

BEHAVIOR AND ELECTRICAL ACTIVITY IN THE HYDROZOAN
PROBOSCIDACTYLA FLAVICIRRATA
(BRANDT). II. THE MEDUSA

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Despite a growing interest in the behavioral electrophysiology of such hydro-medusae as those of *Sarsia* (Passano, 1965; Mackie, Passano and Pavans de Cecatty, 1967; Mackie and Passano, 1968), *Euphysa* (Mackie and Passano, 1968), *Cladonema*, *Tiaropsis*, *Staurophora* (Passano, 1965), and *Spirocodon* (Ohtsu and Yoshida, 1973), a comparison of behavior and associated electrical activity in both the polypoid and medusoid phase of one species has not been reported. This study of the limnomedusan *Proboscidactyla flavicirrata* enables such a comparison to be made.

There is a degree of homology and analogy within pulse types and their conducting systems that is surprisingly exact. This applies particularly to epithelial and epitheliomuscular systems (Spencer, 1974).

The medusa of *P. flavicirrata* has proved an admirable experimental animal for furthering our understanding of all the conducting systems and their pulses that have so far been recognized in the hydromedusae.

MATERIALS AND METHODS

The medusa of *P. flavicirrata* (Fig. 1) is locally abundant in coastal waters of the Pacific Northwest between the end of May and late September. Developmental stages between the post-release four-tentacled jellyfish and the sixteen-tentacled stage have not been found. However, such stages are readily obtained from laboratory culture.

Jellyfish were collected from two localities. Those collected from the dock at the Friday Harbor Laboratories (San Juan Island) were taken at night from April to July, whereas those collected at Oak Bay (Vancouver Island) from August to October were collected during daylight. Medusae were kept in battery jars placed on a water-table at 9-13° C. The water, in the jars, was replaced once a day a few hours after the jellyfish had been fed.

Electrical activity was recorded using polyethylene suction electrodes with tip diameters between 20 and 100 μm with Pt or Ag/AgCl wire as the conductor.

Seawater in the recording dish was cooled (11-14° C) by passing water through a glass coil partially sunk into the wax-base of the recording dish. Jellyfish were never pinned down during recording since the electrodes themselves secured the specimens.

Although most of the behavioral observations were made in the laboratory, S.C.U.B.A. equipment was used to observe adult medusae.

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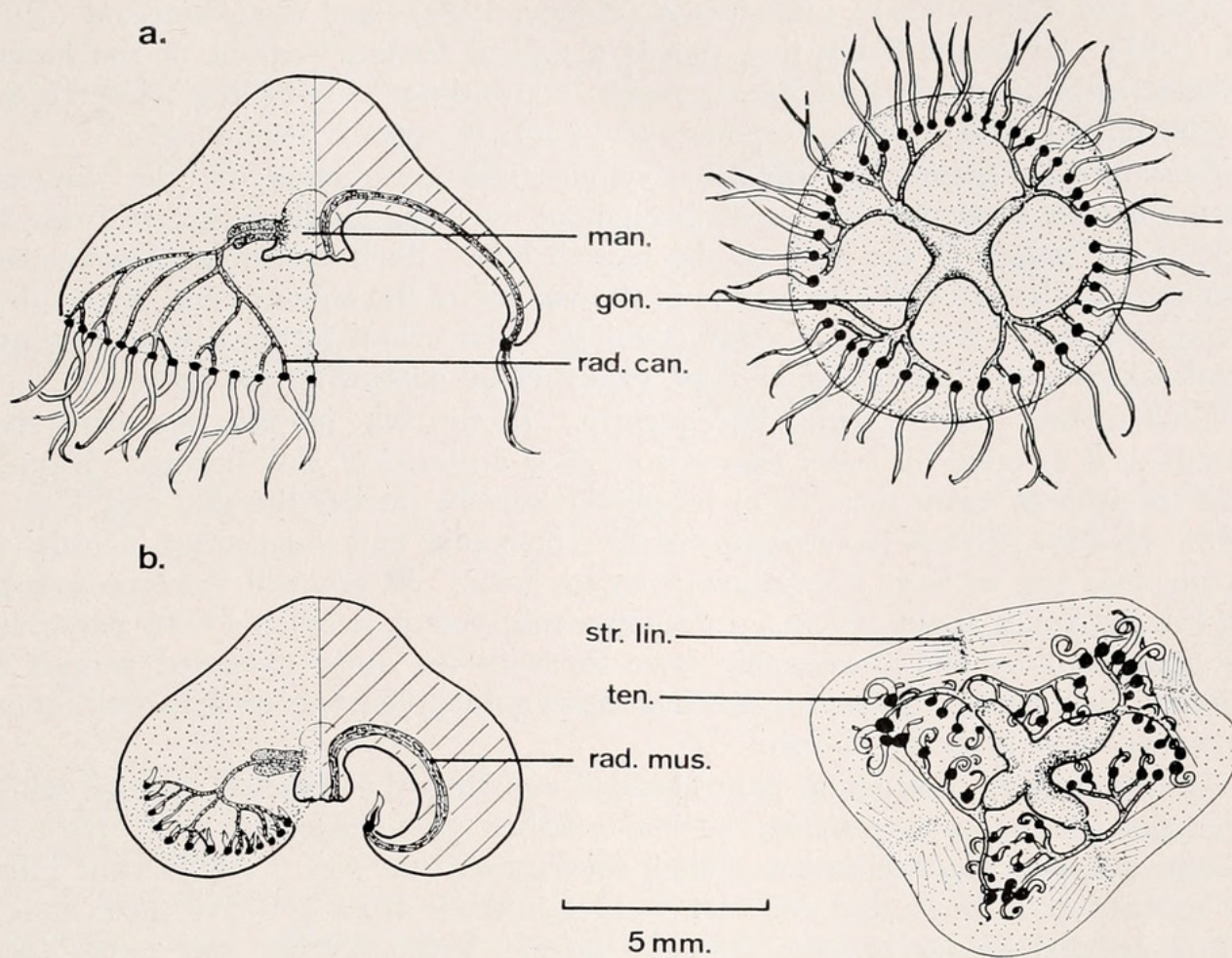


FIGURE 1. Medusa of *Proboscidactyla flavicirrata* at rest (a) and "crumpled" (b) as viewed from the side and above. The side views are diagrammatic and show one hemisphere as a sagittal section. The radial muscle of one perradial canal and the contiguous longitudinal muscle of a tentacle can be seen. The views from above were drawn from photographs: gon.—gonad; man.—manubrium; rad. can.—radial canal; rad. mus.—radial muscle (contracted); str. lin.—stress lines of the exumbrella epithelium; ten.—tentacle (contracted).

