

THE CO-ORDINATION OF THE RESPONSES
OF *CERIANTHUS* (COELENTERATA)

BY G. A. HORRIDGE

Gatty Marine Laboratory, St Andrews University, Scotland

(Received 30 October 1957)

Cerianthus membranaceus, as commonly available at Naples, is a brownish polyp which can extend to 15–20 cm. and contract to 5–7 cm. The numerous tentacles are less contractile, being usually 3–5 cm. long. The gross anatomical structure is well described by Hyman (1940). The polyp normally lives in a soft tube, which it secretes, and has no foot or sphincter muscle. Lacking the diversity of muscle groups of a typical sea anemone its movements are very restricted. In contrast to other coelenterate polyps the Ceriantharia have a substantial ectodermal musculature of the column, which is responsible for the vigorous withdrawal of the animal into its tube. There are also ectodermal radial fibres on the disk. Endodermal muscles are relatively insignificant and play no part in the responses considered here. In common with all other coelenterate polyps *Cerianthus* has two kinds of rapid response to external changes: the feeding movements and the protective retraction. In *Cerianthus* the two are aroused by different stimuli, and in part they are effected by different muscles. The present study is an analysis of some of the physiological properties of the pathways which co-ordinate these responses.

The histology of the nervous system of *Cerianthus* is a controversial topic and, apart from sensory cells, structures with the appearance and staining properties of neurones have not so far been described with certainty. But this is not for lack of a search. A number of histologists have studied *Cerianthus* during the course of the last century, and have used most of the currently available techniques for the selective staining of nerve cells. This work has been recently summarized by Torelli (1938, 1952), who has added her own observations. She comes to the conclusion that the only identifiable nerve elements are sensory cells with branched fibres connecting directly with the ectodermal muscles. This arrangement is exceptional among coelenterates, and moreover there is no indication of how it could co-ordinate the observed movements. On the other hand, the results to be described suggest that a through-conducting network of large axons is present. However, the results of stimulation cannot as yet be correlated with a histological nerve net such as is usually presumed to account for at least some of the responses of coelenterates. Even ganglion cells, or their nuclei, have not been found with certainty. Therefore in the present study, which is solely physiological, we cannot consider axons or synapses but only the excitability and actions of the conducting pathways.

The responses of the Ceriantharia have been largely neglected, perhaps because

they are a small aberrant group, though common as aquarium exhibits. Reference will be made to the work of Moore (1927*a, b*) on the responses to light and to gravity. That a symmetrical twitch follows a single electrical shock was noted by Ross (1957), but the methods of electrical stimulation as introduced by Pantin (1935) for the study of coelenterate responses have not so far been applied.

These methods have one serious disadvantage in that the resulting analysis does not give a balanced picture of the co-ordination of the animal. Electrical stimulation evokes the protective retraction of coelenterate polyps. However, other examples of co-ordinated activity are continually observed, particularly in feeding, creeping, burrowing and peristaltic movements. The physical properties of the through-conducting systems, as deduced from electrical stimulation experiments, are now known for several species of anemones and corals, but the other activities are much less amenable to present experimental techniques. This disadvantage is encountered also in the present study of *Cerianthus*: the protective retraction can be readily analysed, but the pathways which co-ordinate the feeding response and the slower movements remain unknown.

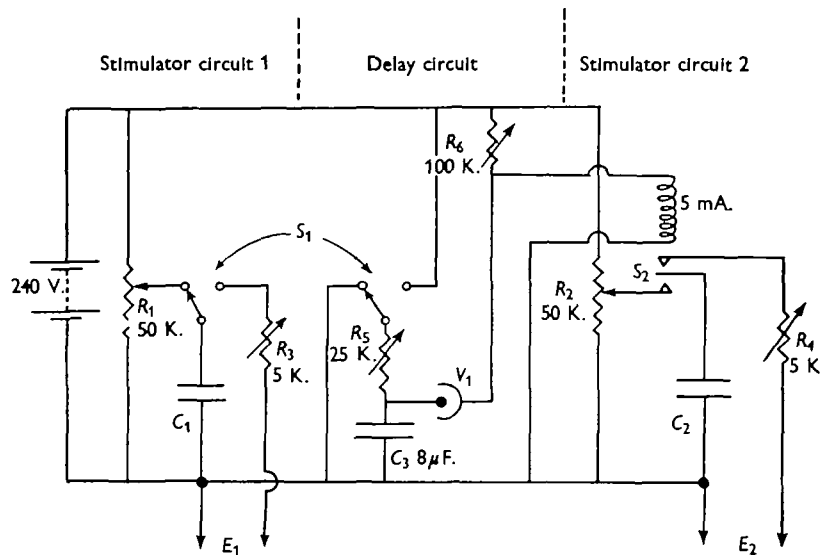


Fig. 1. For explanation see text.

METHODS

The most convenient stimulus for the study of coelenterate through-conducting systems is the condenser discharge. The effects can be related by theoretical equations or by direct experimental comparison to those produced by pulses of constant current. The arrangement used in the present work is shown in Fig. 1. It consists essentially of two stimulator circuits linked together by a delay mechanism.

