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Functional Anatomy of the Spinal Tracts Based on Evolutionary Perspectives

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ABSTRACT

The development of spinal cord represents evolutionary progression. The primitive tract is responsible for functions related to basic survival such as locomotion. In contrast, the developed tracts are involved in perceiving the external environment and controlling conscious movements. There are also differences in the arrangement of spinal tracts between the 2 categories. Tracts serving developed functions are located in the deep layer of the lateral funiculus, whereas primitive tracts occupy other areas. Decussation correlates with tract pathways, with primitive tracts projecting ipsilaterally and developing tracts decussating early. Understanding these principles provides insights into spinal tract organization.

Keywords: Spinal cord; Embryology; Neural pathways; Biological evolution; Anatomy

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GRAPHICAL ABSTRACT

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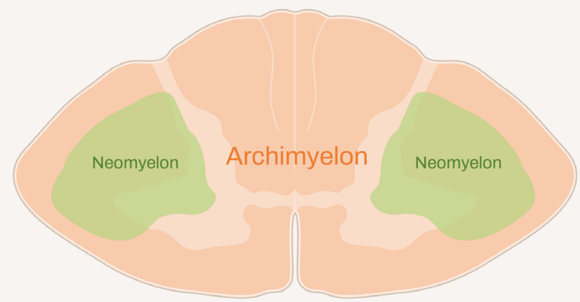
	Primitive ⟷		Developed
Sensory	Proprioception		Exteroception
	unconscious / conscious	undiscriminating	discriminating
Motor	Reflex Equilibrium Coordination		Volitional movement Fine movement

	Primitive	Intermediate	Developed
Arrangement	Archimyelon	Archimylon	Neomyelon
Decussation	None	Late	Early



Conclusion In the “Neomyelon”, tracts responsible for developed functions are located, while in the “Archimyelon”, tracts responsible for primitive functions are located.

INTRODUCTION

The spinal tracts located in the cord intricately convey various functions, and their course is complicated. The arrangement and pathway of the spinal tract also appear disordered and chaotic. These factors make it difficult for clinicians to systematically understand spinal tracts. Traditional classification based on ascending and descending pathways or sensory and motor functions still obscures the fundamental understanding of the spinal tract.

It is well known that the anatomical arrangement of the neural system has a good order than other systems. Particularly, the nucleus in the brain stem is well arranged by its functional component.[7]

The spinal tract in the cord, which is a continuum of the brain stem, also has a coherent arrangement and conformable pathway. This article reviews the functions of the spinal tract based on embryological concepts and provides rules for its arrangement and pathways. Students and specialists majoring in neuroscience or spinal diseases will have more comprehensive insights into the spinal tract and the function of the spinal cord with this concept.

EVOLUTION OF CORD FUNCTIONS

Like other components of the neural system, the spinal cord has evolved over time. Consequently, the human spinal tract contains a condensed representation of the sequential stages of evolutionary development, ranging from primitive to advanced.[13,29] To gain a comprehensive understanding of the spinal tract, it must be examined from an embryological perspective.

Primitive organisms require only basic neural function to control life-supporting organs.[4] More developed animals require a neural structure that receives signals from the locomotor organs and utilizes them to maintain equilibrium and regulate posture. The next evolved sense is exteroception, which involves perceiving stimuli originating from the external environment through sensory receptors in the skin. Sensing vibrations or touch from whiskers or hairy skin is crucial for the survival of animals that live in underground tunnels or narrow spaces in the dark. As vision became more important, a visual correlation between the body and extremities developed. The final part of evolution is interaction with a foreign environment and sophisticated movements controlled by the volition generated by the cerebral cortex. Advanced function also needs to be correlated with new sharp and discriminative sensations on the skin. The newly developed tract begins to intervene among the older primitive tracts.[17,22]

EMBRYOLOGICAL VIEW OF SENSE AND MOTOR

Proprioception represents "one's own sense" and is called as "kinesthesia."[1] Proprioception originates from receptors in the inner ear and locomotive organs such as muscles, joints, and tendons. This enables the maintenance of a balanced posture by integrating equilibrium and coordination. Even with our eyes closed, we can perceive whether our arms are bent. This is an example of conscious proprioception. When we walk, our leg muscles automatically stretch and contract, which makes the knees bend and straighten although we are not consciously aware of this. This is a typical example of unconscious proprioception. The signal evoked by the Golgi tendon and muscle spindle projects into the cerebellum, which is called unconscious proprioception. Owing to unconscious proprioception, the body automatically maintains balance, posture, and reflexes without conscious effort or awareness.[19]

