

Diversity and Evolution of the Insect Ventral Nerve Cord

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Key Words

ganglion, central nervous system, phylogeny, energetic costs, modularity, convergence

Abstract

Is the remarkable diversity in the behavior of insects reflected in the organization of their nervous systems? The ventral nerve cords (VNCs) have been described from over 300 insect species covering all the major orders. Interpreting these data in the context of phylogenetic relationships reveals remarkable diversity. The presumed ancestral VNC structure is rarely observed; instead the VNCs of most insects show extensive modification and substantial convergence. Modifications include shifts in neuromere positions, their fusion to form composite ganglia, and, potentially, their separation to revert to individual ganglia. These changes appear to be facilitated by the developmental and functional modularity of the VNC, a neuromere for each body segment. The differences in VNC structure emphasize trade-offs between behavioral requirements and the costs incurred while maintaining the nervous system and signaling between its various parts. The diversity in structure also shows that nervous systems may undergo dramatic morphological changes during evolution.

Ventral nerve cord (VNC): the chain of ganglia linked by paired connectives and lying beneath the alimentary canal

Central nervous system (CNS): region of the nervous system composed of the brain, subesophageal ganglion, and ventral nerve cord along with several smaller ganglia

Neuromere: part of the central nervous system belonging to one body segment that contains the neural circuitry responsible for the processing of sensory signals of a segment and for controlling the movements of that segment

INTRODUCTION

The insects are the most speciose group of animals on the planet, making up 63% of all named species (53). They have a vast behavioral repertoire that encompasses numerous locomotory, feeding, and reproductive strategies, as well as learning, navigation, and communication. Their behavior may differ radically in the wide range of habitats that different insects inhabit. Closely related species, as well as castes, sexes, and morphs within species, may also show dramatic differences in behavior. Furthermore, larval and adult insects frequently differ radically in lifestyle, body form, and behavior. The evolution of this behavioral diversity must have required morphological or physiological changes in the nervous system or sometimes both. The nervous systems of both invertebrates and vertebrates, however, are constrained by limited energy budgets for neural processing (74, 87, 88), physical limitations of their design (45) and the space they can occupy (118), and the processes by which they are formed during development (49).

Large amounts of energy are needed to maintain a nervous system and to process information within neural circuits (6, 76, 88, 90). Constraints on the energy budget of animals therefore suggest that there is strong selective pressure to reduce neural structures and neural processing to the minimum necessary to behave appropriately (87, 88, 121). In contrast, improved performance in specific behavioral tasks is correlated with the expansion of particular regions of both insect and vertebrate brains (e.g. 46, 47, 56, 79), which is likely to incur additional energetic costs, thus implying strong selective pressure to improve behavioral performance. Physical constraints within the nervous system have also been identified. For example, noise generated by the random fluctuations of voltage-gated ion channels places lower limits on axon diameter (45). Similarly, in mammals, concomitant changes in the volumes of specific brain regions relative to body mass may represent a

developmental constraint (49, 117), although some individual brain regions can change dramatically in volume relative to body mass (8, 117). Although no such relationships have been described for insects, it seems likely that the structure of the nervous system in modern insect species has been influenced by the design of the ancestral nervous system (43, 55, 67, 115).

Strong selective pressures to generate adaptive behavior with a limited energy budget suggest that the nervous system should be diverse and specialized, within the bounds set by both physical and developmental constraints on these evolutionary processes. Many comparative studies of the neurons or neural circuits of insects and other invertebrates have concluded that neuronal morphology is highly conserved during evolution (43, 67, 106), although at more recent phylogenetic scales, anatomical variation may be sufficient to infer phylogenetic relationships (4, 25, 26, 112, 115). Thus, the extent of morphological and physiological diversity within insect nervous systems remains unclear. The insect ventral nerve cord (VNC) provides an ideal starting point from which to assess the extent of diversity of central nervous systems (CNSs), particularly given its modular structure, with a neuromere associated with each body segment. Indeed, the small size and low resting metabolic rates relative to body mass of many insects and the high energetic demands of behaviors such as flight (1, 89, 104) mean that several factors such as space and energy constraints may be more acute in the nervous systems of insects compared with those of vertebrates. The overall structure of the insect VNC has been documented for many species from all of the major insect orders (**Figure 1**) (13–18, 29, 42, 81, 86, 123, 138). Here, we combine data on the overall structure of the insect VNC with phylogenetic approaches and recent advances in understanding the costs associated with nervous systems to assess the diversity and evolution of the insect VNC.

NEUROMERES, GANGLIA, AND FUSION

Insects are segmental animals and their CNSs reflect, although sometimes only obliquely, their segmentally based developmental program. The number of pregnathal segments (anterior to the mouthparts) is still debated, but there are likely to be four (53, 129). There are three additional gnathal segments (bearing the mouthparts) in the head and three thoracic segments (pro-, meso-, and metathorax) associated with each pair of legs. Ancestrally there are 11 abdominal segments, but in almost all extant species this number is reduced by one or more segments, depending on the order (53, 83, 114).