In the stimulator circuits the condensers C_1 and C_2 (variable by substitution from

0.01 to 32 μF .) are charged from the strength controls R_1 and R_2 and are discharged through the stimulating electrodes E_1 and E_2 . In series with the electrodes are the variable resistors R_3 and R_4 , by means of which the total resistance of each discharge circuit is adjusted. In the experiments the total external resistance was usually 3000 Ω . The first stimulator circuit is operated by a snap-action double-pole-double-throw switch, S_1 , which also initiates the operation of the delay circuit. In the delay circuit the rate of charging of the condenser C_3 is controlled by the variable resistor R_5 ; when the voltage across C_3 reaches the striking voltage of the neon V_1 (VS 110) the condenser is discharged through the coil of a relay which operates the contacts S_2 of the second stimulator circuit. The relay is aided by a trickle current adjusted by the variable resistor R_6 .

This instrument, which is portable and weighs less than 1 kg., provides two stimuli of independently variable strength and duration and separated by a controlled interval of time. By adjustment of R_5 and C_3 a continuous sequence of stimuli at a frequency of about 1/sec. can be produced at the electrodes E_2 .

The accuracy depends upon the linearity of the potentiometers and the precision of the condensers; by selection of ordinary components a precision of 5% can be easily achieved. The control of the delay interval by R_5 is calibrated by means of an oscilloscope. Reproducibility is limited by contamination of the contacts, by changes in V_1 and by the friction of the relay. Repeated tests gave a standard deviation of about 5% of the mean delay interval.

Non-polarizable Zn/ZnSO_4 electrodes, sealed into glass tubes by sea-water agar, were used for all experiments in which stimulus strength was measured.

Experiments were conducted at a temperature of 21–23° C.

RESPONSES TO STIMULATION

Cerianthus has two sets of tentacles, an inner and an outer group. In specimens of about 10 cm. expended length the inner tentacles are 1–1.5 cm. long and form a dense cluster round the mouth; the outer tentacles are 4–6 cm. long and are arranged in several rows round the margin of the disk. The tentacles of the inner group are continually making small spontaneous bending and waving movements which are intensified following light mechanical stimulation; those of the outer set are usually quite still unless disturbed. Both groups show the typical dual response to be described, but the following observations were made primarily on the tentacles of the outer row, which, being of greater size, are more easily studied.

When a tentacle is touched with a clean rounded glass rod no response follows. This agrees with von Uexküll's (1909) finding that chemical stimulation is necessary to elicit movement from *Anemonia* tentacles. A touch with the rod moistened with saliva produces a movement. Typically the tentacle contracts on the side touched and tends to curl round the rod. It shortens a little on both sides of the point of stimulation and swings towards the mouth by a movement at its base. This seems to be effected by longitudinal muscle fibres present in the tentacle itself and continuing on to the disk. A stronger mechanical stimulus alone, e.g. a gentle pinch,

evokes the above movements and, in addition, tentacles on either side of the one stimulated also swing towards the mouth. At the same time the edge of the disk is raised locally in the region stimulated and this movement helps to tilt the tentacles inwards. The muscles responsible for the edge-raising movement have not been identified. The movements spread round the disk to a greater extent as the irritation is continued. When one outer or inner tentacle is pinched with forceps all the outer tentacles at once respond with a co-ordinated inward movement, particularly in an animal which has been allowed to rest quietly for about an hour. The movement is propagated in both directions round the disk with a velocity of 2-4 cm./sec.

Besides the feeding movements spontaneous changes are continually going on at a much slower rate so that the outer tentacles change their positions with respect to the rest of the animal. In normal animals in an aquarium the innermost ring of the outer tentacles is sometimes raised vertically over the disk, with other tentacles partly raised, and at other times all the outer tentacles project at right angles to the column.

A single condenser discharge above threshold applied to any part of the tentacles or column initiates an immediate symmetrical twitch of the longitudinal muscle of the column. The extent of the contraction is independent of the strength of the stimulus, provided that it exceeds threshold. A single shock below threshold gives rise to a local bending of the tentacle at the point stimulated, together with a local shortening of the tentacle and an inward swing exactly as in the feeding response. Sometimes several such subthreshold shocks at intervals of about 1 sec. are required before the whole tentacle moves. With about ten shocks, at 1 per sec., neighbouring tentacles begin to respond also. Such effects are found with the condenser charged to two-thirds of the voltage required for threshold stimulation of the through-conducting system.

Although this difference in threshold suggests two pathways of propagated excitation in the tentacles the observations as they stand do not necessarily indicate two conducting pathways. The through-conducting system cannot be excited by a stimulus to the tentacle without an accompanying local movement. Without other evidence the local movement could be merely an excitation of a smaller proportion of the units of a conducting system composed of many units. However, a stimulus applied to the column initiates an impulse that invades the tentacles antidromically and then they give only a slight twitch. This observation appears to confirm the view that the slower movements of the tentacles are co-ordinated by a physiological pathway that is independent of the through-conducting system. In addition we may tentatively suggest that at the input from the sensory cells to the through-conducting pathway there is a physiologically polarized junction which prevents the initiation of feeding movements by an antidromic impulse.

