THE NERVES AND MUSCLES OF MEDUSAE

II. GERYONIA PROBOSCIDALIS ESCHSCHOLTZ

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INTRODUCTION

*Geryonia proboscidalis* Eschscholtz, formerly known as *Carmarina hastata* Haeckel, is common in the Mediterranean for much of the year. It lives well in an aquarium and remains active for several hours under experimental conditions. Because of the large size and the vigorous responses to stimulation it is a convenient animal for experimental work, and as in most medusae the responses are consistent and well defined.

Since the classical work of Romanes (1885) upon some smaller species of Hydromedusae and the work of Nagel (1894) on *Geryonia*, the behaviour and the co-ordination of movements of the Hydromedusae have been largely neglected, and attention has been turned to the larger and more accessible Scyphomedusae. This paper deals with the movements brought about by different muscle systems and the transmission of the excitation that gives rise to these movements. As in most species of Hydromedusae there are several distinct responses and there is a corresponding specialization of the nervous system into distinct but co-ordinated parts which transmit excitation to the various groups of muscles. It is assumed that co-ordination of movement must have its basis in the anatomical arrangement of the nervous system, and an attempt is made to identify the observable nerve elements with the physiological pathways as determined by experiment, but the correspondence that we can find between the activities and the arrangement of the nerves is by no means complete. In no case has it been shown by experiment that a particular fibre is actually a nerve. This uncertainty makes it necessary to use cautious terms such as 'pathways of excitation' and 'system which conducts in all directions' instead of 'axons' or 'through conducting nerve net with synaptic connections', although further work may bring the Hydromedusae in this respect more into line with the better known Scyphomedusae.

METHODS

In the following account, 'mechanical stimulation' implies a gentle touch with a seeker or bristle. 'Electrical stimulation' was applied with a pair of fine platinum wires excited by an induction coil, adjusted to produce a response only at 'break'. Electrical stimulation always involved some mechanical stimulation.
The contraction wave of the circular muscle

The circular muscle of the bell is responsible for the rhythmical beat. The tangentially orientated muscle fibres lie under the epithelium of the concave side of the bell and form a muscle sheet from the base of the manubrium almost to the velum. The fibres are cross-striated, and except near the rim the muscle sheet is divided into six regions by narrow areas along the lines of the radial canals. A single electrical stimulus anywhere within the area covered by the circular muscle, and a few millimetres beyond, gave rise to a single total contraction apparently identical with a normal beat. By cutting strips from the bell it was confirmed that excitation is conducted in all directions. The direction of the cut relative to the direction of the muscle fibres is not important, and the excitation passes readily across the muscle-free strips in the region of each radial canal. When a strip of tissue is made progressively narrower the contraction wave becomes blocked at a definite point, in a strip several millimetres wide. The minimum width at which the bridge will still conduct varies greatly from experiment to experiment. Romanes (1876) considered similar observations on Aurelia to be evidence for a plexus of nerves.

Working with Scyphomedusae, Bullock (1943) showed that it is possible to stimulate a strip of tissue at a moment when the muscle fibres are in the refractory period following a contraction, but when the conducting elements have come out of their own refractory period. In this way the refractory periods of both conduction and contraction elements can be measured separately. This experiment can be repeated for Geryonia. A strip 10 cm. long was stimulated at one end. A contraction wave travelled along the strip with a velocity approximately 50 cm./sec., so that excitation in the conducting system took 0.2 sec. to reach the far end of the strip. There was a short period when the conducting system had come out of its refractory state but the muscle was still refractory. A second stimulus was applied during this interval at the other end of the strip; there was a single contraction under the second electrode but a double one under the first. The shortest interval between two stimuli was 0.5 sec., for the second stimulus to be effective. This gives a refractory period of about 0.3 sec. This result can be interpreted in terms of excitation in the nerve and contraction in the muscle, but the experiment actually shows only that the conducting and contracting systems are distinct. The above result is too great because an insufficiently long strip of tissue was used and this introduced an effect from the refractory period of the muscle.

In another series of experiments the velocity of the contraction wave was measured in strips of the bell, with and without the marginal region. The summary of the results, Fig. 1, shows that there was no significant decrease of the velocity of transmission of the contraction wave after the operation. This does not exclude the possibility that in the ring nerve there may be a transmission slower than that of the contraction wave across the bell; however, it is safe to conclude that transmission in the margin of the bell is not important for the propagation of the contraction wave during co-ordination of the normal beat.
Fig. 1. Measurements of the velocity of the contraction wave. Each vertical unit represents five measurements. The velocity is not greater when the rim is intact.

