THE SPINAL CORD

Development of the Spinal Nerves (Fig.2)

The spinal cord has 31 pairs of spinal nerves. These are attached at regular intervals corresponding to the paired somites and to the paired nodules of the neural crest. Each spinal nerve is similar in developmental sequence, structure and fundamental plan. Each derives from the dorsal and ventral roots

Formation of the Dorsal Roots (Fig. 2)

Each paired nodule of neural crest produces neuroblasts for a dorsal root ganglion. Each neuroblast in the dorsal root ganglion produces a process that bifurcate into peripheral and central branches. The central branch pierces the dorsolateral aspect of the spinal cord, forming the dorsal root. Upon entering the spinal cord, the dorsal root axon characteristically branches. The branches may run up or down the cord, but at the level of the entry, the axon synapses variously on dorsal horn neurons, spinal interneurons and ventral horn motorneurons. The peripheral branch extends to a receptor in the skin or viscera.

Formation of the Ventral Roots (Fig. 2)

Neuroblasts in the ventral horn gray matter differentiate and produce axons that exit from the ventrolateral aspect of the spinal cord. Two types of axons enter the ventral rootes -axons destined for skeleteal muscles and axons destined for autonomic ganglia. The axons going to skeletal muscles issue from motorneurons in the ventral horns. They travel directly to the muscle without further synapses. The autonomic axons issue from neurons in the intermediate horn. These autonomic axons do not run directly to their glands or smooth muscles. Instead, the autonomic axons synapse upon a peripheral neuron in a para or prevertebral ganglion of the sympathetic nervous system. The peripheral neuron then innervates the effector. Thus the autonomic pathway of the PNS involves two neurons; the skeletal muscle pathway involves only one. The preganglionic neuron runs to the ganglion by a small ramus (r. comminicans albus) from the peripheral nerve trunk. The postganglionic axon rejoin the trunk by another ramus (r. comminicans griseus).

Development and Innervation of Somites (Fig. 1,3)

Somites are mesodermal derivatives, develop as a series of regular, paired lumps on each side of the neural tube. Somites produces the somatic structures of the body. Their mesoderm differentiates into dermatomes, myotomes and sclerotomes. The dermatome produces the dermis, the deep layer of the skin beneath of the epidermis. The epidermis derives from the surface ectoderm. The myotome differentiates into skeletal muscle. The scelorotome differentiates into the skeleton and related connective tissue. The somites extend from the caudal end of the spinal cord to the midbrain level. Each somite nerve innervates all of the tissues derived from its original somite and only those tissues. It innervates the dermis derived from a particular somite's dermatome, the muscles derived from the somite's myotome, and the bone derived from its

scelorotome. This rule holds even when the somite derivatives migrate and undergo extensive transformations in the arm and leg regions. Figure 4A shows the transformation of the dermatomes. Only the thoracic region retains the original somite simplicity since it is unaltered by face, arm or leg growth. Opposite each somite, a single paravertebral autonomic ganglion forms, but some ganglia coalesce in the cervical region. The single-somite-single-ganglion arrangement is confined roughly to the thoracic region.

Formation of Somatic Nerve Plexuses (Fig. 3)

Figure 3 shows that a spinal nerve trunk upon entering a plexus contain axons from only one spinal nerve serving only one spinal segment. The axons of the individual nerve trunks intermingle in the plexus, but each axon retains its own identity and does not anastomose with axons of another segment. The peripheral nerves issuing from a somatic plexus may contain axons from more than one nerve trunk or spinal segment. Nerve trunks form three plexuses along the spinal cord: the cervical, brachial and lumbosacral. The brachial and lumbosacral plexuses are the largest because the somite derivatives, undergo the greatest redistribution in the limb buds, which forms the arms and legs. No plexuses occur in the throracic region, where the somites retain their original serial simplicity. Figs. 5-6 show the segmental and peripheral innervation of the skin.

In summary: 1) One spinal nerve innervates the dermatome, myotome, and sclerotome derived from one somite; 2) Wherever the somite derivative migrates during embryogenesis, it retains its original somite nerve; 3) The most extensive rearrangement of the somites is in the head, arms, and legs. The thorax retains the simple serial somite plan, undisturbed by somite rearrangements; 4) The somatic nerve plexuses redistribute the axons from the spinal nerve trunks into convenient pathways to the migrated somite derivatives of the head, arms and legs.