Signals originating from mechanoreceptors in the skin and joints are transmitted to the cerebrum in a process known as conscious proprioception. This mechanism enables us to be aware of our body movements.[24] Conscious proprioception is a more developed function than unconscious proprioception. In contrast, exteroception senses the signals generated by sensory receptors triggered outside the body, such as vibrations, touch, pain, and temperature. Exteroception reaches the cerebral cortex and can be felt at the level of consciousness. Exteroception is more advanced compared to proprioception.[5]

The function of muscle tone can be subclassified into the extensor and flexor groups.[3] Most reflexes tend to activate the extensor muscles, such as when falling from a height or tumbling. The elbows are extended to protect the body. The knee jerk, patella tendon reflex, ankle jerk, and Achilles tendon reflex are activated by proprioception generated by the Golgi tendon organ of each tendon. When the tip of the toes touch the ground while walking, these reflexes are automatically activated and prevent the body from leaning forward.[20] The flexor muscle is activated when walking or grabbing an object, and is related to volitional or delicate movements. The extensor component, which mainly acts as an enduring motion, develops early, and the flexor component is subsequently added. Thus, the control of flexor muscle tone is more developed than that of extensor muscle tone. Volitional motion, which is directly controlled by the cerebral cortex, is the most developed function. While the proximal

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	Primitive ←→			Developed
Sensory	Proprioception		Exteroception	
	Unconscious	Conscious	Undiscriminating	Discriminating
Motor	Reflex		Volitional movement	
	Equilibrium		Fine movement	
	Coordination	Extensor muscle	Flexor muscle tone	
		Trunk, proximal muscle	Distal muscle	

FIGURE 1. Motor and sensory functions in order of development stage based on embryological perspective.

muscles are related to enduring motion, the distal muscles are related to fine movement. The control of the distal muscles is a more developed function than that of the proximal muscles. The motor and sensory functions are arranged in the order of developmental stage based on embryological perspectives in **FIGURE 1**.

TRENDS IN ARRANGEMENT AND DECUSSATION

One characteristic of spinal tract arrangement is that the tracts serving developed functions are located in the deep layer of lateral funiculus and the tracts serving primitive functions occupy the other area, regardless of ascending and descending tract or motor and sensory function. It was proposed to divide the spinal cord into 2 parts from an embryological perspective, distinct from the conventional approach, and label them as "neomyelon" and "archimyelon" (**FIGURE 2**). The neomyelon is responsible for tract development and the archimyelon is associated with the primitive tract.

There is a trend toward decussation of primitive and developed tracts. The primitive tract does not decussate and projects to the ipsilateral side. Contrarily, the developed tract decussates in its course and connects with the contralateral side. For example, the reticulospinal tract, a primitive motor tract, controls body movements at the unconscious level and descends into the archimyelon of the spinal cord without decussation.[2] In contrast,

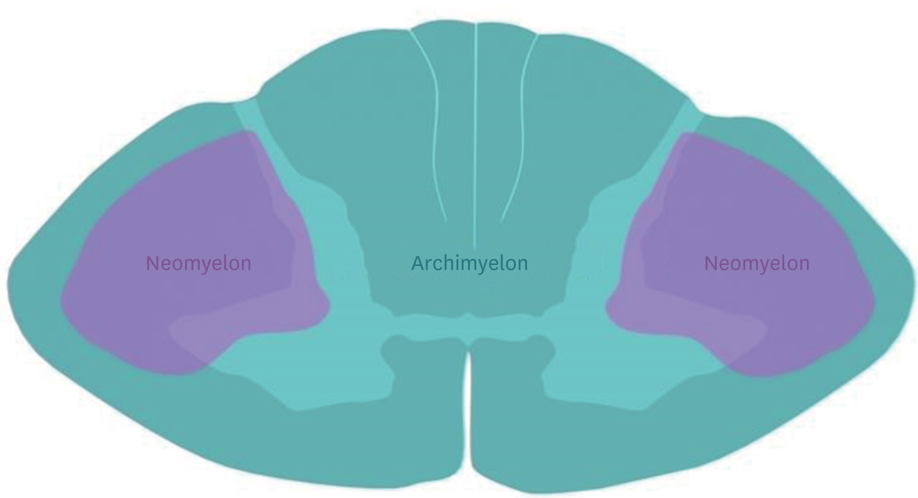

FIGURE 2. Neomyelon and arhinyelon.

