Robert Josephson writes about Carl Pantin’s 1935 ground breaking publications on sea anemone neurophysiology. Pdf files of Pantin’s papers can be accessed as supplemental data at jeb.biologists.org

In the early 1930s Carl Pantin spent several months at the Stazione Zoologica in Naples studying neuromuscular transmission in crustacea. These investigations reached a convenient stopping point several weeks before Pantin was to return to England, and he cast about for something else to do in the meantime. The previous occupant of the laboratory in which he was working had left some sea anemones in an aquarium, and Pantin chose to examine the neural control of muscular contraction in these (Pantin, 1968). The results of this fortuitous change in direction was a series of papers on the behavioral machinery of coelenterates that changed, in a major way, views on the neural control of behavior in coelenterates and on the early evolution of nervous systems in general. The first and arguably the most important of these papers is the principal subject of this column (Pantin, 1935a).

Coelenterates (Phyla Cnidaria and Ctenophora) are the most simply constructed animals with nervous systems, and they offer the most simply organized nervous systems in the animal kingdom. Both cnidarians and ctenophores are basically composed of two epithelial layers, an outer ectoderm and an inner endoderm, separated by a largely acellular, gelatinous mesoglea. Histological studies in the 19th and early 20th centuries established that there are nerve cells in coelenterates, and that these form diffuse, two-dimensional nerve nets that lie in the basal regions of the epithelial layers. In the sea anemone polyps studied by Pantin all the nerve cells occur as parts of diffuse nerve nets. In the late 19th century, G. J. Romanes, Darwin’s protégé, had examined conduction in jellyfish as part of his exploration of the evolution of mental processes in animals. Through clever cutting experiments Romanes demonstrated that contractile waves are conducted diffusely across the subumbrella epithelium of the jellyfish Aurelia and will spread between any two blocks of subumbrellar tissue so long as these are joined by a bridge of intact tissue larger than a millimetre or so in width (Romanes, 1885).

The diffuse conduction demonstrated physiologically by Romanes was consistent with the diffuse distribution of the nerve cells found in histological studies. G. H. Parker, another giant in early neurophysiology, used the cut and stimulate approach of Romanes and found that conduction in the column of anemones is also diffuse (Parker, 1919). Parker stimulated coelenterate tissue with mechanical prodding, light and chemicals. He noted, as had others before him, that contractile responses in coelenterates were sometimes local and often increased in amplitude with increasing strength of stimulation. To account for local, graded behavioral responses thought to be mediated through a widely distributed, diffusely conducting nerve net.

Pantin brought to his studies of anemones an appreciation for the importance of facilitation in neuronal functioning obtained from his work on neuromuscular transmission in crustacea. He also brought to this project electrical stimulators, which, though quite primitive by later standards, were adequate to produce single shocks and trains of shocks of controlled intensity and frequency for activating anemone conducting systems.

The work described in the first anemone paper from Pantin’s time in Naples demonstrated that contractile waves are conducted diffusely across the subumbrella epithelium of the jellyfish Aurelia and will spread between any two blocks of subumbrellar tissue so long as these are joined by a bridge of intact tissue larger than a millimetre or so in width (Romanes, 1885).

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Although the wave of activity initiated by a stimulus number or, with natural stimuli, spread and intensity are graded with thus accounting for local responses whose and decline with distance from this site, than do those further away, the contractile the stimulus origin receive more impulses by sensory structures during natural increasing number of impulses generated number of imposed stimuli or with whose spread increases with increasing number of imposed stimuli or with increasing number of impulses generated by sensory structures during natural behaviour. Further, because muscles near the stimulus origin receive more impulses than do those further away, the contractile responses are greatest at the stimulus site and decline with distance from this site, thus accounting for local responses whose spread and intensity are graded with stimulus number or, with natural stimuli, with stimulus strength.

Although the wave of activity initiated by a single shock to the column apparently reaches all the muscles of the column, it generally results in no overt muscle response. Two or more stimuli at an appropriate frequency are required to initiate muscle contraction, presumably because of requirements for neuromuscular facilitation at the junctions between the nerve net and the muscles. The second paper in the anemone series considered the varying requirements for facilitation among the different muscles of the column (Pantin, 1935b). Very low frequency of stimulation, one shock each 10 s or so, activated just the circular muscles. Increasing the stimulus frequency brought in, progressively, the parietal muscles, the mesenterics and finally the powerful sphenicter muscle. Thus different frequencies of activation caused qualitatively different behavioral responses.

Following the publication of Pantin’s research on anemones in 1935 (Pantin, 1935a–c) one could have entertained, at least for a while, the idea that the behavioral machinery of anemones was largely understood. It appeared that a reasonably complete model of anemone behavior could be constructed with a few, simple components: a through-conducting nerve net, a locally conducting nerve net with interneural facilitation, and a group of muscles with differing requirements for neuromuscular facilitation. But the inadequacies of this simple view soon became apparent. Unstimulated anemones are not inert. Batham and Pantin, in a series of papers published in 1950, used slow mechanical recording and time-lapse cinematography to view the behavior of unstimulated anemones. They found that even under constant conditions animals periodically expand, contract, sway, and even move about by gliding on the pedal disk (reviewed in Pantin, 1952). These behaviors occur on a time scale so slow that they are not easily perceived by direct observation. How these slow behaviors are coordinated is still quite unknown. More recently it has been shown that there is not just one but rather several conducting systems in the column of anemones; a rapidly conducting system, probably the column nerve net, and at least two slow systems (see, for example, McFarlane, 1969, 1975). The slow systems may reflect activity in a subset of the neurons of the general nerve net or they may represent conduction in the epithelial cells themselves. Impulses in the slow systems appear to modulate such activities as oral disk expansion and retraction, and foot detachment. The goal of totally explaining the behavior of anemones seems to be receding as more is becoming known about the behavior of these interesting creatures. But it should be emphasized that the newer findings on slow and often spontaneous behaviors, and the presence of multiple conducting systems in anemone tissues, are additions to and not changes in the basic plan for the behavioral machinery of anemones given to us by Pantin in his classic papers published nearly 70 years ago.

10.1242/jeb.01059

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THE NERVE NET OF THE ACTINOZOA

I. FACILITATION

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(Received 10th November, 1934.)

(With Seven Text-figures.)

INTRODUCTION.

The most primitive form of nervous system in the Metazoa appears to be the nerve net, and in it undoubtedly many features of the nervous systems of the higher animals may be exhibited in a simplified form. But in comparison with such systems the nerve net seems to show certain far-reaching contrasts which suggest not merely a more primitive organisation but a fundamentally different method of transmission of excitation. It is our object to investigate the nature of the special properties of the nerve net. They may be summarised as follows:

(1) Excitation is conducted diffusely in all directions from the site of stimulus. This is well known from the classical experiments of Romanes (1885) on Medusae and of Parker (1918) on Metridium. There are, however, some evidences of polar conduction.

(2) The response varies in character according to the strength of the stimulus. Strong stimuli may call forth not only a more intense but an entirely different response from that of weak stimuli (Jordan, 1908).

(3) The greater the strength of the stimulus, the further is its effect propagated (von Üxküll, 1909, and others).

These properties seem to imply that excitation increases in intensity with the strength of the stimulus, and that this intensity falls off as the conducted disturbance travels away from the site of stimulation. That is, conduction takes place with a decrement.

So long as it was accepted that the nerve net consisted of an anastomosing network of fibres (Bethe, 1903) these properties were inconsistent with the nature of nervous conduction as revealed in the higher animals. More recently Bozler (1927) has shown, however, that at least in Medusae the nerve net consists of separate cells in simple contact with one another, without anastomosis. Conduction in the nerve net must therefore take place from one cell to another, and for this reason may not be comparable with simple transmission of excitation as found in the axon.
of vertebrate nerve. But it remains to be shown that such cell to cell conduction will endow the nervous system with properties consistent with those just summarised. Bozler (1926) also found that the nerve net of Medusae possessed considerable differentiation. While certain tracts in the net possessed a marked decrement of conduction, there were others in which it might be argued that no decrement took place at all. The tracts possessing a decrement may show a marked tendency towards uni-directional or polar conduction, and Bozler stresses the analogy between the properties of these tracts and those of the synaptic nervous system. The fundamental question of the nature of the decrement, however, remains unsolved. In attempting to analyse this in the present experiments, one particular property of the nerve net has forced itself into evidence, that is the property of summation. Romanes showed that in *Aurelia* the property of summation of stimuli was developed to an unusually high degree. While the existence of summation has been frequently noted in connection with nerve networks, this property has never been systematically analysed; yet we shall see in this paper that it transcends all others in its importance.

The animal used in this work was chiefly the anemone *Calliactis parasitica* (Stevenson, 1928). It is the common large Actinian found commensal upon the shells of *Eupagurus bernhardus*. It is frequently referred to under at least two other names: *Adamsia rondeletii* and *Sagartia parasitica*.

**MUSCULATURE OF CALLIACTIS PARASITICA.**

To understand the responses of the Actinozooa it is necessary to remember that the mechanics of muscular contraction in these animals differs greatly from that in the Vertebrata. In the latter even the simplest movement of the limbs or body involves the complex reciprocal action of many muscles acting against a moving skeleton. On the other hand, the body of an Actinozoon is a muscular sac enclosing fluid which is chiefly responsible for its skeletal support. Movement of different parts of this sac is produced through the local development of muscle. These muscles move the parts of the animal directly and not indirectly as in an animal with a hard skeleton. The complex series of antagonistic muscles is not required to move the part. Retraction of any part is produced by the contraction of one muscle, and extension is due to relaxation under the influence of the hydrostatic pressure within the body cavity. Each simple response of the animal tends to be the result of the action of a single muscle, or group of synergetic muscles. And the more complex responses can fairly easily be analysed into such constituent simple responses. The musculature of the Actinozooa differs considerably in different species. That of *Calliactis* resembles fairly closely the system described by Parker and Titus (1916) in *Metridium*, which is closely related to *Calliactis* though these two animals differ significantly in certain features. Hertwig and Hertwig (1879) described the musculature of *Calliactis* (*Sagartia*) parasitica, but the relation of the particular muscles to their function was not considered. The following account deals with the muscles involved in the various responses. The musculature is illustrated in Fig. 1.
MUSCULATURE OF THE COLUMN.

The only muscle layer in the column itself appears to be the circular fibres of endodermal origin. Over the greater part of the column this consists of a thin layer of fibres, but in the upper quarter where the column joins the disc the circular muscle has become elaborated into a highly complex and specialised marginal sphincter. This is a mesogloel sphincter. Its muscle fibres are large and specialised, and in vertical section the sphincter is seen to possess a fairly well-defined limit confining it to the upper part of the mesogloea.

The general layer of circular muscle and the specialised marginal sphincter constitute two muscular systems which are functionally absolutely distinct. It is the contraction of the sphincter which covers the disc when the anemone is irritated.

Fig. 1. A. Partial cross-section of Calliactis parasitica to show muscles of a complete mesentery: 1, longitudinal mesenteric; 2, parietal; 3, circular muscle of column; 4, marginal sphincter; 5, marginal mesenteric; 6, radial mesenteric; 7, transverse mesenteric. B. Sector of disc: 8, tentacle; 9, radial mesenteric; 10, radial extensions of longitudinal tentacular; 11, radial and circular muscles of disc. C. Disc, showing well-developed "edge-raising" reaction.

The response produced by contraction of the general circular layer is not concerned in this and will be considered later on. There is no evidence of any longitudinal muscle in the column.

MESENTERIC MUSCULATURE.

The numerous mesenteries of Calliactis provide the animal with its longitudinal musculature. In the primary mesenteries, and indeed to some extent in all the older mesenteries, there are well-developed longitudinal mesenteric fibres running from the disc to the foot, and their contraction is responsible for the lowering of the disc. In transverse section, these longitudinal mesenteric muscles appear as well-developed "diffuse" muscles on the side of the mesenteries.

In addition to this system there exist on either side of the very base of all the mesenteries, young or old, well-developed parietal muscles, which are responsible
for the retraction of the column as opposed to the disc. Occasional transverse fibres occur throughout the length of the mesentery. Just beneath the attachment of the mesentery to the disc these form a fairly well-developed band of radial mesenteric fibres.

**Disc musculature.**

The surface of the disc is divided radially into sectors of greater or less extent by the various mesenteries. The whole disc is pervaded to some extent with radial and circular fibres. The radial mesenteric muscles also affect the contractions of the disc.

The tentacles consist of the usual longitudinal and circular fibres; but the longitudinal fibres extend into the disc itself for a considerable distance, and function with the tentacle as a single unit. This radial-tentacular musculature is particularly well developed on that part of the intermesenteric space towards the mouth.

