A Monument of Inefficiency: The Presumed Course of the Recurrent Laryngeal Nerve in Sauropod Dinosaurs

A monument of inefficiency: The presumed course of the recurrent laryngeal nerve in sauropod dinosaurs

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The recurrent laryngeal nerve is an often cited example of "unintelligent design" in biology, especially in the giraffe. The nerve appears early in embryonic development, before the pharyngeal and aortic arches are separated by the development of the neck. The recurrent course of the nerve from the brain, around the great vessels, to the larynx, is shared by all extant tetrapods. Therefore we may infer that the recurrent laryngeal nerve was present in extinct tetrapods, had the same developmental origin, and followed the same course. The longest-necked animals of all time were the extinct sauropod dinosaurs, some of which had necks 14 meters long. In these animals, the neurons that comprised the recurrent laryngeal nerve were at least 28 meters long. Still longer neurons may have spanned the distance from the end of the tail to the brainstem, as in all extant vertebrates. In the longest sauropods these neurons may have been 40–50 meters long, probably the longest cells in the history of life.

Key words: Dinosauria, Sauropoda, larynx, neck, neuron.

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Introduction

The recurrent laryngeal nerve (RLN) has become a touchstone in evolutionary biology, as an example of suboptimal morphology caused by a developmental constraint. The RLN, a branch of the 10th cranial (vagus) nerve, innervates the sixth pharyngeal arch, which in tetrapods includes most of the muscles of the larynx (Goodrich 1930), and also provides some sensory innervation to the trachea and esophagus (Murray 1957; Sun et al. 2001). The paired RLNs develop caudal to the aortic arches early in embryonic development. Later the head and heart are separated by the development of the neck. As the heart and its great vessels descend into the thorax, the RLNs are dragged along. The neurons that make up each RLN are forced to elongate in order to maintain their connections to the brainstem on one end and the larynx, trachea, and esophagus on the other. In adult tetrapods, the neurons of the RLN exit the brainstem with the other roots of the vagus nerve, pass out of the skull through one of the ventral or caudal foramina (the identity of this foramen varies among tetrapods), descend into the thorax, branch off from the vagus nerve, loop around the vessels derived from the fourth and sixth aortic arches (in mammals, the aortic arch and ductus arteriosus on the left, and subclavian artery on the right), and pass back up the neck (i.e., recur) to their innervation targets in and near the larynx (Hooper 1887; Fig. 1).

Necks vary in form, proportion, and function among tetrapods, and the length of the RLN follows suit. In humans, the extra length of the nervous pathway imposed by the loop around the great vessels is relatively minor, because our necks are short. The length of the nerve fibers is roughly double the length of the neck, so the RLN is disproportionately long in long-necked animals. Among extant animals, the longest RLNs occur in giraffes, which maintain the same topological relationships between the nerves and the great vessels as in humans; this was first demonstrated by Owen (1841). The tallest giraffes have necks up to 2.4 m long (Toon and Toon 2003), so the total length of the nervous pathway from the brainstem to the larynx along the descending vagus and ascending recurrent laryngeal nerves approaches 5 m in the largest individuals. The extreme length of the RLN in the giraffe is frequently cited as the kind of post-hoc evolutionary kludge (= workaround) that an intelligent designer would surely have avoided (e.g., Berry and Hallam 1986; Darwen and Yao 1993; Forsdyke 1993; Coyne 2009; Dawkins 2009; Kinsella and Marcus 2009). However, the RLNs of some dinosaurs were much longer than those of giraffes, and therefore represent even worse design.

Even the neurons that made up the RLNs in the largest sauropods were not the longest cells in their bodies. In all extant vertebrates, some primary sensory neurons connect specialized receptors in the skin with higher-order neurons in the brainstem, and these cells therefore span the distance from the back of the skull to the most distal extremity. In the largest extant whales, primary sensory neurons are estimated to approach or exceed 30 m in length; in the longest sauropods
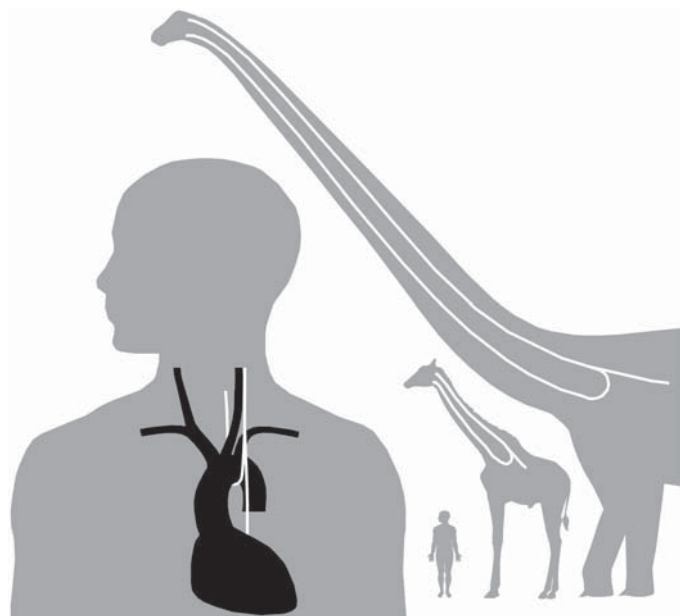
Fig. 1. Course of the left vagus nerve and left recurrent laryngeal nerve in a human, a giraffe, and *Supersaurus*. The right recurrent laryngeal nerve passes caudal to the right subclavian artery rather than the aorta and ductus arteriosus, but otherwise its course is identical to that of the left.