RESULTS

Behavioral observations

Feeding. If jellyfish are placed in an aquarium and then several beakers of fresh plankton poured in, jellyfish will start feeding almost immediately. Single tentacles or groups of neighboring tentacles contract while the margin of the bell associated with these tentacles swings in towards the manubrium. As the margin rolls up into the subumbrella cavity the manubrium bends out towards incoming tentacles. If the prey is small the manubrial lips engulf the tentacles, or if large, the tentacles pass the prey directly to the mouth. The food captured in this way consists of small cyclopoid copepods, cladocerans, trochophore larvae, crab zoeae, copepod nauplii and various eggs.

Medusae of *P. flavicirrata* can often be seen motionless in the sea with the tentacles extended horizontally. In this posture they sink slowly. This behavior has been noted in other limnomedusae and is frequently described as "sink-fishing". The others include *Eperetmus typus* (Mackie and Mackie, 1963); *Gonionemus*

(Yerkes and Ayer, 1903); *Limnocyda* (Edney, 1939); and *Craspedacusta* (Russell, 1953). It seems likely that this is a typical feeding pattern of the limnomedusae since *P. flavicirrata* spends much of the time "sink-fishing", interrupted by intermittent radial feeding responses and bouts of upward swimming.

Swimming. Swimming involves symmetrical contraction of the circular, striated muscle sheet that is present throughout the subumbrella ectoderm from the apex of the velum to the base of the manubrium. Each swimming beat causes elongation of the bell and a reduction in the volume of the subumbrella cavity, thus forcing water out through the velar opening. The velum forms a wide-mouthed funnel which tends to increase exhaust velocities by narrowing the opening.

Undisturbed jellyfish swim infrequently. In the sea, jellyfish are only seen swimming if agitated by water currents or after a period of sink-fishing. Jellyfish were rarely seen more than 10 m below the surface during the day and 1 m at night. Mature jellyfish have slight negative buoyancy and must swim in order to remain near the surface, a swimming period lasting 30 sec will displace a large jellyfish vertically about 80 cm. In comparison, young jellyfish (4–16 tentacles) sink more rapidly and presumably have to swim for more extended periods to maintain their depth. Indeed in the laboratory young jellyfish tend to swim more frequently than mature jellyfish.

The swimming contraction is not graded and thus the distance through which a jellyfish swims is determined by the number of contractions in a burst of swimming and not by the extent of each contraction. In young jellyfish the interval between each swimming contraction in a burst is from 250–350 msec and in mature jellyfish it varies from 300–400 msec. Velar-steering was never seen, even if the jellyfish were tilted through 90°. The medusa of *P. flavicirrata* is very stable with the bell uppermost, since a large volume of mesogloea is well separated from the more dense manubrium and tentacles, thus giving a large turning moment.

Synchronous tentacle shortening, involving all the tentacles of a medusa, usually occurs either immediately (less than 1 sec) prior to or during a swimming burst. While the jellyfish rests between swimming bursts the tentacles are held a few degrees below the horizontal.

Crumpling. "Crumpling" is a term first used by Hyman (1940) to describe a defensive response seen in a number of hydromedusan species, both antho- and leptomedusae, involving contraction of radial muscles together with the longitudinal muscles of the tentacles so that the margin and tentacles are drawn up into the subumbrella cavity. Unlike other hydromedusae, the radial muscles of *P. flavicirrata* are endodermal and lie on the subumbrella side of the radial canals where they are restricted to bands either side of the canals (Spencer, 1971). If the radial muscles of all four quadrants contract, then the jellyfish takes on a square outline when seen from above (Fig. 1b). Any portion of the ectoderm of the jellyfish can be stimulated mechanically to elicit a crumple, with the exumbrella and margins being the more sensitive regions, though tentacles must be shaken before a jellyfish will crumple. During crumpling all other muscular activity ceases.

Synchronous tentacle shortening. Synchronous tentacle shortening has already been described in connection with swimming, but it can also be seen in all medusa stages during rest periods. These contractions usually involve every tentacle and

TABLE I
Parameters of the pulse-types.

Pulse type	Initial polarity	Duration (msec)	Conduction velocity (cm/sec)	Amplitude (mV)	
				+	-
Swimming pulses, N = 450	-	30-110 \bar{x} = 60	22-26 (14° C)	0.04-0.36 \bar{x} = 0.16	0.25-0.80 \bar{x} = 0.30
Marginal pulses, N = 120	+	40-90 \bar{x} = 71	3.9-5.6 (14° C) (only applies to attached medusae)	0.01-3.20 \bar{x} = 1.3	0.02-1.20 \bar{x} = 0.40
Tentacle contraction pulses, N = 80	+	40-120 \bar{x} = 100	—	0.05-5.00 \bar{x} = 2.50	0.03-0.60 \bar{x} = 0.20
Crumpling pulses, N = 130	-	10-50 \bar{x} = 17	5-22 (14° C)	0.09-1.00 \bar{x} = 1.80	0.10-4.00 \bar{x} = 2.50

Pre-swim pulses are not included in this table because of lack of sufficient data.

can be single or appear in bursts. Relaxation is immediate, unlike the tentacle contractions during crumpling when relaxation is far slower. Sometimes these contractions are only seen over a short length of the tentacle near the tip, particularly in adult medusae. Often tentacles curl aborally as they contract. Synchronous tentacle shortening is not dependent on external stimulation of any kind.

Electrical activity

In the following account of electrical activity in the medusa of *Proboscidactyla flavicirrata* the term "mature" refers to a released medusa with a complement of at least 40 tentacles and bell diameter exceeding 4 mm, and does not necessarily imply sexual maturity. A summary of the major parameters of the pulse types is given in Table I.