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TABLE 1. Trends in arrangement and decussation

Variables	Primitive	Intermediate	Developed
Arrangement	Archimyelon	Archimylon	Neomyelon
Decussation	None	Late	Early

the corticospinal tract is the main pathway conveying voluntary movement from the cerebral cortex. The tract crosses to the contralateral side during pyramidal decussation and descends into the neomyelon of the spinal cord.[28] This trend applies to both the descending tract, responsible for motor function, and the ascending tract, responsible for sensory function. The decussation trends are summarized in **TABLE 1**.

Humans possess the most evolved nervous system among all life forms on Earth,[25] and even in the case of primitive tracts responsible for primitive functions, significant changes have occurred in accordance with this evolved nervous system. While primitive tracts tend not to decussate, developed tracts tend to exhibit decussation, although some exceptions exist. The exceptions are explained in detail for each category.

PRIMITIVE TRACTS

Unconscious proprioception

The posterior spinocerebellar tract transmits unconscious proprioception from the trunk and lower extremities.[9] Signals originating from the Golgi tendon organ (Ib) and muscle spindle (Ia) pass through the relay nucleus known as the dorsal nucleus of Clark, and continue to pass through the posterior spinocerebellar tract. The dorsal nucleus of Clark is located between the C8 and L3 spinal cord levels. This tract does not decussate and ascends through the same-side lateral funiculus, and terminates in the ipsilateral cerebellar cortex through the inferior cerebellar peduncle. Through this pathway, proprioceptive signals are transmitted to the cerebellum, allowing for reflexes and the regulation of muscle tone in the lower extremities. Both this tract and the relay nucleus are located in the archimyelon, showing the characteristics of a primitive tract (**FIGURE 3**).

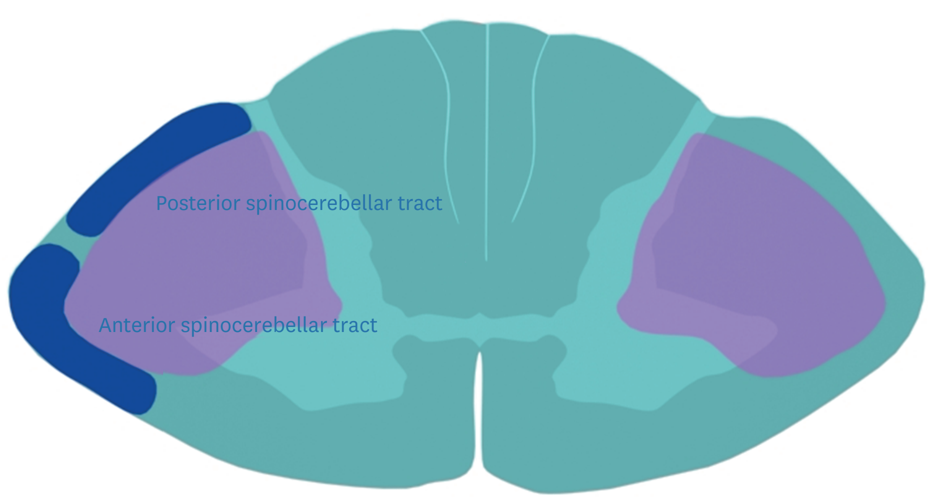

FIGURE 3. Posterior and anterior spinocerebellar tract.

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TABLE 2. Unconscious proprioception tracts

Afferent	Lower extremity	Upper extremity
Muscle spindle (1a) Golgi tendon organ (1b)	Posterior spinocerebellar tract → ICP	Cuneocerebellar tract → ICP
Golgi tendon organ (1b)	Anterior spinocerebellar tract → SCP	Rostral spinocerebellar tract → SCP and ICP

ICP: inferior cerebellar peduncle, SCP: superior cerebellar peduncle.