the homologous neurons may have been more than a third again as long, and were probably the longest cells in the history of life.

Institutional abbreviation.—BYU, Earth Sciences Museum, Brigham Young University, Provo, USA.

Other abbreviation.—RLN, recurrent laryngeal nerve.

Background

In the nervous systems of higher animals, the neuron cell bodies are located in the central nervous system and in the ganglia of the autonomic nervous system. Nerves radiate from the central nervous system to convey commands and sensory information to and from the extremities, and between the autonomic ganglia and visceral organs. These nerves consist of bundles of axons and their supporting cells (neuroglia) enclosed in sheaths of connective tissue (for a general overview of vertebrate neuroanatomy, see Butler and Hodos 1996).

The RLN is similar to other peripheral nerves, in that it comprises bundled axons that connect nerve cell bodies in the central nervous system with distant target cells, in this case in the larynx and pharynx. The larynx is present in all tetrapods. Its primary functions are to protect the trachea and lungs from ingested food and water, to regulate intrapulmonary and intrathoracic pressure, and, in some taxa, to produce and modify sounds (Negus 1962; Wind 1970; Kirchner 1993). Given the importance of these functions, especially airway protection, it is not surprising that the RLN is also

present in all extant tetrapods, including amphibians, reptiles (including birds), and mammals (Ecker 1889; Kaupp 1918; Adams 1939). In all of these animals it follows the same path around the vessels derived from the embryonic aortic arches. This implies that the passage of the nerve caudal to the aortic arches and its recurrent path to the larynx evolved in the common ancestor of tetrapods, and that the recurrent laryngeal nerve is therefore a shared feature of all tetrapods, living and fossil.

Could some extinct tetrapod have evolved a nonrecurrent laryngeal nerve that took a more direct path from the brainstem to the larynx? It appears unlikely, given the developmental and clinical correlations of nonrecurrent laryngeal nerves—those that run directly from the brainstem to the larynx without descending into the thorax and looping around the great vessels. Nonrecurrent laryngeal nerves are rare in humans, and never occur bilaterally. A nonrecurrent laryngeal nerve is present on the right side in less than 1% of humans, and is associated with abnormal arterial supply to the right forelimb (Sanders et al. 1983; Toniato et al. 2004). If the major artery to the right forelimb develops directly from the dorsal aorta distal to the left subclavian artery, there is no remnant fourth aortic arch (normally the right subclavian artery) to pull the nerve down into the chest, and the nerve can take a direct path from the brainstem to the larynx, although the nerve is still recurrent on the left side in these individuals. A nonrecurrent laryngeal nerve on the left is extremely rare (0.04%) and is always associated with situs inversus (Toniato et al. 2004), in which the normal bilateral asymmetries in the internal organs are reversed left to right. In other words, the nerve is nonrecurrent for the same reason as the nonrecurrent right RLN described above, only reversed left to right inside the body; in this case of reversed symmetry the right RLN would still pass caudal to the aorta and ductus arteriosus and take a recurrent path back up the neck. Situs inversus is itself frequently associated with primary ciliary dyskinesia (Kartagener Syndrome; Guichard et al. 2001), which may account for the paucity of cases. In both of these examples of nonrecurrent laryngeal nerves, the contralateral RLN must still loop around the aorta and ductus arteriosus (on whatever side those vessels occur), so these anomalies do not represent variations that could lead to bilaterally nonrecurrent laryngeal nerves, even if they somehow became fixed in a population.

