

Evolutionary trends in invertebrate ganglionic structure

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Abstract:

Early Bilateria developed the basic characteristics of ganglionic organization. Features such as the divergence of longitudinal axon bundles into functionally unique tracts, the separation of centers for motor pattern generation and exteroceptive sensory integration, the segregation of limb motor centers to lateral neuropils, and the genesis of glomerular microarchitecture occur in representatives from many protostome phyla. Ancestors of the protostome and deuterostome lineages may have evolved these features of neuronal organization independently but parsimony would argue in favor of a conservative evolution, whereby phylogenetically early events formed the basis for the complex neural architectonics displayed by extant Chordata.

Key words: axon tracts / nervous system / neuro-anatomy / neuropil / phylogeny

Article:

The basic organizational features of invertebrate nervous systems were well and overwhelmingly reviewed in 1965 by Bullock and Horridge.¹ Since then, the introduction of intracellular marking and axonal filling techniques have allowed researchers working on a variety of organisms to examine ganglionic architecture from a functional viewpoint. Early Bilateria (bilaterally symmetrical animals, including all invertebrate phyla except for Cnidaria and Ctenophora)² seem to have developed the basic characteristics of ganglionic structure, that is, the condensation of neurons and their processes into discrete structures (ganglia) linked by axon tracts (connectives).³ Among the protostomes, this organization has reached peaks of expression in the Arthropoda and Mollusca.

Much of our understanding of ganglionic functional organization has emerged from studies of sensory integration and motor pattern generation which have clearly demonstrated that invertebrate ganglia are complex processing centers. In the annelids, molluscs and arthropods, patterned motor outputs involved in activities such as swimming,⁴⁻⁶ feeding^{7,8} and respiration^{9,10} are generated within individual ganglia and can be expressed, to various degrees, independently of cerebral input. In the arthropods, several types of motor actions are known to arise from the interplay of functionally distinctive ganglionic subregions.^{5,11-13} Complex behaviors, such as prey, mate and habitat selection, are undoubtedly regulated by descending cerebral input.

Ganglionic architecture

In general, neuronal cell bodies surround the ganglionic core, sending their main neurites centripetally through vertical and horizontal axon tracts to make up one or more neuropils, which are synaptic fields of densely packed tiny neuronal branches (Figure 1). Commissures carry neuronal branches between the left and right sides of each ganglion; connectives, extensions of the horizontal ganglionic tracts, carry intersegmental axons which link ganglia along the nerve cord.¹ Ganglia are significantly less complex in the Platyhelminthes (flatworms) than in the more advanced phyla.^{14,15} The brain, which is the only ganglion in members of this phylum, contains areas of neuropil but longitudinal axons do not seem to be neatly bundled away from neuropil areas as they are in molluscs and arthropods. Many neuronal cell bodies are scattered within the synaptic neuropil, a feature that some authors believe to have been retained by primitive deuterostomes and living vertebrates.³

Invertebrate ganglia range in size from small flatworm brains, about 100 μm in diameter,¹⁵ to giant molluscan ganglia, some of which are several millimeters across. Depending upon its size and the complexity of the behaviors it controls, a ganglion may have one to several neuropils. Many neuropils have distinct morphological boundaries and a principal sensory or motor function.¹¹ The central regions of small ganglia, such as the crustacean stomatogastric ganglion or leech segmental ganglia, are usually not divided into morphologically identifiable neuropils,^{16,17} although recent work suggests that motor neuronal arborizations may be compartmentalized within the stomatogastric ganglion (K. Graubard, personal communication). Larger ganglia, such as the segmental ganglia of locusts, cockroaches, crayfish and lobsters, do have internally compartmentalized neuropils. Many, such as the lateral neuropils of crayfish ganglia (Figure 1) can be defined by their limiting tracts. Some neuropils, however, like the dorsal flight neuropils of insect thoracic ganglia, have no visible histological boundaries and can only be recognized as discrete neuropils from the overlapping arborizations of functionally related neurons.^{11,20}

