PRIMITIVE NERVOUS SYSTEMS:
ELECTROPHYSIOLOGY OF THE PHARYNX OF THE POLYCLAD FLATWORM, ENCHIRIDIDUM PUNCTATUM

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SUMMARY

1. Electrical activity accompanying motor activity can be recorded from the excised pharynx of Enchiridium punctatum. Multiple stimuli elicit behaviour which consists of an initial aperture closure followed by extension and then peristalsis. If the stimulus parameters are increased the preparation bends from side to side instead of proceeding through the behavioural sequence. Bending appears to inhibit other movements differentially.

2. The conduction involved with peristalsis is polarized and proceeds in a proximal direction.

3. With stimulus intensities greater than those needed to produce the behavioural response an initial muscle potential (IMP) is evoked. The IMP is frequency sensitive. Maximum facilitation occurs within 100 ms and drops to 50% of maximum within 250 ms.

4. Conduction velocities of the IMP range from 0.05 m s$^{-1}$ to 1.9 m s$^{-1}$. Conduction velocities appear to increase with facilitation.

INTRODUCTION

Flatworms are able to carry out a number of behaviour patterns in the absence of the brain. These activities range from egg-laying (Gruber & Ewer, 1962) to feeding (Koopowitz, 1970; Koopowitz, Silver & Rose, 1975, 1976). The behaviour of decerebrate flatworms appears to be composed of fragments of a larger series of activities which are normally coordinated by the brain. Yet each of these fragments must involve coordinated activity from a number of different muscle sheets, which suggests that peripheral machinery for coordinating motor neurones must exist within the peripheral plexus. The peripheral plexus lies adjacent to and within the muscle layers (Koopowitz & Chien, 1974) and it is difficult to dissect out and study its interactions directly.

Wulzen (1917) described a variety of movements performed by the isolated pharynx of a freshwater planarian. The isolated pharynx of a polyclad flatworm Enchiridium punctatum is also able to perform a number of similar activities, and we have attempted to use it as a model system for studying the peripheral machinery underlying behaviour in this group of animals. The pharynx of Enchiridium is a tube about 10–15 mm long and 2 mm wide in the relaxed state. It is a complex
structure with five muscle layers and at least one nerve net (Koopowitz, unpublished observations). As such it presents many of the problems encountered by workers on the neuromuscular physiology of the coelenterates which are also tubular animals with a diffuse nervous system. The flatworm pharynx is also interesting from another aspect. Not only is this one of the first discrete muscular organs to have evolved but it also represents the most primitive gut musculature available for investigation. The isolated pharynx of *Enchiridium* undergoes a series of coordinated activities if it is electrically stimulated in the proper fashion. This paper reports on an investigation of the behavioural repertoire of this organ and some of the control mechanisms regulating its movements.

**METHODS**

**Animals**

*Enchiridium punctatum* is a large (up to 8 cm long) cotylean polyclad flatworm found beneath rocks in the Southern Californian intertidal zone. Animals can be maintained in the laboratory for a number of weeks. The pharynx was extracted after first placing the worm on its dorsal side on a dry paper towel. By depressing the tissue at the base of the pharynx, the pharynx was everted. With vigorous eversion the pharynx usually autotomized, at its base. The isolated pharynx was then returned to sea water. It was possible to keep the donor animal until it had regenerated a new pharynx.

**Mechanical recordings**

Mechanical recordings were made of either entire pharynges or segments of the tube. Two strands of human hair were threaded through the lumen of the preparation and tied into loops. One loop was passed over a glass hook and the other connected to an isometric force transducer (Statham gold-cell). Following amplification the output of the transducer was displayed on a chart recorder (either a Bausch & Lamb, VOM 6 or a Brush 220). The output of the transducer was linear with respect to the force exerted upon it.

Decreases in pharynx diameter (presumably due mainly to shortening of circular muscles) is displayed as upward deflexions in the figures. One could adjust the amount that the pharynx could be stretched by moving the force transducer along a ratchet.

**Electrical recording**

Electrical records were made using conventional polyethylene suction electrodes (tip diam. = 200 µm). Electrodes were connected to a 3A9 vertical differential amplifier (DC, 3 kHz) of a Tektronix 565 CRO. The output of this amplifier could be stored on an SP 300 Ampex FM tape deck. Permanent records were made on a Brush 220 two-channel chart recorder. In order to minimize high frequency amplitude attenuation the tape records were made at 7.5 IPS but transferred to the chart records at 1.3 IPS (attenuation ± 10% at 1 kHz).
Stimulation

Square wave constant current electrical stimuli were generated by a Grass S48 physiological stimulator connected to a Grass photoelectric stimulus isolation unit (current range 50–150 μA), and applied with a polyethylene suction electrode.

