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BEHAVIOURAL PHYSIOLOGY OF THE COLONIAL HYDROID *OBELIA*

I. SPONTANEOUS MOVEMENTS AND CORRELATED ELECTRICAL ACTIVITY*

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INTRODUCTION

There are a number of descriptions of the electrical activity that can be recorded from the gymnoblastic hydroids *Hydra* (McCullough, 1965; Passano & McCullough, 1962–5; Rushforth, 1965*a*, *b*), *Tubularia* (Josephson, 1962, 1965*a*, *b*; Josephson & Mackie, 1965), and *Cordylophora* (Mackie, 1968). The recorded potentials are unusual in that they are large, up to several millivolts, show a long time course, up to several hundred msec, and show extensive distributions within a hydranth. Evidence is accumulating which suggests that these are potentials produced by electrically active epithelial tissue (Mackie, 1965; Josephson & Macklin, 1967). Similar responses have been recorded within the Hydrozoa from some members of the siphonophores (Mackie, 1965), hydromedusae (Mackie & Passano, 1968) and the stylasterines (Morin, unpublished). Within the Cnidaria these large, slow potentials appear to be restricted to the Hydrozoa for none have been reported from either the Scyphozoa or the Anthozoa. On the other hand, smaller, faster and regionally restricted potentials similar to action potentials have been recorded from the Scyphozoa (Horridge, 1954; Passano, 1965) and the Anthozoa (Robson & Josephson, 1969). But no records of the electrical activity have been published for the Calyptoblastea, a large hydrozoan suborder. The present study of *Obelia geniculata* was therefore undertaken to determine the type(s) of potentials found within a member of this group. The typical large, slow hydrozoan potentials were found and examined.

Within the hydrozoans for which there is published information, the genesis of these potentials is obscure. However, many of the potentials do show a direct correlation to overt effector responses (especially movement) and therefore, as in this study, have proved useful in analysing the behaviour of the organisms. The present account of *O. geniculata* describes (1) the electrophysiological events associated with specific spontaneously occurring behavioural responses, (2) the interactions between distinct electrical events within a hydranth, and (3) the electrical interactions between adjacent individual hydranths.

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MATERIALS AND METHODS

O. geniculata (L.) colonies were obtained from *Laminaria* fronds in the northern end of the Cape Cod Canal or on *Fucus* or *Laminaria* in the vicinity of Woods Hole, Massachusetts. The colonies consisted of from one to several hundred uprights all connected by stolons attached to the substrate. Each upright had from one to more than a dozen alternating hydranths (Plate 1). The hydranths were about 0·5 mm in diameter. During the summer the hydroids were kept at Woods Hole; the colonies, either attached to *Laminaria* fronds or cultured on microscope slides (Crowell, 1957), were maintained in running sea water at 17–21 °C. During the remainder of the year the colonies, cultured on slides, were kept in a 400-gallon recirculating artificial sea water system (Rila Marine Mix) in a constant-temperature room (10 ± 1 °C) in Cambridge, Massachusetts. There were no apparent differences in the responses between those observed in Woods Hole and those observed in Cambridge. The colonies were fed with *Artemia* nauplii once or twice daily. The cultures were maintained on either a 15–9 or 12–12 h light-dark cycle.

All electrical recordings were performed on colonies immersed in a 2 cm-deep sea-water bath held at 11 or 20 ± 1 °C. The bath was equipped with a gravity-flow sea-water circulation system since *O. geniculata* hydranths will regress within a few hours if a flow of sea water is not provided. A microscope slide or a cut piece of *Laminaria* frond on which *Obelia* colonies were growing was placed in the bath and positioned horizontal to the surface of the medium. The colonies were allowed to acclimate for at least ½ h before recordings were begun.

Electrical activity was recorded using fine-tipped suction electrodes similar to those used by Josephson (1965*a*). The electrodes were made by drawing plastic tubing ('Tygon', American Stoneware; i.e. $\frac{1}{16}$ in) over a small flame into a small hollow filament (Fig. 1). Because *Obelia* hydranths are quite small, it was found that even these fine tips were usually too large. Therefore, the tip of the suction electrode was formed from a glass micro-electrode which was broken off so that the internal diameter of the tip aperture was less than 50 μ. The tip was then fire-polished with a microburner under a compound microscope until an internal tip diameter of 10–25 μ was achieved. The glass electrode shaft was broken just above the taper; the glass tip was then pressed tightly onto the tip of the plastic tubing. This method yielded the advantage of a fine tip diameter as well as flexibility so that the electrode followed the movements of a hydranth to which it was attached. A silver wire was inserted through the plastic tubing near the taper and then chlorided (this was referred to as the active electrode). Sea water was drawn into the electrode until the inserted wire was submerged. The glass portion of the electrode was then positioned on the desired region of the hydranth and a weak suction was applied by means of a pipette syringe equipped with a micrometer adjustment. Potentials were recorded between the active (suction) electrode and an indifferent (external) electrode in the bath with a differential input into a high-gain amplifier (Grass 5P1) and registered on a polygraph ink writer (Grass 5B). The response time of the recorder was well above that of the relatively slow potentials produced by *Obelia*. Polarity was expressed as the response of the active electrode with respect to the external electrode. The suction electrode could be attached to any area of the hypostome or to any of the tentacles. In most cases the

glass electrode would accommodate one tentacle. The primary difficulty encountered when using these suction electrodes was the variability in amplitude of the recorded potentials within a single recording period. Such variability was presumably caused by changes of impedance within the tip of the suction electrode as the tissue which was drawn into the tip changed shape due to muscular contractions. This was particularly noticeable when a tentacle was within the electrode.

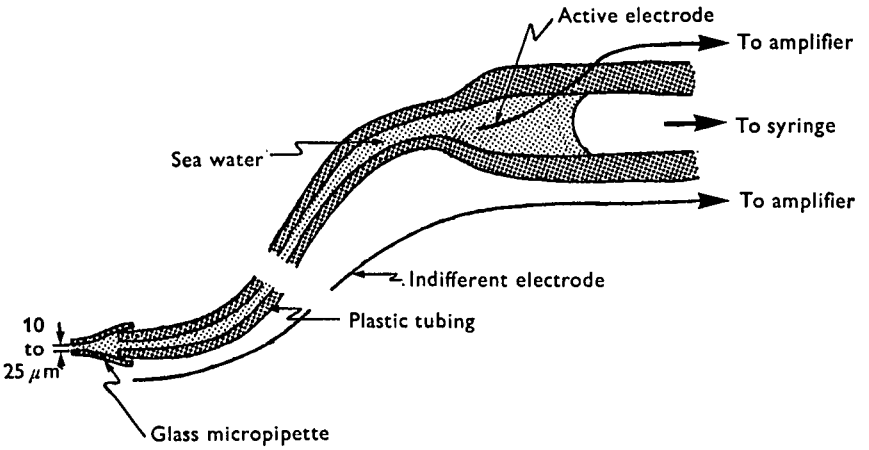

Fig. 1. Suction electrode used to record electrical potentials.