The anterior spinocerebellar tract conveys unconscious proprioception to the lower extremities. It originates in the lumbosacral segment and decussates to the opposite side, ascending to enter the superior cerebellar peduncle. Within the cerebellum, it decussates and terminates in the ipsilateral cerebellar cortex. This is one of the exceptions among the primitive tracts in which decussation occurs but controls the ipsilateral side.[6)]

The cuneocerebellar tract has the same function as the posterior spinocerebellar tract, conveying unconscious proprioception from muscles and tendons in the upper extremities.[21)] This tract passes through the cuneate fasciculus in the posterior funiculus and continues into the same-side accessory cuneate nucleus of the medulla. From the accessory cuneate nucleus, it extends further into the cerebellum via the inferior cerebellar peduncle. The minor tracts also transmit unconscious proprioception and afferent signals. However, all these tracts are located in the archimyelon, as summarized in **TABLE 2**.

Vestibular system

The lateral and medial vestibulospinal tracts are major components of the extrapyramidal system.[14)] The lateral vestibulospinal tract (**FIGURE 4**) originates from the lateral vestibular nucleus and descends through the ventral funiculus of the spinal cord without decussation. It synapses with the anterior horn of the spinal cord. When the lateral vestibular nucleus in animals is stimulated, the extensor muscles of the same-sided limbs contract, whereas the flexor muscles relax. If the brainstem is transected above the vestibular nucleus, it leads to a state of generalized contraction of the extensor muscles, known as decerebrate rigidity. Destruction of the vestibular nucleus results in relaxation of the extensor muscles. In summary, the lateral vestibulospinal tract regulates extensor muscle tone, allowing for resistance against gravity and maintenance of an upright posture.

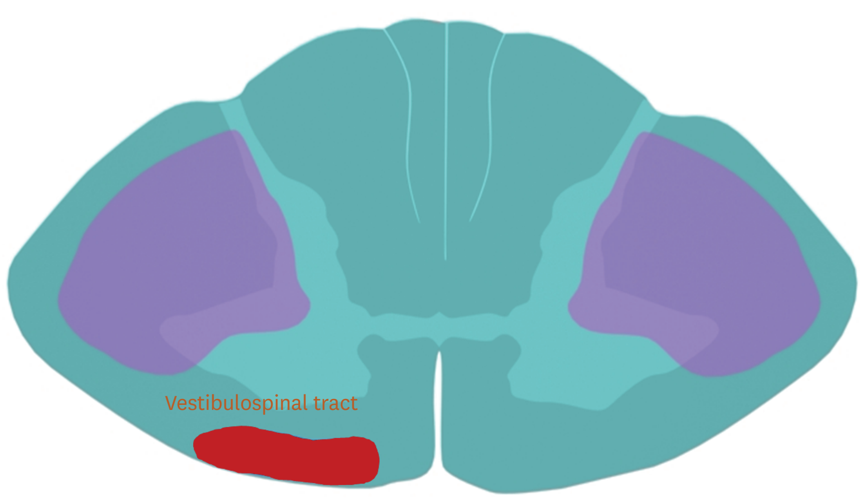

FIGURE 4. Vestibulospinal tract.

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The medial vestibulospinal tract originates from the medial vestibular nucleus and becomes part of the bilateral medial longitudinal fasciculus. It extends through the ventral funiculus of the spinal cord and controls the motor neurons in the cervical segments of the spine. It is involved in controlling head movements to keep the gaze fixed and to maintain body balance.

Reticular formation

The reticular formation of the brainstem is directly or indirectly connected to almost all levels of the central nervous system and performs various essential functions required for basic life activities such as motor control, awakeness, sleep-arousal cycle, pain perception, and visceral activity. The reticular formation is primitive and diffuse. The more primitive the animal, the greater the proportion of reticular formation in the brainstem. Representative connections between reticular formation and spinal tract include the reticulospinal and spinoreticular tracts.[7)]

The reticulospinal tracts is composed of nerve fibers originating from the oral pontine reticular nucleus, caudal pontine reticular nucleus, and gigantocellular reticular nucleus of the medulla. They descend through the ventral and lateral funiculi and terminate at interneurons in the ventral horn.[10)] The pontine reticulospinal tract, originating from the oral and caudal pontine reticular nuclei, descends to the same side without decussation. The medullary reticulospinal tract, originating from the gigantocellular reticular nucleus, decussates immediately before terminating in the ventral horn. Unlike the corticospinal tract, which regulates voluntary movements, the reticulospinal tract controls involuntary movements. They control the coordinated movements of various muscles governed by different segments of the spinal cord. The spinal tract is present in almost all mammals.