**The responses to mechanical stimulation.**

**Stimulation of column.**

If the column is stimulated by means of a glass rod or a silver wire, it is found that the general sensitivity and the nature of the response varies in different parts. Sensitivity is greatest at the pedal edge and decreases as we pass upwards towards the disc. Very light stimulation on the middle of the column, if long continued, tends to cause local contraction of the circular muscle of the column in a ring from the site of excitation. This constriction may slowly pass up the column from the point of excitation as a peristaltic wave. Light stroking of the column may also produce occasional slight upward contractions of individual tentacles scattered round the disc. A somewhat stronger stimulus causes a very slow contraction of the column, so that the disc is lowered though it remains expanded. This is due to the contraction of the parietals. A still stronger stimulus causes, in addition to this effect, a depression of the disc itself, owing to the contraction of the longitudinal mesenteric muscles (Fig. 1). Parker (1916) records similar effects in *Metridium*, where the contraction of these longitudinal muscles appears to be largely responsible for the protection of the disc by invagination. In *Calliactis*, however, these responses are slow and from the point of view of protection of the disc unimportant compared with that which follows great mechanical stimulation. This is a series of violent discrete contractions of the marginal sphincter, so that the disc becomes completely covered before any other reaction of the anemone is apparent. The sphincter reaction is called forth more easily from stimulation of the column than from any other region.

In *Calliactis*, stimulation of the column never causes special responses of the disc. Further, such stimulation evokes only symmetrical responses, that is an even activation of one effector or group of effectors all round the axis of the animal, with no greater activity in the region of stimulation than elsewhere. The reactions to stimulation of the column illustrate the diffuse conduction of excitation from a
stimulus, and the variation in the nature of a response with the strength of stimulus. There is, however, in this case, no evidence that the strength of stimulus affects the distance through which excitation is propagated.

**Stimulation of the disc and tentacles.**

The most striking difference between the responses of the column and those of the disc and tentacles is found in the variety and asymmetrical character of the latter. A light stimulus on the side of a tentacle causes it to bend owing to the very local contractions of the longitudinal muscles. A prolonged stimulus tends to cause rapid and complete contraction distal from the point of stimulation, though the proximal portion of the tentacle remains unaffected (cf. von Uexküll). Only by repeated stimulation of a tentacle can excitation be caused to spread to other tentacles, and the responses are thus restricted to the sector of the disc including the site of stimulus.

The varied responses of the disc represent various degrees of a feeding reaction. Thus local stimulation of a tentacle as presented in the expanded animal results in the tentacle bending towards the mouth, carrying with it the object which caused the stimulus. If the stimulation is at the base of the tentacle on the side towards the mouth, the whole tentacle may move bodily mouthwards by its base. The effect is curiously local, and does not involve wide contractions of the disc. It appears to be brought about by the radial extensions towards the mouth of the longitudinal muscles of the tentacle. Continued light stimulation causes these effects to spread to adjacent tentacles.

In many individuals there is a marked local response of the disc itself. In this the edge of the disc is raised at the site of the stimulus above the level of the disc-surface, and over towards the mouth, so that the tentacles on this part of the disc are curved bodily inwards. This "edge-raising" reaction was first described by Nagel (1894). He pointed out that it is at first a purely local contraction. It cannot certainly be said which muscles are involved, but repeated observation of the movement of the disc when this reaction takes place and examination of fixed sections of contracted individuals lead me to believe that the muscles responsible for this are the radial muscles of the mesenteries where these join the disc (Fig. 1). Continued stimulation causes this raising of the edge to extend progressively sector by sector round the disc; though it can rarely be made to involve more than about one-third of the disc before the entirely distinct sphincter contraction is called up; and this rapidly and completely closes the whole surface of the disc symmetrically. In the complete feeding reaction this edge-raising is accompanied by a sinking of the disc between the site of stimulus and the mouth, which is thus drawn towards the stimulating object and may engulf it.

For these responses of the disc an increase of the stimulus may not only vary the response, but apparently increase the distance to which excitation is propagated. As opposed to the symmetrical responses of the column there appears to be some kind of "decrement" in the propagation of excitation of the disc. This same character endows the tentacles and separate parts of the disc with a considerable degree of
autonomy. However, strong and prolonged stimulation finally involves excitation of the symmetrically responding muscles of the column. This occurs much more readily in some individuals than in others. The contraction of the marginal sphencter may be preceded by mesenteric contractions, as after stimulation of the column.

The sensitivity within the disc varies considerably. It is less near the mouth than towards the edge of the disc. Further, the contractions of the marginal sphincter are more easily obtained from the outer tentacles than from the inner ones. The sensitivity of the individual varies considerably with physiological conditions, such as starvation, also the amount of previous stimulation. In particular, frequent application of moderate or weak stimuli produces a condition of local insensitivity. This is peculiarly marked in Calliactis.

**Response to electrical stimulation.**

**Method.**

The stimulation apparatus was based upon the neon lamp relaxation oscillator (Briscoe and Leyshon, 1930). The discharge circuit usually consisted of a 0.4 μF condenser discharging through a resistance of about 5000 ohms in series with a neon lamp. The condenser was charged by a 300-volt battery through a variable resistance of about 10 megohms. The 5000-ohm resistance included a potentiometer of a few hundred ohms, from which came leads to the electrodes. These usually consisted of silver wires fixed in narrow glass tubes with sealing wax, the ends being planed off to give a silver surface of about 1 sq. mm. surrounded by a flat area of sealing wax. Where fully non-polarisable electrodes had to be employed, these were
constructed of zinc—zinc sulphate—agar plus sea water, a 2 mm. hole being blown in the bottom of a test-tube to allow conduction of the current from the electrode to the organism.

In most experiments it was desirable to record graphically the exact moment at which each stimulus was given. This was done in the following way. A metronome was placed in the condenser discharge circuit. The natural frequency of the discharge was then adjusted to be about 5 per cent. in excess of the frequency of the metronome. The metronome by making a mercury contact was then allowed to discharge the condenser at its own frequency. With this mechanically controlled arrangement, it is an easy matter to provide a simultaneous record of the moment of discharge by a separate contact in a high-speed time marker circuit (Fig. 2). It was found most convenient to record the contractions by means of very weak isotonic levers.

Responses of the column.

The responses evoked by electrical stimulation of the column exactly resemble those obtained by mechanical stimulation except that the local fatigue is much less evident. The contractions of the marginal sphincter are easily recorded graphically. The sphincter contracts so rapidly and powerfully that there is no danger of its response being confused with that of other muscles. Stimuli of a frequency 1 per sec. evoke excellent discrete contractions in the sphincter which show a well-marked "staircase" (Figs. 3 and 4).

In view of the supposed importance of the strength of stimulus it is of particular interest to determine its relation to the response when electric stimuli are employed. If with an electrical stimulus of constant frequency the intensity is gradually raised a well-defined threshold of excitation is found. Above this, good contractions abruptly appear, and further increase in the strength of the stimulus in no way increases or modifies their response. The effect is striking. Fig. 3 shows the complete independence in the response of the sphincter over a 15-fold increase in current intensity. It would seem scarcely possible to obtain a clearer demonstration of that independence between strength of stimulus and response so characteristic of ordinary nerve than is shown in this way by the nerve net. Although the response does not vary with the strength of the stimuli, it is very sensitive to their number and time relations. Indeed, a single stimulus has no visible effect. It is only when it is followed by another that a contraction takes place; and the size of this depends upon the time interval between the two stimuli. Fig. 4 shows the responses of the marginal sphincter to increasing frequencies of stimulation. The rate of contraction increases greatly. This is not merely due to mechanical summation of the more frequent individual contractions. The magnitude of these contractions themselves progressively increases with the frequency. The response is quite evidently a simple and striking facilitation phenomenon. That is the excitation wave from each stimulus not only activates some of the muscle-fibres, but leaves behind it an after-effect which gradually subsides. This after-effect facilitates the transmission of the next excitation wave to the muscle, so that yet more muscle fibres are activated.
Fig. 3. Sphincter. Relation of response to strength of stimulus.

Threshold 1.8
Stimuli 1 per Second

Fig. 4. Sphincter. Relation of response to frequency.
The importance of frequency and the independence from intensity is found for the responses of the mesenteric and parietal as well as the sphincter. The responses can be produced from any point on the column.

These experiments show conclusively, first, that when a response occurs it is the result of many stimuli, and not of a single stimulus. Secondly, that the nature of the response depends upon the number of stimuli and upon the interval of time between them. Thirdly, that the strength of the individual stimulus is without influence. This raises the question how we can interpret the usual statement that the response varies with the "strength" of the stimulus. There seems no doubt that it is due to the employment of mechanical and similar methods of stimulation. A mechanical stimulus acts upon one or more sense organs, and from these not one but a number of nervous impulses are sent out. The greater the "strength" of such a stimulus, the greater the number and frequency of discharges from the stimulated sense organ. That mechanical stimulation does give rise to a battery of impulses is shown by Fig. 5. This illustrates the response of Calliactis to mechanical stimulation of the pedal edge. A weighted point is allowed to fall upon it at the moment shown in the time signal. There is a series of discrete contractions. By noting the moments at which each contraction takes place it is possible to follow the succession of impulses discharged by the sense organs involved. It will be seen that the time interval between the discharges increases with the time that has elapsed from the beginning of the mechanical stimulus. Indeed, this response gives a direct demonstration of sensory adaptation (Adrian, 1932). Fig. 5 also shows that as in electric stimulation the size of the contraction depends upon the time interval between the impulses set up. At the beginning of the mechanical stimulus the impulses are close together, and the response is greater than when the impulses become less frequent and facilitation falls off.
For these reasons, any statement with regard to the relationship between response and strength of stimulus must be very carefully considered. A strong mechanical stimulus involving sense organs is not comparable to a single electric stimulus applied to a nerve. Hence there is no reason to suppose that the relation of response to stimulus in the nerve net necessitates properties which are not in full accordance with what we already know of conduction in nerve.

Responses of the disc region.

The responses of the disc differ from those of the column in showing autonomy, greater variety, and apparent decremental conduction. The question arises, how far is it possible to interpret these in terms of the conclusions at which we have just arrived? Electrical stimulation of the disc presents certain difficulties. It is much harder to place electrodes on it without involving tactile stimuli than on the column, where sensory adaptation is rapid (cf. Fig. 5). Also slight movements of the disc are apt to alter the effective threshold of excitation. It is also possible that, owing to the autonomy of the various sectors of the disc, an intense stimulus may independently excite separate regions. These difficulties can be partly overcome by careful isolation of the part stimulated, and in spite of their existence definite evidence can be obtained to show that variation of intensity of the stimulus at any one site is of relatively little importance, while variation of frequency profoundly modifies the response. In Table I is recorded the response of various animals to stimuli applied to the disc at the base of the tentacles. The frequency and intensity of the stimulus is given. There is a tendency for stimuli of a higher intensity to continue to produce responses for a longer period than stimuli of a lower intensity. But, on the other hand, at all intensities a low frequency restricts the response to types characteristic of weak mechanical stimulation, whereas increase in frequency of stimulus promptly evokes the full range of active responses whatever the intensity.

Table I.

\[ a = \text{no response.} \]
\[ a = \text{local contraction of one tentacle.} \]
\[ b = \text{movement of a few tentacles all round disc.} \]
\[ c-c''' = \text{local raising of edge of disc of increasing extent, with movement of local tentacles.} \]
\[ d = \text{slow contraction of column.} \]
\[ e-e''' = \text{increasing stages of sphincter contraction.} \]
\[ x = \text{complete contraction of whole anemone.} \]

<table>
<thead>
<tr>
<th>Potentiometer</th>
<th>Frequency</th>
<th>Response to successive stimuli</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>1 in 4 sec.</td>
<td>( a, a, a, b, b, b, b, d, o )</td>
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<tr>
<td></td>
<td>1 in 4 sec.</td>
<td>( a, a, a, b, b, b, b, b, b, e, b, b, b, o, a, a, a, o )</td>
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<tr>
<td></td>
<td>1 in 0-74 sec.</td>
<td>( a, a, b, x )</td>
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<td></td>
<td>1 in 0-74 sec.</td>
<td>( a, a, b, x )</td>
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<tr>
<td></td>
<td>1 in 10 sec.</td>
<td>( a, c, c, c, a, o, o )</td>
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<tr>
<td></td>
<td>1 in 10 sec.</td>
<td>( a, c, c, c, c, o, o, o )</td>
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<tr>
<td></td>
<td>1 in 2-5 sec.</td>
<td>( a, c, c, c, c, e, c, c, c, c, c, c, c, c, c, c, c, c, c )</td>
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<tr>
<td></td>
<td>1 in 2-5 sec.</td>
<td>( a, c, c, c, c, c, c, c, c, c, c, c, c, c, c, c, c, c, c )</td>
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<tr>
<td></td>
<td>1 in 10 sec.</td>
<td>( a, c, c, c, c, e, c, c, e, x )</td>
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<tr>
<td></td>
<td>1 in 4 sec.</td>
<td>( a, a, b, b, b, b, b, b, b, b, b, b )</td>
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<tr>
<td></td>
<td>then 1 in 1-4 sec.</td>
<td>( e, e', e'', x )</td>
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so long as this is above the threshold value. This is very clear when a change in
frequency is made during a succession of stimuli, and a series of minor responses
is abruptly converted into the most active ones, as in Table I.

