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THE NERVOUS ANATOMY OF THE BODY SEGMENTS OF NEREID POLYCHAETES

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CONTENTS

The nerve cord of nereid polychaetes consists of intersegmental ganglia linked by narrower connectives. Each ganglion gives rise to four pairs of peripheral nerves designated in their order of origin IV, I, II and III, but numbered I–IV in their segmental succession. Nerve I arises from the cord immediately behind the intersegmental septum, II (the parapodial nerve) and III leave the posterior end of the ganglion near the middle of the segment and IV originates from the anterior (preseptal) part of the succeeding ganglion at the posterior margin of the segment. Nerves I and IV cross the floor of the body wall transversely and terminate in the dorsal integument, II supplies the parapodium and III links ipsilaterally with homologous nerves of other segments through a lateral nerve which runs longitudinally in the ventral body wall adjacent to the bases of the parapodia. Nerves II are the largest, IV are next in size while I and III are very fine and visible only after staining.

All the nerves are mixed and contain relatively few fibres. Each, on the afferent side, supplies a determinable region of the integument, I and IV between them drawing on integumentary receptors over the greater part of the ventral and the whole of the dorsal surface. Nerve II alone receives excitation from the parapodial integument and III is primarily proprioceptive, fibres

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entering the nerve from the surface of the dorsal and ventral longitudinal muscles. Sensory cells are most numerous in the parapodia, particularly in the cirri, and are present in large number in the ventral body wall. There are very few in the dorsal integument. Almost all are bipolar, usually single but occasionally grouped. Two morphological types of sensory cell are described. The internal (centrifugal) fibres of the sensory cells either run directly into the segmental nerves or, more frequently, discharge excitation into the nerve through tracts of a lattice-like subepithelial plexus made up of fibres of multipolar association cells. Excitation originating in scattered receptors thus appears to be canalized into the few fibres of the main nerves by way of the plexus.

The internuncial systems of the cord through which the afferent (and efferent) fibres make their central connexion are of two kinds, (1) giant-fibres and (2) fine-fibres. The paired lateral and paramedial giant-fibres and the single median dorsal giant-fibre have a similar arrangement and distribution in *Platynereis dumerilii* and *Nereis diversicolor* to that described by Hamaker (1898) in *Neanthes virens*. The fine-fibre internuncial neurons are of two types: (1) with short, richly branching axons forming an extensive network in the dorsal neuropile and (2) with long axons, possessed of few collateral processes, forming six longitudinal tracts extending suprasegmentally as dorso-lateral, dorso-medial and ventral tracts disposed symmetrically about the midline. Within the ganglion internuncially transmitted excitation is carried, by virtue of the orientation of the fibres, ventro-dorsally within the neuropile. Afferent fibres connect directly with one or other of the six fine-fibre longitudinal tracts. Proprioceptor fibres probably discharge into the dorso-medial region of the ganglion, exteroceptor fibres into its dorso-lateral area. In addition, afferent fibres, of unknown sensory connexion, enter the ventral fine-fibre tracts from nerves II and IV but not from I and III. Incoming afferent fibres, except perhaps in this latter instance where the ventral tract is adjacent to the lateral giant-fibre, appear never to excite giant-fibres directly. The latter are considered to be indirectly excited through the diffuse pathways of the neuropile.

Motor axons arise, as do internuncial fibres, from cell bodies in the crescentic cell cortex of the ganglion. Every segmental nerve contains at least one motor axon which crosses the dorsal neuropile of the ganglion from a contralateral cell body, the axon giving off longitudinally alined collateral branches which connect directly with one or more of the dorsal fine-fibre tracts. Synapses between the dorsally crossing motor axons and the giant-fibres have not been observed, though a motor fibre of ventral emergence in nerve IV is synaptically connected with the lateral giant-fibre. The probable significance of these direct and indirect neuron interrelationships is discussed in relation to the responses of nereids and to previously described properties of the giant-fibres.

Each segmental nerve contains, at its root, from one to four motor fibres. There is evidence of multiplication of the fibres at the periphery of the nerve, not by branching, but by the interpolation into the motor tracts of relay neurons. In one instance (the parapodial nerve distal to its ganglion) second-order motor neurons contribute additional fibres to the branches. These in turn connect with third-order neurons supplying the muscles. The terminal motor innervation has, however, been seen only in a few places.

The peripheral connexions, both on their afferent and efferent sides, thus embody relay neurons, and it is considered that the arrangement may permit of the short-circuiting of excitation and of the possibility of extensive local control of movement. Evidence is presented to show that nerve IV may be mainly concerned with the innervation of the longitudinal muscles of the body wall through the contraction of which locomotory flexures are developed. Nerve II is responsible for the motor innervation of the parapodium. The occurrence of peripheral nervous connexions between the two nerves further suggests that the co-ordination of body flexures and parapodial movements may not be entirely dependent on central nervous linkages.

INTRODUCTION

While the more general kinetic aspects of locomotory activity and of other frequently occurring movements of nereids have been satisfactorily resolved (Gray 1939), the role of the nervous system in initiating localized movements and in integrating them into more complex behavioural patterns is but imperfectly understood. Gray's observations and experiments throw light on certain aspects of the nervous control of movement, in particular the part played by peripheral events in the genesis and maintenance of locomotory movements. Headless worms and short lengths of the body can exhibit normal locomotory patterns both of the body wall and parapodia and, though movement may cease through loss of 'tone', it may be made to reappear by appropriate peripheral stimulation. In the starting up of locomotory waves, either in normal or headless worms, the parapodia at approximately four-segment intervals acquire in rapid anteroposterior succession postures which lead immediately to the execution of a step. The locomotory wave then links up over the intervals and spreads over the entire body from back to front. The continuity of the pattern is disrupted by transection of the nerve cord, though each nervously isolated part may show within itself a perfectly normal pattern. There are, evidently, in the establishment of locomotory waves, peripheral-central adjustments in each segment of the body and a segment-to-segment co-ordination dependent upon the integrity of the nerve cord. Some early experiments of Maxwell (1897) involving the severing of peripheral nerves show that, in addition, localized movements of the parapodia may on occasions originate from excitation localized in peripheral nervous pathways.

Experimental analysis of the co-ordinating functions of the ventral nerve cord has been directed, in the main, to an examination of the properties and functions of the giant-fibres. Through measurements of action potential, speed of conduction, stimulation threshold and rate of fatigue, Bullock (1945, 1948) has been able to postulate the presence, in *Neanthes virens*, of three systems of giant fibres, two being paired and one single. They are all internuncial in character responding to different spatial patterns of exteroceptive stimulation and mediating the passage of excitation to motor pathways the precise distribution of which has not, however, been determined.

Anatomical investigations have yielded information concerning the organization of the central and peripheral nervous systems in part of a like kind and in part different from that which can be ascertained by experiment. The nerve cord consists of a series of intersegmental ganglia invested by a crescent of cell bodies and giving rise to peripherally distributed nerves. The ganglia are linked by narrower connectives lacking cell bodies and segmental nerves. The conducting elements of the cord group by size and staining properties into giant-fibres and fine-fibres and functionally into sensory, internuncial and motor systems. Knowledge of the form and arrangement of the fine-fibres in nereids is founded primarily on the methylene-blue studies of Biedermann (1891), Retzius (1891) and Hamaker (1898), the points of similarity and difference of which have recently been enumerated (Smith 1956). All three accounts suffer from the serious deficiency of being essentially two-dimensional representations based on an examination of dorso-ventrally flattened pieces of cord; the sensory, internuncial and motor-fibre interrelationships are, in consequence, in some features distorted and in many respects incomplete. The anatomy of the giant-fibre systems (Hamaker 1898) is more accurately determined. Two fibres, one in each of the ventro-lateral corners of the neuropile, are the largest in diameter. Next in size is an unpaired median dorsal fibre. Paired paramedial fibres are the smallest. The separable action-potentials and the conduction rates recorded by Bullock (1945, 1948) accord with the observed number and relative diameter of the fibres. The dorsal fibre and the lateral fibres run the length of the cord, the former without interruption and the latter as a series of segmental fibres linked by intersegmental macrosynapses (Stough 1926). The segmental paramedial fibres on the other hand have a postero-anterior extension over only two body segments and consequently overlap segment by segment.

There is a considerable diversity of opinion as to the number of peripheral nerves in each segment, though all accounts agree that the nerves arise from the ganglion and not from the interganglionic connective. Retzius (1891) figures a single pair of nerves, Quatrefages (1850) three, Biedermann (1891) three or possibly four and Hamaker (1898) five pairs. There would, in fact, appear to be four pairs of nerves in all the various species studied by these workers, the discrepancies in the accounts being attributable to circumstances which have been fully discussed in a recent paper (Smith 1956). It is generally agreed that one pair of nerves (nerves II) are primarily concerned with the innervation of the parapodia; none of the nerves has, however, been accurately traced in respect either of its sensory or motor distribution.

Information on the sensory, motor or mixed character of the peripheral nerves is inconclusive and fragmentary. Retzius (1891), Biedermann (1891) and Hamaker (1898) figure fibres in the cord with extensions into one or more pairs of nerves and without apparent connexion with central cell bodies. They are assumed to be afferent fibres. Sensory cells in the integument have centrifugal* fibres which enter into relation with the peripheral nerves (Retzius 1892, 1895; Langdon 1900), and Langdon claims to have traced the centrifugal fibres to their endings in the cord as 'baskets' surrounding central ganglion cells. In this she is almost certainly in error, and the relationship between the various component fibres of the afferent tracts requires further examination. Fibres arising from a cell body in the neuron cortex of the cord and extending into the roots of one or more of the peripheral nerves (Retzius 1891; Biedermann 1891; Hamaker 1898) are motor in character. Their connexions, direct or indirect, with muscles have not, however, been demonstrated. Retzius alone figures motor endings on muscle, though he was not able to refer them to any particular segmental nerve or region of origin in the cord.

It will be evident from this summary of previous work on the nereid nervous system that virtually nothing is known of the details of neuron patterning either centrally or peripherally nor, therefore, of the form and distribution of the nervous pathways through which excitation is conducted. The present account has accordingly two ends in view, namely, to give an objective anatomical description of the fine-fibre systems of the nerve cord and segmental nerves as they are seen in methylene-blue preparations, and to identify in the complex of giant- and fine-fibre systems the more fundamental features of neuron patterning. It has been found convenient in some sections of the paper to present these simpler, derived features as a preface to the more detailed description.

Material and methods

Three species, *Platynereis dumerilii* (Audouin & M.-Edwards), *Nereis diversicolor* O. F. Müller and *Neanthes* (*Nereis*) *virens* (Sars) have been examined. The greater part of the *Platynereis* material was collected and stained for later examination at the Stazione Zoologica at Naples in 1949 and 1953. The specimens of *N. diversicolor* were prepared in 1952 at the Plymouth Laboratory and those of *N. virens* on various occasions at the Whitstable Laboratory of Queen Mary College.

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* In describing the fibres of a bipolar sensory cell the terms 'centripetal' and 'centrifugal' refer to the direction of conduction of excitation towards or away from the cell body.

Intra-vitam methylene-blue techniques have been used throughout for demonstrating fine-fibre neurons. With the rather small *Pl. dumerilii* the best results have been obtained by immersing whole worms for periods varying from 1 to 6 h in 50 ml. of filtered sea water to which 10 to 15 drops of 0·5% rongalit-white reduced methylene blue (I.C.I., zinc-free 'A'), prepared after the method of Unna (1916), were added. The larger *N. diversicolor* and *N. virens* were first narcotized in equal parts of sea water and 7·5% magnesium chloride and strips of the ventral body wall, to which the nerve cord and segmental nerves are attached, removed by making longitudinal cuts along both sides of the body through the bases of the parapodia. The alimentary canal and any other tissues overlying the nerve cord were dissected away and, in some instances, the ventral longitudinal muscles were removed to expose the underlying nerves to the direct action of the stain. The strips of body wall, tightly stretched on pieces of cork and attached by entomological pins, were floated on the staining fluid. Preparations were examined for progress of staining under a 16 mm objective at half-hourly intervals and, when adequately stained, treated for colour and tissue fixation as follows. Whole animals or strips of tissue still attached to their corks were immersed for about 12 h in 20 to 50 ml. of 8% ammonium molybdate solution at 4° C, then washed in running water for 5 min. Whole animals, which at this stage are flaccid, were lightly brushed on a glass plate to extend them; pieces of body wall were left on the cork. Dehydration was effected either by the passage of the tissues through a graded series of Lang's ethyl alcohol+butyl alcohol mixtures as recommended by Lang (1937) or by direct transfer, after blotting, to two changes of absolute ethyl alcohol for 5 to 10 min. The specimens, cleared in xylol, were stored in liquid paraffin, in which they can remain almost indefinitely without change of consistency or loss of colour, and subsequently prepared for examination either as whole mounts in balsam or as serial sections cut in various planes at thicknesses of from 5 to 100 μ, but usually at 20 μ. Whole mounts of these pieces of body wall were set between two number 0 cover-slips in order to facilitate the viewing of both external and internal surfaces, the cover-slips being temporarily fixed to a slide by a few drops of cedar-wood oil. For examination of the finer anatomical details compensated eyepieces were used in conjunction with Cooke Troughton 3·75 mm fluorite or 4 mm apochromatic oil-immersion objective lenses. Drawings were made on squared paper scaled to a calibrated squared eyepiece. Whenever sections were cut, a few segments of the original preparation were retained as a whole mount to aid in the reconstruction of the neuron configurations and fibre tracts. In all, about 150 methylene-blue preparations of *Pl. dumerilii*, about thirty of *N. diversicolor* and ten of *N. virens* were made use of for reference drawings. For the study of the form and distribution of the giant-fibres of the cord 10 to 20 μ thick transverse sections of *Pl. dumerilii* and *N. diversicolor*, fixed in Witmark's fluid and stained with Masson's or Heidenhain's Azan stains, were used.

The nerve cord and peripheral nerves

Figure 1, a stereogram of a number of body segments of *N. virens* dissected at various levels, shows the principal muscle systems of the body wall and parapodia, the form and setting of the nerve cord, and the more general distributional features of the nerves which arise from the ganglia.

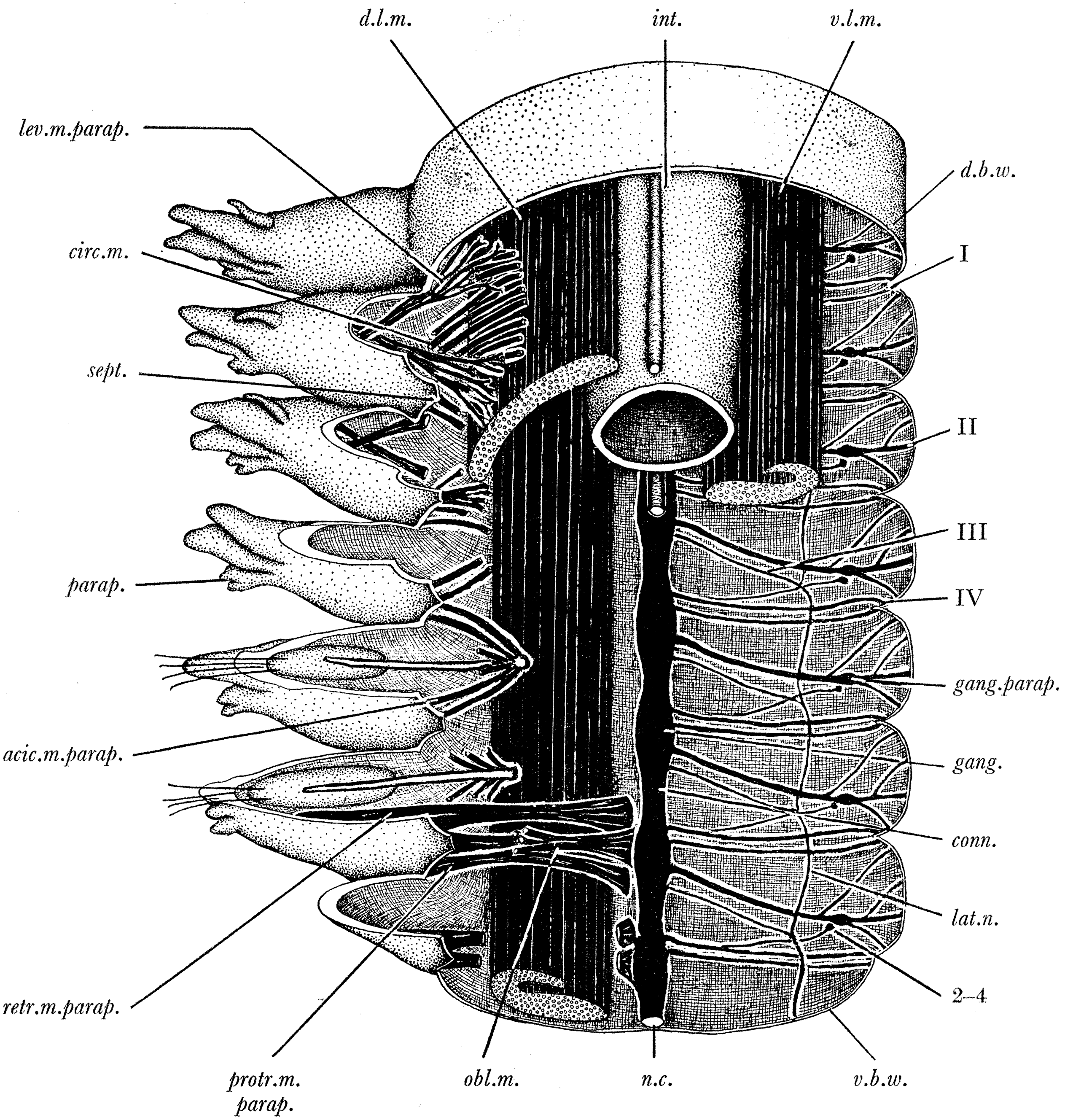

FIGURE 1. Stereogram of seven body segments of *N. virens* dissected at various levels to show the nerve cord and segmental nerves and the muscles of the body wall and parapodia. The anterior end is at the top of the figure. I–IV, the segmental nerves in antero-posterior succession; *2–4*, peripheral connexion between nerves II and IV; *acic.m.parap.* acicular muscle of the parapodium; *circ.m.* circular muscles of the body wall; *conn.* nerve cord connective; *d.b.w.* dorsal body wall; *d.l.m.* dorsal longitudinal muscle; *gang.* nerve cord ganglion; *gang.parap.* ganglion of the parapodial nerve (II); *int.* intestine; *lat.n.* lateral nerve; *lev.m.parap.* levator muscle of the parapodium; *n.c.* nerve cord; *obl.m.* oblique muscle; *parap.* parapodium; *protr.m. parap.* protractor muscle of the parapodium; *retr.m.parap.* retractor muscle of the parapodium; *sept.* intersegmental septum; *v.b.w.* ventral body wall; *v.l.m.* ventral longitudinal muscle.

Dorsal (*d.l.m.*) and ventral (*v.l.m.*) longitudinal muscles act synergically in the production of undulatory waves. Circular muscles (*circ.m.*) external to the longitudinals are less well developed and are not present in all parts of the body segment. Their distribution follows that of the collagen-restraining bands later to be described (p. 179). Some of the muscles responsible for the parapodial movements are extrinsic to the parapodium, others are intrinsic. To the former series belong (*a*) the parapodial protractors (*protr.m.parap.*) and retractors (*retr.m.parap.*) originating from the ventral body wall or from collagen material surrounding the nerve cord and inserted respectively into the anterior and posterior faces of the parapodium, and (*b*) the levator muscles (*lev.m.parap.*) arising from the circular muscle sheath and inserted into the dorsal wall of the parapodium. The principal intrinsic muscles are the spoke-like fibres (*acic.m.parap.*) radiating from the acicula and chaeta sacs which bring about localized movements of the aciculum and parapodium.

The nerve cord (*n.c.*), which lies in the mid-line of the ventral body wall (*v.b.w.*) and extends throughout the parapodium bearing segments, consists of a series of intersegmental ganglionic swellings (*gang.*), the greater part of each ganglion lying posterior to the intersegmental septum (*sept.*). The ganglia are linked by narrower intrasegmental connectives (*conn.*). Four pairs of peripheral nerves (IV, I, II and III) originate from each ganglion; IV is pre-septal, the remaining ones post-septal. The seriation I–IV therefore corresponds to the antero-posterior succession of the nerves within a segment and follows the system of numbering adopted by Quatrefages (1850) and Hamaker (1898). The largest of the nerves is the parapodial nerve (II), except in the more anterior segments where IV may exceed it in diameter. Nerve III is very fine and would not be seen in dissection without previous staining; I can only be traced with difficulty. Each nerve, on leaving the ganglion, dips ventrally and towards the mesio-ventral border of the ventral longitudinal muscle (*v.l.m.*) and comes to lie on the internal face of the ventral body wall (*v.b.w.*). The slope of nerves II and IV (figure 2, II and IV) at their origin from the cord is flatter than that of nerves I and III (figure 2, I and III), the difference in inclination being related, on more detailed examination (p. 157), to the vertical levels in the cord of the internuncial fibres with which the afferent and efferent components of the nerves are connected. The fibres of the steeply sloping nerves I and III have dorsal central connexions only, nerves II and IV are connected both dorsally and ventrally.

Nerve I (figure 1, I), arising from the ganglion a short way behind the intersegmental septum, runs transversely across the floor of the segment below the ventral longitudinal muscle to the margin of the segment, where it ascends along the internal face of the lateral body wall between adjacent parapodia to the dorsal integument. Nerve II, the parapodial nerve, runs outwards from the cord under the muscle in a posteriorly slanting course. A little way beyond the lateral margin of the muscle, and at its point of entry into the parapodium, the nerve expands into a ganglion (*gang.parap.*) from which a number of branches, later to be described in detail (p. 186), extend into the appendage. Nerve III emerges from the ganglion a little behind the parapodial nerve near the junction of the ganglion and connective. After dipping sharply to the basement membrane of the integument it continues in a slanting course, posteriorly and laterally, to reach the outer border of the ventral longitudinal muscle near to nerve IV and the intersegmental septum. The third nerve divides at this point into anteriorly and posteriorly directed branches which, pursuing a somewhat sinuous course parallel to the muscle border, link up with the corresponding tracts in other segments, so forming a lateral nerve (*lat.n.*) which extends from the first to the last of the parapodium-bearing segments. The lateral nerve runs in the connective tissue beneath the ectodermal epithelium, dipping below nerves I and III but passing over (dorsal to) nerve II mesial to its ganglion. The lateral nerve of nereids is not to be identified with the lateral longitudinal nerve described by Storch (1913) as linking the parapodial ganglia of successive segments in the so-called 'tetraneurous' polychaetes included within the family Amphinomidae. In nereid polychaetes the nerve runs mesial to the ganglia and is never connected directly or indirectly with the parapodial nerve. Nerve IV, the most posterior of the nerves within a segment, originates from the anterior, pre-septal part of the succeeding ganglion. The nerve has a similar distribution to nerve I, crossing the ventral body wall transversely and passing to the dorsal wall along the circular contour of the body of the intersegmental region.

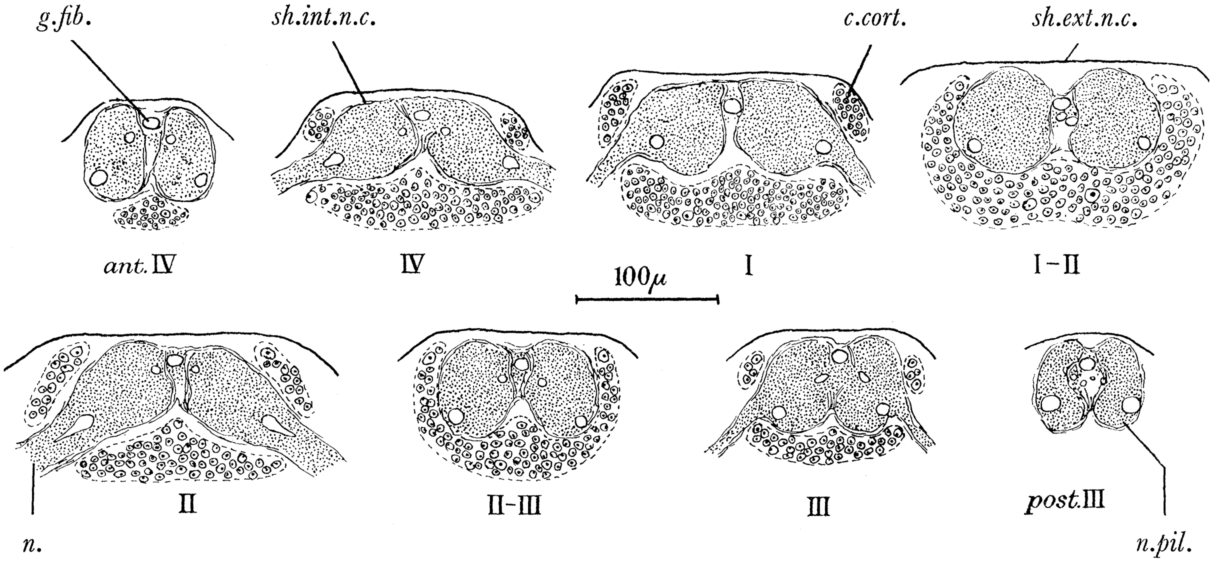

FIGURE 2. Transverse sections through the nerve cord of *Pl. dumerilii* at different levels of a body segment. The levels are indicated by Roman numerals corresponding to the four pairs of nerves. The sections *ant.* IV and IV are through the pre-septal part of the ganglion; I, I–II, II–III and III through the post-septal part. *Post.* III is through the connective. *c.cort.* cell cortex; *sh.ext.n.c.* outer sheath of the cord; *g.fib.* giant-fibre; *n.pil.* neuropile; *sh.int.n.c.* inner sheath of the nerve cord.

There is complete identity of pattern of the segmental nerves of the three species *N. diversicolor*, *N. virens* and *Pl. dumerilii* studied during the present work in respect of their number, place of origin from the ganglion, course, distribution and relative size. Since there is good reason to believe that the nerves of *N. cultrifera* and *N. pelagica* conform to a like plan (Smith 1956), the arrangement described is, in all probability, common to all nereid worms.

STRUCTURAL ELEMENTS OF THE NERVE CORD

The nerve cord in all its parts is invested by fibrous material arranged to form an outer and an inner sheath. The sheaths enclose, and in part penetrate, a central neuropile made up substantially of exceedingly fine and branching strands of glia, the reticulum of which serves as a support for the giant-fibres and fine-fibres of the cord.

Bordering the ganglia (figure 2, I, II, III, IV), but not the connectives (figure 2, *ant.* IV), is a crescent of closely compacted cell bodies (*c.cort.*). The crescent is thickest on the ventral surface, tapers towards the dorso-lateral angles of the cord and is absent from its dorsal side. All the cortical cells of the ganglion (figure 3*B*, *c.cort.*) are contained within the connective tissue of the outer sheath (*sh.ext.n.c.*).

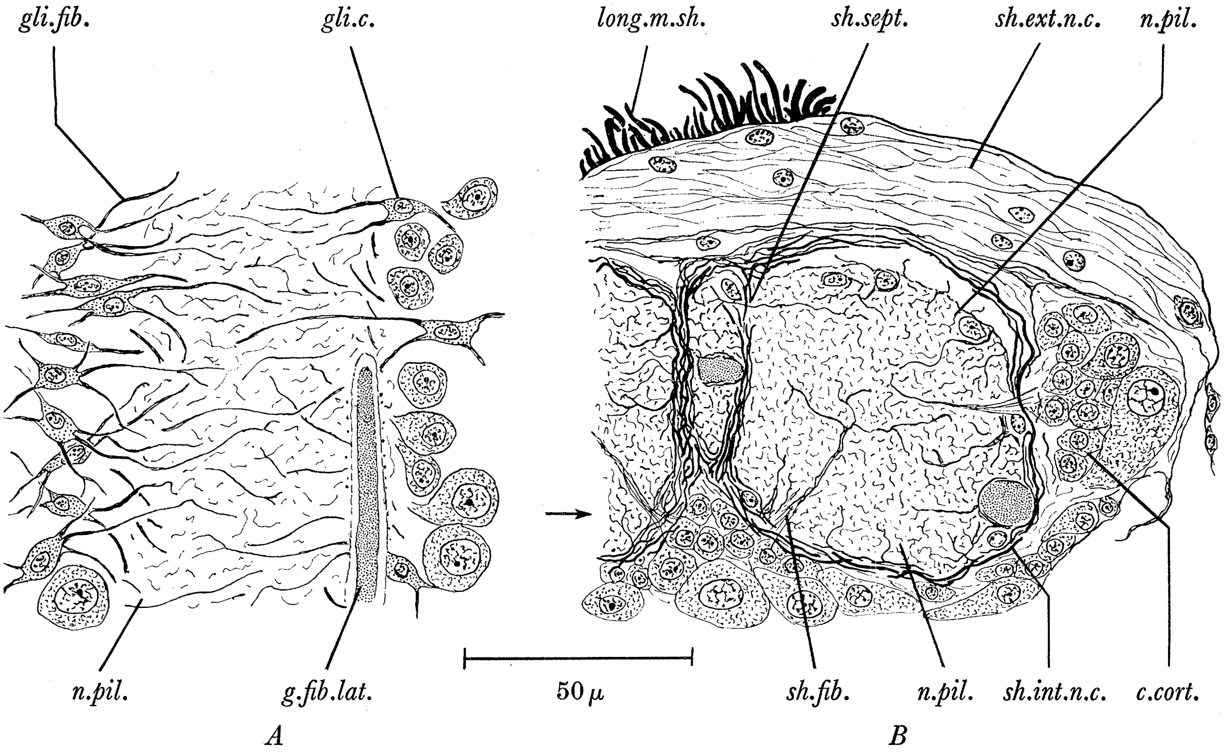

FIGURE 3. *A*, horizontal half-section through a ganglion of *N. diversicolor* at the level in *B*, indicated by the arrow. *B*, transverse half-section through a ganglion of *N. diversicolor*. Witmark fixed, Masson stained. *c.cort.* cell cortex; *g.fib.lat.* lateral giant-fibre; *gli.c.* glia cell; *gli.fib.* glia fibre; *long.m.sh.* longitudinal muscle of nerve sheath; *n.pil.* neuropile; *sh.ext.n.c.* outer sheath of nerve cord; *sh.fib.* sheath fibre invading the neuropile; *sh.int.n.c.* inner sheath of nerve cord; *sh.sept.* sheath septum.

