Spinal Sensorimotor System Part I: Overview
A Tech Brief Prepared for the
Neurofuzzy Soft Computing Program
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The Spinal Sensorimotor System as a Model Application

The spinal sensorimotor system (SSMS) is an appealing homologue for our identified application area of the design of PCNNs for handling large amounts of incoming sensory data and responding to this data in real time with a large number of responding outputs. The biological SSMS has all three of these elements in spades, and has an obvious lead-in to the bipedal locomotion application. While I do not propose that we try to duplicate or biomimic a system as complex as the SSMS, I do propose that a bipedal system modeled somewhat along the lines of the biological example makes an appealing research pathway. The bipedal locomotion system we investigate would be "biomimetic" in the general sense of that word, rather than "biomimic" in the narrow sense of my use of that term.

The purpose of this tech brief is to acquaint everyone with the general schema and structure of the SSMS. Part I is the general overview. Part II deals with more of the specifics of the neural network organization of the system. Think of Part I as a sort of "systems level over-view" of the topic. In it I will try to identify some key issues for EC-based network design.

Spinal Cord Organization

It's probably no surprise that we should begin with the spinal cord itself, since this structure houses all the direct motor control circuits and does the initial sensory feedback signal processing. The spinal cord is the lowest-level neural structure in the central nervous system. The spinal cord runs down the center of the spine, and the spinal cord neurons are distributed over the vertebrae. Running laterally into the body from each of these "segments" are the spinal nerves. A **nerve** is a bundle of axons running between the central nervous system and peripheral target cells.[1] The spinal cord system has four principal classes of nerves as shown below in Table I.

Figure 1 illustrates the spine and its relationship to the hips and brain. At the brain the spine melds into the lowest part of the brainstem, which is called the medulla oblongata (or just the medulla for short). Each vertebra has a pair of nerves, one on each side, each with two roots. In biological terminology the "coordinate system" for the body has the following designations: Ventral (toward the belly), dorsal (toward the back; think of a shark's "dorsal fin"), lateral (to the sides) and medial (in the middle). Nerve bundle pairs run lateral to the spinal cord from each side.

TABLE I: Spinal Nerves

Nerve Group	No. of Nerve Pairs	To/ From muscles, glands and afferents of
Cervical	8	neck, shoulders, arm, and hand
Thoracic	12	chest and abdominal walls
Lumbar	5	hips and legs
Sacral	5	genitals and lower digestive tract

[1] Interestingly enough, the central nervous system (including the spine) has no nerves. Bundles of axons in the central nervous system are called "**tracts**" or "**pathways**" instead of being called "nerves."
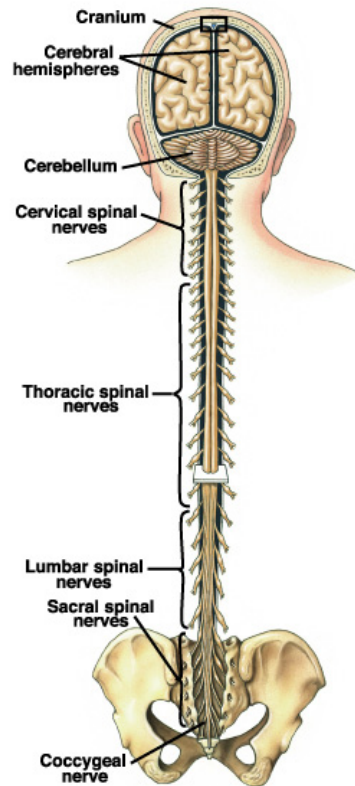
Figure 1: Spinal Nerve Organization. The picture illustrates the four principal classes of spinal nerve locations plus the location of the coccygeal nerve. The spine enters the cranium at the medulla oblongata, which is the first stage of the brainstem. Signals originating in the brain are called supraspinal signals. Tracts coming down from the brain are called descending pathways; tracts going up to the brain are called ascending pathways. The white plate indicates figure 2. (Picture courtesy of Dr. Dee Silverthorn).

Figure 2 illustrates the structure of the spinal nerves. Each side consists of a dorsal root and a ventral root. The dorsal root is the pathway for incoming sensory signals. Just before entering the spinal cord the dorsal root bulges out in a structure called the dorsal root ganglion, which contains the cell bodies of the sensory neurons. The ventral root is the pathway for outgoing motor control signals that innervate the muscles controlled by this particular spinal segment.

Spinal cord gray matter is illustrated in Figure 3. For our purposes the most important regions of the spinal cord are the dorsal and ventral horns. The dorsal horn is the region of the spinal cord that receives incoming (afferent) signals from the body's sensory neurons. It processes these signals and passes some of them on to the ventral horn, and others on to the brain or other vertebra segments. Some of the afferent axons entering via the dorsal root are also passed directly on to the ventral horn.

The ventral horn is the motor drive circuitry of the spinal cord. It contains a number of different types of neurons including motoneurons (MNs) that actuate the muscles, and various interneurons (INs) that perform signal processing for muscle control. The ventral horn receives information from the dorsal horn and from descending pathways that convey signals from the brain to the motoneurons and to the interneurons.
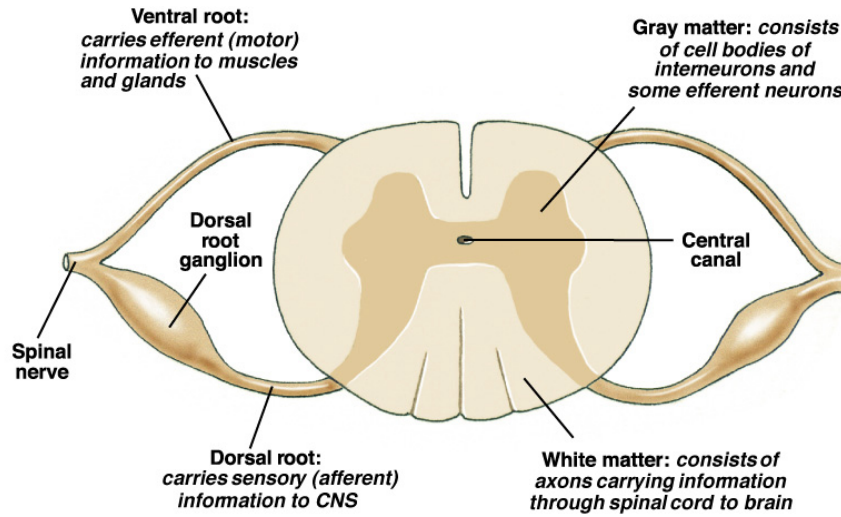
Figure 2: Organization of the dorsal and ventral spinal nerves. The large structure in the center is the spinal cord. The ventral root side is toward the front of the body; the dorsal root is closer to the back. The gray matter is the region of the spinal cord that contains the spinal neurons. The white matter consists of axons that carry signals up or down the spinal cord, either to/ from other vertebrae segments or to/ from the brain. (Picture courtesy Dr. Dee Silverthorn).
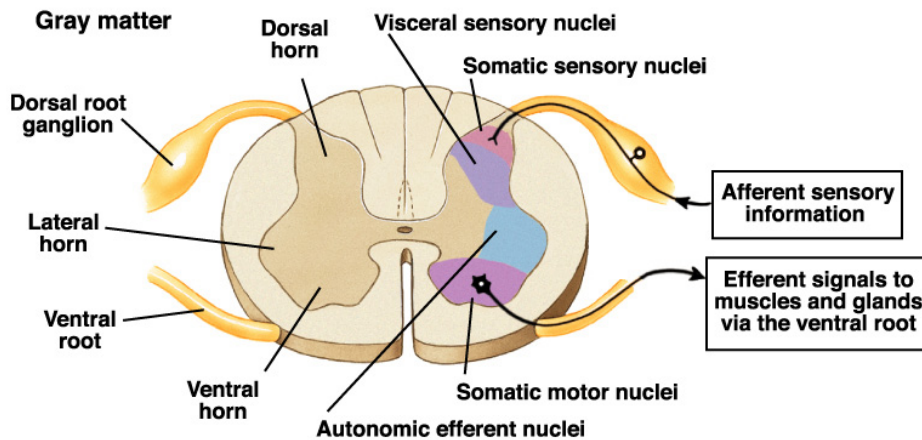

Figure 3: Spinal cord gray matter. The gray matter is arranged symmetrically about the central canal. Each side has three regions: the ventral horn, the dorsal horn, and the lateral horn. The primary functions of each region are indicated in the figure. (Picture courtesy Dr. Dee Silverthorn).

The two sides of the spinal cord are interconnected, so each side can receive signals from or send signals to the ventral horn motor control circuits and the dorsal horn servo circuits on the other side. This arrangement allows for the coordination of muscle movements on both sides of the body. Signals confined to one particular side are called that side's **ipsolateral** signals. Signals that come in from the other side of the spinal cord are called **contralateral** signals.