In the disc, therefore, a single stimulus produces only a slight response or none
at all. All the more complex responses require a battery of stimuli, and it is the
time interval between stimuli which governs the nature of the response, and not
their strength. It seems reasonable to suppose, therefore, that the various responses
of the disc are called up in succession through facilitation.

The second special feature of the disc responses is the apparent existence of a
decrement of conduction. This is apparent in the “edge-raising” reaction. The
stronger the mechanical stimulus, the more widely is the reaction propagated
round the disc. The reaction is easily evoked electrically, but only by a battery of
several stimuli. Here again above the threshold, the strength of the stimulus is of
no importance; but as the frequency of the stimuli in the battery increases there
is a great increase in the size of the response and also it is propagated further. Its
propagation is easily studied with low-frequency stimuli. There is not a single
contraction wave propagated outwards with an intensity that decreases as it gets
further from the point of stimulation; though this might have been expected were
the conducted excitation to undergo a decrement. Actually each stimulus of the
series calls up a contraction, but with each successive stimulus the contraction
extends by stages further and further round the disc, and ceases to extend the
moment the battery of stimuli comes to an end. While, therefore, the muscles under
the electrodes respond with contractions to the first few stimuli, those some distance
away round the disc do not begin to respond till several stimuli have already
passed, after which they respond in a normal manner. One cannot interpret these
effects by supposing that a stimulus is conducted with a decrement. Evidently,
in a battery of successive stimuli, each member paves the way for the propaga-
tion of its successors into fresh sectors of the disc. The most simple explanation of
this is that the conducting path extends by progressive facilitation between the
conducting units of the adjoining sectors; that is, the response of a sector on the
outskirts of the contracting area differs from the response immediately under the
site of the electrodes only in that several stimuli are required before a conducting
path is established to it. It will not therefore begin to respond to each stimulus until
several stimuli have taken place. This implies that facilitation is taking place between
different sections of the nerve net itself. This “interneural” facilitation will be
considered again in a later paper.

This interpretation of decremental conduction may be extended to other cases.
Bozler (1926) has pointed out that decrementless conduction must obtain in certain
tracts of the nerve net of Medusae. But there are other tracts in which he discovers
a strong decrement, and this he correlates with the appearance of synapse-like
properties between the conducting units. These tracts in many ways resemble the
disc nerve net in their properties. It seems likely that, as in the disc, the apparent
decrement is associated with the response to a battery of many nervous impulses
the spread of which to adjacent conducting units depends on facilitation.
This same interpretation can apply to the nerve net of Echinoids. Both *Strongylocentrotus lividus* and *Arbacia pustulata* show strong conduction decrements as measured by the response of the spines to mechanical stimulation. A number of experiments was performed on these, using electrical stimulation. With stimuli varying in frequency from 1 in 4 sec. to 1 in 0.3 sec., both the extent of the movement of each spine towards the electrodes and the distance to which excitation is propagated increase very rapidly with the frequency of excitation and the number of stimuli given. Variation of the intensity of stimulus, on the other hand, produces but little effect.

There is in fact no good evidence for the existence of a conduction decrement at all, except perhaps in the totally new sense that in such regions of the nerve net a battery of impulses may suffer a decrement of number as it passes into adjacent conducting units, though not of individual intensity. But the use of the term "decrement" in this case is so far removed from its accepted use that it is better not to employ it. In any case, a "decrement" in the number of successfully conducted stimuli passing from one part of the conducting system to another gives no ground for the supposition that the nature of conduction in the nerve net differs from that in ordinary nerve. It is therefore valid to use the hypothesis that the nerve net possesses such properties, and that its peculiar features are due to the special importance of facilitation.

**Physiological properties of the nerve net.**

The peculiar properties that have been ascribed to the nerve net make it necessary to determine how far it is physiologically similar to ordinary nerve. Inherent properties of nerve such as refractory period have been frequently assumed to exist in the nerve net but the evidence is unsatisfactory, and these properties seem to be incongruous with many of its apparent features.

*Chronaxie.*

If the nerve net is physiologically similar to nerve, we would expect the appearance of the familiar relationship between the intensity of a stimulating current and the duration necessary for it to cause excitation. The contractions of the marginal sphincter give a splendidly critical indication of the success of excitation, but a succession of stimuli is necessary for a response. The periodic condenser discharges of a neon lamp oscillator provide a simple means of simultaneously controlling the frequency, strength and duration of a series of stimuli.

The threshold intensity for excitation at each capacity can be found at any desired frequency of stimulation. The duration of the discharge is approximately proportional to the capacity of the condenser over a fairly wide range. In these experiments this was directly determined by estimating the duration of the flash of light in the neon lamp which takes place at each discharge. This was done by means of a revolving mirror. An approximate scale of discharge durations for the particular lamp and circuit employed was thus constructed and placed alongside a scale of capacities, as in Fig. 6.
The Nerve Net of the Actinozoa

In the circuit generally used, the condenser was charged by a 300-volt battery through a 10-megohm variable resistance. The resistance in the discharge circuit, including a small potentiometer from which arose the stimulating electrodes, was about 400 ohms. The resistance of the non-polarisable electrodes in contact with the anemone was usually about 200–300 ohms. The electrodes were placed on the lower half of the column of the anemone, and the frequency of stimulation was adjusted to 1 per sec. The method worked well over an enormous range of frequencies. In unpublished experiments on crustacean nerve comparison of intensity duration curves determined by the neon lamp method with those obtained by means of a Lucas spring rheotome showed that only about 0.5 of the duration of the discharge of the neon lamp was effective for excitation. The chronaxie therefore probably corresponds to about 0.5 time duration of the condenser discharge when the threshold intensity is double rheobase strength.

The result of a typical experiment is shown in Fig. 6. It shows that the actinozoan nerve net can yield an intensity duration curve of the usual form. To estimate a chronaxie, a rheobase must be determined for currents of very long duration. In the present case, this is done by using condensers of very great capacity. To approach constancy of threshold in the nerve-net very long stimuli are required. This condition is fulfilled in Fig. 6, but it is often difficult to determine the rheobase because repeated application of currents of long duration may produce local insensitivity. The sudden development of local insensitivity after repeated stimulation was fairly often met with. A small change in the position of the electrodes or even a reversal of their sign allows excitation to take place again.

![Fig. 6. Intensity duration relation for column nerve net.](image)

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Flash duration

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In Fig. 6 the duration of a condenser discharge which succeeds in exciting at
double rheobase strength is 5-6σ. Comparison of many such experiments shows
that this value falls between 4 and 7σ. Applying the factor 0-5 to this, the chronaxie
appears to fall between the limits 2-4σ. This value may be compared with a chronaxie
of 2σ for vaso-constrictor fibres in the frog. The excitability of the nerve net thus
shows no special features which would lead us to distinguish it from nerve. Indeed
the resemblance is closer than might have been expected. Considering the slow
responses of the anemone and considering that stimulation at a frequency of only
1 per sec. is sufficient to evoke the most active responses of the animal, the chronaxie
is surprisingly small.

Refractory period.

The refractory period of the nerve net was determined as follows. Two pairs
of electrodes, each 2 mm. apart, were placed against the base of the column of the
anemone at a distance of about 4 cm. from each other. The vertical distance from
each electrode to the marginal sphincter was the same. A condenser discharge was
then passed through each pair of electrodes in succession. The intensity of each
discharge and the interval between them was varied as desired. Fig. 2 shows the
usual arrangement. A battery of 300 volts slowly charges two 2μF condensers
through 5-megohm resistances. A clockwork turn-table carrying contact arms
successively discharges the two condensers each through its own resistance of
400 ohms, which includes a 30-ohm potentiometer. The minimal intensity required
on each potentiometer is first found by discharging first with one condenser leading
and then with the other at an interval of 1 sec. Having done this, the intensity from
the leading condenser is maintained just in excess of the threshold value, while the
strength required to give a facilitated response following the discharge of the second
condenser is determined for various time intervals. Fig. 7 shows a curve obtained
in this way. There is a well-defined absolute and a long relative refractory period.
The threshold has returned to normal about 0-5 sec. after the first stimulus. The
absolute refractory period in Fig. 7 is about 60σ, a typical value. In different
experiments this varied somewhat, the lowest value being about 40σ.

The true value of the absolute refractory period is hard to ascertain. In a simple
nerve trunk, only one path is possible for all impulses; in the nerve network
alternative paths are possible. In the present experiment, if excitation is conducted
from each pair of electrodes directly up to the sphincter, the paths traversed are
of equal length. Any delay between stimulus and response due to conduction would
be the same for each electrode pair. The absolute refractory period as measured
would then be a true one. It will be shown later that conduction in the nerve net
of the column does closely approach this condition. But small inequalities of path
may affect the apparent value of the absolute refractory period owing to the com-
parative slowness of conduction in the nerve net. Such errors, however, cannot be
very large, because similar values are obtained for the refractory period with either
condenser leading. In general, the absolute refractory period appears to lie between
40 and 65σ.
The refractory period sets a limit to the frequency of effective stimulation of the nerve net. When a battery of stimuli is applied to the column a facilitated response is produced as in Fig. 4. The threshold remains the same until the stimulation interval becomes less than 0.5 sec. As we see from Fig. 7, this corresponds to the beginning of the relative refractory period. If several stimuli are sent in at intervals within the relative refractory period, the threshold appears to rise steadily. Thus, in Fig. 4, three series of contractions are shown at a stimulation interval of 0.21 sec. Just above threshold intensity, the sphincter responds only to every third stimulus, at double this intensity to every other stimulus, while the intensity has to be raised to five times the threshold value to ensure a response to every stimulus. For a stimulation interval of 0.21 sec. every stimulus falls well within the relative refractory period of its predecessor, and even every second stimulus will be not quite clear of it.

A comparison of the above threshold values with Fig. 7 shows that the threshold rises much more rapidly when a battery of more than two stimuli are sent in at intervals within the relative refractory period. It is as though the absolute refractory period was considerably lengthened with increasing numbers of stimuli. But it is hard to be certain of this, because repeated stimulation at intervals within the

Fig. 7. Refractory period and facilitation of sphincter.
refractory period not only temporarily raises the threshold but tends to induce complete local insensitivity which may be maintained for some time.

The absolute refractory period for two stimuli would correspond to a limiting frequency of about 20 per sec. The natural rate of response does not seem to reach more than half this at most.

*The mode of facilitation.*

By recording the response of the sphincter with a weak isometric lever, the same experiments on which refractory period is determined serve to estimate the relationship of facilitation to the interval between stimuli. No response takes place to the first stimulus. The contraction height is thus a statistical measure of the success of the second stimulus in reaching the muscle fibres. It is shown in Fig. 7.

Facilitation becomes evident when the stimulation interval far exceeds the refractory period. As the interval is shortened, the facilitated response increases more and more rapidly, right into the relative refractory period. It reaches a maximum, however, between $0.2$ and $0.1$ sec., and below this the height of contraction falls off sharply, even though there is no question that the second stimulus is effective. The cause of this effect may be that when the stimulation interval is so short all the branches of the nerve net in contact with the sphincter muscle fibres may not have emerged from the absolute refractory period.

It is interesting to notice that facilitation commences long before the refractory period is entered and reaches a maximum actually in the relative refractory period itself. There is no supernormal phase; so that facilitation cannot be related to this, after the manner suggested by Keith Lucas (1917) for crustacean muscle. On the other hand, the results bear a definite resemblance to those obtained by Bremer on the partially curarised sciatic-gastrocnemius of the frog (Bremer, F., 1930), and may agree with his hypothesis that there is an actual summation of the effects of the action current.