The outer sheath varies considerably in thickness in the different parts of the cord, being best developed in the places where muscles are attached to it. To the lateral wall are attached some of the fibres of the protractor and retractor muscles of the parapodium (figure 1, *protr.m.parap.*, *retr.m.parap.*) while dorsally it supports longitudinally running muscle fibres (figure 3*B*, *long.m.sh.*) the contraction of which would appear to shorten the cord. The slender fibres of which the external sheath is composed have an overriding circumferential orientation and are arranged in an open mesh. They contain fibroblasts usually to be recognized by their nuclei; the cell cytoplasm does not stain readily. The inner sheath (*sh.int.n.c.*) is composed of fibres of varying diameter, the largest of which, however, are noticeably thicker than those of the outer sheath. Its inner border is attached to the surface of the neuropile (*n.pil.*), though in the preparation of sections it frequently becomes detached. Many of the formative fibroblasts of the inner sheath are contained within the neuropile, usually at its periphery. They are in size and shape similar to those of the outer sheath. It will be seen from figure 3*B* that the inner sheath cuts into the neuropile, as a double septum (*sh.sept.*). In places, however, the septum is single and it is rarely complete. Even where best developed it has the form of an open lattice, extensively penetrated by glia strands and allowing of the passage of nerve fibres from one side of the cord to the other. Sheath fibres other than those of the vertical septum (figure 3*B*, *sh.fib.*) invade the neuropile from all parts of the periphery. They are readily identified by their staining qualities and by their tendency to form many-stranded cords, in both of which respects they differ from the glia fibres. These latter arise from fusiform cells (figure 3*A*, *gli.fib.*) lodged in the cell cortex. Each cell is drawn out into a number of branching processes which together form the framework supporting the conducting fibres. The glia cells are by far the most numerous of the cells contained within the ganglion cortex. Where counts have shown a total number of some 2000 cell bodies associated with a ganglion, it has been estimated that not more than 100 to 200 are nerve cells giving rise to internuncial and motor fibres. The neurons of the cortex to which brief reference has been made are described more fully in the succeeding part of the account which is concerned with the nervous organization of the cord.

Nervous organization of the cord

The internuncial systems

In entering upon a description of the nervous anatomy of the nereid body segment some remarks may be offered on the arrangement of the subject-matter and, in particular, on the order in which the component elements are described. The sequence which at first sight would seem most appropriate would be that which accords with the routing of excitation. This would entail a tracing of the conduction paths from the sensory cells through the afferent tracts and central internuncial neurons to the efferent fibres of the segmental nerves and thence to the motor endings on the various systems of muscles. There are, however, at least two reasons for rejecting this form of presentation. In the first place, since all the peripheral nerves are 'mixed', it would necessitate, for purposes of description, an arbitrary separation of the component parts which are best dealt with together as they occur in the nerve. The second reason, which is the more cogent, bears on the fundamental architecture of the nervous system.

An inspection of the neuron arrangements within the various parts of the nervous system makes it apparent that the pattern of intra- and intersegmental distribution of excitation within the cord is defined, in the main, by the form and orientation of the internuncial systems. The tracts or neuropile condensations to which they give rise are so constituted or positioned as to determine the level of entry into the cord of the afferent fibres and the course which the motor axons follow in their passage through the ganglion to the segmental nerves. The account therefore begins with an analysis of the form and arrangement of the central internuncial neurons and continues by working outwards to the periphery along the sensory and motor pathways, leaving to the discussion at the end of the paper a review of the nature and possible significance of the observed patterns of peripheral and central neuron linkages in the several parts of the system.

Central internuncial neurons can be defined as neurons having fibres that are wholly contained within the substance of the neuropile and originating from cell bodies lodged within the cell cortex surrounding the ganglia. Usually there is little difficulty in recognizing an internuncial neuron for what it is, though, on occasions, incompletely stained motor fibres, which also arise from central cell bodies, may be confused with them.

Giant-fibre internuncial neurons

There are two main categories of internuncial fibre within the nereid nerve cord, the giant-fibres and fine-fibres, sharply distinguished by their size range, staining properties and distribution. In the rather small worms which have been used for sectioning during the course of this work the giant-fibres show a diameter range of from 7 to 50 μ compared with the 0·1 to 2 μ of the fine-fibres. The giant-fibres do not, as do the fine-fibres, stain with methylene blue. Figure 4, which shows somewhat diagrammatically the arrangement of the giant-fibres within a segment of the cord, was reconstructed from 20 μ transverse sections of *N. diversicolor* fixed in Witmark's fluid and stained with Masson's trichrome stain. Other reconstructions of *Pl. dumerilii* gave an almost identical picture, both closely resembling Hamaker's (1898) figure of the giant-fibre system of *N. virens*. In the following description, features that Hamaker does not mention are the considerable variation in shape and diameter of individual fibres in different parts of their course, the changing levels of the fibres within the neuropile, particularly of the median dorsal fibre, and the occurrence in the lateral fibres of intersegmental macrosynapses, the last-named feature having been described by Stough (1926).

The largest of the fibres are the paired laterals (*g.fib.lat.*) situated laterally or in the ventro-lateral angles of the cord. Each is of segmental origin, the segmental pieces being connected in series by broad wedge-shaped macrosynapses (*syn.*) into a single conducting unit running the length of the body segments and terminating anteriorly in the circumpharyngeal commissure (Nicol 1948). The cell bodies from which the lateral fibres take their origin have not been identified. Each lateral fibre varies along its length in shape and diameter. They are greatest in cross-sectional area anterior and posterior to nerve II and smallest at the junction of the connectives with the anterior ends of the ganglia. The variation in the various regions is of the order of 3:1. A notable and constant feature is the flattening of the fibres opposite nerves II and IV and their extension in these places towards the roots of the nerves.

The median dorsal fibre (*g.fib.d.*), originating (Hamaker 1898) from one or more cells in the neuron cortex of the suboesophageal ganglion, is continuous throughout the length of the nerve cord and is without macrosynapses. Its average diameter is about half that of the laterals and its cross-sectional area shows, within its segmental length, a 4:1 variation. In the ganglion, represented in figure 4 by the interval between nerve IV anteriorly and nerve III posteriorly, the fibre dips into the neuropile to lie at a depth almost one-third removed from the dorsal surface (figure 4*B*). In the connective, on the other hand (figure 4*E*), the fibre is adjacent to the dorsal surface.

The paired paramedial fibres (*g.fib.p.m.*) arise, in each segment, from large pear-shaped neurons (*neur.p.m.*), some 20 to 25 μ in diameter, situated ventrally or ventro-laterally in the neuron cortex. The fibres ascend from the parent cell body to the neuropile and effect a cross-over in the region of nerve III (figure 4*D*). They then run forwards in the cord at the mid-vertical level to a point midway between nerves I and II where they cross again in the mid-line below the dorsal fibre (figure 4) and continue forwards to the level of nerve II in the more anterior segment (*g.fib.p.m'.*) to end in a tapering point in contact with the paramedial fibre of the anterior segment (*g.fib.p.m.*). There appears to be direct contact

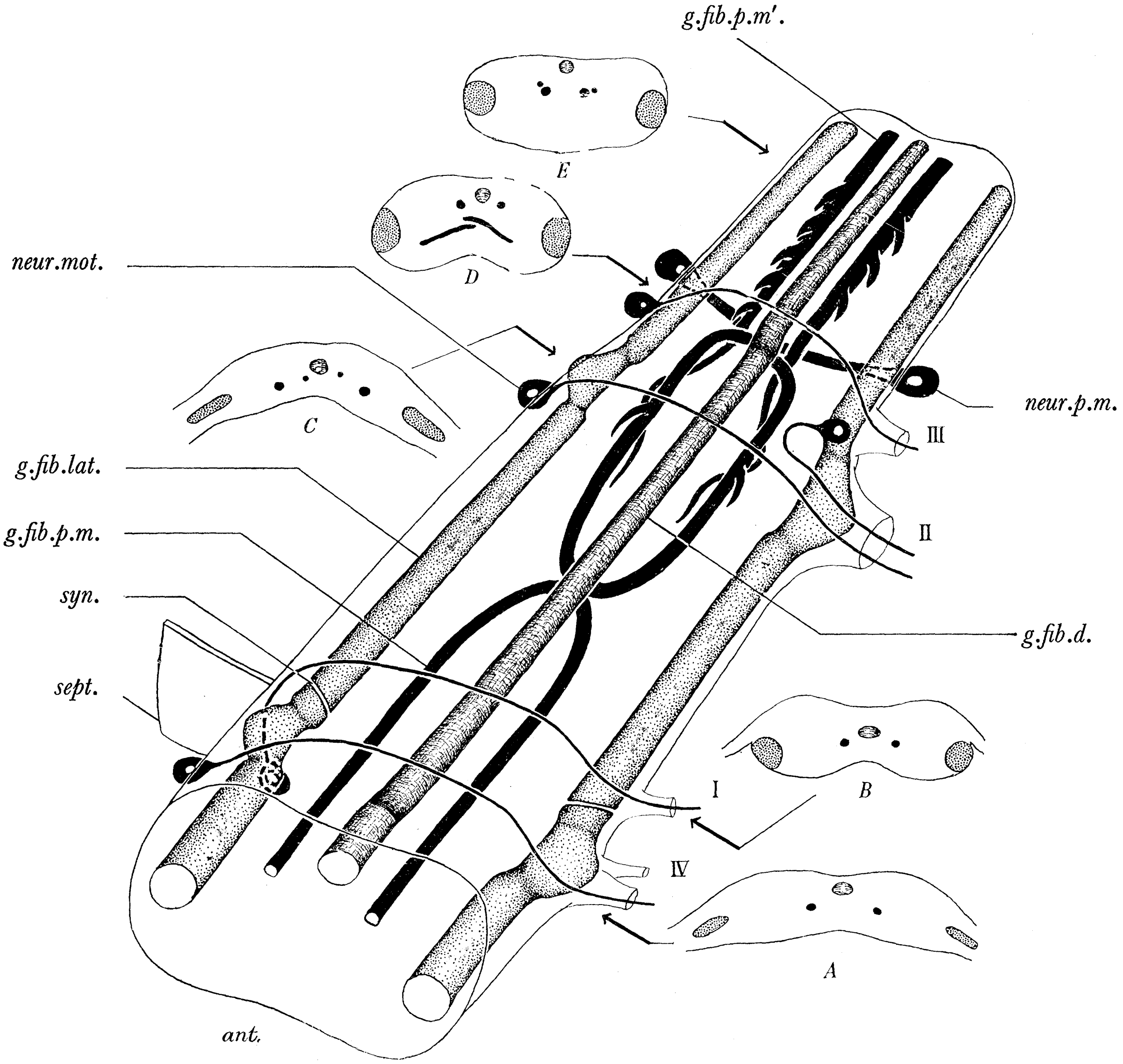

FIGURE 4. Stereogram of a ganglion and connective of *N. diversicolor* showing the form and arrangement of the giant internuncial fibres and the principal motor fibres of the segmental nerves. The anterior (pre-septal) end of the ganglion is at the bottom of the figure. *A*, *B*, *C*, *D* and *E*, outline transverse sections through the cord to show the position of the giant-fibres at the levels indicated by the arrow. *A* to *D* are through the ganglion, *E* through the connective. I–IV, the roots of the segmental nerves; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.*, *g.fib.p.m'.* paramedial giant-fibre; *neur.mot.* motor neuron; *neur.p.m.* cell body of paramedial fibre; *sept.*, septum; *syn.* macrosynapse.

between the fibres of the two sides at the more anterior of the two cross-overs. In no other instance, however, is there a direct connexion between any one fibre and another either in respect of the fibres of a pair or between fibres of different systems. In figure 4 the distal parts of the paramedial fibres (*g.fib.p.m'.*) are shown as having lateral sprigs. Hamaker

(1898) also shows them. There is some doubt, however, whether they represent true collaterals of the main fibre or are spaces in the neuropile. This particular feature, though included in the figure, must, therefore, be subject to reservation. Taking the three systems as a whole, the cross-sectional area ratios of the lateral, dorsal and paramedial components vary in the different regions of the cord between 20:4:1 and 5:2:1 with an estimated average ratio of 12:3·5:1.

Two anatomical features which appear to be of significance in the routing of efferent excitation from the ganglion to the peripheral nerves may, in conclusion, be noted. It has been observed that the median dorsal giant-fibre which in the connective lies at the surface of the neuropile descends in the ganglion to a deeper level. The change of level undoubtedly arises from the necessity of providing for the passage through the neuropile of the dorsally crossing commissural motor fibres (figure 4, *neur.mot.*) which are present in the ganglion but not in the connective. The second notable feature in the anatomy of the giant-fibres is the outward extension of the lateral fibres into the roots of nerves II and IV. Since, as will be shown, these nerves are responsible respectively for the innervation of the parapodial musculature and of the greater part of the muscles of the body wall, the entry of the lateral fibres into their roots may perhaps be relevant to the development of generalized movements involving a number of body segments and the rapid transfer of excitation along the cord.

Fine-fibre internuncial neurons

The nature and variety of the fine-fibre internuncial neurons of the nereid ganglion can be seen from figure 7*A*. The drawing is a simplification of the neuron complex in that neither sensory nor motor elements are included and, for further clarification, the internuncial neurons are shown only on the one or other side of the ganglion, though they are, in fact, duplicated bilaterally. The neurons can be classified into two main categories. Those whose cell bodies are shown on the right of the figure (*neur.intern. a. 1–20*) share the common character of having a long axon the eventual course and alinement of which is directed along one or other of six longitudinally oriented fine-fibre tracts symmetrically disposed in the two lateral halves of the cord as dorso-lateral (*tr.d.lat.*), dorso-medial (*tr.d.m.*) and ventral (*tr.v.*) tracts. The second group comprises internuncials with relatively short but richly branching axons (*neur.intern.b.*, *neur.intern.c.*) having an orientation either predominantly horizontal (*neur.intern.b.*) or vertical (*neur.intern.c.*). The form, occurrence and distribution of each type of neuron will be considered in turn.

Some twenty long-axon neurons (figure 7*A*, *neur.intern.a. 1–20*) can be identified in each lateral half of a ganglion, though not all may be stained in any one preparation. Their cell bodies (figure 5, *a–g*) are roughly spherical or sometimes pear-shaped with a diameter of 15 to 25 μ, the greater number being about 18 μ. They are always unipolar, giving rise on the side facing the neuropile to a single axon fibre some 2 μ wide and narrowing over the greater part of its length to about 1 μ, finally to taper to an extreme fineness. The appearance of the cell body varies greatly according to the depth of staining and whether or not there is fixation or dehydration shrinkage. In a deeply stained preparation (figure 5*b*) the whole of the cell body is deep blue or almost black with no distinction of nucleus and cytoplasm. Not infrequently the interior of the cytoplasm contains blue-staining granules (*a*, *d*, *e*) or the cytoplasm may be finely granular (*c*, *f*) or pale and translucent (*g*). Shrinkage of the cell often produces a corrugated outline (*b*) or wrinkling of the surface (*f*); in well-fixed preparations, however, the boundary of the cell is smoothly convex. The appearance of the nucleus also varies according to the the depth of staining (*f*, *g*).

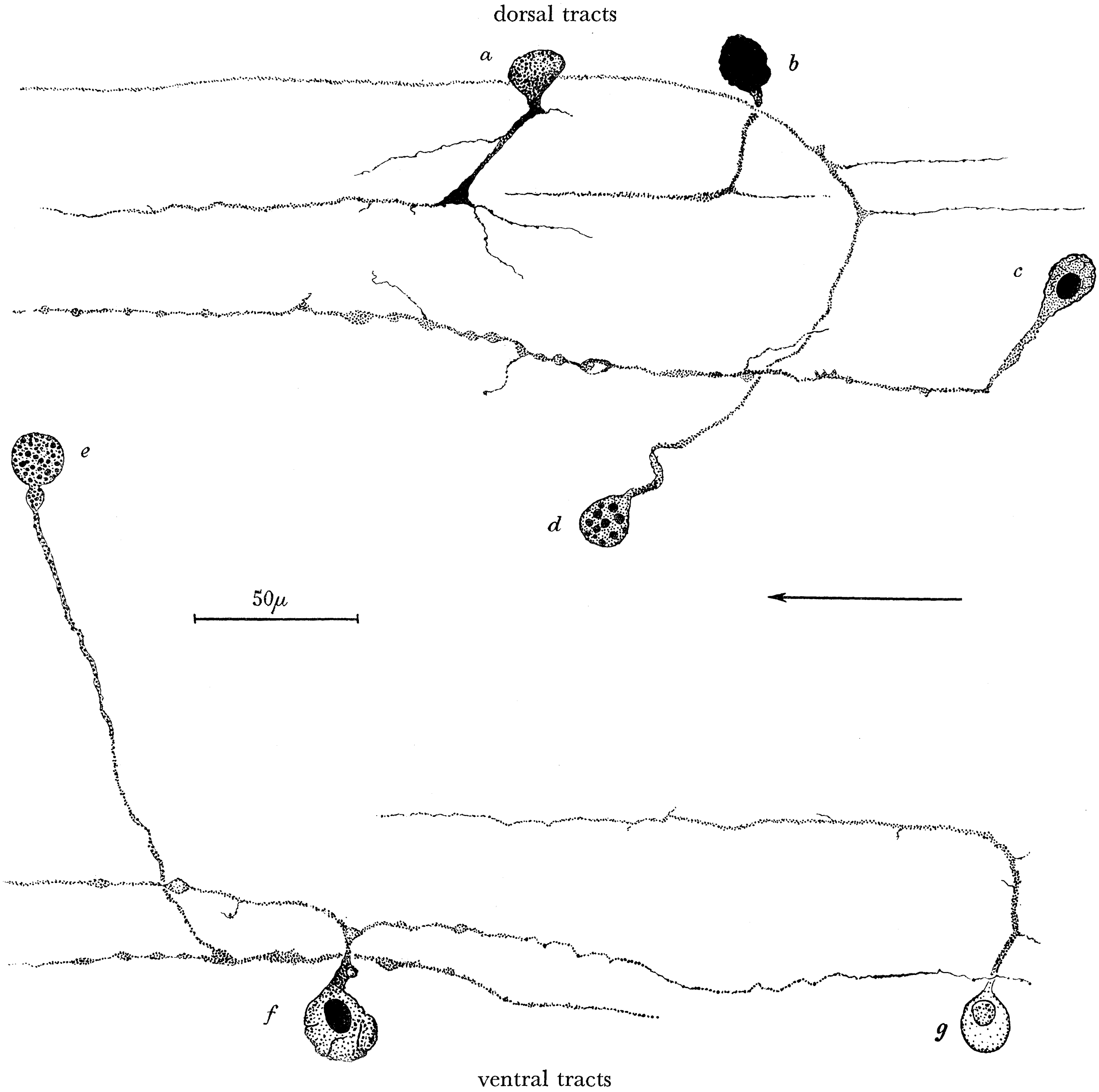

FIGURE 5. Long-axon internuncial neurons of the nerve cord of *Pl. dumerilii*. *a*, *b*, *c* and *d* neurons with axons entering the dorso-lateral and dorso-medial longitudinal fine-fibre tracts; *e*, *f* and *g*, neurons with axons entering the ventral longitudinal fine-fibre tracts. The arrow marks the longitudinal axis of the cord.

The axon fibre, on first taking the stain, is light in colour and of even texture. Later, granules appear on its surface, the granules increasing in number, size and depth of colour as staining progresses. Even in the early phases of staining, and before obvious artifactual swellings appear, the fibre is not completely even in diameter, the more obvious enlargements frequently marking the origin of axon collaterals (*a*, *d*). The axon often persists to the end of its course as a single principal fibre (*d*, *g*), but in many neurons (*e*, *f*) it bifurcates on reaching an internuncial tract into two branches diverging at 180° and directed anteriorly and posteriorly. The two branches may be equally well developed (*e*, *f*) or one of them may (*b*) be a little or (*a*) noticeably smaller than the other, in which latter case the subsidiary fibre assumes the character of a collateral branch. Collaterals are commonly developed (*a*, *d*), and the occurrence of small sprigs at intervals along the main fibre (*c*, *g*) may indicate a much more extensive collateral system in the living neuron than is normally visible in fixed preparations. The finer collaterals almost always exhibit 'beading'.

The most important configurational characteristic of the long-axon internuncial neurons and, as will be seen later (p. 193), the key to their function is the eventual alinement of the principal fibres along one or other of the longitudinal fine-fibre tracts. This unidirectional tendency is shown in figure 5, where the arrow points along the longitudinal axis of the cord. The longer collateral branches have a like orientation (figure 5, *d*). As figure 7*A* shows, about one-half of the neurons have axons directed in the initial part of their course across the neuropile to a contralateral tract, the remainder enter ipsilateral tracts.

Neurons of the second category fall into two series (figures 6*A*, *B*). Features common to the two series and which serve to distinguish them from the long-axon neurons are (1) a smaller cell body, 10 to 15 μ in diameter and pear-shaped rather than globular, (2) the orientation of the axon either vertically or horizontally but never longitudinally, (3) the relatively short axon length, and (4) the large number of branching collateral processes of the main fibre.

The first of the two groups of internuncial neurons with extensive collateral axon branching to be considered are those (figure 6*A*) with vertically ascending axons originating from cell bodies lodged in the ventral sector of the cell cortex either in the mid-line of the cord or a little to one side of it. Both the axon and the collateral branches 'bead' readily. Some of the subsidiary branches extend from the proximal part of the axon into the ventral neuropile of the ganglion, but the greater number are distal or subterminal, fanning out by successive dichotomies as an umbrella-like network within the dorsal neuropile. There appear to be some thirty to forty neurons of this type in each ganglion arranged on either side in single or double file (figure 7*A*, *neur.intern.c.*). They are most numerous in the regions adjacent to the root of the segmental nerves.

Figure 6*B* shows a neuron of the second type within the general category of the branched-axon internuncials. The cell bodies of these neurons are always to be found within the dorso-lateral sectors of the cell cortex (*c.cort.*) on the two sides of the ganglion. Each cell body projects its axon horizontally through the neuropile (*n.pil.*) to the contralateral side. There is often a recurrent branch curving back ipsilaterally. Collateral processes extend dorsally and ventrally from the main fibre. They thus form with their subsidiary branches a nervous reticulum which, like that of the vertical axons, is substantially confined to the dorsal half of the neuropile. There are about ten to fifteen neurons with horizontally directed axons in each ganglion, and they are for the most part concentrated near the origins of the segmental nerves.

The foregoing description of the component elements of the internuncial system cannot readily be reconciled with earlier accounts of the fine-fibre organization of the nereid nerve cord. Retzius's (1891) drawings (Taf. III, figs. 1 and 2) portray a complex series of cell bodies and fibres among which it is possible to recognize sensory and motor fibres, long-axon internuncials and internuncials with horizontally projected branching axons. Internuncials with vertically ascending branched axons are not, however, represented.

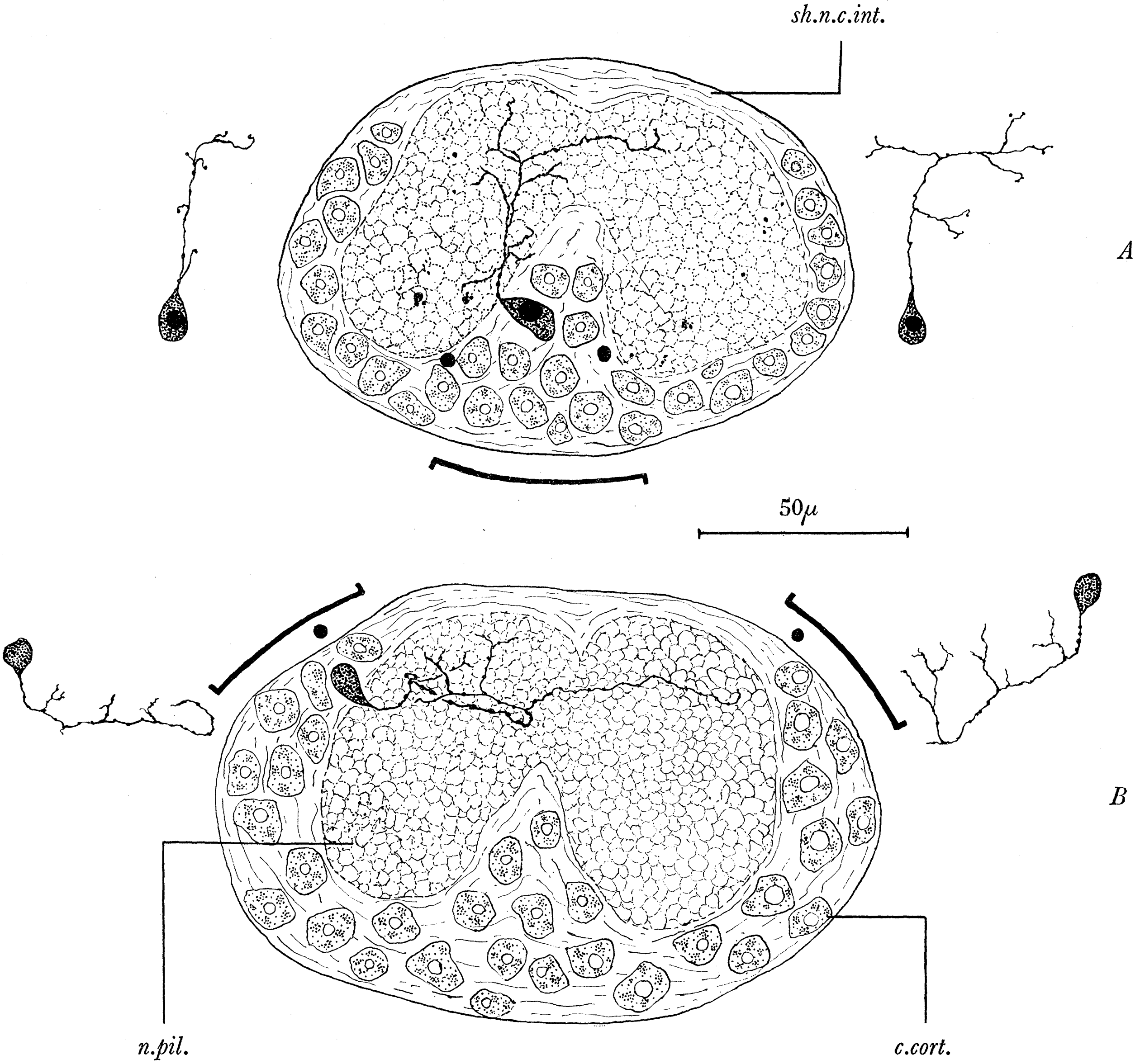

FIGURE 6. Transverse sections through a ganglion of *Pl. dumerilii* to show the form and axon distribution of the branched axon internuncial neurons of the nerve cord. *A*, a ventral neuron with a vertical axon branching in the neuropile, principally in the dorsal neuropile. The subsidiary figures show neurons of a like kind from adjacent sections. The thick line under the section is the arc of the cell cortex to which the cell bodies of these neurons are restricted. *B*, a dorso-lateral neuron with a horizontal axon branching within the dorsal neuropile. The subsidiary figures and the thick line arcs have a similar significance to those in *A*. *c.cort.* cell cortex of the ganglion; *n.pil.* neuropile; *sh.n.c.int.* inner sheath of the nerve cord.

Biedermann (1891) figures a few of the long-fibre neurons in addition to sensory and motor fibres, while Hamaker's (1898) account, though excellent in respect of the giant-fibres, barely mentions the fine-fibre system.

With the description of the component parts of the internuncial system so incomplete it is not surprising that its patternal characteristics remained unrecognized. Retzius alone of the earlier investigators figures preparations in sufficient detail for satisfactory analysis. But his drawings are, unfortunately, projected in a horizontal plane and so lack the distinction of vertical levels. One consequence of this flattening, as we have seen, is the omission of the internuncial neurons with vertically ascending branched axons. But from the point of view of pattern analysis a more serious error is the figuring of the three paired systems of longitudinal fine-fibre internuncial tracts, two of which are dorsal and one ventral, as a broad horizontal band of fibres stretching in a single plane over the width of the cord. A misconception of this kind makes it impossible for the several fibre systems, sensory, motor and internuncial, to be appreciated in their three-dimensional relationships. It has been necessary, therefore, in attempting an analysis of the anatomy of the internuncial systems of the nereid cord to reject earlier interpretations and to rely wholly on original material.

THE NATURE AND SIGNIFICANCE OF THE PATTERNS OF INTERNUNCIAL NEURONS AND FIBRES

The functional interpretation of nervous anatomy centres essentially upon the form and relationships of fibre systems and the relating of visible neuron patterns to the routing of excitation. Moreover, the reliance that can be placed upon a judgement of the functional role of a neuron system will depend upon the extent to which its anatomical pattern appears to be designed for the transfer of excitation in a particular direction or to a determinable region or place.