RESULTS

(I) *Structure and behaviour of* Obelia *hydranths*

The primary structures of a single hydranth, pedicel and portion of upright are shown in Fig. 2. The hydranth is situated in a cup-like extension of the skeletal perisarc, the hydrotheca, into which an extended hydranth can withdraw. The hydranth rests on a diaphragm which projects across the base of the hydrotheca. The coenosarc (ectoderm plus endoderm) of the pedicel is continuous with the hydranth tissue through a small (40 μ) central perforation in the diaphragm. The whorl of filiform tentacles consists of an alternating series of vertical and horizontal tentacles which are equipped with nematocysts on their distal regions. Prey trapped by these tentacles is brought to the mouth which lies at the terminus of the hypostome. Food is engulfed and then digested in the hydranth. Food particles are transported to other regions of the colony by ciliary activity within the coelenteron. The hydranth muculature is located in basal portions of epitheliomuscular cells of the epidermis and gastrodermis. The cells have longitudinally arranged muscle fibrils in the epidermis and circularly arranged fibrils in the gastrodermis. The tentacles are solid with a central row of vacuolated gastrodermal cells surrounded by epitheliomuscular cells and nematocysts of the epidermis. The mesoglea of *Obelia* is very thin. The gastrodermal cells lining the hydranth body and hypostome comprise mostly mucous, secretory and digestive cells. Immediately below the diaphragm the gastrodermal cells become cuboidal-epithelial cells (Brock, Strehler & Brandes, 1967).

Among the changes in posture and shape of a hydranth, three predominant stereo-

typed movements are distinguishable: (1) hydranth contraction, (2) mouth opening and (3) individual tentacle flexion.

Hydranth contraction is the most frequent and conspicuous event. The longitudinal (epidermal) musculature of the hydranth body and the tentacles contract; this produces a tight ball within the hydrotheca with the distal portions of the tentacles

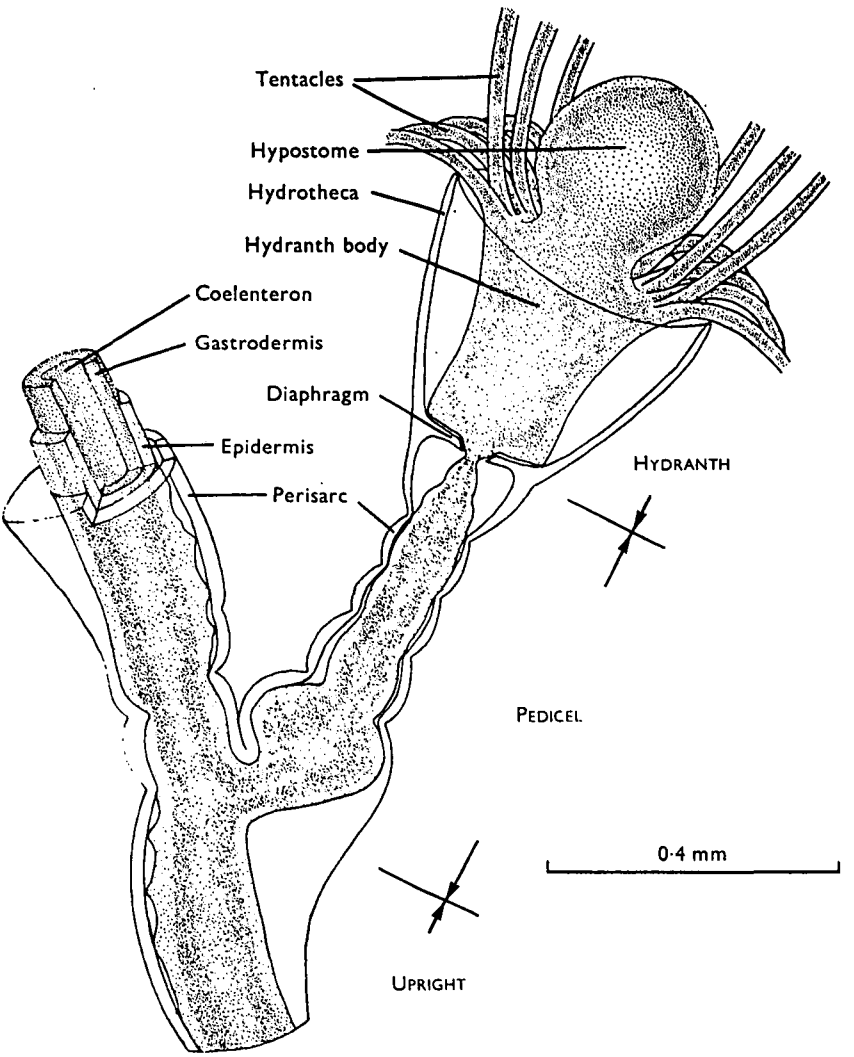

Fig. 2. A single hydranth, pedicel and portion of an upright of *Obelia geniculata*. The nearest tentacles and tips of the others are not shown.

covering the hypostome. This withdrawal usually occurs in a series of several distinct contractions of the hydranth; the total contracting time can last as long as 10 s. Return to the resting state occurs gradually over several seconds. This sequence is repeated at fairly regular intervals of about 1–2 min. It is not clear what significance this behavioural pattern has for the organism. It may function in fluid transport

within the hydranths and coenosarc or it may allow the tentacles to sweep or 'fish' greater volume of sea water.

Aboral flexing of the hypostome which produces mouth opening is a second observable behavioural event. The extent of the contracture of the hypostomal longitudinal muscles is variable and sometimes proceeds to total eversion of the hypostome. Mouth-opening responses are not frequent and are often associated with the rejection of foreign material or the ejection of undigested food. This response may be asymmetrical with only one portion of the hypostomal lip opening. Mouth opening is a rapid process which occurs in less than a second; return to the resting state is somewhat slower.

Another observed response is the oral flexion of individual tentacles. These responses are not frequent and are usually independent of the movement of adjacent tentacles. Flexion takes place in less than a second; gradual return to the resting state takes place in several seconds.

More subtle changes of hydranth posture are also observable. Such changes principally involve the hypostome. Over a period of minutes the hypostome may change from a nearly spherical form to a long bullet-shape or a somewhat flattened ellipsoid. In addition there are complex behavioural responses to feeding and unfavourable conditions.

(II) *Spontaneous electrical activity and behaviour*

The electrical potentials associated with the three behavioural patterns described above are shown in Figs. 3, 6 and 7. In all records positive potentials of the active electrode relative to the bath are displayed as downward deflexions.

Contraction potentials (KPs)

The electrical potential change which precedes contraction of the hydranth will be referred to as the contraction potential (KP) (Fig. 3). We use the term KP to avoid confusion with the contraction potential, CP, used for *Hydra* (Rushforth, 1966). The present usage has been adopted until precise homologies become established for the various hydroid species. Contraction potentials (KPs) are large (0·5–10 mV), usually monophasic potentials, but they can be complex (Fig. 3 and Table 1). The first component of the KP, the 'fast phase', is always present, distinctive and relatively constant. It is always positive when recorded from the hypostome or tentacles, has a rapid rise time (15 ± 5 ms), and a total duration of about 50 ± 20 ms. The 'slow phase' (Fig. 3 B, C, E, G) following this positive 'fast phase' in a complex KP is slow (up to 500 ms duration).