**DISCUSSION.**

In the description of the foregoing experiments it was assumed that electrical stimuli directly excite the nerve net, and further that the physiological properties which have been investigated, such as the refractory period, are characteristic of the nerve net and of no other part of the excitable system. But the experiments have involved the stimulation of an entire organism, and caution must be exercised in comparing them with the results of stimulation of an isolated nerve trunk attached to a muscle. The whole excitable system consists of sense organs, the nervous units which constitute the nerve net and the muscles, and we must consider which of these actually responds to stimulation. It is certain that the muscle itself is not directly stimulated. The electrodes are situated at a considerable distance from the sphincter, and it is easy to show that the response of the latter depends upon the integrity of the intervening tissues of the animal. On the other hand, the response to an electrical stimulus differs materially from that following direct stimulation of a sense organ, for that is followed by the discharge of a battery of impulses which
comes to an end while these organs undergo their characteristically rapid adaptation whereas each electrical stimulus only produces a single response. A great deal of light can be thrown on the problem by a study of the refractory period. Since it is obtained by successive stimulation at two independent sites, the refractory period cannot be that of separate localised excitable elements which transmit excitation to the nerve net. For the refractory period of an element restricted to the neighbourhood of the first electrode cannot affect the success of a stimulus applied to a similar element elsewhere. The refractory period must therefore apply either to the nerve net itself, or to the responding muscle. But, from Fig. 7, stimuli applied to two independent sites on the column show the existence of a relative refractory period with a continuously increasing threshold up to the absolute refractory period. This can only be explained by supposing that the excitation wave following the first stimulus reaches the very region itself of the excitable system which is influenced by the second stimulus. We have seen that the muscle itself is not directly excited, there remains therefore the only possibility that the stimuli are directly exciting the nerve net, and that the refractory period measured is that of some part of the nerve net itself. It does not necessarily follow that the refractory period of all parts of the nerve net is the same, but the stimuli excite a physiologically continuous system, and the measured refractory period applies to those parts of the system immediately below the stimulating electrodes.

The evidence also shows that the wave of excitation passes over the entire nerve net of the column, for stimulation at any point on it throws the whole column into a refractory period. In addition to this there is a mass of evidence to show that the nerve net of the column not only conducts excitation diffusely in all directions, but behaves as a single conducting unit. In the response of the sphincter, although there is no response to the first stimulus, a conducting path is certainly established through from the site of stimulation to the muscle by the second. Again, in responsive animals, a single stimulus may produce a reaction in the form of a slight waving of tentacles scattered round the disc. This reaction is evoked from any point on the column and requires no previous stimulus to ensure its appearance. We are thus brought to the remarkable conclusion that the whole nerve net of the column acts as a conducting layer in its most simple form, directly transmitting excitation from the site of stimulus to the muscle. Such an arrangement is far simpler than the most elementary reflex arc, and indeed it is simpler than anything which the nerve net has previously been considered to exhibit. This simplicity is restricted to the nerve net of the column and does not obtain in that of the disc. It is the cause of the symmetrical character of the responses to stimulation of the column. The contraction of the sphincter, of the parietal, or of the longitudinal mesenteric muscles does not develop gradually from the region of the stimulus. The muscles are activated equally all round the axis of the animal. But with so simple a conducting mechanism, the question naturally arises: how can any variety of response, such as undoubtedly follows stimulation of the column be obtained? We shall consider this fully in a subsequent paper. But since the nerve net of the column behaves as a single conducting unit, it is evident that the facilitation found in the response of such
muscles as the sphincter must occur between the nerve net and each individual muscle, and it is evident that there is scope here for a considerable variety of response.

In conclusion, let us consider the special properties of the nerve net in the light of the results obtained. Of diffuse excitation there is no doubt, though it is clear that it may be of two kinds, complete, as in the nerve net of the column, or restricted, as in conduction in the disc. But the statement that the response varies with the strength of the stimulus needs complete reconsideration. An excitation wave set up by stimulation of the nerve net is independent of the strength of stimulus. In actual fact, a stimulus which succeeds in producing only a single excitation wave in the nerve net produces no response at all or only a trivial one, whatever may be its strength. But a stimulus applied to the surface of the animal excites the sense organs to send out not one, but a group of impulses and it is entirely upon the number of, and interval between these, that the response depends. Finally, the supposed conduction of excitation with a decrement is not true under any circumstances. The distance through which a single excitation wave is propagated is independent of the strength of the stimulus. In the column nerve net of Calliactis the excitation wave passes over the whole system. In the nerve net of the disc, on the other hand, the excitation wave is restricted to the region stimulated. Excitation, however, is propagated to adjoining regions when several stimuli succeed each other at short intervals. Though there is no evidence of a decrement in the intensity of an individual excitation wave, the distance excitation is propagated in the disc increases with the number and frequency of the excitation waves set up. By facilitation between adjacent parts of the nerve net, each successive excitation wave is enabled to travel further than the last. But the stronger a mechanical stimulus on the disc, the greater is the number and frequency of impulses discharged from the sense organs; and hence the further does the response spread.

The nerve net consists of units which behave like true nerve. It is characteristic that it tends to conduct stimuli in all directions; but its most striking feature is the extreme degree to which facilitation is developed both within the net and between the net and the muscles.

SUMMARY.

1. Certain features have been supposed to characterise the nerve net. Response is said to vary with the strength of stimulus; and while conduction may occasionally take place in an all or nothing manner, yet in general conduction is supposed to take place with a decrement. To investigate these points, the responses of Calliactis parasitica to mechanical and electrical stimuli have been investigated.

2. Electrical excitation of the column of the anemone shows that a response results from a succession of stimuli and not from a single stimulus. The character of the response is independent of the strength of the individual stimuli. It depends solely upon the number of stimuli and upon the interval of time between them. All responses are highly developed facilitation phenomena. Each electrical stimulus induces a single excitation impulse in the nerve net.
3. But a mechanical stimulus is followed by the discharge of a battery of impulses from the sense organs. These increase in number and frequency with the intensity of the mechanical stimulus. A response may therefore vary with the strength of a mechanical stimulus, but only in relation to the number and frequency of impulses discharged by the sense-organs.

4. Stimulation of the intact column of the anemone shows complete conduction over its whole nerve net. Mechanical stimulation of the disc appears to show conduction with a decrement. Such a stimulus excites a battery of impulses. Each impulse is conducted without decrement, but it facilitates the entrance of succeeding impulses into adjoining sections of the disc nerve net.

There is no decrement of excitation strength under any conditions in the nerve net. But there may be a numerical decrement as a battery of impulses spreads from a stimulus.

5. The nerve net is physiologically similar to ordinary nerve. A method is described for determining the strength duration relationship for the threshold of electrical excitation of the nerve net. The relation is of the usual form with a chronaxie of about 2-4α. The nerve net has well-defined relative and absolute refractory periods: the latter is about 40-65α. The relation of facilitation to refractory period is considered.

6. The whole nerve net of the column of the anemone acts as a conducting layer in its most simple form, directly transmitting excitation from the stimulus to the muscle. Facilitation takes place between the nerve net and its appropriate muscles. Conduction in the disc nerve net involves facilitation between parts of the nerve net in addition.

7. The true characteristics of the nerve net are diffuse conduction and the extreme development of facilitation. Diffuse conduction may be total, as in the column, or restricted, as in the disc of Calliactis. Facilitation may be between the nerve net and the muscles, or between parts of the nerve net.

Most of this work was done while holding the Cambridge University Table and the Bidder Fund at the Stazione Zoologica, Naples. I wish to express my sincere thanks to Dr R. Dohrn and his staff for their hospitality, and the great facilities they gave me. The cost of some of the apparatus was defrayed by a grant from the Government Grant Committee of the Royal Society.
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THE NERVE NET OF THE ACTINOZOA

II. PLAN OF THE NERVE NET

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(Received 1st December, 1934.)

(With Four Text-figures.)

INTRODUCTION.

In the previous paper an analysis was made of the mechanism of excitation and response in the anemone Calliactis parasitica. The general physiological properties of its nerve net were shown to differ in no fundamental way from those of true nerve. The property of diffuse conduction of excitation alone is unique, and this depends upon morphological organisation. But in the neuromuscular system as a whole, certain features are developed to an unusually high degree. This is particularly true of the facilitation of the transmission of excitation, both between the nerve net and the muscles it serves and between the units of the nerve net itself. This power of facilitation appears to be responsible for the characteristic relations of response to stimulus in several animals possessing nerve nets.

The nerve net of Calliactis shows differentiation into different regions of distinctive properties. In this paper an attempt is made to find out the significance of these and the way in which the whole net is organised. The methods employed have been described in the previous paper (Pantin, 1935).

RESPONSES OF THE COLUMN.

Previous experiments have shown that the whole nerve net of the intact column of the anemone behaves as a single conducting unit. When excited, this system can call into action the circular muscle of the column, the parietal muscles which run vertically up the inner surface of the column at the base of the mesenteries, the longitudinal muscles of the mesenteries themselves, and the powerful sphincter just below the margin of the disc. Particular attention was paid to the sphincter muscle, the response of which was proved to be governed by the number and frequency of the impulses excited in the net by stimulation. But the sphincter is not the only muscle which can be brought into action by stimulation of the column. A variety of responses is possible, possessing the one feature in common that the muscles which bring them about react symmetrically all round the axis of the animal, that
is, contraction is not locally more intense at the site of the stimulus. The question naturally arises how so simple a conducting system as the column nerve net can permit various distinct responses. Fig. 1 B shows the responses elicited by stimulation of the column. Very light mechanical stimulation often calls up local contraction of the circular muscles which may initiate a peristaltic wave. Moderately weak stimulation causes the animal slowly to shorten with the disc expanded, through contraction of the parietal muscles, and a slightly stronger stimulation causes this to be accompanied by withdrawal of the disc through contraction of the mesenteries. Very strong mechanical stimulation is immediately followed by contraction of the sphincter. Jordan (1908) described the somewhat similar successive responses to mechanical stimuli in Actinoloba (Metridium) dianthus. He described the succession as an unloosing mechanism typical of many lower organisms, and supposed that the different muscles were called into action by possessing different thresholds.

![Diagram of Anemone](image)

Fig. 1. A, method of sphincter and mesenteric recording; B, diagrammatic representation of symmetrical responses.

All such responses are easily called up by suitable electrical stimulation. It has been shown in the earlier paper that the response of the sphincter is independent of the intensity of the electrical stimulus, so here we find that the particular muscle which is called into action and the extent of its response is independent of the intensity of the stimulus. The responses for all the muscles served by the column nerve net are evoked at exactly the same threshold. If, on the other hand, the frequency and number of electrical stimuli is varied, the mechanism by which the different muscles are called into action immediately becomes apparent. None of the muscles respond to a single electrical stimulus but only to a series of stimuli of low frequency. Just as the sphincter contraction is governed by its power of facilitation, so also do the other muscles show facilitated responses. But the critical frequency at which each muscle commences to respond, and the number of stimuli required to bring it into action, differ in an orderly manner.

The responses of the individual muscles can be recorded by arranging a series of ties to restrict the movement of particular parts of the anemone, as in Fig. 1 A.
A record of such an experiment is shown in Fig. 2. This shows the simultaneous record of the sphincter contractions (upper tracing) and the response of the mesenteric muscles (lower tracing). The latter registers both the contractions of the longitudinal mesenterics and the parietals. Owing to the changes of shape which the anemone undergoes it is not possible to restrict the responses of either lever to one muscle. In the figure, the contractions of the mesenteric and parietal muscles appear as a slight background on the record of the sphincter lever, and, as the experiment proceeds, the lever registering the contraction of the mesenterics and parietals becomes greatly influenced by the powerful contractions of the sphincter itself. Nevertheless, it is not difficult to disentangle the responses of each muscle.

The series of records in the figure shows the responses of the various muscles simultaneously to stimuli of progressively increasing frequency. One of the most

remarkable features is the extraordinarily low frequencies with which the nerve net appears to be concerned. The anemone employed in the experiment illustrated required a rather higher rate of stimulation than the average. In some cases a stimulus every minute ultimately produced a response. In Fig. 2 stimuli given at a frequency between 1 in 10 and 1 in 6 sec. called forth very slow contractions of the circular muscle of the column which gave no record. But at a frequency of stimulation of 1 in 3 sec. a very slow contraction of the parietals took place. At 1 in 2 sec. the contraction recorded in the lower tracing is very clearly double, a slightly more rapid contraction of the longitudinal mesenterics (which depress the disc) appearing as a hump prior to that of the parietals. And this longitudinal mesenteric response is enormous at 1 in 1.45 sec. The stimulation at a frequency of 1 in 1.10 sec. shows all the muscles responding. The longitudinal mesenteric contraction is much greater than that of the parietal, and in addition the sphincter
is beginning to respond. Finally, at 1 in 0.60 sec. the sphincter response predominates and is followed by a small longitudinal mesenteric response alone.

