

NEUROBIOLOGY OF THE GORGONIAN COELENTERATES, *MURICEA CALIFORNICA* AND *LOPHOGORGIA CHILENSIS*

I. BEHAVIOURAL PHYSIOLOGY

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SUMMARY

1. Electrical or mechanical stimulation of *Muricea californica* or *Lophogorgia chilensis* colonies resulted in withdrawal of polyps in the immediate vicinity of the stimulation point. Additional stimulation did not result in further spread of polyp retraction.

2. Electrical activity was recorded from a colonial conduction system not restricted to the area of polyp withdrawal. Conduction velocity in this conduction system decreased with increasing stimulus number and distance from the stimulation point.

3. Polyp withdrawal in *Muricea* occurred concomitantly with a burst of facilitating electrical impulses. The withdrawal burst was always preceded by impulses of the colonial conduction system.

4. The pattern of colonial behaviour in gorgonians depends upon the conduction properties of the colonial conduction system, the conduction system(s) of each individual polyp, and the pathways connecting the two.

5. Polyp tentacles bend to the oral disk when presented with liver extract. A burst of electrical impulses was recorded from *Muricea* polyps during chemical stimulation. These bursts exhibited apparent adaptation and presumably represent muscle potentials resulting from chemoreceptor activation.

INTRODUCTION

Anthozoan behaviour is often more complex than might be expected in the light of the traditional concepts of organization of coelenterate nervous systems. Recent evidence indicates that, in anemones, such behaviour involves multiple, interacting, conduction systems which possibly include non-nervous conducting epithelia (McFarlane, 1969). Further, in colonial anthozoans, the behaviour of individual polyps is influenced by their interactions with the common tissue mass. Although the polyps can act independently, a colonial control system may override polyp autonomy and produce colonial responses such as bioluminescence and protective polyp retraction (Parker, 1920; Nicol, 1955*a, b*, 1958; Horridge, 1956, 1957; Davenport & Nicol, 1955; Buck, 1953, 1973).

The degree and pattern of control exerted by colonial anthozoans over their constituent polyps varies. Horridge (1957) described several colonial behaviour patterns and proposed two models for their neural control. Josephson, Reiss & Worthy (1961) conducted a computer simulation of excitation spread in a nerve net which more accurately modelled the observed behaviour. Both studies were based on the assumptions that behaviour is closely meshed to underlying neural activity, and that interneural facilitation (Pantin, 1935*a, b*), and thus incremental spread of excitation, is responsible for non-through-conducted colonial activities.

A major focus of recent research into the organization of the anthozoan nervous system has been on the electrophysiological basis of colonial behaviour (Shelton, 1975*a, b, c*; Shelton & McFarlane, 1976; Anderson & Case, 1975; Anderson, 1976*a, b*; Satterlie, Anderson & Case, 1976). Most colonial anthozoans investigated, including at least one with incremental behaviour (*Porites*: Shelton, 1975*c*), have through-conducting colonial nervous systems. On such evidence, Shelton (1975*c*) postulated that polyp withdrawal resulted from a series of impulses of colonial origin activating the polyp neuro-effector system within a critical facilitation period. Different patterns of withdrawal were considered to result from changes in conduction velocity within the colonial conducting systems which caused variations in the number of polyps that would receive impulses within the critical facilitation period. Shelton concluded that interneural facilitation was unimportant and that neural activity does occur in the absence of detectable behavioural responses. On the other hand, Anderson (1976*b*) has shown that incremental spread of electrical activity is responsible for incremental polyp retraction in *Goniopora*, thus supporting the earlier theories.

To further clarify understanding of anthozoan colonial coordination, we have studied two gorgonians electrophysiologically and morphologically. The gorgonians are of great interest because they occupy an extreme in the spectrum of colonial control patterns, one in which the colonial conduction system has little control over the polyps. Thus, Parker (1925) states that responses are '... as local as one could well imagine'. We report here on the electrophysiology of colonial coordination and behaviour of individual polyps of two gorgonian species.

MATERIALS AND METHODS

Specimens of *Muricea californica* Aurivillius and *Lophogorgia chilensis* Verrill were collected locally by divers at depths of from 4 to 11 m (*Muricea*), and 9–22 m (*Lophogorgia*). They were kept in recirculating sea-water tanks (15–20 °C) and were not fed during the course of the experimentation, a maximum of 30 days.