Feeding potentials. Potentials associated with feeding have only been recorded from two released medusae, and thus the following must be treated with caution. These low amplitude, positive going potentials can be recorded from the bases of perradial tentacles actively involved in feeding. They do not appear to be conducted through to neighboring tentacles.

Swimming pulses (SP's) and pre-swim pulses (PSP's). Swimming pulses can be recorded from any part of the circular muscle sheet of the subumbrella and velum in both attached and free medusae. There is a one for one relationship between swimming pulses and swimming contractions. The pulses are always biphasic, with a characteristic shape, which may be preceded by a negative-going spike (Fig. 2). This spike (the pre-swim pulse) is only seen if suction electrodes are attached close to the margin of the subumbrella.

Conduction velocities of SP's have been calculated for mature medusae between electrodes placed on the subumbrella surface near the junction of the velum with the subumbrella. The stimulating electrode is placed between tentacles over the endodermal "ring-canal" at 45° from one of the recording electrodes, and the

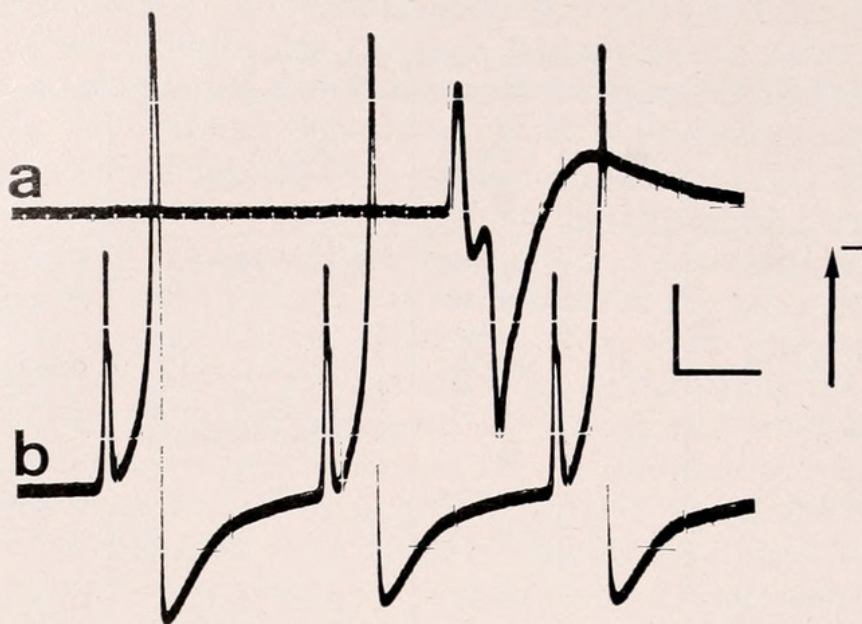


FIGURE 2. A swimming burst consisting of three contractions of the circular muscle. One electrode (a) was attached to a tentacle and recorded a single tentacle contraction; the other electrode (b) was attached to the margin on the subumbrella surface and recorded three swimming pulses (SP's), each preceded by a pre-swim pulse (PSP). The horizontal bar represents 200 msec and the vertical bar, 100 μ V.

recording electrodes are positioned 90° apart. For this preparation a mean value of 25 cm/sec (14° C, N = 27) was calculated if it is assumed that the conduction route is circular between recording electrodes. If three recording electrodes are positioned 120° apart at the same vertical height on the subumbrella then the synchrony of excitation of the circular muscle sheet can be observed, with excitation reaching all three sites within 20 msec, normally it is much less than this (4–6 msec at 14° C).

When a mature jellyfish is placed in a solution containing one part of isotonic magnesium chloride and one part seawater spontaneous swimming stops after some

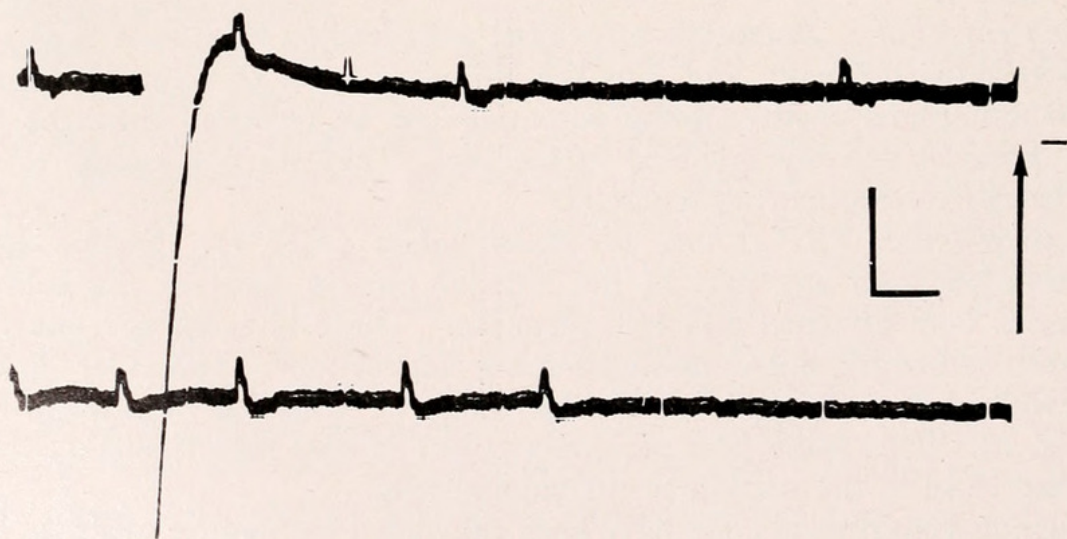


FIGURE 3. Reappearance of pre-swim pulses (PSP's) after Mg^{++} anaesthesia. The two traces form a continuous recording. The large potential on the upper trace is a marginal pulse. The horizontal bar represents 100 msec and the vertical bar, 50 μ V.