The radial conducting system

Geryonia has a stout manubrium about 5 cm. long which normally hangs straight down in the centre of the bell. One of the most noticeable features of the animal is the activity of this organ, which responds to the lightest touch on the edge of the bell by a rapid and precise movement towards the side touched, and brings the terminal mouth in contact with the source of irritation. The effector muscles are arranged round the solid core of the manubrium with fibres parallel to the main axis and continue over the bell as strands along each side of the radial canals.

Preliminary experiments with entire animals showed that the mouth is quickly applied to the position of a stimulus on the underside of the bell. The response persists as long as the stimulus continues; the localization is accurate only to about 5 mm. When two places are stimulated at the same time the manubrium points somewhere between them. A tangential cut 1 cm. long through the subumbrellar
epithelium blocks the inward transmission of excitation from a point peripheral to the cut. This demonstrates that the excitation cannot spread far, if at all, in a circular direction, but must reach the muscles along radial pathways. However, radial pathways alone do not provide a full explanation of the response for mechanical stimulation of the regions indicated in Fig. 2 by small letters was followed by contraction in the regions indicated by the corresponding capital letters. Stimulation near the centre of the bell produced a bending of the middle of the manubrium, but on the other hand stimulation at the margin of the bell was followed by a pointing reaction brought about by a contraction at its base.

Fig. 2. A stimulation in the regions indicated by the small letters produces a contraction in the region indicated by the corresponding capital letters.

On the stem of the manubrium, experiments showed that the arrangement of pathways is not so precisely radial as on the bell. A transverse cut 5 mm. long in the epithelium of the manubrium at right angles to the muscle fibres prevented transmission along the manubrium towards the mouth. However, with strong or repeated stimulation the excitation soon spread round the sides of such a cut. It seems that here the pathways are not entirely radial, but there is a possible alternative explanation that the slow spread round such a cut is due to the mechanical stimulation by the active muscles. As the core of the manubrium is solid, muscles on
opposite sides are antagonistic, so that a little spread of the excitation strengthens the response with no impairment of the accuracy of the pointing as a whole.

These results demonstrate the properties of the subumbrellar epithelium, for the co-ordinated pointing response of the manubrium is not affected by section of the six radial nerve strands, which appear to be local concentrations of physiological pathways that are generally spread over the epithelium.

Fig. 3. Plan of the bell cut almost into two halves with two opposite radial cuts, and with two circular cuts from Y to X and Y to Z. Left side with margin and tentacles, right side without. Further explanation in text.

A preparation to demonstrate many of the characteristics of the pathways which conduct excitation to radial and circular muscles can be made from a single specimen (Fig. 3). Two radial cuts (vertical in the figure) were made reaching from the edge of the bell to the base of the manubrium, and the rim, including velum, ring nerve, and tentacles, was removed from the right half. From the lower of the radial cuts a circular cut extended into each half from Y to X and from Y to Z, almost severing it from the manubrium, but leaving a bridge on each side about 2 cm. wide.

In such a preparation electrical stimulation of one side of the bell produced a contraction wave which did not spread across the base of the manubrium to the opposite side. To the left of the dotted line at B electrical stimulation on the base of the manubrium failed to produce a contraction wave. A response of the manubrium
followed stimulation central to the circular cuts $XY$ and $YZ$ and also at points $M$ and $C$ in a radial line with the bridges at $X$ and $Z$, but not at $K$ or $D$. On the other hand, if stimulation at $D$ was electrical the resulting contraction wave spread in all directions, and although it crossed the bridge at $Z$ had no effect on the manubrium.

The sharp distinction between the two conducting systems that carry excitation to the radial and to the circular muscles is shown by an interesting phenomenon that was accidentally noticed. A wave of contraction made to circulate continuously round the circular muscle of an undamaged specimen of Geryonia would continue to circulate for long periods while the bell slowly rotated in the opposite direction, vibrating all the time. Nevertheless, the manubrium would still swing out towards a touch at the edge of the bell, despite the fact that the diffuse motor pathway was continually active. This experiment has been repeated with Liriope tetraphylla (Geryonidae) and would no doubt be successful in other forms which have a directional response of the manubrium.

