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# Brainstem Organization and Branchiomic Nerves

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## Key Words

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## Abstract

The branchiomic portion of the vertebrate head represents a region of specialized function and, at the same time, a transition between head and body. Recent experimental work has called into question the 'visceral' nature of the branchiomes, interpreting them instead within the framework of the segmentation of the body, as is seen clearly in rhombomeres. The vagus nerve is critical to our understanding of this region. It is usually viewed as a serial homologue of dorsal roots of spinal nerves, and the hypoglossal, with its several roots, has been seen as arising from associated ventral roots. The accessory is often considered to have been derived directly from the vagus, having become individuated in tetrapods in general and especially in amniotes. Work on amphibians is examined with respect to these issues, and within structuralist, functionalist and phylogenetic frameworks. The accessory in mammals and birds is a composite; the spinal motor nucleus, which can be traced at least to elasmobranchs, is distinctly different in origin from the more recently added bulbar portion, which is derived from the vagus. The spinal portion appears to have evolved independently of the system associated with branchially derived musculature. The hypoglossal is derived from ventral-column material, but it is not clearly associated with the vagus phylogenetically.

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## Introduction

My interest in the posterior brainstem and cervical spinal cord arose from my attempts to understand the function of the highly specialized projectile tongues of plethodontid salamanders [1, 2]. Tongues of these species are constructed from the hyobranchial skeleton (parts of the hyoid and first two branchial arches), branchiomic muscles (for

protraction), and hypobranchial muscles (for steering and retraction). I wanted to learn what features of the motor control of these organisms enabled them to fire protractors and retractors simultaneously [3], achieving the most rapid musculoskeletal action in vertebrates [4] while maintaining exquisite control. So, with several colleagues I began a program of mapping the motor nuclei involved [5–8], and also tracing peripheral nerve routes [9].

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My venture into the nervous system built on earlier work that had traced the peripheral nervous system to the muscles of the tongue of salamanders [10–12], and was motivated mainly by ‘functionalist’ or ‘externalist’ concerns [13]. At about the same time, developmental biologists were entering a new and increasingly productive phase of work dealing with segmentation, the mesodermal organization of the head and trunk [14], and genetic correlates of development of rhombomeres and myelomeres [15, 16]. This work is based on unstated premises about evolution and development, such as concepts of ground plans and generative rules, and hence is strongly ‘structuralist’ or ‘internalist’ in perspective. Both perspectives are needed for a full understanding of morphological evolution [13, 17, 18], and thus the debate about the evolution of cranial nerves is an appropriate milieu for exploring how different ‘ways of seeing’ might be combined for a richer understanding of evolutionary morphology and vertebrate phylogenesis and evolution.

The classical interpretation based on embryological studies in sharks [19–21] was that the back end of the skull is segmented, and that the epimeres (somites) and hypomeres (lateral plate mesoderm) of the trunk continued anteriorly, where the pharyngeal clefts complicate matters. The idea was that the ‘branchiomic’ musculature of the clefts was serially homologous with smooth muscle of the hypomere that had become striated, and this was seen in the retained ‘visceral’ innervation through mixed sensory-motor nerves (V, VII, IX, X) that are entirely separated from their associated ventral roots (this was thought to display the ancestral condition, with joining of dorsal and ventral roots in the trunk being a derived condition). Cells of epimeric origin were observed to migrate ventrally, into the floor of the mouth, where they were innervated by ventral roots (hypoglossal, or nerve XII) associated with branchiomic dorsal roots. According to this view, the most posterior branchiomic became progressively reduced in size, in tetrapods, giving rise to the trapezius (*sensu lato*) and laryngeal muscles. The vagus (X) represented a consolidation of a number of branchiomic nerves, and the accessory (XI) was a tetrapod derivative, in essence the hindmost part of the vagus motor nucleus. The branchiomic muscles were served by a more or less continuous visceral motor column [22] that was seen as an anterior continuation and elaboration of the spinal column.