The basic organizational unit of the central nervous system is the neuromere, an accretion of neurons that are responsible for processing sensory signals of a segment and for controlling the movements of that segment. These segmental neuromeres are combined in various ways to form the pre-oral, dorsal brain, the subesophageal ganglion, and the thoracic and abdominal ganglia of the VNC, which together form most of the CNS (22, 109, 114). Each of these structures is linked in a chain by pairs of connectives that consist of the axons of many different types of neurons. Each segmental ganglion of the ventral chain may consist of a single neuromere or it may be a fusion of two or more neuromeres. In ganglia composed of two or more fused neuromeres, the connectives between neuromeres are reduced in length but still exist as tracts of axon bundles within the fused neuropile areas (22, 70, 95, 97, 99, 120, 128, 136).

The position of a neuromere relative to adjacent ones is continuous rather than discrete. To transform this relation into discrete categories, a cutoff point that marks the boundaries must be determined. In this review unfused refers to a neuromere for which there is a clear pair of connectives linking it to an adjacent neuromere. Fused refers to adjacent neuromeres close enough that their edges distort, and the outline of the composite ganglion is a

distortion of the two original outlines with, at most, a small indentation between neuromeres.

DIVERSITY IN VENTRAL NERVE CORD STRUCTURE

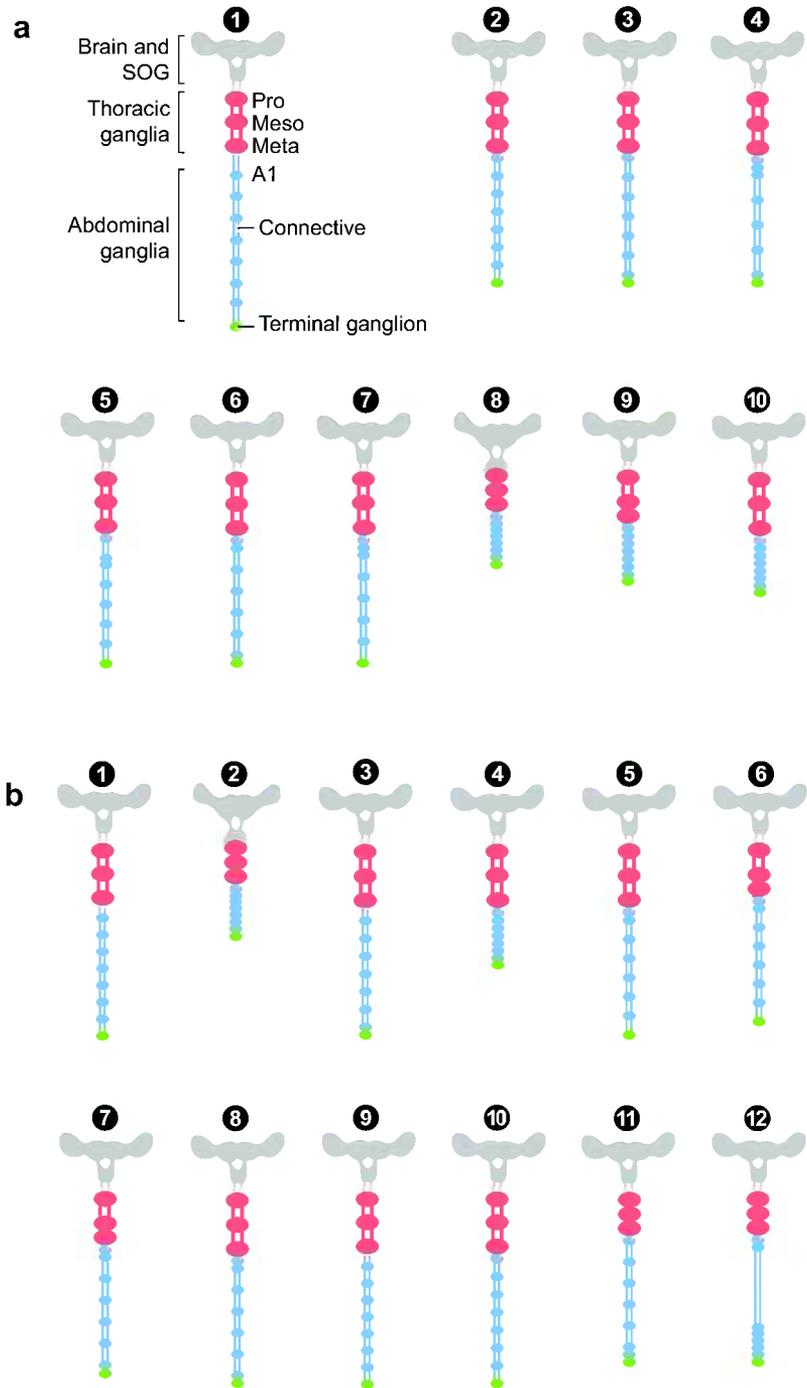
Establishing the structure of the ancestral insect VNC is essential for understanding the structural changes that have taken place during the evolution of the insects. The VNCs documented from the apterygote insect orders, Archaeognatha (51, 59) and Zygentoma (7, 59, 140), all possess three thoracic (T1–T3) and eight abdominal ganglia (A1–A8), ranged across the whole length of the abdomen and ending in a fused terminal ganglion (**Figure 1a.1**). The anterior seven abdominal ganglia (A1–A7) are unfused and the terminal ganglion (A8) consists of at least three fused neuromeres. Thus, the ancestral condition is likely to have been that all thoracic and abdominal neuromeres were unfused except for the three to four neuromeres contributing to the terminal abdominal ganglion. What is the arrangement of thoracic and abdominal ganglia in extant groups of winged insects?