The two categories of internuncial neurons in the nereid nerve cord are, on the basis of this argument, clearly adapted for different purposes, the long-axon neurons with poorly developed collaterals for the transfer of excitation to distant parts of the cord, and the short-axon neurons with an extensively branched collateral system for local but diffuse transfer of excitation. The further implications of the arrangement of the two systems may be considered in turn.

In respect of the long-axon neurons (figure 7*A*, *neur.intern.a.*, *1–20*) it may be noted that the cell bodies, here shown on one side of the ganglion only, are located either in the ventral (*4*, *8*, *10*, *11*, *16*), ventro-lateral (*1*, *3*, *5*, *6*, *9*, *14*, *15*, *17*) or dorso-lateral (*2*, *7*, *12*, *13*, *18*, *19*, *20*) sectors of the cell cortex. Their fibres may have an ipsilateral destination running (*4*, *8*, *12*, *20*) to the dorso-lateral tract (*tr.d.lat.*), or (*3*) to the dorso-medial (*tr.d.m.*) or (*9*, *17*) ventral tract (*tr.v.*). Contralateral fibres similarly terminate in the dorso-lateral (*2*, *5*, *8*, *10*, *18*, *19*), dorso-medial (*11*, *13*, *16*) or ventral (*1*, *14*, *15*) tracts. The initial course of the axons through the neuropile is very varied, usually transverse but sometimes obliquely oriented either in an anterior (*14*) or posterior (*4*, *6*, *9*) direction. Among these various configurations, however, two constantly occurring features can be recognized. Both relate to the directions taken by the axons, namely, that in their distal parts they are longitudinally oriented while proximally they show an overriding ventro-dorsal displacement

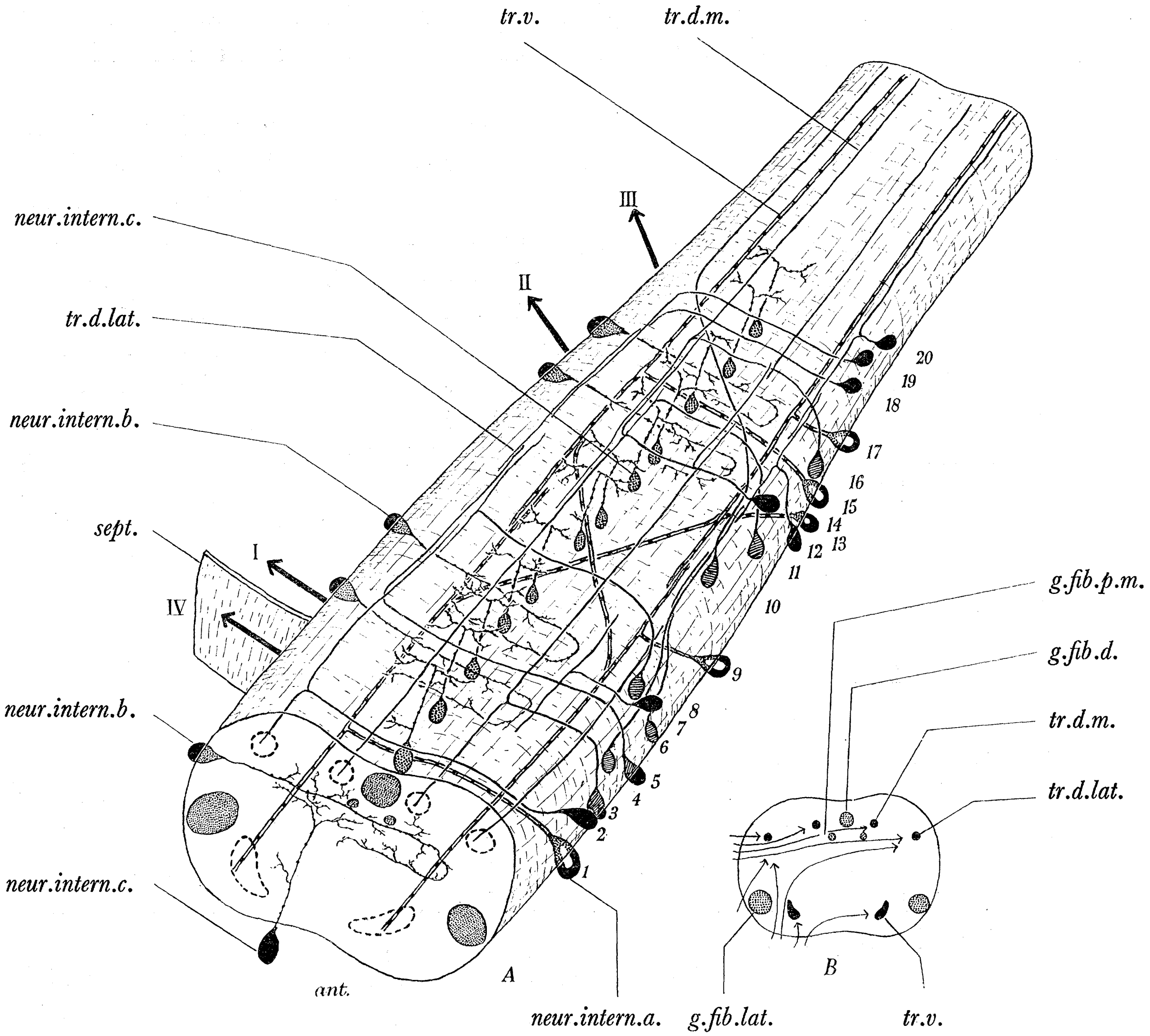

FIGURE 7. *A*, a diagrammatic stereogram showing the principal neurons and fibres of the internuncial systems of the nerve cord of *Pl. dumerilii*. The anterior end of the ganglion is at the bottom of the figure and the ganglion extends posteriorly to the narrower connective. The cell bodies of internuncial neurons with long axons supplying the longitudinal fine-fibre tracts are shown (*1–20*) to the right of the figure. Internuncial neurons with horizontal branching axons (*neur.intern.b.*) are on the left of the figure and internuncial neurons with vertical axons extending from ventral cell bodies (*neur.intern.c.*) are shown in a longitudinal row along the length of the ganglion. All three systems, shown here on the one or other side of the cord, are duplicated bilaterally. The cut end of the cord shows giant-fibres (stippled), the position of the fine-fibre tracts (broken lines) and one each of the two types of branched axon neurons. I–IV, position of the segmental nerve roots; *ant.* anterior end of the ganglion; *neur.intern.a.* long-axon internuncial neuron; *neur.intern.b.*, *neur.intern.c.* branched axon internuncial neurons; *sept.* intersegmental septum; *tr.d.lat.* dorso-lateral fine-fibre longitudinal tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract. *B*, outline transverse section of the ganglion showing the position of the giant- and fine-fibre longitudinal tracts and the principal directions taken by the long internuncial axons of one side of the cord in passing to one or other of the fine-fibre tracts. *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.* para-medial giant-fibre; *tr.d.lat.* dorso-lateral longitudinal fine-fibre tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

in their course from the parent cell body. Taking these in order it may be noted in the first place that *all* the axons terminate in one or other of the fine-fibre longitudinal tracts. This is no mere fortuitous circumstance but is an intrinsic characteristic of the growth and development of the axon. Its determinate nature can best be seen in the instances where the axon in its proximal course is oriented transversely to the tract which it is to enter (figure 7*A*, *neur.intern.a.*, *2*, *35 et al.*); on reaching the tract it turns sharply at right angles or bifurcates at 180° to continue with a strictly longitudinal alinement. It would be premature at this stage of the account and before the sensory and motor connexions of the internuncial fibres have been considered to ascribe to the individual longitudinal tracts functions more precise than that of transmitting excitation along the cord from segment to segment, but information bearing on their special function is to be

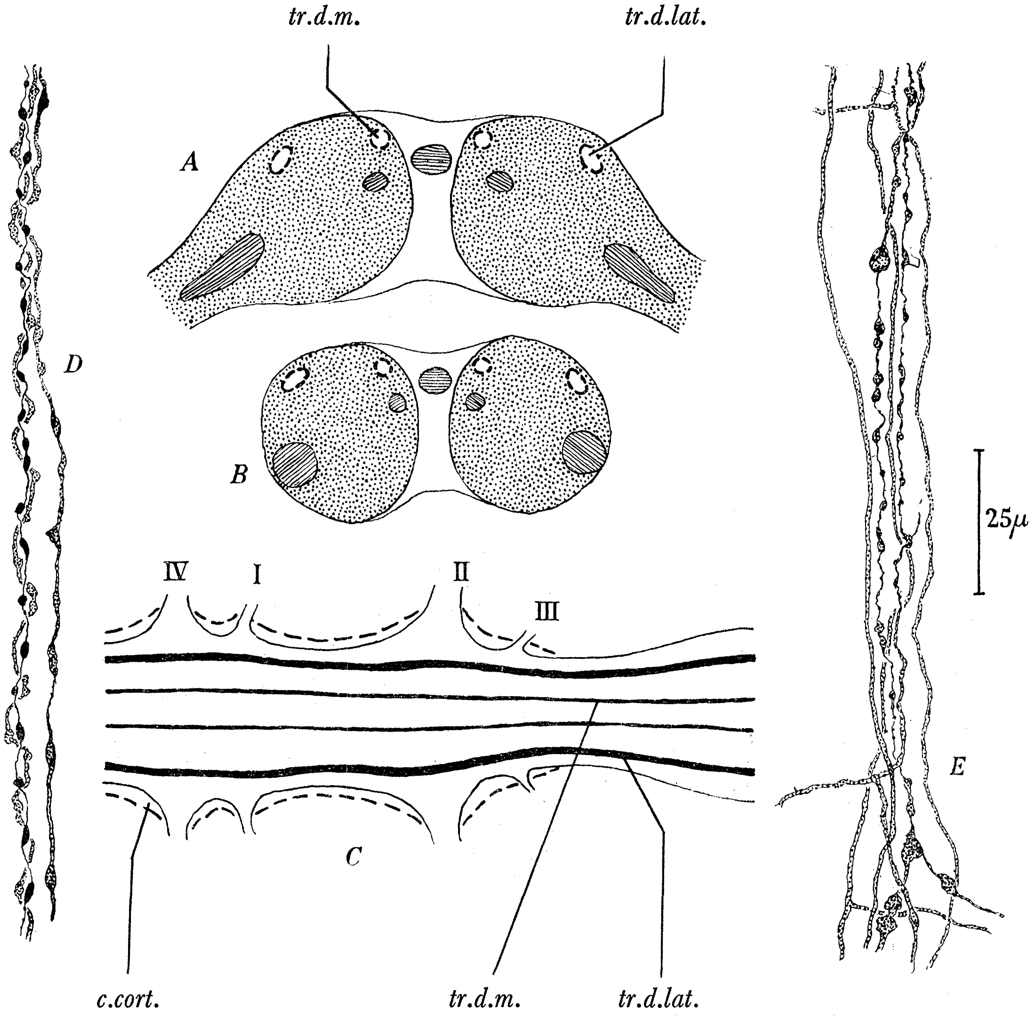

FIGURE 8. The dorsal longitudinal fine-fibre tracts of the nerve cord of *Pl. dumerilii*. *A*, transverse section of a ganglion at the level of the parapodial nerves (nerves II). *B*, transverse section through a connective. *C*, dorsal view of a ganglion and connective showing the course of the dorso-lateral and dorso-medial tracts; the anterior end is to the left of the figure. *D*, details of a part of a dorso-medial tract. *E*, details of a part of a dorso-lateral tract. I–IV, segmental nerves; *c.cort.* cell cortex; *tr.d.lat.* dorso-lateral tract; *tr.d.m.* dorso-medial tract.

obtained from a more detailed study of the composition of the individual tracts and of their relations to other nervous structures.

The position within the neuropile of the dorsal tracts is readily seen in transverse sections through a ganglion or a connective (figures 8*A*, *B*). The dorso-lateral (*tr.d.lat.*) and dorso-medial (*tr.d.m.*) tracts occupy localized areas within the dorsal neuropile and are without direct nervous connexion one with the other. Each follows a slightly sinuous course along the cord (figure 8*C*), and the pairs are more widely separated in the broader ganglion than in the narrower connective. The dorso-medial tract (figure 8*D*) contains the fewer fibres. Three fibres were present in the short length of tract selected for illustration and, of these, two (the broader) are internuncial fibres; the third, which is slender, darker and more obviously 'beaded', was traced as a continuation of an afferent fibre entering the cord from one of the peripheral nerves. There are usually four or five internuncial fibres in the dorso-medial tract, a number corresponding to the number of cell

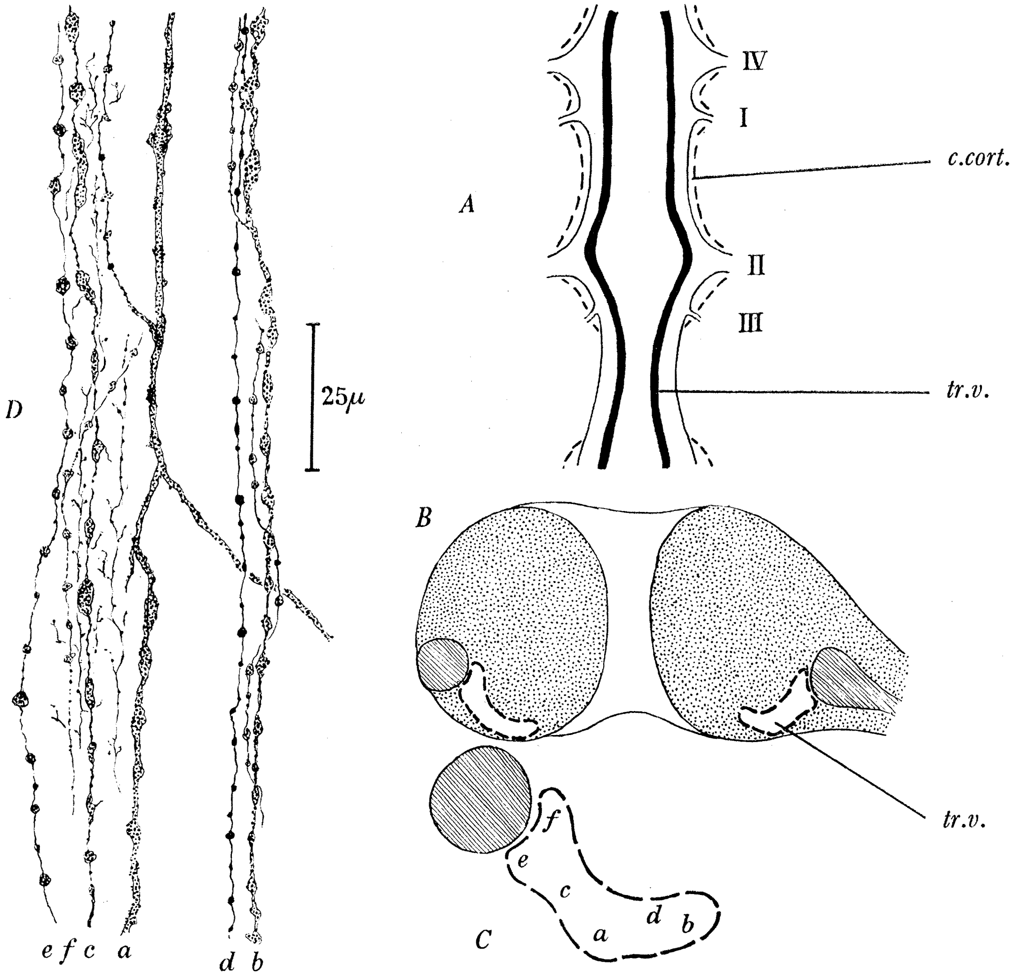

FIGURE 9. The ventral longitudinal fine-fibre tracts of the nerve cord of *Pl. dumerilii*. *A*, dorsal view of a ganglion and connective showing the course of the ventral tract. The anterior end is to the top of the figure. *B*, transverse section of a ganglion at the level of the parapodial nerves (nerves II). *C*, the disposition of the fibres *a*–*f* of figure 9*A* as seen in transverse section. I–IV, segmental nerves; *a*–*f*, the component fibres of the ventral tract; *c.cort.* cell cortex; *tr.v.* ventral tract.

bodies (figure 7*A*, *3*, *11*, *13*, *16*) which in each ganglion contribute axons to the tract, and suggesting that the axons are not as a rule more than one segment long, though this is not always the case. Of the five fibres contained within the part of the dorso-lateral tract shown in figure 8*E* three or possibly four are internuncial, though ten to twelve is the commoner number. Some ten neurons (figure 7*A*, *neur.intern.a.*, *2*, *4*, *5*, *6*, *8*, *10*, *12*, *18*, *19*, *20*) contribute to this tract in each segment. None of the fibres in either of the dorsal tracts is richly furnished with collateral processes.

The ventral tracts (figure 9*B*, *tr. v.*), crescentic in section, are mesial to the lateral giant-fibres which they may in places adjoin. They draw together towards the mid-line in the connective (figure 9*A*), but diverge in the ganglion, especially in the neighbourhood of nerve II, where they accompany the lateral giant-fibres in their displacement towards the roots of the nerves. Unlike the dorsal tracts the ventral systems exhibit marked regional differences of fibre constitution. This is illustrated in figure 9*D*, in which the various fibre systems *a–f* correspond to the regions similarly lettered in figure 9*C*. The fibres *c*, *e* and *f* touch on or are in close apposition to the mesial surface of the lateral giant-fibre and are, on the whole, exceedingly fine and much branched. Some of these fibres are without doubt sensory, since they lack central cell bodies and can be traced out into a segmental nerve, though their extreme delicacy and lightness of staining makes it impossible for them to be followed along their entire length in every instance. The larger central fibre (figures 9*C*, *D*, *a*), the most ventral of the series, is internuncial, and the mesial fibres *b* and *d* are either principal or collateral axons of internuncial neurons. Individual fibres have been traced over as many as three segments though most of them are shorter. The fibres are closely intertwined along the length of the ventral tracts which, like the dorsal internuncial tracts, are evidently designed for transmitting excitation along the length of the cord.

The second of the configurational characteristics of the long-axons to which reference has been made concerns the orientation of the fibres relative to the dorso-ventral axis of the cord prior to their entry into the longitudinal tracts. The feature common to them all is the passage of the fibre from a more ventral to a more dorsal position within the neuropile in its extension distally from the cell body. The principal directions followed by the fibres in their more proximal course are shown in figure 7*B*. Some of the fibres, and in particular those which arise from cell bodies in the dorso-lateral angles of the cortex, run almost horizontally with only a slight upward inclination, but not a single internuncial axon has been found to run dorso-ventrally. It is legitimate to assume therefore that in the nereid cord there is, in addition to longitudinal conduction, a transfer of excitation towards the dorsal neuropile and in a direction opposite to that of vertebrates. The dorsal neuropile of the nereid ganglion would, in consequence, be regarded as the region offering the maximum opportunity for excitation transfer to the more efferent neurons, either internuncial or motor, of the conducting pathways. In respect of the internuncial relationships the dorsal transfer is clearly relevant to the observed form and distribution of the short-axon internuncial neurons furnished with richly branched collateral processes. These latter neurons, as can be seen by reference to figure 7*A* (*neur.intern.a.*, *neur.intern.b.*) are, in fact, so designed and oriented as to produce within the region of internuncially transmitted excitation, a dense plexus of fibres capable of mediating the transfer of excitation to other systems. They are, moreover, most numerous at the levels of the cord opposite the segmental nerve roots and where, as will be seen, the motor fibres make their commissural passage across the neuropile of the ganglion.

In summarizing the features of internuncial patterning which are regarded as of major functional significance the following conclusions may be drawn: (1) the long-axon internuncial neurons form, in the distal and greater part of their course, longitudinally conducting fine-fibre systems organized as dorso-lateral, dorso-medial and ventral tracts bilaterally disposed in the cord; (2) there is a general tendency for all the long-axon fibres to run, in the proximal part of their course, ventro-dorsally through the neuropile and for excitation to be transferred to the dorsal neuropile; (3) the dorsal neuropile is the region of maximum fibre concentration by virtue of the distribution within it of the richly branching collateral processes of the short-axon internuncials; (4) the plexus is best developed at the levels of origin of the segmental nerves. Except for (1) above these considerations apply only to the ganglia. The connectives, which lack peripheral nerves and cortical cells, contain only longitudinally conducting fibres and are devoid of short-axon internuncials with their attendant terminal fibre network within the dorsal neuropile.

The nature and central relations of the afferent and efferent fibre systems of the cord

It is proposed under this heading to consider the occurrence and distribution of the afferent and efferent fibres within the substance of the cord, leaving a description of their peripheral distribution to a later stage of the account.

Figure 10 shows sensory and motor fibres selected from different preparations but drawn in their normal position and orientation relative to the transverse and longitudinal axes of the cord. In speaking of the cord in this context the ganglia are, in fact, referred to, for the connectives have no motor fibres within them, and sensory fibres entering from peripheral nerves in the ganglionic regions are not present throughout their length.

The motor axons (figure 10, *mot.ax.*) are similar in appearance, size and staining properties to the long-fibre internuncial axons (figure 5) and originate from rounded cell bodies (figure 10, *neur.mot.*) of about 20 μ diameter. The distinction between the motor and long-axon internuncials is essentially one of axon distribution; the motor axons never terminate as do the internuncial fibres in the longitudinal fine-fibre tracts but extend beyond the margin of the neuropile into one or other of the segmental nerves (*n.*). Many of the motor neurons, including all the neurons figured, extend commissurally across the neuropile (*n.pil.*) to a contralateral nerve. Their collateral processes are always longitudinally alined and, what is more significant, they invariably run in conjunction with one or other of the longitudinal internuncial tracts.

Sensory fibres (*s.fib.*) are finer and more regularly 'beaded' than the principal motor axons, and their cell bodies are external to the cord and its cell cortex. Since beading also occurs in the finer motor fibres, and it is rarely possible to trace sensory fibres to their parent cell bodies, these criteria are of little practical value in distinguishing between the two systems, but the free endings of the sensory fibres within the neuropile are unique and serve to identify them.

The over-all pattern of the principal sensory and motor fibres of the nereid nerve cord is illustrated diagrammatically in figure 11. From what appears at first sight to be a somewhat confused fibre complex it is possible to recognize some constantly occurring characteristics of which the following apply to the sensory components. (1) All the segmental nerves supply afferent fibres to the ganglion. (2) In every instance some at least of the incoming fibres run upwards into the neuropile to enter either one or two of the dorsal internuncial fine-fibre tracts (*tr.d.lat.*, *tr.d.m.*), the positions of which are shown in the figure by the broken lines on the cut anterior surface of ganglion. (3) With rare exceptions (see, for instance, one of the afferent fibres of nerve IV) the sensory fibres terminate in ipsilateral tracts. In this latter connexion it may be noted that Retzius (1891), who figures some of the afferent fibres of the nerve cord of *N. diversicolor* in great detail, reports a great measure of collateral branching of the central terminal fibre, the branches ramifying through the general neuropile. After examining living preparations I believe this to be a true picture, and the figures which illustrate the present paper, drawn entirely from fixed material, may, because of the loss of stain in the finer branches during dehydration of the tissues, inadequately represent the full extent and complexity of the ultimate branching. (4) In addition to sensory fibres that enter ipsilateral dorsal tracts there are, in two of the four pairs of nerves (figure 11, II and IV), fibres which enter the ganglion ventrally and terminate with a good deal of collateral branching in the ventral longitudinal fine-fibre internuncial tracts (*tr.v.*) adjacent to the mesial surface of the lateral giant-fibre

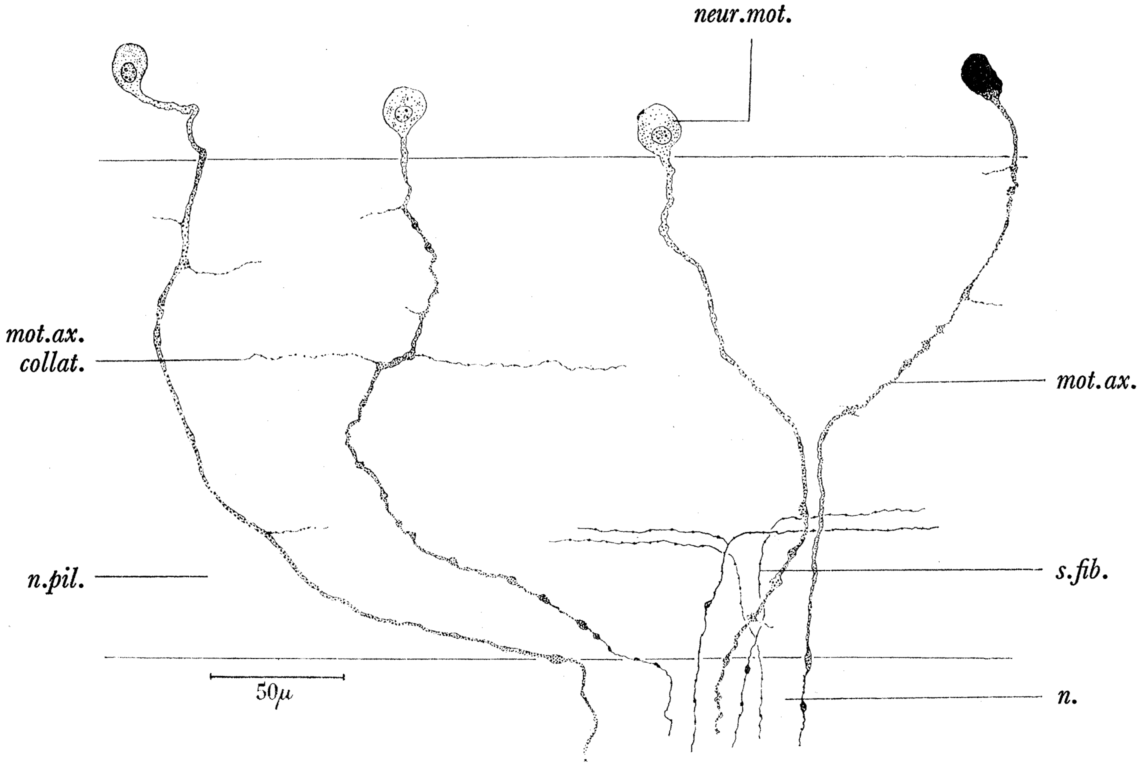

FIGURE 10. Sensory and motor fibres selected from different preparations of the cord of *Pl. dumerilii* and *N. diversicolor* drawn in dorsal view. The lateral margins of the neuropile are indicated by the horizontal lines. *mot.ax.* motor axon; *mot.ax.collat.* axon collateral; *n.* nerve root; *n.pil.* neuropile; *neur.mot.* motor neuron; *s.fib.* sensory fibre.

(see p. 164 and figure 9*C*). No ventrally connected afferent fibres have been seen in nerves I and III.

The number of motor neurons made visible by methylene-blue staining is remarkably small. Seven are shown in figure 11 supplying the nerves of one side of the cord, making a total of fourteen neurons in each ganglion. In some instances there may be two neurons supplying axons to a nerve where, as in the instance of nerve III in figure 11, only one has

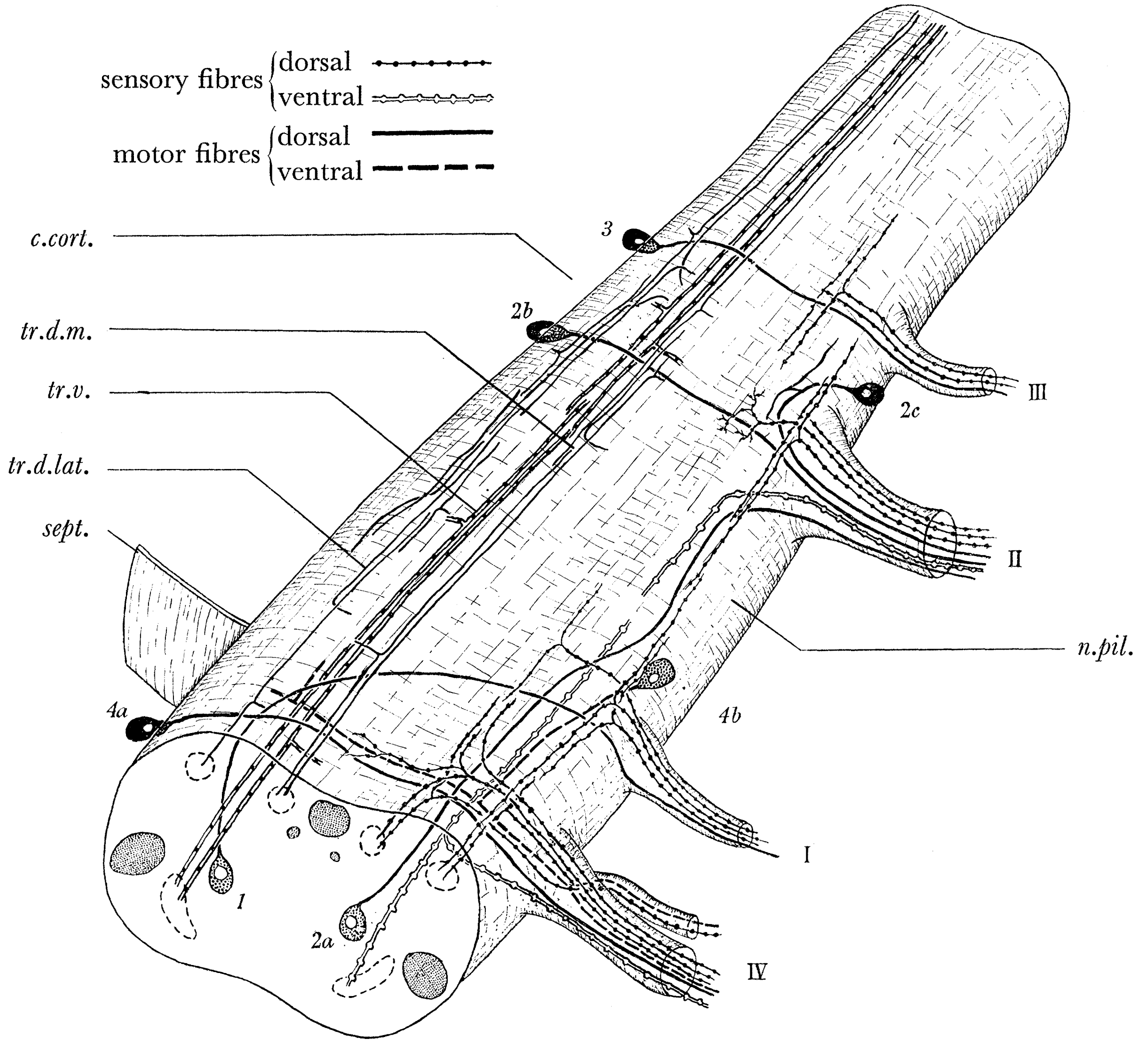

FIGURE 11. Diagrammatic stereogram of a ganglion and connective of *Pl. dumerilii* showing the sensory and motor fibres of the segmental nerves, the position in the cell cortex of the principal motor cells, the distribution in the neuropile of their axons, the levels of entry into the cord of the sensory fibres, and the fine-fibre longitudinal internuncial tracts with which the afferent fibres are associated. Sensory fibres of dorsal and ventral entry are distinguished in the manner shown in the 'key'. Motor fibres, which may traverse the neuropile either dorsally or ventrally in their efferent passage, are also distinguished by different types of lines. The anterior end of the ganglion is at the lower end of the figure and the cut surface shows, in section, the giant fibres (stippled) and the internuncial tracts (broken line). I–IV, the segmental nerves; *1–4b*, the segmental nerves supplied by the motor cells opposite which the numbers appear; *c.cort.* cell cortex; *n.pil.* neuropile; *sept.* intersegmental septum; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

been shown. More commonly, however, the neurons appear, in preparation after preparation, with their cell bodies in the same position in the cortex and with their axons constant in position, orientation and distribution. The impression is gained that while fourteen motor neurons may be too low an estimate for the total number in each ganglion, twenty might be too many and that there are, in reality, very few motor axons of the first order entering the peripheral nerves—always one but never more than three or four. The probable significance of this feature in relation to the innervation of the body wall and parapodial musculature is discussed later (p. 187).