The spinoreticular tract ascends through the lateral funiculus and terminates during the reticular formation. The ascending reticular activating system (ARAS) is an essential component that regulates the overall activity of the cerebral cortex, including consciousness, sleep, and arousal, through interactions with the reticular formation and various nuclei. The spinoreticular tract is responsible for a part of the ARAS.[27)]

INTERMEDIATE TRACTS

Posterior column-medial lemniscus pathway

The posterior column-medial lemniscus pathway conveys conscious proprioception, discriminative touch, and vibration.[16)] These sensations represent more advanced forms of sensory perception than unconscious proprioception transmitted by the posterior spinocerebellar tract, and crude touch and pressure transmitted by the anterior spinothalamic tract. The posterior column consists of gracile and cuneate fasciculi. The gracile fasciculus conveys sensory information from the lower body (T7 and below) and synapses with the gracile nucleus. The cuneate fasciculus conveys sensory information from the upper body (C2–T7) and synapses to the cuneate nucleus. Axons originating from the gracile and cuneate nuclei cross to the opposite side through the internal arcuate fibers and form the medial lemniscus (late decussation). Subsequently, it passes through the ventral posterior lateral (VPL) nucleus of the thalamus and terminates in the somatosensory cortex (Brodmann areas 3, 1, and 2). However, the posterior column is considered more primitive than the lateral spinothalamic tract, which transmits sharp exteroceptive sensations and is located in the archimyelon (**FIGURE 5**).

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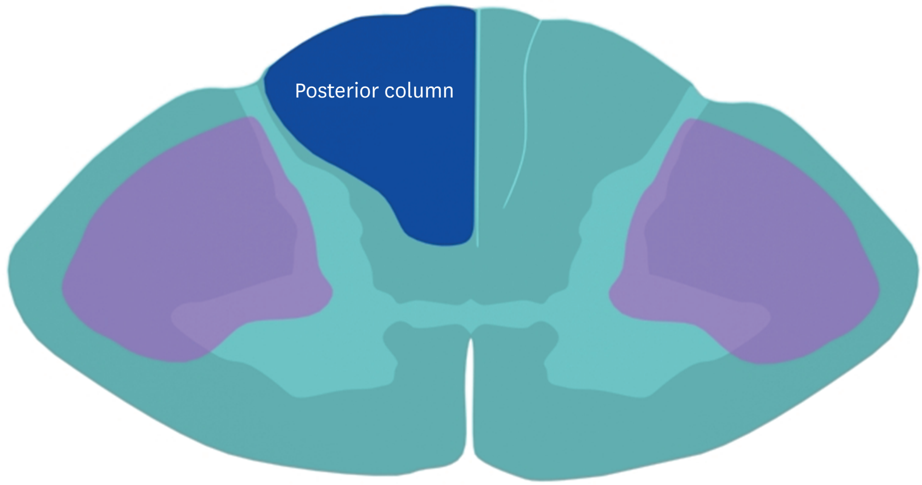

FIGURE 5. Posterior column-medial lemniscus pathway.

Patients with tabes dorsalis provide clear evidence of the function of the posterior column. Below the affected region, they experience a loss of discriminatory touch and vibration bilaterally, as well as difficulties in conveying conscious proprioception, resulting in a characteristic gait disturbance known as tabetic gait. The lateral and anterior fasciculi remain unaffected, allowing for normal perception of temperature, pain, crude touch, and pressure.[15,18)]

Tectospinal tract and spinotectal tract

As vision develops and becomes an important sense next to proprioception, the tectospinal and spinotectal tracts emerge under the need for coordination between vision and posture. These tracts connect the tectum of the midbrain and the cervical spinal cord and mediate head position in response to visual stimuli (**FIGURE 6**).