Relationship of Spinal Roots, Nerves, and the Spinal Cord to Vertebral Levels (Fig. 7)

The average adult has 31 to 32 pairs of spinal nerves, each one corresponding to an embryonic somite. The spinal nerves are numbered in relation to the vertebrae. There are 8 pairs of cervical nerves, 12 thoracic, 5 lumbar, 5 sacral, and 1-2 coccygeal. There are only 7 cervical vertebrae but 8 cervical nerves because cervical nerve 1 (C1) comes out rostral to the first cervical vertebra and cervical nerve 8 (C8) comes out caudal to the seventh cervical vertebra.

Because the vertebral column elongates faster during gestation than the spinal cord, the caudal tip of the cord, which originally lay opposite the cocyx, comes to lie opposite the first lumbar vertebra. Because of this relative elevation (ascensus), the more caudal a nerve root the further it must run to reach its intervertebral foramen and the greater its downward angulation. Since the tip of the cord lies at L1, a physician can insert a needle into the subarachnoid space at L4/L5 or L5/S1 to obtain CSF for diagnostic analysis without fear puncturing the cord. The nerve roots will move aside and generally are undamaged by the needle (Fig. 7).

Gross Anatomy of the Spinal Cord (Figs. 8-10

The spinal cord is a cylindrical elongated part of the central nervous system. It extends from the level of the foramen magnum to the body of the first lumbar vertebra, an average length of 43 cm. Rostrally, the spinal cord continues uninterruptedly into the medulla oblongata. The level of

the foramen magnum arbitrarily divides the medulla and the cord. Caudally, the spinal cord ends at the conus medullaris. The tip of the conus medullaris extends to the sacrum as a thin strand, the filum terminale, composed only of glia. After the ascensus, dorsal and ventral spinal nerve roots angle downward on either side of the filum terminale, extending from the lumbosacral cord to their original vertebral foramina. This groups of roots is called the cauda equina. The spinal cord varies in diameter from about 1cm -1.5 cm. The thoracic region is the narrowest. The spinal cord has two gross enlargements, the cervical and the lumbosacral, to accomodate the extra neurons that innervate the limbs (Fig. 8).

Cross Sectional Anatomy of the Spinal Cord. Gray and White Matter (Fig. 11).

When cut transversely, the spinal cord consists of an outer zone of white matter and a central, H-shaped region of grey matter. The arms of the H, extending dorsally and ventrally, are called the dorsal horn and ventral horn. The grey matter is organized into nuclei and laminae and extends as a column through the length of the spinal cord. For the laminar and nuclear pattern of the spinal gray matter and longitudinal extent of nuclei in the spinal cord see Fig. 9. The spinal gray matter contains three main types of neurons (somaotmotor, visceromotor, sensory and interneurons: see below).

The white matter of the cord contains axons running longitudinally. Some of these axons convey signals from the cord to higher levels of the CNS, others from higher levels to the cord. Finally, a large proportion of the fibers serve cooperation between the segments of the cord. Since the first two groups of axons become successively more numerous in the rostral direction, the proportion of white to gray matter increases from caudal to rostral. The white matter is divided into funiculi, or columns.

Distribution of the Dorsal Root Axons in the Cord (Fig. 12)

Afferent fibers from the receptors follow the peripheral nerves toward the CNS. The sensory fibers of the spinal nerves have their perikarya in the dorsal root ganglia. Likewise, the sensory fibers in the cranial nerves have their perikarya in ganglia close to the brain stem. The ganglion cells are pseudounipolar and send one long process peripherally, ending freely or in encapsulated sense organs. The central process enters the cord and then divides into an ascending and a descending branch. These branches give off several collaterals ventrally to the gray matter of the cord. The different kinds of sensory receptors are supplied with axons of characteristic thickness. Impulses from low-threshold mechanoreceptors are, for example, conducted in the thick myelinated fibers (A-alfa [Ia, Ib] and A-beta [II). These large fibers that constitute the medial division of dorsal roots, mediate sensory modalities consisting of touch, perception of texture, perception of form, and modality termed proprioception, which gives a sense of where the- body parts are (position sense) and of tension of joints and muscles. They divide into ascending and descending branches and terminate in lamina III-VI (A-Beta) and L VI-VII, IX (A-alfa fibers).

