THE NERVE-NET OF THE ACTINOZOA

III. POLARITY AND AFTER-DISCHARGE

By C. F. A. PANTIN, M.A., Sc.D.
(From the Experimental Laboratory, Cambridge, and the Stazione Zoologica, Naples.)

(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, 1933). 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 Actinzoa 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
The Nerve-net of the Actinozoa

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 anemone 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 Calliactis 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. 1 A 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. 1 C). Even two stimuli may result in such a rhythmic discharge (Fig. 1 B). The whole effect may vastly augment the response of the anemone, so

![Diagram A](image1)

![Diagram B](image2)

![Diagram C](image3)

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.

Table I.

<table>
<thead>
<tr>
<th>Interval between stimulus and response sec.</th>
<th>Interval between direct response and supernumerary contraction sec.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.12</td>
<td>0.46</td>
</tr>
<tr>
<td>0.03</td>
<td>0.46</td>
</tr>
<tr>
<td>0.28</td>
<td>0.41</td>
</tr>
<tr>
<td>0.32</td>
<td>0.43</td>
</tr>
</tbody>
</table>

(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
The Nerve-net of the Actinozoa

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 rôlè 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

![Diagrams](image)

Fig. 2. A. (1) Normal facilitation of sphincter (stimulation 1 per second); (2) the same with a supernumerary contraction (second white spot) initiated 0-08 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 satisfi-
ying 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.