The Pterygota or winged insects are extraordinarily diverse in their size, body form, and behavior. Within and between the different orders there is a corresponding diversity in the size, structure, and position of ganglia along the VNC relative to the segments they innervate, and in the fusion patterns of neighboring ganglia (**Figure 1**). The following account deals primarily with changes in the fusion pattern of neuromeres in relation to phylogeny, however, as this information is most prevalent in the literature.

The Ephemeroptera always have three distinct thoracic ganglia but have six to eight abdominal ganglia, depending on the number of neuromeres fused to form the terminal ganglion and whether the A1 is fused to the third thoracic neuromere (T3) (**Figure 1a.1–a.3**) (18, 42, 138). Most species described within

Ganglion: part of the central nervous system consisting of one or more neuromeres

Neuropile: a region of the insect central nervous system bounded by the cortex of cell bodies and mainly consisting of dendrites, axons, and synaptic connections



the Odonata have three thoracic and seven abdominal ganglia (**Figure 1a.2**). Three species diverge from this pattern; two species within the Libellulidae have two thoracic ganglia (the meso- and metathoracic ganglia are fused) and in *Petalura gigantea* A1 is not fused to T3 as it is in all other species (**Figure 1a.1**) (29, 81, 123).

The Phasmida (2, 86), Embiidina (52, 82, 85), and Grylloblattaria (131, 132) also have three thoracic and seven abdominal ganglia (**Figure 1a.2**). The Dermaptera (40, 64, 65, 69, 86), Blattaria (11, 86, 110), and Isoptera (86) have only six abdominal ganglia because an additional neuromere is fused to the terminal ganglion (**Figure 1a.3**). The Mantodea (68, 86) show extensive fusion of the abdominal neuromeres to T3, reducing the number of abdominal ganglia to four (**Figure 1a.4**), and the Zoraptera (113) have further reduced them to just two. The Orthoptera show greater diversity, with between five and seven abdominal ganglia (**Figure 1a.2, a.5–a.7**) (44, 48, 81, 86, 108, 130). Unusually, several orthopterans show fusion within the abdominal VNC (between the second and third abdominal neuromeres) rather than at either end (**Figure 1a.5**). The plecopterans usually have one or two abdominal neuromeres fused to T3. Surprisingly, in some species there appear to be fewer neuromeres in the terminal ganglion than in the ancestral VNC (62).

The most striking feature of the hemipteran VNCs is the complete fusion of all the abdominal neuromeres and, in many species, fusion of one or more thoracic neuromeres (**Figure 1a.8–a.10**) (13, 18). The fusion patterns of several hemipteran species are convergent, requiring independent fusion or separation depending on the assumed ancestral state. The Phthiraptera (13, 119), Psocoptera (50), and Thysanoptera (63, 111) also show complete fusion of their abdominal neuromeres, but unlike the Hemiptera, their thoracic neuromeres remain separate (**Figure 1a.10**).

The Coleoptera are the most diverse order in terms of neuromere fusion, ranging from fusion of all thoracic and abdominal neuromeres into one thoracic ganglion in some members of the Curculionidae (weevils) (28) to three thoracic and eight abdominal ganglia in one member of the Lycidae (**Figure 1b.1, b.2**). The number of ganglia varies from 2 to 10 in the Carabidae (ground beetles) (57), from 1 to 5 in the Curculionidae (28), and from 2 to 7 in the Chrysomelidae (leaf beetles) (80). Relatively few specimens from the other families have been studied but nevertheless variation abounds (15).

The little information on VNC structure within the neuropteroid orders is concentrated within the Neuroptera. There is a broad range of fusion patterns, from complete

Figure 1

Diversity of ganglion number within the insect VNC. Stylized diagrams of the brain and suboesophageal ganglion (gray), thoracic neuromeres (red), abdominal neuromeres (blue), and terminal abdominal ganglion (green). Peripheral nerves are not shown. (a) Apterygotes and exopterygotes: (a.1) *Japyx* spp. (Diplura), *Machilis* spp. (Archaeognatha), *Thermobia domestica* (Zygentoma), *Siphonurus lacustris* (Ephemeroptera), *Petalura gigantea* (Odonata); (a.2) *Lestes tenuatus* (Ephemeroptera), *Anax junius* (Odonata), *Carausius morosus* (Phasmida); (a.3) *Baetis muticus* (Ephemeroptera), *Anisolabis maritima* (Dermaptera), *Periplaneta americana* (Blattaria); (a.4) *Mantis religiosa* (Mantodea); (a.5) *Ceuthophilus brevipes* (Orthoptera); (a.6) *Acheta domestica* (Orthoptera); (a.7) *Schistocerca gregaria* (Orthoptera); (a.8) *Gyropus ovalis* (Phthiraptera), (a.9) *Pentatoma* spp. (Hemiptera); (a.10) *Pemphigus* spp. (Hemiptera). (b) Endopterygotes: (b.1) *Dictyopterus sanguineus* (Coleoptera); (b.2) *Nanophyes nigrovarius* (Coleoptera); (b.3) *Hemerobius stigma* (Neuroptera); (b.4) *Nemoptera lusitanica* (Neuroptera); (b.5) *Ichneumon* spp. (Hymenoptera); (b.6) *Bombus terrestris* females (Hymenoptera); (b.7) *Notodonta camelina* (Lepidoptera); (b.8) *Zygaena* spp. (Lepidoptera); (b.9) *Merope tuber* males (Siphonaptera); (b.10) *Merope tuber* females (Siphonaptera); (b.11) *Ogcodes fuliginosus* (Diptera); (b.12) *Platystoma umbrarum* (Diptera). Modified, with permission, from References 13–18.