Impulses from cold receptors are conducted in thin myelinated fibers (A delta), whereas unmyelinated (C) fibers conduct from heat receptors. Impulses from nociceptors are conducted in A delta and C fibers. These fibers constitute the lateral division of dorsal roots. In the spinal cord, the termination of A delta and C fibers are almost completely separated from those of the A- alfa and A-beta fibers. These fibers accumulate at the apex of the dorsal horn and they form the dorsolateral tract of Lissauer. A-delta fiber terminate primarily in Lamina I and lateral LV, C-fibers terminate in LII.

Efferent Fibers via the Ventral Root Innervate Muscles and Glands

The motor neurons have large, multipolar perikarya and are in the ventral horn proper. The dendrites extend for a considerable distance in the gray matter. The axons leave the cord through the ventral root, follow the spinal nerves, and end in skeletal muscles. These neurons are also called alfa motorneurons and are the largest in the spinal cord and among the largest in the CNS. They are located in Rexed Lamina IX. The smaller gamma motorneurons send gamma-sized axons in the peripheral nerves and innervate the intrafusal fibers in the muscle spindles. The alpha motorneurons sends a collateral axon to an interneuron, the Renshaw cell, which sends an inhibitory syanpase back to the alpha motorneurons.

There is also another group of neurons that sends its axons out of the cord through the ventral root. These supply smooth muscles and glands with motor signals, and belong to the autonomic nervous system. The autonomic system controls the vascular smooth muscles and visceral organs throughout the body. The cell bodies lie in the lateral horn. These neurons form the intermediolateral column (T1-L2) and constitutes the sympathetic part of the autonomic NS. A corresponding, smaller group of neurons is present in the sacral cord (S2-S4) and belongs to the parasympathetic part of the autonomic NS (see below).

The Spinal Cord Consists of Cooperating Subunits that are Controlled by Descending Pathways from Higher Brain Centers

Many of the functional tasks of the spinal cord are under strict control and supervision from higher levels of the CNS. This control is mediated by fibres from the brainstem and the cerebral cortex, which descend in the white matter of the cord and terminate in the gray matter.

Arrangement of the spinal pathways

a)Law of the peripheral position of long fibers
b)Law of lamination by level of entry or body topography
c)Law of separation of sensory pathways by sensory modalities

SPINAL REFLEXES

Myotatic Stretch (Proprioceptive) Reflexes: determines muscle length (Figs 13-16,18)

The most famous stretch reflex is the quadriceps reflex (knee jerk reflex), produced by tapping the patellar tendon, which in turn stretches the quadriceps. The reflex is initiated by special muscle receptors called muscle spindles, which are sensitive to stretch. Muscle spindles are composed of 8-10 modified muscle fibers called intrafusal fibers arranged in parallel with the ordinary (extrafusal) fibers that make up the bulk of the muscle. Sensory fibers (Ia) are coiled around the central part of the spindle. Streching the muscle deforms the intrafusal muscle fibers, which lead to increased activity of the sensory fibers that innervate each spindle. The impulses are transmitted through Ia afferent fibers to the spinal cord, where the fibers establish synaptic contact with alpha motor neurons, which in turn produce contraction of quadriceps and extension

of the leg at the knee. At the same time as the quadriceps contracts there is a reciprocal inhibition of the antagonistic muscles, the flexors of the knee. The inhibition of the flexors is mediated by polysynaptic reflex arcs, and since the motor neurons for the flexors are located in more caudal segments than the motor neurons for quadriceps, the inhibitory reflex is intersegmental, in contrast with the stretch reflex, which is intrasegmental (reciprocal innervation).

Borrowing a concept from engineering, the stretch reflex arc can be viewed as a negative feedback loop that tends to maintain muscle length at a constant value. The desired muscle length is specified by the activity of descending pathways that influence the motor neuron pool. Deviations from the desired length are detected by the muscle spindles; thus increases or decreases in the stretch of the intrafusal fibers change the level of activity in the sensory fibers that innervate the spindles. These changes, in turn, lead to appropriate adjustments in the activity of the alpha motor neurons, returning the muscle to the desired length.

The gain is adjusted by changing the level of activation of the gamma motor neurons. These small gamma motor neurons are interspersed among the alpha motor neurons in the ventral horn of the spinal cord. An increase in the activity of gamma motor neurons produces an increase in the amount of tension in the intrafusal fibers. Although the intrafusal fibers are much too sparse to generate a net increase in muscle tension, contraction of the intrafusal fibers increases the sensitivity of Ia sensory fibers to muscle stretch. The same stretch can then produce a larger amount of Ia afferent activity, which causes an increase in the activity of the alpha motor neurons that innervate the extrafusal muscle fibers.