Of the seven neurons shown as supplying the nerves of one side four (figure 11, *1*, *2b*, *3* and *4a*) arise from contralaterally sited cell bodies, three (*2a*, *2c* and *4b*) from ipsilateral cells. Four (*2b*, *2c*, *3* and *4a*) are in the dorso-lateral angle of the cortex; three (*1*, *2a* and *4b*) are ventral in position. The former direct their axons into and across the neuropile before entering the nerve, the latter are more varied in their course. Neuron *1* ascends vertically, following the outer border of the neuropile before crossing the ganglion dorsally in a transverse and oblique course to enter nerve I. Neuron *2a*, near the root of nerve IV, runs posteriorly in conjunction with the ventral fine-fibre tract to swing outwards and upwards to the level of the dorso-lateral tract, finally to emerge after a right-angled turn in nerve II. Neuron *4b* is unique. Its relations are described fully in the detailed description of nerve IV (p. 170). It can be mentioned here, however, that its ventrally placed cell body, positioned at the level of nerve I, gives rise to an axon which runs forward in company with the ventral longitudinal tract until it reaches the level of nerve IV at which point it turns outwards, encircling closely the ventral border of the lateral giant-fibre before dividing into two branches, one to each of the two factors of nerve IV. The axon is joined to its contralateral partner by a connecting ventral commissural fibre, these being the only neurons in the nereid ganglion which have been found to have axons organically fused one to the other. The fibre stains rather poorly with methylene blue except in its commissural part. It is undoubtedly to be identified with the 'fibre B' of Hamaker's (1898) account.

In concluding this initial survey of the sensory and motor fibres of the ganglion it will be appropriate briefly to consider their more general relationships with the fine-fibre internuncial systems described in the previous section. Figure 12 shows in more detail than figure 7*B* the directions taken by the long-axon internuncial fibres prior to their entry into longitudinal tracts and the orientations and distribution of the short-axon internuncials. The types of line used to denote the different systems of fibres are shown in the key at the bottom of the figure.

The common tendency of the long-axons to extend dorsally in the neuropile is evident. Some few reach only as far as the ventral tracts (*tr.v.*), the majority ascend to or are projected horizontally into the dorsal systems (*tr.d.lat.*, *tr.d.m.*). The short-axons are either vertically or horizontally oriented and branch extensively through the dorsal neuropile, which in the figure is closely stippled. The vertical axons provide a few collaterals into the ventral (lightly stippled) substance of the ganglion. Almost all the sensory fibres and all but one of the motor axons enter or pass through the dorsal neuropile. The sensory fibres before terminating in one or other of the dorsal internuncial tracts throw collaterals into the internuncial neuropile of the region; the motor fibres, encompassed by the internuncial network, have collaterals which enter and are alined along longitudinal tracts. The exceptions to the rule of dorsal entry and emergence of afferent and efferent fibres are certain sensory and motor components of nerves II and IV. In the former instance a sensory fibre enters the ventral longitudinal tract (*tr.v.*), and in the latter a sensory fibre enters the tract and a motor axon (Hamaker's 'B fibre', figure 11, *4b*) leaves the cord by way of the ventral neuropile. The more general implications of this arrangement are obvious. Each nerve is enabled by virtue of the central connexions of its afferent fibres

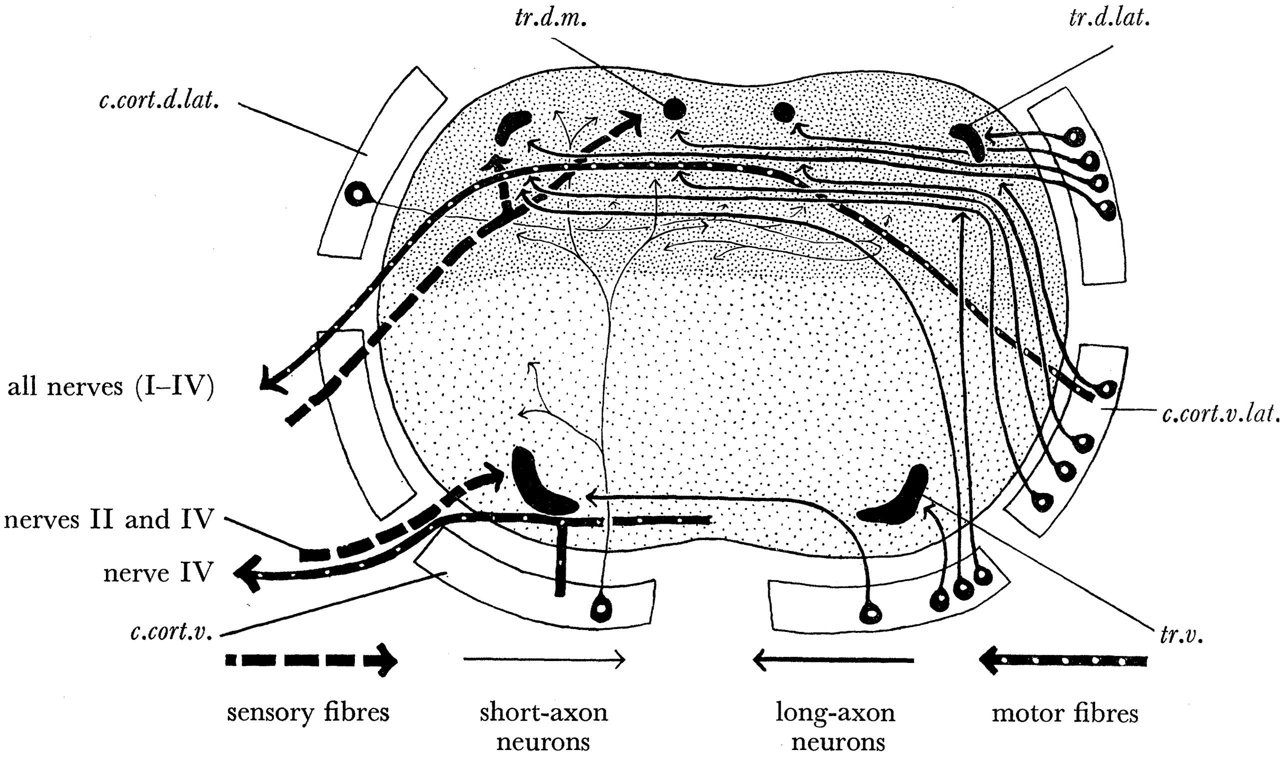

FIGURE 12. Diagrammatic transverse section of a nereid ganglion to show (1) the position of the long-axon longitudinal tract, (2) the directions through the neuropile of the long internuncial axons prior to their entry into the tracts, (3) the distribution of the short-axon internuncials, primarily confined in their collateral branchings to the dorsal neuropile, (4) the course and destination in fine-fibre longitudinal tracts of the sensory fibres, and (5) the course through the dorsal neuropile of the motor axons. The dorsal neuropile containing the greatest concentration of internuncial branchings is the more densely stippled. *c.cort.d.lat.* dorso-lateral sector of the cell cortex of the ganglion; *c.cort.v.* ventral sector; *c.cort.v.lat.* ventro-lateral sector; *tr.d.lat.* dorso-lateral fine-fibre longitudinal tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

to transfer excitation along the cord from one segment to another through the longitudinal fine-fibre internuncial tracts and to discharge excitation locally into the diffuse dorsal neuropile. Since each nerve contains at least one motor axon which crosses the dorsal neuropile commissurally the motor fibre can respond both to longitudinally transmitted excitation by synaptic transfer to its collaterals, and to locally distributed excitation by the passage of impulses through the neuropile net which surrounds its main fibre. Both local and spatially extended reflexes are, therefore, provided for. The presence of additional ventral nervous arcs in nerves II and IV may be noted for further comment after the peripheral distribution of the several nerves has been described (p. 194).

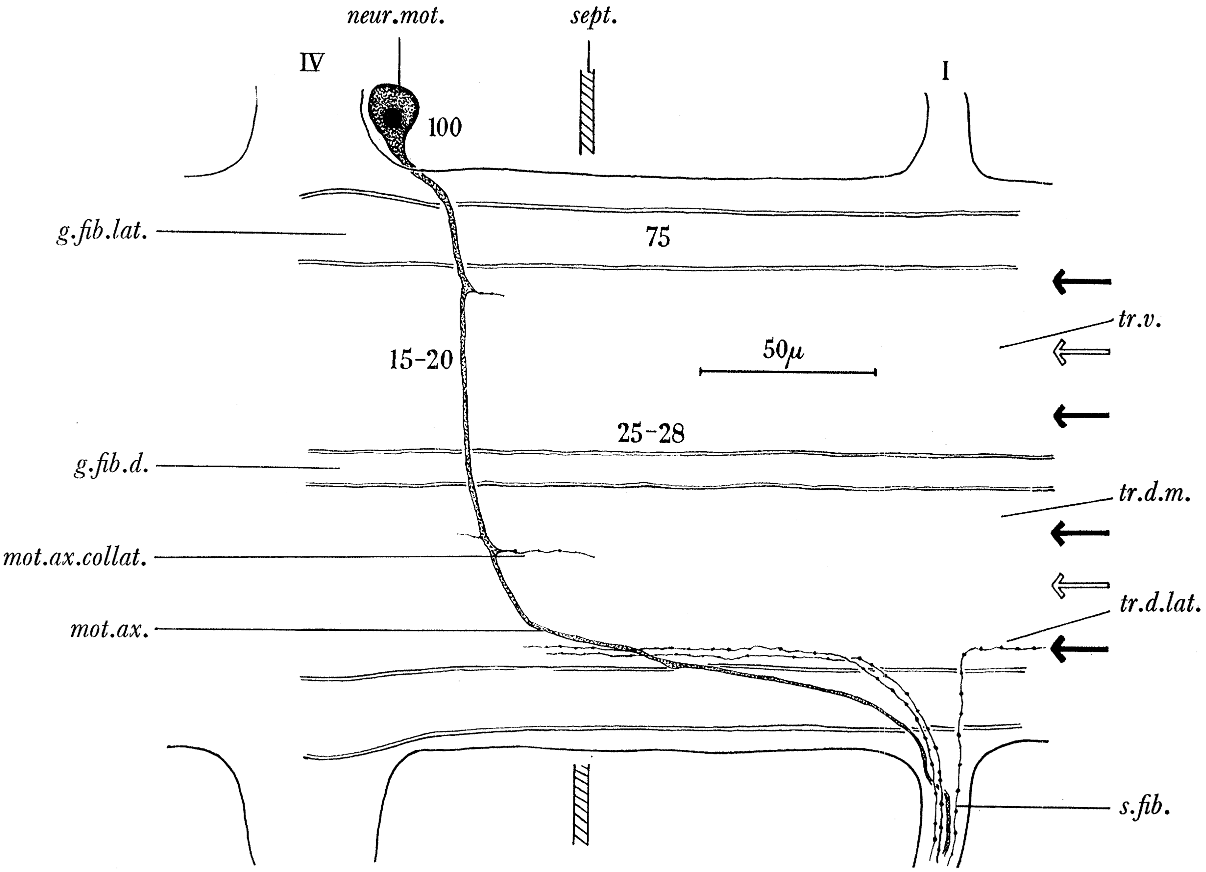

FIGURE 13. The afferent and efferent components of the first (post-septal) segmental nerve of nereids seen in dorsal view of the anterior end of the ganglion. The positions and orientations of the dorsal longitudinal fine-fibre tracts are indicated by the black arrows, the ventral tract by outlined arrows. The numbers adjoining the different structures indicate their depth in the cord from the dorsal surface of the neuropile: 0 is dorsal, 100 is ventral. The anterior end of the ganglion is to the left of the figure. I and IV, roots respectively of the first and last segmental nerves of adjacent segments; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *mot.ax.* motor axon; *mot.ax.collat.* motor axon collateral; *neur.mot.* motor neuron; *s.fib.* sensory fibre; *sept.* intersegmental septum; *tr.d.lat.* dorso-lateral longitudinal fine-fibre tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

THE CONSTITUTION OF THE INDIVIDUAL SEGMENTAL NERVE ROOTS

Under this heading it is proposed (1) to review in some detail the anatomical evidence bearing on the nature of the central connexions of the segmental nerves the more general features of which were referred to in the previous section, and (2) to ascertain the composition of the nerve roots in respect of the character and approximate number of their contained fibres. Information of this latter kind is necessary for the interpretation of the changing composition of a nerve in its peripheral passage and of the manner in which excitation is gathered from scattered receptors and disseminated to the various muscle systems of its motor field. The central relations and composition of each of the four pairs of segmental nerves will be examined in turn, the drawings being simplified in every instance to show the component fibres of one nerve of each pair.

Nerve I (figures 13 and 14)

The nature and approximate number of the fibres within the small post-septal, most anterior nerves of a segment are made clear in figure 13, a composite drawing from preparations of the ganglia of *Pl. dumerilii* and *N. diversicolor* viewed from the dorsal surface. Giant-fibres (*g.fib.d.*, *g.fib.lat.*) are represented in double outline and the position and orientation of the dorsal (*tr.d.lat.*, *tr.d.m.*) and ventral (*tr.v.*) fine-fibre tracts indicated respectively by the black and outlined arrows.

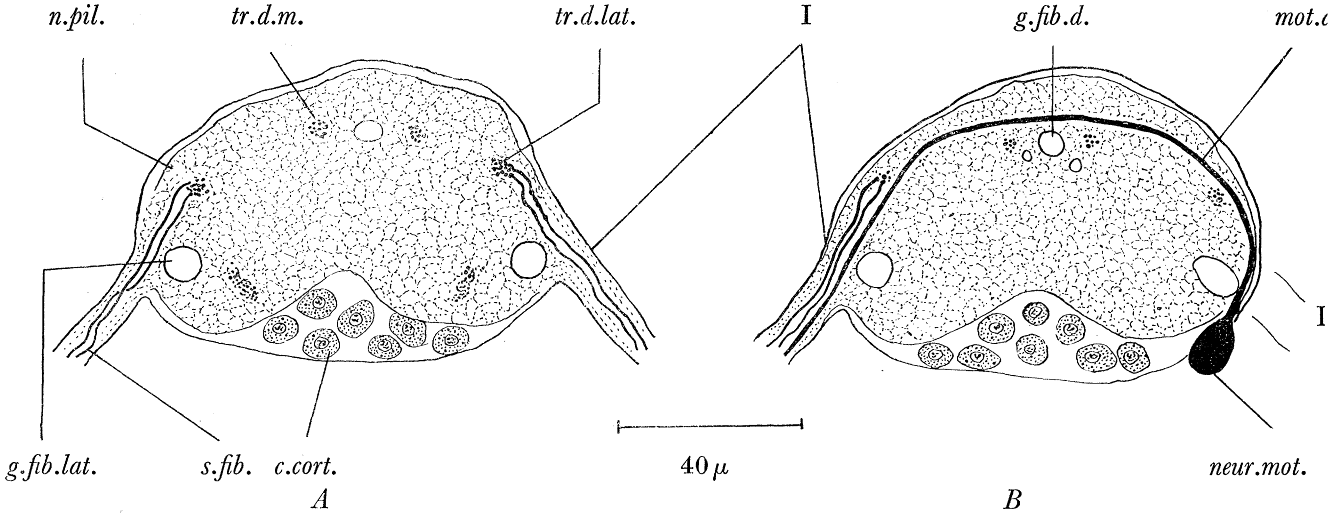

FIGURE 14. *A*, transverse section of a ganglion of *Pl. dumerilii* at the level of the first pair of segmental nerves showing the entry into the ganglion of afferent fibres. *B*, oblique transverse section passing, on the right-hand side, through the pre-septal nerve (IV) and, on the left, through the post-septal nerve (I) and showing the cell body and axon of the motor neuron supplying the first nerve. *c.cort.* cell cortex; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *mot.ax.* motor axon; *neur.mot.* motor neuron; *n.pil.* neuropile; *s.fib.* sensory fibre; *tr.d.lat.* dorso-lateral longitudinal fine-fibre tract; *tr.d.m.* dorso-medial tract.

Three or perhaps four sensory fibres (*s.fib.*) enter the cord from the nerve. They ascend (figures 14*A*, *s.fib.*, 14*B*) in the neuropile, and on approaching the dorso-lateral tract (figure 13, *tr.d.lat.*) bend gently or sharply in a right-angled turn to continue anteriorly or posteriorly in company with the internuncial fibres. None of the fibres runs for more than a short distance in this tract; they diminish in diameter and are no longer visible some 0·1 to 0·2 mm. from their point of entry, passing anteriorly a little way forward of the intersegmental septum and posteriorly not farther than the level of nerve II.

Only one motor axon has been seen to supply this nerve. Its cell body (figure 13, *neur.mot.*) lies in the ventral or ventro-lateral sector of the cell cortex adjacent to the posterior border of nerve IV. The motor axon (*mot.ax.*) ascends steeply towards the dorsal side of the ganglion, hugging the lateral margin of the neuropile in its proximal course (figure 14*B*). On reaching the dorsal neuropile it crosses to the farther side (figure 13), descending to the ventro-lateral corner of the ganglion (figure 14*B*) to enter the root of the nerve. During its commissural passage the axon gives rise to collaterals (figure 13, *mot.ax.collat.*) which are alined along the dorsal longitudinal internuncial tracts on either side of the mid-line.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Nerve II (figures 15 and 16)

The parapodial nerves, the largest of the nerves, except in the anterior segments where the fourth pair may exceed them in size, arise from the ganglion about one-third of the way back from the anterior end of the segment (figure 1, II). They contain rather more

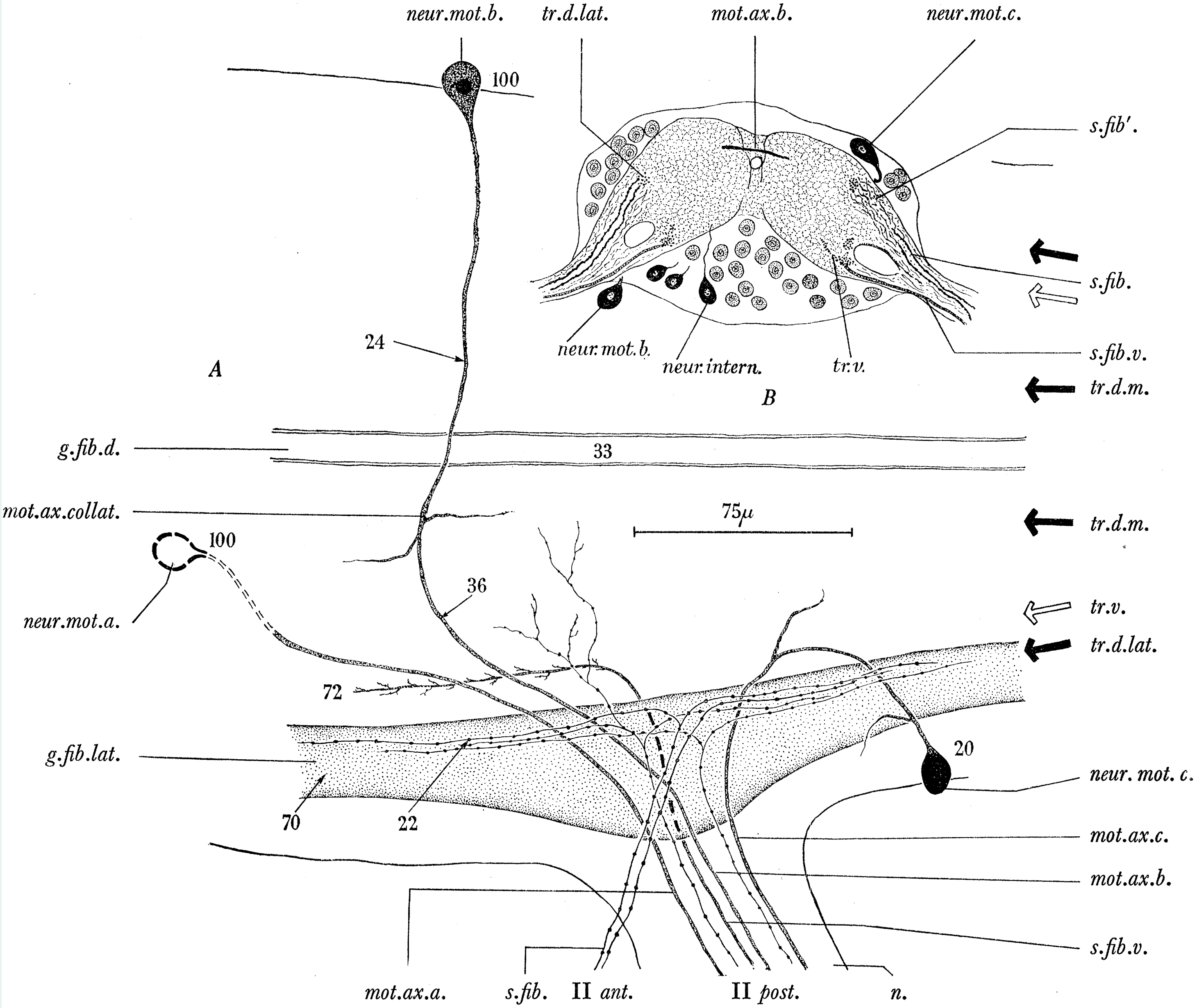

FIGURE 15. *A*, afferent and efferent components of the second segmental (parapodial) nerve of nereids seen in dorsal view. The arrows and numbers placed in conjunction with the various structures bear the same connotation as in figure 13. The anterior end of the ganglion is to the left of the figure. *B*, transverse section of a ganglion of *Pl. dumerilii* at the level of the second segmental (parapodial) nerves. II *ant.* and II *post.* anterior and posterior branches of nerve II; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *mot.ax.* (*a*, *b* and *c*), motor axons of the correspondingly lettered neurons; *mot.ax.collat.* motor axon collateral; *n.* nerve root; *neur.intern.* internuncial neuron; *neur.mot.* (*a*, *b* and *c*), motor neurons; *s.fib.*, *s.fib'.* sensory fibres with a dorsal entry; *s.fib.v.* sensory fibre with a ventral entry; *tr.d.lat.* dorso-lateral fine-fibre longitudinal tracts; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

fibres than the remaining nerves, there being at least three motor and from four to six sensory fibres visible in the main root after methylene-blue staining.

The majority of the afferent fibres (figures 15*A*, *B*, 16, *s.fib.*), on entering the cord, ascend in the neuropile above the lateral giant-fibre (*g.fib.lat.*) to join the dorso-lateral longitudinal internuncial tract (*tr.d.lat.*), usually with a dichotomy at the point of entry. The sensory fibres of this nerve are distinguished by the great number of collateral processes which they throw into the neuropile. In transverse section (figure 15*B*, *s.fib′.*) they appear as a diffuse and fragmentary series of fine branches too complex for their continuity to be traced from one section to another. Figure 15*A* shows the branching systems of one such fibre. Afferent fibres approach the cord from two directions. A smaller anterior group (figure 15*A*, II *ant.*) rise almost vertically from the ventral body wall to bend into the ganglion with a posterior inclination. There are rather more fibres in the main (posterior) branch of the nerve (II *post.*). They ascend to the cord in a more gently curving course and are directed transversely and slightly anteriorly within the cord.

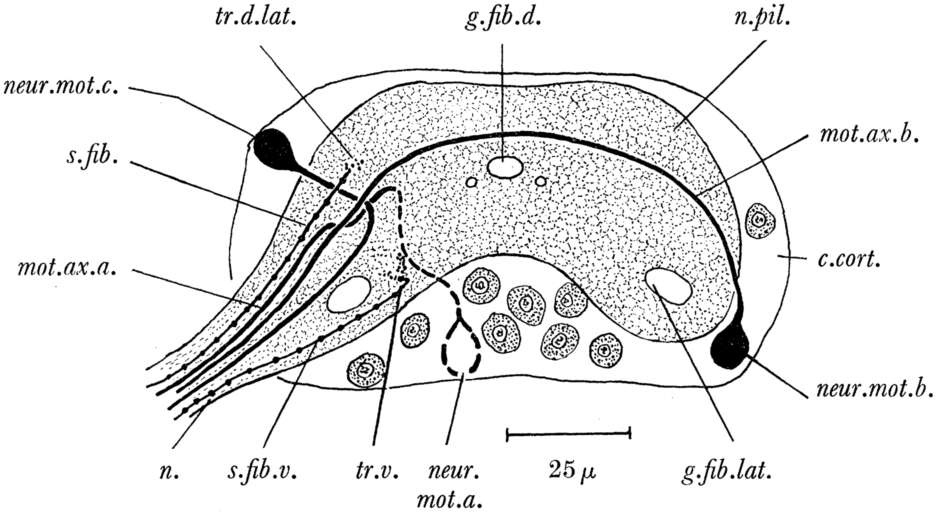

FIGURE 16. Oblique transverse section through a ganglion of *Pl. dumerilii* at the level of the second segmental (parapodial) nerves showing the afferent and efferent components of the nerve of one side and their central connexions. *c.cort.* cell cortex; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *mot.ax.* (*a* and *b*), motor axons; *n.* nerve root; *n.pil.* neuropile; *neur.mot.* (*a*, *b* and *c*), motor neurons; *s.fib.* sensory fibre with dorsal entry; *s.fib.v.* sensory fibre with ventral entry; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.v.* ventral tract.

In the main nerve root there are one or perhaps two afferent fibres with a ventral entry into the ganglion (figures 15*B*, 16, *s.fib.v.*) running under the lateral giant-fibre (*g.fib.lat.*) to enter the ventral longitudinal internuncial tract (*tr.v.*) at its lateral margin. Within the ganglion (figure 15*A*, *s.fib.v.*) they continue forwards for a short distance, giving off on the way a number of short collateral processes.

Three widely separated cell bodies contribute motor axons to the parapodial nerve. The neuron labelled *neur.mot.a.* in figures 11, 15*A* and 16 is the most remote from the nerve. Its axon (figure 11) enters the neuropile ventrally from a cell body in the next anterior segment, near the level of nerve IV, and runs posteriorly in conjunction with the ventral fine-fibre tract to a point opposite nerve I before ascending to the level of the dorso-lateral tract. It runs in association with this system of longitudinal fibres to curve outwards (figure 15*A*, 16, *mot.ax.a.*) above the lateral giant-fibre (*g.fib.lat.*) into the parapodial nerve. The second of the motor neurons (figures 15*A*, *B*, 16, *neur.mot.b.*) is a more typical component of the motor supply in that it has a counterpart in each of the remaining nerves. Its transversely oriented axon (*mot.ax.b.*) gives off collaterals (*mot.ax.collat.*) in its passage through the dorsal neuropile which enter and are alined along the dorsal fine-fibre internuncial tracts. The third motor neuron supplying the parapodial nerve (figures 15*A*, *B*, *neur.mot.c.*) has an ipsilateral cell body positioned dorsolaterally and a little to the posterior side of the nerve root. Its axon bends in a semicircle through the margin of the neuropile before entering the nerve root. The short collateral(s) of the main fibre are unusual in not being alined along longitudinal tracts.