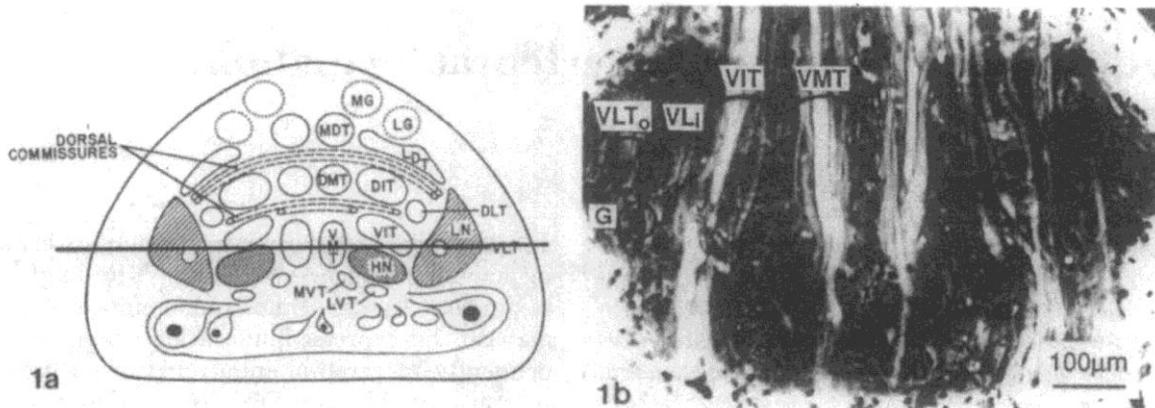


Figure 1. (a) Diagrammatic transverse section through the middle of a crayfish abdominal ganglion. Three layers of horizontal tracts of longitudinal axons surround two layers of transversely running commissures. The lateral neuropils (LN) control segmental limb movements whereas the horseshoe neuropil (HN), seen here as cross sections through the two arms, contains sensory afferent projections. Neuronal cell bodies are found only at the ventral surface of this ganglion. Horizontal line marks approximate location of section in b. Reprinted from Leise *et al.*³⁹ (b) Horizontal section through the LNs and HN of the fourth abdominal ganglion in a crayfish. One vertical tract (G) is circled. The ventral intermediate tracts (VITs) separate the LNs and HN. From Leise *et al.*³⁸ MDT, medial dorsal tract, LDT, lateral dorsal tract, DMT, dorsal median tract, DIT, dorsal intermediate tract, DLT, dorsal lateral tract, VMT, ventral median tract, VIT, ventral intermediate tract, VLT, ventral lateral tract, MG, medial giant axon, LG, lateral giant axon, MVT, medial ventral tract, LVT, lateral ventral tract.

Whereas ganglionic size can give some indication of potential internal complexity, the breadth of a ganglion's behavioral roles and the number of its intrinsic neurons are more important determinants of internal ganglionic architecture. A stomatogastric ganglion contains about 30 neurons that govern a limited behavioral repertoire—the grinding and chewing movements of the foregut.^{8,18} In contrast, a similarly sized leech ganglion contains nearly 250 neurons and is concerned with several types of behaviors, such as bodily shortening, swimming, twisting and walking.^{6,19}

Neuropils can be thought of as the basic building blocks of invertebrate nervous systems,²¹ just as cortical columns are in mammalian brains.²² Invertebrate neuropils also satisfy most of Mountcastle's²³ definitions for vertebrate brain modules: (i) they are local neural networks containing one or a few electrically compact circuits; (ii) neuropils occur in all ganglia and (iii) range in diameter from about 150 μm to 1 mm; (iv) segmentally repeated neuropils contain homologous sets of neurons, as was shown for crayfish abdominal ganglia,²⁴ although segmental variation in neuronal components usually reflects differential segmental activities; (v) many neuropils also retain topographical or functional ordering of neuronal connections (see section 'Partitioning of neuropil function') and often have characteristic sub-structures.²¹ In general, regions such as the lateral neuropils of crayfish abdominal ganglia (Figure 1) and the large ventral neuropil, the ventral association center (Figure 2), of insect thoracic ganglia, satisfy these criteria, although we have little information about somatotopic mapping in crayfish lateral neuropils. The lateral neuropils in crayfish are

thought to be the loci for the pattern generating circuits that drive swimmeret movements.^{5,25,26} The insect ventral association center receives incoming sensory afferents and is responsible for the integration of information about the external milieu.^{11,13,27}