The lateral horn is of little concern to us on this project. The neural circuitry in the lateral horn is primarily concerned with sensory processing and motor control of the autonomic and visceral system (i.e. with the smooth muscles of the internal organs).

Figure 4 illustrates the arrangement of the white matter in the spinal cord. The white matter consists of bundles of myelinated axons that can carry signals for relatively great distances. The principal descending pathways originating in the brain and involved in spinal motor control are: the **vestibulospinal tract**, which mediates reflexes involved in posture and the sense of balance; the **rubrospinal tract**, which is involved with fine motor control of distal extremities (e.g. the fingers) and supplements the postural control of the vestibulospinal tract; the **corticospinal tract**, which carries signals from the motor cortex and other related areas of the cerebral cortex involved in voluntary motions; the **reticulospinal tract**, which is involved in switching on central pattern generation used in walking; and the **tectospinal tract**, which regulates upper body and neck orientation and visually-guided head movements. These are the main "command and control busses" from the brain to the spinal motor system.
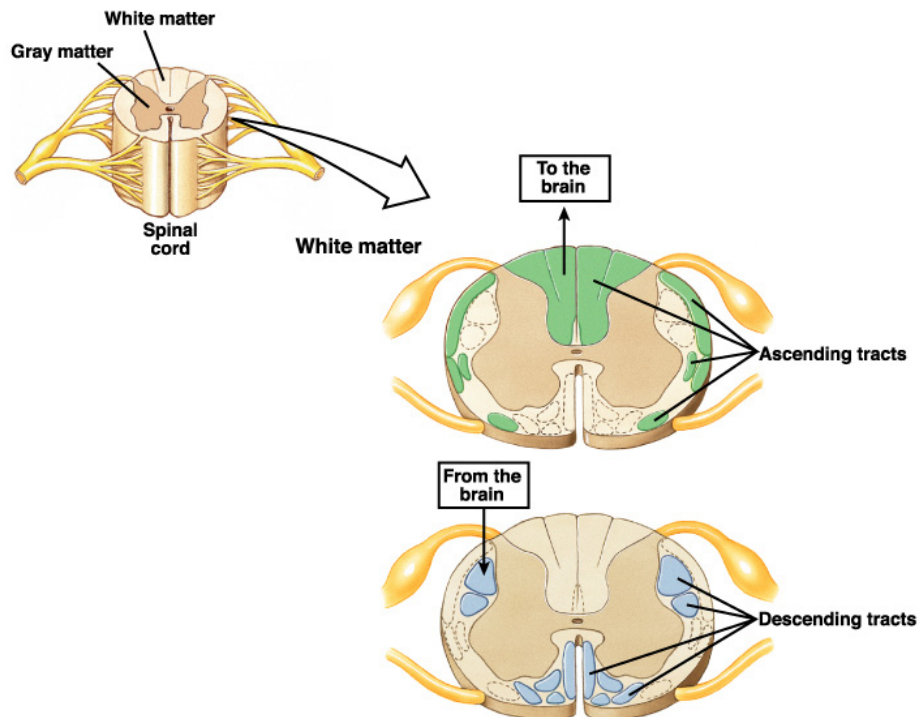

Figure 4: Spinal cord white matter. The white matter consists of myelinated axons conveying signals up and down the spinal cord. Ascending tracts are axon bundles carrying signals up the spinal cord to the brain or to other vertebra segments. Descending tracts are axon bundles carrying signals down the spinal cord from the brain or from other vertebra segments. The figure illustrates the locations of the ascending and descending tracts. (Picture courtesy Dr. Dee Silverthorn).

The principal ascending pathways are: the **spinothalamic tract**, which mainly carries pain and temperature signals and some tactile and joint sensory signals to the thalamus[2] and brainstem; the **lemniscal pathway** consisting of the gracile fascicle and cuneate fascicle axon bundles (also known as the dorsal columns), which carries precise and complex information about touch and pressure; and the **spinocerebellar tract**, which carries muscle and joint proprioceptor (i.e. muscle and joint sensory) information from the legs, central locomotor rhythm information, and information about descending commands reaching the spinal interneurons to the brainstem and from there to the cerebellum.[3] These pathways make up the primary "data busses" for sensory, motor state, and spinal "copies of the orders" command information going back to the brain.

Figure 5 illustrates, in greatly simplified form, the ascending pathways for the spinothalamic tract and the lemniscal pathway. All-capital letters designate the different locations in the spine or
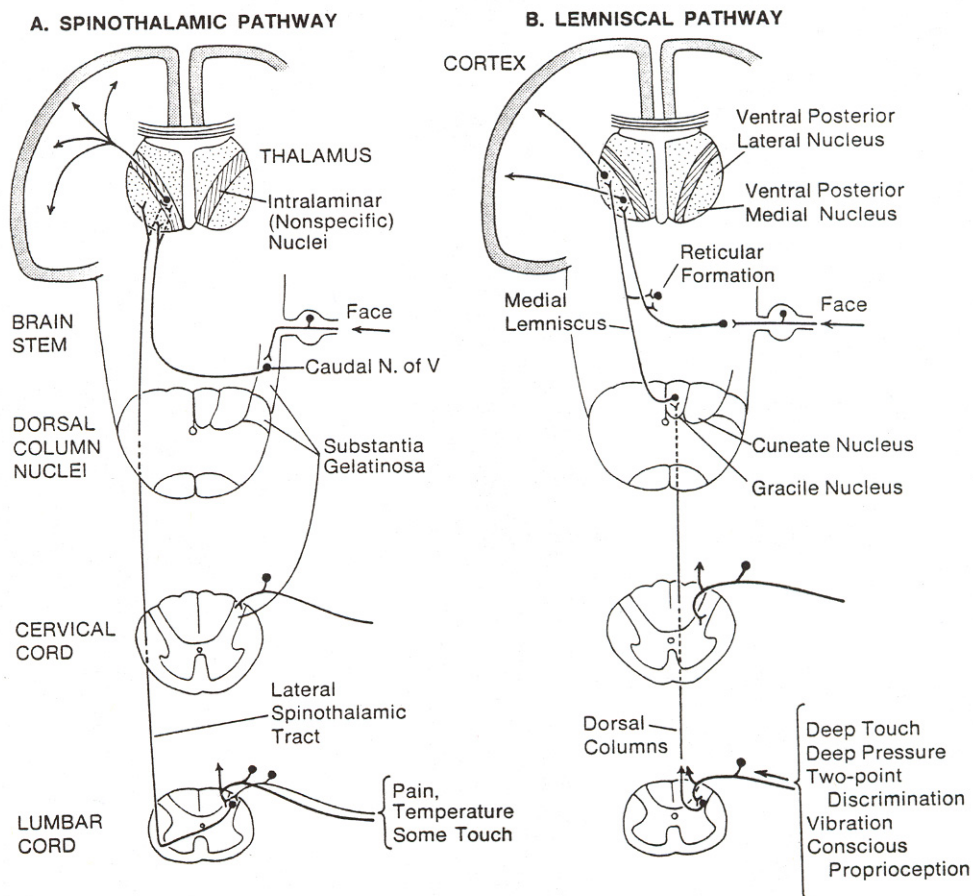

Figure 5: Illustration of spinothalamic and lemniscal pathways. For discussion see text.

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[2] The thalamus is a kind of central switchboard and relay station in the brain. No somatosensory information reaches the cerebral cortex without having first passed through the thalamus.

[3] The cerebellum is the part of the brain chiefly responsible for carrying out the details of executing complex movements commanded by the motor cortex in the cerebrum. The motor cortex is the "executive" brain structure for locomotion, issuing high-level commands to the cerebellum, which then carries them out step-by-step. The cerebellum is a center for "motor learning." In a sense, we could say that the cerebellum "programs itself" for executing movements, which is why we do not have to consciously think about the details of walking, whereas a baby is very clumsy while first learning how to walk.
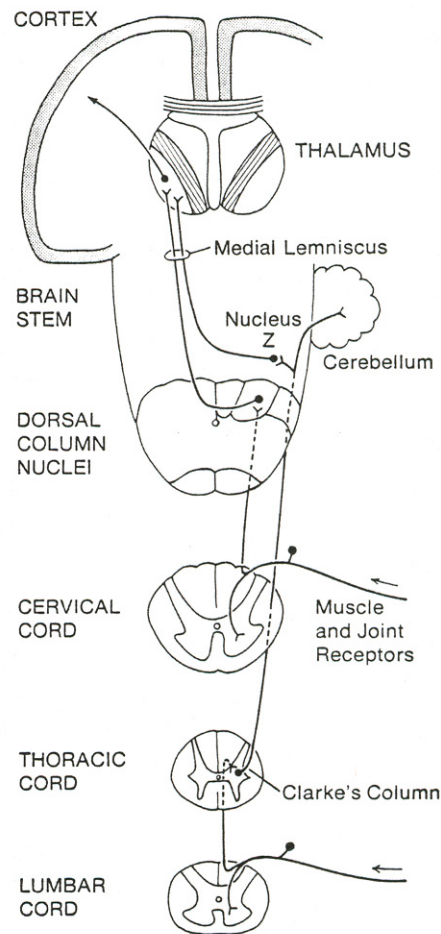
Figure 6: Simplified illustration of the spinocerebellar pathway. The figure also includes part of the lemniscal pathway to the thalamus. The spinocerebellar pathway is the pathway going into the brainstem and contacting nucleus Z (a rather poorly understood nucleus in the brainstem) and the cerebellum. Clarke's column is an integrating nucleus for sensory information from muscles and joints.

brain. The dorsal column nuclei receive signals from the lemniscal pathway and project to the reticular formation in the brainstem (which is involved with arousal and consciousness) and to the thalamus. The types of sensory data carried by these pathways is shown in the figure.