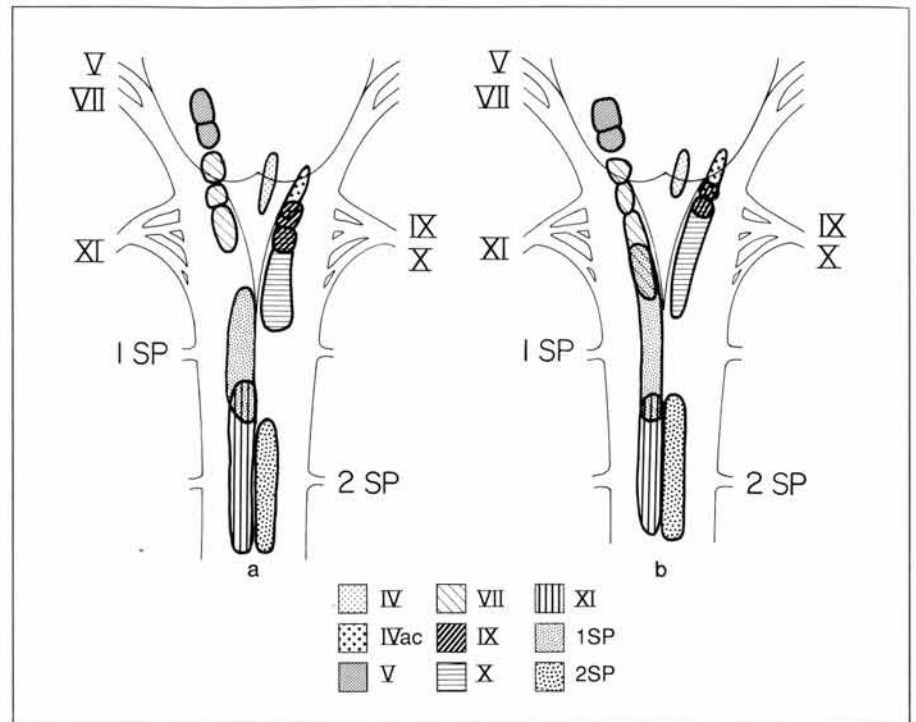
A detailed analysis of the head of *Amia* presented the most elaborate and formal model of the vertebrate ground plan [23]. This was incorporated into the magnum opus of Jarvik [24]. This scheme differed in some important aspects from the familiar and influential conception of Goodrich [25] and also from alternative approaches [26], but every-

one seemed to accept the fundamental points outlined above. However, as this scheme reached its most fully elaborated form, new data were beginning to cast doubt on some of its key features [27, 28]. This has all been summarized recently by Northcutt [29], and I will only deal with those issues of particular importance to my presentation. These are to demonstrate (1) that the vertebrate head is very ancient (pre-Cambrian, if the conodonts should prove to be myxinooids), (2) that the branchiomic muscle is derived from somitic tissue rather than lateral plate mesoderm, and (3) that the distinction between the end of the branchiomic series and the trunk musculature is more discrete than previously believed. At the same time, I will present evidence that some of the alleged distinctions between head and trunk are less clear than they appear. I will mainly discuss the group on which my work has been focused, amphibians, which have a generalized morphology with both a fully developed larval branchial system and a fully metamorphosed terrestrial adult system.

### **The Distinction between Brainstem and Spinal Cord**

Recent research on the developmental genetics of chickens and mice has demonstrated a distinction in gene expression between rhombomeres and myelomeres, and in paraxial mesoderm generally [30]. The complexities of homeobox (Hox) gene expression are under intense scrutiny, and it is premature to extend present findings too far. However, there is an apparent difference between the pattern of Hox gene expression in the rostral and caudal parts of the hindbrain. Thus, it is argued that ‘Segmentation seems, therefore, to have been retained in the upper hindbrain of higher vertebrates, but lost from more caudal parts of the neural tube’ [ref. 31, p. 409, citing ref. 32]. Rhombomere 8 (X is associated with rhombomeres 7 and 8, with the ganglion arising in R7) is longer than the others [32], and it is unclear at this point whether there is any pattern of gene expression that clearly demarcates R8 from the posterior segments [possibly Hox gene 2.1, ref. 30, fig. 5; however, these authors point out that Hox 2.1 is also expressed in the ganglion of X]. Clonal analysis in the chick hindbrain has shown that cells do not cross rhombomere boundaries, and therefore rhombomeres appear to be domains of lineage restriction [33], while in contrast to the developing hindbrain ‘myelomeres are not matched by segmental groupings of differentiating nerve cells, and result from mechanical moulding of the neuroepithelium by the neighbouring somites’ [ref. 34, p. 277].