**The tentacles**

When a specimen of Geryonia is quietly floating upright the six marginal tentacles hang down from the rim. Gentle mechanical stimulation of a tentacle sometimes produced a longitudinal contraction so localized that a swelling appeared for a short time at the place stimulated. Strong stimulation was followed by contraction of the whole tentacle. Both local and propagated responses could be evoked in isolated tentacles and transmission of the excitation could occur in both directions from the point of origin. In the undamaged animal transmission was occasionally in one direction only, towards the base of the tentacle. These responses could be clearly seen by the increase in diameter of the tentacle as the longitudinal muscle contracted. Nagel (1894) distinguished between a symmetrical contraction and one which resulted in a corkscrew shape, the former due to irritants, the latter due to food juices. Judging from what I have seen the two responses are not as separate as he maintained.

The vigorous contraction of a tentacle in response to stimulation of any kind was usually followed by a similar contraction of the other tentacles almost simultaneously round the bell. This transmission between tentacles was prevented completely by making appropriate cuts through the ring nerves. When stimulation produced a contraction that reached as far as the base of the tentacle there was usually also a response from the manubrium, which would swing out towards the stimulated tentacle. The importance of this reaction in feeding is clear.

**Centrifugal transmission to the margin**

Gentle mechanical stimulation of the epithelium of the lower surface of the bell or the tentacles produced an acceleration of the rhythmical beat, in addition to a pointing response. In some way excitation was able to spread towards the rim and influence in a reflex manner the spontaneously active centres responsible for the rhythm. Radial pathways are indicated since the effect could not be produced by
stimulation at the inner side of a suitably placed cut a few millimetres long at right angles to a radius. Shortly before the appearance of the first ensuing beat there was a co-ordinated contraction of all the tentacles. This centrifugal transmission was much slower than that for the pointing reaction in the opposite direction. There was usually a latency of 5-10 sec. between the stimulation and the response of the tentacles which was followed immediately by the beat. Since such observations could only be made with the margin entire, there was some chance of occurrence of spontaneous beats, but a consistent value of the latency was sufficient guarantee against this, and moreover spontaneous beats do not affect the tentacles. By making short incisions in the epithelium at the base of the manubrium it can be shown that in this region the pathways of centrifugal conduction, like those of centripetal conduction, are not strictly radial. Although there is a great difference between velocity of transmission in the two directions of the radial system, there is no evidence of two anatomically separate radial pathways, one going towards the manubrium the other towards the margin.

Compensatory movement and the responses of the velum

An active specimen of Geryonia often reaches the surface of the tank in which it swims. When this happens, as Veress (1911) and Bauer (1927) found, an asymmetry appears in the movement of the bell. The water currents at each beat now act to turn the bell, and the creature swims downwards. The same sequence happens when the water is agitated or the animal is strongly irritated.

Continuous observations of these asymmetrical beats were made by holding a specimen on a horizontal wire thrust through the main axis. Under these circumstances all specimens tended to swim downwards, and it was observed that the lower edge of the bell remained curled inwards more than the upper at the termination of each beat. As a result of this failure to relax fully, the amplitude of the subsequent contractions at the lower edge was not so great as at the upper. A considerable number of observations have convinced me that the difference is largely, and probably entirely, due to a maintained contraction of the velum. No consistent asymmetry of the contraction of the circular muscle could be observed. The bell was rotated and the observations repeated with a different sector. After each beat the velum on the lower side remained contracted and taut, whereas on the upper side it relaxed completely between each beat and waved loosely in the water current. Illumination from above or below had no effect on the behaviour. It seems that the velum at least is under the direct influence of the statocysts and may be the only effector organ of steering in this animal.

Large specimens of Geryonia often hang motionless at the surface of the aquarium. Close examination of the velum showed that rapid local movements appeared spontaneously from time to time; in some specimens an irregular flicker was usually noticeable. Sometimes these contractions appeared to be propagated for a few centimetres.

According to Nagel the velum is not sensitive to mechanical stimulation, but I have found a response that was sometimes quite localized and sometimes conducted
with decrement for a little way round the annulus. There was no response of the bell or the manubrium. A strong contraction of the whole velum was found only at each beat of the bell. An isolated strip of the velum responded to electrical stimulation with a localized contraction only, irrespective of the intensity or frequency of the stimulation, but the contraction may be maintained for some time, which does not happen in the case of the circular muscle.

Fig. 4. The marginal region of Geryonia, mainly after O. and R. Hertwig, who observed the connexion between the two ring nerves in many sections. l.n.r., lower nerve ring; mes., mesogloea; m.s., muscle fibres of subumbrellar epithelium; m.v., muscle fibres of velum; r.c., ring canal; st., position of statocyst; ten., position of tentacle; u.n.r., upper nerve ring.