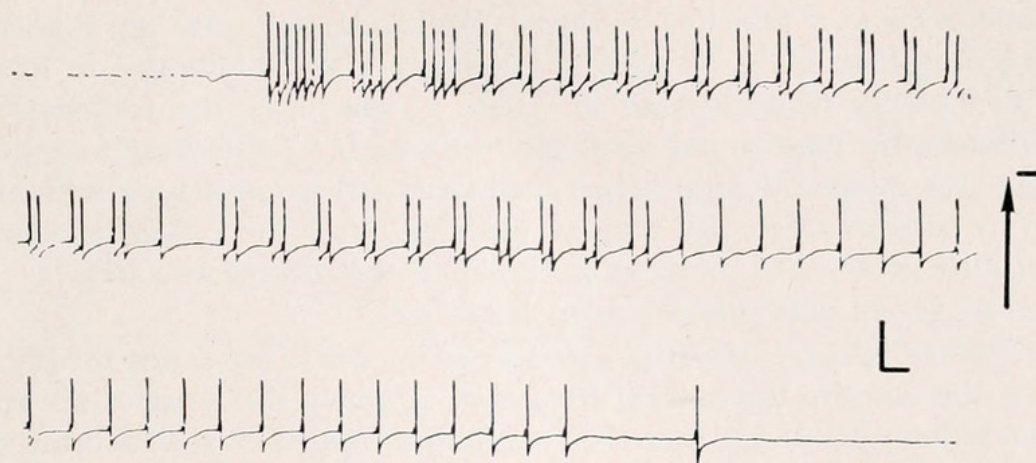


FIGURE 4. Swimming period of a mature medusa. Swimming pulses (SP's) are recorded by an electrode attached to the subumbrella surface. The horizontal bar represents 1 sec and the vertical bar, 500 μ V.

15 min. If the water containing excess Mg^{++} is flushed out with fresh seawater, potentials can be recorded from the margin that have a frequency reminiscent of SP's. This happens about 4 min after flushing (Fig. 3). These potentials have a very low amplitude (9–60 μ V) and are grouped as bursts of from 4–9 pulses which become bursts of 3, 2, and 1 pulse after 7 min. There is no visible muscular contraction associated with these potentials. Then about 15 sec after bursts with three potentials first appear, swimming contractions can be seen together with the associated SP's. At first these SP's are of low amplitude but some 9 min after flushing with fresh seawater they resemble normal SP's. These swimming potentials seen during recovery from Mg^{++} anaesthesia are probably identical to the pre-swim pulses seen preceding SP's that have already been described.

Swimming pulses can be recorded over long periods of time from both attached and free medusae giving data on temporal patterns of swimming. These swimming patterns are surprisingly regular and typically consist of bursts of swimming pulses with distinct interburst intervals (700 msec—several min) and interpulse intervals (200–500 msec) which in a series form a swimming period (3 sec to several hours), as shown in Figure 4. Table II summarizes the temporal patterns of swimming pulses that were recorded from 4 mature medusae (approximately

TABLE II
Temporal patterns of swimming in medusae.

		Burst type					
		7	5	4	3	2	1
Frequency of burst type	Mature Attached	1% —	2% 0.6%	5% 2%	19% 20%	49% 64%	24% 13%
Mean interpulse interval	Mature	308 msec SD 13	365 msec SD 30	390 msec SD 26	425 msec SD 35	384 msec SD 49	n.a.
	Attached	— —	225 msec SD 15	266 msec SD 35	301 msec SD 64	360 msec SD 48	n.a. n.a.
Mean interburst interval following stated burst type	Mature	1060 msec —	1003 msec SD 230	902 msec SD 190	982 msec SD 160	1120 msec SD 83	1350 msec SD 90
	Attached	— —	1500 msec SD 290	1135 msec SD 150	975 msec SD 140	1180 msec SD 190	1230 msec SD 240

6 mm diameter) and 6 attached medusae (approximately 600 μ m diameter) over a total recording time of 15 hr with swimming periods totalling 2 hr 40 min.

The main points demonstrated in Table II are: (a) the frequency of burst types is different for mature and attached medusae; (b) the mean interpulse interval is longer for mature than attached medusae; (c) a burst type with two pulses is favored in both attached and mature medusae; (d) there is a tendency for the mean interpulse interval to increase as the burst size decreases; and (e) the interburst interval varies only slightly with burst size.

When mature jellyfish are stimulated to swim with just supra-threshold shocks delivered to the margin, the natural frequency at which the muscles are contracting can be overridden. However there is a maximum frequency at which the swimming pulse system can be driven. This occurs when the interpulse interval is some 260 msec, which is also the minimum interpulse interval seen during spontaneous swimming.

Marginal pulses (MP's). Marginal pulses can be recorded from the tentacles and marginal regions of both attached and free medusae. Such pulses are often not directly associated with any motor activity, and thus may have an integrative or pacemaker function. Nevertheless, synchronous contractions of all the tentacles are always accompanied by a marginal pulse(s). MP's recorded from attached medusae are seldom grouped in bursts and the system is rarely silent, whereas MP frequency in free medusae is often burst-like and the interpulse interval is rarely as constant as it is in attached medusae. In attached medusae MP firing is synchronized between the four tentacle bases and only occasionally is MP excitation not conducted through to all four tentacles.

Four days after release, medusae begin to develop 4 interrarial tentacles. If suction electrodes are attached to the bases of these tentacles, marginal pulses can be recorded, but there is no synchrony of MP firing between these tentacles and any other tentacles at this stage. Marginal pulse firing within this group of four tentacles is also unsynchronized, however, recording taken from the four primary tentacles (perradial) show synchronous firing with each other, and by the 6th day after release MP firing of all eight tentacles is synchronized (Fig. 5). In individuals with the full complement of tentacles MP firing is not necessarily synchronized between all the pacemaker sites since small groups of adjacent tentacles can show unilateral, synchronous firing.

Conduction velocities of MP's have been calculated by electrical stimulation of tentacle tips and from recordings of spontaneous activity in pre-release medusae. A mean value of 4.7 cm/sec (14° C, N = 15) is obtained if it is assumed that marginal pulses are conducted in the marginal nerve-ring(s). These velocities only apply to attached medusae since it is difficult to stimulate MP's in mature medusae without exciting the crumpling pulse system.