The Inverse Myotatic Reflex: limits the muscle tension (Fig. 19)

Another sensory structure that is important in the reflex regulation of motor unit activity is the Golgi tendon organ. Golgi tendon organs are encapsulated endings located at the junction of the muscle and tendon. Each tendon organ is related to a single group Ib sensory axon (the Ib axons are slightly smaller than the Ia axons that innervate the muscle spindles). In contrast to the parallel arrangement of extrafusal muscle fibers and spindles, Golgi tendon organs are in series with the muscle fibers. When a muscle is passively stretched, most of the change in length occurs in the muscle fibers, since they are more elastic than the fibrils of the tendon. When a muscle actively contracts, however, the force acts directly on the tendon, leading to an increase in the tension of the collagen fibrils in the tendon organ and compression of the intertwined sensory receptors. As a result, Golgi tendon organs are sensitive to increase in muscle tension that arise from muscle contraction and, unlike spindles, are much less sensitive to passive stretch.

The Ib axons from Golgi tendon organs contact inhibitory interneurons in the spinal cord (called Ib inhibitory interneurons) that synapse, in turn with the alpha motor neurons that innervate the same muscle. The Golgi tendon circuit is thus a negative feedback system that regulates muscle tension, decreasing the activation of muscles when exceptionally large forces are generated. This reflex circuit also operates at reduced levels of muscle force, counteracting small changes in muscle tension by increasing or decreasing the inhibition of alpha motor neurons. Under these conditions, the Golgi tendon system tends to maintain a steady level of muscle force, counteracting effects such as fatique, which diminishes muscle force. If the muscle spindle system is viewed as a feedback system that monitors and maintains muscle length, then the Golgi tendon system is a feedback system that monitors and maintains muscle force. Like the muscle spindle system, the Golgi tendon organ system is not a closed loop. Ib inhibitory interneurons also receive synaptic inputs from a variety of other sources, including cutaneous

receptors, joint receptors, muscle spindles, and descending pathways. Together these inputs regulate the responsiveness of Ib interneurons to activity arising in Golgi tendon organs.

Although there are stretch reflexes in all muscles, they are especially prominent in antigravity muscles, where they form the basis for postural reflexes. Stretching of a muscle does not necessarily elicit a reflex contraction. Many factors influence whether there will be a response, such as the velocity of stretching, how long the stretch is, whether the muscle is active when being stretched, and whether- a reflex contraction is functionally appropriate. Short (30 msec) and long-latency stretch reflex. Fig. 21 shows a theoretical possibility of how the same muscle pair may work synergistically or antagonistically in various situations.

Some commonly tested stretch reflexes (Fig. 20)

Some stretch reflexes are routinely tested in neurologic examinations. The most commonly tested stretch reflexes have the following segmental reflex center:

1) The biceps brachialis reflex :flexion of the elbow by tapping the biceps tendon (C5-C6).

2) The brachioradial reflex :flexion of the elbow and supination of the forearm by tapping the styloid process of the radius (C5-C6)

3) The triceps brachialis reflex: extension of the elbow through a tap on the triceps tendon. (C6-C7)

4) Quadriceps (patellar tendon) reflex: extension of the knee by tapping the ligamentum patellae L2-L4)

5) Triceps surae (Achilles tendon) reflex: plantar flexion of the foot by tapping the Achilles tendon (L5-S2).

Flexion and Crossed Extensor (Withdrawal) Reflex (Fig. 25)

The po1ysynaptic flexor reflex serves important protective functions. One of its purposes is to achieve a rapid withdrawal of a limb in response to painful cutaneous stimuli. To maintain position the flexor withdrawal reflex is usually accompanied by extension of the opposite limb through action of the crossed extensor reflex. Receptors: free nerve endings in the skin. Afferent arch: Adelta and C fibers which terminate in the marginal zone (Lissauer) and in the dorsal part of the central gray matter. Central mechanism: the central processes of the primary sensory neurons synapse with interneurons and funicular neurons that in turn innervate ipsilateral flexor and crossed extensor muscles.

Like the other reflex pathways, interneurons in the flexion reflex pathway receive converging inputs from several different sources, including cutaneous receptors, other spinal cord interneurons and descending pathways. Although the functional significance of this complex pattern of connectivity is uncertain, changes in the character of the reflex following damage to descending pathways provide a clue. Under normal conditions, a noxious stimulus is required to evoke the flexion reflex; following damage to descending pathways, however, other types of stimulation, such as moderate squeezing of a limb, can produce the same response. Thus, the descending projections to the cord may function, at least in part, to gate the responsiveness of interneurons in the flexion reflex pathway to a variety of sensory inputs.