Nerve III (figures 17 and 18)

The third pair of segmental nerves originate from the posterior end of the ganglion at its junction with the connective. Not more than two stainable afferent fibres have been seen in this nerve. The fibres in their passage from the integument rise sharply from the ventral body wall to enter the ganglion about half-way up its lateral border. On entering the neuropile they take (figure 18*A*, *s.fib.*) a direct and less vertical course to the dorsomedial fine-fibre longitudinal internuncial tract (*tr.d.m.*). In dorsal view (figure 17, *s.fib.*) the fibres are seen to slope forwards slightly in their passage through the neuropile, dichotomizing at their point of entry into the internuncial tract into short anteriorly and posteriorly directed branches which merge with the internuncial fibres (*tr.d.m.*). On occasions a third fibre is present. Unlike those so far described it reaches to the contralateral side of the ganglion and has one or more bifurcations thrusting into the neuropile. This is the fibre labelled in figure 17 as *mot.ax.b.* and shown (by a broken line) as having a possible connexion with a motor-cell body (*neur.mot.b.*). This particular fibre is visible in very few preparations, and its connexion with the cell body has in no instance been made out with certainty so that its efferent character must be open to doubt. The reasons for including it in the motor series are (1) that it is rare for sensory fibres to be dissociated centrally from the longitudinal tracts as this one is, and (2) that it is somewhat thicker than the majority of sensory fibres.

The cell body, *neur.mot.a.* (figure 17), appears in most preparations. It is recognized by the forward curve of its axon (*mot.ax.a.*) proximally, and the obliquely transverse commissural approach of the fibre to the contralateral nerve. Figure 18*B* (*mot.ax.a.*) shows the vertical level of the commissure a little above the dorsal giant-fibre (*g.fib.d.*). It may be noted that it crosses the giant-fibre at the posterior intersect of the paramedial fibres (*g.fib.p.m.*), though the association of the motor axon with the giant-fibres is sufficiently remote to discourage speculation as to any possible functional significance of the juxtaposition of the fibre crosses. The motor fibre (or fibres if we allow an efferent function to *mot.ax.b.*) enter the segmental nerve on the ventral side of the afferent fibres (figure 18*B*), close to but not in apparent contact with the lateral giant-fibre. The nerve root never contains more than three or four stainable fibres.

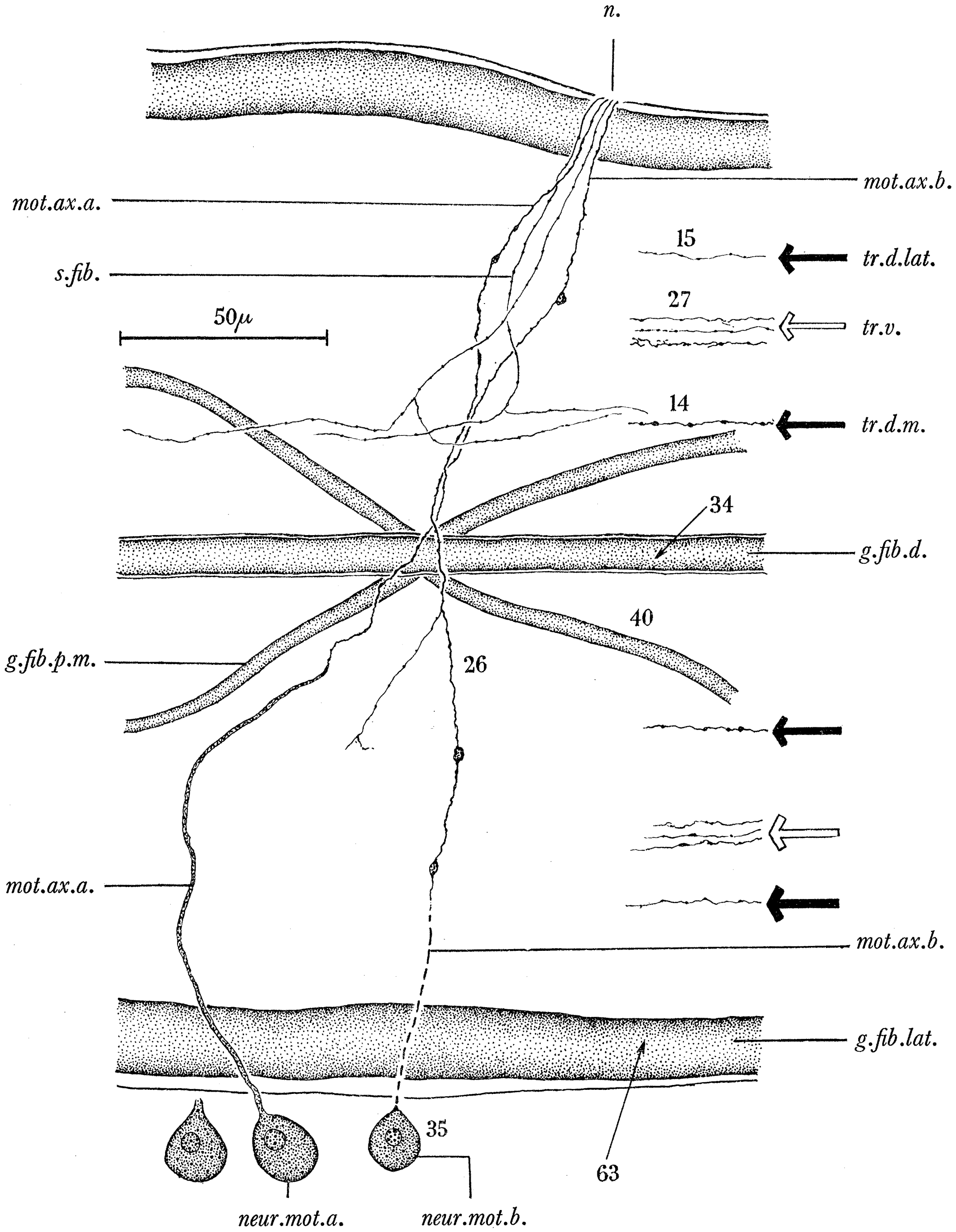

FIGURE 17. Afferent and efferent components of the third segmental nerve of nereids seen in dorsal view of the ganglion. The arrows and numbers placed in conjunction with the various structures bear the same connotation as in figure 13. The anterior end of the ganglion is to the left of the figure. *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.* paramedial giant-fibre; *mot.ax.* (*a* and *b*), motor axons; *n.* nerve root; *neur.mot.* (*a* and *b*), motor neurons; *s.fib.* sensory fibre; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

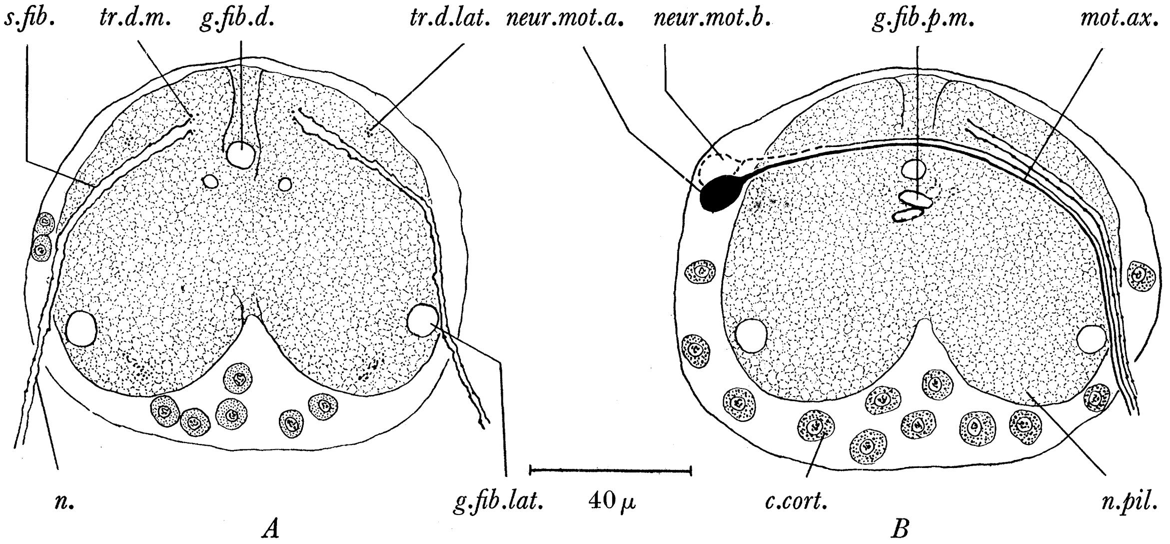

FIGURE 18. Transverse sections through a ganglion of *Pl. dumerilii* at the level of the third segmental nerves. *A*, the afferent fibres of the paired nerves and their central connexions. *B*, the motor neurons and afferent and efferent fibres of one side. *c.cort.* cell cortex; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.* paramedial giant-fibre at a point of crossover of the two fibres; *mot.ax.* motor axon; *n.* nerve root; *n.pil.* neuropile; *neur.mot.* (*a* and *b*), motor neurons; *s.fib.* sensory fibre; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.d.m.* dorso-medial tract.

Nerve IV (figures 19, 20, 21 and 22)

The fourth pair of nerves, the most anterior in order of origin from the ganglion but the most posterior in a body segment, are, in the variety of their component parts, the most complex of the series. Their afferent fibres, for example, connect with one or other of all three ipsilateral longitudinal internuncial tracts and include, in addition, fibres with freely branched central terminals extending to the contralateral neuropile. A further unique feature is the occurrence, in addition to the normal types of motor neuron, of bilaterally disposed neurons joined across the two sides by organically fused axons. Moreover, the axon on either side divides at the lateral margin of the neuropile to serve each of the two branches of the peripheral nerve. Figure 19 shows representative fibres of all the component elements with the exception of these last-named neurons which, having little affinity for methylene blue, are difficult to make out in whole mount preparations.

The main nerve root (figure 19, IV and figure 20*A*, *n.*) is set transversely to the cord and at about 45° to its vertical axis. Its afferent fibres continue into the neuropile along the line of the nerve (figure 20*A*, *s.fib.*), the majority of them reaching almost to the mid-line to enter the ipsilateral dorso-medial internuncial tract (figures 19, 20*A*, *B*, *tr.d.m.*). One or two fibres ascend more sharply to the dorso-lateral tract (figure 19, *tr.d.lat.*) on the side of entry. Most of the fibres dichotomize to give anteriorly and posteriorly directed branches. One, or at the most two, fibres are to be seen in the posterior branch of the nerve (figure 19, IV *post.*) which runs forwards and inwards to the ganglion from the intersegmental septum (*sept.*). The fibres continue in this direction within the substance of the nerve giving off numerous collaterals in their passage. They are unusual in having no direct connexion with the dorsal internuncial tracts and in their terminal extension into the neuropile of the contra-lateral side of the cord.

The motor components of the nerve are in two series. The first consists of an axon or axons (figures 19, 21 *A*, *mot.ax.a.* and figure 19, *mot.ax.b.*) crossing into the nerve from cell bodies (*neur.mot.a.*, *neur.mot.b.*) sited contralaterally in the dorso-lateral angle of the neuron cortex anterior to the nerve root. One of the neurons (figures 19, 21 *A*, *neur.mot.a.*) can almost always be traced in its entirety, a second (figure 19, *neur.mot.b.*) appears in a few preparations as an incompletely stained fibre but so like the first in its form and distribution that its motor nature can hardly be doubted. Axon collaterals accompany and effect connexion with dorsal internuncial tracts. To the second series belong the neurons having axons corresponding to Hamaker's (1898) 'fibre B'. Their cell bodies (figures 21 *A*, *B*, *neur.mot.B.*) are rounded, and with a diameter of 25 to 30 μ are larger than those of other motor neurons. They lie posterior to the intersegmental septum (figure 21 *B*, *sept.*) ventral

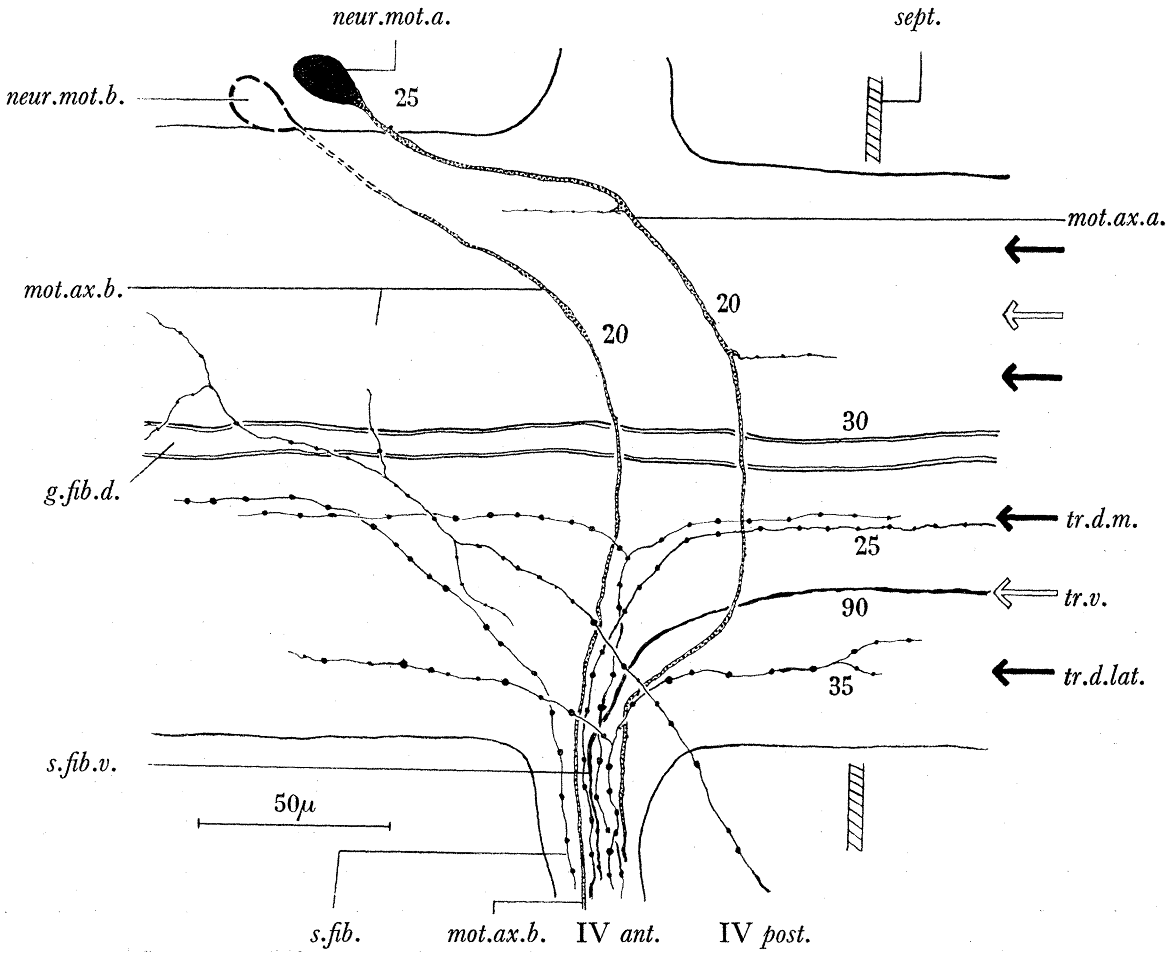

FIGURE 19. Afferent and efferent components of the fourth segmental (preseptal) nerve of nereids seen in dorsal view of the ganglion. The arrows and numbers placed in conjunction with the various structures bear the same connotation as in figure 13. The anterior end of the ganglion is to the left of the figure. IV (*ant.* and *post.*), anterior and posterior branches of nerve IV; *g.fib.d.* dorsal giant-fibre; *mot.ax.* (*a* and *b*), motor axons; *neur.mot.* (*a* and *b*), motor neurons; *s.fib.* sensory fibre; *s.fib.v.* sensory fibre with ventral entry; *sept.* intersegmental septum; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

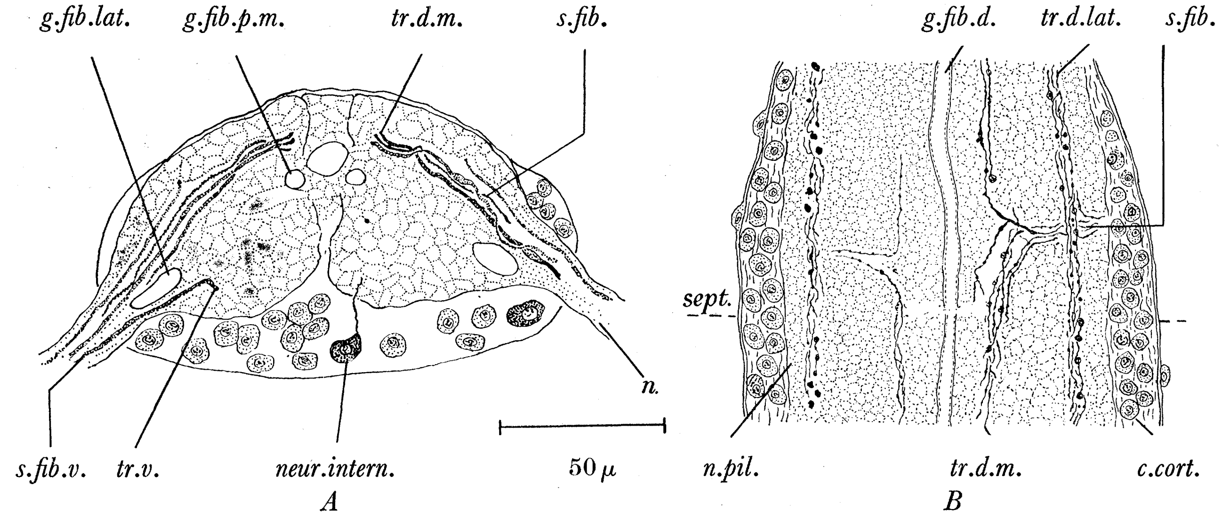

Figure 20. *A*, transverse section through a ganglion of *Pl. dumerilii* at the level of the fourth segmental nerves to show the afferent fibres and their central connexions. *B*, horizontal section through the dorsal neuropile of a ganglion of *Pl. dumerilii* at the level of entry of the afferent fibres of the fourth pair of segmental nerves into the dorso-medial tract. The anterior end of the ganglion is at the top of the figure. *c.cort.* cell cortex; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.* paramedial giant-fibre; *n.* nerve root; *n.pil.* neuropile; *neur.intern.* internuncial neuron; *s.fib.* sensory fibre; *s.fib.v.* sensory fibre with ventral entry; *sept.* intersegmental septum; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

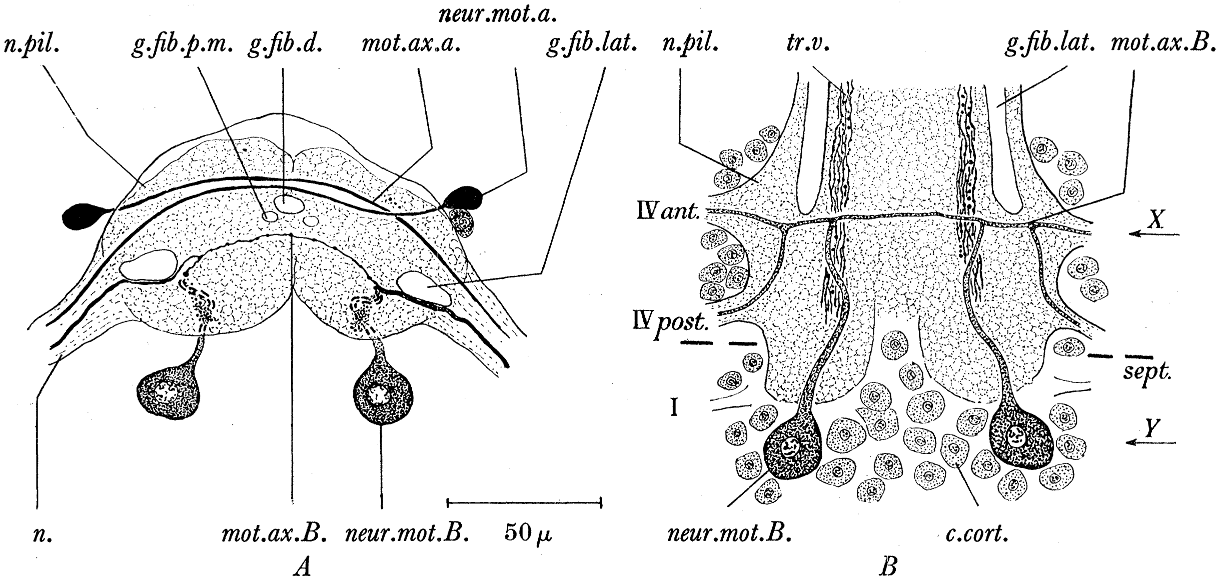

Figure 21. The motor components of the fourth pair of segmental nerves of *Pl. dumerilii*. *A*, transverse section of a ganglion at the level of nerves IV (level *X* in figure 21*B*) but including the post-septal motor cell bodies (*neur.mot.B.*) at the level *Y* of figure 21*B*. *B*, oblique horizontal section through the ventral neuropile of the anterior end of a ganglion. The anterior end of the ganglion at the top of the figure is cut at the more dorsal level. I, IV (*ant.* and *post.*) roots of the segmental nerves; *c.cort.* cell cortex; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.* paramedial giant-fibre; *mot.ax.a.* motor axon with a dorsal commissural fibre; *mot.ax.B.* motor axon with a ventral commissural fibre uniting the motor fibres of the two sides; *n.* nerve root; *n.pil.* neuropile; *neur.mot.a.* motor neuron; *neur.mot.B.* motor neuron with a ventral cell body and with ventrally emerging fibres (Hamaker's 'fibre B'); *sept.* intersegmental septum; *tr.v.* ventral fine-fibre longitudinal internuncial tract.

to the roots of the first pair of segmental nerves (I). Each gives rise to a stout axon more akin in size and staining properties to a giant- than to a fine-fibre. The axon enters the neuropile ventrally, encircles spirally the ventral longitudinal internuncial tract (*tr.v.*) in its forward passage and, on reaching the level of nerve IV, becomes joined to its partner by a ventral transversely running commissural connecting fibre. Hamaker described this bridge as an anastomosis of two fibres which can be individually recognized. In all the preparations examined during the course of the present work the fibre is single and is often thin enough (figure 21*A*, *mot.ax.B.*) to 'bead' readily. The commissural fibre extends laterally beyond its junctions with the parent fibre, closely encircles the ventral border of the lateral giant-fibre (*g.fib.lat.*), and divides at the margin of the neuropile into two branches, one supplying the anterior root of the nerve (figure 21*B*, IV *ant.*) and the other

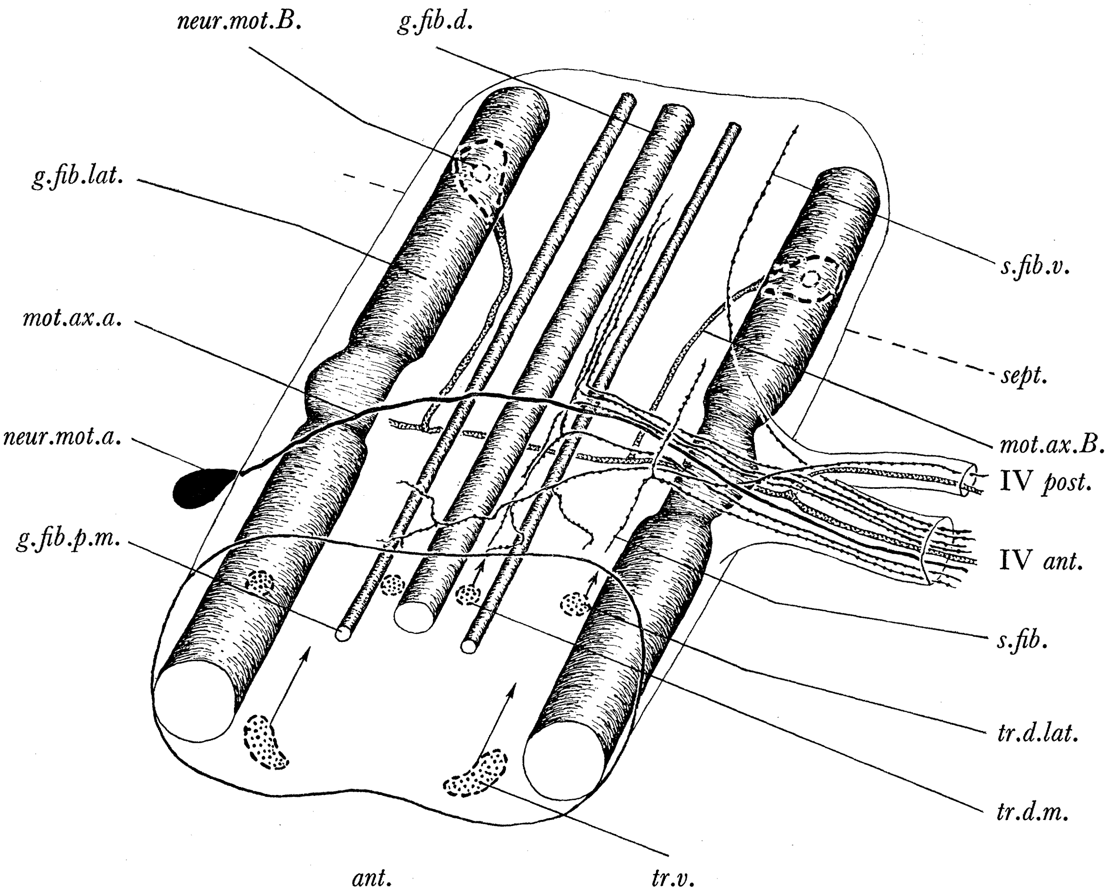

FIGURE 22. Diagrammatic stereogram of the anterior region of a nereid ganglion showing the afferent and efferent components of the two branches of nerve IV and their central relationships. The anterior end of the ganglion is at the bottom of the figure. IV (*ant.* and *post.*), the anterior and posterior roots of nerve IV; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.* paramedial giant-fibre; *mot.ax.a.* motor axon with a dorsal commissural fibre; *mot.ax.B.* motor axon with a ventral commissural axon uniting the motor fibres of the two sides; *neur.mot.a.* motor neuron with a dorso-lateral cell body; *neur.mot.B.* motor neuron with a ventral cell body; *s.fib.* sensory fibre with dorsal entry; *s.fib.v.* sensory fibre with ventral entry; *sept.* intersegmental septum; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract.

the posterior root (IV *post.*) in the manner described by Hamaker. The latter regards the two branches as separate nerves, but the close association of the afferent fibres of the two nerve roots and their common supply from a divided axon would not seem to justify this interpretation.

Some seven fibres (four sensory and three motor) are contained within the root of the main (anterior) branch of nerve IV, three (two sensory and one motor) in the smaller posterior branch. All the nervous components of the two branches are shown, together with the central relationships to other fibre systems, in the stereogram (figure 22).

The afferent connexions of the segmental nerves

The respective numbers of afferent and efferent fibres described in the previous section as being present in the nerve roots were nerve I (3–4 and 1), nerve II (6–8 and 3), nerve III (2 and 1–2) and nerve IV (6 and 4). At a rough estimate there are in the epithelium of the body wall some 1000 sensory cells per square millimetre of surface, while, not to mention the parapodial muscles, there are not fewer than 500 fibres in the two longitudinal muscle bands on the one side of a segment. The limited fibre content of the segmental nerves at their roots would seem inadequate for the service of such extensive sensory and motor fields without some peripheral branching or other form of fibre multiplication. It may of course be argued that the estimated number of fibres in the nerve roots is altogether too low because of the possibility that not all of the fibres are, in any one preparation, made visible by staining. This possibility is, however, largely discounted by the fact that the nerve tracts at the periphery always contain a significantly greater number of fibres, and since experience has shown that fibres stain as readily in one part of a nerve as another, one must allow that there is, in reality, a considerable multiplication of fibres towards the periphery. Smallwood (1926, 1930) has considered the implications of this disparity of fibre number at the peripheral and central ends of the segmental nerves of *Lumbricus* and concludes (1) in respect of the afferent fibres, that 'such facts as these compel a revaluation of the generally accepted notion of the relation of epidermal sense organs to the central nervous system', the 'accepted notion' in this context being (Langdon 1900) that each sensory cell is directly connected with the nerve cord, and (2) in so far as the motor fibres are concerned, that there is extensive peripheral branching. It will be convenient in order to clarify the problems raised by these considerations to examine, in the first place, the afferent tracts at their periphery, and in particular to trace the mode of connexion of the sensory cells with the more peripheral fibres of the segmental nerves.