Electrical recordings were made with tygon suction electrodes (Ag/AgCl, tip diameter 100–300 µm) leading to Grass P511R preamplifiers, and displayed on a Tektronix 434 oscilloscope. Stored displays were photographed directly with a Polaroid camera, and continuous recordings were photographed with a Grass C4R Kymograph camera. Electrical stimuli were applied to polyp oral disks with a Grass S9 stimulator through suction electrodes (Ag/AgCl). For chemical stimulation, beef liver extract (5 g wet weight per 100 ml sea water, double-filtered with Whatman No. 1 paper) was applied under water with a finely drawn glass pipette 1–2 cm away

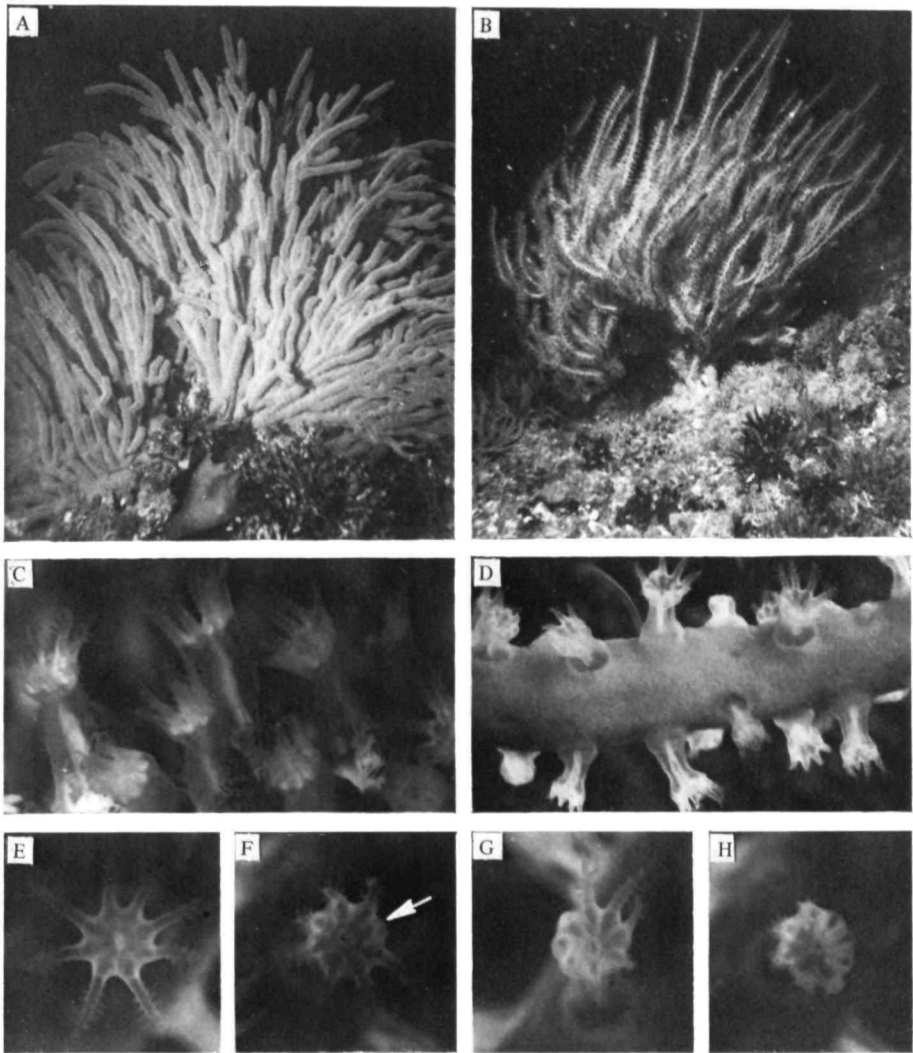


Fig. 1. Habitat photographs of *Muricea* (A) and *Lophogorgia* (B). (C–D) Branch arrangement and polyp structure of *Muricea* (C, $\times 10$) and *Lophogorgia* (D, $\times 7.5$). (E–H) Feeding sequence of a *Lophogorgia* polyp (oral view, $\times 15$) in response to beef liver extract (see text). (E) Expanded posture. (F) Single tentacle response (arrow). Note mouth opening. (G) Response of four tentacles (H) Complete response of all eight tentacles.

From the test polyp. Seawater controls causing mechanical disturbance in excess of that used for chemical tests produced no electrical activity in the polyps. All experiments were performed in subdued light at 17–19 °C.

RESULTS

Gross morphology

Muricea and *Lophogorgia* (Fig. 1) are gorgonians with irregular branches lying roughly in one plane and lacking cross connexions. Polyps extend in all directions around the branches. In *Muricea* they protrude from prominent calyces giving the colony a warty appearance. The coenenchyme of *Muricea* is brown with small yellow-brown polyps of up to 0.5 mm oral disc diameter. Each polyp has eight pinnate tentacles extendable to 3 mm. The coenenchyme of *Lophogorgia* is red with transparent polyps lacking calyces and which are slightly smaller than *Muricea* polyps.

Behavioural observations

The gorgonian colony is virtually inexcitable (Parker, 1925; Horridge, 1957). A single electrical stimulus to a *Muricea* or *Lophogorgia* polyp produces only a response in that polyp. Subsequent stimuli evoke responses in as many as 50–60 neighbouring polyps located 5–10 mm around the stimulation site, with all polyps in this area reacting simultaneously, as judged by visual inspection. The border between reactive and non-reactive polyps is not definite since some polyps in this area respond with tentacle or column twitches.