THE STRENGTH-DURATION RELATIONSHIP

That the threshold strength increases as the stimulus duration is reduced is an observation common to all excitable tissue, so the existence of a strength-duration relationship is not evidence that nerve axons are being excited. Other mechanisms,

such as that of *Vorticella* stalk, show the familiar curve (Lapique, 1926). Again, an absolute measure of the stimulus duration at a threshold of twice the minimum strength does not reveal the nature of the excitable process though it indicates its approximate time scale. I hoped that the excitability of *Cerianthus* could be defined more precisely if the observed strength-duration relationship proved to be a close approximation over a large range to the theoretical curve worked out by Hill (1936). However, Hill's theory does not apply specifically to nerves or to muscles; it only assumes certain formal quantitative relations. The form of the strength-duration curve could indicate how closely these relations account for the excitatory process and it might show to what extent *Cerianthus* resembles other coelenterates.

The stimuli, which were electrically negative condenser discharges of various time constants, were applied through non-polarizable Zn/ZnSO₄/sea-water agar electrodes in glass tubes drawn to an orifice of diameter 0.5 mm. For each series of measurements the total external resistance was adjusted to 3000 ohms with a high-resistance meter, a procedure shown to be adequate because the measuring current was the same in either direction and did not decay with time. The body of the animal and the sea water covering it were maintained at earth potential by a relatively large electrode. The small electrode tip was pressed against the region to be stimulated and held gently in place as the preparation moved. The variations following small movements were not large and an average over six to ten measurements was found for each type of stimulus.

Typical results from the stimulation of *Cerianthus* column are shown in Fig. 2 (*a*), where they may be compared with the results (*c*) from the column of Naples specimens of *Calliactis*. These results from *Cerianthus* do not fit Hill's theoretical curve, which is drawn as a smooth line (*b*), whereas those for *Calliactis* are in reasonable agreement with the theory. Furthermore, the *Cerianthus* results are displaced well to the left of those for *Calliactis*. In Fig. 2 (*a*) which appears typical, the time constant RC at twice the rheobase is 1.4×10^{-4} sec. This is not the same as Lapique's chronaxie which relates to constant current pulses and is theoretically $0.35 RC = 5 \times 10^{-5}$ sec. The theoretical curve (*b*) has larger corresponding values; 2.2×10^{-4} and 8×10^{-5} sec. The theoretical curves all have the same shape; the constants determine only their position on the paper. For *Calliactis* (*c*) the time constant at twice rheobase is 4.0×10^{-3} sec.; Lapique's chronaxie is 1.4×10^{-3} sec. These constants were obtained by the method of curve-fitting described by Hill (1936).

The results are substantially the same wherever the stimulating electrode is applied on the surface from tentacle tip to aboral end. Fig. 3 (*a*) shows results from stimulation of a tentacle. As in Fig. 2 (*a*) they do not agree well with the theoretical curve. Chronaxie values ($0.35 RC$) ranging from 4×10^{-5} to 9×10^{-5} were found at different points on the surfaces of eight specimens, but no particular significance has emerged from these variations. The shape of the strength-duration curve differed slightly in some of the positions studied; for example, in Fig. 3 the observations indicated by crosses agree well with the theoretical curve (*c*).

The chronaxie for *Calliactis* is somewhat shorter than the figure of 2.4×10^{-3} sec.

previously given by Pantin (1935); the chronaxie for *Cerianthus* is surprisingly short. A partial explanation of this curious result is to be found in the effective size of the electrode. Grundfest (1932) found that decrease of the electrode size is accompanied by a reduction of the chronaxie. With a capillary electrode 20–30 μ diameter on frog muscle fibres he obtained values 0.05 times normal, and for nerve 0.4 times normal. Pantin used large electrodes in pairs with the sea water not earthed, thereby producing effectively larger electrodes. In addition, in *Calliactis* a thick layer of mesogloea intervenes between the electrodes and the excitable