The more general characteristics of the exteroceptive sensory cells and of their internal nervous connexions can most readily be seen in the head region of nereids, which is richly endowed with sensory endings and with afferent tracts which, in this instance, connect with the brain. As figure 23, a horizontal section through the prostomium, shows, there are numerous bipolar sensory cells (*s.c.*) with spindle-shaped cell bodies drawn out at the two ends into a centripetal and centrifugal fibre. The cell body is contained within the epithelium, its centripetal fibre ending either at the inner or outer surface of the cuticle (*cut.*), the centrifugal fibre passing internally to terminate below the epithelium. At the subepithelial level a number of fine-fibres, grouped into subsidiary or principal tracts (*n.tent.*), can be seen. The centrifugal fibres are directed towards these tracts and contribute to them, but they are never very long and their individual endings are far removed from the central nervous system (*br.*). By far the greater number of the subepithelial fibres of the nerve tracts are, in fact, made up of processes of multipolar cells lying close to the surface of the basement membrane which underlies the epithelium. These association neurons (*neur.assoc.*) are most numerous at the afferent end of a tract and, since their processes are relatively short, the number of fibres within a tract diminishes as the tract approaches the central nervous system. This is clearly seen in the course to the brain of the tentacular nerve (*n.tent.*) on the right-hand side of the figure. The left tentacle has been cut parasagittally and shows the sheathing material of the tract (*sh.n.tent.*). The mode of connexion of the sensory cells revealed in the figured preparation is general to all parts of the integument and shows the circumstances which determine the reduction in the

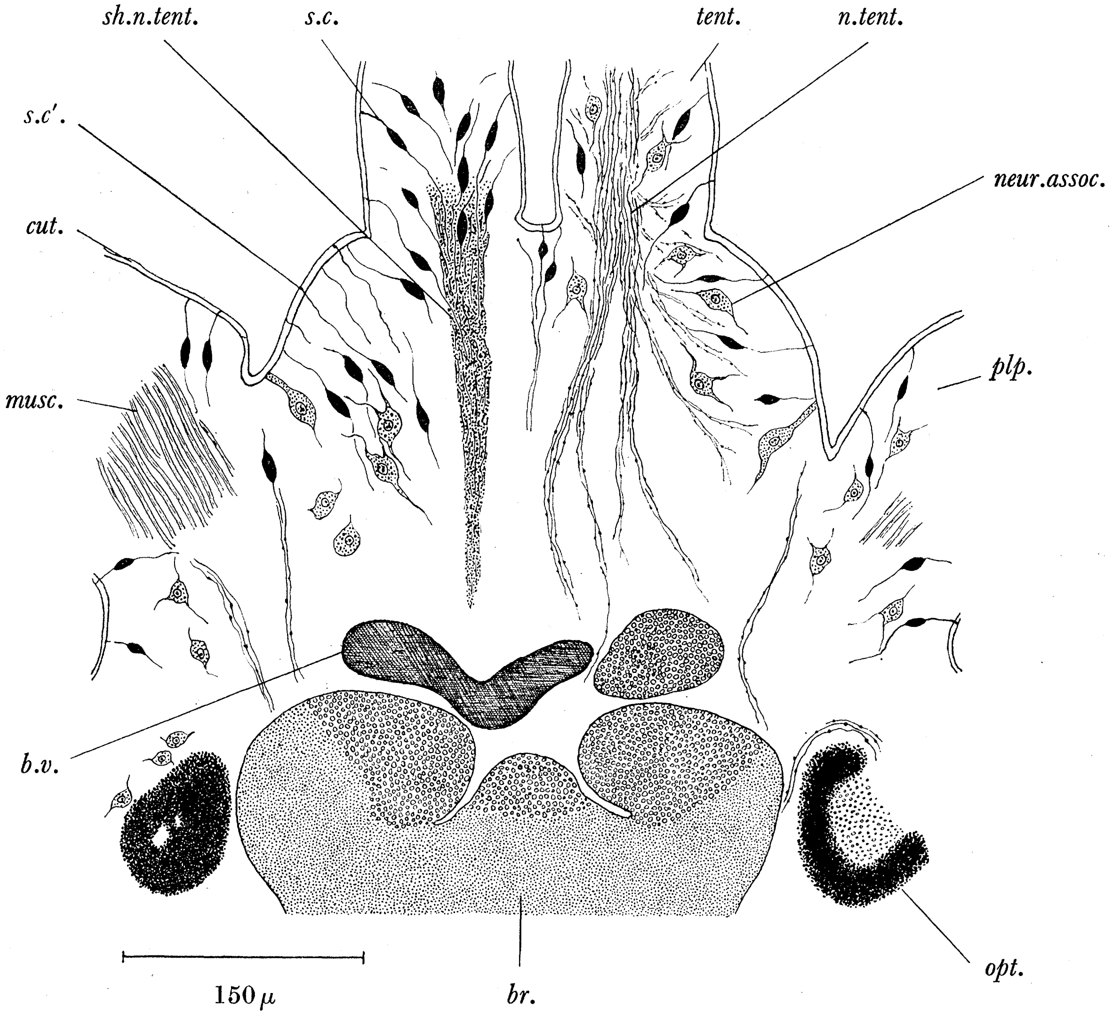

FIGURE 23. Horizontal section through the prostomium of *Pl. dumerilii* at a dorsal level showing the form and relationships of the integumental sensory cells, the subepithelial association neurons and the fibres of the peripheral nerve branches. For further explanation see the text. *b.v.* blood vessel; *br.* brain; *cut.* cuticle; *musc.* muscle fibre; *n.tent.* tentacular nerve; *neur.assoc.* association neuron; *opt.* eye; *plp.* palp; *s.c.*, *s.c'.* sensory cells; *sh.n.tent.* tentacular nerve sheath; *tent.* tentacle.

number of afferent fibres in a nerve in its central passage. To summarize these circumstances: (1) there are large numbers of integumentary sensory cells which (2) connect subepithelially with fibres derived from multipolar association neurons, (3) the latter, most numerous at the periphery of a nerve, form tracts diminishing in fibre content and diameter as they pass centrally, (4) at all stages in the inward course of a nerve there is a recruitment of excitation into a diminishing number of fibres, the excitatory state being transmitted finally, in so far as the afferent tracts are concerned, into localized regions of the cord.

THE EXTEROCEPTOR SENSORY CELLS

Form, variety, orientation and grouping

The most commonly occurring type of sensory cell is of the kind shown in figure 24*A*, single in the sense that it is not obviously grouped with other sensory cells, and with a bipolar spindle-shaped cell body some 10 μ long and 4 μ wide at the centre, wedged between epithelial cells. The darkly staining cell body is without distinction of nucleus and cytoplasm. The sensory cell is oriented perpendicularly to the epithelial surface or has an orientation identical with that of the surrounding cells. Although most of the sensory cells have all these characteristics, each feature, with the exception of the epithelial position of the cell body, may be subject to variation. The nature of these variations is illustrated in figures *B* to *H*. *B* shows variations in the shape and staining reactions of the cell body. A rounded cell is unusual, but the cells with a lightly staining granular cytoplasmic content, with or without a visible nucleus, are merely indicative of a prior immersion in a weak stain or of a short period of staining. *C* shows, on the left, a normally oriented neuron; less frequently the cell body may lie at an angle to the surrounding epithelium. Not infrequently (*D*), the centripetal fibre (*centrip.fib.s.c.*) enlarges terminally

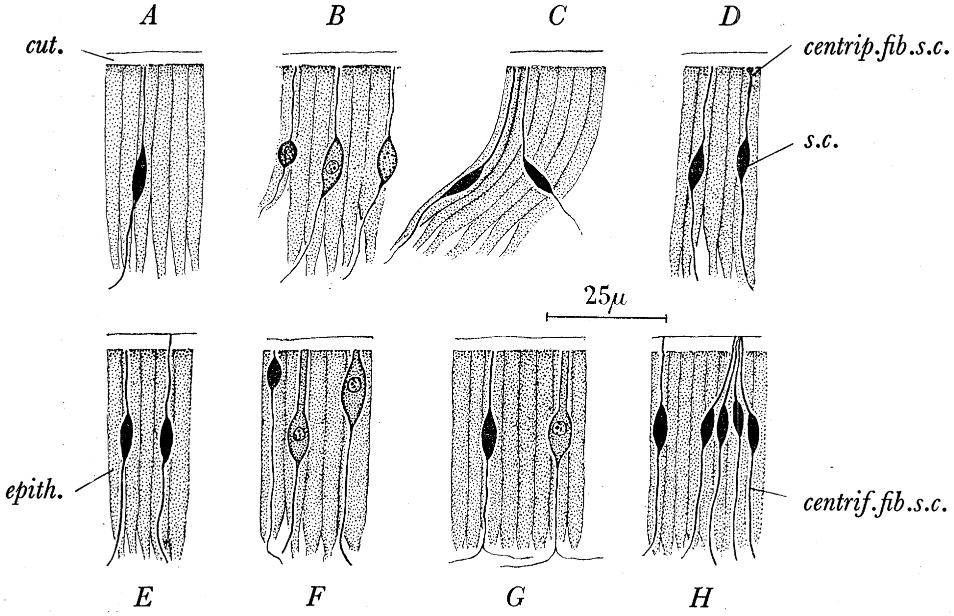

FIGURE 24. *A* to *H*, variations in the form, grouping and orientation of the integumental sensory cells of nereids. *centrif.fib.s.c.* centrifugal fibre of a sensory cell; *centrip.fib.s.c.* centripetal fibre of a sensory cell; *cut.* cuticle; *epith.* epithelial cell; *s.c.* sensory cell.

into a knob, but the unexpanded ending is the more common. Centripetal fibres may (*E*) terminate below the cuticle (*cut.*) or reach to the surface or a little beyond; the two forms occur in almost equal number. Occasionally, as in the left-hand neuron of (*F*), the centripetal fibre is short, with the cell body almost touching the epithelial border. The remaining two neurons of the figure may represent a different functional type of exteroceptor. They are usually less reactive to methylene blue, and the nucleus can always be seen within the faintly blue cytoplasm. The centripetal fibre of this type of sensory cell is, moreover, stout and sharply truncated at its tip and may be extended or extremely short. Both this and the more common type of cell may (*G*) have a centrifugal fibre (*centrif.fib.s.c.*) which dichotomizes below the epithelium into the underlying nerve tracts. Forked fibres are, however, rather rare. Finally, sensory cells may be grouped as shown in (*H*). This is, in my experience, an unusual condition in nereids and must be distinguished from the mere crowding of sensory cells as in the parapodial cirri, where, however, there is no tendency for the centripetal fibres to converge at the periphery as they do in the grouped systems. The latter occur most commonly, though never in great number, in the head appendages.

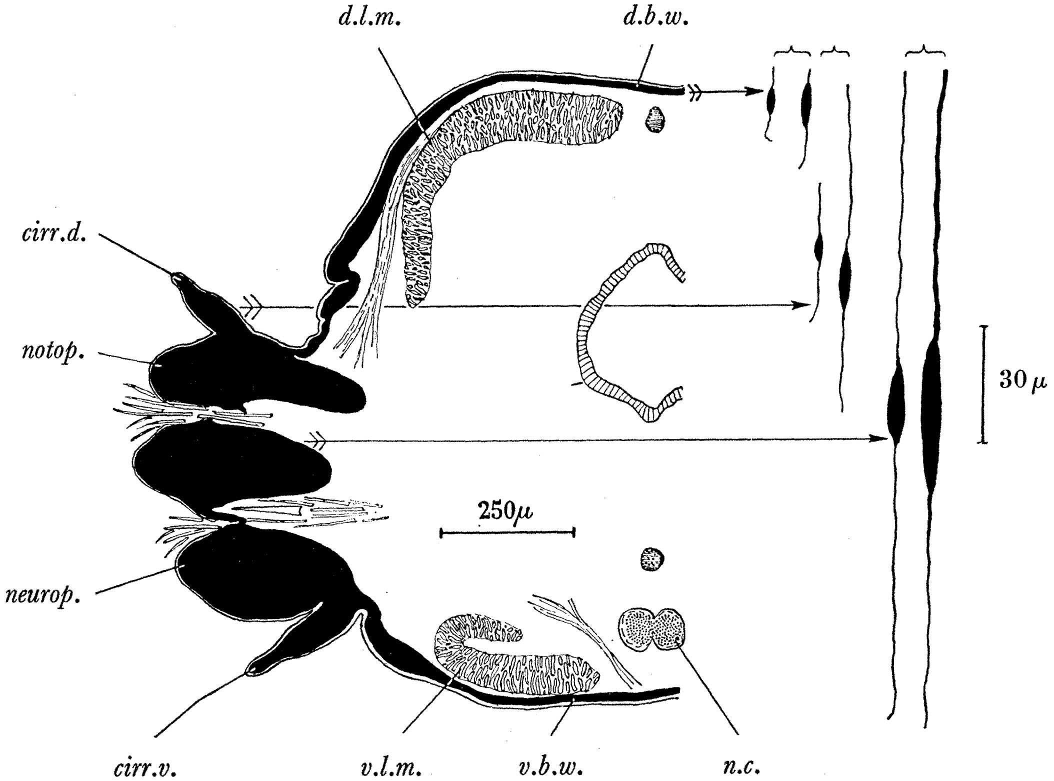

FIGURE 25. Diagrammatic half-transverse section of a body segment of *Pl. dumerilii* showing (in black) the depth of the epithelium in the different parts of the body wall and, to the right of the figure, the relative size range of the sensory cells in the different regions indicated by the arrows. *cirr.d.* dorsal parapodial cirrus; *cirr.v.* ventral parapodial cirrus; *d.b.w.* dorsal body wall; *d.l.m.* dorsal longitudinal muscle; *n.c.* nerve cord; *neurop.* neuropodium; *notop.* notopodium; *v.b.w.* ventral body wall; *v.l.m.* ventral longitudinal muscle.

It is interesting, in view of these observations, to record the divergence of opinion among earlier workers as to the form and grouping of the sensory cells. Retzius (1891) speaks of the sensory cells as being single in *N. diversicolor*; Langdon (1900) says that in *N. virens* they are always grouped. She also describes spiral sensory organs surrounding pockets of invaginated cuticle. I have not seen this last-named type and, though I have not examined the sensory endings of *N. virens* in detail, am inclined to agree with Retzius and to regard the solitary condition of the sensory cells as being generally the more characteristic of nereid polychaetes.

Size

Retzius (1891) and Hamaker (1898) have described the sensory cells of nereids as having, in some instances, cell bodies below the epithelium. Langdon (1900), on the other hand, is convinced that they always lie in the epithelium. The present observations accord with this latter view. The epithelium of nereids varies considerably in thickness in the various parts of the body wall. Figure 25 shows the extent of the variation. The epithelium, shaded in black, is never more than about 30 μ thick over the dorsal surface (*d.b.w.*) and is very little thicker in the ventral wall (*v.b.w.*). There is a perceptible lengthening of the individual cells at the angles of the segment, but in the parapodium (*neurop.*, *notop.*) they attain a relatively immense length, projecting some 300 μ or more into the body cavity. The dorsal (*cirr.d.*) and ventral (*cirr.v.*) cirri are, as Langdon rightly observes, wholly of epithelial construction, and one may add that the notopodial and neuropodial lobes are essentially similar, the only difference being the intrusion of blood vessels into their epithelial substance. It does not appear previously to have been noted that the differential development of the epithelial cells affects the sensory cells in a like way. To the right of figure 25 six sensory cells are drawn, two from each of the three regions of the body from which the directive arrows are led. In each pair the smallest and the largest of the neurons from the region are shown as a measure of the local size range of the cells and fibres. All parts of the neuron are affected by the differential development. Cell bodies ranging from 5 to 60 μ in length have a related fibre-length variation of about 1:10 to 12. Moreover, the largest of the neurons have markedly thicker fibres than the smaller ones.

Distribution and numbers in the different parts of the integument

Figure 26 illustrates the approximate relative concentration of sensory cells in the different areas of the integument. The parapodial cirri (*cirr.d.*, *cirr.v.*) carry by far the greatest number of receptors. Many endings are also to be found in the neuropodial (*neurop.*) and notopodial (*notop.*) lobes of the parapodium. The numbers are smaller at the junction of the parapodium with the body segment, though the sensory cells are still relatively abundant and remain so over the ventral body wall (*v.b.w.*). In the dorsal integument (*d.b.w.*), however, the sensory cells are both small and sparsely scattered; one may scan a section 20 μ thick over the entire width of the wall without finding more than two or three such cells.

There seems to be general agreement among previous workers that the parapodia, and particularly their cirri, are the regions most richly furnished with sensory endings. Langdon (1900) makes the generalization that the number of sensory cells present in a given area is related to the degree of exposure of the surface, the greater the exposure the larger the number of endings. This is certainly not true of the nereids studied during the course of the present work; the ventral body wall has invariably been found to have more sensory cells than the dorsal integument.

The numerical distribution of receptors illustrated in figure 26 invites a number of questions which cannot be answered by anatomical studies unsupported by experiment. The two morphologically differentiated types of receptor represented in figure 24*G* might, perhaps, justify the assumption that they respond to stimuli of different quality, and the ending of the centripetal fibres in some instances below the cuticle and in others at its surface may imply a difference of function. Nereids are known to react to a variety of stimuli, including touch, temperature, light and the presence of substances dissolved in water. The restriction of the variant forms of receptor to two or at the most three morphologically differentiated types, and the apparently random distribution of the variant forms in the different regions of the integument, makes further speculation as to their specific functions unprofitable. The considerable concentration of endings in the parapodia, and especially in the cirri, and the difference in the number of sensory cells on the dorsal and ventral surfaces of the body are, however, realities, the significance of which might well be tested by experiment.

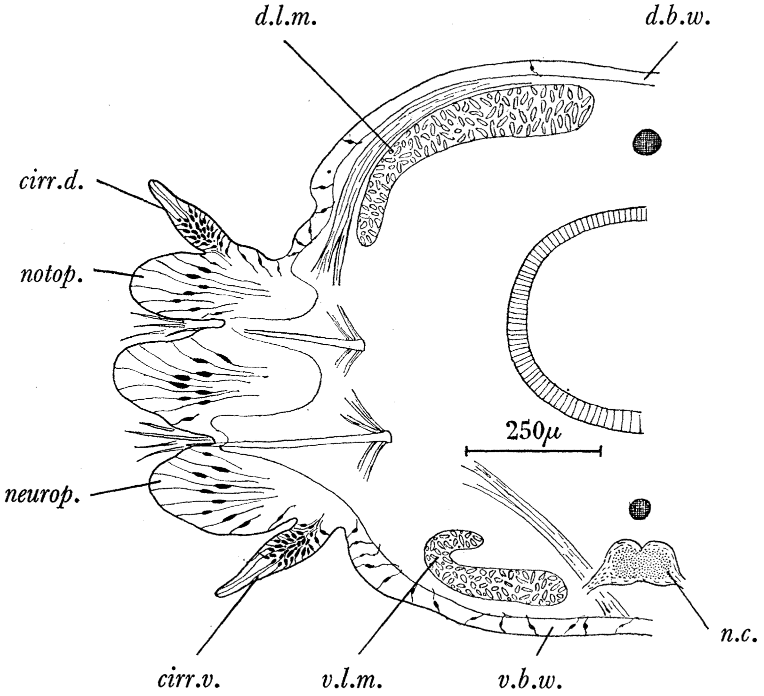

FIGURE 26. Diagrammatic half-transverse section of a body segment of *Pl. dumerilii* showing the relative numbers of sensory cells in the different parts of the body wall. *cirr.d.* dorsal parapodial cirrus; *cirr.v.* ventral parapodial cirrus; *d.b.w.* dorsal body wall; *d.l.m.* dorsal longitudinal muscle; *n.c.* nerve cord; *neurop.* neuropodium; *notop.* notopodium; *v.b.w.* ventral body wall; *v.l.m.* ventral longitudinal muscle.

The variation in the size and distribution of the sensory cells in the different parts of the integument has an important bearing on the interpretation of the anatomy of the sensory and association fibre connexions in the different parts and on the constitution of the nerve tracts which occur at the periphery of the afferent systems of fibres. A description of the sensory cells and afferent fibre complex in the various parts of the wall of a nereid body segment follows.

(*a*) *Parapodia*

The nereid parapodium consists of bilobed neuropodia and notopodia bearing respectively a ventral and a dorsal cirrus. The two cirri differ in size but are otherwise identical. A cirrus (figure 27) is a fusiform appendage wholly composed of epithelial cells (*epith.*) in which numerous mucus cells (*muc.*) occur. The epithelial cells are longest in the narrow bluntly tapering tip, the internal ends of the cells converging towards the base of the cirrus along its central axis. A thin cuticle (*cut.*) covers the cirrus externally. All of the sensory cells (*s.c.*) are bipolar and are oriented for the most part parallel to the epithelial cells by which they are invested. The cell bodies are mid-epithelial in position and are in consequence farthest removed from the surface where the epithelium is deepest. There are, for this reason, no cell bodies in the tip of the cirrus, the surface of which is innervated by long centripetal sensory fibres. In the middle region of the cirrus the cell bodies are more superficial and their centripetal fibres shorter. The centrifugal fibres converge within the epithelium to the base of the cirrus forming a central tract of fibres—the cirrus nerve (*n.cirr.*). This nerve, unlike those described in the head (p. 172 and figure 23, *n.tent.*), is wholly composed of sensory fibres. Subepithelial association fibres have no part in its composition though they appear subepithelially when the cirrus nerve enters the

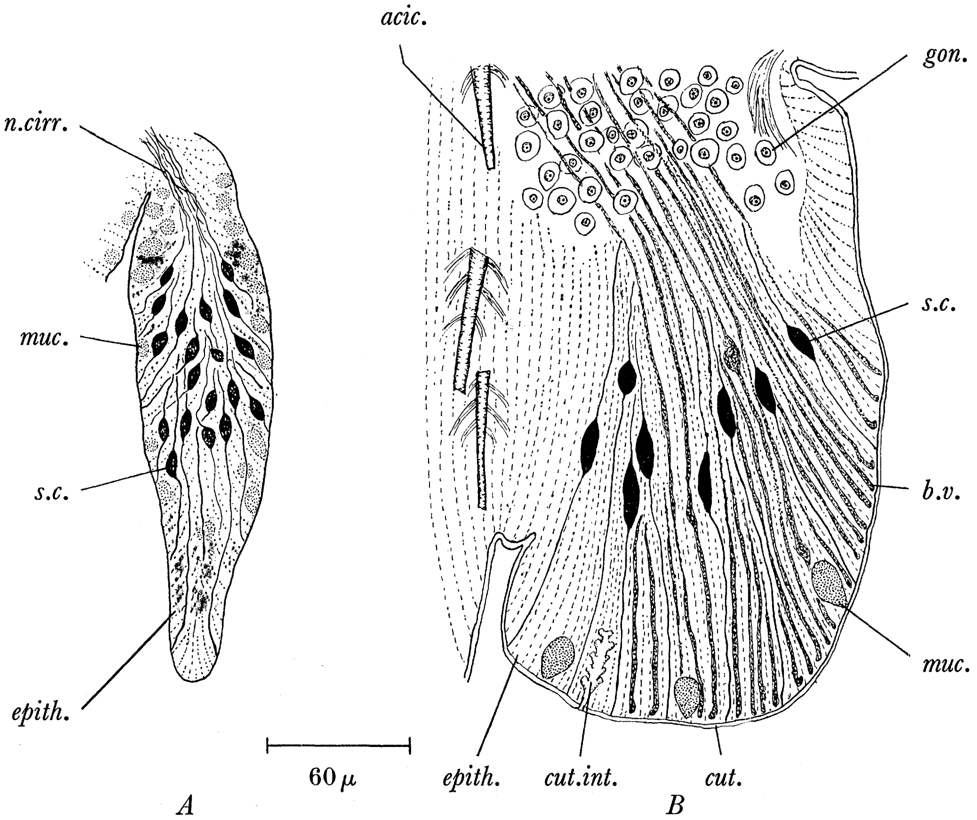

FIGURE 27. *A*, longitudinal section of a parapodial cirrus. *B*, longitudinal section through a neuropodium. The sections show the form and arrangement of the sensory cells and associated structures of the integument. *acic.* aciculum; *b.v.* blood vessel; *cut.* cuticle; *cut.int.* cuticular intuck; *epith.* epithelial cell; *gon.* gonad; *muc.* mucus gland; *n.cirr.* cirrus nerve; *s.c.* sensory cell.

parapodium and becomes linked to one of the branches of the parapodial nerve leading to the parapodial ganglion.

A notopodial or neuropodial lobe (figure 27*B*) is of a more complex tissue construction. There is a similar elongation of epithelial cells (*epith.*) and there are mucus cells (*muc.*) opening at the surface of the cuticle (*cut.*). The epithelium of the parapodial wall is, however, invaded by numerous slender blood vessels (*b.v.*) connected mesially with the dorsal and ventral longitudinal vessels and drawn out into loops, the ends of which closely underlie the cuticle and allow of the respiratory interchange of gases at the surface. In places the cuticle is invaginated to form 'sertularian-like' structures to which are attached muscle fibres. The sensory cells of the parapodial lobes (*s.c.*) are, as has already been noted, very long, in keeping with the elongation of the epithelial cells. Sensory endings of centripetal fibres are fairly evenly distributed over the surface, and the centrifugal fibres converge to form tracts which connect centrally, as do those of the cirri, with nerves emanating from the ganglion of the parapodial nerve.

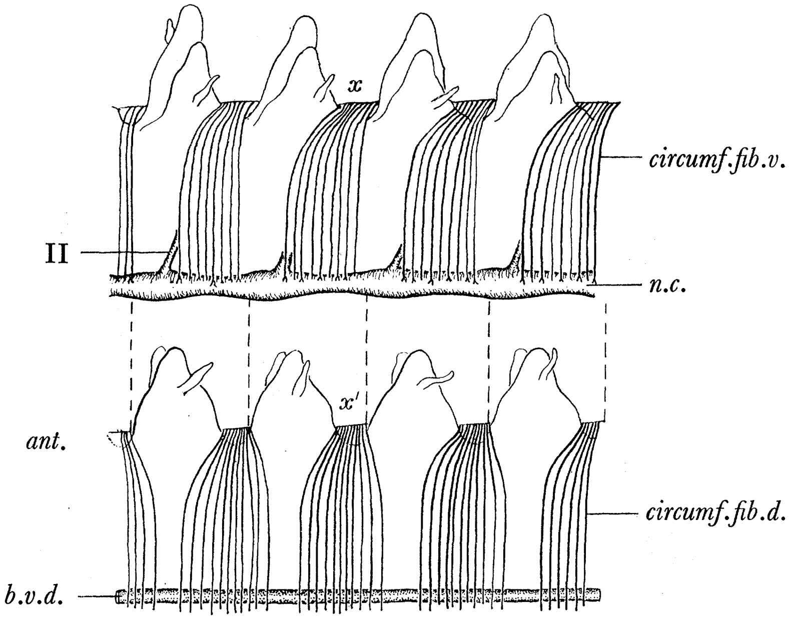

FIGURE 28. The circumferential restraining fibres of the body wall of *Pl. dumerilii*. Above, ventral view of a lateral half of the ventral body wall. Below, dorsal view of a lateral half of the dorsal body wall. The anterior end of the worm is to the left, the limits of the body segments are indicated by broken lines and the letters *x* and *x'* are corresponding regions of the lateral body wall in which the fibres pass from the ventral to the dorsal surface. II, nerve II (parapodial nerve); *b.v.d.* dorsal blood vessel; *circumf.fib.d.*, *circumf.fib.v.* dorsal and ventral lengths of the circumferential fibres; *n.c.* nerve cord.

The great concentration of sensory fibres in the parapodia suggests that they are the most sensitive parts of the body segment. The qualities of the stimuli that can be perceived by the parapodia have not been accurately analyzed.

(*b*) *Body wall*

Before describing the innervation of the body wall, brief reference will be made to certain fibrous structures which do not appear to have been described previously. They are not normally visible in stained sections of fixed material but, notwithstanding their non-nervous character, have a strong affinity for methylene blue. The structures concerned are the circumferential fibres (figure 28, *circumf.fib.v.*, *circumf.fib.d.*) lying in the basement membrane below the epithelium of the body wall. They are attached to the collagen tissue of the outer nerve sheath on the under-side of the nerve cord (*n.c.*) in the posterior two-thirds of each segment and run transversely across the floor of the segment as a series of parallel, evenly spaced, bands. On reaching the margin of the segment, at the base of the parapodium, they swing posteriorly to converge into the narrow intersegmental strip of the lateral body wall and so continue to the dorsal surface. Here (*circumf.fib.d.*) they diverge to overlap adjacent segments, cross the mid-line and continue around the periphery of the segment to be inserted in the collagen of the mid-ventral line near to the place of origin of the fibre. Sometimes the two ends overlap, but more often there is a small gap between them. The circumferential fibres correspond in their position and course to the circular muscles, which are also absent from the anterior third of the segment.

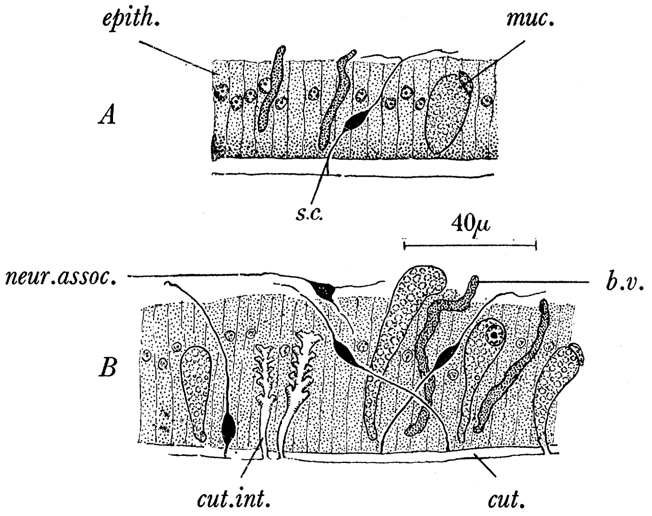

FIGURE 29. *A* and *B* are respectively transverse sections through parts of the dorsal and ventral body wall of *Pl. dumerilii* showing the structures associated with the epithelium. Nerve cells staining with methylene blue have been superimposed on Witmark fixed–Masson stained sections in which the non-nervous structures are more clearly seen. *b.v.* blood vessel; *cut.* cuticle; *cut.int.* cuticular intuck; *epith.* epithelial cell; *muc.* mucus gland; *neur.assoc.* subepithelial association neuron; *s.c.* sensory cell.

In the earliest phases of staining, the fibres appear (figure 30, *circumf.fib.a.*) as delicate strands very like nerve fibres except that they are never 'beaded'. Later (*b*, *c*) they thicken by the extension of the stain from the border of the fibre to its deeper lying substance, and finally, after prolonged staining (*d*, *e* and *f*), the bands broaden considerably by the spread of the stain to the underlying muscles (*musc.*). The strong affinity of the circumferential fibres for methylene blue is somewhat puzzling and makes it doubtful whether they are composed of collagen which does not, in nereids, readily take the stain. They appear, nevertheless, to be connective tissue and to function as restraining bands to which the circular muscles are attached and through which they exert their pull on the body wall during contraction.