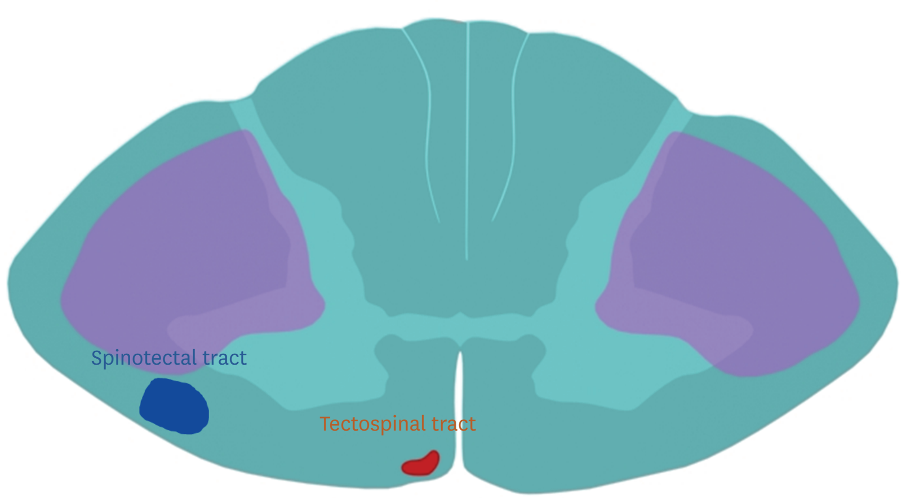

FIGURE 6. Tectospinal tract and spinotectal tract.

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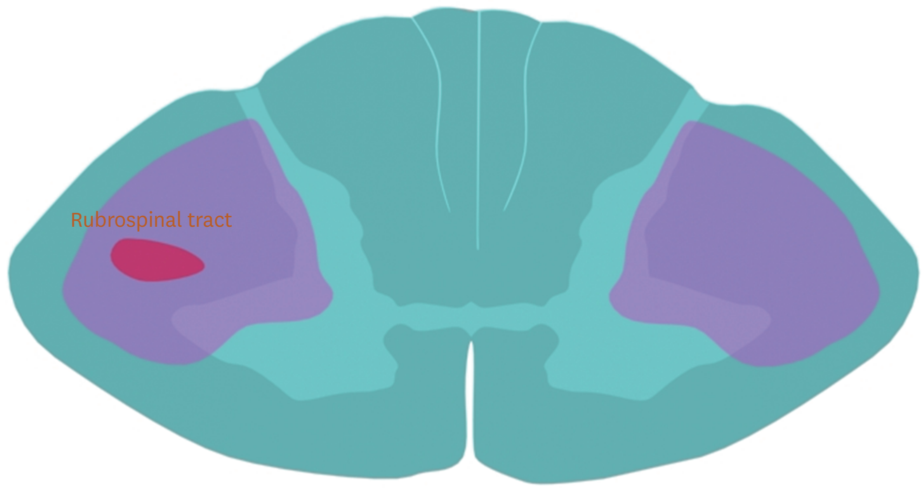

FIGURE 7. Rubrospinal tract.

TABLE 3. Descending tracts from brain stem

Midbrain	Pons	Medulla
Tectospinal tract	Vestibulospinal tract	Medullary reticulospinal tract
Rubrospinal tract	Pontine reticulospinal tract	-

Rubrospinal tract

The rubrospinal tract originates from the red nucleus and crosses the ventral tegmental decussation to become the rubrospinal tract. It descends into the lateral funiculus of the spinal cord and terminates in the cervical ventral horn, controlling flexor muscle tone (**FIGURE 7**).

Descending tracts from brain stem

Non-mammalian vertebrates rely mostly on motor pathways originating from the brainstem, such as the reticulospinal, vestibulospinal, and rubrospinal tracts, to regulate motor function. These pathways exhibit remarkable similarities between species.[26)] The reticulospinal and vestibulospinal tracts represent the most primitive motor pathways, primarily projecting ipsilaterally and indirectly connecting to spinal motor neurons. The rubrospinal tract is an intermediate between the corticospinal and primitive tracts. The tract crosses over and directly connects to the motor neurons. Although highly prominent in lower quadrupedal mammals and present to some extent in primates, the rubrospinal tract is almost absent in humans (**TABLE 3**).

