Is the Tubular Nervous System Related with the Development of Skeletal Muscle in Chordates? – A Review

Rajani Singh[1]

[1] Department of Anatomy, All India Institute of Medical Sciences (AIIMS), Rishikesh, Uttrakhand, India

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Address for correspondence Dr. Rajani Singh, Department of Anatomy, All India Institute of Medical Sciences (AIIMS), Veerbhadra Marg Pashulok, Rishikesh, 249201, Rishikesh, Uttrakhand, India (e-mail: nani_sahayal@rediffmail.com).

Abstract

Many theories and arguments have been proposed regarding the ancestors of the vertebrates and the factors that lead to the evolution of the tubular nervous system. Invertebrates had simpler smooth muscles. Vertebrates acquired additional skeletal muscles. The skeletal muscles were found to be associated with a new type of tubular nervous system. There were three stages in the evolution of the nervous system. The most primitive was the network type, in which there was neither a polarization nor a centralization of neurons. The second stage was characterized by the evolution of a ganglionic nervous system. Then, the tubular type of nervous system appeared for the first time in chordates. Therefore, the author hypothesizes that the skeletal muscle developed simultaneously with the tubular nervous system. The chorda mesoderm and, thereby, the skeletal muscle, induced the formation of a tubular nervous system in chordates. In the present article, the author aims to analyze the nervous system, starting from invertebrates and moving on to chordates.

Keywords
- nervous system
- skeletal muscle
- chordates
- mesoderm

Introduction

Starting from unicellular organism up to most complex chordates, the evolution of nervous system is important for understanding the functions of the body including communication of external messages for defense from external enemies, as well as pathologies. Moreover evolution of the nervous system is also helpful to understanding progressive development of communicating channels to regulate body activity. This information will be useful for understanding changing sensitivity of different parts of the body.

Invertebrates represent 95% of all the living animals, and present a wide morphological diversity, ranging from jellyfish to insects and snails. These invertebrates are divided into 30 or more phyla, while vertebrates share a single phylum with the invertebrates, urochordates, and cephalochordates. However, invertebrates have played a vital role in increasing our understanding of the basic principles of neurobiology[1,2] and offer exciting avenues of new research, such as neural regeneration[3–5] and functional testing of individual neurons.[6] Invertebrates are critical to understand the evolution of the animal nervous system, which is intimately related to the evolution of intelligence. In the present article, the author has tried to analyze the nervous system starting with the most primitive animal, *Porifera*, which lack a nervous system, moving on to the chordates, which acquired the tubular nervous system found in all vertebrates, along with skeletal muscles. The author hypothesizes that skeletal muscles, which appeared for the first time in chordates, might have caused or induced the formation of the tubular nervous system. Thus, the aim of the present study is to establish this hypothesis by analyzing the nervous system, starting from *porifera* and moving on to the phylum *Chordata*.

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Porifera and the Origin of Neurons

Molecular, morphological, and developmental evidences suggest that the sponges (phylum *Porifera*) are the oldest living lineage of animals.[7–9] *Porifera* are multicellular and diploblastic organisms that have two layers: the pinacoderm (dermal epithelium), and the choanoderm (gastral epithelium), with a non-cellular mesenchym in between. These animals do not possess a mesoderm and, therefore, no muscle tissue of any type is present in these creatures. Although sponges lack neurons, they can use calcium ion channels to conduct electrical signals through their body and generate coordinated behaviors in a preneural manner.[10,11] Demosponges are known to go through rhythmic changes in body size, and some species can rapidly contract their openings and body sizes in response to stimulation.[12,13] Although *Hexactinellid* (or glass) sponges cannot contract like many demosponges, they can stop the beating of their flagella, halting the process of water intake.[12,13] *Hexactinellida* might also be capable of responding to light by using their spicule skeleton as optical glass fibers.[14] The idea that neural precursors exist in sponges is supported by genetic evidence. The *Amphimedon queenslandica* sponge has many of the genes required in other animals for synaptic targeting,[15] and larval sponges use proneural genes to develop some of their sensory cells in a manner similar to neurogenesis.[16]