The dorsal and ventral surfaces of the body wall (figures 29 *A*, *B*) are made up, primarily, of columnar epithelial cells (*epith.*), between which are intruded mucus glands (*muc.*) and blood vessels (*b.v.*). Only in the ventral body wall (29 *B*), however, are there cuticular intuckings (*cut.int.*), mainly grouped around the mid-ventral line and near the bases of the parapodia, and having, in some instances at least, muscle fibres attached to them.

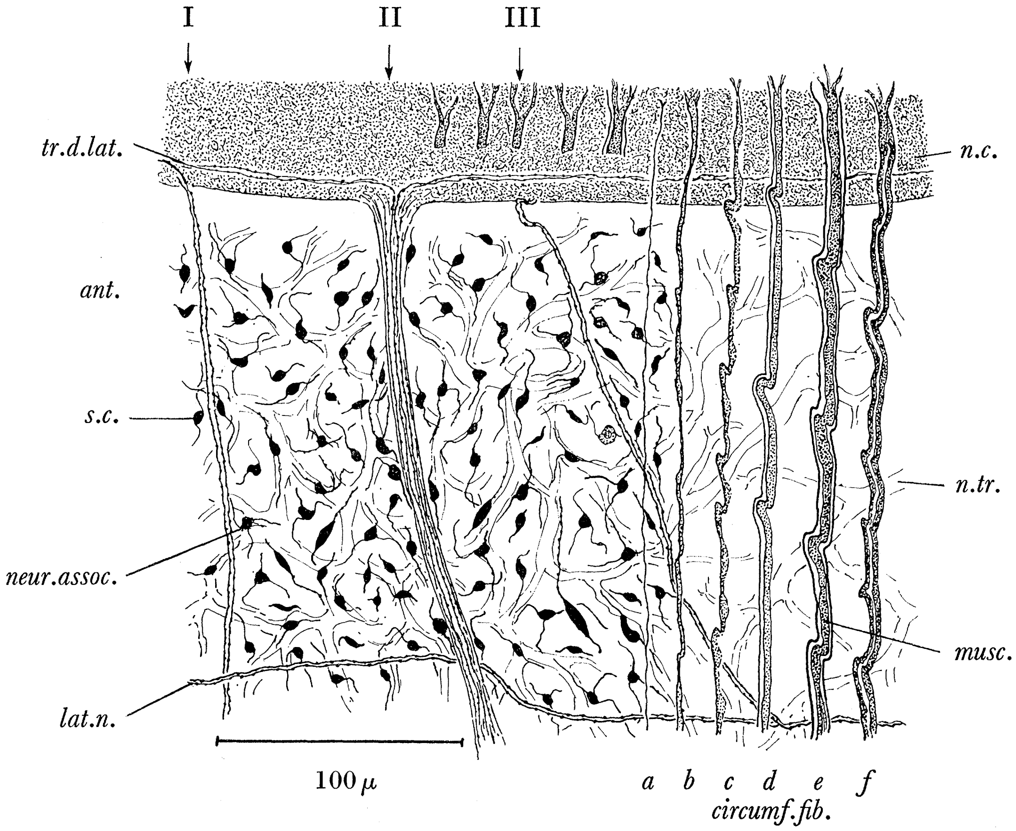

FIGURE 30. Part of a thick horizontal section through the ventral body wall of *Pl. dumerilii* showing sensory cells, subepithelial association neurons and fibre tracts, the fibre systems of nerves I, II and III and circumferential staining bands (*a–f*) in various phases of staining. The anterior border of the segment is to the left, the mid-ventral line at the top and the lateral margin of the body wall at the bottom of the figure. The arrows mark the levels of origin of nerves I, II and III. *circumf.fib.* (*a–f*), circumferential fibres in various phases of staining; *lat.n.* lateral nerve; *musc.* muscle fibre; *n.c.* nerve cord; *n.tr.* subepithelial nerve tract; *neur.assoc.* subepithelial association neuron; *s.c.* sensory cell; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract.

Neurologically, the two surfaces differ chiefly in the number of their sensory cells, there being many more on the lower than on the upper surface. Figure 30 shows the appearance of the ventral body wall after methylene-blue staining. Sensory cells (*s.c.*) are readily distinguished from the deeper lying multipolar association cells (*neur.assoc.*) by their bipolar form and more superficial position. The internal (centrifugal) fibres of the sensory cells combine with the association fibres to form a net-like subepithelial plexus shown in the figure by an outlined lattice. To the right of the figure where the section cuts more deeply into the wall the lattice is seen without its covering of sensory and association cells. The fine-fibre lattice connects up, in a pattern later to be described (p. 187), with the segmental nerves (figure 30, I, II, III), each nerve collecting afferent excitation from circumscribed regions of the body wall. In order not to over-elaborate the drawing, individual association fibres have been omitted from the figure. They are, however, very numerous. The afferent pathways thus consist, as in other parts of the nereid integument, of tracts with fibres diminishing in number as they approach the segmental nerves, the nerves I, II and III included in the figure consisting of considerably fewer fibres than the supply tracts of the association plexus.

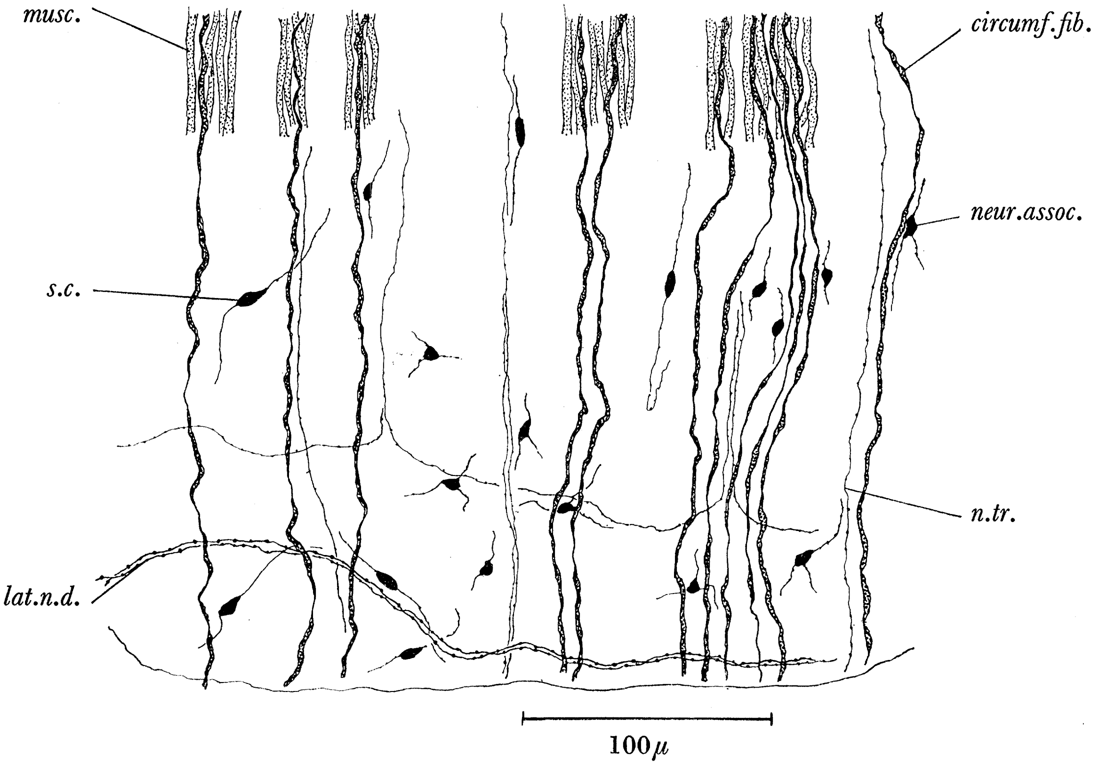

FIGURE 31. Part of a thick horizontal section through the dorsal body wall of *Pl. dumerilii* showing the sensory cells, subepithelial association neurons and fibre tracts, circumferential fibres and circular muscles. The anterior border of the segment is to the right, the mid-dorsal line at the top and the margin of the body segment at the bottom of the figure. *circumf.fib.* circumferential fibre; *lat.n.d.* dorsal lateral nerve; *musc.* muscle fibre; *n.tr.* subepithelial nerve tract; *neur.assoc.* association neuron; *s.c.* sensory cell.

On the dorsal surface the paucity of sense cells (*s.c.*) and of association cells and fibres (*neur. assoc.*) is immediately obvious on examination of whole mounts or of thick sections of the body wall (figure 31). The few systems of transversely running fibres seen in this section appear to be continuations over the dorsal side of the segmental nerves I and IV, though it has not been found possible to trace accurately the connexions around the lateral body wall owing to the close approximation of the two fibre systems in the narrow strip of the intersegment.

THE PROPRIOCEPTOR SENSORY CELLS

In addition to the exteroceptive system of integumentary sensory cells and fibres there are—in the nereids studied during the course of the present work—other well-defined systems of nerve fibres to which it seems justifiable to assign a proprioceptive function. The fibres in question are associated with the musculature and are best seen on examining the dorsal and ventral longitudinal muscles of the body wall. Figures 32*A*, *B* and *C* show the manner of their association with the latter muscle. The proprioceptor fibres (figure 32*A*, *s.fib.propr.*) arise from nerve tracts in the region of the ventral body wall adjacent to the lateral margin of the ventral longitudinal muscle (*v.l.m.*), rising vertically into the body cavity to encircle the muscle round its reflected outer border. Their initial course takes them transversely across the muscle towards the mid-line of the body, but, on approaching the inner margin of the reflected muscle, they turn at right angles to run parallel to the muscle fibres. In so doing they connect up with neighbouring fibres or fibre groups, so forming a partially connected network of fibres over the muscle surface (figure 32*B*). Though many of the fibre systems are conjoined, individual fibres with free nerve endings may frequently be seen (figure 32*C*). There is some difficulty in ascertaining with which fibre tracts of the body wall the individual proprioceptor fibres are connected. Most of them undoubtedly arise from the lateral nerve (figure 32*A*, *lat.n.*), which, it will be recalled, is an extension of nerve III, connecting the third nerves of the successive segments of the body. Proprioceptor fibres from the greater part of the muscle connect with this nerve. In the neighbourhood of the intersegmental septum, however, proprioceptor fibres would appear to discharge excitation into the fourth (pre-septal) nerve (IV) and possibly also—though this is more doubtful—into the first segmental (the post-septal) nerve (I). Circumstantial evidence of the connexion of the proprioceptor fibres with one or both of these nerves is provided by the occurrence of proprioceptor fibres on the dorsal longitudinal muscles. These muscles adjoin the dorsal integument which is innervated solely by nerves I and IV.

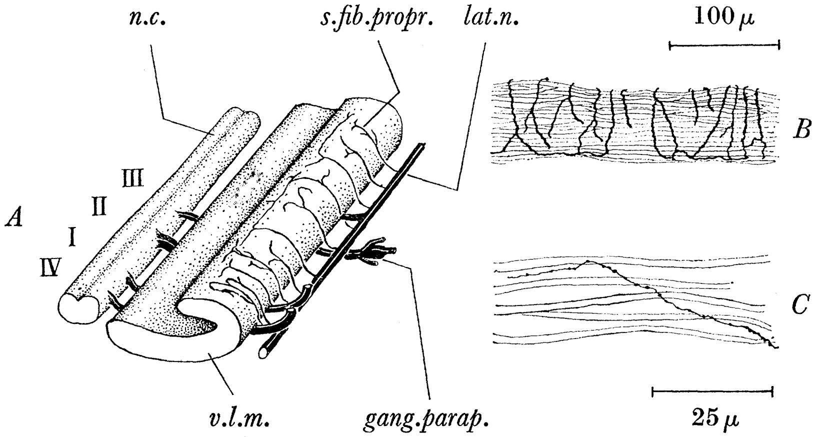

FIGURE 32. Proprioceptor sensory fibres. *A*, stereogram showing a segmental section of the nerve cord and ventral longitudinal muscle, the segmental nerves and the origin and distribution of the proprioceptor fibres. The anterior end of the ganglion is at the bottom of the figure. *B*, surface view of the dorso-lateral wall of the ventral longitudinal muscle with its investing network of proprioceptive fibres. *C*, high-power drawing of an isolated proprioceptor fibre. IV–III, segmental nerves in their order of origin from the ganglion; *gang.parap.* ganglion of the parapodial nerve (nerve II); *lat.n.* lateral nerve; *n.c.* nerve cord; *s.fib.propr.* proprioceptive sensory fibre; *v.l.m.* ventral longitudinal muscle.

The question arises as to whether the nerves here described may be motor rather than proprioceptive in function. The main reason for not regarding them as such is that they fail to penetrate the connective tissue which surrounds the muscle but remain attached to the epimysium. In this position they are unable directly to excite the muscle fibres but are so disposed as to respond to distortions accompanying the contraction and relaxation of the musculature. The cell bodies of the proprioceptors have not been identified. It would appear that they lie in the body wall and that the fibres which extend internally over the perimysium are wholly centripetal.

Fibres of a similar kind surround the acicula and chaeta sacs. Retzius (1892) figures endings on the chaeta sac and ascribes to them a sensory function. Proprioceptors on the longitudinal muscles have not, however, been previously recorded.

Motor fibres and the innervation of the musculature

Nothing is known from previous accounts of the manner in which nereid muscles are innervated. In the majority of methylene-blue preparations blue-staining fibres are seen to accompany the muscles of the body wall and parapodia along a greater or lesser part of their length. These fibres have, however, more the appearance of connective tissue strands than nerve fibres. They resemble the circumferential bands in their staining properties and in being neither 'beaded' nor visibly connected with the nerve tracts of the body wall. There are, nevertheless, at times (figure 33, *mot.fib.*), fibres associated with the muscles which are 'beaded' and can be traced to the nerve plexus of the ventral body wall (*v.b.w.*) and which differ from proprioceptor fibres in having direct contact along their length with

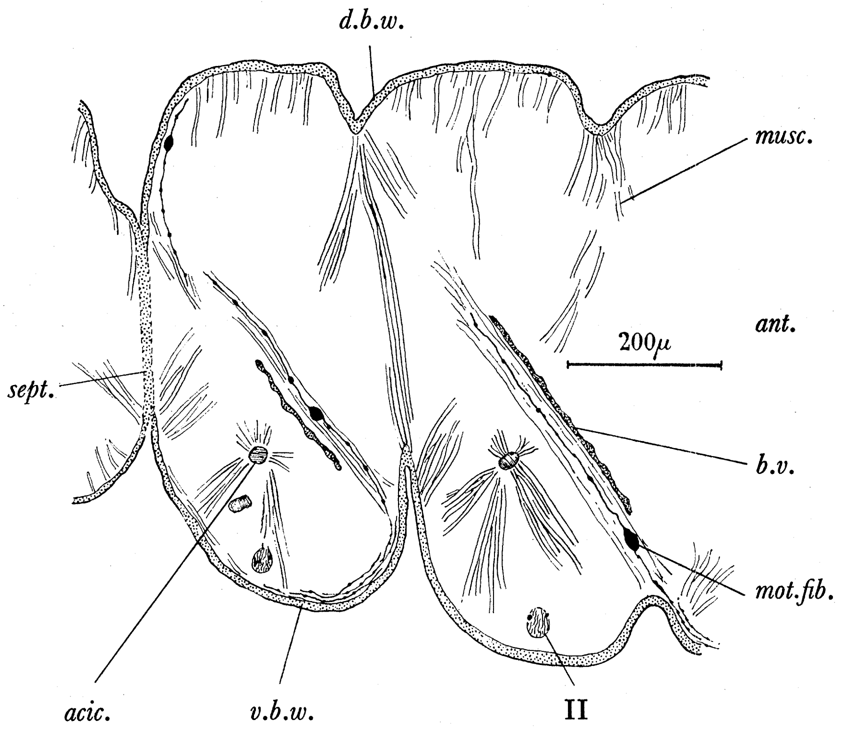

FIGURE 33. Parasagittal longitudinal section through three body segments of *Pl. dumerilii* at the level of junction of the parapodia with the body segments showing motor nerve fibres accompanying the oblique muscles of the parapodium. *acic.* aciculum; *ant.* anterior end of the segment; *b.v.* blood vessel; *d.b.w.* dorsal body wall; *mot.fib.* motor fibre; *musc.* muscle fibre; *sept.* intersegmental septum; *v.b.w.* ventral body wall.

one or more muscle fibres. It has not been found possible to trace the course of these supposedly motor fibres within the subepithelial tracts and, in consequence, it is not known with certainty whether efferent excitation is always relayed peripherally from the primary motor axons of the segmental nerves to the ultimate endings by way of intercalated neurons or whether the primary axons, on occasions, exhibit extensive terminal branching. There are, however, strong indications that efferent excitation is distributed by the former method, the evidence coming mainly from the neuron arrangements within the parapodial ganglion (see p. 187 and figure 35*E*).

As has been noted, all the segmental nerves contain motor fibres and all may, therefore, be considered to innervate one or more of the muscle systems of the body or parapodia. The fields served by the individual segmental nerves have not been determined by direct tracing, but some provisional conclusions may be inferred from the general distributional characteristics of the nerves. Muscles wholly intrinsic to the parapodia such as the acicular muscles must, for example, be innervated by the parapodial nerves (nerves II), since these alone of the four pairs enter the parapodia. Again, nerves I and IV in places innervate the circular muscles of the body wall and certain parapodial muscles such as the oblique and levator muscles which are derived from the circular sheath. The consideration given in the following section to the peripheral distribution of the several segmental nerves provides further information as to the pattern of distribution of the motor nerves which is, however, more appropriately discussed in conclusion to the account. It must, nevertheless, be admitted that the conclusions are not as firmly founded upon direct observation as one would have wished. The conditions favourable to the staining of the afferent and central tracts are evidently not suitable for the demonstration of motor nerves; other conditions of staining must be sought before the efferent pathways can be fully elucidated.

THE PERIPHERAL COMPOSITION AND DISTRIBUTION OF THE INDIVIDUAL SEGMENTAL NERVES

The figures used in illustration of this concluding section to the account of the anatomy and peripheral distribution of the segmental nerves are arranged to show, in each instance (figures 34 to 37*A*), their exteroceptive sensory fields within the ventral integument, (*B*) the nature and central connexions of their component fibres and the composition of the nerve roots, and (*C*–*D* or *C*–*E*) the anatomy of the peripheral tracts and aspects of their proprioceptor and motor distribution. The figures 34 to 37 (*B*) are simplified versions of figures 13, 15*B*, 17 and 19 of the earlier part of the account, and are included in order to summarize within the compass of a single composite figure all of the more important anatomical features of the nerve in its course from the ganglion to the periphery.

Nerve I (figures 34*A*–*D*)

Almost all of the subepithelial tracts supplying this nerve are on its posterior border (figure 34*A*), a few fibres only innervate the narrow anterior region of the intersegment. The tributary branches of the main tract reach back to the parapodial nerve but do not extend into the parapodium, the sensory cells of which (p. 185) connect with branches of the second (parapodial) nerve. The nerve contains at its periphery substantially the same number of fibres as at its root, and it would therefore appear that the association cells of the tributary plexus (figure 34*C*, *neur.assoc.*) do not contribute in any number to the main tract. Sensory cells (*s.c.*) discharge excitation either directly into the main nerve or, more usually, by way of the association fibres. Figure 34*D*, a transverse section through the intersegment, shows the course of the nerve. Its fibres, lying on the basement membrane external to the circular and longitudinal muscles, follow the line of the body wall in their passage to the dorsal surface. Proprioceptor fibres (shown by the black arrows) enter the nerve from the dorsal and ventral longitudinal muscles and motor nerves (outlined arrows) have been seen to leave the nerve at the base of the parapodium to innervate its oblique muscles. Nerve I extends to the dorsal integument, but the boundaries of the sensory field on the upper surface of the segment are not readily determinable.

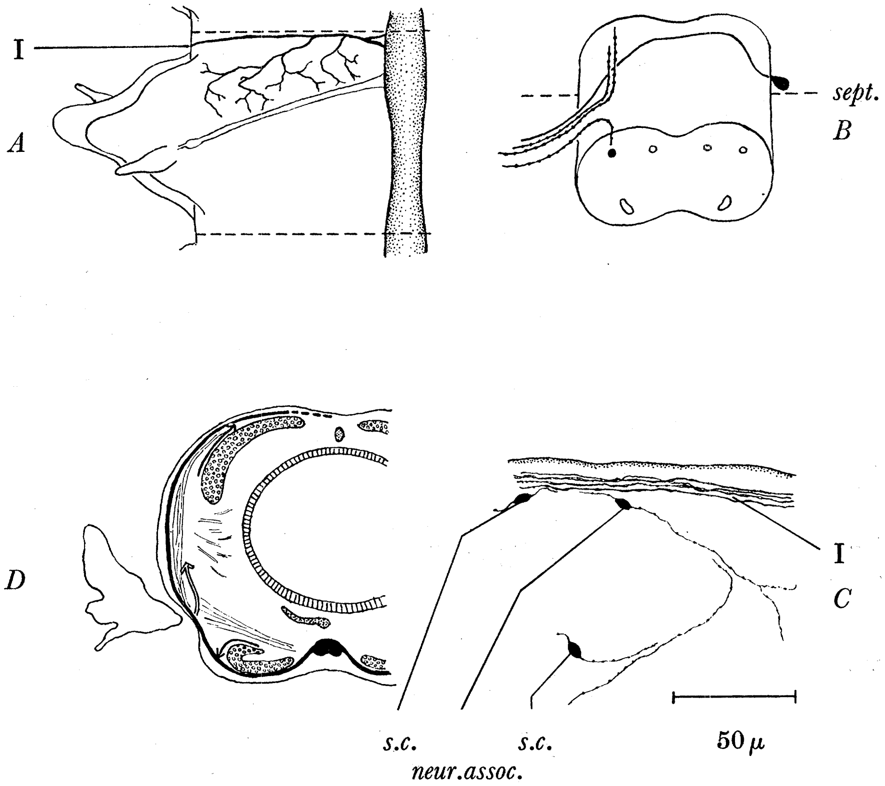

Figure 34. Synoptic diagrams showing the constitution and central and peripheral relations of the first segmental nerve. *A*, sensory distribution. *B*, distribution of the sensory and motor components in the ganglion and nerve root. *C*, sensory cells and association neurons of the subepithelial nerve tracts feeding into the nerve. *D*, partial transverse section of a segment to show the distribution of the nerve and of its proprioceptor (black arrows) and motor (outlined arrow) components. I, first segmental nerve; *neur.assoc.* association neuron; *s.c.* sensory cell; *sept.* intersegmental septum.

Nerve II (*the parapodial nerve*) (figures 35*A*–*D*)

These nerves alone of the four pairs receive excitation from the surface of the parapodia. On the other hand, they play a subordinate role in the innervation of the body wall, being connected with a very few receptors restricted to narrow strips of the ventral integument anterior and posterior to the nerve (figure 35*A*). There are, in addition, subsidiary twigs supplying the mid-line of the body wall below the nerve cord. The main branches of the nerve, five in all, arise from or in the neighbourhood of the parapodial ganglion, three (figure 35*A*, *p.n. 1*, *2* and *3*) from the anterior border, one (*p.n. 4*) as a continuation of the main nerve and one (*p.n. 5*) from its posterior side. The first of the branches (*p.n. 1*) arises proximally to the ganglion and extends in a dorsally curving arc to the upper surface of the notopodium where it terminates, receiving on its way, through the subepithelial association tracts, excitation drawn from sensory cells of the anterior wall of all four parapodial lobes. A similar course is followed and a sensory field of like pattern innervated by the second branch (*p.n. 2*), which, however, arises distally to the ganglion and is

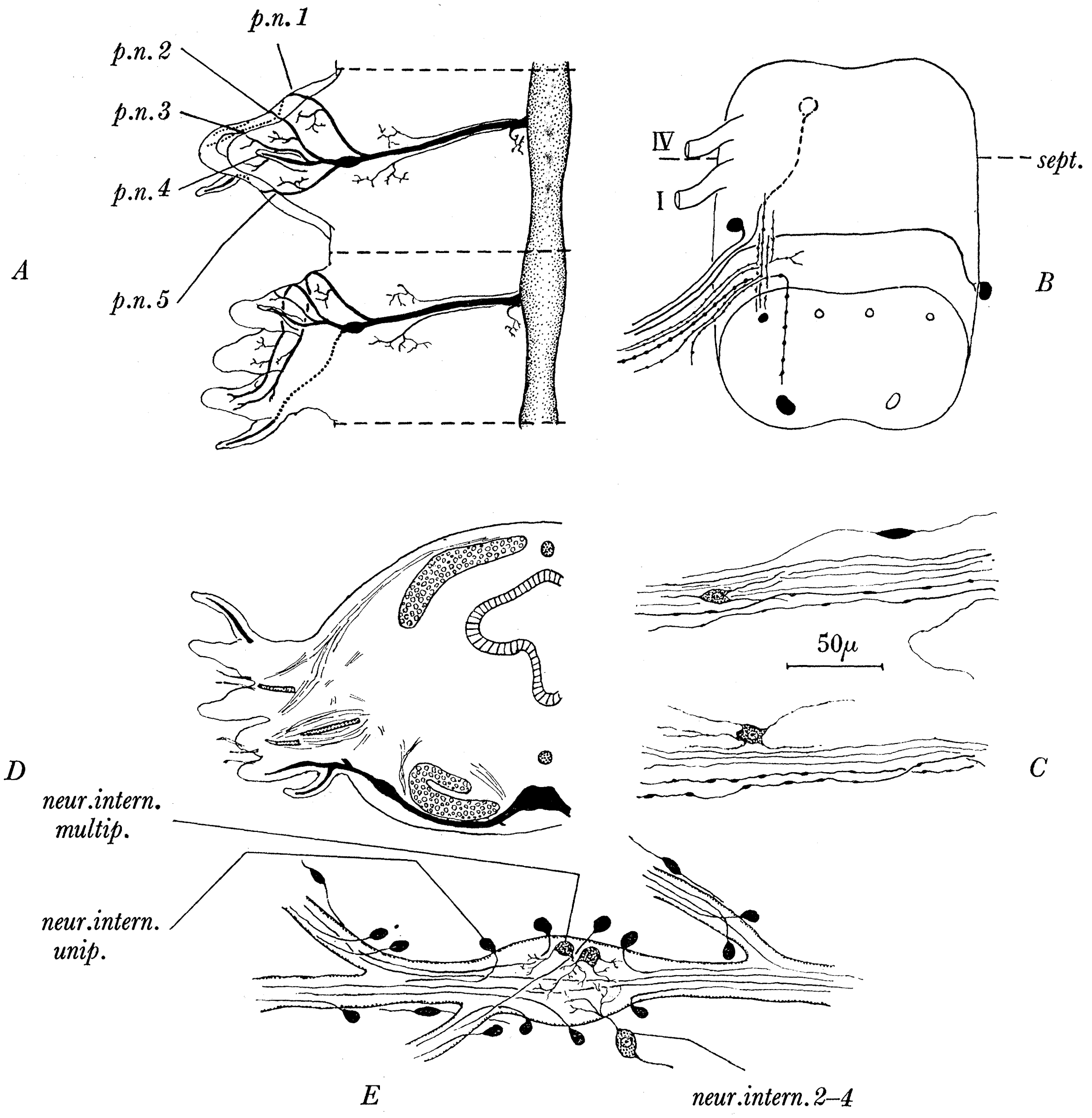

FIGURE 35. Synoptic diagrams showing the constitution, central relations and peripheral distribution of the second segmental (parapodial) nerve. *A*, sensory distribution. *B*, distribution of the sensory and motor components in the ganglion and nerve root. *C*, the fibres of the main nerve and of a tributary branch. *D*, partial transverse section to show the distribution of the nerve. *E*, the parapodial ganglion and its associated neurons. I–IV, the first and fourth segmental nerves; *neur.intern.unip.*, *neur.intern.multip.* unipolar and multipolar internuncial neurons; *neur.intern. 2–4*, internuncial neuron connecting the parapodial ganglion with nerve IV; *p.n.* (*1–5*), branches of the second (parapodial) nerve; *sept.* intersegmental septum.

consequently rather shorter than the first nerve. The third factor (*p.n. 3*), diverging from the main nerve at the base of the ventral cirrus, is restricted in its distribution to the undersurface of the parapodium. The tract forming the core of the cirrus and alined along the axis of the main nerve at its distal extremity is not, strictly speaking, a part of the parapodial nerve, since it is made up entirely of the centrifugal fibres of sensory cells (p. 177 and figure 27*A*, *n.cirr.*). One nerve only (*p.n.5*) encircles the posterior wall of the parapodium, receiving excitation from all parts of its posterior wall in its upward passage to the dorsal cirrus. The fibres of the principal nerve trunk and of its branches are connected with sensory cells (figure 35*C*) either directly or through association cells.

The parapodial ganglion is situated laterally to the ventral longitudinal muscle (figure 35*D*). Its main neurological features are represented in figure 35*E*. Fibres of the main nerve tract, seemingly the same as those which enter or leave the cord at the nerve root, are distributed to the different branches of the nerve, one or two to each branch. The number of fibres entering each branch is, however, augmented by fibres of unipolar internuncial neurons (*neur.intern.unip.*), the cell bodies of which border the thin sheath which invests the ganglion and the main and subsidiary nerve branches. Most but not all of the internuncial fibres are directed distally towards the termination of the nerve, an orientation which argues a motor function and would show that in the parapodial nerve, at least, efferent excitation is distributed by relay neurons interposed between the few motor fibres of the principal nerve and the several muscle systems which require to be innervated. Within the substance of the ganglion are multipolar internuncial neurons (*neur.intern.multip.*) with short arborescent processes forming local concentrations of neuropile. The ganglion, with its afferent and efferent fibres interconnected and augmented by long-axon and short-axon internuncial neurons, is in its nervous organization a microcosm of the central nervous system. There is, in short, evidence that it is so constituted as to allow on the one hand for the through passage of excitation to and from the central nervous system and, on the other, for the peripheral short-circuiting of excitation between the receptors and motor endings. Moreover, since unipolar internuncial neurons are also to be found within the non-ganglionated parts of the parapodial nerve branches, it may be supposed that localized nervous arcs between sensory endings and muscle are not necessarily confined to tracts passing through the ganglion.