The Vegetative Reflex (Fig. 26)

Receptors: skin (mainly pain and temperature) and visceroceptors. Afferent arch: primary neurons are in the spinal ganglion. The fibers are medium-thin myelinated and unmyelinated. Central mechanism: Between the afferent and the efferent neurons there is always one or several interneuron. Efferent branch: the efferent arch of the reflex consist of two neurons: one is located in the lateral horn (n. intermediolateralis:between T1-L3) the second in the para- or prevertebral sympathetic chain. The postganglionar axons returning to the spinal nerve function as sudomotor, vasomotor or piloarector. Those neurons which synapse in the prevertebral chain innervate though their postganglionic processes the viscera.

Referred Pain. Hyperesthesia (Fig. 27). Recording from spinothalamic cells in the spinal cord has shown that many can be activated by nociceptive stimuli applied to visceral organs and to the skin. Higher centers, however, impulses arriving from a particular spinothalamic cell always interpreting as coming from the skin. When signals arise for the first time in the heart, they are misinterpreted as coming from the skin. This phenomenon, commonly experienced with diseases of visceral organs, is called referred pain. Infarction of the heart, for example, is usually accompanied by pain localized to the left arm, diseases of the gallbladder may manifest themselves with pain below the right shoulder blade. Convergence on spinothalamic cells may also explain the phenomenon of hyperesthesia - that is, a region of skin becomes abnormally sensitive, such that even light touch may provoke pain. This is commonly observed with diseases of visceral organs. Thus, impulses from the visceral organ excite the spinothalamic cell so that less excitation from the skin is necessary to fire the cell.

Sensory Neurons in the Cord Give Rise to Ascending Pathways to Higher Brain Centers

The second main type of spinal neurons sends axons to higher levels of the CNS. Their perikarya are mainly located in the dorsal horn and in the transition zone between the dorsal and ventral horn. Their job is to inform the brain of the activities of the spinal cord, and especially about what is going on in the body. The dorsal root fibers form synaptic contacts -in part directly, in part indirectly via interneurons -with neurons in the spinal cord, sending their axons to various parts of the brain. Such axons, destined for a common target in the brain, are grouped together in the spinal white matter, forming ascending tracts0.

THE SOMATOSENSORY SYSTEM

Cutaneous and deep receptors (Figs. 22-23)

Type of receptors. In the skin: free and encapsulated receptors according to their structures. Functionally, skin receptors can be classified by their adequate stimulus as mechanoreceptors, thermoreceptors, and nociceptors.

Nociceptors are free receptors. Functionally, skin nociceptors are high-threshold mechanoreceptors or polymodal receptors. Axons responding to mechanical stimulus only if it is very intense. Most of them are in the Adelta range (15-30m/sec). Almost half of the unmyelinated axons of peripheral nerve respond well not only to intense mechanical stimuli, but also to heat and noxious chemicals. Axons of these polymodal nociceptors make up the majority of very slowly conducting (,1m/s) C fibers in a peripheral nerve. Their

receptors respond to minute punctures of the epithelium, with a response magnitude that depends on the degree of tissue deformation. They also respond to temperatures in the range of 40-60^{o}C and change their response rates as a linear function of warming (in contrast with the saturating responses displayed by non-noxious thermoreceptors at high temperatures). The relatively rapidly conducting Adelta and the slowly conducting C fibers are responsible for two very different qualities of pain. The rapidly transmitted signal, often with high spatial resolution is called first pain or cutaneous pricking pain. It is well localized and easily tolerated (fast conducting Adelta fibers). The much slower, highly affective component is called second pain or burning pain (poorly localized and poorly tolerated). The third or deep pain, arising from viscera, musculature and joints. It is poorly localized, can be chronic and often associated with referred pain.

Thermoreceptors. According to combined physiological and histological analysis the free endings are also responsible for the perception of heat and cold. Specific thermoreceptors respond with a sustained response over a narrow rangeof skin temperature but do not respond to skin indentation. Axons of warm receptors are unmyelinated, slowly conducting C fibers, wheras axons of cold receptors are lightly myelinated, mostly Adelta fibers. Thermoreceptors are very poor indicators of absolute temperature but are very sensitive to changes in skin temperature.