Figure 6 is a simplified illustration of the spinocerebellar pathway. This pathway provides for integration of muscle and joint information with cerebellar mechanisms that are essential for sensorimotor coordination and the maintenance of muscle tone and posture.

The principal descending motion-command pathways are illustrated in simplified form in Figure 7. The figure shows the terminal connections of these pathways in the white matter and the ultimate destination of these signals in the gray matter of the ventral horn. The figure also shows the sites where the descending tracts originate in the brain. (These sites themselves receive inputs from elsewhere within the brain). Note that although most of the descending signal paths originate in the brainstem, particularly the medulla and another part of the brainstem called the pons, the descending pathway of the corticospinal tracts carry information directly from higher cerebral brain centers (i.e. the motor cortex).
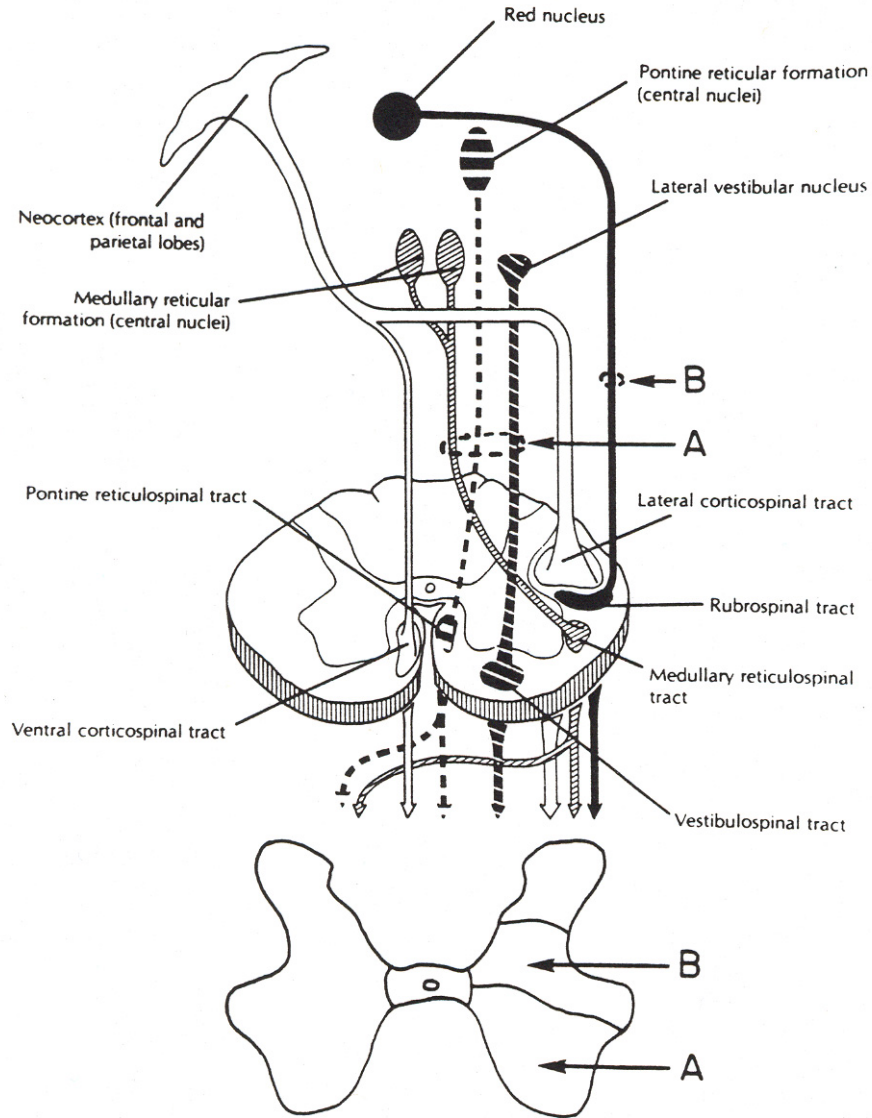
Figure 7: Principal descending pathways involved in motion control. The neocortex is the outermost part of the cerebrum. The part of the neocortex indicated here is that which is involved with the motor cortex and part of the somatosensory cortex (the part of the cerebrum concerned with processing perceptual information). The red nucleus and pontine reticular formation are located in the part of the brainstem called the pons, which connects at the top of the medulla. The medullary reticular formation is located in the medulla. The tectospinal tract is not shown in this figure. The other four tracts are labeled. The lower figure shows the gray matter target areas for the tracts labeled A and B in the upper figure.

Sensory Nerves

The body has a rich variety of sensors that convey information to the spinal cord. For our purposes we can classify these as: cutaneous (skin) mechanoreceptors responding to pressure, vibration or touch; cutaneous thermal nociceptors (pain receptors responding either to heat or to cold, but typically not both); cutaneous mechanical nociceptors responding to intense pressure or prickly pain; subcutaneous mechanical and subcutaneous thermal nociceptors (pain and temperature sensors in the joints or muscles); and muscle mechanico-receptors responding to

stretch, velocity, or tension. For convenience we can categorize these in terms of their locations as skin sensors, joint sensors, and muscle sensors.

Signals from different types of sensors are conveyed to the dorsal horn via fibers with different propagation velocities by sensory neurons of different types. Figure 8 tabulates the spectrum of different sensory signal-carrying elements (and also includes the three motor fibers that carry action potentials from the ventral horn to the skeletal muscles). The figure does not include the joint sensors, which will be discussed separately.

Although perhaps not immediately apparent, sensors of all these types (including joint sensors) are involved in skeletal muscle control by the ventral horn. Skin receptors are often very
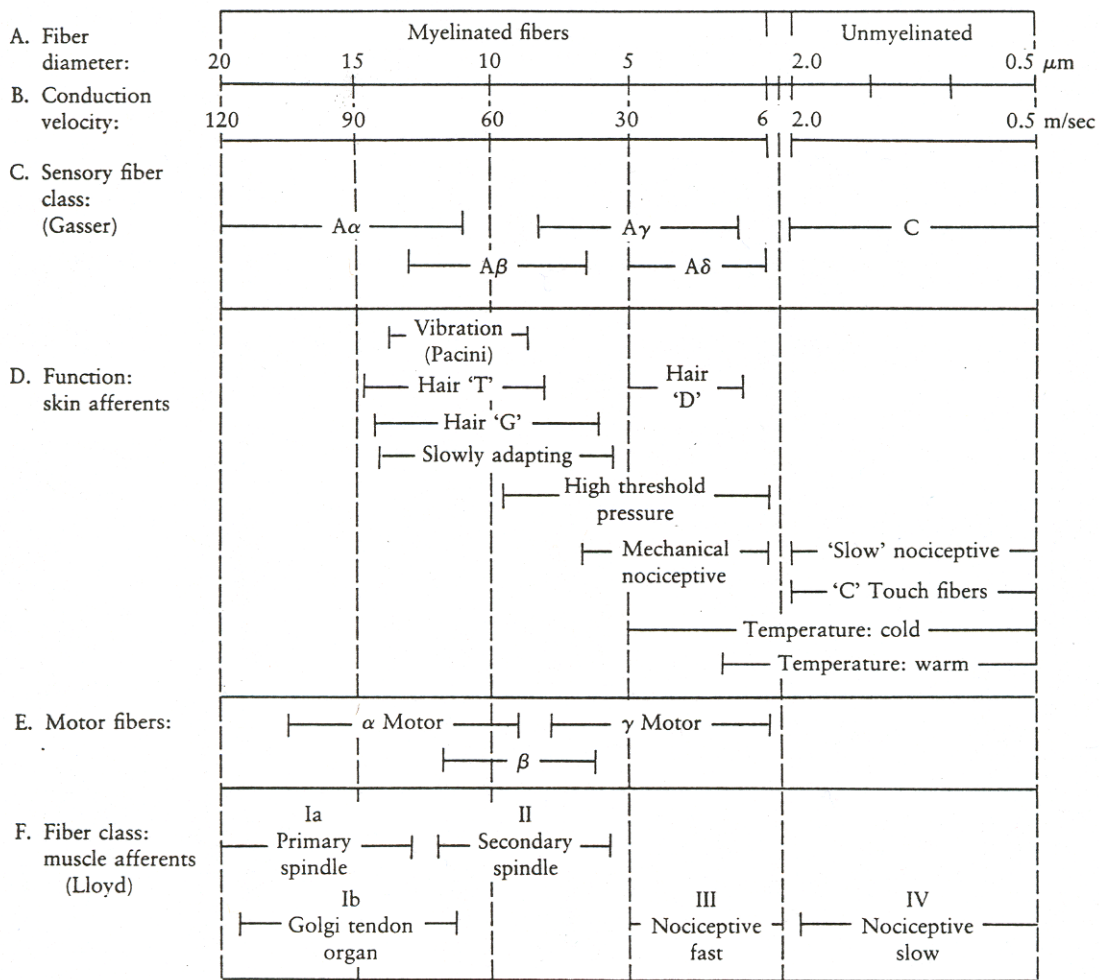
After Somjen (1972)