Within 10 mm of a stimulation site, a train of 4–6 supra-threshold stimuli at a rate of 0.7 s⁻¹ initiates the only obvious colonial activity, a smooth, continuous retraction of the polyps into the coenenchyme. Graded responses occur; 2–3 stimuli result in tentacle contractions while 3–4 stimuli provoke twitches of the polyp column in addition to tentacle movements. If stimulation is terminated prior to a complete retraction, the polyps immediately return to an expanded posture. Once withdrawn, the polyps remain retracted for five minutes or more.

In behavioural experiments with two stimulating electrodes approximately 4 cm apart, normal polyp withdrawal in the area surrounding one electrode was achieved when one or two of the 4–6 stimuli were delivered by the distant electrode. The existence of an undetected, incrementally-conducting, control system is therefore doubtful.

Individual polyps respond to beef liver extract with graded feeding (acceptance) responses. Single tentacles can act independently, twitching toward or bending to the oral disc (Fig. 1 F). With less localized application, two or more tentacles simultaneously bend to the oral disc (Fig. 1 G). In the presence of the larger amounts of feeding stimulants, all tentacles contract to the mouth (Fig. 1 H), the anthocodium partially retracts and the polyp remains semi-retracted for more than a minute. This may represent a rejection or avoidance response because it differs from acceptance in that the tentacle shortens rather than bends directionally to the mouth.

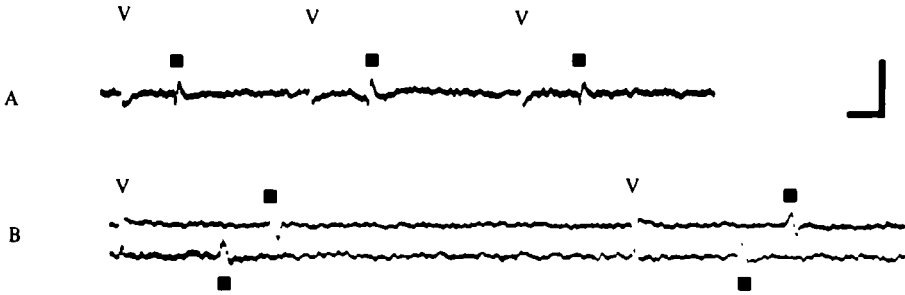


Fig. 2. Electrophysiological recordings from the colonial conduction system of gorgonians in response to electrical stimulation. (A) Electrical activity recorded from the oral disc of a *Lophogorgia* polyp. (B) Recordings from two *Muricea* polyps. (V) stimulus artifact, (■) colonial impulse. Scale: Ordinate 10 μ V, abscissa 200 ms.

Electrophysiology of the colonial conduction system

Electrically evoked through-conducted colonial impulses were recorded from the oral discs of polyps of both *Muricea* and *Lophogorgia* colonies, even from widely separated branches. Unlike some other colonial anthozoans, in which a second through-conducted impulse was also recorded (Anderson & Case, 1975; Shelton, 1975*b*; Shelton & McFarlane, 1976; Satterlie *et al.* 1976), only one impulse was recorded for each stimulus. Colonial impulses in *Lophogorgia* were small, 2–4 μ V in amplitude, with durations of 50–70 ms (Fig. 2A). Conduction velocity in the colonial system, recorded between pairs of electrodes, was 5–7 cm s⁻¹ (18 °C). These results are based on data from only five recording sessions owing to the difficulty of recording from the small polyps. Consequently, the majority of the work was done on *Muricea*.

Through-conducted, generally biphasic, impulses were consistently recorded from the polyp oral discs of *Muricea* colonies. However, depending upon electrode attachment and stimulus number, either portion of an impulse might dominate, giving the impulse a monophasic appearance. The colonial impulses (2–7 μ V in amplitude and 40–60 ms in duration, Fig. 2B) were conducted without decrement, with an absolute refractory period of around 80 ms.

Conduction velocity, measured as the latency between two recording electrodes, varied from 4 to 20 cm s⁻¹ (17–19 °C) depending upon distance from the stimulating electrode, stimulus number, and stimulus frequency. The stimulus normally used was 5 V/1 msec although threshold for the through-conducting system was as low as 1.6 V/1 msec. Repetitive stimulation resulted in a decrease in conduction velocity in the colonial conduction system with each successive stimulus (Fig. 3). The decline was greatest with the first few stimuli, but lessened prior to total failure. The rate of decline in conduction velocity and the time to total conduction failure varied with stimulus frequency. Responses to frequencies of 0.5–0.7 s⁻¹ were the most consistent, with conduction velocities falling to 60–70% of the initial value after 10–15 stimuli. Once in approximately 50 tests, a *Muricea* colony responded to more than 25 stimuli at 0.5 s⁻¹ before failing. As stimulus frequency increased, the initial drop in conduction velocity was greater, and conduction failure occurred more rapidly. Conduction failure always occurred between the stimulating and nearest recording electrodes. Occasionally, a skipped response occurred before total failure. In these instances, conduction velocity after the pause was always greater than or equal to that

