

Certain Histological and Anatomical Features of the Central Nervous System of a Large Indian Spider, *Poecilotheria*

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SYNOPSIS. Some of the finer details of the anatomical organization of the subesophageal ganglion of the spider, *Poecilotheria* sp. were studied in Palmgren silver-stained sections at the light microscopic level. The ganglionic mass is differentiated into a central fibrous core and a peripheral layered mass of cellular cortex. The neuropile is heterogeneous, consisting of both diffuse and glomerular types, and is considered the primary place for integration. The dorsal region is motor, and the ventral is sensory. The processes of motor cells and endings of sensory neurons are restricted mostly to a single ganglion. Each large motor neuron possesses a long stem-process, short and highly branched dendritic ramifications, and a smooth, unbranched axon. Larger interneurons are more diversified, and extend from one to several ganglia. These are of ascending or descending or even decussating types. Smaller interneurons are mostly restricted to one or a few ganglia. On the basis of this organization the probable synaptic junctions between neurons are discussed.

The earliest work on the anatomy of the central nervous system of spiders was that of Saint-Rémy (1890) who described different types of cells, nerve centers of the brain, and the subesophageal ganglion. Hanström (1919, 1921, 1928, and 1936) described the brain of different groups of araneids with particular reference to the globuli cells, mushroom bodies, optic centers, and central body, and included a very brief account of the subesophageal ganglion.

Babu (1965) described the comparative anatomy of the central nervous system in arachnids, and gave an account of the gross morphological and histological aspects of the central nervous system of *Poecilotheria*. Attention was paid to the fiber tracts, groups of cells, and their pattern of distribution in the cephalothoracic mass. The following observations are supplementary to these, giving finer details of organization of the subesophageal mass observed at the light microscopic level.

One of the locally available large species of spider, *Poecilotheria* sp. (Theraphosidae) was used. The nerve mass was fixed in Bouin's fluid, and paraffin serial sections of 20 to 40 μ thickness were cut in the three important planes. The serial sections were stained by the reduced silver method of Palmgren (1948).

GENERAL FEATURES OF THE CEPHALOTHORACIC NERVE MASS

In the sedentary spider, *Poecilotheria*, the central nervous system is represented by a single large fused cephalothoracic nerve mass at the anterior end of the animal (Babu, 1965). This nerve mass can be divided into a dorsally located supra-esophageal ganglion or the brain, and a ventrally placed subesophageal mass. The latter includes a pair of large pedipalpal and four pairs of leg ganglionic masses and 11 pairs of small abdominal ganglia. The central nervous system conforms to the typical arthropod plan in that it consists of a cellular cortex surrounding a highly complex neuropile (Bullock and Horridge, 1965). In the ganglionic mass the fibrous matter occupies 50-60% of the total area, whereas the cellular rind occupies 25-35%, and the remaining spaces are occupied by the glial tissue.

NEUROPILE

The central core of a highly complex tangled mass or meshwork of nerve processes presents two aspects—tracts of fibers and neuropile. The core is completely devoid of nerve cell bodies and is formed from the processes of motor and interneurons and terminal arborizations of sensory

neurons. None of these processes has been seen to enter the ventral cellular cortex as in other invertebrates. Tracts consist of parallel fibers in passage and are thus devoid of synaptic endings (Bullock and Horridge, 1965). The neuropile, which can be distinguished by its finer and more tangled texture, thus becomes the most important region, because this is the only known place of neuronal contacts. Hence it has acquired functional significance as the primary place for the process of integration (Bullock and Horridge, 1965).

As reported for certain other arthropods (Maynard, 1962), in *Poecilotheria* two types of neuropile can be distinguished, on the basis of gross fiber configuration—the diffuse and the glomerular.

Diffuse neuropile. This predominates over the other type of neuropile and presents the classical picture of “tangled confusion” (Horridge, 1960). It includes the processes of large and small motor and interneurons and axon terminations of sensory neurons. Fibers occur separately and also combined as tracts. The processes of central neurons are quite extensively branched and spread to varying degrees throughout the neuropile. Even though the neuropile gives the appearance of a complex mass of fibers, careful observations reveal that each neuron tends to have its domain of arborizations. Synaptic junctions, however, cannot be recognized easily with the light microscope.