Figure 8: Spectrum of sensor and fiber characteristics. Row C shows the five major fiber types (axons) that transmit the sensory information. Rows A and B give the range of fiber diameters and associated propagation velocities characteristic of these fibers. Row D illustrates various types of skin receptors and their characteristic signaling properties. Row E depicts the motor fibers that carry action potentials to the skeletal muscles. Row F gives the sensors that provide feedback from muscles to the dorsal horn. The figure does not show the joint sensors and I will discuss these separately.
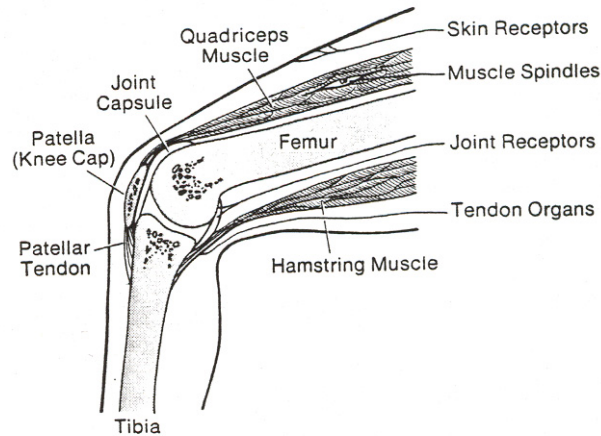
Figure 9: Sites of sensory receptors for muscle sense and kinesthesia. Kinesthesia refers to the sense of position and movement of the limbs as well as sensations of effort, force, and weight. The muscle spindles and tendon organs (i.e. the Golgi tendon organs) were discussed in our previous tech brief on muscles. We will discuss the skin and joint receptors in this tech brief. The sum total of all sensory information associated with the skeletal muscle system, including conscious sensation, is called **proprioception**.

much involved in kinematical muscle actions, as suggested by the proximity of the skin receptors to the quadriceps muscle in Figure 9. That there is an interrelationship among muscle spindle receptors and joint receptors is perhaps obvious to you.

Although most people do not commonly think of it as such, the skin is an organ – the largest single organ in the body. It is subdivided into three layers, the covering epidermis (the outer integument), the connective dermis (the "below-the-surface" skin layer), and the subcutaneous fat layer. It performs a number of vital functions, including the conveyance of information about the animal's environment, temperature regulation, and protection of the inner organs. In human beings the skin is further classified in terms of glabrous (non-hairy) skin (e.g. the palms of the hands, fingertips, bottom of the feet, etc.) and hairy skin (which makes up most of the skin mass in mammals). Note that it does not matter whether or not the hairy skin actually has hair present. The top of the head is hairy skin regardless of whether you are Touraj or you are Terry. The two types of skin employ different suites of skin receptors, and this is the key distinction between them so far as our interests are concerned.

Figure 10 illustrates the main types of sensory receptors found in glabrous skin. As we are about to see, free nerve endings and Pacinian corpuscles are also found in hairy skin. Some free nerve endings respond to only one type of stimulus (e.g. temperature); other types may respond to more than one sensory modality, and these are called polymodal receptors. It is worthwhile here to clear up a bit of biological terminology regarding free nerve ending stimuli. "Pricking pain" refers to immediate sharp pain (e.g. from touching something very hot; pricking does not imply that something mechanically stabs into the skin); burning pain refers to a constant aching, which would typically follow a pricking pain. Also, "cooling" and "warming" receptors are defined by the fact that their peak sensitivity to temperature is either below or above body temperature, respectively.

Figure 11 illustrates the main types of sensory receptors found in hairy skin. Sensors in the first two columns are more or less the same as those in figure 10. The last two columns depict sensors that differ from those of figure 10, even though their characteristics are quite similar.
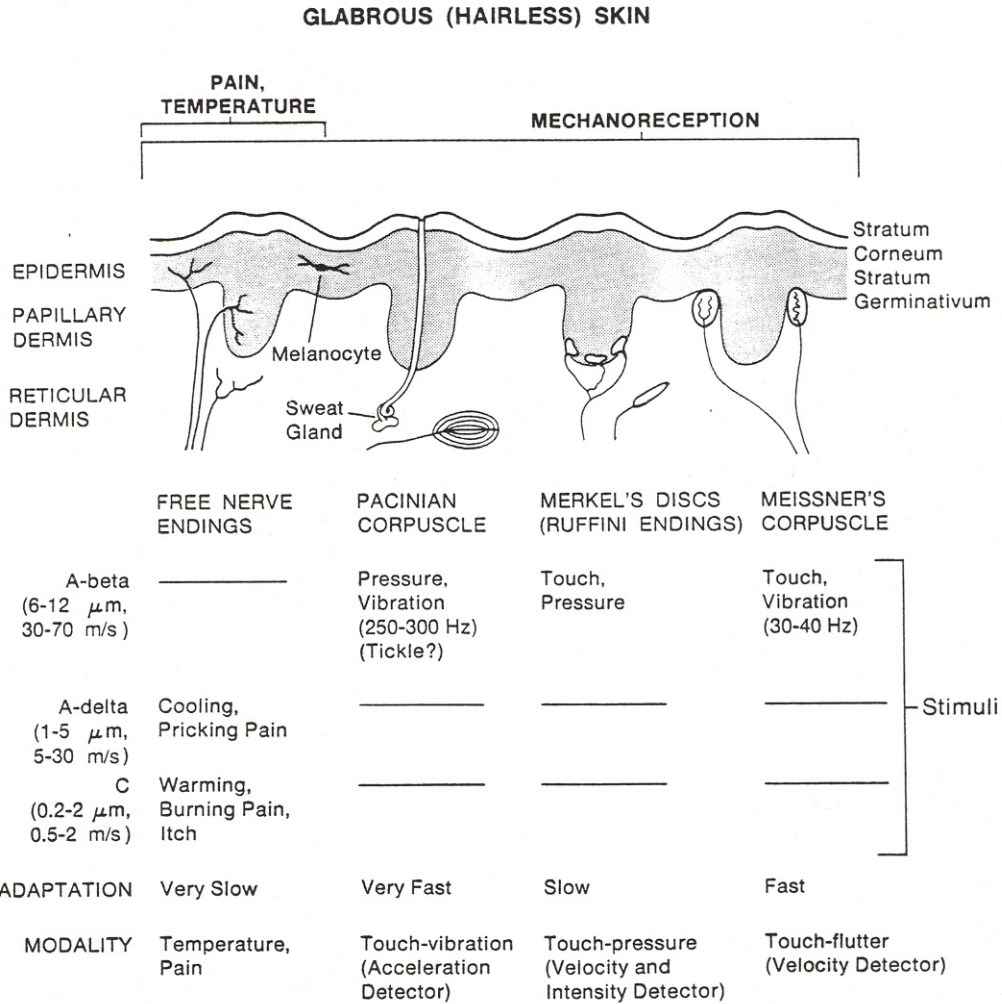
GLABROUS (HAIRLESS) SKIN

PAIN, TEMPERATURE

MECHANORECEPTION

EPIDERMIS

PAPILLARY DERMIS

RETICULAR DERMIS

Melanocyte

Sweat Gland

Stratum Corneum
Stratum Germinativum

	FREE NERVE ENDINGS	PACINIAN CORPUSCLE	MERKEL'S DISCS (RUFFINI ENDINGS)	MEISSNER'S CORPUSCLE	
A-beta (6-12 μm, 30-70 m/s)	———	Pressure, Vibration (250-300 Hz) (Tickle?)	Touch, Pressure	Touch, Vibration (30-40 Hz)	
A-delta (1-5 μm, 5-30 m/s)	Cooling, Pricking Pain	———	———	———	Stimuli
C (0.2-2 μm, 0.5-2 m/s)	Warming, Burning Pain, Itch	———	———	———	
ADAPTATION	Very Slow	Very Fast	Slow	Fast	
MODALITY	Temperature, Pain	Touch-vibration (Acceleration Detector)	Touch-pressure (Velocity and Intensity Detector)	Touch-flutter (Velocity Detector)	

Figure 10: Main types of sensory receptors and their functional properties in human glabrous skin.
The figure shows the division between mechano- and non-mechano-receptors. Each column provides information concerning axon fiber type, stimuli, the adaptation properties of the receptors, and the sensory modalities for each class of receptor. These nerve fibers project to the cell bodies of their respective sensory neurons located in the dorsal root ganglion.