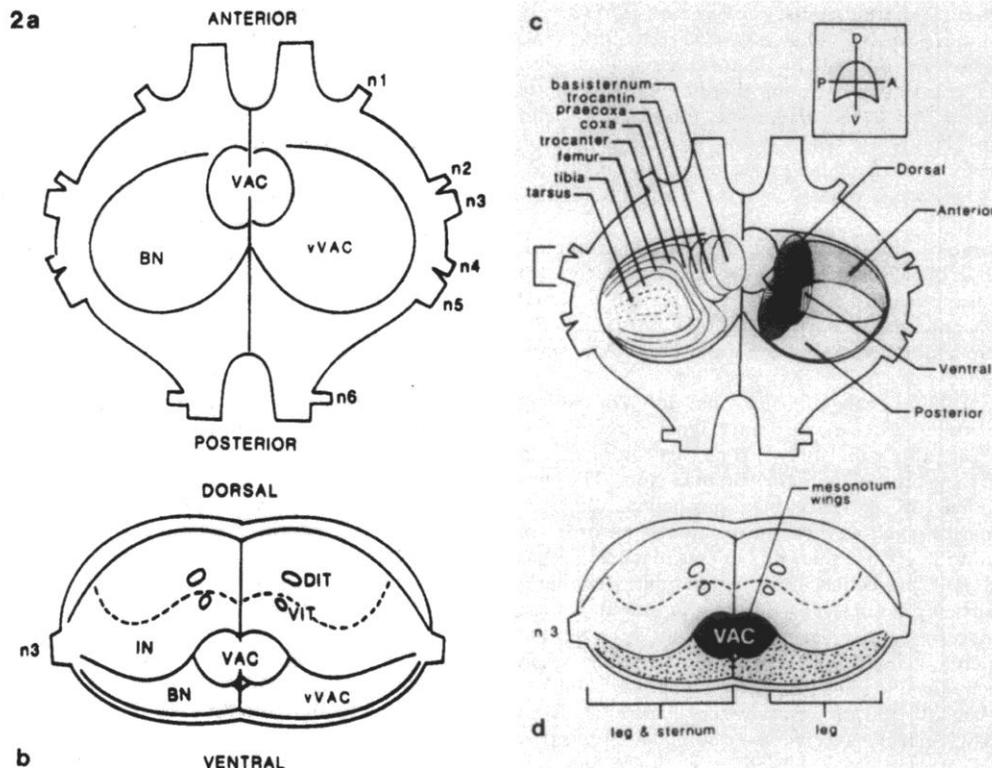


Figure 2. Map of sensory afferent projections in the mesothoracic ganglion from bristles on the second leg of a cricket. (a) Diagrammatic horizontal section. n1-6, nerve 1-6; IN, intermediate neuropil; VAC, ventral association center; vVAC ventralmost VAC; BN, bristle neuropil. (b) Transverse section through the same ganglion at the level of n3. Tracts as in Figure 1. (c) Summary of bristle afferent organization in horizontal section. Lines do not represent strict borders, projections areas overlap. Dashed lines are inferred borders. Inset, circumferential order of bristles on leg. Right side of ganglion shows representation of target regions of bristle afferents with respect to dorsal-ventral and anterior-posterior axes. (d) Diagram as in b, showing dorsal-ventral order of bristle projections to VAC and vVAC. From Johnson and Murphey.²⁷

Neuropil substructure

Three types of microarchitecture are common in invertebrate neuropils: synaptic glomeruli, radial columns and tissue layers.²¹