Ametaboly: nymphs closely resemble adults but lack genitalia

Hemimetaboly: nymphs resemble adults but possess wing buds rather than fully functioning articulated wings

Holometaboly: larvae may be radically different from adults and undergo metamorphosis during pupal stage

fusion of all the abdominal neuromeres with the third thoracic neuromere in *Nemoptera lusitanica* to seven distinct abdominal ganglia in the Megaloptera, Chrysopidae, and Hemerobiidae (**Figure 1b.3, b.4**) (77, 78, 139).

The Hymenoptera vary in the fusion pattern of both their thoracic and abdominal neuromeres (**Figure 1b.5, b.6**) (14, 39, 137). In the Apidae, Megachilidae, and Vespidae the second and third thoracic neuromeres are fused, but in the Ichneumonidae, Sphecidae, Mutillidae, and Formicidae all three thoracic ganglia are separate, suggesting that fusion of the thoracic neuromeres may be convergent. The number of abdominal neuromeres varies from seven in the Cimbicidae to just two in the Cynipidae.

All the available data on the Trichoptera show three thoracic ganglia and either five or six abdominal ganglia (12). The Lepidoptera, like the Coleoptera and Hymenoptera, have variable numbers of both thoracic and abdominal ganglia (**Figure 1b.7, b.8**). Nonditrysian and basal ditrysian Lepidoptera have three separate thoracic ganglia, whereas in most other ditrysian Lepidoptera the second and third thoracic neuromeres are fused (16, 72). The nonditrysian Lepidoptera possess two to six abdominal ganglia and the ditrysian Lepidoptera possess four.

All members of the Siphonaptera (17, 73), Mecoptera (98), and the basal Diptera (17, 41) have three thoracic ganglia and between four and eight abdominal ganglia. The Stresiptera show a dramatic reduction in this number to either a single combined thoracic and abdominal ganglion or two ganglia. Within both the Stresiptera and the Siphonaptera there are differences in the number of abdominal ganglia between sexes (**Figure 1b.9, b.10**) (17, 73). In contrast, the Brachycera (17, 41, 141) possess a wide range of fusion patterns, from three thoracic ganglia and six abdominal ganglia in the Asilidae to complete fusion of all the ganglia within more derived families such as the drosophilids (**Figure 1b.11, b.12**).

DEVELOPMENTAL ORIGINS OF NERVE CORD DIVERSITY

Insects have three main developmental strategies: ametaboly (apterygotes), hemimetaboly (exopterygotes), and holometaboly (endopterygotes) (30, 126, 127). The embryonic VNC develops from ectodermal cells that differentiate to form neuroblasts and midline precursor cells present in each segment (10, 91, 122, 124, 125). The neuroblasts divide asymmetrically to form ganglion mother cells, which in turn divide to produce two neurons. Outgrowth of fibers from these neurons forms paired horizontal commissures within each segment and longitudinal tracts between segments that eventually form a ladder-like structure of neuromeres that closely resembles the ancestral insect VNC (9, 10, 122, 124, 125). This developmental program is remarkably conserved (122, 124) and produces a modular structure (5, 134) that may be a crucial factor in generating the diversity of VNCs. During the later stages of embryonic development the neuromeres shift anteriorly or posteriorly from their segments, sometimes fusing with neighboring neuromeres. This means that during different stages of embryonic development the positions and fusion patterns of neuromeres vary considerably. At the end of embryonic development in exopterygote insects the positions and fusion pattern of the neuromeres closely resemble those of the adult, although there may be significant postembryonic growth (54, 92, 108). At the end of embryonic development in endopterygote insects, however, the VNC resembles that of the larvae, not that of the adult. Further restructuring occurs during pupation to produce the adult VNC, which may differ radically from that of the larvae (**Figure 2**) (3, 14, 17, 37, 41, 58, 96, 100). Such restructuring creates a further level of developmental modularity (5, 134) that may contribute significantly to the increased VNC diversity in the endopterygote insects relative to that in the exopterygotes.

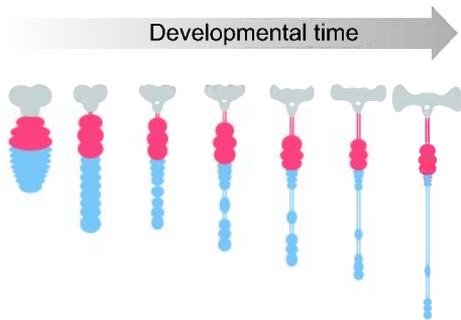


Figure 2

Separation of neuromeres during metamorphosis in *Syrphus ribesii* (Diptera). Stylized diagrams of the brain and subesophageal ganglion (gray), thoracic neuromeres (red), and abdominal neuromeres (blue). Data are from Reference 17.