**Fig. 1.** Topography of the brainstem in salamanders, showing the location and limits of motor nuclei discussed in this paper. Based on tracing with horseradish peroxidase [7, 8]. **a** Composite generalized pattern based on species of the families Ambystomatidae, Dicamptodontidae, Salamandridae, and Plethodontidae that are fully metamorphosing species. **b** Pattern found in the tribe Bolitoglossini of the Plethodontidae. The bolitoglossine salamanders are direct-developing species that have the most highly specialized tongues. There is considerable overlap of the motor nuclei in all taxa studied, but the overlap is extreme in the bolitoglossines, where the motor nucleus of VII completely overlaps that of IX and nearly all of X.



I believe that generalizations from studies of chicks and mice to all vertebrates, or to ancestral ground plans, are premature. For example, there are differences between taxa in the arrangement of myelomeres, and it is unclear what the ancestral state for vertebrates might have been. In the case of salamanders, it is questionable that the borders of myelomeres are respected. Figure 1 [generalized from ref. 7, 8] shows that there is extensive overlap in the brainstem motor nuclei in salamanders. Note, for example, that the motor nucleus of VII (which is very discrete) does not overlap rostrocaudally with that of V, but it does with that of IX and X. It even overlaps with the anterior part of spinal 1, especially in bolitoglossine salamanders. Thus, IX and X have no exclusive territory; IX is overlapped by VII and X, and X is overlapped by VII, IX and spinal 1, and in some species, slightly by XI. The cells are all intermingled in a single column, but there are cytological distinctions between them and each nucleus is clearly and discretely outlined. This pattern in salamanders differs substantially from that in frogs, in which the motor nuclei are more discrete and show little rostrocaudal overlap [35].

There are alternative ways to explain the patterns of overlapping motor nuclei in salamanders. A functionalist interpretation might focus on the initial condition of small

organismal size, large cells, and the functional advantage of firing all motor nerve cells simultaneously. A structuralist interpretation would instead see the large genomes of salamanders imposing fundamental shifts according to generative 'rules', with the condensation of somites because of too few cells playing a major role in the loss of prior segmentation. The large cells of amphibians might be responsible for the fact that only 4 cranial somitomeres are found in amphibians, whereas 7 are found in teleosts, chicks and mice (the ancestral condition is unknown, but is generally assumed to be more rather than fewer; with present data it is equally parsimonious to assume that 4 went to 7 and then reversed in amphibians, that 7 went to 4 in sharks and amphibians, or that 4 went to 7 in teleostomes and then reversed to 4 in amphibians) [14]. These explanations beg the question of evolutionary direction with respect to other vertebrate taxa and point to the need for an explicit and well-coordinated cladistic analysis of ontogeny.

The above statements make it clear that (1) more detailed investigation of the hindbrain-spinal cord boundary, and (2) formal comparative phylogenetic and ontogenetic analysis are needed [29]. We have some information from early development in zebra fish [36], which raises doubt about the view that the hindbrain and spinal cord develop

in fundamentally different ways. Study of early embryology is suggested [36], and the implication is that the ground plan would be revealed by such an investigation. I would emphasize study of complete ontogeny in taxa carefully selected for phylogenetic analysis – hagfish, lamprey, sturgeon, lungfish, salamander, caecilian, frog and perhaps a turtle or lizard. Then we would have filled out the zebra fish-chick-mouse picture and have a framework for an evolutionary interpretation of the findings. It has long been considered possible that there is not a single border between the head and body, and that there have been shifts during vertebrate evolution [e.g., ref. 37]; I remain dubious concerning this possibility, and would seek the explanation elsewhere.