Glomeruli

Synaptic glomeruli are spherical clusters of complex synapses that are often set apart from the surrounding neuropil tissue by distinct glial capsules,^{21,28} just like the glomeruli in mammalian olfactory bulbs. Glomeruli range from 15 to 50 μm in diameter, occasionally reaching 100 μm across. In the invertebrates, glomeruli appear almost exclusively in sensory systems, occurring in conjunction with well-developed sensory organs.¹ They probably evolved as the most efficient means of packaging three-dimensional neuronal tissue and they occur where numerous afferents must converge on to relatively few interneurons.²⁹ They may also contribute to an increase in the safety factors associated with signal transmission among three or more synaptic elements.²³ Glomeruli can be found in annelid brains (Figure 3),³⁰ in molluscs, for example, in the parietovisceral ganglion of scallops,³¹ and in arthropod sensory neuropils such as the crayfish horseshoe neuropil.²⁶

Some of the best studied invertebrate glomeruli occur in the olfactory and accessory lobes of arthropod brains,³² where they process information received by the antennal sensory receptors (Figure 3). In the cockroach, information from hundreds of thousands of sensory receptors converges into less than 150 glomeruli. Local interneurons interconnecting glomeruli improve the incoming signal-to-noise ratio, whereas projection interneurons carry information from the glomeruli to higher brain centers. The convergence of afferents in mammalian olfactory glomeruli, such as those in rabbits, is an order of magnitude greater than it is in

cockroaches^{21,33} but local and projection interneurons play similarly important roles in the first processing stages. Rabbit glomeruli are also larger than most invertebrate glomeruli, being 100-200 μm in diameter, although in male moths, the so-called 'macroglomerular complex' reaches 200-300 μm in diameter (Figure 3). Each macroglomerulus receives over 80,000 afferents that select strongly for female sex pheromones.³² Glomerular size thus correlates with the number of convergent afferents. Although the basic arrangement of synapses within mammalian and insect olfactory glomeruli differ, neuronal elements in both types of glomeruli allow for horizontal and vertical processing.

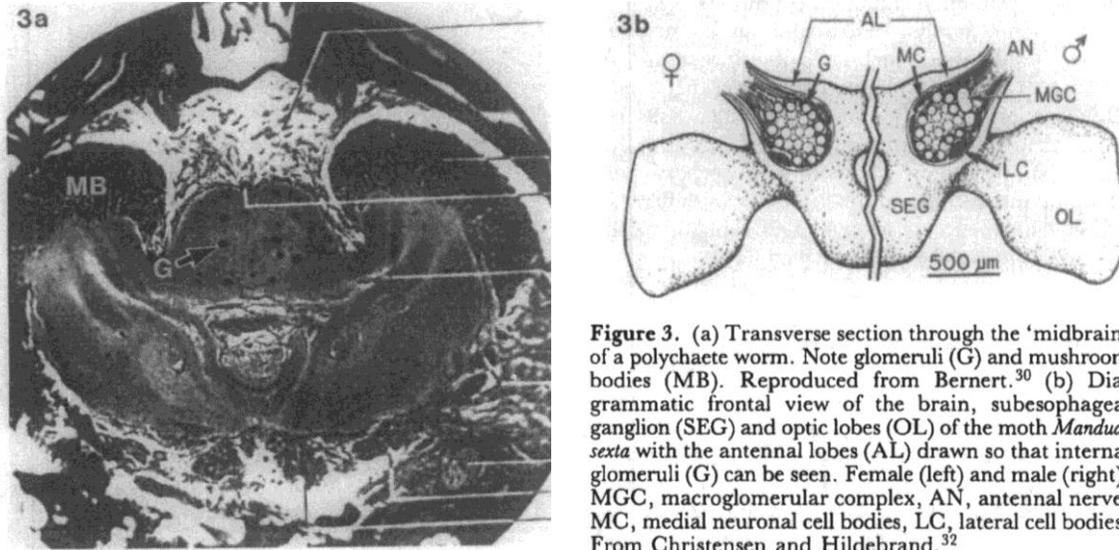


Figure 3. (a) Transverse section through the 'midbrain' of a polychaete worm. Note glomeruli (G) and mushroom bodies (MB). Reproduced from Bernert.³⁰ (b) Diagrammatic frontal view of the brain, subesophageal ganglion (SEG) and optic lobes (OL) of the moth *Manduca sexta* with the antennal lobes (AL) drawn so that internal glomeruli (G) can be seen. Female (left) and male (right). MGC, macroglomerular complex, AN, antennal nerve, MC, medial neuronal cell bodies, LC, lateral cell bodies. From Christensen and Hildebrand.³²