The deep developmental conservation of the RLN is further illustrated by the fact that a nonrecurrent laryngeal nerve has not evolved in any known tetrapod, even in proportionally long-necked taxa such as giraffes and ostriches. The rarity of nonrecurrent laryngeal nerves in humans, their association with other developmental abnormalities, and the retention of the recurrent pathway in all known extant tetrapods, even those with long necks, together suggest that the recurrent pathway is too deeply entrenched in tetrapod development for a viable alternative to have evolved.

The recurrent laryngeal nerve in sauropod dinosaurs

To date, attention has focused on the giraffe as the ultimate example of the "unintelligent design" of the recurrent laryngeal nerve, perhaps because this nerve in the giraffe is the longest that can be directly observed. However, the longest-necked animals of all time are the extinct sauropod dinosaurs, and necks over 10 m long evolved independently in at least four sauropod lineages (Wedel 2006). The longest-necked sauropod for which cervical vertebrae are available is *Supersaurus*. The longest cervical vertebra of *Supersaurus*, and the longest single vertebra discovered to date for any animal, is BYU 9024, which has a vertebral centrum 138 cm long (personal observation). Scaling up from the complete neck of the closely related *Diplodocus* and making the conservative assumption that BYU 9024 is the longest vertebra in the neck yields an estimated neck length of at least 14 m (Wedel and Cifelli 2005). The *Supersaurus* individual represented by BYU 9024 probably had neurons whose length along the path from the brainstem to the larynx exceeded 28 m (92 ft).

It may be impossible to determine how the 28 m path from the brainstem to the larynx, if present, affected *Supersaurus* in life. There are apparently no physiological barriers to the existence of such immensely long cells, because the longest neurons in extant whales may exceed 30 m (see below). However, the conduction of nerve impulses to the larynx by such a circuitous route has interesting implications for nerve conduction velocities and the coordination of swallowing. As the axons that comprise nerves grow longer, conduction time of nerve impulses increase unless mechanisms evolve to increase the conduction velocity (Hartline and Colman 2007). In the giraffe, the great length of the RLN is compensated to some extent by larger, more heavily myelinated nerve fibers, which allow faster conduction velocities (Harrison 1981). The swallowing reflex involves coordination of laryngeal contraction, governed by the extremely long RLN, with contraction of the pharynx under the control of the much shorter (<1 m) superior laryngeal nerve, which takes a more direct path from the brainstem to the larynx. In sauropods, this coordination may have been accomplished by varying conduction velocities in the two nerves or by higher-level neural control of the impulses governing muscular contraction. Whatever the mechanism of coordination, it must have been able to accommodate massive changes in the disparity between the lengths of the two nerves over ontogeny, as the sauropods grew from hatchlings with necks much less than 1 m long into massive adults.

Laryngeal vocal folds are present in anurans (frogs and toads), mole salamanders, geckoes, bull snakes, crocodilians, and mammals, but they appear to have evolved independently in all these groups (Weishampel 1997; Fitch 2006; Senter 2008). In other tetrapods, including birds, the closest extant relatives of sauropods, sounds are generated by other regions of the respiratory tract that are not innervated by the recurrent laryngeal nerve (Romer and Parsons 1977), although the larynx may be used to modify those sounds (e.g., White 1968; Beckers et al. 2004). In a comprehensive review of animal sound production, Senter (2008: 255) found "no anatomical evidence for vocal ability" in non-avian dinosaurs. In the absence of data, the most that can be said is that if sauropods produced or modulated sounds using their larynges, those activities were subject to relatively long physiological delays. This effect of large body size on nervous system function has been demonstrated for living animals (More et al. 2010), but it probably reached its ultimate expression in the very long nervous pathways of sauropod dinosaurs, including those to the limbs and tail (see below).

Pain signals from the larynx to the brain in sauropods may have been considerably delayed. Unmyelinated vagal afferent fibers have conduction velocities as low as 0.5 m/s (Iggo 1958), and some unmyelinated fibers are present even in the recurrent laryngeal nerve of the giraffe (Harrison 1981). Unless selected for faster response, similar unmyelinated fibers would have taken almost a full minute to relay "slow pain" signals to the brain of *Supersaurus*! However, innervation of the skin of the throat region would have been provided by cervical nerves with much shorter pathways (<1 m) to the central nervous system, so even the largest sauropods would have felt external injuries to the throat almost immediately.

Even longer neurons in the longest whales and sauropods

Incredibly, the neurons of the recurrent largyneal nerve were not the longest cells in the bodies of sauropods. Some sensory pathways from the extremities to the brainstem were even longer.