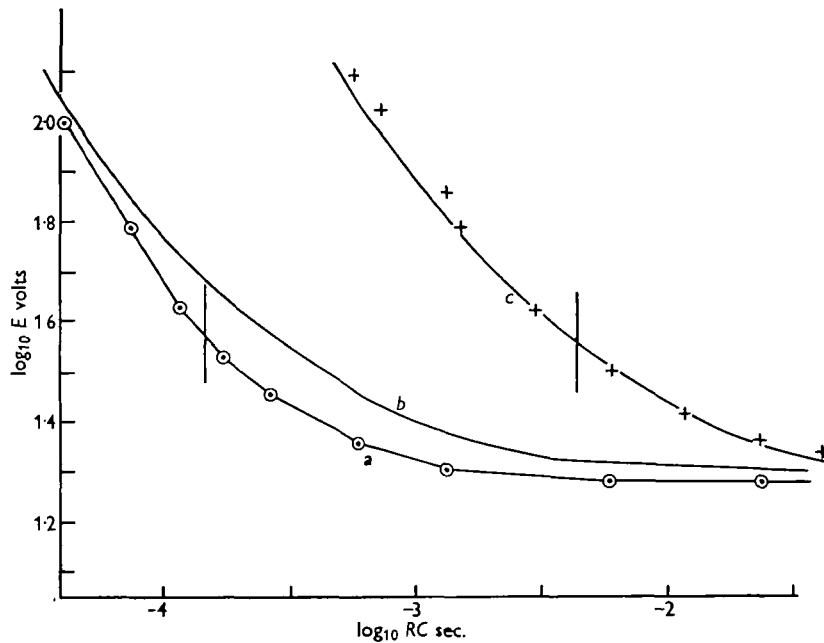


Fig. 2. The relation between intensity and time constant for the least stimulus required to excite. (a) Experimental results on *Cerianthus* column, with lines connecting the points; (b) curve of the theoretical equation $\log E = \log E_0 + [1/(RC/K - 1)] \log RC/K$ (Hill, 1936), with $K = 1.0 \times 10^{-4}$, E_0 is the rheobase; (c) curve of Hill's equation, $K = 2.5 \times 10^{-3}$, with new experimental results on *Calliactis* column. The vertical lines show the points at twice the experimental rheobase strength at (a) 1.4×10^{-4} sec. and (c) 4.0×10^{-3} sec. Each experimental point is the mean of six observations.

endoderm and this increases the effective electrode size since the current is more diffusely spread further from the electrode. In *Cerianthus*, the excitable tissue is ectodermal and is much nearer the electrode as here applied. The size and position of the electrodes do not account completely for the difference between the two species. Chronaxie measurements have also been made with the same electrodes on a variety of anemones, e.g. *Cereactis*, *Metridium*, in which the mesogloea is thin. The values so obtained agree with those from *Calliactis*. The mechanism of excitation peculiar to *Cerianthus* remains obscure; we are entitled only to draw the conclusion that it differs in time-scale from the corresponding mechanism of anemones.

These results at least show how difficult it is to identify the excitable tissue by indirect means and gross stimulation. The strength-duration curve fails as an aid in the identification of the excitability as nervous or muscular. But this need not always be the case; a composite curve with two chronaxies, as for some frog muscles, would be better evidence of two separately excitable tissues.

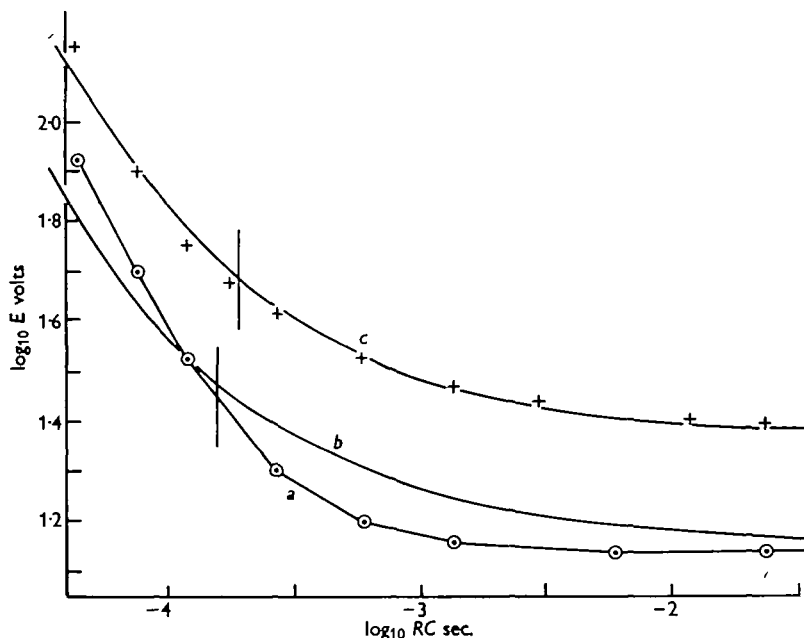


Fig. 3. The relation between intensity and time constant for the least stimulus required to excite. (a) Experimental results on *Cerianthus* tentacle, with lines connecting the points; (b) curve of Hill's equation (see Fig. 2) with $K = 1.25 \times 10^{-4}$; (c) curve of Hill's equation with $K = 1.6 \times 10^{-4}$ and experimental results on *Cerianthus* column. Note that in this example (c), in contrast with the results in Fig. 2(a), the results from the column agree with the theoretical expectation. As in Fig. 2(a) the results from the tentacle 3(a) follow a more inflected curve than the theory predicts. The vertical lines show the points of twice the experimental rheobase strength. Each experimental point is the mean of six observations.

THE REFRACTORY PERIOD

The refractory period was measured by applying a second shock of sufficient strength to excite at various intervals after an initial stimulus. The total contraction height is greater if the second stimulus produces a second impulse. The difference in the two contraction heights readily indicates whether the second stimulus has successfully excited the conducting system. The time constant of each stimulus was 1.25×10^{-3} sec., produced by discharge of a $0.5 \mu\text{F}$. condenser through a total external resistance of 2500 ohms. The second stimulus can be applied either at the same point as the first or at a nearby point. There is an absolute refractory period of 70–75 msec. and the relative refractory period is discernible up to about 120 msec. after the first stimulus. Results are shown in Fig. 4, together with the results found for *Calliactis* by Pantin (1935).