The structure of the nervous system

The following summary is taken mainly from the Hertwig brothers' fine monograph. There are two nerve rings, the upper separated from the lower by the supporting lamella of the velum (Fig. 4).

The upper nerve ring is a strong bundle of fibres covered with a thin ciliated epithelium to which it remains attached in macerated preparations. This epithelium contains cells of two kinds: there are sensory cells, each with a process going into the nerve ring, and there are flat epithelial cells. The upper nerve ring is divided into two strands; one part contains relatively small bipolar ganglion cells, the other part consists of thin fibres which are principally the processes of the epithelium cells overlying the nerve.

Fibres from the tentacles and from the statocysts join the upper nerve ring, which seems to be mainly concerned with the sensory parts of the nervous system. The lower nerve ring lies in a clear band between the muscle fibres of the velum and
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the bell. This nerve contains many ganglion cells, some of which send fibres over the circular muscle of the bell (Hertwigs, pl. 5, fig. 7). Overlying the nerve is a very thin epithelium of distinct, flat cells, among which are occasional bipolar sensory cells, each with a thin peripheral process in the surface of the epithelium.

Small bundles of nerve fibres run from one nerve ring to the other through the mesogloea of the velum. The Hertwigs found these fibres in many sections, but gave no indication of a regular arrangement. They did not find any nerve fibres in the velum, but Hyde (1902) in Gonionemus found some which came from the lower ring nerve.

From the base of each tentacle a radial nerve strand runs across the subumbrellar surface of the bell to the base of the manubrium. These radial nerves consist of relatively few fibres; from them axons run through the neighbouring epithelium of the bell. Over the whole of the subumbrellar surface there is a network of small multipolar nerve cells, each with three to five processes, which in the Hertwig's drawings often run in a radial direction, but these authors could not discover any differentiated endings of nerve fibres on the muscle fibres.

DISCUSSION

(1) Conduction across the subumbrellar epithelium

The greatest emphasis must be placed on the observation that the pointing response of the manubrium to stimulation at the margin is not impaired by the continuous circulation of a wave of contraction round the bell. The pointing reaction is brought about by radial pathways, the contraction wave is propagated in all directions, and for an anatomical basis of both these activities the experimental evidence limits us to the epithelium of the subumbrellar surface, where there is found a nerve net. Simultaneous propagation in opposite directions is not possible in a nerve or a through-conducting network of nerves in the way that electrical impulses may pass in a wire, because the refractory period prevents one impulse from passing another. The observation of simultaneous transmission seems to be conclusive evidence of two functionally separate conducting systems, so long as these are behaving in the way that other nerves are known to do. It must be remembered, however, that there is no proof of nervous activity in either radial or isotropic system.

Bearing in mind the problem of two distinct physiological pathways in one nerve net, let us examine in more detail each of the reactions concerned.

By making cuts in different directions, Romanes (1877) first showed that the contraction wave in a Hydromedusa Sarsia sp. is transmitted in all directions across the bell. Nagel (1894) showed the existence of the same state of affairs in Geryonia. These observations can be explained in terms of the network of nerve cells and their processes which can be seen in the subumbrellar epithelium. In Geryonia the repetition of Bullock's experiment, in which the conducting pathway was stimulated while the contractile system was refractory, indicates but does not prove the activity of nerve fibres. It has been shown that the transmission of the contraction wave in the Scyphozoan Aurelia aurita is by way of a through-conducting net of large axons and not from fibre to fibre of the muscle (Horridge, 1954). However, in Geryonia,
or any of the Hydromedusae, it is only by analogy with the better-known groups that a similar state of affairs is thought to exist.

Working with *Tiaropsis indicans*, Romanes (1877) found that the manubrium would point accurately to a stimulated place on the edge of the bell. His observations of the behaviour are detailed, and show that the movements of the manubrium depend upon a conducting system which is mainly radial. In work based directly on that of Romanes, Nagel (1894) showed that a similar state of affairs exists in *Geryonia*. The marked sensitivity of the radial pathways to gentle mechanical stimulation which does not directly initiate a contraction wave suggests that here the transmission to the muscle of the manubrium depends upon nerves closely linked with primary sense cells. The radial direction of the pathway across the muscle fibres and the centripetal polarization also suggest a nervous basis, and here the histological observations agree, for many of the nerve cells in the subumbrellar epithelium have axons that run in a predominantly radial direction.