In attached medusae, using three electrodes, it can be seen that each tentacle base contains a site capable of initiating marginal pulse excitation. One site may lead for many minutes to be rapidly followed by another, yet other sites may show attenuation of MP amplitude and stop firing for a period. Such relationships are far more difficult to see in free medusae since there are numerous tentacles each undergoing independent tentacle contraction (to be described later), and also the bursting pattern of marginal pulses leads to confusion over which pulses are

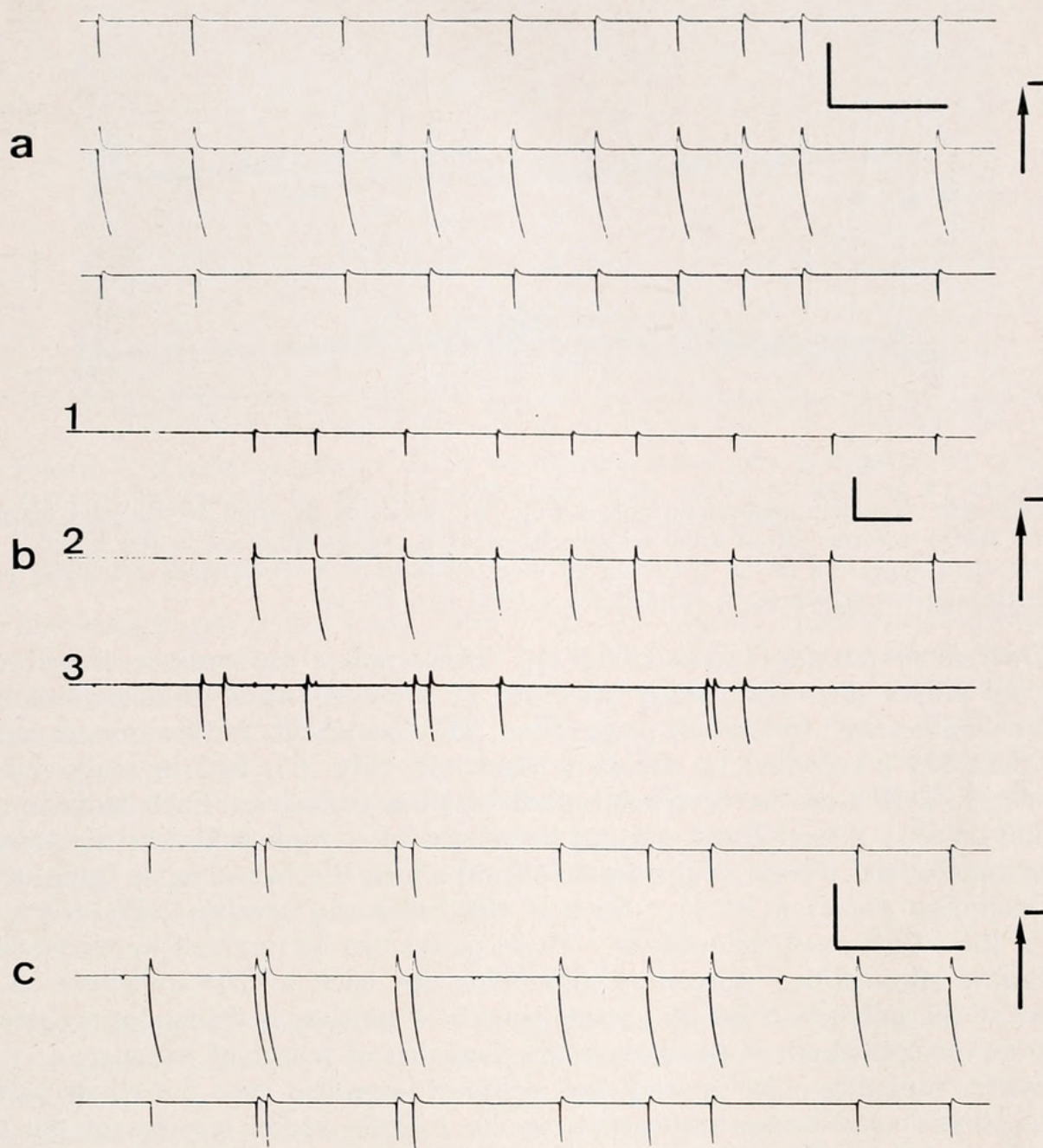


FIGURE 5. a) Synchronous marginal pulse (MP) activity recorded by electrodes attached to three of the four tentacles (perradial) of a recently released medusa. b) MP activity of the same medusa recorded by two electrodes attached to perradial tentacles (traces 1 and 2) and the third electrode (trace 3) attached to a developing interr radial tentacles. c) MP activity recorded from the same tentacles as in b) but approximately 20 hr later, with all three sites showing synchrony. In a, b, and c the horizontal bar represents 5 sec and the vertical bar, 1 mV.

related in bursts from different sites. Synchrony of MP's in all the tentacles of free medusae is not the rule; quite frequently populations of tentacles adjacent to one another show connectivity, with each population apparently isolated.

If medusae, both attached and free, are placed in seawater containing excess Mg^{++} then the synchrony of MP's is lost, with all marginal pulse sites eventually becoming silent. If, for example, a mature medusa is placed in a one to one solution of isotonic magnesium chloride and seawater, MP activity ceases after 10 min. This effect is reversible if jellyfish are flushed with fresh seawater, but the rates of recovery are extremely variable.