Records can be taken from the hydranth body only when the hydranth is excised from the protective hydrotheca. Such records show that the KP is identical with KP records made from the other areas except that the polarity is reversed. This is shown in Fig. 4 where two electrodes were placed on two different and opposite tentacles and a third electrode was placed on the hydranth body. The potentials appear at each electrode apparently simultaneously, at least within the resolution (about 5 ms) of the recording equipment.

KPs most often occur in bursts of two to eight potentials, but they may range from single events to bursts composed of up to fifteen potentials. The number of con-

tractions observed in a hydranth withdrawal sequence is equal to the number of KPs recorded during the contraction sequence. KPs have never been recorded without the appearance of contraction. Thus, it is reasonable to assume that each KP is the electrical manifestation of a single hydranth contraction.

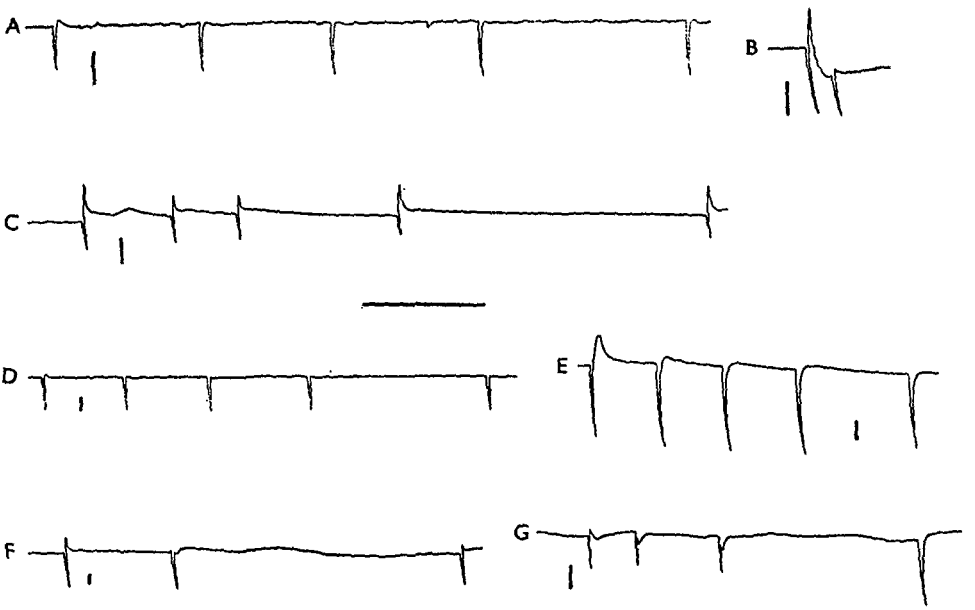

Fig. 3. Examples of contraction potential (KP) bursts all recorded from different hydranths. The vertical bars represent 1 mV and the horizontal bar, 1 s. A–C recorded from tentacles, D–G recorded from the hypostome.

Table 1. *Characteristics of spontaneously occurring electrical potentials recorded from the hypostome of* Obelia geniculata

(Plus–minus figure indicates maximum range based on approximately ten to twenty-five recorded potentials.)

	KP	MOP	TKP
Half rise time: (ms.)	6±1	25±5	20±10
Rise time: (ms.)	15±5	75±20	70±20
Half decay time: (ms.)	10±5	110±50	115±75
Decay time: (ms.)	35±15	350±100	460±200
Duration: (ms.)	50±20	425±100	530±200
Amplitude: (mV)	0·5–10	1–10	0·2–0·7
Initial polarity	+	+	−

Several examples of KP sequences are shown in Fig. 3. The relationship of the slow phases to the fast phases shown in Fig. 3G is particularly interesting. The interval between the onset of the fast phase and that of the slow phase decreases with successive KPs in the burst. This phenomenon was observed a number of times in different animals.

The inter-KP intervals vary from burst to burst but in the usual pattern the second

interval is usually the shortest (0·86 ± 0·23 s) and is followed by successively longer intervals (up to 1·52 ± 0·42 s, $N = 14$) (see Morin & Cooke, 1971*a*, Fig. 6).

Contraction burst responses are rhythmic. This is clearly shown in Fig. 5A in which simultaneous recordings were taken from two adjacent hydranths. Inter-burst

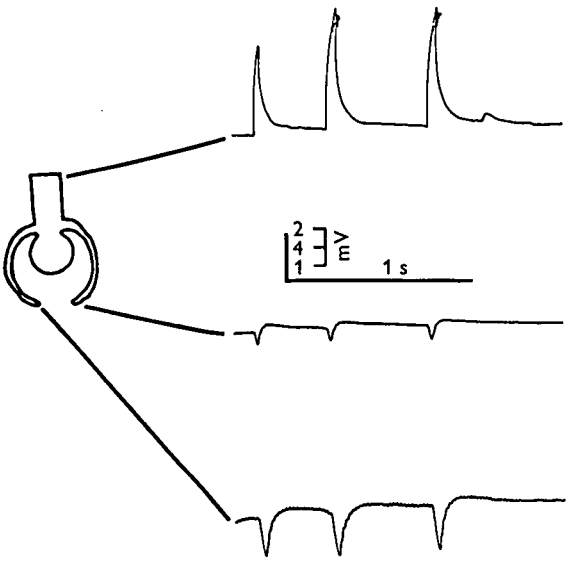

Fig. 4. Spontaneously recorded KPs from the hydranth body (upper trace) and tentacles opposite one another (middle and lower traces) from an excised hydranth. Note the polarity reversal between the upper and the lower two traces.

intervals were measured from records of several hours duration. The inter-KP burst interval is defined here as the period between the first KP of successive bursts. Fig. 5B shows a frequency histogram of the inter-burst intervals for the two hydranths of Fig. 5A. These data show that the bursting frequency is loosely rhythmic, but that there is a considerable degree of variation. Other records show that the mean interval for different hydranths is not identical. However, the distribution around the mean is similar for most hydranths. Even adjacent hydranths do not always show similar mean intervals. A range of mean intervals from 40 to 180 s has been recorded from different colonies all under similar conditions.

The effect of light on inter-burst interval has been examined only briefly. The results show that the mean interval between bursts is slightly longer (by a few seconds) in the dark than in the light.

Mouth opening potentials (MOPs)

A slow, positive, and usually simple potential is correlated with mouth-opening behaviour (Fig. 6). Such a potential will be referred to as the mouth-opening potential, MOP. The MOP is easily distinguished from the KP even at slow oscillograph speeds because it is smaller (200–700 μV) and slower (350–750 ms duration) (Fig. 6 and Table 1). The shape and positive polarity of the potential is the same when recorded from the hypostome, tentacles or excised hydranth body.