The rate of contraction of the sphincter increases with the frequency of stimulation. The same thing happens in the longitudinal mesenterics, and probably also in the parietals (Fig. 2). But at the highest frequencies the contraction of the mesenterics and parietals is apparently diminished. This seems to be brought about by two things. First, the natural rate of contraction of these muscles reaches a maximum at comparatively low frequency beyond which it does not materially increase and may even diminish. Further, although these muscles commence to respond at a very low frequency, yet, compared with the sphincter, the number of stimuli required to produce a response is very large. This has an important consequence, because a short battery of high-frequency stimuli, as in the last tracings in Fig. 2, can in this way produce a maximal response of the sphincter before any serious contraction of the mesenterics and parietals is called forth. This is significant, because owing to sensory adaptation even a strong mechanical stimulus only sets up a brief train of impulses (Pantin, 1935).

Not only do the muscles increase in contraction rate with frequency of stimulation, but also there is a definite relationship between the natural speed of contraction of each muscle and the relative ease with which it can be activated. Jordan pointed out that there was an apparent relation between the relative rapidity of action of various muscles in Actinoloba and the "strength" of stimulus necessary to activate them. It is evident from Fig. 2 that the full description of the phenomenon is that the lower the natural speed of the muscle, the lower is the frequency of excitation at which its response begins to be facilitated. At its maximum speed the circular muscle of the column takes many minutes to reach its maximum contraction, whereas this is reached in 1 or 2 min. by the parietals, in \( \frac{1}{4} \)–1 min. by the longitudinal mesenterics, and in a matter of seconds by the sphincter.

These experiments show that through gradation of the effective rates of facilitation to the various muscles served by the column nerve net, together with gradation of their natural speed of contraction, a remarkable gradation of varied responses is in turn rendered possible in the anemone even though the intact column net acts as a conducting unit in its simplest form. By virtue of the universal conduction of the column nerve net all muscles of each class are symmetrically activated about the axis of the animal.

**DIFFERENTIATION IN THE NERVE NET.**

A wave of excitation initiated in the column nerve net seems to spread over the whole of it. On the other hand, in the disc the response to a stimulus remains localised, so that there is a high degree of autonomy. Only by a succession of stimuli can excitation spread. The impulse set up by each stimulus not only evokes a response locally but facilitates the passage of the next impulse into adjacent regions of the disc. In a battery of impulses therefore each successive impulse is able to travel farther from the site of stimulation. This kind of facilitation has been
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referred to in the previous paper as "interneural" facilitation, because it appears to take place between units of the nerve net as opposed to neuromuscular facilitation such as that which takes place between the column nerve net and the sphincter.

The degree to which this type of facilitation is developed varies very greatly in different parts of the disc. Tangentially, very many stimuli are required to propagate excitation round the disc. Thus, the "edge-raising" feeding response may require ten or more stimuli to extend it round one-third of the disc circumference; whereas radially very few stimuli are required to establish a conducting path, and after long experimentation there may even be through conduction from the outset. Provided excitation is maintained for long enough, and at a high enough frequency, a conducting path can become established between any point on the disc and the column nerve net, that is, continued excitation of the disc can ultimately evoke the sphincter reaction. As this reaction is easily recorded, this enables us to obtain some estimate of the power of interneural facilitation along different paths in the disc nerve net.

When the sphincter contraction commences in response to stimuli applied to the disc, the contraction once initiated is precisely similar to the contraction elicited from any part of the column by stimuli of the same frequency. The fact that conduction takes place in the disc in a manner different from that in the column in no way modifies the response once initiated. But whereas from any point on the column the facilitated response of the sphincter begins at the second stimulus, it may not begin until the third, or even later stimulus when excitation is applied in the disc. Fig. 3 A shows the delay in commencement of the response by one stimulus when the sphincter contraction is elicited by stimulation at the mouth. This is compared with the same response elicited by stimulation of the column. The difference is merely a delay of the appearance of the response by one stimulus, and not an alteration of its form. When on stimulation of the disc one or more extra stimuli are required before a response appears, the intervening, apparently ineffective stimuli, must in fact be establishing a conducting path between the site of stimulus and the column nerve net controlling the sphincter muscle. That is, the extra stimuli required appear to represent stages of interneural facilitation within the disc nerve net.

Interneural delay is most evident where autonomy is greatest, as in an isolated tentacle. By allowing a single tentacle to adhere to the stimulating electrodes these can be kept at some distance from the rest of the body, so that there is no fear of irradiation of the stimulus to other regions. Under these circumstances ten or fifteen stimuli may be required before a conducting path is established to the sphincter, though as soon as this is done the muscle responds in the usual way.

The extent to which interneural facilitation is developed varies considerably with the individual and with the previous history. It is greatest in resting animals. But once through conduction is established it tends to endure for long periods, so that in animals which have been subjected to prolonged experimentation abnormally few extra stimuli are required to establish a conducting path to the sphincter. It seems that facilitation lasts longer between units of the disc nerve net than between the column nerve net and its muscles.
The nerve net of the disc shows considerable physiological complexity. It would seem natural therefore to regard the condition of universal conduction in the column nerve net as simpler. In one sense this is so; but the simplicity of the conducting mechanism has in all probability only been achieved through considerable morphological organisation. Despite the universal conduction of the intact column, the existence of interneural facilitation in parts of its nerve net can be demonstrated if the column is subjected to cutting or the partial isolation of various pieces. Numerous experiments were carried out in which the edge of the pedal disc, together with the base of the column, was separated from the rest of the body round most of its circumference. As Parker (1918) had shown in *Metridium* a “tail” prepared in this way still allows transmission of excitation to the body of the anemone along the nerve net, though lateral transmission higher up the column is often imperfect (Parker, 1917 a). This was fully confirmed in *Calliactis*. But, in addition, the important fact emerged that frequently several preliminary stimuli were required before a conducting path was established between the end of the tail and the main nerve net of the column. This delay depends simply upon the transverse conduction. If the anemone is completely divided through the disc, pharynx and column, down to within 1 cm. of the base of the column on either side, conduction from one-half of the animal to the other frequently shows this interneural delay in which a few stimuli are required to establish a conducting path.

Fig. 1. A₁₁, interneural delay in the disc (one stage); A₄, normal response from column. B₁₁, interneural delay in lateral conduction across a cut in the column (as in Fig. 4 B); B₅, the same after occasional stimulation: note establishment of through conduction; B₆, normal response from column. C, occasional conduction in column deprived of mesenteries. Dots show successful stimuli. All stimuli 1 per second.
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This is seen in Fig. 3 B₁. The necessity for establishing a lateral conducting path by preliminary stimuli in organisms on which such operations have been performed is most clearly seen in specimens which have rested for some days before experimentation. A brief amount of stimulation rapidly induces more or less permanent through conduction in these cases. In Fig. 3 B₂, following the experiment shown in Fig. 3 B₁, through conduction has become established so that the stimuli directly facilitate the sphincter.

These facts suggest that the property of through conduction in the intact column is in some way related to vertical conduction, and therefore perhaps with the mesenteries. This is borne out by experiment. If a vertical strip of the wall of the column is cut, which includes the underlying mesenteries, through conduction to the sphincter is obtained in a normal manner by stimulation at the end of the strip. If, however, the mesenteries of such a strip are cut across, however wide the strip may be, it is only with the greatest difficulty that through conduction to the sphincter can be established at all, and it repeatedly breaks down, so that the sphincter fails to respond to every stimulus in a battery (Fig. 3 C). The through conduction characteristic of column stimulation depends upon the intactness of the mesenteries. Lateral conduction in the column, and still more vertical conduction apart from mesenteries, show well-marked interneural facilitation, just as does the disc. Despite its apparent simplicity of action when intact, the nerve net of the column itself exhibits an underlying complexity.

THE VELOCITY OF CONDUCTION.

Considerable light can be thrown upon the plan of the nerve net by study of the velocity of conduction of excitation in its different parts. The recorded velocities in Actinians are comparatively low. Parker (1918), for *Metridium*, gives the value of 12–14 cm. per sec. This was obtained by cutting a long strip round the pedal edge and stimulating by a battery of stimuli from an induction coil. The responding muscles in this anemone are the longitudinal mesenteries. Conduction in some Coelenterate nerve nets, however, can take place very much faster than this. Harvey (1912), in *Cassiopeia*, records 77 cm. per sec. Since we have demonstrated that facilitation plays an important part in Actiniozoan responses, the possibility that interneural facilitation may superimpose a delay which would falsify apparent conduction velocities must not be overlooked. From this cause, propagation of excitation in the disc necessarily seems to be a slow process, since it only progresses by stages corresponding to each separate impulse set up by the stimulus. It is evident that this difficulty can only be satisfactorily overcome by using a muscle which gives distinct contraction increments corresponding to each impulse reaching it from the nerve net. The marginal sphincter of *Calliactis* is perhaps more suitable than any other muscle for this purpose. Each separate contraction is readily visible, and its latent period after the stimulus can easily be determined.

In the following experiments the animal was stimulated by silver-wire electrodes, 2 mm. apart, applied at various points on the body. A metronome controlled neon-
lamp stimulator was used, as described in the previous paper. It was adjusted to give a frequency of excitation of exactly 1 per sec. The records obtained are similar to those shown in Fig. 3. The difference in time between each stimulus and the contraction corresponding to it is easily seen. The experiments were conducted at 18–20°C. In determining conduction velocities, some difficulty attaches to the variability of the anemone’s shape. Passive stretching can proceed to almost any extent, till rupture occurs. In these experiments, the anemones were placed on flat glass plates to which they were allowed to adhere. They were then left in large glass jars in aquarium water overnight, after which they were fully expanded. In this condition their dimensions were measured.

![Diagram](image)

Fig. 4. A, B, C and D, latent periods of sphincter contraction in operated animals. Times in hundredths of a second. Temperature 18–20°C. E, scheme showing conduction velocities in *Calliactis* (cm. per sec.).

When strips are cut round the circumference of the pedal edge of *Calliactis* leaving an attachment to the body, low conduction velocities are found which consistently agree with those found by Parker in *Metridium*, that is, they are of the order of 10–20 cm. per sec. But in *Calliactis* the sphincter is very well defined, and the distance between the junction of the strip with the intact pedal edge on the one hand and the sphincter on the other can be accurately measured. When this is done, and the records are examined, it is found that the velocity of conduction vertically up to the sphincter has a much higher value. Thus, in Fig. 4 A, an anemone with a “tail” 14 cm. long exhibited a latent period of contraction of 1-28 sec. when stimulated at the very end of the “tail,” and corresponding times when stimulated at intermediate positions. This corresponds to a velocity of about 12 cm. per sec. On the other hand, when the anemone is stimulated at the pedal intact edge the sphincter responds within 0.11 sec. The dimensions of the sphincter in *Calliactis*
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are clearly defined, and the minimum path that the impulse must have travelled in this case was $5\frac{1}{2}$ cm. Even if the muscle itself and the recording apparatus exhibited no latency of response, it is evident that the conduction velocity in a vertical direction is of the order of at least 50 cm. per sec. Actually, if we stimulate the outside of the column immediately above the previous site of stimulus and directly over the sphincter itself, a latent period is found of 0.05 sec. Subtracting this from 0.11 leaves a conduction time of 0.06 sec., which corresponds to a minimum velocity of about 90 cm. per sec. It is clear, therefore, that lateral and vertical conduction take place at very different rates.

Not only are the vertical and lateral velocities very different but these in turn differ from the rate of conduction through the column wall. This appears to be very slow. A stimulus placed on the column outside the sphincter, as in Fig. 4 A, has a latency of 0.05 sec. But a very strong stimulus applied by electrodes across the edge of the disc can directly excite the sphincter. The response commences with the first stimulus and the latent period has now the reduced value of 0.03 sec. The difference of 0.02 sec. may be attributed to conduction from the outer surface of the column to the sphincter embedded in its mesogloea. This distance can only roughly be estimated, but it is not more than 1 or 2 mm. This corresponds to a velocity of 5–10 cm. per sec.

The significance of these different conduction rates was determined by operating on the animals in various ways. Fig. 4 C shows an anemone cut in two by a vertical incision to within 1 cm. of the edge of the pedal disc. Care was taken to separate the oesophagus on the two sides so that the only point of contact between the two halves is by the column wall or by the pedal disc. Such an operation greatly delays the conduction of excitation from one half of the disc to the other. But Fig. 4 C shows that this delay takes place in passing laterally across just that part of the column which connects the two halves. There is as much as 0.22 sec. difference in latent period between two points 1 cm. above the pedal edge and 2 cm. apart, one of which is one side and the other the other side of the cut. Here again we have the low lateral velocity of conduction which in different experiments varied from 9 to 20 cm. per sec.