The existence of the refractory period implies that an all-or-nothing impulse is initiated under the first electrode, and the observation that the second stimulus can be at a point distant from the first shows that the impulse has this property along the conducting pathway.

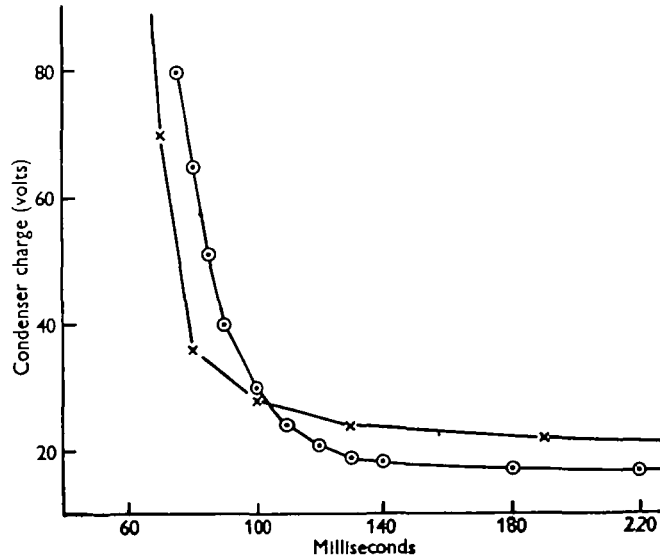


Fig. 4. The relation between intensity of stimulation and refractory period of the through-conducting system. ○, *Cerianthus*, the stimuli being applied to a tentacle; ×, *Calliactis* from Pantin (1935).

VELOCITY OF TRANSMISSION

The velocity of transmission of the through-conducting system was measured along the column by taking into account the apparent increase in the refractory period as the second shock is applied progressively further away from the first. With a charge of 40 V. the results appeared to be unaffected by local variations in sensitivity. With both electrodes at the same place the refractory periods for six trials were 85, 92, 86, 85, 90, 90 msec. With the same electrodes separated by 6 cm. of the column the apparent refractory periods were 125, 134, 120, 145, 140, 135 msec. This gives an average velocity of transmission of about 1.3 m./sec.

CONTRACTION OF THE ECTODERMAL MUSCLE OF THE COLUMN

Column contraction was recorded with an isotonic lever arranged to pull the muscle with a load of approximately 10 g. The preparation was held by pins or threads and submerged in aerated sea water. Under these conditions the whole animal or a longitudinal strip of body wall would relax and steadily lengthen for the first half hour or so and would then usually show slow irregular changes in length, each of which might take an hour to complete. Some of this slow, apparently spontaneous,

movement may have originated at the mechanical supports, but I consider that the time courses and heights of contractions recorded in this paper represent real physiological changes of the preparation. Some slow movements, particularly at the aboral end, were observable in untouched whole animals kept in glass tubes.

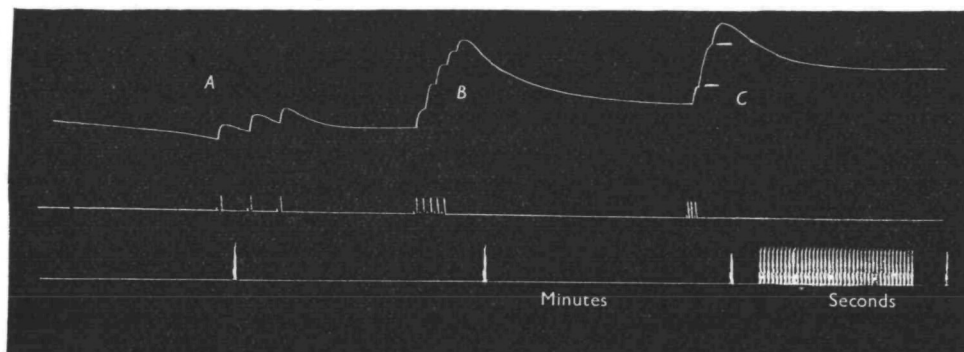


Fig. 5. A kymograph record of longitudinal contractions of the column of an intact *Cerianthus*. This record illustrates the contraction at each shock, the slow relaxation, the staircase of successively smaller steps at constant time interval, and the larger contraction (facilitated) at C following stimuli that are very close together. In C the steps are indicated.

The twitch of the muscle in response to a single shock is symmetrical on all sides of the column. The relaxation is slow, as shown in Fig. 5. The contraction height of a single twitch is independent of the stimulus strength above threshold. The height of the contraction, as measured by the maximum excursion of the trace on a smoked drum, depends upon the initial length at the moment of stimulation as shown by the points \times in Fig. 6. This relation, which is common to many slowly relaxing muscles, appears to have no particular significance here, but must be allowed for when considering the question of temporal summation of successive contractions. As shown in Fig. 5 the second contraction begins at various stages in the course of relaxation after the first contraction; it is reasonable to assume that the height of the second contraction depends upon the initial length in the same way as the first. In Fig. 6 the circles show the extents of second contractions which follow the first after an interval of 1 sec. The agreement between the two sets of points shows that the second contraction is similar to the first, although on the trace it would rise above the first and the extent of the second contraction would be less than the first. A typical trace which illustrates these features is shown in Fig. 5 at A and B. However, the second contraction is larger than normal for intervals less than 1 sec. as in Fig. 5, C. When a second shock is applied at various time intervals after the first, at the same point on the column or tentacle, the resulting total contractions are greatest for intervals of about 100 msec. The curve of the facilitation of contraction, Fig. 7, is comparable with that which Pantin (1935) obtained for *Calliactis*, though more sharply inflected. The present observations on *Cerianthus* do not provide any information as to the site of the mechanism of facilitation because

they do not show whether it occurs in the conducting system or in the contraction process; in *Calliactis* this distinction was possible.

