THE NERVE NET OF THE ACTINOZOA

II. PLAN OF THE NERVE NET

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(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 Actinolobus (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.

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 1-1 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
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.
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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 of 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 Actinozoan 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 neo-
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.

![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.).](image)

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
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 sphencter 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 sphencter, 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 sphencter. 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 sphencter 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 sphencter 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 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
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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-
metrically 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 smoothes 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 *Metradium* (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 *Anemonea 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 *Anemonea* 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 *Anemonea* 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 *Anemonea*, 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 e). 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 sensitivty, 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.
The Nerve Net of the Actinozoa

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, 1917c.; 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 Actinozoans 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 Calliactis 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.

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