Unless otherwise stated all results have been obtained at least three times. Where electrical stimulation was used the preparation was allowed to rest at least 2.5 minutes between stimulus presentations.

RESULTS

Isometric recordings

When an entire isolated pharynx is suspended under moderate tension recurrent peristaltic waves can be observed. The contraction originates at the distal end of the pharynx and is propagated towards the proximal end. The frequency and pattern of contractions is quite variable from preparation to preparation. These waves may occur with a steady rhythm or they may be arhythmic. Occasionally one finds preparations where activity occurs in bursts with long pauses lasting up to 30 min between bursts. Although isometric recordings of the contractions from the active pharynx often appear as smooth increases in tone they may, in fact, be composed of several series of contractions which usually do not have a constant phase relationship (Fig. 1a).

Attempts were made to localize the pacemaker sites which initiate the peristaltic waves. A rhythmically active pharynx was cut into three equal lengths and activity recorded from each section (Fig. 1b–d). The contractions measured from the proximal portion (Fig. 1b) tend to be irregular but the multiple nature of the contractions can still be discerned. The middle part of the pharynx (Fig. 1c) produces contractions which appear rather like those of the intact preparation. No significant activity could be recorded from the distal third (Fig. 1d), although this is where it originates in the intact, isolated pharynx. It is likely, therefore, that the pacemakers are situated in the middle portion but initiate activity at the distal tip.

The response to stretch is an increase in the amount of tension generated during the contractions (Fig. 1c). Comparable results were obtained from the intact preparation. A consistent relationship between stretch and contraction frequency could not be found.

Electrical recordings

The following series of experiments utilized extracellular suction electrodes. Unless otherwise stated the stimulating electrode was placed at the proximal end of the pharynx and the recording electrode in line midway along the pharynx. The initial response to electrical stimulation is closure of the aperture followed by extension of the pharynx (Fig. 2). Closure lasts approximately 500 ms and involves an inward bending of the distal margin. It is not simply due to a decrease in diameter of the opening.

Elongation, which generally follows mouth closure, also involves straightening of the pharynx. Some seconds later a peristaltic wave is initiated at the distal end of
Fig. 1. Isometric recordings of muscular activity from portions of the isolated pharynx in response to moderate stretch: (a) recordings from an intact pharynx; (b) recordings from the proximal third of the pharynx; (c) recordings from the central third, arrow indicates where increased stretch was applied to the central portion; (d) recordings from the distal third of the pharynx. Upward deflexions represent increases in tension and were accompanied by the movement of a peristaltic wave in a proximal direction along the length of the preparation.

the pharynx and proceeds proximally. The electrical correlates of this behaviour (Figs. 2 and 3) appear to be as follows. Mouth closure (a) occurs some 800 ms following the initial stimulus and is usually accompanied by a biphasic, compound potential which may last 100 ms. This, in turn, may be followed by a quiescent period of variable length (up to 20 s) before elongation (b) occurs. However, elongation may be preceded and followed by considerable phasic activity, much of which is difficult to correlate with the behaviour. In Fig. 2 the elongation occurs in the midst of a 10 s burst of activity. The peristaltic wave (c) may be initiated up to 45 s after the electrical stimulus, but in most cases it appears approximately 15 s after stimulation. During this latent period, background electrical activity is reduced to small spikes which we suspect are neuronal in origin. The peristaltic wave, which appears to be a smooth isometric contraction from the mechanical records (Fig. 1),
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Fig. 2. Electrical activity associated with the behavioural sequence. Response is to 14 stimuli; each 20 V, 1 ms duration. (a) Closure of the distal aperture; (b) pharyngeal elongation; (c) peristalsis.

Fig. 3. Electrical activity and behaviour associated with paired stimulus trains. Initial train: eight stimuli presented, 10 s⁻¹, each stimulus 1 ms in duration. Second train identical except that 15 stimuli are presented. Stimulus intensity is 20 V for both trains. (a) Closure of the distal aperture. (b) Elongation. (c) This biphasic potential accompanies the initial peristaltic wave. Peristalsis is blocked by the second stimulus train which evokes vigorous bending and thrashing movements.

is actually made up of a number of oscillations. We do not know whether these represent a series of discrete contractions involving the same muscle field or the ordered activity in different muscle groups. The length of time between elongation and peristalsis varies from preparation to preparation. In a few we were unable to elicit peristalsis. None of the three components appear to be prerequisites for the others and under certain conditions (see below) each has been observed separately.