### The Evolution of the Vagus and Accessory Nerves

The glossopharyngeal nerve (IX) of a generalized vertebrate – a shark or *Amia*, for example – can be taken as the paradigm for a rhombomeric nerve, with its diagrammatic organization and its motor control of branchiomeric musculature. Nerves V, VII, and X are all specialized, and the last was long thought to be a composite of some sort, having arisen by the condensation of several nerves that were formerly independent. Evidence of this is seen in the ganglia of Frierip, which appear in segmental positions behind the vagus but in front of the first complete spinal nerve, and in the multiple roots that combine to form the hypoglossal nerve (XII). Goodrich [25] was disturbed that he could find no evidence of compression of myomeres in the vagal region, and so offered an alternative interpretation, ‘partial polymerisation’. His very brief explanation [pp. 768–770] is based on the situation in lampreys, in which a series of vagal branchiomeres is served by branches from a long epibranchial nerve that is the most posterior branch of the vagus and extends backward, below the spinal nerves, giving off branches to successive branchial pouches. Goodrich supposed that all but the cutaneous sensory components of the first few spinal nerves have been gathered forwards into what he calls the anterior root of the vagus. He considers the epibranchial nerve to be a ‘partial collector nerve’. This collecting is supposed to take place over the entire branchial region.

A problem with the idea of condensation, or of the collecting of more posterior components, to form a vagus is the fact that the vagus retains its distinctiveness in all vertebrates, including lampreys and hagfish [38, 39]. This implies that the organization of the vagus must have taken place very early in vertebrate evolution, and since then has

remained very stable. Given this fundamental conservatism, a reinvestigation of changes in the vagus associated with the origin of vertebrates is in order. It is worth observing that while the issues involved are profound, rejection of anyone of competing hypotheses depends on rather subtle points and narrow interpretations. It is unlikely that these problems will be easily solved.

Most recent work on the developmental genetics of the hindbrain has failed to pay attention to the vagus. I suppose this is because in birds and mammals the branchiomeric muscles associated with the vagus are few and small. But in salamanders and other nonamniote vertebrates, the problem is important. For example, several muscles supplied by the vagus and responsible for gill movement in salamander larvae dramatically change function to project the tongue in adults, and there are intriguing problems associated both with metamorphosis and the evolution of direct development in relation to organization and function of the vagus.

Fox [40, 41] followed earlier workers [especially Drüner; ref. 42] in arguing that there is a segmental pattern of serially homologous branchial nerves and muscles in the development of salamanders. There are, at most, four functional gill clefts in salamanders, and earlier workers had reported finding as many as five branchial levator muscles, the first served by the glossopharyngeal and the remaining four by branches of the vagus. Fox reported three vestigial blind gill pouches behind the last functional one, and therefore postulated that in the ancestry of tetrapods there had been eight vagal segments. The picture is pretty clear for the first three branchial segments, each of which has a separate branchial levator. However, Fox [41] found that levators 4, 5, and 6 were joined ventrally and that they all served the fourth branchial arch in *Hynobius*. The dilator laryngeus and the trapezius (cucullaris) were seen as homologues of branchial levators 7 and 8. According to this view, the dilator laryngeus and the trapezius are serial homologues of more anterior branchial levator muscles that evolved in the context of tetrapod origins. Rather romantically, Fox [ref. 41, p. 198] declared that ‘Vestiges of ancestral pharyngeal structure remain during the ontogeny of *Hynobius* and *Cryptobranchius*, but with the subtle and elegant economy which nature regularly practises, components which served for an aquatic existence are used by tetrapods to survive and flourish on land’. The general assumption of Fox and other workers, never really refuted, was that the larval organization of salamanders generally preserved the ancestral condition, or at least reflected the ‘Bauplan’ with greater fidelity than any other condition found in tetrapods.