Spherical knots of synapses have been described in some flatworm brains,¹⁵ which may be the phylogenetically earliest appearance of glomeruli or glomerular-like structures. The prevalence of such structures is unknown and needs further study. Their behavioral role is unknown but they most probably contain synapses from sensory afferents on to local interneurons, two types of neurons known to exist in this phylum. Here again, flatworms may hold the key to our ability to understand the origin of higher-level organization in nervous systems.³

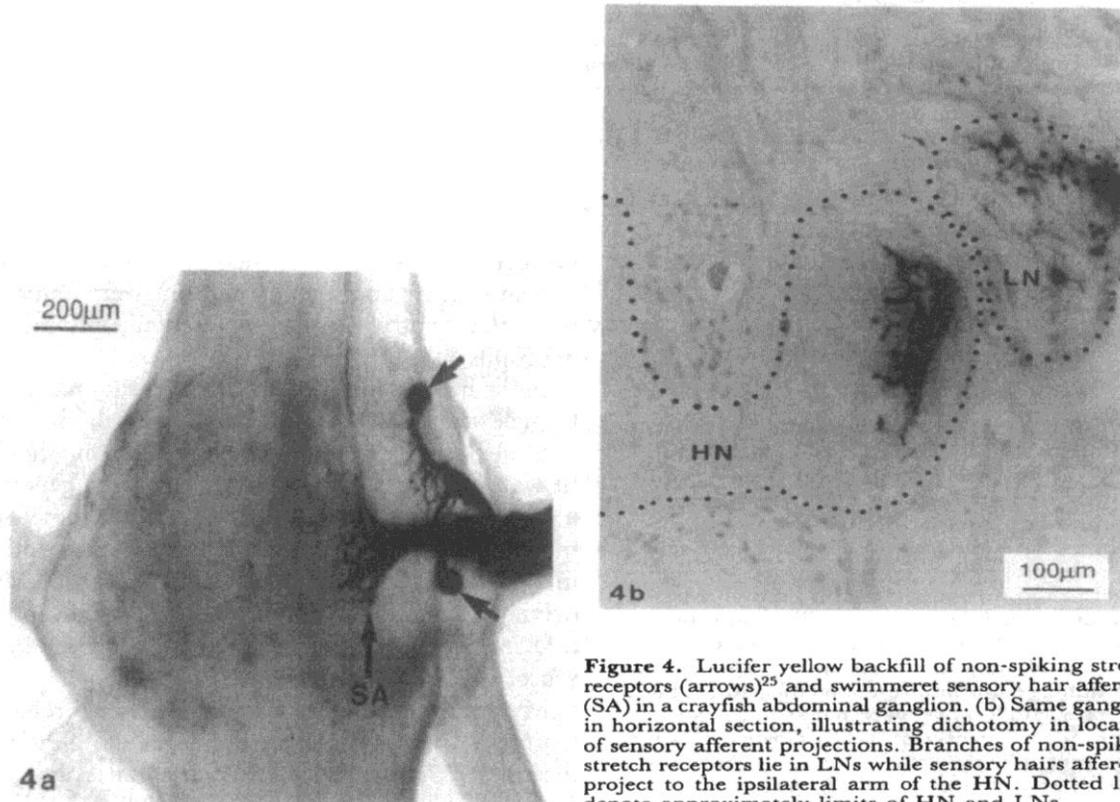


Figure 4. Lucifer yellow backfill of non-spiking stretch receptors (arrows)²⁵ and swimmeret sensory hair afferents (SA) in a crayfish abdominal ganglion. (b) Same ganglion in horizontal section, illustrating dichotomy in location of sensory afferent projections. Branches of non-spiking stretch receptors lie in LNs while sensory hair afferents project to the ipsilateral arm of the HN. Dotted lines denote approximately limits of HN and LNs.