In *Goniumemus murbachi* (Hyde, 1902) there are bipolar and multipolar cells in the radial nerve strands, the superficial ones of each kind connecting with the circular muscle and with the network of nerve cells and their processes which spread over it, the deeper ones with the radial muscle, gonads and the radial canal. The reactions of *Goniumemus* are similar to those of *Geryonia*, with marked contrast between feeding and swimming activity (Yerkes, 1902), and here is an indication of two separate parts of the nervous system. Section of the six radial nerve strands in *Geryonia* did not prevent co-ordinated pointing of the manubrium, but in this region there is certainly a concentration of radial pathways to the manubrium, as shown by stimulation with a needle electrode. In *Tiaropsis indicans* Romanes found that the mouth responded more readily to stimulation in the region of the radial canals; the same was true for *Geryonia*.

A question of fundamental importance is whether experimental demonstration of transmission in a definite direction in a nerve net is sound evidence of a structural orientation that we may expect to observe histologically. In *Tiaropsis indicans* Romanes found that the pointing reaction of the manubrium depended upon radial transmission, but was careful to restrict his conclusions. 'We must not, however, conclude that these lines are radial structurally: the evidence only proves that they are so functionally.' This is strictly true, but there is now considerably more information about the action of nerves in Coelenterates and other groups of animals. It would be likely that a nerve net with functional polarization should show some structural polarization of the fibres. For precise location of physiological pathways a direct record of the electrical activity of a nerve is most satisfactory, but in practice conclusions must be based mainly on the general agreement of separate histological and physiological evidence. The through-conducting system of the mesenteries of *Calliactis* (Pantin, 1952) is an example where the histological basis was demonstrated after the physiological behaviour was known. With all this in mind, it is clear that to understand the subumbrellar nerve net in *Geryonia* a more detailed histological study is required.

* Now known as *Eutonina indicans* Romanes.
(2) Integration of the physiological evidence

Light mechanical stimulation of the tentacles or the underside of the bell was followed by a response of the manubrium and a co-ordinated contraction of the six tentacles. Exploration with an electrode, and the sensitivity to chemical stimuli (Nagel, 1894) indicate that there are sensory cells widely spread over the surface. The experiments on Geryonia have shown that receptors on the tentacles and on the subumbrellar epithelium connect to pathways which conduct excitation in each direction along the tentacles, in each direction round the ring nerve, and radially towards the base of the manubrium. This inter-related system of physiological pathways is here called the tentacle-radial system and is sharply contrasted with the separate contraction wave system which is the basis of the co-ordination of the beat. It can now be seen that most of the physiological pathways depicted in Fig. 5 fall into one of these two groups. In this diagram an effort is made to represent the inter-relations of these conducting systems where they meet in the margin of the bell.

Romanes (1876) showed that in all Hydromedusae studied the beat originates in the margin of the bell, probably in the ring nerves. The co-ordination of the eight anatomically-separate rhythmic centres in Aurelia implies that the impulse from the leading centre brings about the discharge of all the other centres and resets the rhythm in each. Pantin & Vianna Dias (1952) showed that an extra stimulus injected into the rhythm in Aurelia is followed by a pause of the same duration as the intervals between the other beats. In Hydromedusae the bell may be cut into small
sections which continue to beat each at their own rate, indicating many rhythmical centres. Although the more refined experimental evidence is not available, it is reasonable to conclude that these centres are normally co-ordinated in the same way.

Stimulation of a tentacle or of the subumbrellar epithelium gives rise to a beat in a manner that recalls a reflex action. There is evidence that two distinct systems, radial and rhythmic, are present in the marginal nerves, and that one acts on the other in an irreversible manner. First, section of the ring nerve destroys the co-ordination between the adjoining tentacles, showing that the through-conducting tracts pass all round the margin. Secondly, the rhythmical beat has its origin in another system which is similarly distributed. Excitation in the tentacle-radial tracts in the ring nerve can influence the rhythmical mechanism and bring about a series of beats or accelerate the existing rate, but the excitation responsible for the contraction wave does not leak in the opposite direction into the tentacle-radial system. This is illustrated in Fig. 5 by short arrows from the outer circular pathway to the inner (from the tentacle-radial to the rhythmic system and not vice versa). This may be compared with the polarization of a vertebrate synapse. Observations similar to those which are the basis of this conclusion have been made by the author on a number of different species of Hydromedusae, and also of Scyphozoa; in some species, for example, in Naustithoe (Coronatae), the action is to inhibit the beat rather than accelerate it.