EVOLUTIONARY CHANGES OF NERVE CORD STRUCTURE

What are the evolutionary events that have led to the highly variable number of ganglia in the VNCs of insects? Several factors may affect the position and pattern of neuromeres along the VNC, including developmental processes, the position of sense organs and/or muscles, body size, and/or shape. Most studies of the structure of the VNC have not attempted to determine the underlying causal factors. We can therefore only hypothesize about the contributing factors.

The extensive convergence of ganglion number within the insects appears to have been generated by fusions between neuromeres, but it is also possible that fusion may be reversed and that neuromeres have separated from one another. The latter occurs in some flies during metamorphosis. For example, in the larvae of *Syrphus ribesii* the thoracic and abdominal neuromeres are fully fused, but during pupation the VNC is extended and separates into its composite neuromeres (**Figure 2**) (17). The development of the VNC from a fully separated structure, however, means that separation in adult insects can be achieved by altering the extent to which neuromeres move during embryogenesis or pupation. Mapping the fusion of

the third thoracic neuromere with the first abdominal neuromere onto a recent insect phylogeny (135) suggests that this event occurred early in the evolution of the insects and that it may have been crucial for the development of insect flight (**Figure 3**). Indeed, several interneurons implicated in the generation of the flight motor pattern are located in the first abdominal neuromere (106).

In individual species of several insect orders the third thoracic and first abdominal neuromeres are not fused, suggesting that independent separations have occurred numerous times (**Figure 3**). Likewise, the large amount of convergence between insect species with highly fused VNCs suggests fusions have also occurred many times. In some cases possible factors may be identified that have influenced the structure of the VNC. For example, comparison of the polyneopteran and paraneopteran orders reveals striking differences in the extent of fusion, especially within the abdominal neuromeres (**Figure 1**). One contributing factor to the complete fusion of the abdominal neuromeres in the Paraneoptera may be the absence of cerci in these orders (53, 114), reducing sensory inputs to the terminal abdominal neuromere and allowing it to shift anteriorly.

Heath & Evans (57) examined the relationship between body length or VNC length and the number of discrete abdominal ganglia in carabid beetles. These beetles show a high degree of diversity in the number of abdominal ganglia but relatively little variation in their external anatomy. The number of discrete abdominal ganglia is positively correlated with their body length or VNC length (57). It is unclear what selective pressures influence this relationship, or whether it represents a developmental constraint, with the number of ganglia determined solely by the body length.

Is fusion between any two adjacent neuromeres equally probable? Two examples, one involving thoracic neuromeres and the other abdominal neuromeres, suggest that certain fusions are more common. Fusion between

Cerci: paired appendages on the eleventh abdominal segment that are usually covered in hair sensilla and have a sensory function

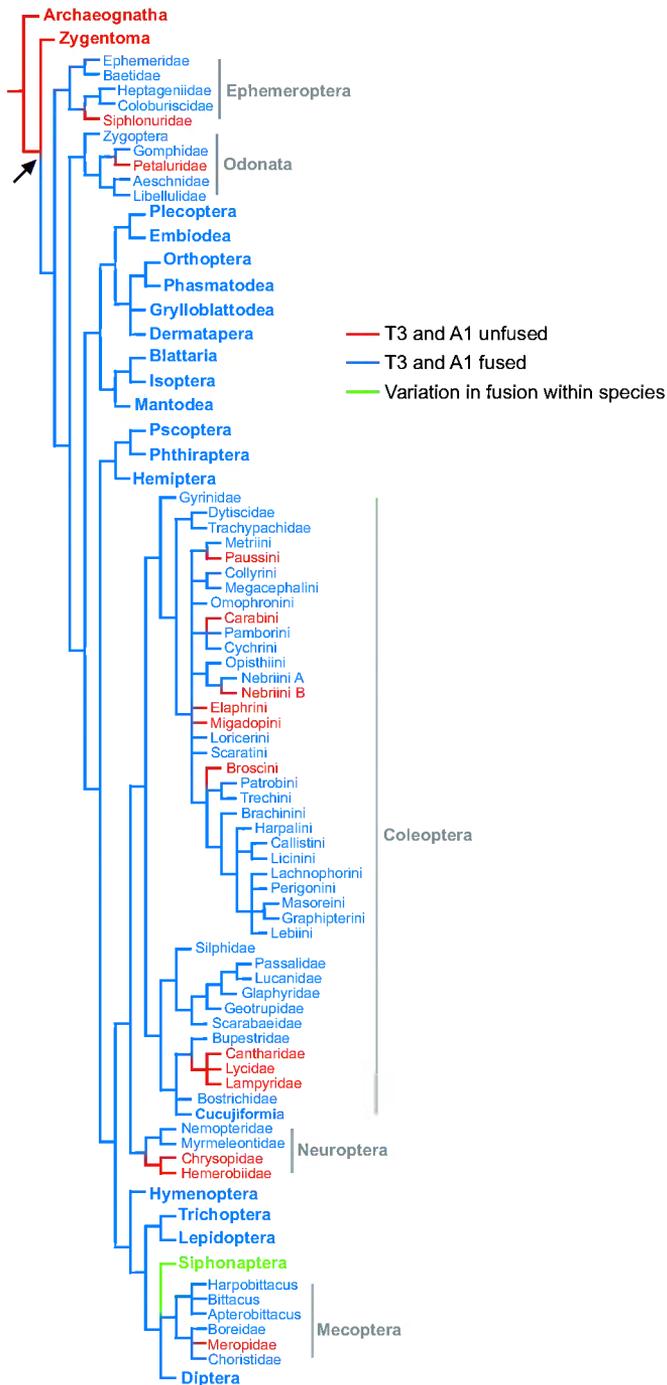


Figure 3

Fusion of the third thoracic and first abdominal neuromeres mapped onto a phylogeny of the insects. The black arrow indicates the point at which insects evolved flight. Phylogenetic relationships are based on References 135 and 53. See text for VNC data.