Radial columns and layers

The optic lobes of arthropods and cephalopods display two other types of neuropil substructure—radial columns and layers.^{21,34,35} Radial arrangement of cell groups allows for both hierarchical and parallel analysis in signal processing as well as the retention of a retinotopic representation of the visual field. Like glomeruli in olfactory systems, radial columns allow for convergent amplification of the incoming signal.³⁵ In the retinae of crustaceans and insects, visual receptors and their supporting elements are arranged in columnar groups called ommatidia. Each receptor neuron in an ommatidium projects into a particular column or cartridge of neurons in the first optic neuropil. Projections from cartridges in this neuropil can be traced into the adjacent second and third optic neuropils,³⁵ which are organized in laminae because incoming axons synapse on intrinsic interneurons that branch on different spatial levels. For example, in crayfish, photoreceptors terminating distally in the first optic neuropil respond maximally to horizontally polarized light; those ending proximally respond to vertically polarized wavelengths.³⁵ Circuitry within layers can also subserve lateral inhibition and feedback loops for light adaptation.

Cephalopods display similar types of organization in their optic neuropils. In squid, the outer neuropil of the optic lobe is arranged in concentric layers whereas the large inner mass of the lobe is organized into alternating columns of neuropil and axon tracts.³⁶ Columnar neuropil structure is likely to have evolved independently in the cephalopods and arthropods; the arrangement of visual ommatidia and neuropils in arthropods is unique to this phylum.

Partitioning of neuropil function

Historically, ganglionic motor areas were thought to be dorsal whereas sensory information was processed ventrally.^{11,37} We now know that the traditional designation of a neuropil as sensory or motor is misleading. Traditional 'motor' neuropils are more aptly designated 'sensori-motor' areas,¹¹ as the generation of a behaviorally relevant output depends upon the integration of a variety of sensory inputs. For instance, the insect flight neuropil, a 'motor' neuropil, contains branches from motor neurons that drive wing elevators and depressors but also receives projections from flight proprioceptors—wing hinge receptors and wing sensory hairs.^{11,20}

The term sensory neuropil remains valid for regions like the insect ventral association center (Figure 2) and its crayfish homologue, the horseshoe neuropil (Figures 1, 4). The horseshoe neuropil contains projections from numerous sensory afferents³⁸ and, like the ventral association center, its primary function is the integration of information about the external environment. Still, the horseshoe neuropil receives branches from abdominal motor neurons—slow and fast extensor and slow flexor motor neurons,^{38,39} perhaps indicating that some exteroceptive information is sent directly from sensory afferents and interneurons to abdominal positioning neurons. Integration of information in a similar pathway has been described physiologically for locust legs and overlapping arborizations of the relevant motor and sensory neurons were found in both the ventral association center and lateral neuropils.⁴⁰

In the insects, many of the flight sensory receptors branch in the sensorimotor areas as well as in the ventral association center and, although one should be wary of oversimplifications, there is, in general, a spatial dichotomy in the integration of these two main types of sensory information: proprioceptive information is analysed in neuropils concerned with driving muscular activities whereas exteroceptive information is mostly integrated in the separate sensory neuropils (Figure 4).^{11,13,41,42}

Much less is known about the functional roles of neuropils from other invertebrate phyla, although the lobes of the enormous (by invertebrate standards) cephalopod brains certainly have specific behavioral tasks.⁴³ Annelids may also show some dorsoventral segregation of motor and sensory functions: in leech ganglia, the ventral part of the central neuropil contains fibers of smaller diameter than the dorsal part,¹⁷ which may indicate the presence of sensory afferents. Whether there is any such spatial differentiation of neuropil tissue in flatworm brains is unknown.

