissues lining the common cloacal openings, but whether they pass from the territory of one zooid to that of another is unknown. The muscle bands appear to end at the junctions between zooid territories. Those of one zooid do not even abut regularly end to end with those of the neighbour. Thus there is no morphological basis for assuming that impulse transmission can occur between zooids, although this possibility is not precluded.

The extremely slow (by coelenterate standards) velocity of transmission between zooids coupled with the highly variable response latency suggests that coordination is not mediated by conduction of electrical impulses in nerves or muscles but by mechanical interaction. Ascidians are very sensitive to vibration and the tremor or pull set up by one contracting zooid might be enough to trigger contractions in the neighbors

either en masse or in a wavelike series. In fact, this seems to be the most likely mechanism. Functionally it could be as effective as coordination by propagated electrical events.

Where among the Tunicata might we look for "true" colonial responses involving impulse conduction between zooids? The most likely candidate is *Pyrosoma.* This pelagic colony swims by expelling water from the common cloacal cavity through a velum-like diaphragm at one end. Muscles, blood vessels, and possibly nerves run through the colony interconnecting those zooids adjacent to the diaphragm and entering the diaphragm itself. Coordinated contractions are stated to take place in the muscles, thus tightening the diaphragm, compressing the cloacal cavity, and expelling a jet of water. Water cannot flow back outward through the zooids, as they shut their inner openings during the general contraction (Neumann 1934–1935). It seems probable that these locomotory contractions represent a type of escape response and that they evolved from the contractions of the common cloaca in a sessile ancestor, the response serving originally as a means of clearing away debris or providing a protective closure as in conventional sea squirts.

It would not be surprising to find a behavioral *Anlage* for the *Pyrosoma* response in sessile compound ascidians, particularly in such species as *Cyathocormus,* which closely resemble *Pyrosoma* in the regular arrangement of the zooids around a cylindrical central cavity (Brien 1966). This is another reason for not excluding the possibility that spread of responses in aplousobranch colonies involves more than simple mechanical interaction.

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