In the neuropile the fibers cover a wide range of sizes. The largest of these are the stem processes, proximal regions of dendrites, and the axons. A representative figure for their size is 8μ , but the smallest are beyond the resolution of a light microscope. Careful tracing of sensory neurons shows that they end predominantly in the ventral or central region of the neuropile. This region consists mainly of small fibers and densely staining areas called sensory association centers (Babu, 1965). The dorsal region, in contrast, consists mostly of larger fibers which include the dendritic and axonal processes of motor and larger interneurons. The densely staining areas

are less conspicuous, and only a few sensory fibers terminate in these regions. Such a differentiation of the neuropile into dorsal motor and ventral sensory areas was also reported in crustaceans and insects (Bullock and Horridge, 1965).

The neuropile is traversed by small and large commissural and longitudinal tracts with fibers of different diameters. The formation of these transverse and longitudinal tracts by fibers arising from discrete groups of nerve cells and their pattern of distribution were reported earlier (Babu, 1965). In the neuropile the course of single large axons of the interneuronal type can be followed. These axons are smooth and unbranched, some of them running along the entire length of the ganglion without branching. The axonal terminations are simple, ending either in a single ganglion, or distributing branches over a number of ganglia. At its terminal end an axon normally splits repeatedly and the branches occur at shorter and shorter intervals towards the end. The fine branches finally become lost in the neuropile. Although the endings are fine, extensive, and intricate, they are not highly specialized. Normally, the terminations of most of the sensory fibers are confined to one or a few ganglia. But the terminations of a larger interneuron are generally more extensive.

Structured neuropile. The structured neuropile occurs mostly within the sensory association areas and is thus limited mostly to the ventral region. These regions of neuropile show irregularly shaped, dense, fine-fibered masses (Fig. 1) and occur prominently in the leg and pedipalpal ganglia. Such tight, knot-like clusters of fibers are called glomeruli. In spiders these are formed from the terminations of sensory fibers (Fig. 2, sn) and dendritic endings of small (type B) neurons (Fig. 2, in). The number of these fibers entering each glomerular mass cannot be determined. But the type B cells, which are normally arranged in groups, give off their processes in bundles that terminate or pass through the glomeruli. Thus, it seems a large number of central neurons contribute to the

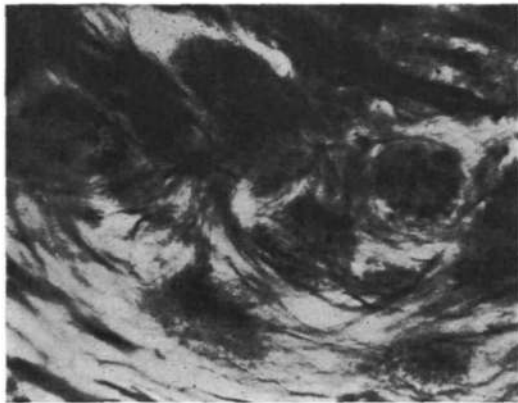


FIG. 1. Glomerular neuropile.

formation of each glomerulus. A few axonic endings of larger interneurons (Fig. 2, IN) can also be seen terminating in several of these glomeruli in a ganglion. Very few dendritic endings of motor neurons (type D) reach these glomerular masses. The type B cells with their dendrites in glomeruli apparently act as interneurons between motor and sensory neurons (Fig. 7).

HISTOLOGY

For the different types of cells and their pattern of distribution in the subesophageal ganglion, see Babu (1965).

Neurofibrils. Neurofibrils, now accepted as important components of a neuron, occur in different groups of invertebrate animals (Bullock and Horridge, 1965). In

FIG. 2

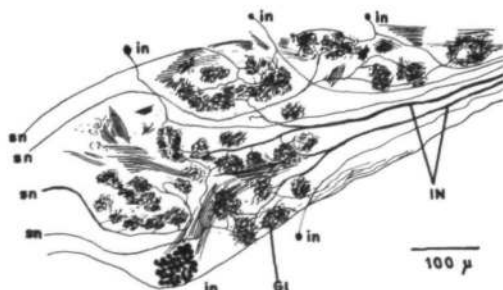


FIG. 2. Ventral sensory area of a leg ganglion showing small type interneurons and glomerular neuropile. Gl, glomeruli; in, small (type B) interneurons; IN, large (type D) interneurons; sn, sensory neurons.

spiders, they are particularly evident in the basal parts of the stem processes of larger motor and interneurons. They are fine fibrillar structures in the axoplasm and run along the longitudinal axis of the neurite (Fig. 3). Under the light microscope,