Some of the key properties that distinguish different receptors are: speed of adaptation to stimulus; receptive field of sensation (i.e., how big a skin area is covered by a particular receptor, therefore how fine or course is the ability to sense stimulus); threshold of stimulus required for stimulating the nerve; and intensity of the sensation produced. For example, the sense of touch has far higher spatial resolution and a finer grade of response to stimulus in the fingers than is the case in, say, the thigh. Note, too, that some of the mechanoreceptors, e.g. the Pacinian corpuscles, Meissner's corpuscles, and the hair follicles, are frequency-selective in terms of their stimuli. In effect, they constitute mechanical filters.

There are four main types of joint receptors. These are illustrated in Figure 12 for the case of the kneecap. Type I receptors resemble Ruffini endings in the skin (see figure 10). Type II receptors take the form of flattened Pacinian corpuscles (see figures 10 or 11). Type III receptors resemble the Golgi tendon organs (which we discussed in the tech brief on muscles) and are tension-sensing receptors. Type IV receptors are unmyelinated nerve endings that resemble pain fiber terminals.
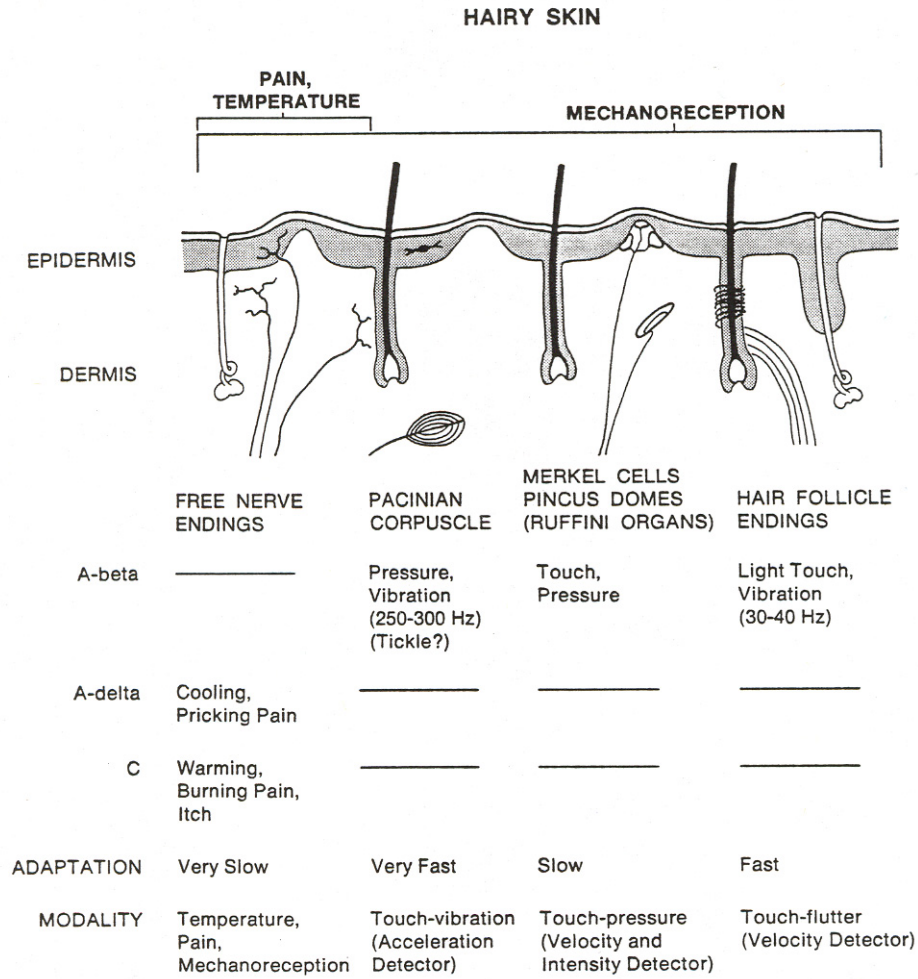
HAIRY SKIN

	FREE NERVE ENDINGS	PACINIAN CORPUSCLE	MERKEL CELLS PINCUS DOMES (RUFFINI ORGANS)	HAIR FOLLICLE ENDINGS
A-beta	————	Pressure, Vibration (250-300 Hz) (Tickle?)	Touch, Pressure	Light Touch, Vibration (30-40 Hz)
A-delta	Cooling, Pricking Pain	————	————	————
C	Warming, Burning Pain, Itch	————	————	————
ADAPTATION	Very Slow	Very Fast	Slow	Fast
MODALITY	Temperature, Pain, Mechanoreception	Touch-vibration (Acceleration Detector)	Touch-pressure (Velocity and Intensity Detector)	Touch-flutter (Velocity Detector)

Figure 11: Main types of sensory receptors and their functional properties in human hairy skin. The gross properties of these receptors are similar to their glabrous-skin counterparts (see figure 10), although their detailed properties differ, e.g. in terms of threshold for sensation, intensity of stimulation, and spatial resolution.
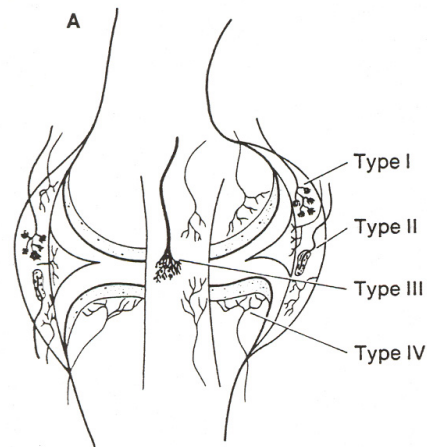

Figure 12: Main types of joint receptors. In terms of gross properties these receptors resemble the skin receptors. See text for discussion.

Type I receptors respond to stretch with a slowly-adapting discharge (action potential bursts) and function as a velocity and intensity detector. Type II joint receptors sense pressure and vibration and are rapidly-adapting. Type III receptors are found in ligaments, respond to tension, have a high threshold for firing, and are slowly-adapting. The joint receptors are tuned to respond to different joint positions and respond only over relatively narrow angles within the range of joint movement.

We introduced three of the muscle mechanoreceptors previously in our brief on muscles. These were: group Ia (velocity) receptors; group Ib (Golgi tendon organ tension sensors); and group II (length, i.e. stretch) receptors. These receptors are included in figure 8. In addition, muscles also contain two types of nociceptors: fast (group III) nociceptors and slow (group IV) nociceptors. Like other types of pain and temperature sensors, these participate in control of muscle motor activity. To date I have uncovered relatively little specific information about these receptors, but I think their role in muscle is probably pretty self-evident on at least a qualitative level, particularly to anyone who has ever torn a muscle while exercising or participating in athletics, or who has felt "the pump" after lifting weights or "the burn" while lifting weights, backpacking, or running.

The Reflex Arc Concept

It's probably safe for me to assume that all of us know what a muscle reflex is. The doctor taps your knee with his little hammer and your lower leg jerks; you touch something hot and your hand and arm jerk back; you step on something sharp and your leg flexes to get off the object and your other leg stiffens to bear your weight while your torso muscles adjust to get your weight off the injured foot. As these examples illustrate, a muscle reflex can range from being simple and localized (the knee jerk) to being a fairly complex symphony orchestrated via a wide range of muscles (the "step on something sharp" example). What some of us may not know is that all these reflexes, from the simple to the very complicated, are entirely actuated at the spinal cord level, usually without any intervention by the brain.[4]

At the neural network level most immediately proximate to the motoneurons, pretty much the entirety of the ventral horn circuitry is devoted to reflexes and muscle servo control. There are four types of spinal reflex, illustrated in Figure 13. These are: the myotatic (stretch) reflex, the inverse myotatic reflex, the Group II reflex, and the flexor reflex. Figure 13 illustrates the sensory afferent involved in stimulating the reflex and provides an estimate of the number of neuron layers between the afferent signal (as it arrives via the dorsal root) and the motoneurons. (The neural networks involved are not as simple as this figure might suggest).

If the ventral horn circuitry (at least at its lowest levels) is devoted to actuating reflexes and regulating muscle responses, how is voluntary movement possible? The answer to this question is that the neural organization has evolved in such a way that descending signals from the brain are able to **co-opt** the circuitry involved in the flexor reflex. This is done by higher-level networks of interneurons mostly in the dorsal and partly in the ventral horns.