DEVELOPED TRACTS

Spinothalamic tract

The lateral spinothalamic tract transmits the most advanced form of sensation: pain generated from the free nerve ending and heat sensation from the thermoreceptor of the skin.[23)] The fibers enter the cord through the dorsal horn and decussate to the contralateral side (early decussation). The location of this tract in the cord is in the deep layer of the lateral funiculus, the neomyelon. The tract ascends to the lateral funiculus and projects to the somatosensory cortex through the relay nucleus of the VPL thalamic nucleus (**FIGURE 8**).

The anterior spinothalamic tract conveys crude touch and pressure, which are poorly localized. These sensations enter the posterior horn of the spinal cord, decussate, and ascend

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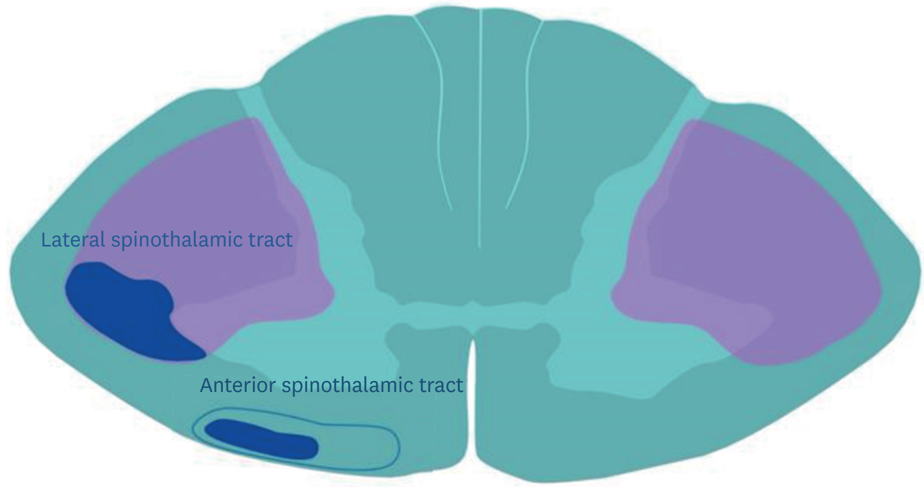

FIGURE 8. Anterior and lateral spinothalamic tract.

along the anterior spinothalamic tract to reach the ventral posterior nucleus of the thalamus. It is thought to be a rudimentary tract of primitive sensory function before the emergence of advanced sensory tracts, such as the lateral spinothalamic tract, which conveys pain and temperature. It is located in the archimyelon and intermingled with the vestibulospinal tract.

In patients with syringomyelia, a fluid-filled cavity develops within the central canal of the spinal cord, leading to the obstruction of the ventral white commissure. It primarily occurs in the cervical region. If the crossing fibers of the lateral and anterior spinothalamic tracts are interrupted at the cervical level, it causes the loss of crude touch, pressure, temperature, and pain sensations in both shoulders and arms. However, the lateral and anterior fasciculi remain intact, preserving sensation below the level of the lesion. In addition, the posterior column is preserved, allowing for normal conscious proprioception, discriminative touch, and vibration in all the 4 limbs.[11,30)]

Corticospinal tract

The corticospinal tract conveys volitional movement starting from the Betz cells in layer V of the precentral area of the cerebral cortex (Broadman area 4), premotor area, and adjacent parietal area.[12)] Most fibers (approximately 90%) decussate at the pyramid of the medulla before a long journey into the spinal cord and form the lateral corticospinal tract. These early decussating fibers occupy the largest portion of the neomyelon, located in the deep layer of the lateral funiculus (neomyelon). The remaining small portion of fibers (approximately 10%) is known as the anterior corticospinal tract, which does not decussate or decussates at the level of the cord exit (late decussation). The uncrossed and late decussating fibers are located at the anterior funiculus, which is located in the archimyelon. Based on this arrangement and pathway, it can be assumed that the early decussating lateral corticospinal tract transmits the most advanced function of discrete volitional motor control of the extremities or digits. In contrast, the uncrossed or late decussating corticospinal tract is involved in transmitting the coordination function rather than volition (**FIGURE 9**).