In the arthropods, centers for limb control are segregated from areas concerned with movement of body-wall musculature.^{11,20,44} In the polychaete worms, separate small ganglia govern the functions of the appendages (parapodia)¹ and the fusion of such ganglia to central segmental ganglia during evolution could account for the relatively lateral position of limb neuropils in extant arthropods (Figures 1, 4).^{5,13,26,44,45}

Axons are also segregated in tracts and commissures. The best known examples are again in the arthropods. From comparative studies on crayfish and insects we know that some of the longitudinal tracts, originally named for their locations,²⁶ contain functionally homologous neurons. For example, exteroceptive sensory afferent axons travel in the intermediate and medial tracts of the third and fourth layers in crayfish and insects³⁹ and proprioceptor axons run in the dorsal medial tracts.³⁹ The relationship between insect and crustacean ganglionic commissures, on the other hand, is unclear. Much more work needs to be done on the thousands of projection interneurons travelling in these ventral nerve cords to obtain a more complete view of the conservation of tract identity in the arthropods.

In leech ganglia, rostro-caudal axons diverge into separate tracts but again, the functional identity of their component axons is unknown. Given the phylogenetic affinities of the annelids and arthropods,⁴⁶ further research may demonstrate that the arrangement of tracts in annelid nerve cords resembles that of arthropods. The axons running through the neuropil in flatworm brains also need further study to determine how or if they are organized. As yet, molluscs have not been shown to display the complex sandwich of tracts and commissures found in the arthropods.

In the arthropods, sensory afferents are distributed within the major neuropils so that they retain a topographic representation of the body surface or of the external receptive fields (Figure 2).^{13,21,27} In crickets, as an example, central projections from leg mechanoreceptors retain their proximal-to-distal, circumferential and dorso-ventral order (Figure 2), suggesting that the analysis of the animal's spatial relationship to environmental conditions begins in the segmental ganglia. Particular subsets of other sensory modalities, such as wind direction⁴⁷ or hearing,⁴⁸ are also mapped in insect neuropils. Motor neuronal arborizations in insect neuropils also retain their somatotopic order.^{20,49,50} Again, much less is known about the bodily or sensory field mapping in neuropils in other phyla,²¹ although we do know that neuronal cell bodies are somatotopically organized in some molluscan ganglia.⁵¹

Development and ganglionic architectonics

Internally compartmentalized ganglia may have persisted because they allow large numbers of developing neurons to grow and reach appropriate targets simultaneously. In all phyla, neurons seem to use the same types of cell-cell and cell-matrix interactions to create functional networks and build complex ganglionic interiors (see articles in *Semin Neurosci* vol 3 no 4, ref 52). Mechanisms such as cellular generation, migration, differentiation and loss, and filopodial extension and retraction ensure that growing neurons reach appropriate target sites.^{21,53} Upon arrival, competition for synaptic sites, trophic interactions and activity-dependent feedback make major contributions to the development of functional synaptic connections.⁵⁴

Cellular and environmental interactions continue to be important during an organism's growth and maturation. For example, during each molt cycle, adult crustaceans generate new sensory hairs whose axonal arborizations must be incorporated into existing circuits and ganglionic pathways.⁵⁴ Experiments in which appendages are transplanted from one bodily location to another show that regenerating neurons are guided by positional cues, possibly cell surface markers.⁵⁴ Within foreign segmental ganglia, the central projections of such ectopic sensory neurons grow into the appropriate neuropils, retain their spatial organization and can even connect with proper target interneurons.⁵⁵ During metamorphosis, a time when many organisms remodel their somatic tissues, physiological states and ecological interactions, neuronal functions are also recon-figured.^{49,56} In some insects, neuropil size and extent changes as neural circuits are remodeled but the general architectonic features of a ganglion are stable.⁵⁶ Motor and sensory neurons may die, be born or change their roles during metamorphosis but the relatively constant interneuronal population stabilizes internal ganglionic structures.

Neuropil maps or microarchitecture should be expected to change in accordance with the reforming neuronal connections.