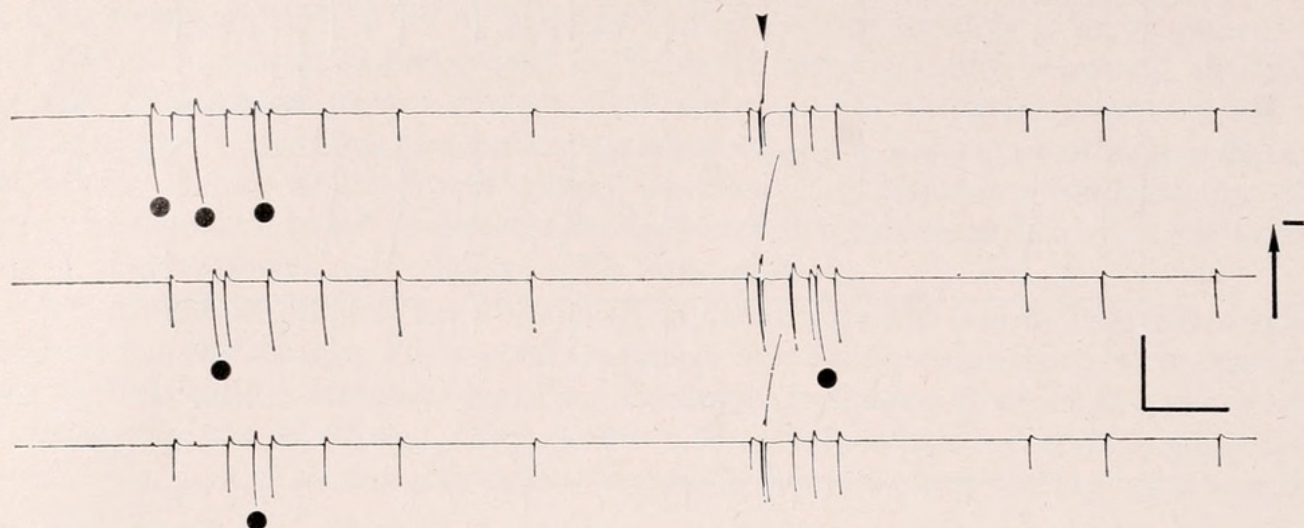


FIGURE 6. Tentacle contraction pulses (TCP's), indicated by solid circles, and marginal pulses (MP's) recorded from three tentacle bases of a medusa attached to the colony. The biphasic event appearing at the arrow on all three channels is a spontaneous crumpling pulse. The horizontal bar represents 5 sec and the vertical bar, 500 μ V.

Tentacle contraction pulses (TCP's). These pulses are easily confused with marginal pulses since both pulse types can be recorded from tentacles and have similar parameters. In any one preparation, TCP's normally have a greater amplitude than MP's recorded by the same electrode (Fig. 6), and in multi-channel recordings, TCP's are never synchronized between tentacles. Each tentacle contraction pulse is a local event and can be related to a single unilateral contraction of the longitudinal muscle of the tentacle from which the recording is being made.

Crumpling pulses (CrP's). Suction electrodes can record CrP's from any part of the ectoderm of the medusa. These pulses can be initiated by electrical or mechanical stimulation. Electrical stimulation can elicit a CrP anywhere on the surface of the jellyfish, although greater potentials and larger electrodes are needed to excite the epithelium of the exumbrella than that of marginal regions.

Every crumpling pulse is conducted without decrement over the whole surface of the jellyfish and causes contraction of the smooth, radial muscles of the subumbrella endodermal lamella, and similar muscles in the tentacles. Such contractions are graded, each successive CrP delivered at short intervals (more than 1 shock/4 sec) causes a contraction that summates with prior contractions. There is no evidence of facilitation in the CrP conducting system. In fact, the threshold for evoking a CrP increases with repetitive stimulation. The first shock always causes a CrP, and such a pulse, like all other CrP's is conducted over the entire surface of the jellyfish with a resultant crumple.

The conduction velocity of CrP's may be dependent on the size and geometry of cells forming the ectoderm at any one point, since velocities are greatest in the direction of the long axes of cells and where cells are large (Spencer, 1971). Crumpling pulses that are conducted circumferentially through the exumbrella epithelium close to the margin (within 40 μ m) have far higher velocities (mean of 21 cm/sec at 14° C, N = 52) than CrP's recorded from other areas of the exumbrella (mean of 13.7 cm/sec at 14° C, N = 76).

Recordings of repetitive stimulation of the CrP's system show that the amplitude of pulses decays exponentially to a constant level. This occurs when the inter-

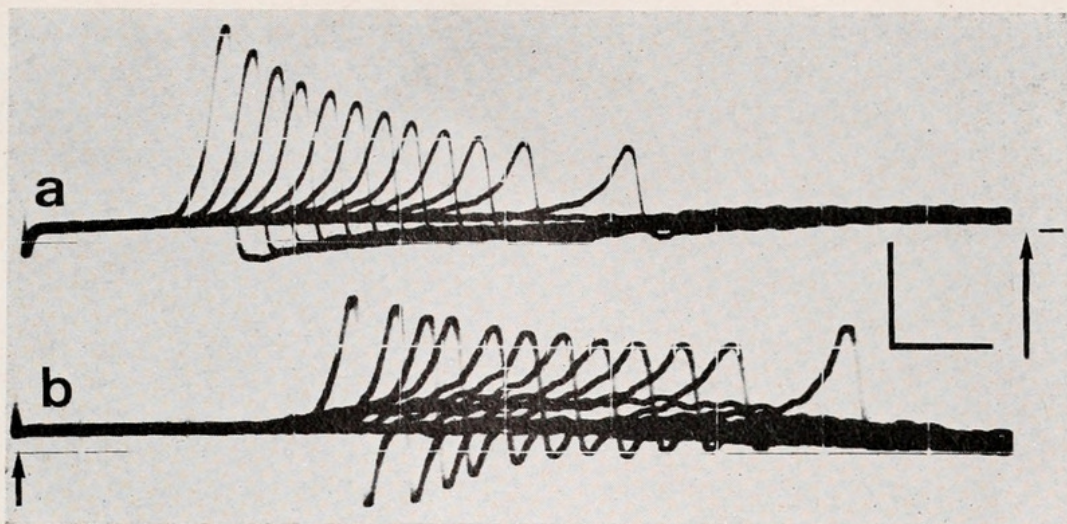


FIGURE 7. Crumpling pulses (CrP's) stimulated at a frequency of 2/sec on the exumbrella and recorded by electrode a) attached to the exumbrella and b) attached to the subumbrella. 12 superimposed traces are shown. An arrow denotes the stimulus artifact. The horizontal bar represents 20 msec and the vertical bar, 1 mV.

val between shocks is less than 1 sec (Fig. 7). During repetitive stimulation at frequencies greater than 1 shock/2 sec the conduction velocity of crumpling pulses decreases with each successive shock until the system becomes inexcitable. This phenomenon will be called fatiguing. All parts of the ectoderm show fatiguing to the passage of closely spaced crumpling pulses, and since the phenomenon of fatiguing can be seen in preparations where the duration of the shock is less than 1 msec, increased initiation delay cannot account for fatiguing. Recovery from a fatigued state is fairly rapid with the conduction velocity returning to 90% of the original value in about 40 sec.