Ctenophora, Cnidaria and the First Nervous System

The first animals to have true neurons were the *Ctenophora* and *Cnidaria* (sea anemones, jellyfish, and hydras). The neurons in these animals can generate electric currents (or action potentials) and communicate using neurotransmitters between synapses. However, these neurons are generally less specialized than the neurons of other animals. *Cnidarians (Coelentrate)* lack a centralized nervous system, and instead have multiple broad "nerve nets" that are identifiable by distinct neurotransmitters.[4,17] *Coelentrates*, such as the hydra, are also diploblastic, with two cellular layers: the outer epidermis and the inner gastrodermis, with acellular mesoglea in between. These animals also lack a mesoderm and muscles of any type and possess a very primitive type of nervous system. These have bipolar and multipolar nerve cells or neurons forming an irregular and discontinuous nerve net or nerve plexus (►**Fig. 1**). Neighboring nerve cells are not fused together, but their processes or neuritis form synaptic junctions. This type of nerve net is known as synaptic nerve net. Thus, the nervous system first appeared in the form of a nerve net in these creatures.

Ctenophore neurons can connect using any part of the cell body (most animals localize synapses at specialized axons and dendrites) and do so using a "presynaptic triad" consisting of synaptic vesicles, the endoplasmic reticulum, and one or several mitochondria.[18] Genomic data supports the hypothesis that these simple nervous systems are related to the more complex systems of other organisms. The genome of the *Nematostella vecensis* sea anemone includes genes that code for a variety of neurotransmitters, as well as receptor proteins that recognize these signaling molecules.[19] The similarities between the neurons of *ctenophores*, *cnidarians*, and other animals suggest that all neurons derive from one or a few cellular common ancestors.[20,21]

Fig. 1 Showing nerve net/plexus in Hydra.

Bilateria and the Origin of the Central Nervous System

The vast majority of existing animals are bilaterians, that is, animals with left and right sides that are approximate mirror images of each other. All bilateria are thought to have descended from a common wormlike ancestor that appeared in the Ediacaran period, between 550 and 600 million years ago.[22] The fundamental bilaterian body form is a tube with a hollow gut cavity running from the mouth to the anus and a nerve cord with an enlargement (a ganglion) for each body segment with an especially large ganglion at the front called the brain.

Bilaterians can be divided, based on events that occur very early in embryonic development, into two groups-superphyla called *protostomes* and *deuterostomes*.[23]

Deuterostomes include vertebrates as well as *echinoderms, hemichordates* (mainly acorn worms) and *Xenoturbellidans*.[24] *Protostomes*, the more diverse group, includes arthropods, mollusks and numerous types of worms. There is a basic difference between these two groups in the placement of the nervous system within the body. *Protostomes* possess a nerve cord on the ventral (usually bottom) side of the body, whereas in *deuterostomes* the nerve cord is on the dorsal (usually top) side. In fact, numerous aspects of the body are inverted between the two groups, including the expression of patterns of several genes that show dorsal to ventral gradients. Insects, for example, have nerve cords that run along the ventral midline of the body, while all vertebrates have spinal cords that run along the dorsal midline.[25]

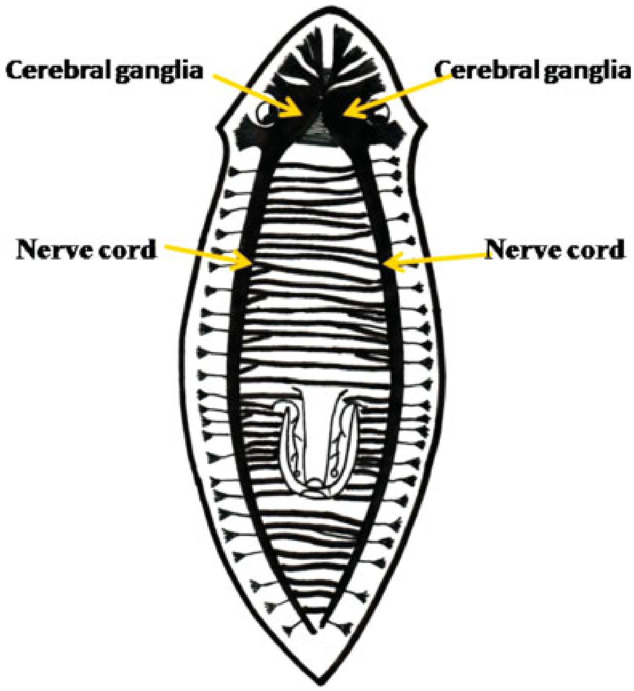

Fig. 2 Showing ganglionated nervous system in platyhelminthes.