Contractions which are much slower, asymmetrical, and often restricted to one end of the column are part of the normal behaviour of *Cerianthus*. Specimens kept in glass tubes continually make slow bending movements of the end of the column. The asymmetrical bending responses to light and to gravity described by Moore (1927*a, b*) are changes of posture which are maintained by the longitudinal ectodermal muscle of the column. As mentioned above, preparations arranged for kymograph recording show slow movements, but it has not been possible to find the cause of these or to discover their relation to the normal behaviour of the whole animal.

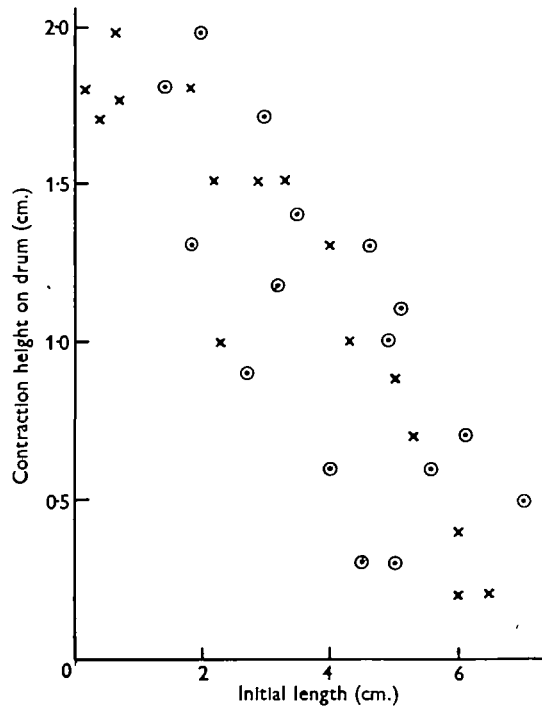


Fig. 6. The extent of the second contraction plotted against the initial length of the muscle: x, after a delay of at least 20 sec.; O, after 1 sec. delay since the previous stimulus. The ordinates refer to arbitrary measures of the excursion on a kymograph drum.

Longitudinal strips and mounted preparations of the whole column show an asymmetrical slow component of contractions following several electrical stimuli. The responses to the first few shocks are followed by a relaxation that is complete in 1–2 min. As shown in Fig. 8, later contractions may be followed by an abnormally slow relaxation. The slow relaxation occurs all along the length of the preparation. In a preparation of two longitudinal strips connected by a transverse bridge in the form of a U the rapid contractions and relaxations are similar in the two strips. The slower relaxation is not propagated from the strip in which it originates. A typical

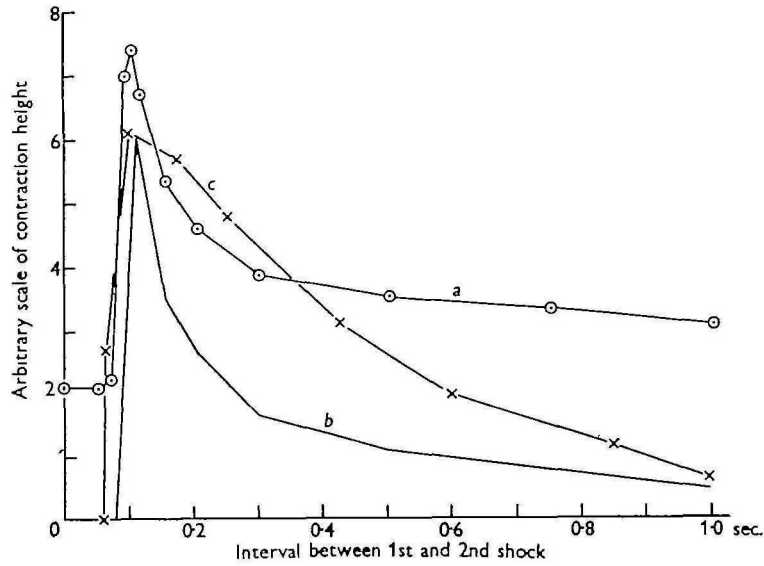


Fig. 7. Facilitation of contraction in *Cerianthus*. (a) The relation between the interval between two shocks and the height of the resulting two contractions taken together; (b) the height of the component due to facilitation alone. This curve is derived from (a) by deduction of the heights expected if each shock had occurred separately; (c) Pantin's (1935) results on *Calliactis* redrawn so that the height of the peak and the base line are similar to those of curve (b) on the arbitrary scale of contraction height. The anemone contracts only at the second shock and (c) is comparable with (b). Note that the facilitation is at a maximum at similar positions on the time scale in (b) and (c), but falls off relatively more rapidly in *Cerianthus*.