the second and third thoracic neuromeres occurs in several orders, but fusion of first and second thoracic neuromeres (without previous fusion of the second and third thoracic neuromeres) occurs just three times in the brachyceran Diptera: the Xylophagidae, the Therevidae, and one species of the Asilidae (17, 41, 141). The absence of a pair of metathoracic wings in the Diptera may facilitate this unusual fusion pattern. Fusion is more prevalent between abdominal neuromeres than between thoracic neuromeres. It is common for anterior abdominal neuromeres to fuse with the metathoracic ganglion or for the more posterior abdominal neuromeres to fuse with the terminal abdominal ganglion. In contrast, fusion between any of the middle abdominal neuromeres is rare (see below) and may have been generated by the separation of two already fused neuromeres from either the metathoracic ganglion or from the terminal abdominal ganglion.

Variation Between Closely Related Species

Relatively few studies describe variation in the fusion patterns of closely related insect species, and species-level phylogenies are often unavailable, making it difficult to determine the evolutionary events that have affected VNC structure. In the stingless bees (*Meliponini*), however, the VNC has been described for over 30 species from numerous genera including *Melipona*, *Trigona*, and *Plebeia* (137). Species within these genera show variation in the fusion patterns of abdominal neuromeres and the relative positions of their abdominal ganglia (Figure 4a). In particular, comparison of the length of the connectives separating the sixth and seventh abdominal neuromeres reveals a continuum of VNC structures from unfused to fused, accompanied by an anterior shift of all the abdominal ganglia in some species. Mapping the structures of these VNCs onto a phylogeny of the stingless bees (38) shows that

in some basal genera the sixth and seventh abdominal neuromeres are completely fused, whereas they are unfused in some more derived genera (**Figure 4b**). This suggests that fusion of these two neuromeres may have occurred many times during the evolution of the stingless bees. Moreover, although the data are sparse, rather than occurring as a smooth transition between unfused and fused states, large changes in VNC structure may occur within genera as may separations of previously fused neuromeres.

Variation Within Species

Differences in the pattern of neuromere fusion occur in males and females of the same species in several orders of holometabolous insects (14, 17, 39, 41, 73). For example, both sexes in the Conopidae (Diptera) have a single fused abdominal ganglion, but it is considerably larger and more posterior in females than in males (**Figure 5a**) (17, 41). Worker and queen bees have a different pattern of neuromere fusions and positions of the ganglia (14, 39). In the stingless bee *Melipona quadrifasciata* males have four abdominal ganglia, whereas queens and workers have five (39). In queens these ganglia are evenly spaced throughout the abdomen, but in workers they are shifted anteriorly, with the terminal ganglion occurring in the first abdominal segment (**Figure 5b**). These differences in fusion pattern are due to the fusion of one or more additional neuromeres to the terminal abdominal ganglion in one sex or caste. In *Apis mellifera* workers and *Mutilla rufipes* females, however, it is also possible that the seventh and eighth abdominal neuromeres have separated, creating an additional ganglion (14). The conclusion is that neuromere position and fusion pattern are plastic traits that can be altered, even within a single species, and may have a behavioral role. For example, in the Conopidae, the more posterior position of the abdominal ganglion in females may be due to the need to control complex musculature for egg laying, which is not present in the males (116).