Mechanoreceptors can be free receptors, for example, those found at the roots of hairs, or encapsulated ones such as those in the glabrous[hairless] skin (e.g.Meissner and Pacinian corpuscles: rapidly adapting [RA]; Ruffini corpuscles and Merkel's disks: slowly adapting[SA]).

Sensory information from Meissner corpuscles and RA afferents leads to adjustment of grip force when objects are lifted. These afferents respond with a brief burst of action potentials when objects move a small distance during the early stages of lifting. In response to RA afferent activity, muscle force increases reflexively until the gripped object no longer moves. Such a rapid response to a tactile stimulus is a clear indication of the role played bt somatosensory neurons in motor activity.

Activating Merkel's disks and the SA axons terminating in them are responsible for form and texture perception. As would be expected for receptors mediating form perception, Merkel disks are present at high density in the digits and around the mouth (50/mm^2 of skin surface) at lower density in other glabrous surfaces and at very low density in hairy skin. This innervations density shrinks progressively with the passage of time so that by the age of 50, the density in human digits is reduced to 10/mm^2. SA axons contacted by Merkel cells display, low threshold responses to cutaneous stimuli. Unlike RA axons, SA fibers respond not only to the initial indentation of skin, but also to sustained indentation up to several second in duration.

Stimulating axons that appear to end in Pacinian corpuscles gives a feeling of vibration. Sensory axons at the core of Ruffini corpuscles display slowly adapting responses to the latareal movement or stretching of skin.

Proprioceptors. The term proprioceptive or kinesthetic sense is used to refer to the perception of joint position, joint movements, and the direction and velocity of joint movement. There are numerous mechanoreceptors in the muscles, the muscle fascia, and in the dense connective tissue of joint capsules and ligaments. There are two specialized encapsulated, low-threshold mechanoreceptors: the muscle spindle and the tendon organ (Golgi). Their adequate stimulus is stretching of the tissue in which they lie. Muscle spindles, joint and skin receptors all contribute to kinesthesia. Muscle spindles appear to provide their most important contribution to kinesthesia with regard to large joints, such as the hip and knee joints, whereas joint receptors and skin receptors may provide more significant contributions with regard to finger and toe joints.

Muscle Spindle (stretch receptors)

Scattered throughout virtually every striated muscle in the body are long, thin, stretch receptors called muscle spindles. They are quite simple in principle, consisting of a few small muscle fibers with a capsule surrounding the middle third of the fibers. These fibers are called intrafusal fibers, in contrast to the ordinary extrafusal fibers. The ends of the intrafusal fibers are attached to extrafusal fibers, so whenever the muscle is stretched, the intrafusal fibers are also stretched. The central region of each intrafusal fiber has few myofilaments and is non-contractile, but it does have one or more sensory endings applied to it. When the muscle is stretched, the central part of the intrafusal fiber is stretched, and each sensory ending fires impulses.

Numerous specializations occur in this simple basic organization, so that in fact the muscle spindle is one of the most complex receptor organs in the body. Only three of these specializations are described here; their overall effect is to make the muscle spindle adjustable and give it a dual function, part of it being particularly sensitive to the length of the muscle in a static sense and part of it being particularly sensitive to the rate at which this length changes.

1. Intrafusal muscle fibers are of two types. All are multinucleated, and the central, non-contractile region contains the nuclei. In one type of intrafusal fiber, the nuclei are lined up single file; these are called nuclear chain fiber. In the other type, the nuclear region is broader, and the nuclei are arranged several abreast; these are called nuclear bag fibers. There are typically two or three nuclear bag fibers per spindle and about twice that many chain fibers.

2. There are also two types of sensory endings in the muscle spindle. The first type, called the primary ending, is formed by a single Ia (A-alpha) fiber, supplying every intrafusal fiber in a given spindle (although it innervates the bag fibers more heavily than the chain fibers). Each branch wraps around the central region of the intrafusal fiber, frequently in a spiral fashion, so these are sometimes called annulospiral endings. The second type of ending is formed by a few smaller nerve fibers (II or A-Beta) on both sides of the primary endings. These are the secondary endings, which are sometimes referred to as flower-spray endings because of their appearance. Primary endings are selectively sensitive to the onset of muscle stretch but discharge at a slower rate while the stretch is maintained. Secondary endings are less sensitive to the onset of stretch, but their discharge rate does not decline very much while the stretch is maintained. In other words, both primary and secondary endings signal the static length of the muscle (static sensitivity) whereas only the primary ending signals the length changes (movement) and their velocity (dynamic sensitivity). The change of firing frequency of group Ia and group II fibers can then be related to static muscle length (static phase) and to stretch and shortening of the muscle (dynamic phases).