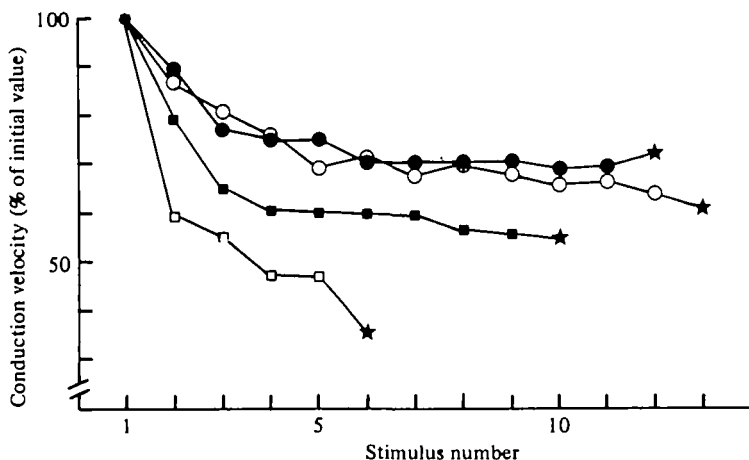


Fig. 3. Conduction velocity measurements in the colonial conduction system of *Muricea* indicating effects of stimulus frequency and stimulus number. ●, 1/2 s; ○, 1/15 s; ■, 1/s; □, 2/s. Stars denote the last impulse prior to total failure of the conduction system.

of the preceding impulse. The increased interpulse interval possibly favoured recovery of fatigued conducting units, resulting either in a more direct pathway for the next through-conducted impulse, or if the pathway is constant, decreased conduction time in the individual units, as might occur, for example, with restoration of impulse amplitude with repolarization.

For each stimulus, conduction velocity diminished with increasing distance from the stimulating electrode. On a few occasions, the two recording electrodes remained attached long enough to permit moving the stimulating electrode to three or four different locations. One such experiment is summarized in Table 1. In these experiments conduction velocity diminished equally with distance both basally and distally to the recording electrodes, indicating a lack of conductile polarization with respect to the colonial structure.

Immersion of the colony in a 1:1 solution of 0.37 M magnesium chloride and sea-water relaxed the polyps within 5 min while the through-conduction system continued to respond for up to 20 min. After 10 min, impulses began to decrease in amplitude and were lost in the noise. Complete recovery of polyps and through-conduction system required about 45 min in fresh sea water.

Table 1. *Variation in conduction velocity with changes in conduction distance in the colonial conduction system of Muricea.*

(Two recording electrodes remained in place while a stimulating electrode was moved to four locations. (+) indicates that the stimulating electrode was proximal to the recording electrodes, and (-) distal to the recording electrodes. S-R Distance = distance from the stimulating electrode to the nearest recording electrode.)

S-R Distance (cm)	Conduction velocity (initial* cm/s)	Conduction velocity (mean cm/s)
0.9 (+)	16.0	11.0
1.7 (-)	13.7	9.7
2.1 (+)	11.2	9.7
3.3 (-)	9.6	7.0

* First in stimulus series.

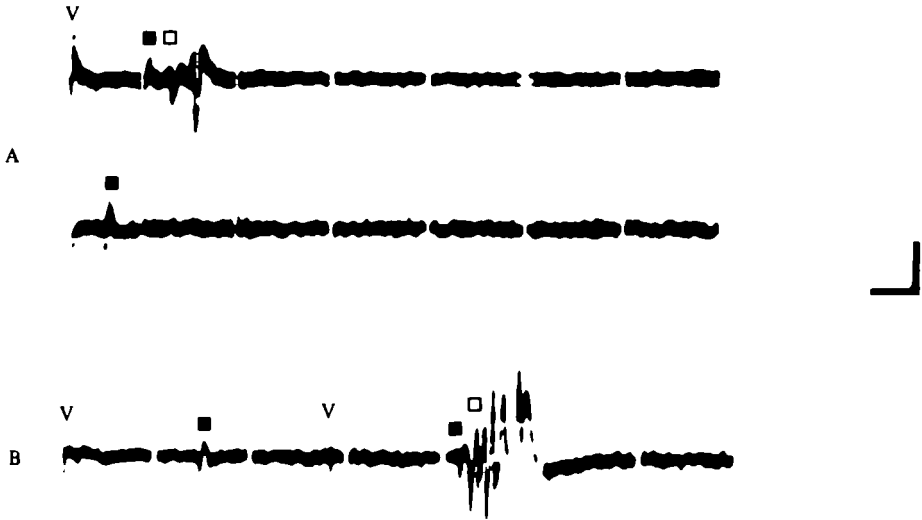


Figure 4. Electrical activity of the colonial conduction system of *Muricea* with resultant impulse bursts associated with activation of the polyp retractor system. ■, Impulse of the colonial conduction system; □, initial impulse of the polyp burst. (A) Recordings from the two polyps, the more distant of which (upper trace) responded with tentacle and column twitches. (B) Burst of electrical activity in the polyp retractor system resulting in total withdrawal. Note that a colonial impulse always precedes polyp activity. Ordinate $5 \mu\text{V}$, abscissa 200 ms (A) and 300 ms (B).