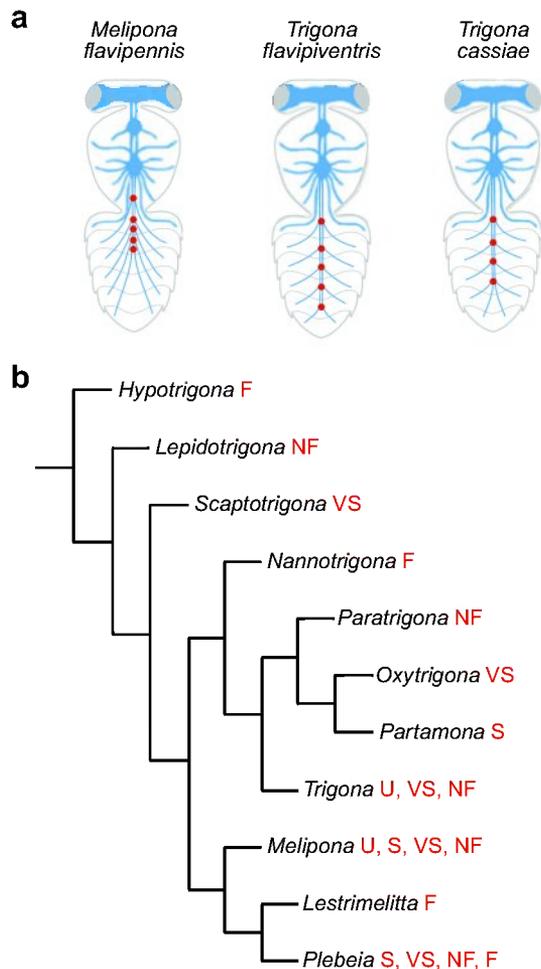


Figure 4

Variation in the structure of the insect VNC between closely related species of stingless bees (Meliponidae). (a) The outline of the abdomen and thorax (gray), VNC (blue), and the abdominal ganglia (red) from *Melipona flavipennis*, *Trigona fulviventris* and *Trigona cassiae*. (b) The distance between neuromeres 6 and 7 in the VNC in 11 genera of stingless bees in relation to phylogeny. Data are from Reference 137. Phylogenetic relationships are from Reference 38. U, unfused; F, fused; NF, nearly fused; S, small; VS, very small.

Selective Forces Affecting Nerve Cord Structure

Several recent modeling studies of nervous systems in both invertebrates and vertebrates have suggested that neurons are placed to minimize the total wiring cost (31–34, 36, 84). This cost can include the time taken to

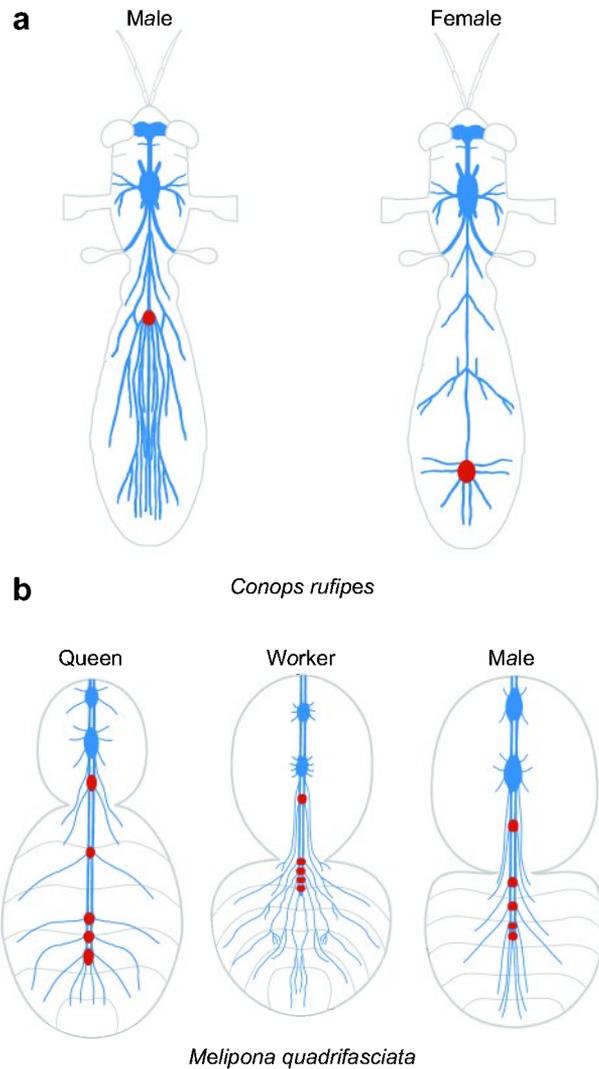


Figure 5

Variation in the structure of the insect VNC within species. (a) Variation in the size and position of the terminal thoracic ganglion between sexes in a conopid fly, *Conops rufipes* (Diptera). (b) Variation in the position of ganglia and in the fusion pattern of neuromeres between castes in the stingless bee, *Melipona quadrifasciata* (Hymenoptera). Brain and thoracic ganglia are colored blue, and abdominal ganglia are colored red. Data are from References 39 and 41.

conduct signals from region to region (107, 133), the metabolic energy consumed during signal transmission (6, 74–76, 88, 90), the total volume of wiring within the nervous system (35, 84), or the number of processing steps (66). If adjacent neuromeres are sepa-

rate rather than fused, this should increase the time taken for signals to travel between neuromeres, the energy consumed, or the space occupied, and the increased costs thereby incurred may affect the evolution of the VNC. Conversely, reducing the distance between neuromeres or the fusion of neighboring neuromeres reduces the length of their connectives, saving time on the conduction of action potentials between them, saving space, and reducing concomitantly the energetic cost. For fusion to occur, a neuromere must shift anteriorly or posteriorly away from the center of the segment that it innervates. In the ancestral insect VNC each neuromere is adjacent to its peripheral targets (7, 51, 59, 140), minimizing, on average, the length of its peripheral nerves. Any shift in the position of a neuromere outside its segment inevitably increases the distance to its peripheral targets, thereby increasing the energetic cost and conduction time of an action potential to and from the periphery. The position of each neuromere therefore results from a balance between the costs of signaling to the periphery and the costs of signaling to neighboring neuromeres. It remains unclear whether the entire insect VNC is a cost-minimized structure or whether other factors play a part. Recent modeling studies of the nervous systems of the nematode *Caenorhabditis elegans* and the primate *Macaca mulatta* suggest that the positions of some neurons or cortical regions deviate substantially from the predicted optimal position (31, 66).