To elicit the behavioural sequence, multiple stimuli must be applied to the proximal end of the pharynx. Stimuli applied to the distal margin merely produce small local contractions. These results suggest that conduction must be polarized and proceeds in the distal direction. Histological examination of the proximal end of the pharynx where the stimulating electrode is attached revealed numerous axons. There is no assurance that these are, in fact, the axons which elicit the behavioural sequence but they could be efferent pathways from the central nervous system.

A distinctly different kind of behaviour can also be elicited. This involves bending and thrashing from side to side. If an increase is made in stimulus frequency, intensity or number, the pharynx does not proceed through the behavioural sequence but instead bends from side to side. The electrical activity accompanying bending
Fig. 4. Changes in electrical activity associated with interstimulus interval. Both trains of stimuli consist of 33 stimuli presented at 20 s⁻¹. Each stimulus has a duration of 1 ms and an intensity of 30 V. Behaviour accompanying the first stimulus train is bending. The second train evokes (a) closure of the distal aperture which is followed by (b) elongation. Note that each stimulus train by itself would normally elicit bending.

(Fig. 4) consists of slow potential waves. There may be only one or two bends but in a few preparations long lasting threshing occurred. The most spectacular example is shown in Fig. 3 where a preparation was stimulated during the peristaltic wave. The second burst of stimuli inhibited the peristaltic wave and induced vigorous side-to-side bending which lasted for more than 10 s. This prolonged flexing was only found in two animals; usually only two or three flexions are elicited. Another burst of stimuli delivered after bending will not initiate further activity for several seconds. This observation suggests that some kind of inhibition might exist.

In the following experiment the preparation was subjected to two identical trains of stimuli with a variable time interval between the trains. Each train consisted of 30 stimuli at a frequency of 20 s⁻¹. The stimulus intensity was 30 V, each shock lasting 1 ms. The response to the initial train at this intensity was sufficient to induce a number of mild flexions (Fig. 4). The response to the second train of stimuli is related to the time interval between trains. There is no response to the second train with an ITI (intertrain interval) less than 2 s. At ITIs between 2 and 18 s aperture closure tends to be followed by pharyngeal extension (Fig. 4). At intervals greater than 18 s the response to the second train was the same as the response to the first train. In a few preparations we observed flexing behaviour at shorter intervals but this was rare and unpredictable.

These results can be interpreted in either of two ways. Bending could induce inhibitory feedback or the stimuli might directly activate inhibitory neurones. There
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Fig. 5. Effects of stimulus frequency on absolute threshold of the behavioural sequence. Open symbols refer to stimulus regimes which did not elicit behaviour; closed symbols refer to stimuli which did evoke the behaviour. Stars are values where the stimulus frequency was 20 s\(^{-1}\) and circles are values obtained with 10 stimuli s\(^{-1}\). The shaded areas imply the thresholds for evoking behaviour at the two frequencies of stimulation. All data were obtained from a single preparation.

is some evidence which suggests that inhibition of mouth closure and extension is primarily due to the stimulus itself. In one preparation, when the train of stimuli was delivered at a frequency of 10 s\(^{-1}\) rather than 20 s\(^{-1}\), we recorded an initial bending which was followed by extension and mouth closure. It seems unlikely, therefore, that bending might reflexly inhibit the behavioural sequence. It is probable that the higher frequencies of stimulation used in these experiments directly evoked activity in the inhibitory neurones. A similar frequency-sensitive inhibitory system has already been described in the flatworm Planocera gilchristi (Koopowitz & Ewer, 1970). High
threshold frequency-sensitive inhibition can be demonstrated in the pharynx of Enchiridium. We investigated the number of stimuli required to elicit the behavioural sequence of mouth closure–extension–peristalsis at varying stimulus intensities and at frequencies of either 10 or 20 stimuli s⁻¹. The results (Fig. 5) clearly demonstrate that a greater minimum stimulus intensity is needed to elicit the behaviour pattern at the higher frequency. At 120 stimuli s⁻¹ one needed a minimum of 20 stimuli at the threshold voltage of about 27.5 V. On the other hand at 10 s⁻¹ one could elicit the behaviour with 22.5 V and 10 stimuli. Similarly, the minimum number of stimuli which could elicit the behavioural sequence was 5 at the lower and 8 at the higher frequency. In these experiments we also looked at the stimulus intensity-number relationship at 30 stimuli s⁻¹ and obtained essentially the same kinetics as at 20 s⁻¹. It seems unlikely that the threshold discrepancies are merely due to refractoriness in the system because at 22 V, 10 stimuli at 10 s⁻¹ are sufficient to elicit the response, while at this voltage even 30 shocks at 20 s⁻¹ would not evoke the behaviour. At all stimulus regimes above threshold both closure and extension were obtained. In most cases peristalsis was also evoked, but at unpredictable times it failed to appear.