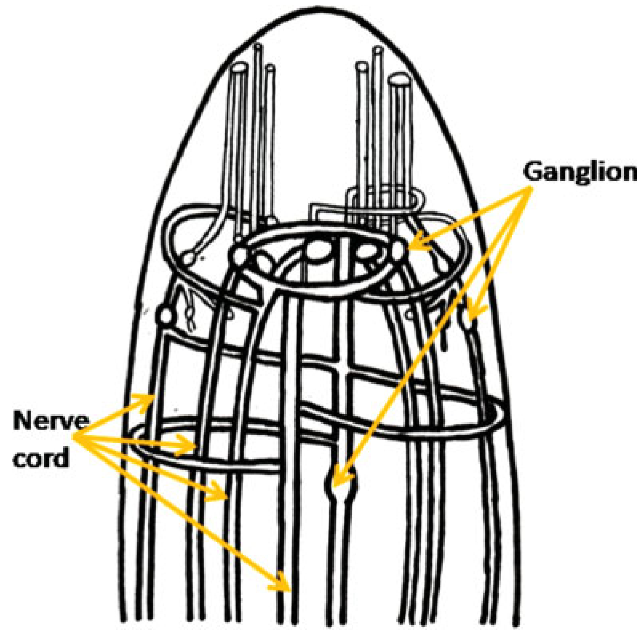

Fig. 3 Showing ganglionated nervous system in nematodes.

Worms are the simplest bilaterian animals. These include *platyhelminthes, nematodes* and *annelids*.

Platyhelminthes, such as the *Dugesia*, are triploblastic animals. The third germ layer is the mesoderm, which appeared for the first time in these animals. The mesoderm produces contractile muscle cells. The muscle cells form an outer layer of diagonal muscles and an inner layer of longitudinal muscles, which are smooth muscles. Thus, in these animals, the mesoderm has given rise only to smooth muscles, in contrast to vertebrates, in which the mesoderm forms both smooth and skeletal muscles. The skeletal muscle has not yet evolved in *platyhelminthes*. The nervous system in these animals marks the beginning of a centralized nervous system found in higher animals. There is a prominent bilobed mass of nervous tissue called brain or cerebral ganglia. The two lobes of the brain are connected by several transverse fibers. From the brain, two lateral longitudinal nerve cords arise, which extend to the posterior end. Each lobe of the brain gives rise to numerous peripheral nerves that supply various sense organs. Each nerve cord also gives rise to nerves on both sides along its whole length. Those arising from inner side anastomose with similar ones from the other nerve cord to form transverse commissures (►**Fig. 2**). Thus, the beginning of a ganglionated nervous system is a hallmark in these animals. The mesoderm gives rise to smooth muscles, which are constituted by longitudinal, circular and dorso-ventral fibers. There is no skeletal muscle in these animals.

The next higher group is constituted by *nematodes*. These are also triploblastic, with only longitudinal smooth fibers. In these worms, the skeletal muscle has also not yet evolved. Their nervous system is of the ganglionated type in form of a circumenteric ring and anterior and posterior nerves (►**Fig. 3**).

In annelids, the mesoderm gives rise only to smooth muscles, in the form of outer circular and inner longitudinal fibers. In these animals, there is also no skeletal muscle. Their nervous system is well developed and differentiated into central, peripheral and visceral nervous system. The central nervous system consists of cerebral ganglia (brain) with a double ventral cord bearing ganglia and lateral nerves in each segment (►**Fig. 4**). These nerve cords are connected by transverse nerves like the rungs of a ladder. These transverse nerves help to coordinate the two sides of the animal. Two ganglia at the head end function similar to a simple brain. In these animals, the ganglionated nervous system has persisted, but it has become more complicated, and a tubular nervous system has not yet appeared.