In all extant vertebrates, some primary afferent neurons —those responsible for sensing vibration and fine touch— convey information from sensory receptors in the skin directly to the brainstem (Butler and Hodos 1996). The cell bodies of these primary neurons are located in dorsal root ganglia adjacent to the spinal cord. These are pseudounipolar neurons in which the nerve cell body is separated from the axon by a short stem (Fig. 2). The axon extends away from the stem in two opposing directions: peripherally to receptor terminals in the skin, and cranially to the brainstem in one of the dorsal columns of the spinal cord. At the cranial end, each axon synapses with an interneuron of the central nervous system. This pattern of neural "wiring" is present in all extant vertebrates, including lampreys and hagfish (Woodburne 1939; Ronan and Northcutt 1990), so it must have been present in extinct dinosaurs as well.

The length of the longest neurons in the body of a vertebrate can be deduced by determining the distance from the brainstem to the animal's most distant extremity. The longest extant vertebrates are blue whales, *Balaeonoptera musculus*, with total body lengths of up to 33.59 m (110 ft; Wood 1982).
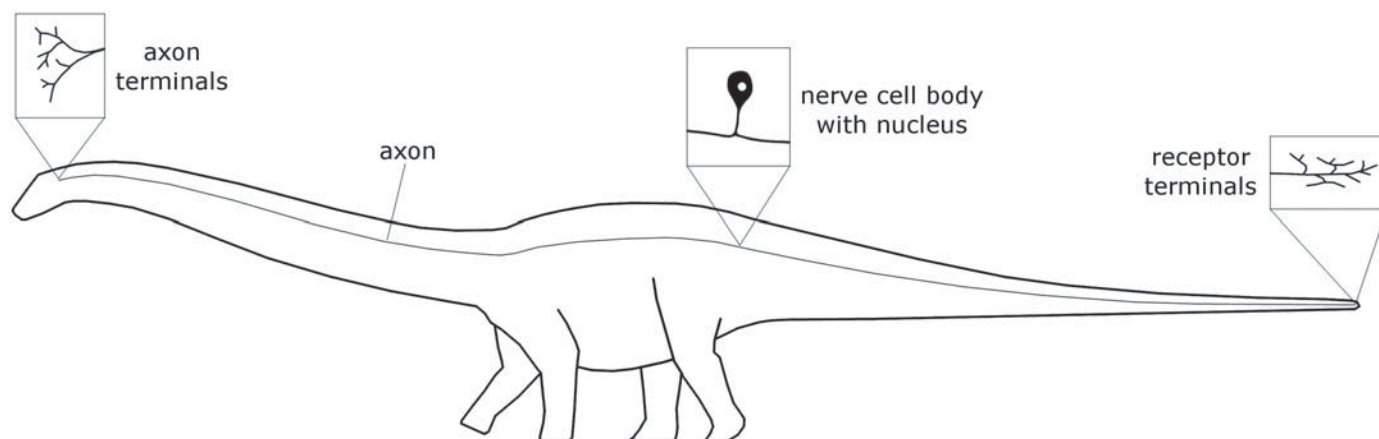
Fig. 2. The longest cells in the bodies of sauropods were sensory neurons that connected receptors in the skin of the extremities with interneurons in the brainstem, a pattern of neural architecture that is present in all extant vertebrates. The nerve cell bodies would have been located in the dorsal root ganglia adjacent to the spinal cord. The diagram of the neuron is based on Butler and Hodos (1996: fig. 2-1B).

Blue whales also have the longest skulls of any animals that ever lived, typically accounting for about 20% of the length of the body. The shortest possible path from the brainstem to the tail would therefore approach 27 m in the largest individuals. However, the axons must travel laterally to reach the ends of the flukes and the anatomical path of the nerve fibers is not perfectly straight, so it is likely that the largest blue whales have individual nerve cells 30 m or more in length. These may be the longest cells in any extant organism, although it is worth noting that their existence is predicted based on comparisons with smaller tetrapods; the continuity of individual neurons spanning the distance from flukes to brainstem has not been empirically demonstrated by dissection or neuronal tracing.

The longest sauropods were almost certainly longer than the longest whales, although precise measurements are impossible because all of the largest sauropods are known from fragmentary remains (see Carpenter 2006: fig. 3). Lovelace et al. (2008) estimated a total length of 33–34 m (108–111 ft) for the specimen of *Supersaurus* from Wyoming; the largest individual from Dry Mesa in Colorado was apparently slightly larger. The skull of *Supersaurus* was probably 1m or less in length, which would yield a pathway length from the brainstem to the end of the tail of perhaps 35 m in the largest specimens.