MOPs usually appear singly, but may occur in random clusters of 2–4 within 10–20 s (Fig. 6B). They occur infrequently relative to KPs, and are nonrhythmic. Recordings were made for periods of more than an hour without the appearance of MOPs. The average interval between MOP responses from several hydranth records was about 135 s; but MOPs sometimes occur at a rate up to one hundred times this average (Fig. 6C). These MOP 'bursts' begin abruptly, continue for about 1–3 min and then cease. Such events are rare and occur no more than once or twice during a record of several hours duration.

The number of MOPs is identical with the number of simultaneously observed repetitive flexions of the hypostome when a cluster of such events occur. There is no apparent difference in MOP characteristics associated with symmetric and with asymmetric mouth opening.

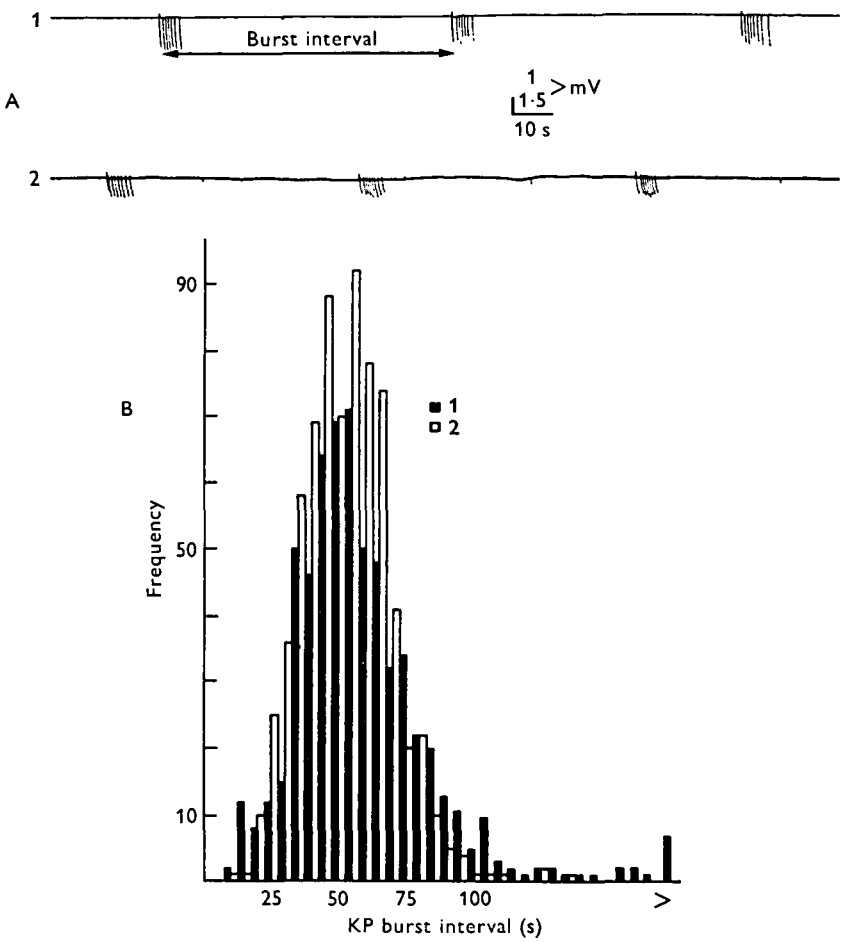

Fig. 5. Intervals between successive KP-bursts. A. A record of two adjacent hydranths (1 and 2) showing their individual KP-burst activity. Burst interval extends from the first KP of one burst to the first KP of the succeeding KP-burst. B. Frequency histogram of KP-burst intervals of the upper trace (1) and the lower trace (2) of A from a twelve hour record. Trace 1 (solid bars) $N = 621$, mean = 62 s; trace 2 (open bars) $N = 709$, mean = 55 s. The modes, but not the means, are the same.

MOPs are conducted too rapidly to allow measurement of a delay between two electrodes placed on the same hydranth.

Tentacle contraction potentials (TKPs)

Oral flexion of a single tentacle is usually observed to accompany a large (1–10 mV), slow, negative-going, simple potential when recorded from the hypostome (Fig. 7 and Table 1). We shall refer to this potential as the tentacle contraction potential,

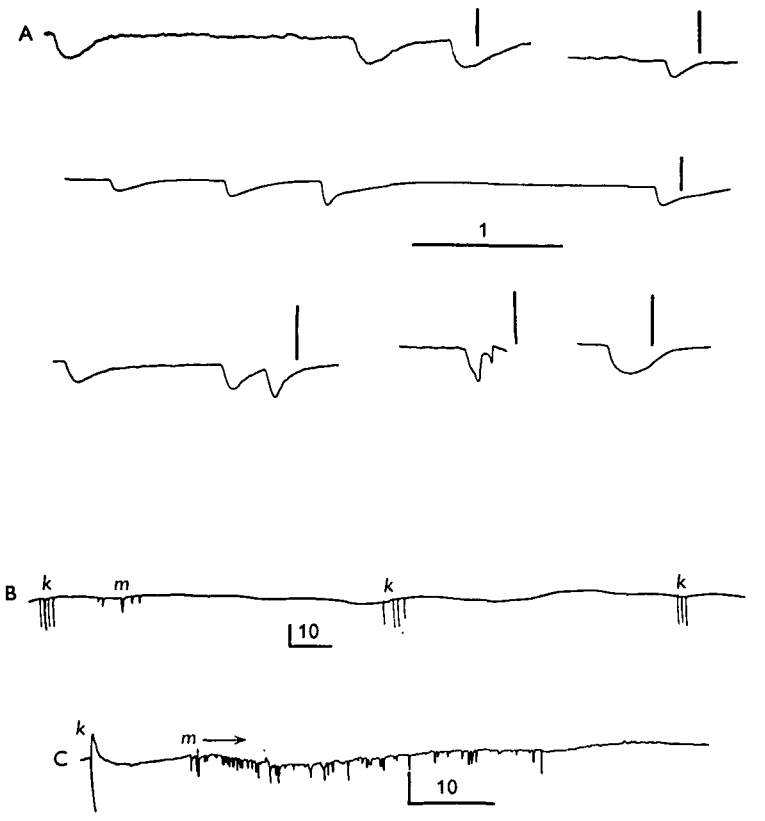

Fig. 6. Examples of mouth-opening potentials (MOPs). A, MOPs recorded from the tentacles, top trace; and from the hypostome, bottom two traces. Each record is from a different hydranth. B, Typical MOP pattern, *k* = KPs, *m* = MOPs. Note that the two are easily distinguished. C. A MOP 'burst'. Vertical bars represent 1 mV. Horizontal bars represent seconds as indicated.

TKP. We have used a term different from the tentacle potential, TP, previously used by Passano and McCullough (1962) and TCP, used by Burke & Rushforth (1966) for *Hydra* to avoid possible confusion should homologies not prove valid.

When recording from a tentacle a response, similar to that recorded from the hypostome, is recorded when that tentacle contracts. When another tentacle in the whorl contracts a potential is recorded of the same duration and shape, but of opposite polarity (positive) and of a smaller amplitude. This was shown by dual recording from two tentacles or a tentacle and the hypostome (Fig. 8). As illustrated in Fig. 8*B*, all TKPs are negative when recorded from the hypostome.