Polyp electrophysiology

During repetitive stimulation of the colonial conduction system, a second impulse, or burst of impulses, was frequently initiated. When the recording electrode was near the stimulating electrode, the secondary impulse activity could be correlated with behaviour of nearby polyps. Stimulation sufficient to initiate tentacle or polyp column twitches in neighbouring polyps elicited single or double secondary impulses in the recorded polyp (Fig. 4A). A burst of 4 to 10 facilitating impulses occurred in conjunction with stimulus-initiated polyp withdrawal (Fig. 4B). The retraction bursts were always preceded by a nerve net impulse indicating that the colonial nerve net triggers the withdrawal behaviour. Similar results have been found in *Renilla* (Anderson & Case, 1975), and some actinians, in which the polyp through-conduction system activates the withdrawal responses (Josephson, 1966; Pickens, 1969; McFarlane, 1969; Robson & Josephson, 1969). In *Muricea*, behavioural responses of polyps within the 5–10 mm reactive area surrounding the stimulus electrode were always accompanied by secondary electrical activity. Outside of this area, similar electrical activity was occasionally observed, but usually without movement in polyps surrounding the one being tested. Spontaneous secondary impulses were frequently recorded immediately following electrode attachment, and were presumably due to the mechanical stimulation of the polyps by the electrode.

The secondary impulses, or polyp retractor impulses, were not conducted between polyps, even within the reactive area surrounding the stimulus site. When the stimulus frequency was less than 0.25 s^{-1} , electrical activity from two polyps within 5 mm

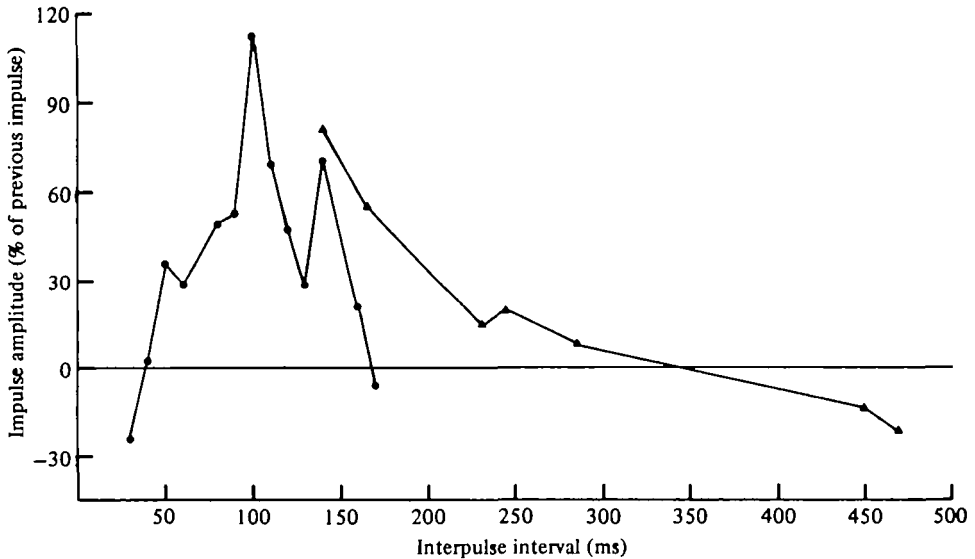


Fig. 5. The effect of interpulse interval on the size of impulses within a burst of electrical activity in the polyp retractor system (circles). At intervals less than 30 ms and greater than 170 ms, no following impulses were triggered. Each point represents the mean of from 5 to 13 measurements. Interpulse intervals were rounded to the nearest 10 ms. The initial burst of electrical activity in response to liver extract is also plotted (closed triangles). Note the long interpulse intervals in comparison with the polyp retractor bursts.

of the stimulation point was random and mutually independent, and required more than six stimuli for activation. The same effect was observed for distant polyps at all stimulus frequencies.

Polyp impulses, which most likely represent electrical activity in the tentacular and septal musculature (retractors), were variable in amplitude and duration. The single or double impulses associated with tentacular and column twitching were 5–10 μV in amplitude, and 40–80 ms in duration. In a retraction burst, the impulses facilitated to a maximum of 20 μV . If an additional stimulus was given during the burst, the response was prolonged and often facilitated to well over 30 μV . Impulse durations within a retraction burst were between 15 and 80 ms. These relatively long duration facilitating impulses probably represent electrical activity in the retractor muscles which presumably reflects activity in underlying neural elements.