DISCUSSION

The feeding pattern seen in *P. flavicirrata* closely follows feeding habits in other hydromedusae. Hyman (1940) distinguishes between feeding in jellyfish having a broad, shallow bell and those having a tall, narrow bell. These characteristics are typical of the leptomedusae and anthomedusae respectively. Feeding in *P. flavicirrata* most closely resembles that of the flat type of jellyfish, except that tentacles holding the food contract and these tentacles are sometimes held by the manubrial lips. Low amplitude potentials have been recorded from the bases of perradial tentacles involved in a feeding response that cannot be associated with other known conduction systems (Spencer, 1971).

The only analytical accounts of the mechanics of swimming in the hydromedusae are those given by Gladfelter (1972, 1973). All the principles of propulsion he suggests are met by *Proboscidactyla* except that velar steering was not seen. Unlike other limnomedusae *Proboscidactyla* does not have statocysts and it is likely that the extra stability gained from a dome-shaped bell obviates the need for a reflex response such as velar steering. Synchronous tentacle contractions accompanying or preceding swimming have been frequently seen in hydromedusae; *Eperetmus typus* (Mackie and Mackie, 1963), *Leuckartiara octona* (Russell, 1953), *Bougainvillia superciliaris* (Agassiz, 1849). Such contractions presumably reduce the drag created by trailing tentacles.

Spontaneous swimming in scyphozoans (Horridge, 1959) is unlike that in small antho- and limnomedusae. Bursting is rarely seen and there is far more variability in the mean interpulse interval over extended periods of time. Horridge found that the standard deviation of the inter-contraction interval is usually 20–30% of the mean, whereas in *P. flavicirrata* equivalent values are from 4–21% (calculated from the raw data for Table II).

Behavioral and electrophysiological evidence (Romanes, 1876; Passano, Mackie and Pavans de Ceccatty, 1967) suggests the presence of a number of coupled swimming pacemakers in the marginal ganglia (Mackie, 1971) and/or marginal nerves of hydromedusae. Mackie and Passano (1968) have shown that the spread of excitation for contraction in the swimming, circular muscle of *Sarsia* does not require the involvement of nerves. Pure myoid conduction in *Sarsia* has a velocity of 7.5–8.5 cm/sec (20° C) in a circular direction. If the margin is present then velocities rise to 50 cm/sec as compared to 25 cm/sec (14° C) in *Proboscoidactyla*. It is possible that in *Proboscoidactyla* circular conduction is facilitated by the presence of the marginal nerve rings (Spencer, 1971). Thus in many hydromedusae the marginal nerves are used for rapid conduction of excitation around the bell and the swimming-muscle sheet is excited near the margin by these nerves with a subsequent myoid spread.

The spikes (PSP's) sometimes seen in *Proboscoidactyla* preceding biphasic swimming pulses and during recovery from Mg^{++} anaesthesia are presumably the motor output of the swimming pacemaker system, conducted in the marginal nerve or nerves that trigger swimming. Similar events have been recorded in *Phialidium* (Passano, 1965), *Spirocodon* (Ohtsu and Yoshida, 1973), and *Stomotoca* (Mackie, unpublished). Since PSP's can be recorded in the margin before the swimming muscle has recovered from Mg^{++} anaesthesia it would appear that Mg^{++} blocks transmission at neuro-muscular junctions more readily than neuro-neuronal junctions.

Spontaneous, synchronized tentacle flexion or shortening is seen in many hydrozoans, both polyps and medusae: *Porpita* (Mackie, 1959), *Tubularia* (Josephson, 1965), *Turritopsis* and *Gossea* (Gosse, 1853), and *Eperetmus* (Mackie and Mackie, 1963). The functions of such movements are obscure in *Proboscoidactyla* as in other hydromedusae. In *Porpita*, orally directed flexions seem to aid food collection whereas in *Tubularia* similar movements are probably used to mix the contents of the proboscis cavity and/or to transport gut contents to neighboring polyps.

Marginal pulses always accompany synchronized tentacle contraction in *Proboscoidactyla* although marginal pulse firing does not necessarily cause tentacles to contract. Passano *et al.* (1967) report that synchronous contraction is seen during MP firing but that, unlike *Proboscoidactyla*, there is not a one for one relationship. No motor function has been ascribed to MP's recorded from *Spirocodon* (Ohtsu and Yoshida, 1973); I assume the nMP's they report to be synonymous with MP's, and that QSCP's are the electrical concomitant of the type of tentacle contraction that can be triggered by nMP's. It is evident that MP's can only be recorded from areas close to the margin and that the conduction system lies within the marginal nerve rings (Passano, 1965; Passano *et al.*, 1967; Mackie and Passano, 1968; Ohtsu and Yoshida, 1973). There is a striking difference between the conduction velocity of marginal pulses in *Sarsia* (50 cm/sec) and *Spirocodon*

(71 cm/sec) with the velocity in *Proboscidactyla* (4.7 cm/sec). An explanation for this difference is that the diameters of neurons conducting MP's are likely to be far smaller than equivalent neurons in *Sarsia* and *Spirocodon* since the individuals used were young attached medusae.

The ontogeny of activity in the marginal pulse system suggests that every tentacle has the potential to contain a marginal pulse pacemaker and that synchrony between MP pacemaker sites is dependent on neuronal connections between sites. These connections probably consist of a number of parallel pathways, thus affording either tight or loose coupling of pacemakers. This coupling is lost under Mg^{++} anaesthesia before the pacemakers become completely silent (cf. Mackie and Passano, 1968).

Romanes (1877) was familiar with crumpling in jellyfish and gives a detailed description of a "spasm" in *Staurophora*, noting all those features which distinguish it from a swimming contraction. Unfortunately he was not aware of the existence of a second muscle system, the radial muscles. Mackie, Passano and Pavans de Ceccatty (1967) did identify the muscles involved and give a description of the events occurring after excitation of the exumbrella of *Sarsia tubulosa*. In *Sarsia* crumpling consists of a flurry of contractions in the radial muscles, and closure of a sphincter in the bell margin whereas in *Proboscidactyla* there is often just a single contraction and the sphincter muscle is absent. It should be noted that, besides protecting delicate tissues, crumpling causes *Proboscidactyla* to sink more rapidly by reducing the frontal area, thus carrying an individual away from noxious stimulation.