The short time taken for excitation waves to travel vertically in either direction is very evident from Fig. 4. In conjunction with the low lateral velocity, this indicates that there exist longitudinal paths of high conduction velocity, and it is natural to suggest that these are in the mesenteries. Experiments support this. In Fig. 4 C a stimulus applied on the mesenteries shows a latency of only 0.08 sec., whereas opposite this point on the column wall there is a latency of 0.14 sec., although the distance travelled to the sphincter is approximately the same in both cases. Not only does direct stimulation of the mesenteries yield very high conduction rates, but the threshold of excitation in their neighbourhood is much lower than elsewhere in the animal.

If the mesenteries are as far as possible removed and their basal portions scored across without cutting into the column, the conduction velocity decreases enormously (Fig. 4 D, right half). This decrease in conduction rate is accompanied by
the appearance of interneural facilitation. Such an operation is necessarily a very drastic one, yet, nevertheless, the results show with certainty that damage to the mesenteries is sufficient to destroy the characteristic high vertical velocity of conduction.

The importance of the mesenteries can be shown in another way. In Fig. 4 B a vertical strip is cut from which the mesenteries have been removed as far as possible. The operation results in the appearance of a low vertical conduction velocity as in Fig. 4 D. But, on the other hand, the converse experiment is possible. A portion of the organism above the pedal edge was carefully isolated from the rest of the body by cuts extending completely through the column. Contact was retained only via the mesenteries. Fig 4 B shows that the latency exhibited when stimuli are applied in this isolated piece is of the same order as on the neighbouring intact pedal base. It seems certain that the high vertical velocity of conduction depends on the intactness of the mesenteries and on these alone.

The slow rate of conduction through the column from the surface is apparent in all these experiments. In Fig. 4 C it will be seen that excitation actually takes considerably longer to pass to the opposite side from a stimulus on the column 1 cm. from the cut (0.36 sec.) than it does from a stimulus on the edge of the half of the oral disc above it (0.27 sec.). Though in the latter case the distance travelled by the excitation wave must be nearly double that of the former, yet the time it takes is actually 30 per cent. or so less. Again, by comparing the latent period following stimulation of the column with that following direct stimulation of the mesenteries within, a direct estimate can be found for the time taken for excitation to cross the column wall. In Fig. 4 C this is from 0.06 to 0.09 sec. The column wall has a thickness of some 2–3 mm. Although the figures can only be approximate, the average conduction rate in this and other cases appears to have low values of between 2 and 10 cm. per sec. We are thus left with a picture of a conducting system in the column itself with a lateral rate of some 15 cm. per sec., and able to conduct stimuli inwards from the surface at about 4 cm. per sec. In addition to this it seems probable that the net of the column itself can conduct vertically even when the mesenteries are removed. Experiments such as Fig. 4 B and D suggest a rate of vertical conduction of the order of 10 cm. per sec. But in view of the drastic nature of the operation of removing the mesenteries and cutting them across, this must be accepted with caution. But in any case, in addition to the column itself, there is the mesenteric system which is characterised by high vertical conduction rates which attain the order of 120 cm. per sec.

The vertical conducting paths of the mesenteries are connected together by a lateral conducting ring in the neighbourhood of the sphincter. This muscle appears to contract as a whole from whatever point on the body excitation is applied. There is great mechanical difficulty in determining the relative latency of one side of the disc compared with another. But experiments indicate that there is a difference in latency of less than 0.05 sec. for points 5 cm. apart round the disc edge. This gives a lateral conduction rate of the order of 100 cm. per sec. The exact region which this conducting ring occupies has not yet been definitely ascertained, but it is
certainly in the neighbourhood of the sphincter, for cuts extending through this on both sides of the disc suffice to isolate the two halves of the sphincter, so that they respond with appreciably different latent periods. This conducting ring completes the mesenteric rapid conduction system. In no other region is there high-speed lateral conduction. Removal of the whole pedal base in no way prevents the sphincter contracting as a whole from whatever point the stimulus is applied.

The conduction rate radially in the disc is also comparatively high, being of the order of 60 cm. per sec. No satisfactory method was devised for determining conduction velocities in other directions in the disc. The approximate velocities in different directions are shown in Fig. 4 E.

PLAN OF THE NERVE NET.

Both the study of the relative development of interneural facilitation and of conduction velocity within the nerve net give consistent pictures of its physiological organisation in Calliactis. Indeed, there is a definite relationship between the velocity of conduction and the development of interneural facilitation. The velocity is greatest where interneural facilitation is least. It is not meant by this that the low velocity is due to the time taken for a succession of stimuli to establish a conducting path, but that the actual velocity in these tracts themselves is low even when through conduction has been established. With the evidence before us we can try to construct a physiological picture of what the nerve net of Calliactis is like and can then compare it with what is known of its morphological organisation. Covering the whole body of the animal there appears to be a nerve net where interneural facilitation is well developed and in which the conduction velocity is low. This primary structure is modified in varying degrees. In the tentacles and in the disc generally, interneural facilitation obtains, with its consequent high development of autonomy. But radially from the mouth there are paths in which conduction takes place at a much higher rate and with a less degree of interneural facilitation. At right angles to these, and about the tentacles, interneural facilitation is so very evident that there must be numerous links in the chains of conducting units running round the disc.

In the column, as distinct from the mesenteries, there is a conducting network with its relatively low conduction velocity and a tendency towards interneural facilitation, particularly in the vertical direction. Lateral conduction is best developed round the pedal edge, which is also the most sensitive to stimuli. The middle region of the column is less sensitive. This primary system is altogether modified by the mesenteric-sphincter through-conduction system. This system is directly accessible to electric stimuli and probably therefore has direct connections extending to the surface of the column. The mesenteric-sphincter system acts as a single conducting unit, communicating with all the symmetrically responding muscles. In the case of the sphincter, communication is direct, except for the facilitation between the net and the muscle. But whether the system is in such direct communication with the mesenteric and parietal muscles as it is with the sphincter is less certain. These muscles can undoubtedly be set in action sym-
metrical by the sphincter-mesenteric system. But it is possible that there exists interneural facilitation between this system and these muscles. They exhibit a very long latent period covering several stimuli, and in Calliactis they contract so slowly that mechanical summation smooths out the responses to individual stimuli. Stimulus and response cannot therefore be correlated directly, as in the sphincter.

This plan agrees with the morphological structure very well.

The Hertwigs (1879) have fully described the nerve network of Calliactis (Sagartia) parasitica. The net is very rich, particularly in ganglion cells, at the bases of the tentacles and in the stretches between them. From the crown of tentacles, strands containing big bipolar cells run in towards the mouth more or less separated from each other. This radial structure clearly agrees with the tendency to radial conduction already noticed. On the other hand, the complication of the net at the periphery round the bases of the tentacles is again what might be expected, for in this region many complex responses can be evoked which must involve separate nervous elements only communicating by interneural facilitation.

In the column, the nerve net becomes sparse, but in the mesenteries it is very well developed and constitutes a system of fibrils running the whole length of the mesentery. These clearly correspond to the through-conducting mesenteric paths which we have established physiologically. The Hertwigs point out that these fibres are thicker than those in the rest of the nerve net, and this is precisely what we should expect in view of their high conduction velocity (cf. Gasser and Erlanger, 1927).

The plan of the nerve net is based on a system with marked interneural facilitation extending over the whole organism. Within this are certain well-defined tracts where through conduction is established to a greater or less extent, namely the mesenteric-sphincter system and to a less extent radial paths in the disc. This suggests that despite their simplicity the through-conduction systems are in fact specialisations. The effect of this specialisation is to divide the neuromuscular system of Calliactis into two distinct parts, the disc, where feeding reactions predominate, and the column; this, with its specialised through conduction and its successive muscular responses of parietals, mesenterics and sphincter, gives a graded series of protective reactions. This system is very well adapted to the special conditions under which the organism lives. Its mode of life on the shell of the hermit crab entails continual mechanical disturbance. To the greater part of this disturbance the animal must remain indifferent if it is to attempt to obtain food at all. But frequently grosser mechanical shocks necessitate abrupt concerted action of its musculature in order to produce sudden protective movements in the animal. The sphincter and mesenteric contractions fulfil this purpose excellently. On the other hand, the column as a whole is largely used as a machine for carrying the disc and bringing its surface in contact with food material on the ground, and protecting it when it is harmed. When the disc is in its correct site, the ordinary feeding reactions can take place. For these asymmetrical responses are evidently necessary and a through-conducting system would be unsuitable. It is here that interneural facilitation is most evident, with its correlative autonomy.
COMPARISON WITH OTHER SPECIES.

Owing to its peculiar mode of life, Calliactis represents an extreme type from which other species diverge to varying extents. The physiological development of the sphincter is greater here than in other species. In some other members of the Metridiidae there appears to be a general similarity to Calliactis, though the sphincter response is less in evidence. In the genus Metridium (Jordan, 1908; Parker, 1919) the primary protective response is supplied by the contraction of the longitudinal mesenteries. Only after the disc has been withdrawn by these muscles does the contraction of the sphincter complete the protective process by covering the disc, whereas in Calliactis the sphincter covers the disc before any other response has become evident. Apart from this somewhat important difference, the general behaviour is very much the same, nor does the structure of the nerve net appear to differ very greatly. Outside this family, however, divergence seems to be greater, chiefly owing to lower development of the specialised through-conduction mechanism. This is correlated with reduction of the sphincter.

Few species differ more widely from Calliactis parasitica than Anemonia sulcata. Experiments with this showed no evidence of a through-conduction mechanism. It seemed impossible to bring any effectors symmetrically into action round the axis of the animal. Wherever stimuli were applied, only local responses were obtained. As in Calliactis, excitation of disc and tentacles produces a local response, which, however, can spread to adjacent sectors by the facilitation of a succession of stimuli. Eight to ten stimuli are required to propagate excitation across about 60° of the disc, and it is only with the greatest difficulty that a response of the whole disc can be obtained, for with very prolonged batteries of stimuli insensitivity supervenes. This applies both to mechanical and to electrical stimulation. These asymmetrical responses of the disc produce very decided feeding reactions, local stimulation of a tentacle causing this to withdraw towards the mouth, while as stimulation proceeds the mouth is pulled towards the site of stimulus and adjacent tentacles move towards it. The independence of the disc effectors is more evident than in Calliactis; but it is in the response to excitation of the column and the pedal edge that their behaviour is most distinct. In Anemonia this simply calls forth a contraction of the parietal muscles at the site of stimulus which does not spread round. By continued stimulation the parietal muscles locally pull down the edge of the disc towards the site of stimulus, and the whole surface of the disc, with the mouth and the tentacles, is thus brought to bear upon it. In fact, every response from the column as well as the disc is a localised feeding response. In Anemonia the sphincter is scarcely developed and the disc does not close. Indeed there appears to be no reaction which is obviously protective. Repeated attacks only cause irregular local contractions and insensitivity, while the water of the enteric cavity is expelled and the whole animal shrivels to an inert mass.

In contrast with Calliactis, isolation and autonomy of different parts is at a maximum in Anemonia, while the wholesale protective responses of the through-conduction system are at a minimum. All the responses which depend for their
existence upon autonomy are highly developed. Pedal locomotion is very well
developed in Anemonia, and the autonomy of the pedal disc in this reaction is well
known (Parker, 1917 c). In contrast with this, the only action which the pedal disc
of Calliactis undertakes is to spread out over the surface with which it is in contact
and adhere to it. Even in the disc, the independence of various parts is much more
in evidence in Anemonia than in Calliactis. This effect is greatly intensified because
the tentacles and disc of Anemonia are more sensitive to mechanical stimuli and
undergo sensory adaptation very much less rapidly than those of Calliactis. As a
result of this sensitivety, the co-ordination of neighbouring tentacles in Actinia in
response to food is to a very great extent mechanical in its origin, the movement of
one tentacle stimulating its neighbours to respond also, to some extent in a manner
analogous to a chain reflex.

Between the extremes represented by Calliactis and Anemonia, Actinia equina
occupies an intermediate position. In the disc responses, it closely resembles
Calliactis. On the other hand, stimulation on the side of the column causes local
parietal contraction as in Anemonia. If, however, the very sensitive pedal edge is
touched, a symmetrical retraction takes place. Like Calliactis, therefore, there
exists a through-conduction system able to bring effectors symmetrically into action,
but this is accessible only from the pedal edge and not from the side of the column.
The retraction produced in this response is a protective reaction. It is not primarily
due to contraction of the marginal sphincter, like Calliactis. As in Metridium, the
first response is a contraction of the longitudinal mesenteric muscles, the contraction
of the sphincter only completing the closure of the disc after this has taken place.
An interesting feature observed in Actinia was that this through-conduction
mechanism was more in evidence under some conditions than others. Symmetrical
retraction was much harder to evoke in very expanded or well-fed animals.