Refractory and facilitative properties of the polyp conduction system are revealed by examination of the retraction bursts. In Fig. 5, changes in impulse amplitude are plotted against interpulse intervals. The resulting curve is bell-shaped with maximum facilitation occurring at interpulse intervals of 100 ms, and with limits of 30 and 170 ms, beyond which no succeeding impulses were triggered. The refractory period of the polyp retractor system can be interpreted as around 30 ms, and the maximum interpulse interval which will maintain facilitation is 170 ms. At interpulse intervals greater than 100 ms, the facilitation effect diminishes gradually, presumably describing the limits of the critical facilitation period of the retractor neuro-muscular junctions.

Application of liver extract to the tentacles of a *Muricea* polyp produced an initial



Fig. 6. Electrical response of a *Muricea* polyp to liver extract (see Fig. 1, E-H). Stimulus application is represented by the arrow; the four traces represent a continuous record. The polyp responded with an initial burst followed by apparent adaptation. Ordinate $10 \mu\text{V}$, abscissa 200 ms.

burst of impulses of similar amplitude and shape to those recorded during polyp retraction (Fig. 6), but with more restricted durations (40–60 ms) and longer interpulse intervals (Fig. 5). They were followed by isolated impulses at successively increasing intervals (Fig. 6). Sometimes the entire response lasted up to 30 s. Electrical responses, graded in impulse frequency and number, were sometimes recorded and presumably represent variation in tentacle flexion. The amount of liver extract applied, and the method of application used during the electrophysiological tests normally produced flexion of all 8 tentacles. The impulse pattern of the initial liver-induced bursts are plotted in Fig. 5. The interpulse intervals are long and incompatible with the demonstrated properties of the polyp retractor system. The decrease in frequency of firing following the initial burst recalls the apparent sensory adaptation observed in *Tealia* prefeeding responses (McFarlane, 1970; McFarlane & Lawn, 1972; Lawn, 1975).

Pathways which conduct feeding impulses probably do not involve activation of the colonial system since through-conducted impulses were not recorded during liver-induced responses, and since a series of impulses involving the colonial system would activate the polyp retractors. It is probable, however, that the tentacular conduction pathways activated by the liver extract are directly connected with the polyp retractor system since mechanical stimulation and excessive chemical stimulation to the tentacles can cause partial or complete polyp withdrawal. This possibility is strengthened by the observation that neurites cross the mesoglea from oral disc ectoderm to septal endoderm in *Muricea* (Satterlie & Case, 1978). The long interpulse intervals would therefore appear essential to feeding responses since impulses at higher frequencies could activate the polyp retractor muscles. On the basis of the incompatibility of the feeding (liver) response with properties of the polyp retractor system, the apparent impulse adaptation, and the behavioural correlates, these impulses are believed to represent electrical activity in the tentacle muscular systems resulting from chemoreceptive responses.

DISCUSSION

Except for one instance in which incremental spread of electrical activity has been established (Anderson, 1976*b*), the conducting systems of colonial anthozoans have been demonstrated to be through-conducting (Shelton, 1975*a, b, c*; Shelton & McFarlane, 1976; Anderson & Case, 1975; Anderson, 1976*a*; Satterlie *et al.* 1976). However, through-conducted signals do not necessarily produce through-conducted behavioural responses (Shelton, 1975*c*). This is particularly apparent in the present study on gorgonians. Useful information conveyed by a through-conduction system must be carried as frequently coded signals, to be interpreted by the polyp effectors. These effectors are, in addition, under the control of polyp conduction systems which can modify, and possibly, inhibit, colonial messages. The pattern of colonial behavioural responses, therefore, depends upon (1) the transmissive properties of the colonial conduction system, (2) the way the polyp conducts and reacts to this information, and (3) how the junctions between the two systems transfer the information (see Anderson, 1976*c*).

The activation of polyp musculature in gorgonians appears to conform to the ideas of Pantin (1935*a, b, c, d*) in that a facilitating series of impulses, within a critical time period are required to achieve polyp retraction. The burst of electrical activity associated with polyp retraction in *Muricea* consists of facilitating impulses which have a limited range of interpulse intervals (30–170 ms) representing this critical facilitation period. The tentacle musculature also requires a series of impulses for activation, although fewer impulses appear to be needed.

The area of interaction between the polyp and colonial conduction systems appears to be in the polyp oral disc region (Satterlie & Case, 1978). Recordings from the oral disc of *Muricea* polyps indicate that electrical activity in the polyp retractor system in response to electrical stimulation is always preceded by an impulse of the colonial conduction system. This is in agreement with data from *Renilla* (Anderson & Case, 1975) in which colonial nerve net impulses were conducted up the polyp column followed by polyp impulses conducted downward. In the majority of colonial anthozoans previously studied, this colony-polyp connection does not appear to play a major role in restricting the response pattern of the polyps. In *Tubipora*, for example, polyps respond to the second stimulus in a series with tentacle twitches, and to each successive stimulus with an increasingly intense behavioural response (Horridge, 1957; Anderson, 1976). In this respect, the polyps react as if there is a direct connexion between colonial conduction system and the polyp effectors. This is similar to the through-conduction system described in anemones by Pantin (1935*a*), and electrophysiologically demonstrated by several authors (Josephson, 1966; Robson & Josephson, 1969; McFarlane, 1969; Pickens, 1969). The oral disc connexion of gorgonian polyps does not appear to provide a direct route for colonial impulses. Similar results were found in *Renilla*; however, responses from different polyps varied considerably (Anderson & Case, 1975). In *Muricea*, from four to six colonial impulses are normally required to activate the polyp conduction system, which then responds with a burst of electrical activity.