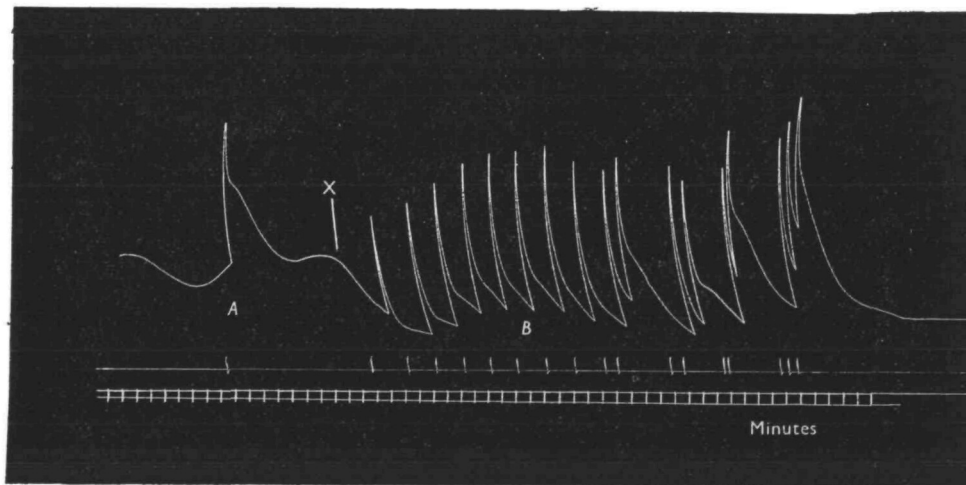


Fig. 8. Various types of contraction in *Cerianthus*. A, Response to a single electrical stimulus during a slow contraction which was elicited by mechanical stimulation; B, typical quick responses. Note the delayed relaxation in A and in the later quick contractions.

trace is shown in Fig. 9. Ten shocks at 2 per sec. is an adequate stimulus to produce a contraction which relaxes slowly.

The muscle is clearly capable of two distinguishable responses; the twitch followed by the delayed relaxation is a combination of these two. Both responses are propagated over the muscle, for the whole length of it responds to a stimulus at one point. These two responses are co-ordinated by distinct mechanisms since either fast or slow contractions occur separately. The picture which emerges of the co-ordination of the slow contractions following stimulation does not agree with all observations of the slow movements of whole animals. The responses to light and to gravity appear to be direct local responses, not propagated along or round the column. The characteristic movement of the aboral ends of animals in glass tubes is a slow contraction which is co-ordinated round the animal, and forms a terminal bulb: this bulb has an obvious functional significance as a movable holdfast in the animal's natural tube.

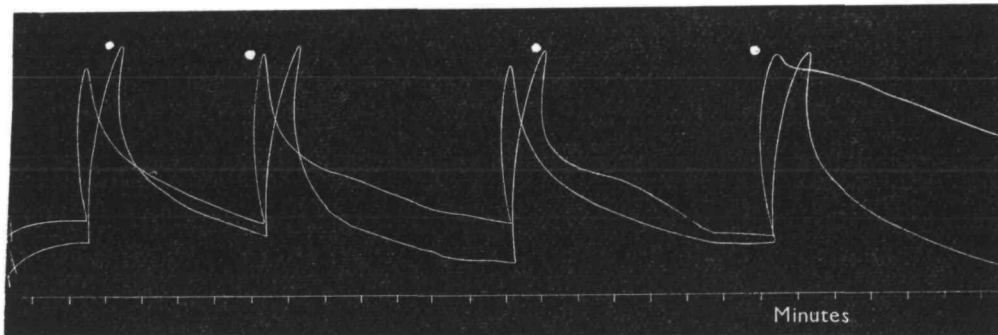


Fig. 9. Contractions of two strips of longitudinal muscle which were joined by a transverse bridge at the aboral end. The stimulus, 20 shocks at 2/sec., was applied to the oral end of one strip or the other as indicated by the white dots. In addition to the symmetrical quick contraction, the stimulated strip alone shows a delayed relaxation which becomes more pronounced as the experiment proceeds.

DISCUSSION

Previous histological work

The ectoderm of the column of *Cerianthus* consists mainly of glandular cells, nematocysts, and the cell bodies of the underlying longitudinal muscle fibres. The contractile fibres lie in radially arranged longitudinal lamellae which are folds of the underlying mesogloea. Below the superficial layer of cell bodies lies a plexus of thin fibres which run parallel to the surface. Some authors, for example, Hyman (1940), have taken these to be nerve fibres but present knowledge of their connexions and histological structure is far from satisfactory. Dr Torelli, the present authority, doubts (1957) the nervous nature of this plexus and supposes it to be connective tissue. She describes (1952) nerve fibres which run over the lamellae of the muscle fibres in the position expected of a motor innervation, but is unable to find the cell bodies of these fibres, or any other ganglion cells. These fibres over the muscle

lamellae (and in the above subepidermal plexus) are very small compared with the nerve nets which are the through-conducting systems of *Metridium* (Pantin, 1952) and *Aurelia* (Schäfer, 1878). After much histological work on *Cerianthus* by a number of authors with varied techniques no fibres or cells which can reasonably be identified with the through-conducting system have been described.