Studies on many developing nervous systems have shown that normal neuropil development depends upon neuronal activity in both vertebrates and invertebrates.²¹ Cricket sensory systems can be viewed as models that demonstrate the great plasticity inherent in the development of invertebrate nervous systems. Afferents from cricket cerci branch in specific neuropils on both sides of the last abdominal ganglion, increasing their contralateral arborizations when that side is deprived of its normal ipsilateral input. Deprivation also decreases the responsiveness of the sensory interneurons. The area of increased afferent arborization also occurs within the normal neuronal target region. New dendritic growth is thus activity-dependent and spatially restricted by the same positional information that specifies their original locations.^{21,54}

Lastly, glial cells can also play a significant role in shaping and maintaining ganglionic architecture. In moths, glomerular borders are defined by changes induced in the local glial cells when sensory axons grow into the olfactory lobes.⁵⁷ Deafferented moths have no glomeruli in their olfactory lobes and afferent synapses occur in abnormal locations within the neuropil. Moths with normally afferented lobes but with experimentally depleted glial populations show similar results.⁵⁷ How afferents activate glia and how glia in turn exert their effects is still under investigation. The generality of this role for glial cells in the formation of invertebrate sensory neuropils is as yet a subject for speculation.

Are significant characters conserved or have they evolved several times?

Morphological and molecular evidence strongly supports a close phylogenetic relationship between the Annelida, Onychophora and Arthropoda.^{2,46} Members of these phyla have certain neuroanatomical features in common but not all of their similar ganglionic structures are homologous. For example, it is unlikely that glomeruli in the midbrains of polychaete worms³⁰ and in insect antennal lobes³² are homologous structures (Figure 3). Conversely, one of the classic examples of conservative neural evolution in these phyla is the large 'mushroom bodies', the corpora pedunculata, in the brain ganglia.¹ Behavioral and physiological experiments on insects indicate that the mushroom bodies are mainly involved in the temporal integration of olfactory information and may be responsible for olfactory memory formation.⁵⁸ The functions of mushroom bodies in annelid and onychophoran brains are still hypothetical but their structural characteristics provide strong grounds for considering them to be true homologues.¹

In the arthropods, the general plan of ganglionic tract layers seems to be highly conservative.³⁹ Even in *Drosophila melanogaster*, the basic arthropod system of tracts and neuropils is retained in miniature.⁵⁹ As mentioned above, the phylogenetic roots of this type of neuronal organization needs further investigation.

An example of analogous structures serves to illustrate the point that great care must be taken before homology is invoked. The so-called giant fibers (Figure 1), axons with diameters between 20 and 1000 μm , occur in many invertebrate nervous systems.¹ These fibers, which are enlarged for high speed signal transmission, tend to occur as part of rapid escape systems (see also Edwards and Palka, this issue⁶⁰). There seems, however, to be no broad conservation of truly homologous giant neurons between the main groups of invertebrates. Giant fibers may be individual neurons with enlarged axons, linked axonal segments from adjacent neurons or the result of ontogenetic cell fusion.¹

Further evolutionary trends

Although it is somewhat beyond the scope of this paper, a mention of the evolutionary trend towards fusion of individual ganglia into single brain masses is warranted. Advanced arthropods and molluscs evolved massive brains in this fashion but seem to have done so independently.¹ Tissue condensation has profound effects on the arrangement of commissures, tracts and neuropil areas⁵⁰ and probably yields several beneficial results: reduced conduction times, the elimination of interposing relay inter-neurons and the increased availability of different types of sensory input to individual neurons and neuronal networks.⁵⁰

The early evolution of distinct ganglia and their subsequent elaboration were successful adaptations to life in complicated environments. Compartmentalized ganglia may have allowed many circuits to be efficiently packaged in a minimal volume of tissue, allowing animals to express more rapid or more appropriate behavioral responses to environmental changes and organismal interactions. The evolution of condensed brains seems to have been a successful continuation of this trend.

Experiments on fossilized organisms would enable us to achieve a better understanding of the origin, form and function of modern-day nervous systems. In lieu of this, comparative studies on extant species will have to suffice.

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