The problematic sauropod *Amphicoelias fragillimus* was probably even longer. Only a single partial vertebra of *A. fragillimus* was ever described (Cope 1878), and that has been lost for well over a century. Size estimates of *A. fragillimus* therefore face the dual uncertainties of being based on extremely fragmentary material and being impossible to check against a physical specimen. Carpenter (2006) produced a size estimate for *A. fragillimus* that is about 2.2 times the size of the famous mounted skeleton of *Diplodocus carnegii* in linear terms. Taylor (2010) independently obtained an estimate of 1.87 times the size of *D. carnegii* for *A. fragillimus*. These estimates suggest a total length, from snout to tip of tail, of 49–58 m (161–190 ft), and a maximum

neuron length only a meter or so shorter. Even with nerve conduction velocities approaching or exceeding 100 m/s, nerve impulses would have taken several tenths of a second to transit between the end of the tail and the brain in the longest sauropods. Unlike the unnecessarily long RLN, this is not an example of suboptimal design caused by a developmental constraint, but rather of animals approaching the real physical and chemical limits on living systems.

Even if we accept the estimated sizes for *Amphicoelias*, it is not known whether it had a longer neck—and therefore a longer RLN—than *Supersaurus*. The neck of *Diplodocus carnegii* is 6.5 m long (Hatcher 1901), and using the scale factors of 1.87 and 2.2 discussed above yields an estimated neck length of 12–14 m for *Amphicoelias*. If *Amphicoelias* was more similar to *Barosaurus* and *Supersaurus* in being proportionally long-necked, it might have had a neck up to 19 m long, and neurons in the RLN of 38 m or more.

The primary afferent neurons in whales and sauropods are much longer than any known cells in invertebrates such as the giant squid (*Architeuthis*) and colossal squid (*Mesonychoteuthis*). The giant axons of squid are widely used in studies of neuron function (Gilbert et al. 1990), but they are remarkable for their diameter—up to 1 mm—rather than their length. Cephalopods lack myelin and the only available mechanism to increase the conduction velocity of their nerves is to increase the diameters of the axons (Hartline and Colman 2007). The existence of squid longer than 13 m (43 ft) has been impossible to substantiate, and reports of larger specimens may represent exaggerations, crude field measurements, and stretching of the tentacles (O'Shea and Bolstad 2008). Nerve pathways from the brain or stellate ganglia to the tip of the tentacles in the largest squid would therefore be much shorter than the longest neurons in extant whales, let alone in extinct sauropods.

The physiology of neurons measuring many meters or tens of meters is difficult to investigate. One area of potential interest is axoplasmic streaming. An axon must not only transmit nerve impulses but also transport materials between

the nerve cell body and axon terminals. This transport is accomplished by streaming of cytoplasm within the axon, called axoplasmic streaming (Oztas 2003; Fletcher and Theriot 2004). Different substances are transported at different rates, which have been investigated in humans and small laboratory animals. Fast transport of neurotransmitters and enzymes can reach 200–400 mm/day, whereas the slow transport of some proteins averages 0.1–1.0 mm/day (Oztas 2003). Even at 1 mm/day, slow axoplasmic streaming would take more than four decades to move proteins from the nerve cell body to the axon terminals in the longest neurons of large whales. This is assuming that the nerve cell body was located at the midpoint of the axon, and that each transport stream only had to cover half the total length of the cell.

It seems very likely that whales, sauropods, and other giant organisms must have higher velocities of axoplasmic streaming than have been observed in humans and small laboratory animals, otherwise the movement of some substances from the nerve cell bodies to the axon terminals would take longer than the projected life spans of many individuals. Indeed, over the ontogeny of an individual animal the neuron would have to increase in length faster than documented speeds for slow axoplasmic streaming, which is probably impossible since the axon would require the transported substances to be enabled to grow in the first place. Although logically attractive, the hypothetical acceleration of axoplasmic streaming has not yet been demonstrated, and may be essentially impossible to demonstrate given the logistical difficulties of performing neurological experiments on whales. Although the largest domesticated animals are far smaller than large whales, they might provide a window into the physiology of multi-meter neurons in vertebrates.

Conclusion

The course of the recurrent laryngeal nerve appears to be an unchanging aspect of tetrapod embryology, being as developmentally fixed as the presence of a heart and paired vessels to the head. The existence of 28 m neurons in the RLN of *Supersaurus* may seem fantastic, but they appear unavoidable given what we know of tetrapod embryology and evolution. Other neurons in the bodies of sauropods were even longer, spanning the entire distance from the brainstem to the tip of the tail, and may have been the longest cells in the history of life. These incredible cells represent the interplay of evolutionary innovation and developmental constraint: the acquisition of giant, long-necked and long-tailed bodies built on a deeply conserved tetrapod bauplan.

Acknowledgements

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