The motor field of the parapodial nerve has not been determined by direct tracing but may be considered (p. 184) to include all the muscles wholly intrinsic to the parapodium. The nerve is thus concerned, both on the sensory and motor side, predominantly and indeed almost exclusively with the innervation of the parapodium.

Nerve III (figures 36, *A* to *D*)

The third segmental nerve is confined in its peripheral distribution (figure 36*A*) to the area of the ventral body wall directly underlying the ventral longitudinal muscle (*v.l.m.*). In its oblique outward course from the ganglion the nerve receives a few sensory fibres contained within a narrow strip of integument on its anterior and posterior borders. The primary function of the nerve seems to be that of proprioception. All the third nerves of the one side of the body are connected peripherally through the lateral nerve (*lat.n.*) which runs roughly parallel to the outer border of the longitudinal muscle. A lateral nerve of similar distribution links, on the dorsal surface, the proprioceptor fibres of the dorsal longitudinal muscles of successive segments. This nerve is, however, connected with the fourth (and possibly also the first) segmental nerve, the third nerve, as has been shown, not extending to the dorsal side. It may well be that the function of the lateral nerves is to register the suprasegmental patterns of body flexure which accompany swimming and rapid ambulation. Since (figure 36*B*) the third nerve also contains a motor fibre it is possible that such patterns may not only be recorded centrally by virtue of the afferent connexions of the cord but lead, in addition, to muscle adjustments by the more localized routing of excitation through peripheral afferent and efferent circuits. The nerve in all its parts contains few fibres (figure 36*C*). Its course in the subepithelial tissues of the body wall is shown in figure 38*D*.

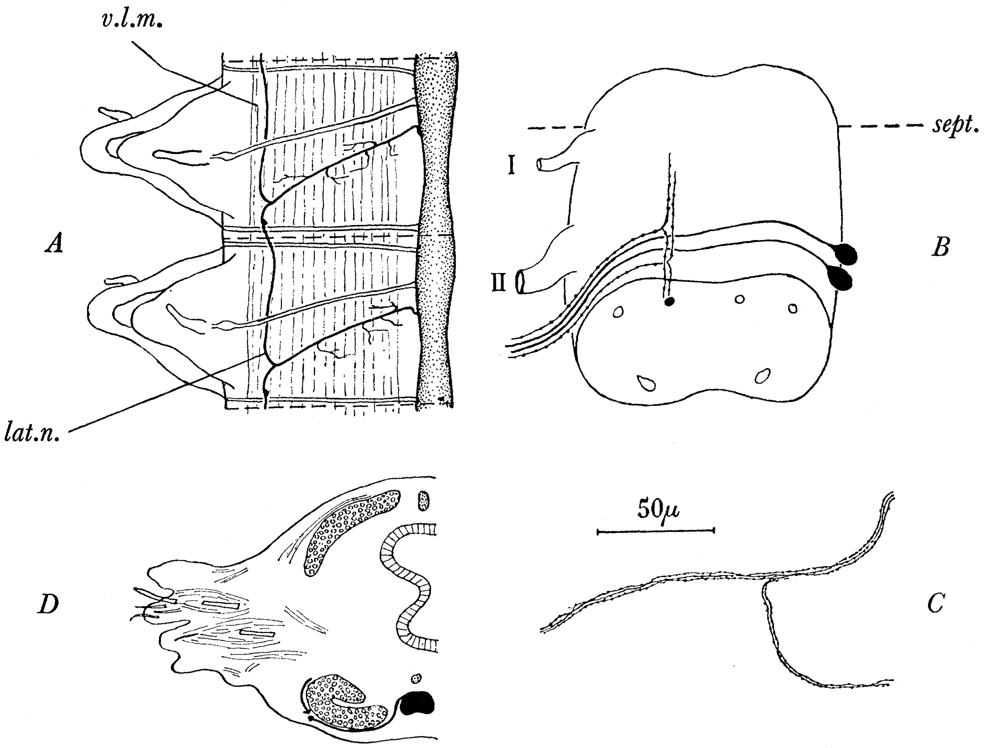

FIGURE 36. Synoptic diagrams showing the constitution, central relations and peripheral distribution of the third segmental nerve. *A*, sensory distribution and the lateral nerve. *B*, distribution of the sensory and motor components in the ganglion and nerve root. *C*, the fibres of the main nerve and of a tributary branch. *D*, partial transverse section of a segment to show the distribution of the nerve and (black arrow) of its proprioceptor components. I–II, first and second segmental nerves; *lat.n.* lateral (connective) nerve; *sept.* intersegmental septum; *v.l.m.* ventral longitudinal muscle.

Nerve IV (figures 37*A* to *E*)

The fourth nerve receives excitation from the receptors of the ventral body wall over an area extending from the parapodial nerve to the posterior border of the segment (figure 37*A*). It innervates, in addition, the integument of the mid-line as far forward as the root of nerve II. Broadly speaking the composition of the fourth (pre-septal) nerve, in so far as it is made visible by methylene-blue staining, is similar to that of the first (post-septal) nerve. Each of the two nerves is connected with subepithelial tracts extending over a substantial area of the ventral integument, each supplies motor fibres to the oblique muscles which cross the parapodia at their confluence with the body segment and there is some evidence that each may have proprioceptor connexions with the longitudinal muscles of the body wall. But it is reasonable to suppose from the central relations of the two

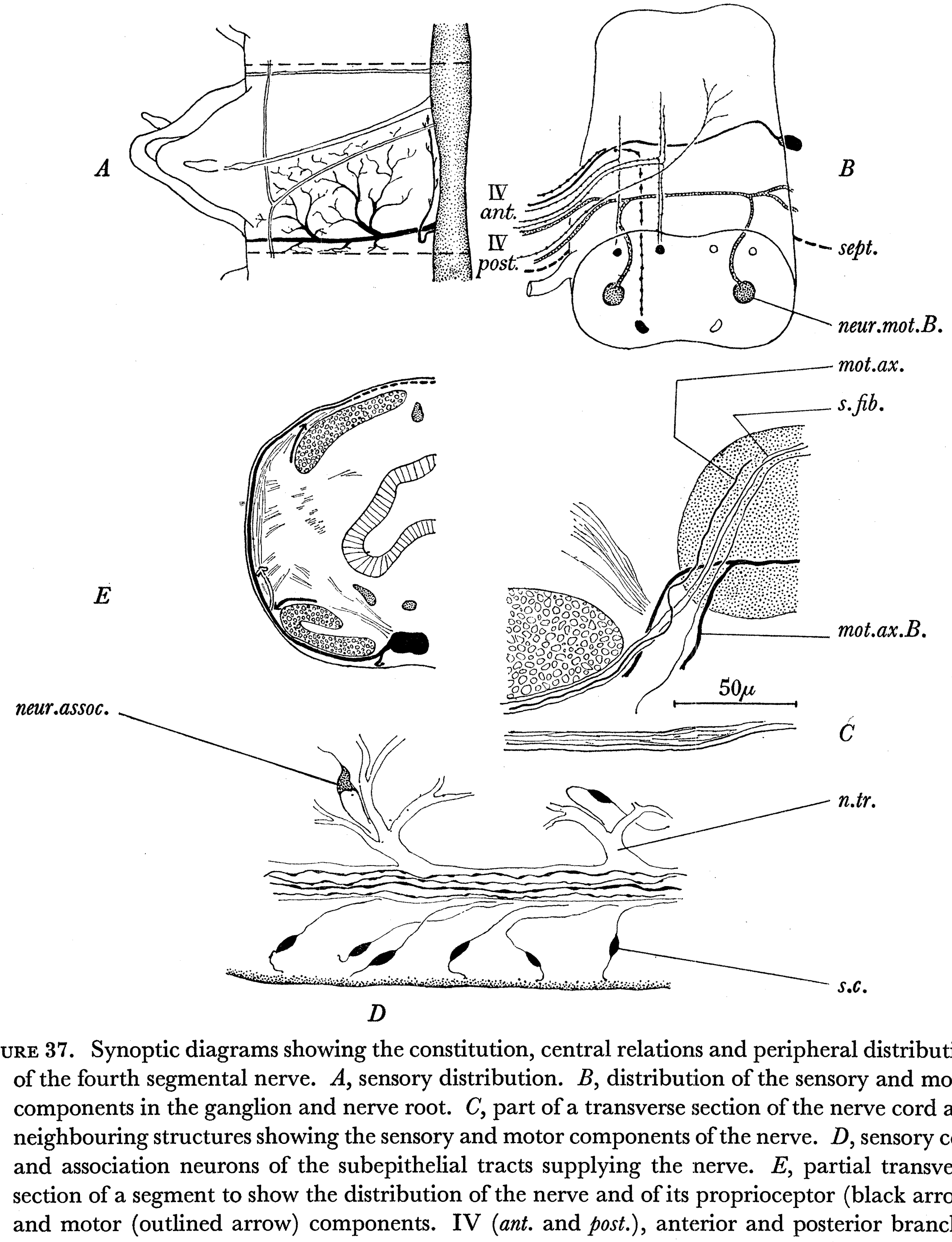

FIGURE 37. Synoptic diagrams showing the constitution, central relations and peripheral distribution of the fourth segmental nerve. *A*, sensory distribution. *B*, distribution of the sensory and motor components in the ganglion and nerve root. *C*, part of a transverse section of the nerve cord and neighbouring structures showing the sensory and motor components of the nerve. *D*, sensory cells and association neurons of the subepithelial tracts supplying the nerve. *E*, partial transverse section of a segment to show the distribution of the nerve and of its proprioceptor (black arrow) and motor (outlined arrow) components. IV (*ant.* and *post.*), anterior and posterior branches of the fourth segmental nerve; *mot.ax.* motor axon; *mot.ax.B.* ventral motor axon (Hamaker's 'B fibre'); *n.tr.* nerve tract of the subepithelial plexus; *neur.assoc.* association neuron; *neur.mot.B.* motor neuron; *s.c.* sensory cell; *s.fib.* sensory fibre; *sept.* intersegmental septum.

nerves (figures 34*B*, 37*B*), connected as they are, on the one hand (I), with the dorso-lateral internuncial tracts of the cord and, on the other (IV), with the dorso-lateral and dorso-medial tracts, and the occurrence in nerve IV of ventrally connected sensory and motor fibres, neither of which are present in the first nerve, that the fourth nerve may have the greater variety of peripheral connexions. This supposition receives some support from the greater number of its constituent fibres. In some degree the larger fibre number of nerve IV is to be related to the larger area of its sensory innervation and, indeed, the expansion of the nerve in the anterior segments where the number of exteroceptor cells is greatest bears this out. The fact remains, however, that there are features in the composition of nerve IV less obviously related to the number of its afferent and efferent fibres than to a presumed greater variety of nerve supply.

It has been shown that nerve II is concerned essentially with the innervation of the parapodium and that nerve III is first and foremost a proprioceptive nerve. The muscles mainly concerned with locomotory activity, the longitudinal muscles of the body wall and the protractors and retractors of the parapodium, are part of the body segment proper which is supplied on the afferent side almost entirely by nerves I and IV. By analogy with the parapodial innervation it is not unjustifiable to suppose that nerves I and IV innervate the muscles associated with the region of their afferent supply and that, of the nerves, IV, with the more extensive and varied motor constitution, is the more important in the development of co-ordinated movements. The manner in which the segmental nerves are peripherally interconnected supports this view (p. 191).

The anatomy of nerve IV in its peripheral course is summarily illustrated in figures 37*C*, *D* and *E*. In (*C*) sensory fibres (*s.fib.*) and motor axons of dorsal (*mot.ax.*) and ventral (*mot.ax.B.*) emergence are seen entering and leaving the ganglion. They come together peripherally in the main nerve tract which lies below the ventral longitudinal muscle. Laterally (figure 37*E*) the nerve receives proprioceptor fibres (black arrows) from the longitudinal muscle and gives rise to motor fibres (outlined arrows) terminating in the oblique muscles. Dorsally the nerve receives exteroceptor fibres from the upper surface of the integument and proprioceptor fibres from the dorsal longitudinal muscle. The nerve throughout its course is connected (figure 37*D*) with sensory cells (*s.c.*) having centrifugal fibres of direct entry or connected with the nerve through association tracts (*n.tr.*) of the subepithelial plexus.

THE PERIPHERAL INTERCONNEXIONS OF THE SEGMENTAL NERVES

Interconnexion between the fibres of the segmental nerves and their terminal sensory and motor fibres has been seen to be effected through relay neurons of an association or internuncial character. The peripheral connexions which are now to be described are of a different kind in that they connect one segmental nerve with another. They are found (figure 38*A*) in two places, namely, between the parapodial ganglion and the fourth nerve (*neur.intern. 2–4*) and between the lateral nerve (*n.lat.*) and the fourth nerve (*neur.intern. 3–4*).

In respect of the latter (figure 38*C*, *neur.intern. 3–4*) two or three neurons are situated in the angle of the two nerves where they cross at the lateral border of the longitudinal muscle a little in front of the posterior border of the septum of the segment. The neurons are bipolar or multipolar, and their fibres on the two sides of the cell body effect the connexion. It might be argued that these internuncial neurons belong to the same category as the subepithelial association neurons, but this would deny the different character of their connexions. The distinction between the two series is, moreover, the more apparent in the instance of the nerve II–IV connexion (figure 38*B*, *neur.intern.2–4*). Here the single interconnecting neuron is bipolar with dendritic processes extending into the parapodial ganglion (*gang.parap.*) from the short entry fibre and with a long axon trailing in its oblique passage mesially and posteriorly to the root of the fourth nerve which it enters. In this case it is apparent from the form of the neuron that excitation is transmitted from the parapodial ganglion to the fourth nerve, and it is possible that the neurons between nerves III and IV conduct in a like direction. If this be so, the connexions would serve to transmit information to the fourth nerve on the one hand (*neur.intern.2–4*) relating to the postures of the parapodia and, on the other (*neur.intern.3–4*), to the state of flexure of the body-wall muscles. Since nerve I is never connected in this way with other segmental nerves the observed pattern of peripheral interconnexion of the remaining nerves adds

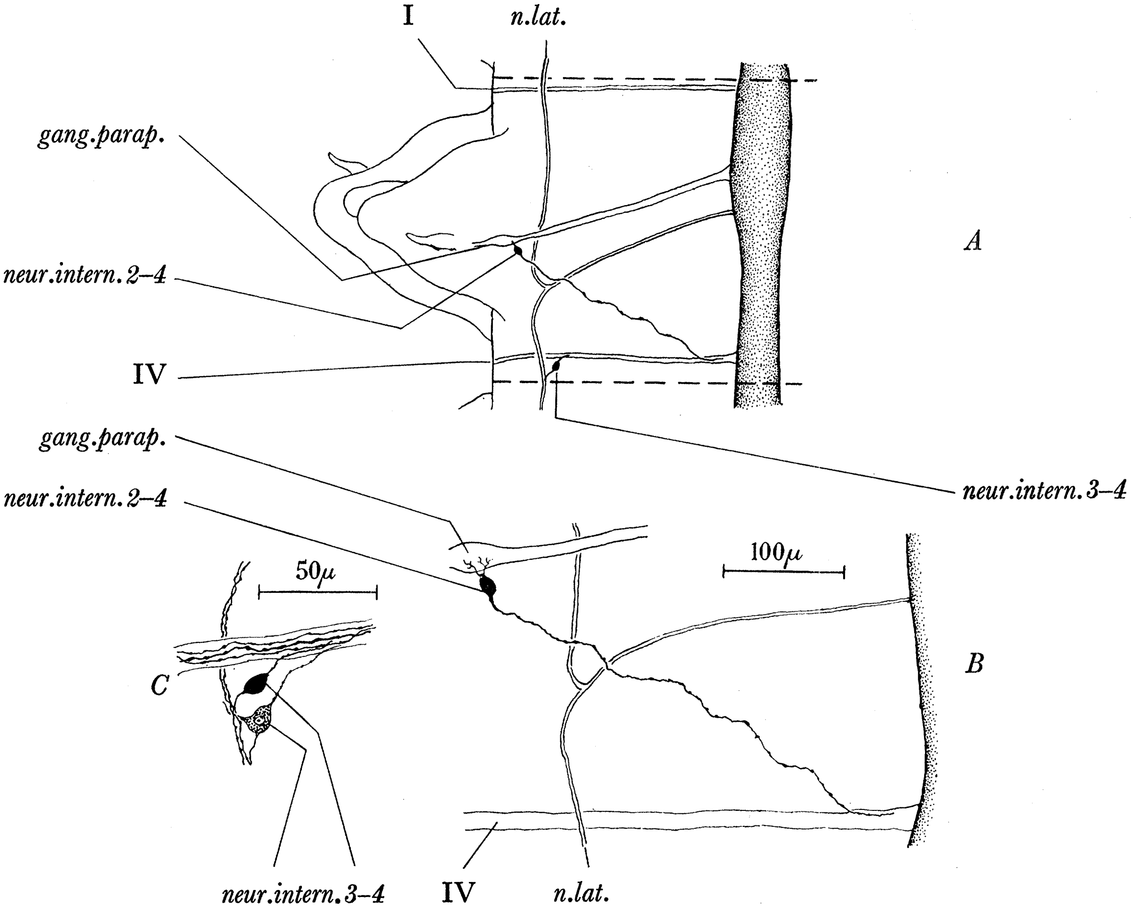

FIGURE 38. The peripheral internuncial connexions between the nerves II and IV and III and IV. *A*, general plan of the interconnexions. *B*, details of the II–IV connexion. *C*, details of the III–IV connexion. I and IV, the first and fourth segmental nerves; *gang.parap.* parapodial ganglion; *n.lat.* lateral nerve; *neur.intern.* (*2–4* and *3–4*), internuncial connexions between nerves II and IV and III and IV respectively.

weight to the supposition advanced in the previous section (p. 190) that nerve IV is primarily responsible for the innervation of the longitudinal muscles and consequently for the development and co-ordination of the locomotory body flexures.

Conclusions

In ending this account of the nervous organization of the nereid body segment it is proposed to re-state some of the conclusions reached concerning the nature and functional significance of the observed central and peripheral patterns of neuron interconnexion, and to speculate on the probable significance of other less well-attested aspects of their nervous anatomy. Figure 39 illustrates the features which will be referred to.

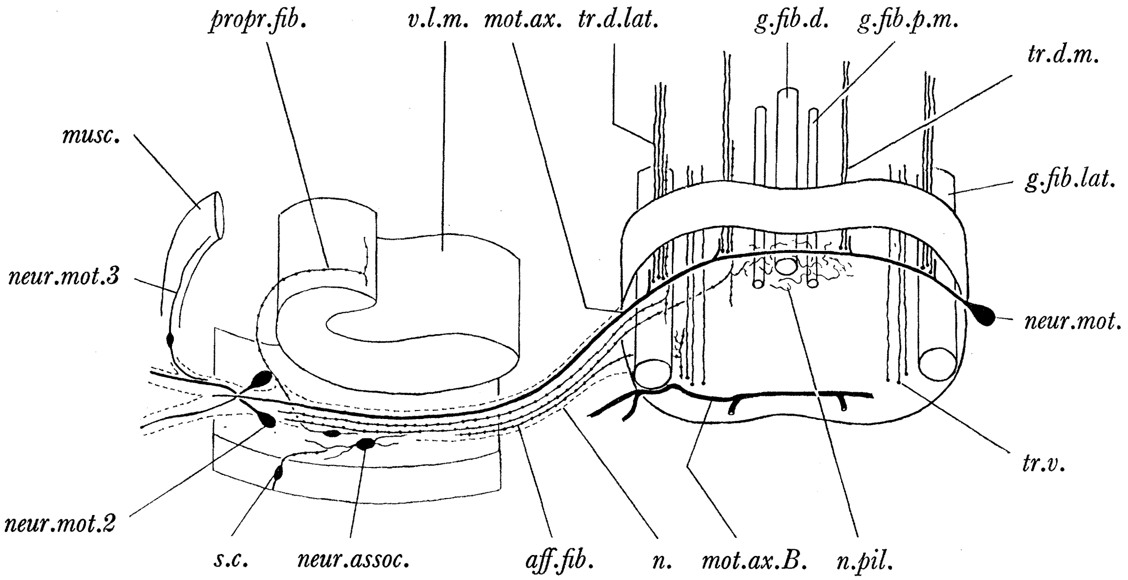

Figure 39. Diagram to show in a generalized form the central and peripheral interneural connexions of the component neurons of a segmental nerve. For further explanation see the text. *aff.fib.* afferent fibre; *g.fib.d.* dorsal giant-fibre; *g.fib.lat.* lateral giant-fibre; *g.fib.p.m.* paramedial giant-fibre; *mot.ax.* motor axon of dorsal emergence; *mot.ax.B.* motor axon of ventral emergence; *musc.* muscle; *n.* segmental nerve; *n.pil.* neuropile; *neur.assoc.* association neuron of the sub-epithelial plexus; *neur.mot.*, *neur.mot.* (*2* and *3*), motor neurons of the first, second and third order; *propr.fib.* proprioceptor fibre; *s.c.* sensory cell; *tr.d.lat.* dorso-lateral fine-fibre longitudinal internuncial tract; *tr.d.m.* dorso-medial tract; *tr.v.* ventral tract; *v.l.m.* ventral longitudinal muscle.

That all four pairs of segmental nerves of nereids are 'mixed' can hardly be doubted. In each nerve (*n.*) there are one or more axons (*mot.ax.*) originating as unipolar extensions of cell bodies (*neur.mot.*) lodged in the cell cortex, and there are fibres (*aff.fib.*) with free central endings, the cell bodies of which, when they can be identified, are lodged in the basement membrane of the integument peripheral to the cord.

Afferent fibres, on entering the cord, connect with one or other of six tracts of a central internuncial character each made up of synaptically connected longitudinal fine-fibres extending the length of the cord. The tracts are symmetrically disposed about the mid-line of the cord, two, the dorso-lateral (*tr.d.lat.*) and dorso-medial (*tr.d.m.*) tracts, in the upper half of the neuropile and, one, the ventral tract (*tr.v.*), in the lower half. The incoming afferent fibres make their internuncial connexion on the side of entry and are never contralaterally connected; afferent fibres of nerves I and II enter the dorso-lateral tract, those of nerve III the dorso-medial, and the fibres of nerve IV contribute to both. Since, as has been shown, nerves I and II are predominantly concerned with the transmission of exteroceptive afferent excitation, III is in the main proprioceptive and IV has both an exteroceptor and proprioceptor supply, there is some indication of a possible localization of functional areas within the ganglion with the suggestion, in this instance, that the dorso-lateral tracts may lie within an exteroceptive and the dorso-medial tracts within a proprioceptive column of the dorsal neuropile.

Two nerves (II and IV) contain afferent fibres which enter the ventral longitudinal fine-fibre internuncial tract (*tr.v.*) and run along its outer side. In this position they are closely adjacent to the lateral giant-fibre and their fine collateral processes may have endings on the fibre. The direct connexion is, however, by no means certain.

There are five giant-fibres in the nereid cord, two laterals (*g.fib.lat.*), two paramedials (*g.fib.p.m.*) and one dorsal fibre (*g.fib.d.*). The lateral fibres are of segmental origin, linked by macrosynapses into a single conducting system, the dorsal fibre is continuous and the paramedials overlap two segments and are segmentally repeated throughout the body. The last-named fibres have a double cross-over, but the giant-fibres are not otherwise connected one with another. All are strictly internuncial in that they are confined to the cord. None of the giant-fibres (with the possible exception of the lateral fibres) has a direct connexion with incoming afferent fibres and none (again with the exception of the lateral fibre-motor axon *B* connexion in nerve IV) has a direct connexion with the efferent fibres of the segmental nerves. The giant-fibres are, however, situated in regions of the cord permeated by a dense fibrillar network (*n.pil.*) derived from the terminal branches of short-axon internuncials which, one may suppose, mediate the transfer of excitation from the afferent endings to the giant-fibres and from the giant-fibres to the motor axons. The fact that nervous connexions have not been demonstrated suggests that they are of a more diffuse kind than those which link the dorsal fine-fibre internuncial systems (*tr.d.lat.*, *tr.d.m.*) with the afferent and efferent nerve components. In this latter instance, as will be seen from the figure, the afferent fibres run directly into the tracts which, on the efferent side, connect in an equally determinate manner with the collateral branches of the dorsal commissural motor axons (*mot.ax.*). One sees in this afferent fibre—fine-fibre internuncial—motor axon connexion as clear a representation of a nervous arc as could possibly be provided, the arcs being, in addition, linked segment by segment through the longitudinal tracts.

In most families of polychaetes giant-fibres are present in one form or another and in varying number. But the fact that syllids and phyllodocids, among other groups, lack them (Nicol 1948) and are yet able to execute undulatory and other types of ambulatory movement is a strong indication that it is the fine-fibre internuncial system which is responsible both in polychaetes possessing giant-fibres and in those without them, for the conduction of excitation necessary for the genesis and maintenance of locomotory movement. The direct fibre-to-fibre linkages of the fine-fibre arcs allow, one may presume, locomotory patterns of muscle contraction and relaxation to develop in response to normal and unexceptional levels of environmental stimulation. There is the possibility, on the other hand, if the more indeterminate character of the nervous connexion implies a greater number of intermediate linkages, that the reflexes involving the internuncial pathways of the dorsal and paramedial giant-fibres would only come into operation under more intensive stimulation. Where, however, as in the instance of the lateral giant-fibres, there are indications of a more direct contact between the sensory endings and the internuncial system (in nerves II and IV) a somewhat lower threshold would be anticipated. This is, in fact, what Bullock (1945, 1948) found in his experimental analysis of the conduction properties of the giant-fibres of *N. virens*. The lateral fibres in this polychaete have a lower threshold than the dorsal and paramedial fibres.

The possible significance of the limitation of afferent fibres of ventral entry to nerves II and IV calls for brief comment. The two nerves, as has been seen, draw upon sensory fields covering the greater part of the integument, nerves II from the surfaces of the parapodia and nerves IV from the larger part of the ventral and from an undefined area of the dorsal integument. It would not be expected that nerves III would connect in this way since the giant-fibres respond to exteroceptive rather than to proprioceptive stimulation, though the exclusion of nerves I from the opportunity of effecting direct sensory transfer to the lateral giant-fibres is less readily explained.

Bullock (1945, 1948) shows that the lateral fibres respond to adequate stimulation of any part of the skin, the dorsal fibre to excitation originating in the anterior quarter of the body and the paramedial fibres to stimulation of segments in the posterior three-quarters of the animal. All the fibres conduct in either direction. It is a little difficult to equate the two attributes of localization of the sensory field and conduction direction with the anatomy of the system. There are no apparent fundamental differences in the pattern of central connexion of the afferent fibres in the different regions of the body, though there are indications, from the varying size of nerve IV, that the sensory connexions may vary in the anterior and posterior segments. In any event the observed differences in the number of sensory endings on the dorsal and ventral surfaces and other less striking variations in other parts of the integument would suggest that a more detailed regional survey of the effects of localized stimuli on the responses of the giant-fibres would assist the further analysis of the nature of the afferent connexions.

Although the giant-fibres of nereids are strictly internuncial, in some polychaetes such as *Myxicola infundibulum* and *M. aesthetica* (Nicol 1947, 1948; Nicol & Young 1946) they extend from the cord to innervate directly the muscles responsible for rapid contraction of the body. This is clearly an adaptation to the tubicolous habit where rapid withdrawal into the tube may be necessary to avoid injury. In nereids the efferent tract which appears, on neurological grounds, to be most suited for the evocation of rapid responses is to be found in nerve IV, where the motor fibres of ventral emergence (figure 39, *mot.ax.B.*) synapse with the lateral giant-fibres on the two sides of the segment. Since nerve IV is, in all probability, mainly responsible for the innervation of the longitudinal muscles, rapid shortening of the body in response to noxious stimuli may perhaps be attributed to the operation of the ventral motor tracts of these nerves.

The nerves of nereids are peripherally so constituted as perhaps to permit of the short-circuiting of excitation between receptor and effector systems without the intervention of the central nervous system. The probable nature of the peripheral connexions is shown diagrammatically on the left-hand side of figure 39. Exteroceptive sensory cells (*s.c.*) connect up with segmental nerves directly or through association neurons (*neur.assoc.*). Proprioceptor fibres (*propr.fib.*) from the longitudinal muscles connect with the tracts directly. The segmental nerves contain afferent and efferent fibres at their roots, and it is presumed that the fibres continue to the periphery although their intertwining makes it impossible to trace them with certainty. Where a nerve divides multiplication of motor fibres is effected through intercalary neurons (*neur.mot.2*). Motor neurons of the third order (*neur.mot.3*) are seen occasionally to leave the main tract and to innervate the muscles (*musc.*). Not all of these features are visible in all the segmental nerves, and the evidence bearing on the character of the ultimate motor supply is, in particular, too fragmentary to be well founded. It can, however, be asserted with some confidence that a considerable measure of peripherally regulated response is, on the anatomical evidence, possible and to be expected. Further experimental analysis is needed to elucidate the nature and distribution of the peripheral pathways and of the kinds of movement which can be locally elicited. On the anatomical side more information is especially needed on the motor distribution of the segmental nerves.

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