The shape and size of the positive TKP recorded from a tentacle or hydranth body are practically indistinguishable from those of a MOP, especially at slow oscillograph speeds. Most individual hydranth recordings were therefore made from the hypostome where the polarity of the MOP and TKP are opposite.

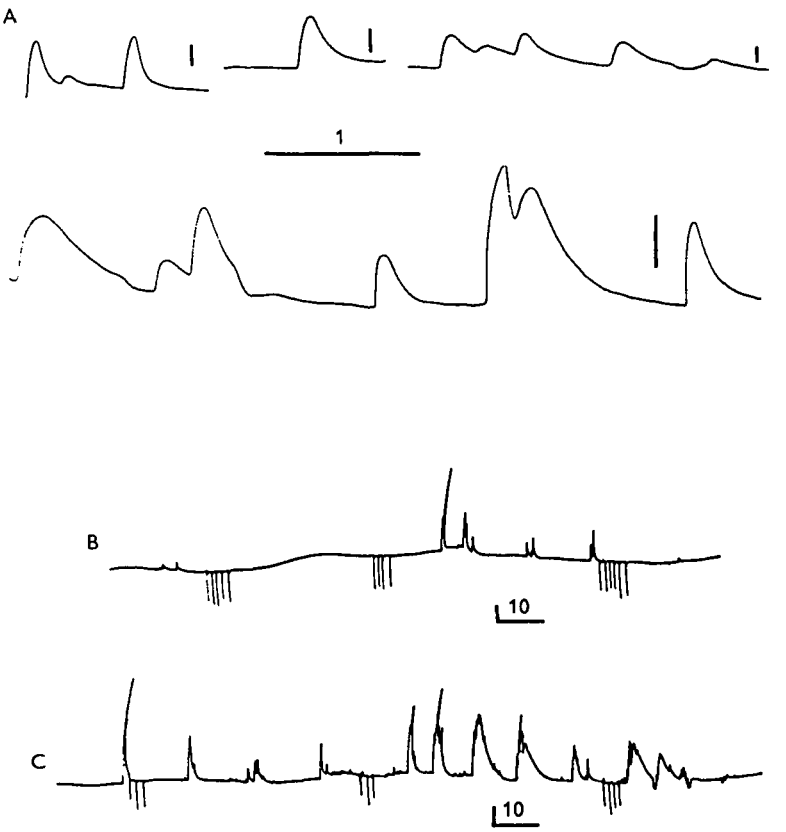

Fig. 7. Examples of tentacle contraction potentials (TKPs). A, TKPs recorded from the hypostome. Each record is from a different hydranth and colony. B, Typical TKP pattern with the electrode on the hypostome (the positive potentials are KPs). C, A TKP 'burst'. Vertical bars represent 1 mV; horizontal bars represent seconds as indicated.

TKPs occur without rhythm and relatively infrequently, although they usually appear more often than MOPs. TKPs normally occur singly but may occur in clusters of 2–15 at a time (Fig. 7B). Occasionally many TKPs will appear over a period of from 30 s to several minutes in a fashion similar to MOP 'bursts' (Fig. 7C). The frequency within the TKP 'bursts' is less than in MOP 'bursts', but they occur more often; up to five or six in 10 h.

(III) *Electrical activity of other species of the Campanulariidae*

A few observations were made on *Obelia longissima* from Casco Bay, Maine, and on *Gonothyraea loveni* from the Eel Pond, Woods Hole. The three types of potentials found in *Obelia geniculata* were also recorded in both of these species and probably

have homologous origins. These potentials and the behavioural responses are correlated in the same way as in *O. geniculata*. Therefore, at least these two species within the Campanulariidae are equipped with similar physiological responses to those in *O. geniculata*, although further studies will be required to reveal possible minor differences in their patterns and interactions.

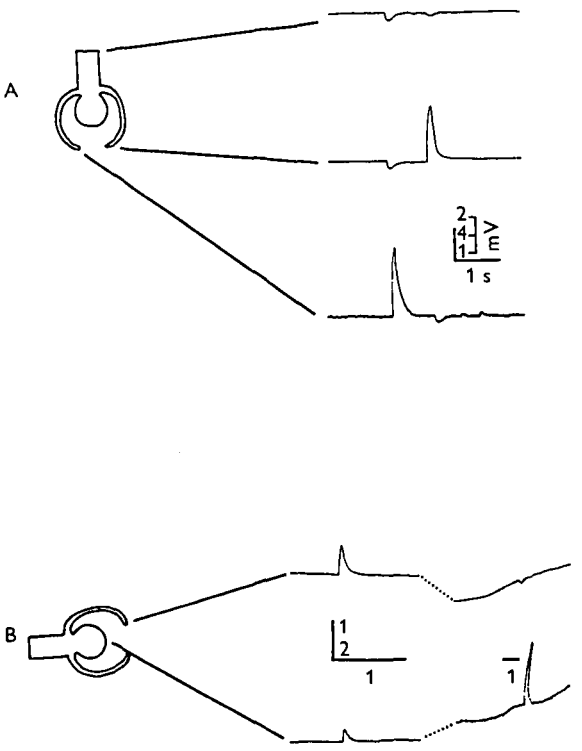

Fig. 8. TKP activity as recorded from various locations on a hydranth. A. Triple record from an excised hydranth showing contraction of first the left and then the right tentacle as indicated by the drawing. Upper trace recorded from hydranth body, lower two traces recorded from opposite tentacles. B. Dual record from an intact hydranth showing the contraction of first the upper tentacle and then some other tentacle in the whorl. Upper trace recorded from the upper tentacle as indicated by the drawing, lower trace recorded from the hypostome. Vertical bars represent millivolts, as indicated; horizontal bar represents 1 s.

(IV) *Interactions between KPs, MOPs and TKPs*

MOP and TKP activity occur during any part of a KP burst (Fig. 9). If coupling between MOPs and KPs does occur, it is loose. Some coupling is suggested by the observation that a MOP occasionally precedes the first KP of a burst, although such an apparent interaction occurs in only a small percentage of the total MOP and KP activity. In one experiment encompassing 10 h, 69 MOPs were recorded within or immediately preceding (within 1 s) a KP burst (Fig. 9F); 48 of these MOPs occurred just prior to the first KP. However, these numbers represent less than 10% of all the MOP activity and less than 7% of all the KP bursts recorded during that 10 h period. These numbers are too small for adequate statistical analysis.

TKP responses showed no detectable coupling to KP activity (Fig. 9E, G). The TKP and MOP responses also showed no obvious interactions.

Under uniform conditions, therefore, it would appear that a loose coupling may exist between the MOPs and the KPs, while no coupling occurs between TKPs and KPs or between TKPs and MOPs.