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[4] Where there is brain intervention, that intervention takes the form of stopping the reflex, not initiating it. When you are caught by surprise by some (usually nociceptive) sensation, it is almost always impossible for the brain to intervene. Once when I was about four years old, I wandered into our dining room, where my older brother and my father were sham-boxing. Having just come from watching an episode of the Three Stooges, and spotting a "pin" (actually, a nail) sitting on the table, I naturally picked it up and poked my brother in the hind end with it. His reflex was to jump forward while drawing back both arms – a response that carried his nose straight into Dad's on-coming left jab. (Fortunately, *I* survived the episode unscathed).

A. STRETCH (MYOTATIC) REFLEX

AFFERENTS:
Ia (70-120 m/sec)
From spindle
primary endings

Extensor

Flexor

DETECTS: Phasic stretch
of muscle
FUNCTIONS:
Control of movement
? Antigravity

B. INVERSE MYOTATIC REFLEX

AFFERENTS:
Ib (70-120 m/sec)
From golgi
tendon organs

Extensor

Flexor

DETECTS: Active stretch
of tendon
FUNCTION:
Control of muscle force
Control of muscle
stiffness

C. GROUP II REFLEX

AFFERENTS:
II (30-70 m/sec)
From spindle
secondary endings

Extensor

Flexor

DETECTS: Steady stretch
of muscle
FUNCTIONS:
Posture?

D. FLEXOR REFLEX

AFFERENTS: II, III, IV
(0.5-70 m/sec)
From cutaneous
nerve endings

DETECTS: Harmful stimuli
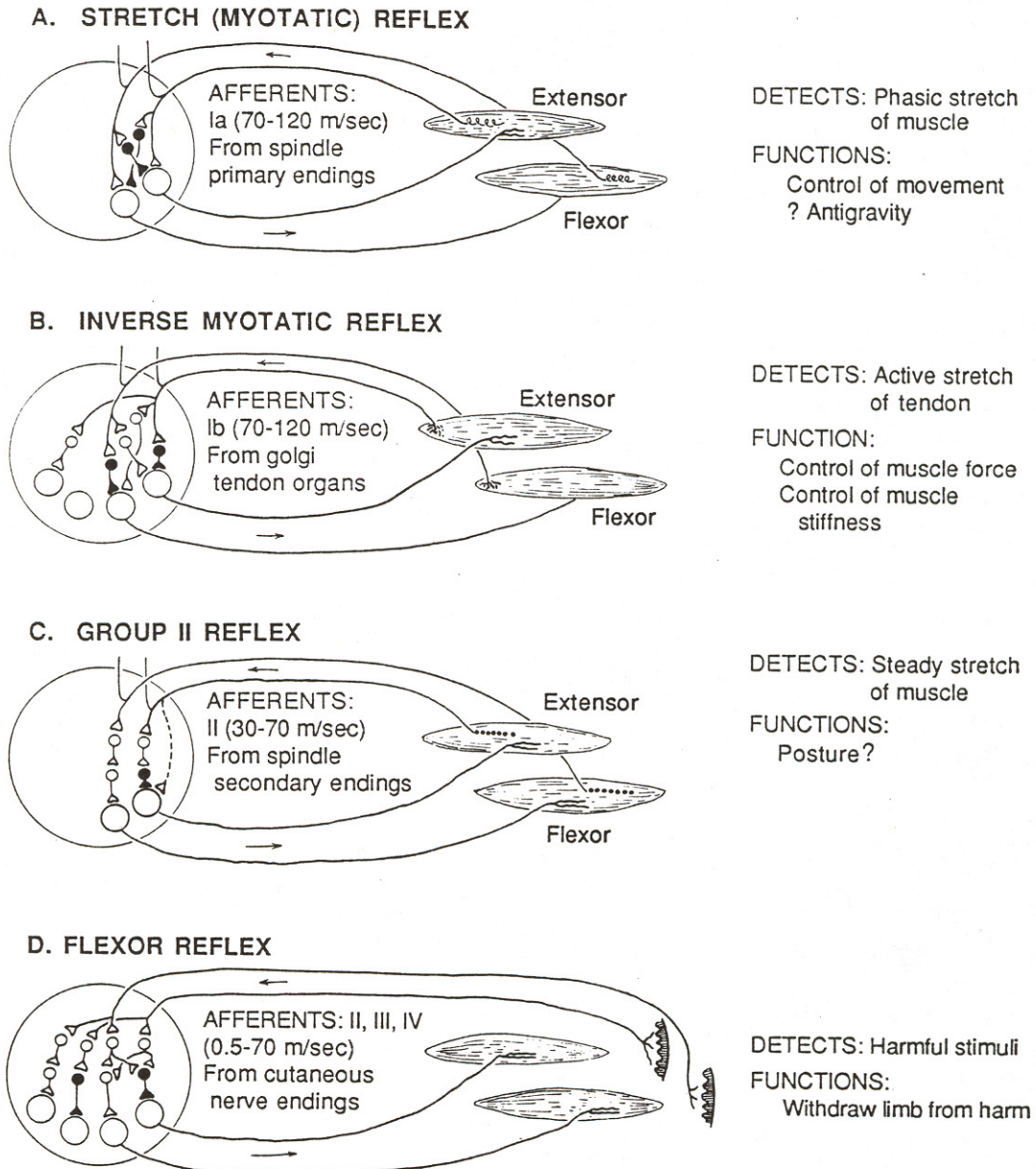FUNCTIONS:
Withdraw limb from harm

Figure 13: The four spinal muscle reflexes. The figure illustrates the type of sensory receptor signal that stimulates the reflex, the type of situation detected and transmitted to the spine via the dorsal root, the putative function of the reflex, and provides an estimate of the number of neuron layers intervening between the afferent signal and the motoneuron. The neural network is <u>not</u> as simple as the figure suggests.

This co-opting of the flexor reflex circuitry by descending command signals has been termed the "reflex arc." In effect, the higher-level interneurons of the SSMS constitute a kind of "steering logic" that allows higher brain functions to block afferent skin, joint, and nociceptive muscle signals (collectively called the **flexor reflex afferents** or **FRA** pathway) and take control of the motor neurons. This rather impressive by-product of evolution allows the higher functions to take advantage of the intricately-connected reflex circuitry for executing the very complex voluntary motions that the body is capable of performing. At the same time, it turns the spinal horns into a "smart terminal" at the disposal of the brain, and off-loads much of the intricate detail of motion control from the higher levels of the motor hierarchy in the brain.
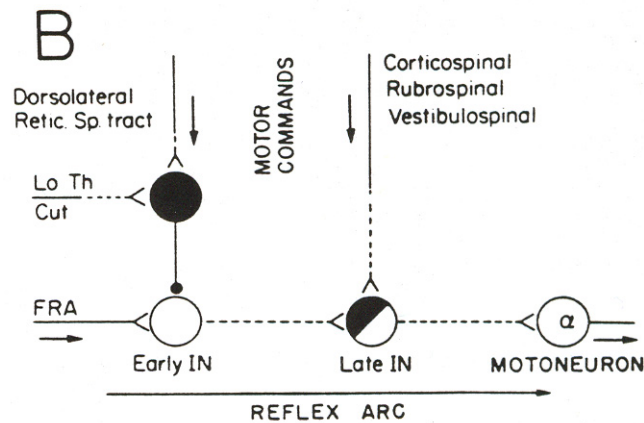
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Figure 14: Schematic illustration of the reflex arc concept. The circles indicate small subnetworks of neurons at the same synaptic level. IN stands for interneuron. Input signals are actually busses rather than individual signals. The dashed lines indicate other possible layers of interneurons interposed between the subnetworks shown. The motor commands are descending signals from the reticulospinal and other tracts (see figure 7). Excitatory synaptic connections are indicated by the "<" synapse symbols. Inhibitory synaptic connections are indicated by the "•" symbol on the lower-left subnetwork. FRA is "flexor reflex afferents", and Lo Th Cut is "low threshold cutaneous inputs". α-motoneurons are the motoneurons that drive extrafusal muscle fibers (refer to the tech brief on "Muscles"). "Early IN" designates interneurons that directly receive afferent inputs. "Late IN" designates interneurons at deeper layers of the network in the signal pathway. (These would perhaps consist of neurons in the output layer of the dorsal horn or perhaps interneurons in the ventral horn). The solid-black subnetwork at the upper left in the figure represents mid-level interneurons in the dorsal horn. Note that this subnetwork sends inhibitory inputs to the early dorsal horn INs.

The details of the neural network circuitry, particularly that part of it involving dorsal horn interneurons, is not well understood. However, the general schema of the signal processing pathway is reasonably well-established. Filling in the missing details is one of the challenges for our team, especially for the EC-based network research. Let us take a look at the general schema for the reflex arc. Figure 14 illustrates (in "cartoon" form) the basic idea. The caption explains the symbols being used in the figure. We will begin our discussion with the so-called "intrinsic" modulation of FRA signals, i.e. the modulation of early FRA inputs by other cutaneous signals. We will then go on to discuss how the higher motor command centers in the brain take advantage of the circuits for intrinsic modulation.