CONCLUSIONS

If the histological evidence is accepted the only fair conclusion from the physiological observations is that the through-conducting system is the ectodermal muscle itself. If so, this would be an exception among coelenterates so far studied and the simplest example of muscular co-ordination yet discovered among multicellular animals. The velocity of conduction, the refractory period and the chronaxie would then be properties of the muscle, despite the quantitative agreement of the first two of these in *Cerianthus* and in the mesenteric system of *Calliactis*, which is accepted as being co-ordinated by a nerve net (Pantin, 1952). But I think that the above conclusion, based upon indirect physiological and negative histological evidence, is premature and would be acceptable only after a direct observation of propagation from muscle fibre to muscle fibre.

The interpretation of results obtained by standard physiological methods of gross stimulation is necessarily severely limited since even if a nerve net is found by histological methods, further evidence is required before it can be accepted as one of the pathways of conduction. Limitations of technique have restricted most studies of nerve nets so that physiological and histological information is obtained independently. In general there is so far no direct evidence that the histologically observed fibres are concerned in the behaviour or that physiological properties can be ascribed to a particular axon structure. There are two exceptions, the physiologically distinct specialized giant fibre systems of actinians (Pantin, 1952) and scyphozoans (Horridge, 1954). In the former the identification is based on the agreement between the fibre orientation in the mesenteric nerve net and the anisotropic distribution of the velocity of conduction in this region; in the latter it was possible to obtain physiological information about a cell which at the same time was identified microscopically.

In the present study I have endeavoured to find the limits of the interpretation which can be placed on the classical experimental methods of gross electrical stimulation. In *Cerianthus*, since a net of definite nerve axons has not yet been found, the position is not complicated by the assumption that the co-ordinating pathway is located in a nerve net. The later discovery of the existence of a net would not alone justify the assumption that it is the site of one of the physiological pathways. Circumstantial evidence, such as directionality, specific connexions to the muscles, or a limited regional distribution would allow a tentative correlation; direct physiological micro-methods could be conclusive.

SUMMARY

1. The responses of *Cerianthus membranaceus* to electrical and mechanical stimulation are described.

2. The longitudinal muscle of the column ectoderm responds with a symmetrical contraction to a single shock from a condenser discharge applied anywhere on the animal. The response is independent of the strength of the stimulus above threshold and is co-ordinated by a through-conducting system which propagates an impulse at about 1.3 m./sec. followed by an absolute refractory period of 70 msec. at 21–23° C.

3. The strength-duration curve of the excitatory process, the relative refractory period curve and the curve of facilitation of contraction are given and compared with corresponding results from actinians.

4. Slow responses of the tentacles and column muscle are described.

5. The physiological observations are discussed in relation to the histological background. The conclusion that the physiological pathway cannot yet be histologically identified is discussed as part of the general problem of the analysis of the coelenterate nerve net.

I should like to thank Dr P. Dohrn and his staff at Naples for their kind interest and for the use of the facilities of the Stazione Zoologica.

REFERENCES

- HILL, A. V. (1936). Excitation and accommodation in nerve. *Proc. Roy. Soc. B*, **119**, 305.
 HORRIDGE, G. A. (1954). The nerves and muscles of medusae. I. Conduction in the nervous system of *Aurellia aurita* Lamarck. *J. Exp. Biol.* **31**, 594.
 HYMAN, L. H. (1940). *The Invertebrates*, Vol. 1. *Protozoa through Ctenophora*, p. 628. New York and London: McGraw Hill.
 LAPIQUE, L. (1926). *L'excitabilité en fonction de temps*. Paris: Presses Universitaires.
 MOORE, M. M. (1927a). The tropistic reactions of *Cerianthus membranaceus*. *J. Gen. Physiol.* **6**, 385.
 MOORE, M. M. (1927b). The reaction of *Cerianthus* to two sources of light. *J. Gen. Physiol.* **6**, 393.
 PANTIN, C. F. A. (1935). The nerve net of the Actinozoa. I. Facilitation. *J. Exp. Biol.* **12**, 119.
 PANTIN, C. F. A. (1952). The elementary nervous system. *Proc. Roy. Soc. B*, **140**, 147.
 ROSS, D. M. (1957). *Nature, Lond.* **180**, 1368.
 SCHÄFER, E. A. (1878). Observations on the nervous system of *Aurelia aurita*. *Phil. Trans.* **168**, 563.
 TORELLI, B. (1938). Istologia e senescenza in *Cerianthus*. *Pubbl. Staz. zool. Napoli*, **17**, 1.
 TORELLI, B. (1952). Su alcuni particolare aspetti della istologia di *Cerianthus*. *Pubbl. Staz. zool. Napoli*, **23**, 141.
 TORELLI, B. (1957). Private communication.
 UEKKÜLL, J. VON (1909). Recherches sur les tentacules de l'*Anemonia*. *Bull. Inst. Oceanogr. Monaco*, no. 148.