The nature of the colony-polyp junction is unknown, but may include one or both of the following possibilities. There may be interneural facilitation within the

pathways which connect the two systems. Alternatively, there may be a special group of cells (neural, muscular, or epithelial) which act as a gateway to the polyp system. Either way, the colony-polyp junction is a major factor in the colonial inexcitability of gorgonians.

The activation of the polyp system is largely dependent on the frequency of arriving impulses. This, in turn, is dependent upon conduction velocity changes in the colonial nerve net associated with stimulus number and frequency as well as conduction distance. Changes of this nature represent the sources of behavioural variability in the model of colonial coordination mechanisms proposed by Shelton (1975*c*). Conduction velocity changes in the nerve net of *Muricea* following repetitive stimulation play as important a role in colonial inexcitability as the colony-polyp connexion.

The properties of the colonial conduction systems of *Muricea* and *Lophogorgia* lend support to Shelton's ideas, although the need for additional variables is evident. Three concepts must be considered.

(1) As previously discussed, the colony-polyp connexion can influence colonial behavioural response patterns.

(2) Direct (Josephson, 1961; Morin & Cooke, 1971; Anderson, 1976*b*) and indirect (Pantin, 1935*a, b*; Bullock, 1943; Nicol, 1955*a*) physiological evidence supports the involvement of interneural facilitation in colonial control mechanisms. As in the original models of Horridge (1957) and Josephson *et al.* (1961), nerve nets should be considered as a mixed population of transmissive and non-transmissive (facilitation-requiring) junctions. Since only small changes in the ratio of the two were necessary to change computer-constructed nerve nets from incrementally-conducting to through-conducting (Josephson *et al.* 1961), different ratios, even among through-conducting nerve nets, must be considered as a potential source of behavioural variability.

(3) Variations in the density of junctions between conducting units can alter the properties of the conduction systems and thus alter behavioural responses.

Colonial nerve nets are present in gorgonians and consist of a sparse mesh of randomly oriented neurones (Titschack, 1970*a*; Satterlie & Case, 1978). These observations are consistent with the physiological interruption of nerve net transmission in *Muricea* due to high magnesium concentrations, a test generally accepted as demonstrating neural pathways in coelenterates. As an opposite extreme in the degree of colonial excitability, the pennatulids possess extremely well-developed nerve nets (Titschack, 1968, 1970*b*; Pavans de Ceccatty & Buisson, 1964; Buisson & Franc, 1969; Buisson, 1970; Satterlie *et al.* 1976). The relative inexcitability of *Alcyonium* (Horridge, 1956; Shelton, 1975*b*) was similarly attributed to a low density nerve net by Titschack (1970*a*). Kawaguti (1964) noted that the nerve plexus of the gorgonian *Euplexaura* was much less complex than that of more reactive actinians and scleroactinians. The effect of conducting unit density on colonial conduction, based on these findings, is presented diagrammatically in Fig. 7. For each hypothetical conducting unit density, two curves are presented representing different ratios of transmissive to non-transmissive junctions. Other ratios and thus other curves should not be excluded, and are necessary to explain many of the response variations. If we assume that five stimuli are required to produce polyp withdrawal at a fixed distance from the stimulating electrode, the effect of conducting unit density on the frequency of impulse arrival at this distance is apparent.