Effects of Fusion and Separation upon Neural Circuits

Changes in the distance between neighboring ganglia are likely to produce significant changes in the morphology and physiology of local or intersegmental neurons and neural circuits of which they are a part. Reducing axon diameter [which is related to axonal conduction velocity (60, 61, 107)] may reduce the wiring cost of intersegmental circuitry but it will increase the time needed for

neural processing. For example, having a fused terminal abdominal ganglion allows the convergence of many small-diameter short sensory neurons onto a few large-diameter neurons that can then carry rapidly the integrated signals to the rest of the CNS. If the terminal abdominal ganglion is moved anteriorly to fuse with more anterior abdominal and thoracic neuromeres, then the same speed of processing could only be achieved by the many sensory neurons with large-diameter axons. This would be expensive to produce during development, to maintain, and to use for signaling.

The extent of dendritic arborizations is limited by the distance along the dendrites over which graded potentials can propagate (101, 102). In unfused ganglia, dendritic arborizations are restricted to the neuropile of just one ganglion (19, 20, 22–24). Fusion of neuromeres may allow the dendrites of neurons in one neuromere to expand into the neuropile of neighboring neuromeres, forming novel synaptic connections. Neurons in which the dendrites do cross between neuromeres are found in the metathoracic and terminal ganglia of cockroaches and locusts (21, 71, 93, 103). For example, in the metathoracic ganglion of the locust, interneurons involved in the production of the breathing motor patterns have processes that ramify through the neuropiles of the adjoining abdominal and thoracic neuromeres (21, 93, 103).

Graded potentials, rather than action potentials, may also be used to transmit information between neurons (105), as they require less energy to signal the same amount of information (76). Nonspiking neurons that transmit graded information are found within individual ganglia in locusts, crickets, stick insects, and cockroaches as components of local networks that process mechanosensory information and control limb movements (20, 22–24, 27, 71, 94). Fusion of neuromeres may allow graded potentials, rather than action potentials, to be used to transmit information between adjacent neuropiles. The morphology of some nonspiking neurons within the termi-

nal abdominal ganglion of the cockroach suggests that this is possible (71). The reduction in the length of cabling enabled by neuromere fusions may therefore lead to a more energetically efficient form of signaling and thus to further cost saving.

CONCLUSIONS

Substantial evidence indicates that the basic structure of the VNC has undergone many changes many times during evolution to produce extensive structural diversity among modern insects. Although the ancestral VNC probably consisted of a chain of three thoracic and eight abdominal ganglia, this pattern is rarely observed within the winged insects. Instead, there is variation in the size and position of ganglia, and the fusion pattern of neuromeres occurs across orders, families, tribes, and genera, and even within different members of a single species. Fusion between some neuromeres (e.g., the first abdominal and third thoracic neuromeres) is common, whereas between others (e.g., the fourth and fifth abdominal neuromeres) it is rare, possibly because of differing constraints and pressures. Despite the many advantages apparently conferred by fusion of neuromeres, some composite ganglia appear to have separated again into their constituent neuromeres. The fusion and separation of neuromeres during evolution suggest that there are strong cost/benefit trade-offs for improved performance and reduced costs.

These changes have produced widespread convergence in the fusion pattern of the VNC, obscuring phylogenetic relationships that cannot be deduced from the fusion patterns of the VNC. The developmental and functional modularity of the VNC may have contributed significantly to this extensive variability. The variability in the overall structure of the VNC suggests that there may be considerably more variation within neurons and neural circuits than previously documented. Whether the components of neural circuits or the circuits themselves undergo

changes or are conserved during evolution depends upon the strength and direction of selective pressure to which they are subjected.

Within the insect VNC these selective pressures have produced remarkable structural diversity.

SUMMARY POINTS

1. The VNC of the common ancestor of the insects is likely to have contained three thoracic ganglia (T1–T3) and eight abdominal ganglia (A1–A8), including a terminal ganglion consisting of three fused neuromeres.
2. The structure of the adult VNC is variable both within and between insect orders, families, and genera, and even between castes and sexes of the same species. Variation occurs in the positions of ganglia, which may shift relative to the segments that they innervate and relative to other ganglia, and also in the pattern of fusions between neuromeres from neighboring segments to form composite ganglia.
3. Separation of neuromeres from composite ganglia may have occurred independently in several lineages of insects.
4. Changes in the fusion and separation of neuromeres and in the relative positioning of ganglia can be observed during growth and development. In exopterygote insects, larval forms may have VNCs radically different from those of adult forms.
5. Mapping the patterns of fusion and separation onto phylogenies reveals widespread convergence throughout the insect orders.
6. The fusion of neuromeres may reduce conduction delays and energetic costs in existing circuits and also reduce the space consumed by the VNC.
7. Neuromere fusion may promote the formation of new circuits that in turn may lead to the production of novel behaviors.

FUTURE ISSUES

1. Despite the extent of the variation documented in the VNC structure, the relationship between this variation and behavior needs to be determined more fully. Species-level phylogenies coupled with the structure of the VNC and accurate behavioral descriptions are essential for making more substantive links.
2. The selective forces (energetic costs, timing delays related to specific behavior, and space) that may play important roles in generating the variation in the VNC structure need further elucidation to explain the observed variation.
3. Little is known about the genetic changes that underlie the morphological diversity of insect VNC structures. In particular, knowing which genes and gene products are involved in establishing the pattern of neuromere fusion or separation and how their expression is controlled is essential for understanding how different VNC structures are generated during development.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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