The idea of intrinsic modulation of nociceptive FRA signals begins with the simple observation that pain in the skin can often be relieved (if not too severe) by gently stimulating skin around the hurt area (light brushing, massaging, or tickling). This is the first clue that skin cutaneous mechanoreceptors can inhibit the nociceptive free-nerve-ending pathway to some degree (see figures 10 and 11).[5] Free-nerve-ending pathways are generally transmitted by Aδ- and C-type fibers. As figure 8 illustrated, these fiber types have relatively slow propagation velocities, with unmyelinated C-type fibers having the slowest velocities and Aδ-type fibers being only slightly faster. Figure 8 illustrates the types of skin afferents conducted by these axon fibers.

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[5] R. Melzack and P.D. Wall, "Pain mechanisms: a new theory," *Science*, vol. 150, pp. 971-979, 1965.
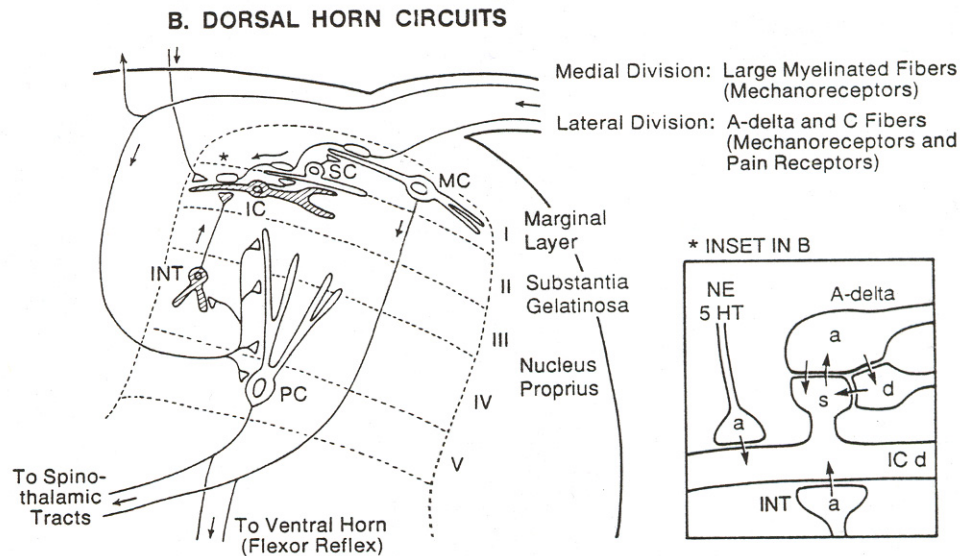
B. DORSAL HORN CIRCUITS

Figure 15: Some of the neurons and synaptic connections found in the dorsal horn. The inset is a close-up of the synaptic connections indicated by the "*" in the left-hand figure in layer II of the horn. The neuron identifiers have the following definitions: IC = islet cell; INT = interneuron; MC = marginal cell; PC = projection cell; SC = stalked cell. The descending axon just below the letter "B" in the left-hand figure is part of the reticulospinal tract (i.e. it corresponds to the left-most command signal input in figure 14). Abbreviations in the inset figure have the following definitions: a = axon; d = dendrite; s = spine (as in a dendritic spine, not as in a bone); NE = norepinephrine; 5-HT = serotonin (both NE and 5-HT are metabotropic neurotransmitters; the figure does not intend to imply that the reticulospinal fiber carries both, but that both are known neurotransmitters for these types of fibers); IC = islet cell; INT = interneuron. The unlabeled dendrite in the right-center of the inset probably belongs to the stalked cell. The s-a junction is a dendroaxonic synapse, and its function is immediate feedback inhibition. The dendrodendritic synapse d-s provides lateral interaction between responding cells. The axodendritic synapses, a-s and a-d, are forward-transmitting signal paths.

Low-threshold cutaneous afferents are typically tactile or other mechanoreceptors that make use of Aβ-type fibers (see figures 10 and 11). These fibers are larger and have faster propagation velocities than the fibers just discussed. Figure 8 illustrates the speed of these fibers and the types of cutaneous afferents they convey.

We next recall that all peripheral nerves enter the spinal cord by way of the dorsal root. While most of the details of dorsal horn circuitry is not yet well understood, some of its organization is reasonably well established. Figure 15 illustrates some of the main neuron types and synaptic connections found in the dorsal horn. (Again, recognize that this figure is <u>not</u> a complete depiction of the dorsal horn neural networks). The incoming afferent signals are divided into two types. The large myelinated fibers are Aβ-type fibers. The lateral division consists of both Aδ- and C-type fibers. The Aβ fibers are glutaminergic (excitatory) and make contact with dendrites in layers III and IV of the dorsal horn. The projection cell (PC) excited by these fibers provides a straight-through transmission of these tactile afferents. The interneurons INT mediate interactions among *different sensory modalities* of the lateral and medial afferents. (Only one INT interneuron is shown, but the horn has many of them, and there are multiple afferents coming in through the dorsal root). Only FRA signals are depicted in this figure.

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The Aδ-type fibers (high-threshold afferents) terminate mostly on the marginal cell (MC). These afferents would correspond to the FRA inputs in figure 14, and MC might be considered to be an "early IN". (The Aδ fibers are "fast" compared to the C-type fibers). The C-type fibers (slow nociceptive fibers; see figures 10 and 11) terminate mostly in layer II of the dorsal horn. If this is to be consistent with the schema of figure 14, the implication would be that the particular low-threshold fibers in figure 14 would be C-type fibers, or some subset of them, from figure 15. Certainly the islet cell (IC) in figure 15 could qualify as an "intermediate" (rather than early or late) interneuron, because of its relative position in the neural network shown in figure 15, from the fact that C-type fibers produce "slow" signals, and because the descending control signal synapses with it. But it is not certain whether the low-threshold afferents of figure 14 are indeed C-type fibers from free-nerve-endings (which, from figures 10 and 11, are involved in warming, burning – i.e. aching – pain, and itch). Furthermore, the picture is inconsistent with the idea that tactile signals activate the inhibitory pathway, because these signals are conveyed by the medial division of Aβ-type fibers, which synapse with the INT interneuron. As I said earlier, figure 14 is a cartoon of an idea and not a known neuron or subnetwork.

An hypothesis I find more appealing is that neuron INT is an integrating neuron (activated by Aβ-type fiber afferents) and that the descending reticulospinal signal of figure 14 excites the islet cell, thereby inhibiting the "early subnetwork" of figure 14 at the stalked cell. It is known that both NE and 5-HT (norepinephrine and serotonin) mediate (that is, help activate) pain inhibition effects of morphine. It is also known that 5-HT stimulates islet cells, and that islet cell outputs are inhibitory whereas stalked cells are excitatory.[6] This idea is also consistent with the fact that the lateral division FRA signals synapse mainly with the IC and MC cells of figure 15, which places these cells first in the FRA signal processing chain (hence arguably "early" in the spatial if not necessarily the temporal sense). However, **what is important for us** is the general idea, not partial network diagrams of the dorsal horn circuits whose role in the reflex arc pathway is both putative and at present unproven. In any event, it is known that the dorsal horn circuitry is much more complex than either figures 14 or 15 suggest.

Now let us turn to the idea of supraspinal takeover of the FRA pathway by descending motor command signals. Descending command signals from the corticospinal, rubrospinal, and vestibulospinal tracts are known to make synaptic connection with interneurons in the ventral horn. It is also known that at least some of the signals from the vestibulospinal tract make synaptic connections directly on motoneurons, thereby constituting a feedforward command signal. However, this direct connection to a motoneuron is not sufficient all by itself to fire that neuron. Motoneurons receive an extraordinary number of input signals (believed to number as many as 50,000 in some cases!), and so it is reasonable to assume that direct supraspinal control synapses to motoneurons can do little more than "bias" or "predispose" that neuron to fire in response to other input signals. Evidence supports the hypothesis that the majority of descending motor command signals synapse with interneurons in such a way as to produce a "global" excitation of some groups of motoneurons (and inhibition of others), and that the ones that actually fire action potentials in response to this global excitation are those singled out by their direct vestibulospinal connection. One source of experimental evidence in support of this hypothesis involves studies of primates that show when the direct connection to the motoneurons is severed, but the connections to the interneurons is left intact, the result is loss of the ability to move the fingers individually.

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[6] E. Jankowska, "Interneuronal relay in spinal pathways from proprioceptors," *Prog. Neurobiol.* (1992) **38**: 335-378.

Active FRA inputs, left to their own devices, tend to produce the flexor reflex. However, it is possible, by suitable mental preparation, for a human being to override at least some of these reflexes via pre-conditioning of the FRA pathway by descending motor commands. An example of this is illustrated when you "walk off a sprain" – i.e. deliberately walk on a sprained ankle instead of giving in to the reflex to lift that foot off the ground. You may limp, but you do walk (and under obvious conscious control).