3. Muscle spindles also receive a motor innervation. The large motor neurons that supply extrafusal muscle fibers are called alpha motor neurons, while the smaller ones supplying the contractile portions of intrafusal fibers are called gamma neurons. Gamma motor neurons can regulate the sensitivity of the muscle spindle so that this sensitivity can be maintained at any given muscle length. Presumably, there are two types of efferent gamma neurons. One consists of gamma-dynamic cells innervating predominantly the intrafusal-bag fibers. The other represent gamma-static cells predominantly stimulating the intrafusal nuclear chain-fibers.

The Golgi tendon organ. Is located at the musculotendinous junction. There is no efferent innervation of the tendon organ, therefore its sensitivity cannot be controlled from the CNS. The tendon organ, in contrast to the muscle spindle, is coupled in series with the extrafusal muscle fibers. Both passive stretch and active contraction of the muscle increase the tension of the tendon and thus activate the tendon organ receptor, but active contraction produces the greatest increase. The tendon organ, consequently, can inform the CNS about the muscle tension. In contrast, the activity of the muscle spindle depends on the muscle length and not on the tension. The muscle fibers attached to one tendon organ appear to belong to several motor units. Thus the CNS is informed not only of the overall tension produced by the muscle but also of how the workload is distributed among the different motor units.

Joint receptors. The joint receptors are low-threshold mechanoreceptors and have been divided into four groups. They signal different characteristics of joint function (position, movements, direction and speed of movements). The free receptors or type 4 joint receptors are nociceptors.

DORSAL COLUMN-MEDIAL LEMNISCUS SYSTEM (FIGS. 30-32)

This pathway is important for touch, pressure, vibration and kinesthesia. The thick dorsal root fibers, conducting impulses from the low-threshold, rapidly adapting mechanoreceptors of the skin, muscles and joints, ascend in the dorsal column to terminate in the gracile and cuneate nuclei. As the fibers ascend in the dorsal columns, they send off collaterals ventrally to the spinal gray matter. Most of these collaterals terminate on interneurons, but some reach as far as the ventral horn motorneurons. Pathways from the face are carried through the lemniscus trigeminalis. Fibers form the spinal cord end in the thalamic ventroprosterolateralis (VPL) and from the lemniscus trigeminalis in the thalamic VPM. Fribers from the VPL and VPM terminate in the primary somatosensory (SI) cortex. In addition, some fibers from the VPL and VPM end in the secondary somatosensory area (SII), situated in the upper wall of the lateral cerebral fissure.

Experiments with cutting of the dorsal columns in monkeys and observations in humans with damage more or less limited to the dorsal columns indicate that the dorsal column-medial lemniscus system is important in spatial and temporal comparisons of stimuli, that is the discriminative sensation. Such sensory information is of crucial importance for the performance of many voluntary movements. Indeed, most studies indicate that damage to the dorsal columns produces severe ataxia.

THE SPINOTHALAMIC TRACT (ANTEROLATERAL SYSTEM) (FIGS. 30-32)

The spinothalamic tract is of primary importance for the perception of pain and temperature. A relatively crude sense of touch and pressure can also be mediated by this pathway The *A-delta* fibers terminate in LI and V, while the C fibers in LII. Spinothalamic cells are located in LI, IV-V, VII and VIII. Most thin dorsal root fibers do not synapse directly onto spinothalamic cells but rather influence them indirectly via spinal interneurons. Interneurons of the dorsal horn, especially those of the substantia gelatinosa, have a decisive role on whether the signals from nociceptors will be transmitted to higher levels of the nervous system.The spinothalamic cells in the cord can be classified by their response properties: 1) low threshold units - cells that react only to light mechanical stimuli (light touch of the skin); 2) wide dynamic range units (WDR) - cells that react to stimuli of high intensity (activating nociceptors) and to light stimuli. The impulse frequency of these cells increases with increasing stimulus intensity; 3) high-threshold units - cells that respond only to stimuli of an intensity sufficient to activate nociceptors, and 4) thermosensitive units.