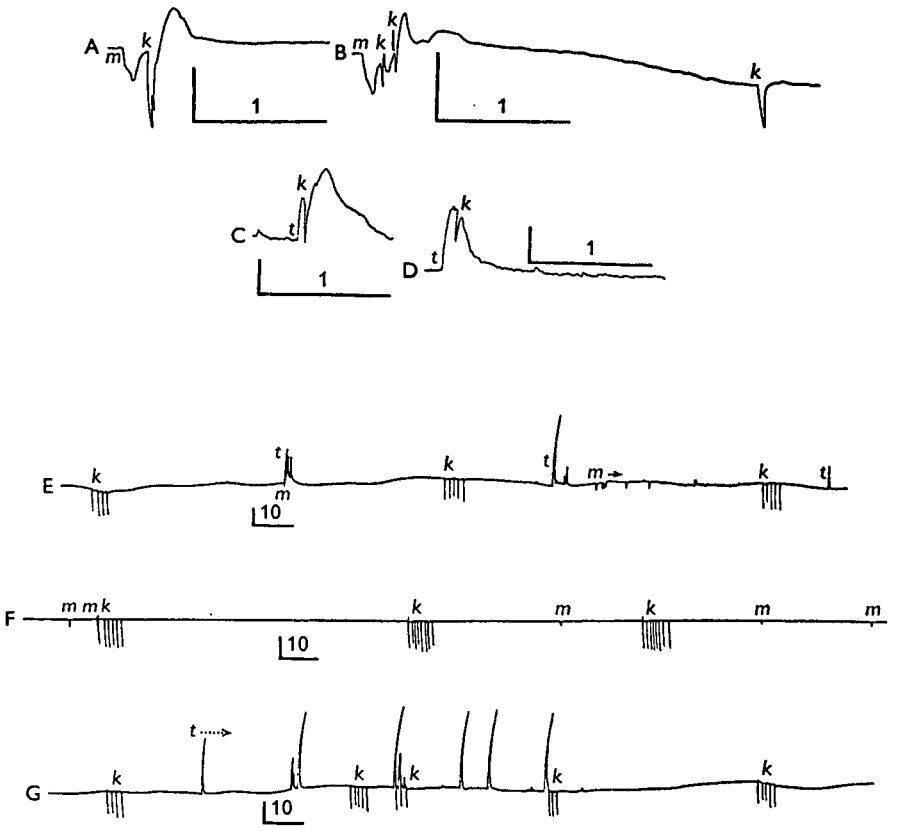

Fig. 9. Examples of different spontaneous potentials occurring simultaneously or nearly so. A and B, MOPs (*m*) followed closely by KPs (*k*). C and D, TKPs (*t*) followed closely by KPs (*k*). E, A normal pattern of KP (*k*), MOP (*m*) and TKP (*t*) activity. F, Shows 5 recorded MOPs (*m*), one of which occurs just prior to the onset of a KP-burst. G, Shows several TKPs four of which occur during or just prior to KP-bursts. Vertical bars indicate 1 mV; horizontal bars represent seconds as indicated.

(V) *Electrical interactions between adjacent hydranths*

Electrical recordings from two or three adjacent hydranths were made simultaneously and analysed for possible interactions between the hydranths.

KP-burst comparisons showed that there was no interaction of these potentials between adjacent hydranths; each hydranth contracted independently of the others. This non-interaction of KP-bursts was shown in the following way. KP-burst frequency histograms, as described above, were constructed for each recorded hydranth (Fig. 5B). Most of these histograms from dual or triple recordings showed a distinct difference in mean interval, some as large as 15 s for adjacent hydranths,

These mean interval differences alone suggest that KP-bursts between adjacent hydranths are not coupled. The example in Fig. 5 was chosen because the mean intervals were nearly identical and the records encompassed almost 12 h. Of all the records it most suggested the possibility of coupling between hydranths.

The next procedure utilized to reveal possible inter-hydranth KP coupling involved comparing the latencies between onset of KP-bursts in one hydranth and onset of KP-bursts in an adjacent hydranth (Fig. 10A) (see Wyman, 1965, Josephson &

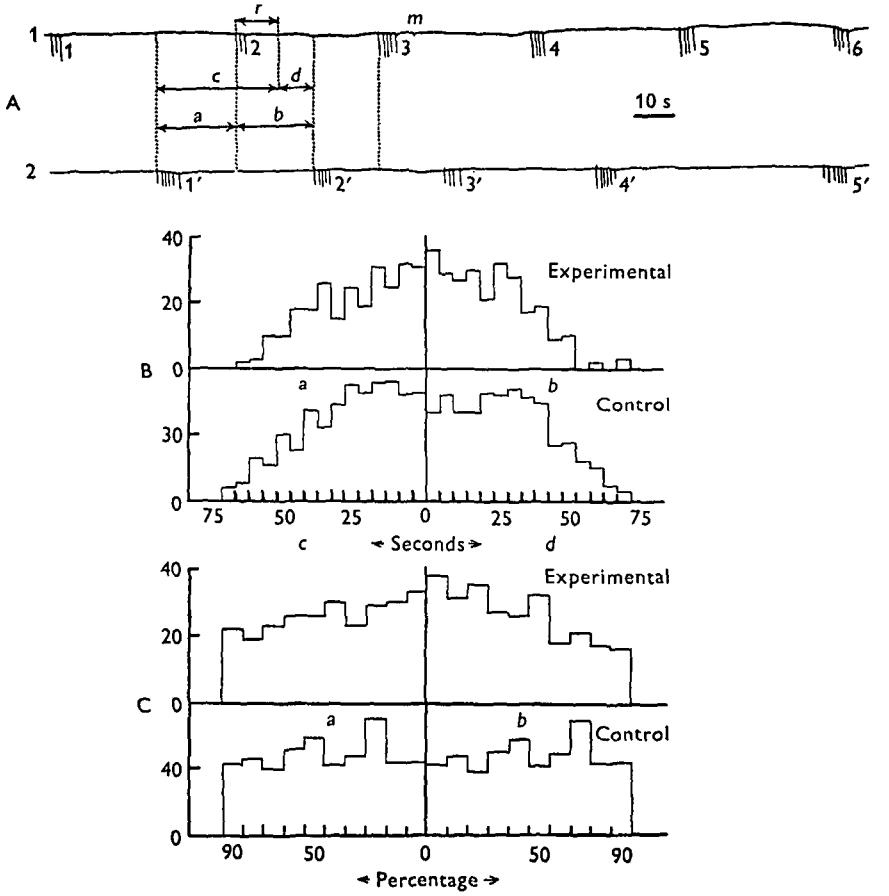

Fig. 10. Intervals between KP-bursts from two adjacent hydranths (same two as in Fig. 5). A, Two traces showing the measured intervals; *a* is the time between the onset of a KP-burst in the upper trace (KP-2 in this example) and the onset of the preceding KP-burst in the lower trace (KP-1′ in this example); *b* is the time between the onset of KP-2 of the upper trace and the onset of the following KP-burst (2′) in the lower trace. The control intervals were measured in a similar way but from a reference point a random time (*r*) from each KP-burst in the upper trace. The random times (*r*) were selected between 0 and 100 seconds in 1 sec increments from a random numbers table. The interval *c* is the time from this reference point to the preceding KP-burst in the lower trace (KP-1′) and *d* is the time from this reference point to the following KP-burst in the lower trace (KP-2′). These measurements were repeated for each KP of the almost 12 hour record. B. Shows a frequency histogram of the latency measurements described for A. $N = 1040$ for the control (*c* and *d*), $N = 527$ for the experimental (*a* and *b*). C, Shows a frequency histogram of the phase measurements for *a*, *b*, *c* and *d*. These values were obtained by dividing each one of the latency measurements (*a* to *d*) by the appropriate inter-KP-burst interval of the two traces ($a+b$; $c+d$). These figures are represented as a percentage of the total KP-burst interval.