Turning again to the histological basis of physiological pathways in the light of the information summarized in Fig. 5, there are reasons for considering that part of the upper nerve ring corresponds with the circular pathway between tentacles. The nerve bundle which runs along each tentacle joins the upper nerve ring. The close association with overlying primary sense cells agrees with the sensory nature of other parts of the tentacle-radial system. In each of the Trachymedusae studied histologically the upper nerve ring is associated with the statocysts, although in Geryonia no actual connexion was described by the Hertwig brothers, but indicated by Eimer (1874). This is sufficient to remind us that the co-ordination between tentacles cannot be the sole function of the upper ring nerve.

The lower ring nerve appears to be partly motor in function, having ganglion cells which send out fibres to the velum on one side and to the circular muscle on the other; perhaps it is wholly motor in function for there is not much histological evidence of connexions with sense cells. The least complicated view of the functions of Hydromedusae is that each bundle of fibres carries only one kind of excitation, but enough has been said to show that the nervous system is not a homogeneous net of similar elements, which are sometimes concentrated into well-defined tracts. Conditions are more complicated than this for, except for the radial nerves, there is physiological evidence of differentiation in each of the nerve trunks. Local action on the velum and symmetrical activity of the bell are quite distinct but both are associated with the lower nerve ring; the through-conducting pathway in the upper nerve ring must be distinct from the local fibres of the epithelial sense cells; excitation from the tentacles can influence the rhythm and also the manubrium; the statocysts influence the velum and possibly the rhythm, and yet the
nerve fibres from both tentacles and statocysts run into the upper nerve ring. The picture that is emerging is one of physiologically separate through-conducting tracts which may be superimposed on each other in a net or concentrated into mixed bundles. They meet and interact in the marginal ring nerves, though the mechanism and full extent of this interaction are still unknown.

(3) The velum

The complexity of the action of the nervous system is brought out by a consideration of the control of the velum, which may contract locally and is active as a whole at each beat. The contraction of the velum as a whole is not necessarily symmetrical, and it seems that this is due to a symmetrical contraction superimposed on a local one. A possible conclusion from the observations is that the through-conducting system of the contraction wave brings about a contraction of the whole velum by acting on a second localized conducting system. The action must be irreversible, for stimulation of the velum produced only a local contraction. Summarizing these conclusions we have:

- Reflex influences on the rhythm
- Gravity receptors presumably statocysts
- Axons to velum
- Velum muscle

It is difficult to decide the function of the velum in the various species of Hydro- medusae. I have also observed a local contraction of the velum independent of the beat in Melicertum octocostatum. The suggestion of a steering function is not new. Yerkes & Ayer (1903) expressed the view that Gonioa emus can direct its course by contraction of the velum; Murbach (1903) was inclined to agree, and the present observations on Geryonia confirm these suggestions. There are two short references to the function of the velum of the freshwater medusa Craspedacusta (Milne, 1938). The velum contracted with the bell, restricting the outgoing water to a jet, and relaxed while the bell expanded. Secondly, animals in an inverted position would sometimes drive vertically downwards against the bottom of the tank, and were able to progress only after an asymmetrical contraction; it was the velum rather than the bell itself which was responsible for the changed direction of the expelled water.

SUMMARY

1. The responses of Geryonia proboscisalbis to electrical and mechanical stimulation have been studied with particular attention to the transmission of excitation.
2. There are two kinds of excitation transmitted across the undersurface of the bell; first, the symmetrical beat is co-ordinated by an isotropic conducting system which acts in a through-conducting, all-or-nothing manner, and produces brief contractions of the circular muscle; secondly, the movements of the manubrium are co-ordinated by a radial conducting system, which produces a maintained contraction of the radial muscles of the manubrium.
3. The independence of these two conducting systems is shown by the simultaneous and yet distinct transmission of the two kinds of excitation in different directions.

4. The contraction wave is not transmitted through the ring nerves faster than over the rest of the bell.

5. The manubrium bends towards a stimulated tentacle, and all the tentacles contract simultaneously, co-ordinated by a through-conducting pathway in the marginal nerve. There is evidence that a polarized pathway carries excitation from this system to the rhythmical marginal centres.

6. Observations of Geryonia held with the axis horizontal show that the steering action is due to an asymmetrical maintained contraction of the velum.

7. The known histological details of the nervous system are compared with the physiological pathways demonstrated by experiment. The differentiation of a primitive isotropic nerve net into distinct tracts with separate functions is essential for the several rapid feeding and swimming activities.

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