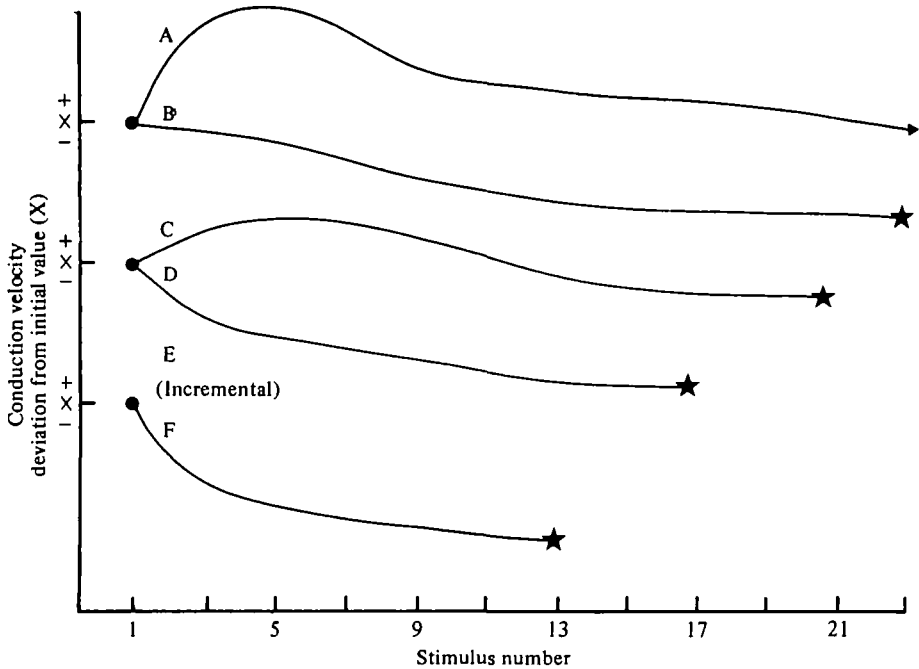


Fig. 7. Hypothetical curves illustrating the effect of conducting unit density on the conduction velocity in colonial conduction systems of a variety of anthozoans. For each density, two curves are plotted representing (1) conduction systems with a relatively high ratio of transmissive to non-transmissive junctions (lower curves), and (2) conduction systems with relatively high ratios of non-transmissive to transmissive junctions (upper curves). The curves are based, in part, on experimental evidence (see text). The stars indicate the last impulses prior to total failure of the systems.

Curve A represents the conduction velocity changes observed for pennatulids (Shelton, 1975*b*; Satterlie *et al.* 1976), and the septal retractors of *Calamactis* (Pickens, 1969, 1974). There is an initial rise in conduction velocity, possibly representing the formation of more direct pathways due to either synaptic or interneural facilitation, a later decrease in conduction velocity, or lengthening of the pathway, and eventually an equilibrium between fatigued and active units. Pickens (1974) found the initial rise in conduction velocity in *Calamactis retractors* served to increase synchronization of muscle fibres several centimetres apart. This observation could help explain the great degree of colonial control maintained by the pennatulid through-conduction systems. The vigour of the pennatulid conduction systems, the ability to respond to more than 50 stimuli without failure, can be attributed to the large number of available pathways. Another likely property of such high density conduction systems is after-discharge or frenzy (Parker, 1920; Nicol, 1955*b*; Buck, 1973) due to the high probability of reverberating circuit formation during sustained activity.

A decrease in conducting unit density results in more rapidly fatiguing systems. A series of curves representing a transition similar to that between curves A and C (Fig. 7) was produced by progressively narrowing a bridge of tissue in the rachis of the pennatulids *Stylatula* and *Virgularia* (R. A. Satterlie, P. A. V. Anderson & J. F. Case, in preparation). Initial results indicate that a point is reached where this bridge is 'incrementally conducting' as in curve E.

The conduction patterns of *Tubipora* (Anderson, 1976), *Isophyllia* and *Dichocoenia* (Shelton, 1975c) can possibly be compared with curve D, Fig. 7 although morphological evidence is lacking. A conduction system of this nature would still be able to control large areas of a colony. It is at low conducting unit densities that the effect of repetitive stimulation restrict the reactive area of colonial control. In a low density conduction system, there are few available pathways, consequently fatigue might build up rapidly. The gorgonians, and possibly *Porites* (Shelton, 1975c), reflect this type of conduction system (curve F, Fig. 7). The rapid fall of conduction velocity and the rapid onset of fatigue limits the area in which polyps receive impulses at a frequency adequate to activate the retractor musculature. Also, indirect routes could create a noticeable decrease in conduction velocity with distance, as found in *Muricea*. In this type of conduction system, with presumably few facilitation-requiring junctions, a wide range of conduction velocities is possible.

The ratio of transmissive to non-transmissive junctions becomes critical as the number of junctions decrease, and as a result, incremental spread of electrical activity, as observed in *Goniopora* (Anderson, 1976b) becomes more probable. Under these circumstances, a high proportion of facilitation-requiring junctions could produce a conduction system in which the number of stimuli determines the degree of activity spread. Much of the evidence for interneural facilitation comes from preparations in which the conducting unit density was reduced by variations in ionic concentrations (Bullock, 1943), and by cutting experiments (Nicol, 1955a; R. A. Satterlie, P. A. V. Anderson and J. F. Case, in preparation). It is equally conceivable that conduction systems exist which are at times through-conducting, and at times incrementally-conducting, depending upon the amount of previous activity.

Colonial behavioural patterns in anthozoans are dependent upon properties of the colonial conduction systems, the polyp conduction systems, and the interactions between the two. Other factors, as yet uncovered, are probably also involved. For instance, many colonial anthozoans possess through-conducting 'slow' systems (Shelton, 1975b; Shelton & McFarlane, 1976; Anderson & Case, 1975; Satterlie *et al.* 1976), the functions of which are unknown. Similarly, polyps may possess multiple conduction systems similar to those in anemones (McFarlane, 1969), which could alter incoming colonial impulses.

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