Mackie, 1965 for a similar treatment). If coupling did occur then a preferred latency should be shown by frequency histograms of the measured latencies. Such histograms were constructed with respect to each KP in the upper trace (hydranth 1) from two pairs of measurements, one pair of which acted as controls (Fig. 10A). The first measured pair were the actual times between the onset of the KP-burst in hydranth 1 (upper trace) and the onset of the preceding KP-burst in hydranth 2 (lower trace) (*a*) and the onset of the KP-burst in hydranth 1 and the onset of the following KP-burst in hydranth 2 (*b*). The second pair, the controls, were measured in a similar way but from a reference point, *r*, a random time from each KP-burst in the upper trace; *c* was the time from that point to the preceding KP-burst of hydranth 2 and *d* was the time from that point to the following KP-burst of hydranth 2. The random times were selected between 0 and 100 s in 1 s increments from a random numbers table. The two latency histograms (Fig. 10B) are similar, and hence there is no correlation between the activity of the two hydranths.

A third procedure was utilized to test for inter-hydranth coupling. This was phase-correlation analysis. This method examines possible coupling between hydranths as a function of the total inter-KP-burst intervals rather than a fixed latency after a burst. Such a phase frequency histogram can be constructed by dividing the intervals *a*, *b*, *c* and *d* (Fig. 10A) by the appropriate inter-KP-burst interval of the two traces ($a+b$, $c+d$). Results of this treatment are shown in figure 10C. There is no correlation of phase between hydranths.

It could be argued that additional communication from the other hydranths in an upright obscures the relationship between the two hydranths being recorded. To test such a hypothesis activity was recorded from a young upright which was isolated from other uprights and possessed only two hydranths. Analysis of the records by means of histograms similar to those in Text-fig. 10 showed that the inter-KP-burst intervals within the two hydranths were indeed random with respect to one another and therefore that there is no coupling of KP activity between hydranths without applied stimuli (see the following paper, Morin & Cooke, 1971*a* for coupling following stimulation).

No correlation analyses of MOP or TKP activity between hydranths were made. These events were irregular and so infrequent that visual comparisons were sufficient to convince us that no correlation existed. There was never any observed change in MOP or TKP activity in one hydranth during the appearance of a MOP or TKP 'burst' in an adjacent hydranth.

In summary, the physiological evidence indicates that there is no interaction of the three potentials between hydranths in the absence of applied stimuli. This leads to the conclusion that these potentials are not normally through-conducted between hydranths, but are instead local events within a hydranth. Thus each hydranth acts as an individual unit rather than part of a tightly coupled colony.

DISCUSSION

Obelia *and other hydroids*

The spontaneous electrical responses recorded from *Obelia* show characteristics common to those of other hydroids which have been described: (1) their large ampli-

tude, (2) their long duration and (3) their widespread distribution within a hydranth.

These responses appear to represent epithelial potentials because they are similar to the epithelial potentials shown for nerve-free conduction in siphonophores (Mackie, 1965) and *Cordylophora* (Mackie, 1968) and similar to the transepithelial potentials shown in *Hydra* (Josephson & Macklin, 1967). The structural origin of the electrical potentials and of the conducting tissues in these forms has not yet been settled. The role of the nervous system has also not been satisfactorily resolved, although the work of Mackie & Passano (1968) on hydromedusae gives evidence for an interaction of a presumed nervous system with an epithelial system. They conclude that the nervous system of hydromedusae performs certain complex responses, integrates sensory input and initiates behaviour while the epithelial system transmits simpler responses. Data obtained so far on *Obelia* are not contradictory to such an organization. Brock, Strehler & Brandes (1967), studying the fine structure of hydranths of *Campanularia flexuosa*, have found little evidence for neural components within the tissue. Physiologically *Obelia* hydranths are not very suitable for an examination of this problem of epithelial conduction primarily because they are very small.

Most of the hydroids that have been examined undergo periodic hydranth contractions which are associated with a particular potential change: in *Hydra*, the contraction potential (CP), in *Tubularia*, the hydranth potential (HP) and in *Obelia*, the contraction potential (KP). These contraction-associated events (1) show periodic bursting patterns, (2) produce contractions of the longitudinal musculature of the hydranth body and tentacles, (3) are similar in shape and duration, and (4) may be recorded from homologous regions of the respective hydranths. The intervals between contraction potentials (CPs) within a burst in *Hydra* are longer than those in either *Obelia* or *Tubularia*. Josephson & Mackie (1965) suggest that the CP of *Hydra* is homologous to the HP of *Tubularia*; we propose that the KP of *Obelia* is also homologous.

The CPs of *Hydra* and HPs of *Tubularia* each have been shown to be coupled to another recorded potential that is capable of driving these potentials. These are the rhythmic potential (RP) of *Hydra* and the neck potential (NP) of *Tubularia* (Passano & McCullough, 1963; Josephson & Mackie, 1965). No analogous potential has been recorded from *Obelia*. Both the RPs and NPs appear to originate from the basal regions of the hydranth. We might not have recorded such potentials because recording from the homologous region in *Obelia* was not possible without excision because of the protective effect of the skeletal hydrotheca. However, both NPs in *Tubularia* and RPs in *Hydra* were often recorded from the more distal regions of the hydranths; this suggests that our records should at least occasionally have indicated these events if they were present; but none were seen. Furthermore, when the hydranth was excised no analogous responses were recorded from the hydranth body while rhythmic KP bursts continued. Thus it seems unlikely that such a coupled potential exists in *Obelia*.

Mouth-opening potential (MOP) activity in *Obelia* has no known counterpart in the gymnoblasts studied.

The tentacle contraction potential (TKP) of *Obelia* is very different from the analogous electrical activity in *Tubularia* and *Hydra*. In these the tentacle contraction potentials are short (about 50 ms) and positive, while those of *Obelia* are long (about

500 ms) and negative when recorded from the responding tentacle or the hypostome. The possibility remains that the present observations on the TKP system do not represent tentacle movements. This appears unlikely, however, because tentacle movements were seen at the same time TKPs were recorded. TKP activity appears similar to the 'suction potentials' recorded from *Tubularia* when increased suction was applied to them through the suction electrode (Josephson & Mackie, 1965). However, there was no correlation of TKP activity with applied suction in *Obelia* and they are not localized as are suction potentials. Tentacle contraction potentials, therefore, are very different from the analogous potentials recorded from *Hydra* and *Tubularia*. Further examination is necessary in order to resolve the basis of this difference.