Fox [41] identified what he termed vagus I, II and III. As the glossopharyngeal innervates branchial levator 1, vagus I serves branchial levator 2, vagus II serves branchial levator 3, and vagus III innervates levator 4. There is a final vagal root that divides into three branches, the first two of which serve levators 5 and 6, and the last the dilator laryngeus. The trapezius is innervated in *Hynobius* larvae by a 'stout nerve from the upper surface of the vagus ganglion'. Fox believed that vagal nerves IV, V and VI had fused, and argued that all the vagal nerves were extant [his table 2, p. 197, makes clear that he considered the trapezius to be innervated by vagus VII].

Curiously, Fox failed to cite what appears to be the most thorough study of morphogenesis of the branchial region in a salamander, that of Piatt [43] on *Ambystoma*, a study that included extensive extirpation experiments. Piatt reported only four branchial arches, but he found that the levator muscle of the fourth arch had at least three heads, one innervated by a branch of the second branchial trunk (which also sends a branch to the levator of the third arch) and the others by a nerve that he termed the 'first ramus (n. accessorius) of the visceral trunk of the vagus'. The trapezius was served by this latter nerve, and Piatt considered it to be a muscle of the fourth branchial arch. However, Piatt considered the dilator laryngeus to be an entirely different kind of muscle, derived from splanchnic rather than somatic lateral plate mesoderm together with all other laryngeal muscles. He reported the muscle to be innervated by the visceral trunk of the vagus. Piatt agreed with Edgeworth [44] that the dilator laryngeus was not a serial homologue of the branchial levators. These workers were not able to differentiate the vagus from the accessory, because they lacked tracing methods and did not use degeneration experiments.

A final muscle that enters into the controversy is the so-called opercularis, a muscle that extends from the shoulder to the middle ear bone in salamanders and frogs. This is a slip of the cucullaris (trapezius) in plethodontids, and shares its innervation, but in other amphibians it is a slip of the levator scapulae, a muscle served by the hypoglossal nerve. (The innervation of the levator scapulae is complicated. In frogs, the second spinal and the hypoglossal have separate roots that join distally, so the muscle might have strict spinal innervation.)

Students of salamander development have reported that the hyoid and all posterior branchiomic muscle is derived from the anterior part of the lateral plate mesoderm, and Piatt [43] makes this derivation explicit [see, especially, table 2, p. 567]. However, his figures [especially those on plate 5, p. 581] raise the possibility of derivation from

paraxial mesoderm, a necessary consideration in view of the findings of Noden [28]. There is a pressing need for a study using tracing methods in salamanders, in which the derivation of branchiomic muscles from lateral plate mesoderm has seemed so clear.

In the light of the above information, the discovery of a discrete accessory nerve (XI) fully within the cervical spinal cord in salamanders [5–7] and frogs [35, 45] has special significance. This nucleus in amphibians has a distinctly spinal as opposed to a cranial cytoarchitecture.

The accessory nerve of mammals has two components, a bulbar motor nucleus which contains preganglionic (parasympathetic) neurons, and a spinal motor nucleus which may contain some preganglionic neurons but mainly contains motor neurons that innervate the trapezius and its derivatives [46, 47]. The bulbar portion seems best interpreted as the caudal portion of the dorsal vagal nucleus [38]. There are conflicting views concerning the origin of the spinal motor nucleus.

It was once generally thought (and is still widely reported in general texts) that the spinal component of XI is composed of the most caudal roots of the vagal motor nucleus in 'lower vertebrates', and that this portion migrated ventrocaudally and became independent in 'higher vertebrates' [38]; hence, the spinal motor nucleus was considered to be a derivative of an original dorsal root with so-called special visceral (serving striated branchiomic muscle) function. Piatt [43] and Fox [41] implicitly accept this view in their interpretation of muscular morphogenesis in salamanders. Recently Szekely and Matesz [47] argued that many histological features shared by accessory and branchiomic neurons, as well as axonal routes identical to those observed for other neurons in the branchiomic column, suggest that the accessory is a detached cranial nerve, controlling the movements of the head by using muscles derived from the posterior branchial arches. As in so many arguments over this region, these authors make much of the distinction between branchiomic and somatic muscle origins, whereas we have seen (above) that this distinction is not as clear-cut as it once seemed.