**Initial muscle potential (IMP)**

Close analysis of the electrical events initiated during a train of above-threshold stimuli revealed a small, positive, potential which is graded, of a relatively smooth character (Fig. 6a), and slow time course characteristic of a muscle potential. The potential, however, is not due to direct stimulation of the muscle cells, as the event may be blocked by increasing ambient Mg²⁺ concentration (Fig. 6b). It seems likely, therefore, that at least one synapse and/or one neuromuscular junction is present between the stimulation site and the position of the recording electrode. The threshold necessary to evoke this initial muscle potential (IMP) appears to be higher than that needed to produce the behavioural responses discussed earlier. In a few preparations it was possible to find a small spike (Fig. 6b, c) associated with each stimulus which persisted following application of Mg²⁺.

The amplitude of the IMP appears to depend upon a number of factors. If a preparation is subjected to a train of stimuli (each of 50 V and 1.0 ms duration) at a frequency of 10 s⁻¹ (Fig. 7), the responses to individual stimuli can be seen to increase in amplitude. Following this there is usually a period during which no response can be elicited. In the following experiments the preparation was subjected to a train of 12 stimuli at either of three frequencies: 10, 20 or 30 s⁻¹. Stimulus intensities varied between 20 and 50 V for a particular train. Three minutes were allowed between stimulus trains. Frequencies and intensities of any particular train to be delivered were chosen at random. It was thus possible to examine the effects of both stimulus frequency and intensity on a number of different aspects of the response. In Fig. 8 (a) the effects of amplitude versus stimulus intensity are shown for the three frequencies. The maximum amplitude achieved always appears to be less at the 10 s⁻¹ frequency than for 20 or 30 s⁻¹, but there is apparently no significant relationship between amplitude and stimulus frequency for these higher stimulus repetition rates. Despite this the amplitude of the transient shows a very clear
relationship to stimulus intensity. The increased amplitudes measured at frequencies higher than 10 s⁻¹ are partially due to summation of the response.

It is possible to evoke the IMP with single shocks of sufficient stimulus intensity. The threshold for an IMP response to a single stimulus is considerably greater than that necessary to evoke behavioural responses. At intensities which also evoke behaviour, a number of stimuli must be applied before the IMP can be elicited. The minimum number of stimuli needed to produce an IMP response of maximum amplitude appears to be dependent on the intensity of the stimulus (Fig. 8b). In Fig. 8(b) the maximum response at 20 shocks s⁻¹ is obtained with eight stimuli, while at 50 V only two are needed. There is no clear relationship between stimulus frequency and stimulus number needed to obtain this maximum response, but
Fig. 7. Electrical recording showing graded nature of the IMP. All four stimuli are identical and presented at a frequency of 10 s⁻¹. Each is 50 V, 1 ms in duration.

Fig. 8. Effects of stimulus frequency on characteristics of maximum IMP in a series. (a) Changes in response amplitude at varying stimulus intensities. (b) Number of stimuli needed to produce maximum IMP in a series at varying stimulus intensities. In both graphs closed circles are data obtained with 10 stimuli s⁻¹; closed triangles, 20 stimuli s⁻¹; and open circles 30 stimuli s⁻¹.

Frequency is important in eliciting a response at certain stimulus intensities. At frequencies of 10 s⁻¹ the preparation will not respond to stimulus intensities below 35 V; however, at higher frequencies responses could be evoked at lower stimulus intensities. A sizeable response could be measured at 25 V with a frequency of 20 or 30 shocks s⁻¹.