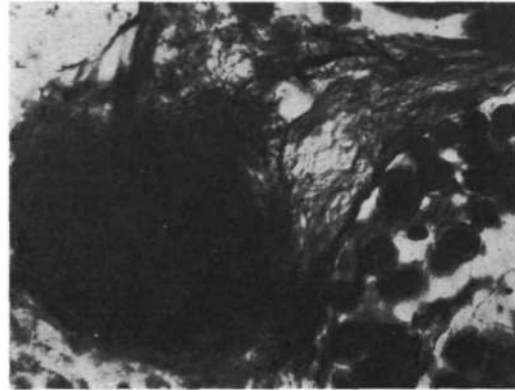


FIG. 3. Type D cell showing neurofibrillae in the axon hillock.

because of their small diameter and large number, it is not possible either to count them or to determine their diameter. As in the cockroach (Wigglesworth, 1960) and scorpions (Babu and Venkatachari, 1966), these fibrils fan out and form a dense mass around the nucleus.

Motor neurons. It is easy to follow the course of the axons and dendritic arborizations of large neurons compared to those of smaller cells. Motor neurons are identified by the central cell body and by the exit of the axon into a peripheral nerve. Each cell typically gives off a single, large, stem process (Fig. 4, St) of 8 μ diameter. This process of some of the ipsilateral motor neurons is very long (800 μ) and it ascends from the ventral cellular zone to the dorsal neuropile. In the dorsal neuropile the single process divides into two nearly equal halves. One of these is short and repeatedly branches, ending within the ipsilateral dorsal neuropile. Hence, it is called a dendrite (Fig. 4, Dn). Most of these dendritic ramifications lie in the regions of termination of similar motor neurons, presumably ending mostly in relation to interneurons. The second process is long, smooth, and unbranched and

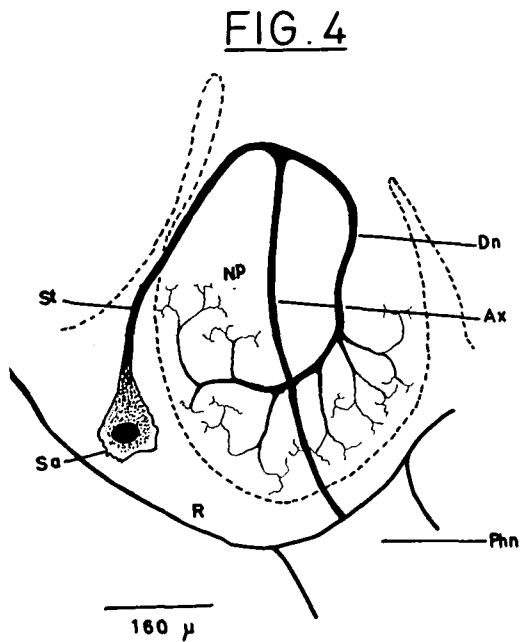


FIG. 4. A typical large type motor neuron with its processes. The dashed line marks the boundary of the third leg ganglion. Ax, axon; Dn, Dendrite; NP, neuropile; Phn, Peripheral nerve; R, Rind (cortex); Sa, Soma; St, Stem-process.

enters the peripheral nerve; it is called an axon (Fig. 4, Ax). Each of the leg nerves is supplied by 50-60 such large motor neurons whereas the pedipalpal nerve is composed of 70-80 neurons.

From serial sections cut in three planes, four types of motor neurons could be identified. In the first type (Fig. 5, Mt1), the dendritic ramifications and the exit of its axon are restricted to the ipsilateral ganglion. A similar type of ipsilateral motor neurons was reported in the lobster (Allen, 1894, 1896); *Carcinus* (Bethe, 1897); dragon fly (Zawarzin, 1924); *Vejovis* and *Heterometrus* (Hanström, 1923; Babu and Venkatachari, 1966) and *Epeira* (Hanström, 1919). In the second type of motor neuron (Fig. 5, Mt2) the axon exits by the opposite (contralateral) leg nerve (of the same segment), with its dendritic endings terminating in the ipsilateral leg ganglion. This type of motor neuron is also found in *Limulus* (Hanström, 1926), *Epeira* (Hanström, 1919), and *Heterometrus*

(Babu and Venkatachari, 1966). In *Poecilotheria* the ipsilateral motor neurons are more common than the contralateral ones.