Addens [38], in an exceptionally thorough analysis and argument, disagrees with this interpretation, and considers the spinal nucleus to be 'nothing else but part of the foremost spinal roots' (p. 341). He cites the fact that the trapezius muscle is innervated by spinal nerves as well as by the spinal component of XI [48], and evidence that the trapezius has a myotomal origin (at this time it was assumed that branchiomic musculature originated from anterior lateral plate mesoderm). Addens identified a spinal component in fishes, and this was widely ignored by subsequent work-

ers, although it has been verified by recent tracing studies [49].

The fasciculation of the outflow of the spinal component of XI with X is ancient, and the long cranial route of the fibers of XI up the spinal cord and into the skull clearly has influenced many workers in their interpreting the nerve as being of cranial origin. However, such a fasciculation is not a unique condition. In caecilians, an occipital nerve exits the skull with the vagus in some species, but has a separate foramen in others, and in others still it exits between the skull and the first vertebra [50]. Furthermore, the spinal accessory does not always exit with the vagus; in several ungulates there is no distinct XI and the trapezius complex is served by nerves that exit through several cervical vertebrae [38]. While XI generally serves the trapezius complex of muscles, it may also serve some others in the neck region; too few tracing studies have been done as yet to have a full picture of this nerve. In caecilians, which lack any vestige of limbs or girdles, and have no trapezius, we have been unable to find any evidence of a spinal accessory system [unpubl. data].

In amniotes the accessory nerve is clearly a composite motor nerve; the so-called bulbar motor nucleus of the accessory is best viewed as a component of the vagus. The spinal motor nucleus of the accessory, in contrast, is ancient and discrete, and I believe that it has nothing to do with the ventral (branchiomic) component of the vagus (nucleus ambiguus). The latter nucleus (best known in mammals) was long thought to have the sole function of supplying branchiomic musculature, while the dorsal motor nucleus was thought to contain all preganglionic (parasympathetic) motor neurons (typically smaller in size). This is now known to be wrong; the nucleus ambiguus contains preganglionic motor neurons as well, making it clear that there is a sharp distinction between it and the more posterior nucleus of the spinal accessory [46, 51]. There remains the fact that the nucleus ambiguus supplies the intrinsic musculature of the larynx in mammals. This musculature is formed from lateral plate mesoderm in all groups investigated (the work of Noden [28] is strongly suggestive on this point for birds). The innervation could be taken as evidence that the larynx is phylogenetically derived from the last branchial arch, and has undergone developmental reorganization in tetrapods. Alternatively, I would argue that the laryngeal musculature, of splanchnopleuric origin, has built upon the foundation of the preexisting vagal innervation of the pharynx and is a tetrapod invention.

The new data support a modified version of the views of Addens [38] and reject the hypothesis that the trapezius complex and the musculature of the larynx are branchio-

meric in origin. The motor nucleus of the vagus has undergone parcellation (probably associated with evolution and elaboration of the parasympathetic system; there is no dorsal nucleus in hagfishes or in salamanders [7]). However, the fundamental organization of the nerve has been relatively stable since the phylogenetic event separating the myxinooids from other living vertebrates, and there was little change in the nerve (loss of some muscles that historically were innervated; gain of some newly differentiated laryngeal muscles) associated with the origin of tetrapods.

### Evolution of the Hypoglossal Nerve

I close with a few observations on the hypoglossal complex and its relation to the branchial region of the skull. Bjerring [23] considered the hypoglossal nerve to be composed of the ventral roots of several (usually three) occipital nerves, the dorsal parts of which constituted the vagus and three more posterior nerves that have been incorporated into it. Bjerring considered the region to be so strictly ordered that he thought the concept of branchiomic musculature should be abandoned. An alternative view would see the posterior branchiomic (served by the vagus) region as being an elaboration associated with gill development and overlain on the general ground plan.