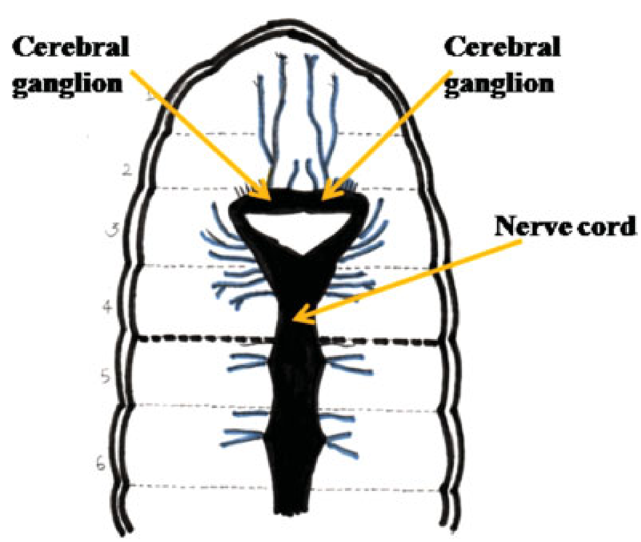

Fig. 4 Showing ganglionated nervous system in Annelids.

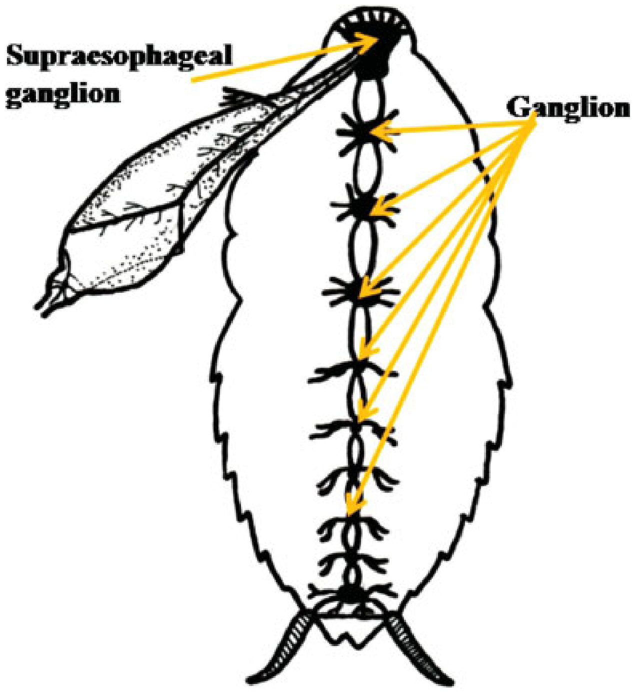

Fig. 5 Showing ganglionated nervous system in Arthropods.

Arthropoda are triploblastic animals. The three layers are the ectoderm, the endoderm, and the mesoderm. The mesoderm gives rise to both smooth and skeletal muscles. Skeletal muscles have appeared but are discontinuous and very poorly developed. Arthropods, such as insects and crustaceans, have a nervous system made up of a series of ganglia, connected by a ventral nerve cord made up of two parallel connectives running along the length of the belly.[26] Typically, each body segment has one ganglion on each side, although some ganglia are fused to form the brain. The head segment contains the brain, also known as the supraesophageal ganglion. In the insect nervous system, the brain is anatomically divided into the protocerebrum, the deutocerebrum, and the tritocerebrum. However, the brain in these creatures is different from the brains found in vertebrates due to the fact that it consists of ganglia containing no ventricles. Immediately behind the brain is the subesophageal ganglion, which is composed of three pairs of fused ganglia. It controls the mouthparts, the salivary glands, and certain muscles.

In the *Periplaneta americana,* which is an arthropod, the nervous system comprises of the central, the peripheral, and the sympathetic nervous system. The central nervous system consists of the brain and the ventral nerve cord. The brain is a bilobed mass located in the head. It represents three pairs of ganglia fused together. From the brain, a double ventral nerve cord runs posteriorly along the mid-ventral line of the thorax and the abdomen. It bears nine ganglia, three in the thorax and six in the abdomen. The ganglia give rise to nerves which constitute the peripheral nervous system. The sympathetic nervous system comprises four ganglia – one lying above the pharynx, the second lying on the esophagus, the third on the crop, and the fourth lying on the surface of the proventriculus (►**Fig. 5**). Thus, the nervous system is of the ganglionated type, with no evidence of the tubular type of nervous system and of skeletal muscles.