In the third type (Fig. 5, Mt3), the dendrites terminate in a nearby ganglion, whereas the axon emerges by the ipsilateral anterior or posterior leg nerve. This probably corresponds to neuron 8 described by Hanström (1923) in the subesophageal ganglion of *Vejovis*. In *Poecilotheria*, a fourth type (Fig. 5, Mt4) of neuron not reported in *Epeira* (Hanström, 1919) was also identified. In all of the three types described earlier, the dendritic terminations are confined to a single ganglionic mass, but in this fourth type the dendrites terminate in two ganglionic masses and the axon enters one of the two leg nerves. Motor neuron 5 entering the second leg nerves of the scorpion (Hanström, 1923) may be of this type. Thus, the ramifications of motor neurons tend to be limited mostly to one and occasionally to two ganglia.

Interneurons: The bulk of the neuropile

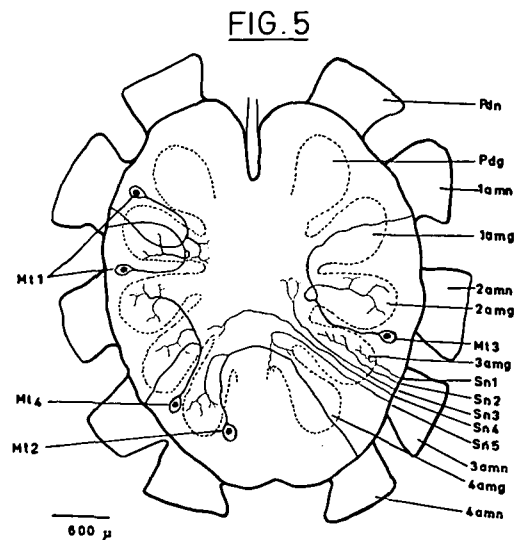


FIG. 5. Horizontal section of the subesophageal ganglion showing the pattern of distribution of the processes of motor and sensory neurons. 1-4amg, four pairs of leg ganglia; 1-4amn, four pairs of leg nerves; Mt1-4, types of motor neurons; Pdg, pedipalpal ganglion; Pdn, pedipalpal nerve; Sn1-5, types of sensory neurons.

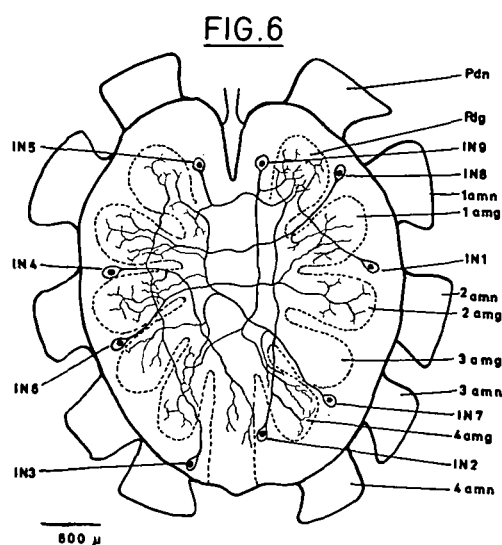


FIG. 6. Selected interneurons of the subesophageal ganglion. 1-4amg, four pairs of leg ganglia; 1-4amn, four pairs of leg nerves; IN1-9, type D interneurons; Pdg, pedipalpal ganglion; Pdn, pedipalpal nerve.

is composed of the processes of interneurons of type B and type D cells. Type D neurons are typically of a unipolar type described earlier for the motor neurons and are abundant in the dorsal neuropile. Unlike motor neurons, several types of interneurons are found with limited or extensive axonic ramifications. The dendritic endings are normally confined to a single ganglion as in motor neurons. Such widespread interneurons are common in most of the arthropods (Bullock and Horridge, 1965). Figures 6 and 7 show some of the selected interneuronal types. The cell bodies of these larger neurons are amidst the other larger motor neurons within the cortex. The type B cells, arranged in groups at different regions of the cortex contribute their processes mainly to the neuropile of the adjacent ganglia or to the central neuropile. The majority of the fibers in the longitudinal tracts consist of either ascending, descending, or decussating intersegmental neurons. In the commissures, motor and sensory neurons are predominantly present.