The series Anemonia, Actinia, Calliactis represents stages of development of the
sphincter-mesenteric through-conduction system. The development of this system
is, however, not simple. This is evident in the responses of the parietal muscles.
In Calliactis, the sphincter, longitudinal mesenterics and parietals can all be excited
to symmetrical contraction by way of the mesenteric through-conducting net. With
the sphincter, this net communicates directly. The mesenterics, like the sphincter,
invariably contract symmetrically, and since in the allied genus Metridium the
mesenteric fibres run in close connection with the longitudinal mesenteric muscle
(Parker and Titus, 1916) the connection here may be direct also. But the parietals
present a more difficult problem. They can not only be activated symmetrically by
the through-conduction mesenteric net, but under appropriate conditions can show
local response. This has just been illustrated in Actinia, but it is also true of Calliactis.
Under natural conditions this animal can show asymmetrical contraction of the
parietals. So far this has not been produced by artificial excitation, but it is evident
enough in the normal animal on the shell inhabited by the hermit crab. The column
is bent over so that the oral sweeps the ground as the crab walks along. Similar
parietal independence exists in Metridium, as Parker (1916) has shown, in the
bending of anemones subjected to lateral illuminations.
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It is evident, therefore, that though the parietals are accessible to the mesenteric conduction system, yet they are partially isolated from it, and can under appropriate conditions be independently excited without excitation flowing over into the mesenteric system. These difficulties would be removed if the parietals were connected only indirectly with the mesenteric system by way of the primary nerve net of the column in which interneural facilitation has been shown to exist. This receives some support from the morphological organisation of the parietals. They are developed on either side of the base of every mesentery, even the most rudimentary. But only in the first few cycles do the mesenterics approach full development with respect to the rest of their structure (Stephenson, 1920), and this may well include the mesenteric conduction system.

To normal stimuli, whether the parietals are called into action via the through-conduction system or locally must depend upon the connection of the sensory nerve endings. In Calliactis, direct excitation of the column nerve net is possible from any point over the column, so that we must suppose that in this species sense organs communicate directly with the through-conduction system. In Actinia equina, on the other hand, this system is usually only accessible to sensory stimulation at the pedal edge. But over the greater part of the column excitation only produces local parietal contraction, so that the sense organs cannot connect with the through-conduction system.

DISCUSSION.

The nerve net of Calliactis shows the overwhelming importance of facilitation and the variety of response which is possible through this alone in even the simplest nervous organisation. This is clearest in the sphincter-mesenteric system which behaves as a single conducting unit. By simple gradation of facilitation rates, the various symmetrically responding muscles can be brought progressively into action so that this simple organisation seems to endow the animal with responses sufficiently complex to have a superficial appearance of purposiveness. But this simplified system is a specialised adaptation. The comparative study of Actinians shows the progressive development of a through-conduction system. What are in fact specialised through-conduction tracts of the same kind are found elsewhere, as in the bell of Medusae (Bozler, 1926) and in the giant fibre systems of Annelids (Eccles, Granit and Young, 1932), and probably of Arthropods. The essential feature of through conduction is common enough as a specialisation in other cases. The neuromuscular arrangement of the Vertebrata exhibits modification of precisely the same character. In these the motor nerve fibres are virtually in direct through connection with the muscle fibres, so that the motor nerves become virtually extensions of the muscle fibres into the central nervous system (Eccles and Sherrington, 1939). Both in Actinians and in Medusae the development of through conduction is associated with the necessity for large co-ordinated responses of the animal as a whole. In Actinians these are concerned with protection, and in Medusae with locomotion. But the peculiar neuromuscular arrangement of the vertebrates has a different
significance. It is related to the fact that gradation of response is effected in this group largely by the number of nerve fibres involved, and not by the graded facilitation mechanism of many other phyla.

The primary arrangement of the nerve net is that in which interneural facilitation predominates. Though this necessarily involves more localised responses than is the case with through-conduction systems, yet the variety of response is very much greater. This follows because differences in frequency and number of impulses not only bring in different muscles but the whole response may be entirely altered by excitation spreading into fresh parts of the net in connection with fresh sets of effectors. The existence of interneural facilitation also permits great variation of the response according to the kind of stimulus applied. Different sense organs can have different connections with the nerve net, and their conducting paths through to the effectors may be partly isolated. This is very evident in the responses of the disc to chemical and mechanical stimuli (cf. Nagel, 1894; Parker, 1917 c.; von Uexküll, 1909).

Comparing Calliactis with the higher animals, the reaction of the animal as a whole can be predicted with surprising correctness when the nature of the stimulus and the region of its application are known. The relation between stimulus and response is largely a quantitative one. For this to be true, the link between stimulus and response must be able to vary appropriately according to the nature of the stimulus. This link is not the nervous impulse by itself. A single impulse in the nerve net is almost ineffective. It is the impulse group set up by the stimulated sense organs which constitutes this link. From the point of view of the animal, each impulse group must be treated as a whole. The nature of the response depends upon the number and frequency relations of the impulses composing it, and upon the region of the nerve net in which it is set up. If instead of the individual impulse we consider such impulse groups as natural units in behaviour it is interesting to observe that their properties closely approach the "excitation" of von Uexküll, and resolve some of the apparently anomalous properties of the latter.

In comparing the behaviour of Actinzoans with that of Arthropods or Vertebrates, an enormous difference in time scale becomes apparent. The frequency of the impulses which characterise the responses in Calliactis is quite extraordinarily low. Consideration of the foregoing experiments suggests that the average frequency in a resting anemone is less than 1 in 10 sec., while an impulse frequency of 1 in 1 sec. is sufficient to evoke the most active response which the animal can give. The whole scheme is thus 100 to 1000 times slower than that which characterises the nervous organisation of the Vertebrates.

SUMMARY,

1. Stimulation of the column of the anemone Calliatis parasitica elicits a graded series of responses. Each response is primarily due to the action of a single set of muscles. The means by which this effect is produced is physiologically simple. Part of the nerve net beneath the intact column behaves as a single conducting unit and the various muscles communicate with it. The muscles, however, are only
activated through the facilitation of a series of impulses. Each muscle has its own appropriate frequency range, to which a facilitated response can be obtained. The range of frequencies is extraordinarily low, from 1 impulse in 1 sec. to 1 impulse in 10 sec.

2. "Interneural" facilitation can be demonstrated between adjacent conducting units of the nerve net of the disc. From various points on the disc several stimuli may be required to establish a conducting path to the sphincter muscle. The apparent continuity of conduction throughout the column in the intact animal is due to specialised tracts running vertically up the mesenteries. These are joined by a conducting ring in the neighbourhood of the sphincter. In addition to this "through-conduction" system, there is a general nerve net within the column wall in which interneural facilitation is evident.

3. The velocity of conduction in the general nerve net of the column has the slow rate of 10–20 cm. per sec. But for the sphincter-mesenteric system the rate is over 1 metre per sec.

4. The relative development of both interneural facilitation and of conduction velocity within the nerve net give consistent pictures of its physiological organisation. These agree with its morphological organisation.

5. Comparison with other species shows that the through-conduction system is a specialisation, developed in varying degrees in different species. It is most highly developed where protective reactions are most perfect, as in Calliactis.

6. The importance of the "impulse group" propagated from a stimulated sense organ as the natural unit in behaviour of Calliactis is discussed.

Most of this work was done while holding the Cambridge University Table and the Bidder Fund at the Stazione Zoologica, Naples. I wish to express my sincere thanks to Dr Dohrn and the staff for their hospitality and the great facilities they gave me. The cost of some of the apparatus used in this work was defrayed by a grant from the Royal Society.

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THE NERVE-NET OF THE ACTINOZOA

III. POLARITY AND AFTER-DISCHARGE

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(Received 4th December, 1934.)

(With Two Text-figures.)

INTRODUCTION.

It has often been remarked that the nerve net possesses certain properties which have their counterpart in central nervous rather than in peripheral systems. In general, an analysis of the responses of Calliactis parasitica showed that the nerve net of this organism behaves as though it consisted of a number of simple conducting units (Pantin, 1935). But transmission in this system, however, is governed by the high development of facilitation between these units. There is facilitation between nerve net and muscle fibres, and between the units of the nerve net itself. This "interneural" facilitation is evidently analogous to certain features of central nervous conduction. Facilitation, however, is only one of many special features peculiar to the central transmission of excitation among the higher animals. Two of the most important of these are polarity and after-discharge. In this paper the relation of properties in Calliactis analogous to these are considered. The methods used have already been described in the earlier papers. The anemone was stimulated by means of a metronome-controlled neon-lamp stimulator.

POLARITY.

The existence of polarity in Actinozoa has long been known, particularly in the tentacles. Parker (1917 a) shows that a mechanical stimulus applied to a tentacle of Metridium causes a contraction of the longitudinal muscles which is greater on the side towards the mouth; that is, there is an apparent tendency towards centripetal conduction. In the same way, the experiments of Rand (1909) and Chester (1912) demonstrated that when a tentacle is cut across, the response of the central stump differs from that of the severed portion. The cut base of the latter remains open, whereas the cut surface of the central stump shows a strong, highly localised contraction of the circular muscles which closes the wound. These facts indicate a definite polarity in the tentacle, such that excitation is conducted more easily centrally than peripherally. Parker (1919) draws attention to the agreement
between this and the observations of Groselj that the conducting fibres from the sense organs to the net tend to run in a central direction down the tentacle from the sense organ. From this he shows that there is a centripetal polarity and that this is of anatomical origin.

This interpretation, however, deserves further examination, for there are certain facts which the idea of centripetal polarity does not seem to cover. Von Uexküll (1909) showed in *Anemone sulcata* that while mechanical stimuli activate the longitudinal muscles, chemical stimuli are followed by contraction of the circular muscles; in particular, local application of chemical stimuli to a tentacle causes a contraction of the circular muscles peripherally from the point of stimulation up to the end of the tentacle. This seems to show for the circular muscles a centrifugal conduction. Experiments on the tentacles of *Calliactis* agree with this. In this species both sets of muscles can be activated by mechanical stimuli. Mechanical stimulation on the side of a tentacle at first produces local bending due to contraction of the longitudinal muscles at the site of stimulus, and slightly centrally from this point. Long-continued mechanical stimulation at a given point on the tentacle, however, is followed by contraction of the circular muscles centrifugally from the point of stimulus out to the tip of the tentacle. On the other hand, severance of a tentacle often fails to produce more than a local response, so that the centripetal spread of excitation seems to be very restricted.

More direct evidence in favour of centrifugal conduction in the tentacle can be obtained. A stimulus applied to the column of the anemones has been shown to excite a through-conducting network which directly supplies the marginal sphincter (Pantin, 1935). But in many organisms such stimuli are found to cause slight contractions of the longitudinal muscles in the tentacles. Even a single stimulus may cause this in a few tentacles scattered round the edge of the disc. From this it appears that the nerve net of the tentacles is often in more or less direct communication with the through-conducting system which is excited by stimulation of the column and which also supplies the sphincter. While this holds for stimuli passing out centrifugally into the tentacles, conduction in the reverse direction is much harder to obtain. If stimuli are applied directly to the tentacle it is found that while it is quite possible to excite the sphincter to respond, it requires 10–20 stimuli to do so. While therefore the nerve net of the tentacle is certainly fairly closely connected with the through-conduction system, its connection is essentially a polar one, even a single impulse may pass into many of the tentacles, whereas a large number of impulses is required to facilitate a conducting path in the opposite direction. It follows that the tentacle possesses a definite centrifugal polarity of interneural facilitation.

It is important to distinguish this centrifugal physiological polarity from the centripetal anatomical polarity of Parker. The two systems in no way conflict, and in fact both seem to be necessary to explain the observed phenomena. The effects of cutting tentacles give as much evidence for physiological centrifugal conduction as for anatomical conduction in the reverse direction. If a tentacle is cut across, it is clear from Groselj's evidence of centrally running sensory fibres that very many
of these will be cut; but the numerous cut ends will all be connected with the nerve net on the central side of the cut, whereas the cut ends on the free part of the tentacle will have their connection with the nerve net severed. If, as it is reasonable to suppose, it is the severance of these fibres which is responsible for the stimulus to the muscles, it is again clear that on anatomical grounds alone the general stimulation of the cut end of the central stump will be vastly greater than that of the cut free end of the tentacle. Consequently, the closure of the cut end of the stump may be the inevitable consequence of the anatomical polarity of the sensory fibres. But further, it is to be remarked that this closure of the circular muscles remains localised, and is not propagated centrally. This suggests an interneural block to stimuli originating from the cut, which is in full agreement with our observation that only with difficulty can a conduction path be facilitated centripetally by electrical excitation. In fine, there is no necessary inconsistency between the varied properties which the tentacle appears to exhibit. All the data so far presented seem to be consistent with the centrifugal physiological polarity of interneural conduction combined with an anatomical polarity in the opposite sense.