In amphibians, the hypoglossal nerve is formed by two or three nerves that join at some distance from their origin. One of these nerves always exits via a foramen in the first spinal vertebra. In some caecilians there is an occipital component, but it is absent in all adult salamanders and frogs. There are two distinct hypoglossal nuclei in frogs; the dorsomedial appears to be the homologue of the hypoglossal nucleus of mammals, while the ventrolateral nucleus appears to be a basically spinal element [reviewed in ref. 8]. In amniotes, the main hypoglossal nerve has its own cranial foramen, but there are some minor but complex connections to the first few spinal nerves. The hypoglossal of chondrichthyans, actinopterygians and sarcopterygians is also made up of several roots, usually two occipitals and the first spinal. In some species these retain dorsal rootlets and ganglia.

Recently, a series of rudimentary ventral rootlets has been observed in whole mounts of chicks stained by an immunohistochemical technique [52]. These rootlets extend in a straight line rostrally from the spinal ventral roots to the caudal rootlets of the abducens (IV). They are not strictly segmental, but rather occur in a zone; the authors interpret them to represent maximally four occipital and three cervical ventral roots. The more anterior of

these rootlets disappear, and the posterior ones join to form the hypoglossal. The subcephalic muscle of *Latimeria* is innervated by the abducens [53], and this is probably the homologue of the retractor bulbi of tetrapods (and I would predict that the lateral part, or accessory, abducens motor nucleus serves the subcephalic muscle). Some rudimentary basicranial muscles appear during salamander development [23], and these, too, are associated with a zone of ventral rootlets like those reported in chicks. However, I doubt that there is a strict segmental order to this region. Rather, there is a ventral and medial column that extends from the brainstem into the spinal cord, and I suspect that outflow from it is organized more by peripheral segmentation and differentiation than by the kind of association between rhombomeres and homeobox genes seen for the ganglion-associated elements (V, VII, IX and X). There does not seem to be a special association (that is ventral root to dorsal root) with the vagus complex, although there might be with the occipital complex and the system of vestigial ganglia (Froriep's ganglia) associated with them. It could be that the division of the hypoglossal motor nucleus in frogs [54], giving rise to ventromedial and dorsolateral nuclei, the latter apparently having migrated during evolution, is the model we should use to understand the earlier origin and segregation of the spinal accessory nucleus, which I believe ultimately arose from the ventral motor column in the cervical spinal cord.

## Conclusions

Functionalist interpretations of the evolution of the brainstem and branchiomeres focus on the evolution of pharyngeal gills and the posterior expansion of the branchial region associated with requirements for ventilatory and then feeding functions. The enlargement and elaboration of the vagus nerve, the separation of the dorsal nucleus, and the establishment of a nucleus ambiguus could be interpreted in such a framework. A structuralist interpretation for the region might be based on the concept of a

morphotype or ground plan, and a focus on the genetic and developmental phenomena responsible for individuation and specialization of rhombomeres and somites. I have focused attention on the transition from head to body, and on the vagus, accessory (especially the spinal component), and hypoglossal nerves to show how ground plan models have driven interpretations of data. There is a need for both functionalist and structuralist approaches. I believe that the greatest success will come when the two approaches are kept relatively 'pure' in initial research efforts, so as to avoid intellectual contamination at too early a stage and, thus, a confusion of issues, but are combined in the synthetic phase. The vertebrate ground plan, or 'Bauplan', is ancient and pervasive. Because ontogeny does not recapitulate phylogeny in a predictable way, and because von Baerian recapitulation has discrete limitations and can give a false sense of security, the 'Bauplan' must be revealed by an appreciation of full ontogenies rather than by simply studying very early embryology. There has been selectively driven evolution of the nervous system, and perhaps fasciculation and parcellation, to give two very general examples, will ultimately be understood in this context. But, we must have well-designed phylogenetic analyses throughout, because the role of history has been profound, even dictatorial. Functionalism, structuralism and history, pursued individually and together, offer a pathway for understanding how complex morphologies evolve.

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