The larger neurons traced are mostly of an interganglionic type (Fig. 6). The den-

dritic endings are limited to the nearby ganglion, whereas the axonic terminations end either in one or several ipsilateral or contralateral ganglia. The neurons IN1-4, are of ipsilateral type, relaying information between one to five ganglia. One of these (IN3) interconnects the four leg and pedipalpal ganglia and enables these appendages to receive information simultaneously. Such widely branching but descending types of neurons were reported for the fused ventral ganglionic mass of *Carcinus* (Bethe, 1897), *Vejovis* (Hanström, 1923), and *Limulus* (Hanström, 1926). The axon of neuron IN2, acts as a through-ascending fiber, relaying information from the fourth leg to the pedipalpal center.

Three types of contralateral neurons (IN5-8) are represented (Fig. 6). One of these (IN5) interconnects the opposite pedipalpal and another (IN8) the corresponding contralateral leg ganglion. Similar local and contralateral interneurons were described in the dragon fly (Zawarzin, 1924). The decussating neuron IN7 is like IN3 in its interconnection, but its cell body is contralaterally placed. The neuron IN9 is different from others, since it terminates in both of the fourth leg ganglia.

The smaller type B neurons, in contrast to the larger cells, are mostly intraganglionic in their distribution (Fig. 7). These cells, which are usually arranged in masses, give off their processes in packed bundles. These appear to act as interneurons between the ventral sensory association masses and the dorsal neuropile where the dendritic branches of motor neurons terminate. The neurons in1-4 are of this ipsilateral type, and the neuron in5 is a contralateral one. Some of these (in6 and in7) are local, interconnecting the different regions of the sensory association mass.

SENSORY FIBERS

Peripheral axons enter a ganglion primarily from the ventral region as in insects (Zawarzin, 1924) and scorpions (Babu, 1965). These are thin fibers, and the majority of them end in different regions of

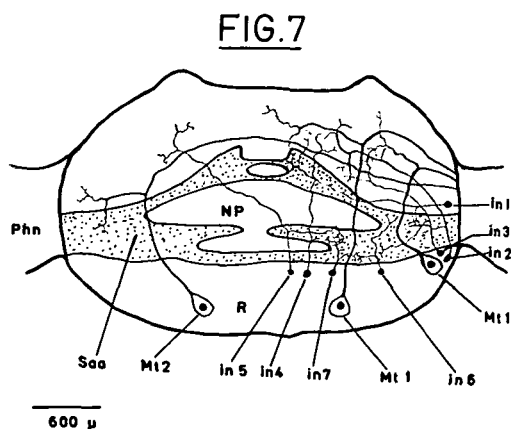


FIG. 7. Transverse section of the subesophageal ganglion showing the regional distribution of selected neurons. in1-7, type B interneurons; Mt1, ipsilateral motor neuron; Mt2, contralateral motor neuron; NP, neuropile; Phn, peripheral nerve; R, rind (cortex), Saa, sensory association area.

the ipsilateral ganglion (Fig. 5) in the ventral neuropile (Sn1-2). Axons ending in the opposite ganglia (Sn4) or in the adjacent anterior (Sn3) or posterior (Sn5) ganglia are also present. Sensory endings of similar type were reported in *Carcinus* (Bethe, 1897) dragon fly (Zawarzin, 1924), *Vejovis* (Hanström, 1923), and *Heterometrus* (Babu and Venkatachari, 1966).

CONCLUSIONS

A topic of fundamental interest in the nervous system is the synaptic relation between neurons. The neuronal arrangement presented permits visualizing a three-dimensional relationship of interconnections for the large ipsilateral segmental motor neurons. The dendritic branches interlace either directly or indirectly with afferent and internuncial neuropile. Termination of some of the ipsilateral and contralateral sensory neurons in the dorsal neuropile may directly excite the motor neurons and thus form a monosynaptic pathway. Electrophysiological tracing of these afferent and efferent connections could be done fruitfully. Information from the ventral sensory area appears to be

mostly relayed to the motor neuropile through the smaller interneurons.

Information from adjacent or distant ipsilateral or contralateral ganglia is relayed through at least one large interneuron. The axonal terminations of several such neurons end within the dendritic area of motor neurons. A few of these large intersegmental neurons also end within the ventral sensory neuropile whence information to motor neurons is perhaps relayed through the smaller interneurons.

Even though the subesophageal ganglion is a compound mass, anatomically the individual ganglia and large single neurons associated with it can be located without difficulty. The motor and interneurons can be easily reached from the ventral side of the animal for intracellular recordings. From the large peripheral nerves it is also possible to impale single motor axons, as was done in our laboratory on the scorpion (Venkatachari, 1968). Thus, the neuroanatomy is favorable for electrophysiological study.

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