This conclusion is of importance in considering the origin of polarity. It is the physiological rather than the anatomical origin which is important here. The appearance in the Actinozoa suggests that polarity may have arisen, not by the abrupt appearance of a valve-like mechanism but by the gradual development of differential rates of facilitation between units of the nerve net.

The existence of polarity is not restricted to the tentacles. There is some evidence that it exists radially in the disc. Although conduction outwards from the mouth takes place easily and with little facilitation, yet prolonged stimulation of the disc edge is required to involve the mouth and the feeding reactions. On the other hand, polarity is notably absent from the intact column. Perhaps this is most clearly shown by the fact that a stimulus applied at any point appears to throw the whole column into the refractory state.

AFTER-DISCHARGE

Among the properties of the nerve net which are supposed to resemble those of a central nervous system rather than a peripheral one is the phenomenon of after-discharge. In Actinozoa care must be taken to distinguish it from natural delayed responses. Conduction velocity is low and many of the muscles contract so slowly that complicated responses may appear to take place long after a stimulus has ceased to act. But in about 30 per cent. of the Caliactis examined, a phenomenon of an altogether different nature was observed which certainly bears some relation to after-discharge. In normal animals, if a battery of stimuli is given to a point on the column at a suitable frequency each stimulus is followed by a response of the marginal sphincter. But in some individuals there may arise one or more additional contractions during the series. It is as though a second stimulus were interjected in the series at some arbitrary point. Fig. 1A shows this. There is a normal response to stimuli at a frequency of 1 per sec., but at two points a supernumerary con-
traction takes place in the series. When such supernumerary contractions occur the response of the sphincter is greatly increased. This, however, is entirely due to spacing of the supernumerary contractions with relation to the applied battery of stimuli; by temporarily raising the frequency, they increase the facilitated response. The response may consist of more than a single supernumerary contraction. It may consist of a more or less rhythmic succession of up to ten or more contractions (Fig. 1C). Even two stimuli may result in such a rhythmic discharge (Fig. 1B). The whole effect may vastly augment the response of the anemone, so

Fig. 1. Sphincter responses: 1 per second. A. (1) normal facilitation at 1 per second; (2) and (3) the same with supernumerary contractions. B. Consecutive responses: (1) simple facilitated response to 2 stimuli 0.1 sec. apart; (2) the same followed quickly, and (3) rather later, by a single supernumerary contraction; (4) as (1), but followed by a rhythmic discharge (4 per second) ending in complete contraction of animal. C. Rhythmic supernumerary contractions following battery of stimuli. Note regularity of rhythm.

that it may respond to two or three stimuli by a rapid and complete contraction of the whole animal.

By calling this phenomenon "after-discharge" it is simply implied that, following the response of the muscle to a given stimulus, one or more additional contractions may arbitrarily appear after it. Many causes for this might be possible, and we may not assume that the appearance of after-discharge in the Coelenterate nerve net necessarily implies that it is analogous in its origin with after-discharge in the central nervous system of the higher animals. Some of the possibilities are as follows:

(1) The appearance of a supernumerary contraction might be due to the
nervous impulse set up by the stimulus arriving at the muscle by two paths in the nerve net of unequal length; the difference in time of arrival resulting in two distinct responses. But the supernumerary contractions can follow 1 sec. or more after the direct response. For a time difference of this order, the difference in length of path would be far beyond anything which could actually be found in the anemone. Further, such an explanation can scarcely account for a rhythmic discharge.

(2) Adventitious waves of excitation might occasionally arise from sense organs. If these occurred during a battery of stimuli a supernumerary contraction would take place. But against this, supernumerary contractions only appear following stimulation, and therefore seem to have some connection with the stimulus even if only indirect. Sometimes supernumerary contractions bear evidence of a definite time relationship to the preceding direct response. Table I shows a case where these contractions tended to occur at a more or less definite interval after a preceding contraction due to a stimulus. This is independent of the position of the stimulus, for the time interval between the two contractions stays roughly the same even though the interval between the stimulus and its direct response varies greatly with the point of stimulation, owing to the time taken in conduction. Such a correlation could scarcely be found if supernumerary contractions were due to adventitious stimuli.

(3) The supernumerary contractions may be artefacts depending upon the contraction of the sphincter muscle itself. These movements are quite violent, and especially in view of the fact that a hook and thread may be attached to the disc for recording, it is possible that each stimulus might evoke a contraction of the sphincter which, when it took place, would in turn set up an excitation wave through mechanical stimulation of the sense organs. Such a process would be somewhat analogous to a chain reflex. While it is hard to rule out such an explanation altogether it cannot hold in many cases because a supernumerary contraction can follow the primary response with extraordinary rapidity. The time interval between the two can approach the absolute refractory period; and since, moreover, this may happen at the very first stimulus which elicits a response, the supernumerary contraction may commence while the mechanical movement due to the primary response is scarcely appreciable (Fig. 2A).

(4) The after-discharge may depend in some way upon "synaptic" conduction. That is, the nervous impulse in passing over the synapse between two conducting
units in the net so excites this junction that one or more subsequent impulses are set up. While this is possible, it must not be forgotten that these effects are observed in the response of the sphincter to stimulation of the column. This is the very case in which the existence of complete through conduction has been most clearly demonstrated via the mesenteric-sphincter system. If synaptic contacts exist in this system, as they probably do, they only play a passive rôle during the normal conduction of excitation.

(5) Both the primary and the supernumerary contractions may be due to the stimulus itself. Multiple responses are common in certain nerves, as in the prolonged after-discharges which may follow a stimulus in crustacean nerve under certain conditions (Barnes, 1934). But if the supernumerary contractions of

![Diagram 1](image1)

![Diagram 2](image2)

Fig. 2. A. (1) Normal facilitation of sphincter (stimulation \(1/2\) per second); (2) the same with a supernumerary contraction (second white spot) initiated \(2\) to \(3\) sec. after first successful primary response (first white spot). Note great and lasting facilitation. B. Discharge following mechanical point stimulus on pedal edge. Time in seconds. C. Response of sphincter to constant current (lower signal) locally applied to column. (1) 0.8 volts, (2) 1.0 volts, (3) 1.6 volts.

*Calliactis* originate in this way, the stimulus must be extraordinarily enduring in its effect. The applied stimulus lasts a few thousandths of a second and the chronaxie is short, whereas the supernumerary contraction may follow the primary by more than 1 sec., or may even be a succession of contractions over several seconds.

A more significant difference rests in the peculiar relation of the supernumerary contraction to the preceding stimulus. While the multiple discharges of crustacean nerve bear a more or less regular relationship to the stimulus, the supernumerary contractions in *Calliactis* do not. They seem to occur with equal probability whether the preceding stimuli have been very strong or only just above threshold value, or whether there have been as few as two in number or very many. Above all they are peculiarly fickle in their incidence. Successive batteries of stimuli which seem to be identical may produce either a single supernumerary contraction, none at all, or
a whole series. Any of these effects may occur in any order under what appear to be the same conditions of stimulation.

Regular discharges of impulses somewhat analogous to those which occur in Crustacean nerve can in fact be produced in Calliactis when excited by a constant current. Fig. 2C shows the periodic contractions of the sphincter which occur when a direct current is applied by two small non-polarisable electrodes on the column of the anemone. In such discharges there is a threshold current intensity beyond which the greater the current the longer is the battery of impulses set up, and to some extent the greater is their frequency. The relation of stimulus to response in such cases as this is too definite for them to be directly comparable with the supernumerary contraction system. In the latter, the curious partial independence from the stimulus gives the impression that its connection with the excited nerve net is imperfect and may fail in an arbitrary manner. Whatever this system is, it can provide a strong stimulus when excited, for an impulse from it can follow close behind the absolute refractory period of a preceding artificial stimulus when the threshold of excitation is at least double that of the normal. The system resembles in some ways an indirectly stimulated sense organ, for this also can give one or more impulses. Fig. 2B shows such a short series in response to mechanical stimulation of the pedal edge, produced by a weighted point. The duration of the stimulus is shown by the black band. The individual impulses set up are shown by the vertical lines above it, except the first, which produces no response. Whether this analogy is significant remains to be determined. At present there is no satisfying explanation for these supernumerary contractions. While the phenomenon resembles superficially the after-discharge of the higher types of central nervous system, its origin, and in particular its relation to the synaptic properties of the nerve net is uncertain.

DISCUSSION.

The responses of Calliactis described in the preceding papers showed a great simplicity. But to a certain extent this is due to the simplicity of the reactions studied. Attention was there particularly focused on the responses to mechanical and electrical stimuli, and on the unusually simple protective responses of the column. How the rules which were deduced from these reactions alone need extension to cover the whole behaviour of the anemone remains to be seen. In some cases additional factors come into play, as in crawling and peristalsis. But in those responses which were examined the simplicity is quite real, and there is a very direct relation between stimulus and response.

This general plan of response can undergo modification. Previous stimulation, by the establishment of paths of interneural conduction and also through the development of local insensitivity, can modify the reactions of an animal to a particular stimulus. More extensive changes can be produced by feeding. In Calliactis, as in most other Actinians, well-fed animals are very insensitive and may even remain fully expanded under drastic mechanical and electric excitation.
Parker (1917b) has shown how food substances can depress the feeding reactions of *Metridium*. Such modifications involve, however, only differences in the case with which particular responses can be called up. They do not seem to cause the appearance of quite new reactions.

So far as the present experiments have gone, the only entirely arbitrary element in the scheme of the responses of *Calliactis* appears to be the supernumerary contraction mechanism. Though its origin is obscure, the direct relation between stimulus and response is certainly upset when this mechanism is in action. It introduces an element of uncertainty into the response of the anemone to a given stimulus which has at least superficial parallels in the behaviour of the higher animals. This may simply mean that small differences, at present undetected, in the conditions of stimulation or in the state of the anemone produce large differences in response. On the other hand, the functional significance of the supernumerary contraction mechanism is not evident. While, when it does act, it endows the anemone with greater responsiveness, the moment and extent of its occurrence do not seem to be directed to any advantage. The very evident purposiveness of the quite machine-like protective reactions presents an interesting contrast to this.

Whatever view is taken of the supernumerary contractions, their existence together with that of polarity and of facilitation shows that some characteristics of the nervous systems of the higher animals are already foreshadowed in the coelenterate nerve net. It is often said that the nerve net possesses central nervous properties not present in peripheral systems. This is due to the fact that the vertebrate skeletal neuromuscular system remains the standard by which all others are compared. Unfortunately this is very specialised, owing to the high development of continuity of conduction between motor nerves and muscle fibres. In several phyla, as in the coelenterates, neuromuscular facilitation is found. It is an inversion to say that the neuromuscular arrangements in all other phyla show central nervous properties because they do not possess the unique peripheral conduction mechanism of the Vertebrata.

The true relation of the nerve net to the central nervous system of more highly organised phyla is found in the morphological absence of centralisation, and the simple relation of response to stimulus; these are questions of degree of organisation.

**SUMMARY.**

1. Polarity exists in *Calliactis*, particularly in the tentacles. In these, there is a centripetal polarity of anatomical origin, but there is in addition a physiological polarity running centrifugally. More stimuli are required to facilitate a conducting path centrally from a point on the tentacle than in the reverse direction. Polarity may originate by the development of differential facilitation rates.

2. In some individuals, a kind of after-discharge is observed. A series of one or more extra contractions follows the primary response to a stimulus. Though these appear only after a stimulus has been given they are only indirectly caused by it.
Their presence or absence cannot be predicted and seems to bear no relation to the strength of the stimulus. They introduce an arbitrary element into the otherwise singularly regular relation between stimulus and response.

3. Several possible sources for the phenomenon are considered, including synaptic junctions between conducting units of the nerve net, but there are difficulties in accepting any of them.

4. The nerve net of Calliactis possesses many of the properties of the nervous systems of more highly organised animals. The danger is pointed out of employing the unique skeletal neuromuscular system of the Vertebrata as the standard by which the nervous arrangement of other phyla are to be compared.

The author wishes to repeat the acknowledgments and sincere thanks expressed in the preceding papers.

REFERENCES.