Thalamic termination sites: VPL, PO, CL. Single unit recordings in the three main thalamic terminal regions of the spinothalamic tract have suggested that there are certain functional differences among them. Schematically, the fibers ending most posteriorly (in PO) may be responsible for the immediate awareness of something painful ("ouch"!); those ending in the VPL signal where exactly the painful stimulus is, whereas fibers ending in the intralaminar nuclei may be responsible for the intense discomfort and emotional aspect of pain sensation. Although both the lemniscal and anterolateral fibers terminate in the VPL and VPM nuclei of the thalamus, they do not convergence on the same cells, thus inputs from discriminative pathways and pain/temperature pathways

terminate on different groups of neurons, producing neurons specific for single modalities.

CENTRAL CONTROL OF SENSORY TRANSMISSION (FIG. 38)

There are descending fiber connections from the cerebral cortex and the brain stem ending in various relay nuclei of the somatosensory pathways. These connections are somatotopically organized and enable selective control of sensory signal transmission from particular parts of the body and from particular receptor types. Among the various aspects of central control of sensory impulse transmission, those related to pain in particular have received much attention in recent years. According to one hypothesis, the periaqueductal gray (PAG) stimulation through connections to the nucleus raphe magnus (NRM) and hence to the cord could elicit inhibition of spinothalamic cells so that they are less readily activated by impulses from nociceptors. Part of the analgesia is mediated through the binding of opiates to their receptors in the PAG, the NRM and parts of the spinal cord (LI, II and V). Microinjection of morphine in the PAG can produce analgesia in experimental animals that depend at least partly on connections from NRM to the spinal cord. The transmitter of fibers from the raphe magnus is serotonin. Also some of the dorsal horn interneurons contain opioid peptides. Suppression of pain may enable continuation of intense physical activity for a while, which may be of vital importance. Also analgesia may also be produced by stimulation of peripheral nerves (acupuncture) or in stressful situations. Depending on the nature of the stress, the analgesia may be mediated by liberation of endorphins or by apparently endorphin independent mechanisms. There is also evidence to suggest that the emotional state of the animal is of importance for whether analgesia is produced or not.

THE SOMATOSENSORY CORTICAL REGIONS (FIGS 37,39,41)

Sensory impulses conducted in the medial lemniscus and the spinothalamic tract finally reach the two somatosensory areas, SI and SII. Both of these cortical regions receive somatotopically organized projections from the VPL and VPM. Somatosensory impulses also reach other cortical regions, such as the motor cortex (M1). Within each of the cytoarchitectonic subdivisions (areas 3a, 3b, 1, 2) of the primary sensory cortex it appears that the whole body has its representation; thus there are probably four body maps within S1.

The body maps contain many distortions, the most dramatic of which are the greatly enlarged representations of the hand, particularly the digits and that of the face. Representations of the digits occupies more than 100 times the cortical surface area devoted to the trunk. By this relative enlargement in cortical representation, the digits and lips are said to be magnified, and the degree of overrepresentation is called the magnification factor.

Neurons in area 3b and area 1 are primarily activated by stimulation of cutaneous receptors. In contrast, areas 3a and area 2 are responsive to deep stimuli, with area 3a particularly responsive to muscle afferents and area 2 to joints. Even though many

neurons in SI are activated only or most easily from one receptor type -that is, they are modality-specific -there are also neurons in SI with more complex properties.

SII is located in the upper bank of the lateral sulcus and adjoining insula. Receive input from SI. Neurons of SII, in turn, give rise to axons that innervate the insular cortex and from there somatosensory information reaches the hippocampus and amygdala. By this scheme, SII is vital as the obligatory route taken by sensory inputs mediating tactil learning and memory. A second major role for SII apparent from its intarcortical connectivity is that of sensorymotor integration.

SI is primarily concerned with the texture of objects, whereas area SII, which is related to both cutaneous and deep receptors, is more important for the discrimination of size and shapes. Lesions of SI in humans entail reduced sensation in the opposite half of the body. Not all sensory qualities are affected equally, however. Discriminative cutaneous sensation and kinesthesia are particularly disturbed; much less reduced (if at all) is pain sensation.

Cortical Map Plasticity (Ramachandran, Merzenich) (FIGS. 40,44,45)

Further Processing of Sensory Information:

The posterior parietal cortex Areas 5 and 7 belongs to the so-called association areas of the cortex. They do not receive direct sensory information from the large somatosensory pathways but via numerous association fibers from SI and SII. The activity of neurons in area 5, and 7 may depend not only on what is occurring in the periphery but also on whether the attention of the monkey is directed toward the actual stimulus.