Brown-Séquard syndrome is characterized by unilateral spinal cord damage. In terms of ascending tracts, the damage to the early decussating spinothalamic tract results in the loss of crude touch, pressure, temperature, and pain sensations on the opposite side below the

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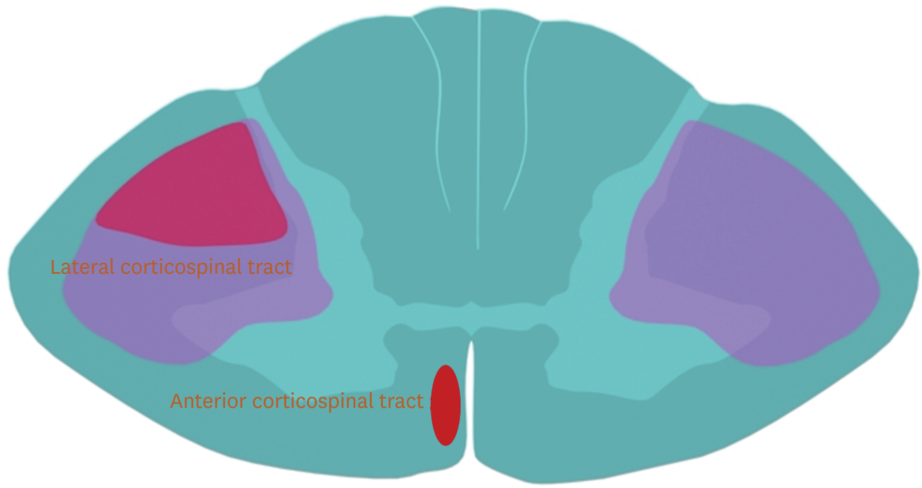

FIGURE 9. Anterior and lateral corticospinal tract.

affected level. Damage to the late decussating posterior column leads to loss of conscious proprioception, discriminative touch, and vibration sensation on the same side below the affected level. In the descending tract, the corticospinal tract, which mostly undergoes early decussation, causes ipsilateral hemiparesis on the same side.[8)]

APPLICATION IN CLINICAL PRACTICE

Distinguishing the spinal cord into neomyelon and archimyelon, despite potential exceptions and ambiguities, offers the advantages of simplicity and intuitiveness. The spinal cord is susceptible to various types of trauma and a wide array of diseases. When examining patients in a clinical setting, inferring the damaged tract based on the patient's symptoms is not an easy task, particularly for trainees and students who are still learning. Applying this evolutionary perspective allows for a comprehensive understanding without the need to memorize the locations and functions of individual tracts.

For instance, if a patient arrives at the emergency room after an accident and exhibits muscle weakness in both the upper and lower limbs, along with bilateral loss of pain and temperature sensation, while proprioception and vibration sensation remain intact on both sides, what condition might this be? Considering that primitive functions are preserved while devolved functions are impaired, one can envision a state of the spinal cord in which the neomyelon is compromised while the archimyelon remains intact. The neomyelon pertains to the central part of the cord, making it easy to infer that it is indicative of central cord syndrome.

CONCLUSION

In summary, the rearrangement of the human spinal tracts based on the stage of development is presented in **FIGURE 10**. From an evolutionary perspective, the human spinal cord has a coherent arrangement and pathway of tracts. It can be divided into 2 regions: where tracts convey primitive functions and where tracts convey developed functions. The tracts carrying developed functions are positioned in the "neomyelon" region of the spinal

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	Primitive	←→		Developed
Sensory	Spinoreticular tract Posterior spinocerebellar tract Anterior spinocerebellar tract Cuneocerebellar tract	Posterior column	Anterior spinothalamic tract Spinotectal tract	Lateral spinothalamic tract
Motor	Reticulospinal tract Lateral vestibulospinal tract Medial vestibulospinal tract	Anterior corticospinal tract	Tectospinal tract Rubrospinal tract	Lateral corticospinal tract

FIGURE 10. Re-allocation of tracts in concept of development.

cord section, while the tracts conveying primitive functions are situated in the “archimyelon,” which encompasses the remaining spinal cord. This article reviews the functions of the spinal tracts based on embryological concepts and provides insights into their arrangement and pathways. This concept may assist specialists who care for patients with spinal cord disorders and injuries to comprehensively understand the spinal cord.

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