The extent of frequency sensitivity was studied in another experiment where the amplitude of IMP was recorded following presentation of paired stimuli. Inter-stimulus intervals varied between 0·001 s and 1·0 s. Stimuli were slightly above threshold for a single shock. In the experiment reported (Fig. 9) the response amplitude to the initial stimulus varied between 30 and 70 µV. A clear facilitatory effect can be seen in the response to the second stimulus of the pair. Facilitation has its maximum effect within 100 ms of the first stimulus and then declines gradually.
Facilitation itself is potent and the response to the second stimulus can be ten times the amplitude of the first. The peak period of facilitation, however, is short-lasting and facilitation drops to 50% of its efficiency within 250 ms. There is little variation in the kinetics of facilitation, measured this way, from preparation to preparation. The reason why differences in response amplitudes (Fig. 8a) for 20 and 30 stimuli s$^{-1}$ appear to be slight is understandable in light of Fig. 9. Both of the above frequencies occur in portions of the facilitation curve which are not significantly different. We were interested to see if facilitation also affected conduction velocity. Three electrodes were used. The stimulating electrode was placed at the proximal end and two recording electrodes were placed in line with the stimulating electrode. The recording electrodes were positioned in the middle and near the distal end of the pharynx. Pairs of stimuli at varying interstimulus intervals were applied. Stimulus intensity was below threshold for a single stimulus. Conduction velocities were derived by dividing the distance between the two electrodes by the time difference for generation of the IMP at the two electrodes. The values presented in Fig. 10 are data from our different preparations. Data from a single representative preparation is also histogrammed in this figure. At first glance the conduction velocities measured appear to be quite variable. One might have expected that conduction facilitation would have occurred at interstimulus intervals between 0.008 s and 0.04 s. Data obtained from pairs of stimuli with interstimulus intervals falling in this range (Fig. 10a) suggests a bimodal distribution with approximately 40-32% faster than
When interstimulus intervals smaller or greater than the presumed facilitated range were tested only 19.04% were faster than 0.6 m s⁻¹ (Fig. 10b).

In one preparation the effect of changing stimulus intensity during peak facilitation was examined in detail. Paired stimuli 0.0125 s apart were presented. Intensities of both shocks were varied together. The most obvious effect of changing stimulus intensity was a change in response amplitude of the IMP to the second shock (Fig. 11a). As intensity increased so did the response amplitude. Accompanying the increase in response amplitude was a decrease in latency, measured as the time period between presentation of the first stimulus and the initiation of the IMP (Fig. 11c). A rather surprising feature was the fact that the time from stimulus presentation to peak amplitude of the IMP did not vary significantly with changing stimulus intensity (Fig. 11b). With increasing stimulus intensity, however, the
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Fig. 11. Changes in IMP characteristics with varying stimulus intensity: (a) ordinate; response amplitude in μV. (b) ordinate; time to peak amplitude in ms. (c) ordinate; latent period measured from stimulus onset to beginning of response. (d) ordinate; response rise-time measured from the beginning of the response to the maximum response amplitude.

rise-time of the IMP also increases (Fig. 11d). Reciprocity between latency and rise-time probably accounts for the constancy in time to peak amplitude. One might have expected that rise-time would also have decreased with increasing stimulus intensity, but if the IMP represents a multi-unit response then the changes in rise-time may merely represent recruitment of additional units. Faster pathways would be revealed by decreases in latency, while slower pathways would create a longer time to peak amplitude.

**DISCUSSION**

Besides those activities described, the isolated *Enchiridium* pharynx is able to perform a number of other kinds of movements. It has not been possible to elicit these reliably and the stimulus parameters are still unknown. Of these movements the most conspicuous is aperture gaping. This consists of a drastic shortening in length, accompanied by an increase in aperture diameter so that the entire organ assumes a conical shape. Gaping can sometimes be elicited in freshly-excised pharynges by mechanical stimuli applied to the distal rim. In the intact animal, gaping appears before swallowing and is generally followed by peristalsis. Peristalsis, however, never occurs directly after gaping in the isolated preparation. Electrical stimulation applied to the distal rim, or anywhere else on the pharynx, was ineffective in evoking gaping.