The next phylum is the chordates, which are triploblastic, that is, their nervous system consists of three layers: the ectoderm, the endoderm, and the mesoderm. In this phylum, such as in the *Amphioxus*, for example, the mesoderm gives rise to smooth as well as to skeletal or striated muscles. Thus, a well developed skeletal nervous system has appeared for the first time in these animals. However, their nervous system is very much simplified and a well-developed brain, such as that found in higher chordates, is absent, but their central nervous system consists of hollow dorsal neural tube lying middorsally above the notochord. Its anterior part ends abruptly in the rostrum. It shows a slight enlargement, called the cerebral vesicle. The posterior part is called the spinal cord. A narrow central canal called neurocoel runs throughout the length of the neural tube filled with cerebrospinal fluid (►**Fig. 6A**, **B**). It

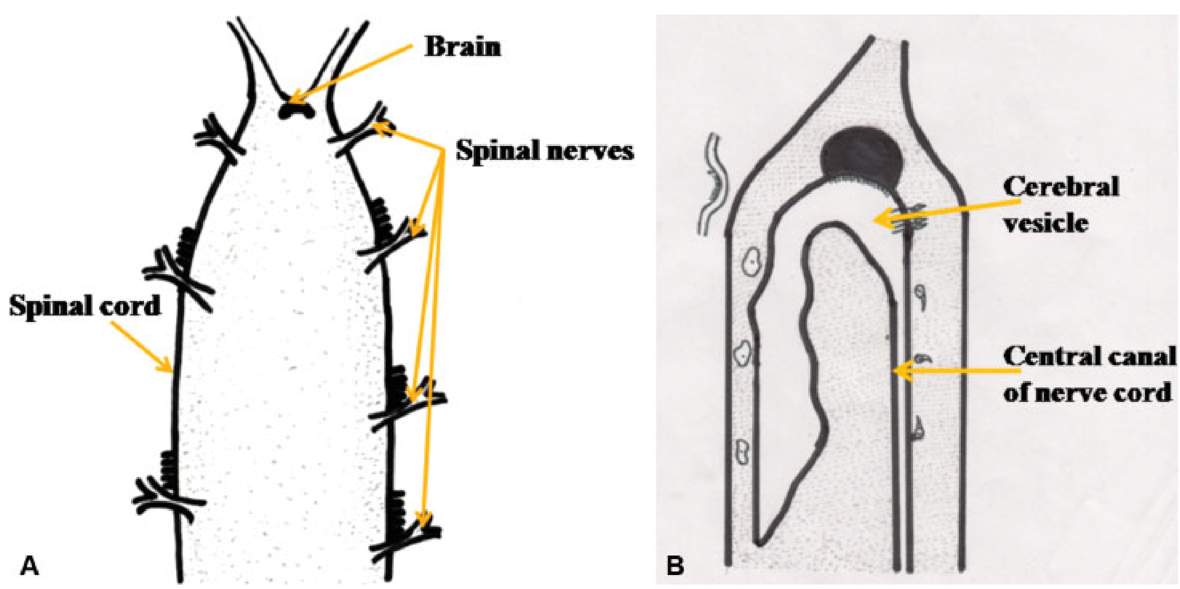

Fig. 6 (A) Showing tubular nervous system in Amphioxus. (B) showing tubular nervous system in Amphioxus in longitudinal section.

has a dilated cerebral vesicle, known as the ventricle. Histologically, the neural tube resembles that of other vertebrates. It consists of inner gray matter of nerve cells and outer white matter of nerve fibers. As we investigate the nervous system of still higher vertebrates, the nervous system becomes more complicated. But well-developed skeletal muscles are first observed in chordates, of which the typical example is the *Amphioxus*. A tubular nervous system was also found for the first time in chordates *(Amphioxus)*. Thus, it can be inferred that skeletal muscle has caused or induced the formation of the tubular nervous system. How this has been done it is an open question for future works.

Thus, in summary, the most primitive invertebrates—the *porifera*—consist of only two layers. There is no mesoderm nor muscles of any type. These animals have no nervous system. The next group, which consists of *coelenterates*, is also diploblastic, having no mesoderm but possessing a nervous system in the form of a nerve net. Although *platyhelminthes, nematodes* and *annelids* are triploblastic, having the mesoderm along with the ectoderm and the endoderm, the mesoderm is present but gives rise only to smooth muscles. There is no skeletal muscle. The nervous system is of the ganglionated type. Chordates are triploblastic. In these animals, the mesoderm also gives rise to skeletal muscles, besides smooth muscles. Well-developed skeletal muscles appeared for the first time in chordates, and the tubular nervous system also appeared for the first time in these animals. It can be said that skeletal muscles somehow induce the development of a tubular nervous system. This fact needs to be elucidated by further studies.

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