The crumpling pulses that can be recorded from *Proboscidactyla* can be equated with similar potentials that have been recorded in most of the hydrozoans so far examined. Histological evidence from Mackie (1965), Mackie and Passano (1968) and Spencer (1971) shows that these pulses can be propagated across sheets of simple pavement epithelium of either the bell or nectophore (in spihonophores). These epithelia do not appear to support any other electrical activity and the excitation that is propagated from cell to cell causes similar motor activity in all the hydromedusae studied, that is crumpling. The electrical parameters of crumpling pulses are characteristic, being of large amplitude (several mVs) and biphasic. In some species they may be compound events as Passano (1965) has shown in *Cladonema*.

None of the epithelia conducting CrP's show any signs of facilitation, the first shock is always effective. Multiple firing to a single shock seems to be a common feature of the systems in *Sarsia* and *Euphysa* (Mackie and Passano, 1968) unlike *Proboscidactyla* where it never occurs. During such multiple firing the duration of each pulse increases successively, this is similar to an increase in the duration of CrP's in *Proboscidactyla* after repetitive stimulation and maybe consequential to a reduction of conduction velocity as the system fatigues. The conduction velocities of CrP's in *P. flavicirrata* of 6–21 cm/sec at 14° C over the exumbrella ectoderm is of the same order as velocities measured in other hydromedusae; *Sarsia*, 15 cm/sec at 18° C (Mackie and Passano, 1968); *Euphysa*, 18 cm/sec at 14° C (Spencer, 1971); *Bougainvillea*, 6 cm/sec at 14° C (Spencer, 1971); *Phialidium*, 19 cm/sec at 20° C (Mackie and Passano, 1968); and *Spirocodon*, 12 cm/sec (Ohtsu and Yoshida, 1973). Differences in conduction velocity of crumpling pulses

due to the geometry of cells in the ectoderm have not been seen in other hydromedusae. The very high velocities of CrP's conducted circumferentially near the margin may be due to facilitated conduction caused by involvement of the marginal nerve rings (Spencer, 1971).

Proboscidactyla is still able to conduct crumpling pulses in excess Mg^{++} (Spencer, 1971) even when all muscular and nervous activity has stopped, though these pulses can only be generated by electrical stimulation. This low susceptibility of epithelial systems to magnesium anaesthesia was noted by Mackie and Passano (1968).

The phenomenon of fatiguing where both amplitude and velocity of epithelial pulses falls with repetitive stimulation has not been recorded in other hydromedusae, though Mackie and Passano (1968) did notice an increase in the duration of crumpling pulses with multiple firing.

The radial muscles responsible for crumpling are smooth muscles but it is not known whether such muscles in hydromedusae require nervous innervation or whether the myoepithelial cells can be depolarized electrically by direct epithelial excitation. Perhaps both types of innervation are present since the graded, local movements seen during prey capture and swallowing obviously require nervous control.

From the physiological and histological evidence obtained from a preceding paper on the polypoid phase of this limnomedusan (Spencer, 1974) and that presented here, some hypotheses on the mechanisms of epithelial conduction in the Hydrozoa can be erected.

We find, as a general rule, that conduction velocities of epithelial pulses are higher in tissues having large cells. For example, crumpling pulses have higher velocities (6–21 cm/sec) than colonial pulses (0.9–9.0 cm/sec) in *Proboscidactyla* and cells of the exumbrella ectoderm are far larger (approximately 25 μm diameter) than the epithelial cells that probably conduct colonial pulses (approximately 12 μm diameter). In *Hippopodius* (Siphonophora) the exumbrella cells of the nectophores are often 100 μm on their shortest axis (Mackie, 1965) and have conducted pulses with velocities as high as 30 cm/sec at 21° C. This suggests that a large component of the conduction time of an epithelial pulse may be due to a delay at each cell-junction. It should be noted that all these cells have similar thicknesses and thus a lower cytoplasmic resistance probably does not account for such high velocities in the larger cells.

The phenomenon of fatiguing in the epithelial conducting systems of *Proboscidactyla* gives further support to the idea that junctional delay may be a prime factor in determining conduction velocity. During fatigue of the colonial pulse system of the polyp colony, to repetitive stimuli, the velocity of pulses may be reduced by 45% of the original velocity but there is no reduction in amplitude, whereas in the crumpling pulse system of the medusa the velocity is maximally reduced by 40% and there is an exponential decrease in the amplitude of pulses. This decrease in conduction velocity of epithelial pulses seen during repetitive firing could be due to: a) an increase in the threshold of each cell, b) an increase in the rise time of the action potential, or c) an increase in the proportion of inexcitable cells, that is cells not recovered from their refractoriness. There is no reason why these mechanisms should be mutually exclusive.

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SUMMARY

1. Feeding in the medusa of *Proboscidactyla flavicirrata* is accompanied by local, small amplitude impulses recorded from the bases of perradial tentacles.

2. Medusae, both attached and free, swim spontaneously with electrodes in place thus giving data on the temporal patterns of contractions of the swimming muscle.

3. Swimming pulses (SP's) can be recorded from the circular muscle of the subumbrella. Each SP is preceded by a pre-swim pulse (PSP) which is a neuronal pulse conducted in the marginal nerve(s).

4. Marginal pulses (MP's) are neuronal pulses conducted in the marginal nerve(s) which can trigger synchronous tentacle contraction.

5. MP's originate from pacemaker sites located in tentacle bulbs. When new tentacles first appear the firing of MP's from these new sites is not synchronized with established pacemakers: eventually they become linked to the original pacemaker system.

6. Synchrony between MP pacemakers is lost under Mg^{++} anaesthesia.

7. Tentacle contraction pulses (TCP's) are the electrical accompaniment to local tentacle contraction.

8. Crumpling pulses (CrP's) are epithelial pulses causing the protective behavior known as crumpling.

9. CrP's show a decrease in conduction velocity and amplitude as a result of repetitive stimulation.

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