In the absence of stimuli, electrical or stretch, the isolated *Enchiridium* pharynx
appears to be inactive. In contrast the isolated planarian pharynx is active and appears to ‘crawl’ across the bottom of the container (Wulzen, 1917). Despite the stimulus requirement of *Enchridium* it is probably unlikely that the activities recorded are simple reflexes. The sequence of aperture closure, extension and peristalsis involves considerable time periods between individual phases of activity which last up to 45 s. There are a number of ways by which one might account for the long durations, but the lags suggest that activity is not merely a chain of reflexes. The simplest explanation for the long periods would be that the system is not silent but the recording electrodes are unable to differentiate neuronal spikes in the noise. Another explanation involves the presence of non-spiking interneurones. For obvious reasons we are unable to investigate this possibility in this preparation at present. Sea-anemone behaviour has received considerable attention in recent years and McFarlane (1973, 1975) has elegantly demonstrated the existence of a number of conducting systems in these animals. Some anemone activities also occur in the absence of recordable electrical potentials and long pauses between bursts of activity are also found (McFarlane, 1975; McFarlane & Lawn, 1972). The longest time period is between extension and peristalsis. Peristalsis can be initiated by stretch and the extent of the contraction is related to the tension placed on the preparation. Those parts of the pharynx which are most sensitive to stretch do not coincide with the site of origin of the peristaltic wave. This suggests that the contraction wave is not a mechanically induced event when this behaviour is elicited following electrical stimulation. Another point which argues against mechanical coupling is that with threshold numbers of stimuli, one can elicit both aperture closure and extension without peristalsis. Increasing the number of shocks in the train evokes peristalsis after closure and extension. In this case the two first parts of the pattern appear to be as vigorous as they are with stimulus trains which do not evoke peristaltic waves. It appears that peristalsis is dependent on the number of stimuli.

Conduction of the peristaltic wave is polarized and only occurs in a distal-to-proximal direction. At present there is no evidence for electrical coupling between adjacent muscle cells. Gap or tight junctions do not occur between muscle cells. Gap or tight junctions do not occur between circular pharyngeal muscle cells in this animal (Koopowitz, unpublished observations), neither is there any physiological evidence for such coupling. Electrical stimuli applied to the distal end cause a localized contraction in the vicinity of the electrode but there is no spread. Perhaps the best evidence that non-muscular cells are involved in propagating the wave comes from observations involving inhibition of peristalsis. When a wave is inhibited by electrical stimulation it will re-emerge following cessation of the stimulus, but always at some distance from the point where the wave had stopped. It appears that excitation may be conducted in the absence of the contraction wave. Inhibition may work directly on the muscle cells. Similar myentric plexus conduction and control of peristalsis has been suggested for the small intestine (Kottegoda, 1969). Peristalsis can also be inhibited following bending movements, but it is not clear if this involves the same or different pathways.

There are a number of parallels between the *Enchridium* pharynx and anthozoan neuromuscular systems. Essentially both are cylinders with sheets of muscles and naked nerve nets. The anatomical organization of *Enchridium* pharyngeal nerves
Electrophysiology of a flatworm pharynx shows a naked nerve net lying close to the outer circular muscles and a more centrally positioned system of longitudinally running fibres (unpublished observations from both light microscopy and ultrastructural investigations). The longitudinal nerve fibres leave the pharynx and run into the somatic plexus. Possible connexions between the net and the longitudinal fibres have not been investigated. Anthozoan nerve nets are diffusely conducting and facilitatory (Hall & Pantin, 1937) although polarized conduction and through conducting pathways have also been reported (Pantin, 1935; Pickens, 1969). Multiple stimuli are needed to elicit behavioural sequences in the Enchiridium preparation, although the IMP can be evoked by a single short duration electrical stimulus. Even in the latter case, it is possible to produce an IMP with multiple subthreshold stimuli. The facilitatory nature of this preparation is much clearer than the neuromuscular system of Planocera (Gruber & Ewer, 1962), another polyclad. The time course for facilitation of the IMP is similar to that of Gyrocotyle (a cestodarian flatworm) neuromuscular preparations (Koopowitz, 1973). Maximum facilitation occurs at interstimulus intervals of approximately 10 ms and decays rapidly. In coelenterates maximum facilitation ranges from 15 to 30 ms on anthozoans (Josephson, 1966; Pickens, 1969) to about 2 s in scyphozoans (Bullock, 1943). In anthozoans interstimulus intervals less than those values result in an abrupt decrease in response amplitude whereas Enchiridium features a gradual decrease. Presumably the flatworm has a shorter refractory period. The conduction velocities measured in Enchiridium pharynx are considerably faster than those recorded from the coelenterate preparations and resemble velocities measured directly from the plexus nerves of Notoplana acticola (Koopowitz & Bernardo, in preparation). Pickens (1974) described increases in conduction velocity following multiple stimulation in a sea anemone. Similar results have also been obtained from the flatworm pharynx. That the changes in conduction velocity might reflect increased synaptic efficacy in the net or some other process is conjectural, but it is interesting that similar effects occur in both phyla. Whether or not the similarities between the anthozoans and flatworms reflect convergence due to similar morphological organizations or a deeper phylogenetic relationship still remain to be elucidated.

REFERENCES