Potentials that have no behavioural correlate have been reported for all the other hydroids examined. All the potentials observed in *Obelia*, however, do have an associated behavioural response. It should be mentioned that, conversely, in *Obelia* slow behavioural acts were observed for which no corresponding electrical potentials were recorded. All rapid behavioural movements are correlated with an electrical response.

Interactions within hydranths

Tubularia is the best understood hydroid with respect to the interactions between specific potentials. Both excitatory and inhibitory coupling have been shown between the triggering system (TS) and the NP system for excitation and between the distal opener system (DOS) and the NP system (Josephson, 1965*b*; Josephson & Uhrich, 1969) for inhibition. Two coupled potentials (the NP and HP) have been shown to excite one another reciprocally, although one (the NP) usually dominates (Josephson & Mackie, 1965). There is interaction within the hydranth (NPs and HPs) and between the stalk and the hydranth (DOSPs, TSPs and NPs). Excitatory and inhibitory coupling have been shown in *Hydra* with inhibition exerting itself reciprocally between the two systems (tentacle potentials [TCPs] and CPs) (Rushforth, personal communication) and when the CP system is externally stimulated by light especially (Passano & McCullough, 1962–5).

The situation in *Obelia* is unclear. In the absence of external stimuli it is unlikely that coupling exists between TKP and MOP or between TKP and KP activity. The evidence suggests that MOP activity may drive KP activity. The major obstacle to resolving coupling is the infrequent occurrence of apparently coupled events. In the example cited earlier, apparent coupling occurred 69 times in almost 12 h, or less than once every 10 min. This is a very small sample for meaningful statistical analysis. A full evaluation of coupling will become available only after many more and longer experiments are performed. We can conclude, however, that if coupling does occur it is looser than in *Hydra*, *Tubularia* or *Cordylophora*.

Interactions between hydranths

Evidence presented here shows no communication between hydranths. It is not surprising, when conditions are uniform, that each hydranth should respond as an individual rather than as an integral part of a tightly coupled colony. By having the freedom to act within its own 'microsphere' (that area within reach of the fully extended tentacles, see Plate 1) without being encumbered by unnecessary information

from its neighbours, the hydranth is able to make maximum use of its limited but sufficient behavioural repertoire. Evidence that there is direct communication between hydranths upon stimulation will be presented in the two papers following (Morin & Cooke, 1971*a*, *b*).

SUMMARY

1. Spontaneous electrical potentials from *Obelia geniculata* hydranths were recorded using fine-tipped suction electrodes.

2. The primary behavioural responses of the hydranths were observed and correlated with specific electrical potentials: the contraction potential (KP) associated with hydranth withdrawal, the mouth-opening potential (MOP) associated with mouth opening, and the tentacle contraction potential (TKP) associated with oral flexion of individual tentacles.

3. KPs occurred in rhythmic bursts while the TKP and MOP responses were infrequent and non-rhythmic.

4. Two other species, *O. longissima* and *Gonothyraea loveni*, were shown to produce the same three types of potentials with corresponding behavioural responses.

5. The MOP activity may occasionally drive the KP responses within a hydranth, but the coupling is very loose. None of the other possible interactions within a hydranth was observed.

6. No interaction of any of the potentials between adjacent hydranths was found in the absence of external stimuli.

7. It seems likely that the KPs in *Obelia* are homologous with the contraction potential (CP) in *Hydra* and the hydranth potential (HP) in *Tubularia*. MOP and TKP activity do not show apparent homologies with potentials of the other hydroids *Hydra*, *Tubularia* and *Cordylophora*.

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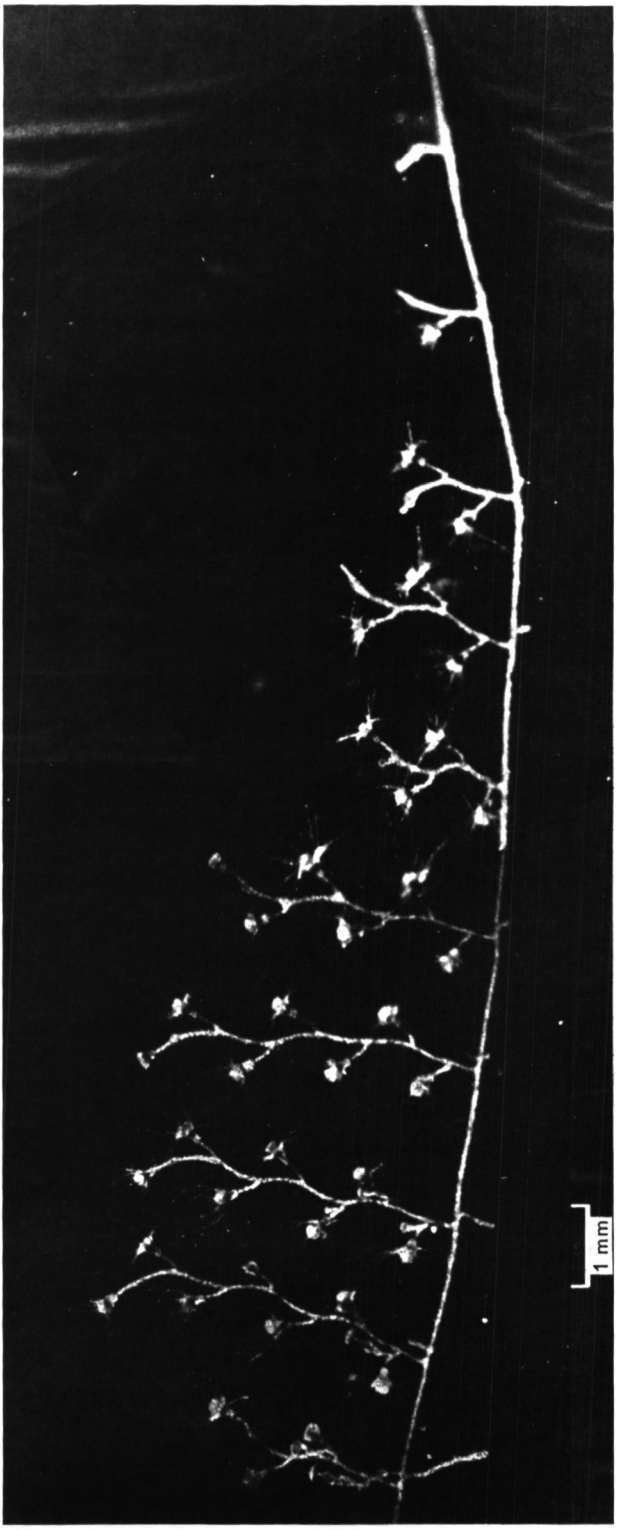

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EXPLANATION OF PLATE

A cultured *Obelia geniculata* colony growing over a microscope slide. Growth of the stolon is toward the right. Uprights (ten shown) bearing the hydranths spring from the stolon. The oldest upright (far left) bears two gonangia and one hydranth undergoing regression. The next upright (second from the left) bears one gonangium, six normal hydranths, and one hydranth undergoing regression. Note the geometric symmetry.