In the reflex arc model the FRA pathway to the interneurons in the motoneuron circuit is inhibited by activation of the same subnetwork used by the intrinsic inhibition of this pathway by the Aβ-type fibers. This is the principle of the idea expressed in figure 14.[7] Inhibition of this "FRA noise" that would otherwise interfere with the descending supraspinal commands clears the path for control of the α motoneurons by these command signals, which act through "late" INs in the ventral horn circuitry. The FRA-INs are used as "switching devices" in order to facilitate this effect, while at the same time maintaining the other neural servo circuitry for switching in appropriate sensory feedback information that allow the same circuits that control reflexes to perform their function in the service of the supraspinal commands.

Motor Control Network Organization

We close this tech brief with a discussion at the network level of the spinal motor control organization. A more detailed look at the neuron level will be the subject of Part II.
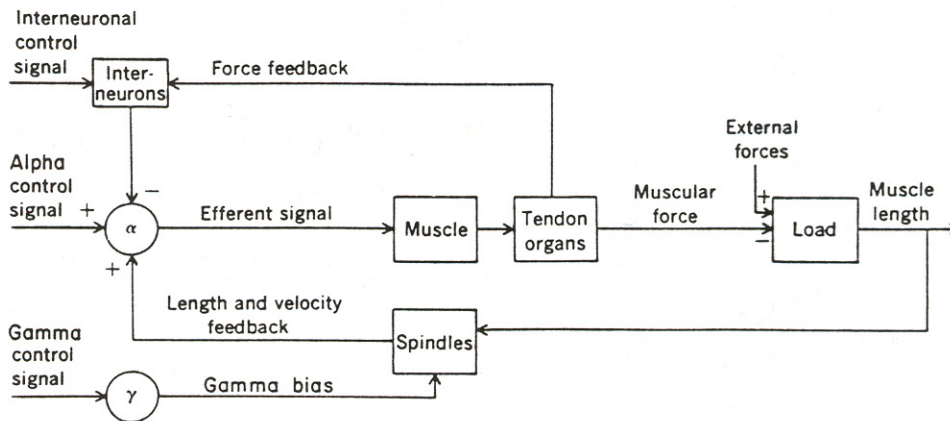

Figure 16: Simplified block diagram of a muscle control system. This figure is a modified version of one published by Houk.[8] The "Load" block represents the mechanical load (weight or torque) that the muscle must overcome. The amount of load affects the muscle length resulting from application of a given muscle force. The Golgi tendon organs and the muscle spindle afferents provide the feedback signals projected to the spinal neurons. These feedback paths depicted in this diagram are not entirely correct as shown. In particular, spindle afferents also feed back to lower-level interneurons in addition to α motoneurons. "+" and "-" represent excitatory and inhibitory connections, respectively. The descending control commands reach all spinal interneurons, not merely the ones associated with this one motor unit.

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[7] T. Jeneskog and H. Johansson, "The rubrospinal path. A descending system known to influence dynamic fusimotor neurones and its interaction with distal cutaneous afferents in the control of flexor reflex afferent pathways," *Exp. Brain Res.*, vol. 27, pp. 161-179, 1977.
[8] J.C. Houk, "Feedback control of muscle: a synthesis of the peripheral mechanisms," in *Medical Physiology*, ed. V.B. Mountcastle, 13th ed., St. Louis: C.V. Mosby Co., 1974.

Figure 16 is a simplified control system block diagram depicting the basic ideas involved in the control of a single motor unit in a muscle.[9] The first thing to mention about this diagram is that it is incomplete. Motor unit servo systems interact with each other, both in the same and in different muscles. None of this interaction is illustrated in figure 16, although a weak stab at it is partially represented by the "interneuronal control signal" input path. The diagram also fails to account for β-motoneurons, although this failing is forgivable since these had not been discovered at the time of Houk's work.

The control system depicted in figure 16 would be a fairly simple example of a servo system if it were not for the fact that most of the elements within it are nonlinear. Further complicating the matter is the fact that there is a multitude of motor units in a muscle, that a muscle spindle probably cannot be uniquely associated with a single α motoneuron, that muscles are arranged in agonist-antagonist pairs that strongly interact with each other, and that even larger groups of muscles form muscle synergist systems whose activities are coordinated in complex movements. All of these facts were mentioned in the previous "Muscles" tech brief. Nonetheless, the servo of figure 16 makes a good starting point since these complications for the most part can be taken into account by adding to the diagram, and nothing shown in it needs to be taken away.

I have yet to come across any "system block diagram" that does justice to the ventral horn servo system, although I have seen several single-motor-unit block diagrams, similar to figure 16, masquerading under the title of "block diagram of the muscle servo." Since neuroscientists tend to be pretty smart people, we can probably attribute this to the fact that neuroscientists are not systems engineers and systems engineers by and large are typically not neuroscientists. In this and the tech brief to follow, I will try to better fill in the "systems" picture of the network of interconnected servo networks.

The first task that faces us is resolving the question of how to view the network organization of the SSMS. To better explain what I mean by this, let us recall that almost every paper on the subject of neural networks begins by presenting some kind of layer organization. Whether the discussion is on multi-layer feedforward neural networks, instar-outstar networks, ARTMAP networks, Eckhorn-Johnson networks[10], or any other well-known neural network, the paper assumes some particular network topology and goes from there. It is a prejudice of the PDP crowd[11] that by and large the topology of a neural network can be safely assumed, without having much regard to the function the network performs, because neural networks are allegedly such general-purpose, one-size-fits-all structures that just about any sufficiently complex network can do any job. Hence the number of published neural network topologies is relatively small.

Minsky and Papert dismiss this attitude as "romanticism". Their work strongly implies (although does not actually prove) that this presumption is fatally incorrect. They speculate that the neural organization of the central nervous system must be viewed in terms of a "network of networks" paradigm, within which the network topologies are important. My own opinion is that in at least this they are correct, and I adopt a network-of-networks paradigm in this brief.

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[9] The discussion in this section assumes you are already familiar with the "Muscles" tech brief.

[10] Two-layer recurrent networks based on the Eckhorn pulse-coded neuron model.

[11] Parallel Distributed Processing. This is the school of the disciples of McClelland, Rumelhart et al. Their thinking dominates mathematical neural network theory today in much the same way that the Bishop of Paris dominated the setting of the curriculum of the University of Paris in the year 1200AD. The principal voices of opposition to the PDP paradigm are those of the much-besmirched Minsky and Papert, whose mathematical theorems high-lighting the shortcomings of PDP are largely ignored (cf. *Perceptrons* by M.L. Minsky and S.A. Papert, Cambridge, MA: The MIT Press, 1988). Over the years, I have also become disenchanted with the PDP attitude, although of course I am not a famous voice of opposition.

Nature does not favor us by staking out boundaries around groups of neurons that say to one and all, "There! These are the different networks we have." Anatomists (the map-makers of the body) are guided by considerations that are in part qualitative and in part functional. The division of the spinal cord into dorsal and ventral horns is one such example of this. In trying to come up with a good "breakdown" of the SSMS into different interacting networks, I base my approach on two considerations. The first is "functional" in the sense of asking "what kind of signal processing seems to be carried out by this network?" The second is a "signal path" consideration. Outputs from one neuron affect other neurons through the path of synaptic connections that carry the effect of that output signal to other neurons. Monosynaptic connections are those where the output axon of the source neuron synapses directly to the sink neuron. Disynaptic connections are chains where there is one layer of neurons (or even a single neuron) interposed between source and sink. We will call this interposed layer a "hidden layer". Paths with two "hidden layers" are trisynaptic, etc. In the normal terminology of neurobiology, all paths with two or more hidden layers are typically called "multisynaptic" or "oligosynaptic".

In terms of coming up with a network-of-network organization for the SSMS, I take as the references for "source neurons" the sensory neurons that produce the afferent signals (on the feedback path side of things) and the descending supraspinal axons of the command pathways (on the command signal side of things). I take the motoneurons as the primary outputs of the system. The ascending signal tracts and the propriospinal signals[12] that run between different spinal segments will be regarded as secondary outputs of the SSMS.

Now although the "network of networks" paradigm is an hypothesis, it is one that finds very strong support from experimental neurobiology. I base my discussion here on two key review papers, one by Jankowska[6] in 1992, and the other by Lundberg[13] in 1979. A **population** of interneurons is defined as a set of INs mediating particular actions. A population may include within it a number of subpopulations, each of which can be independently activated while other subpopulations remain inactive. A **task-related subpopulation** is a subpopulation controlling a specific movement synergy, i.e. coordinating the actions of groups of synergist muscles.

It is known beyond any reasonable doubt that task-related subpopulations of INs do in fact exist within the SSMS. These subpopulations are comprised of small neural networks, and each such network appears to be specialized for performing some small number of muscle control tasks. These networks communicate extensively with other related networks.

There appears to be a somewhat natural division of these subpopulations in terms of a higher and a lower level. This schema is illustrated in Figure 17. I call the lower level the "motoneuron" or MN-level. I call the upper level the propriospinal or PPS-level. The muscle units are illustrated at the bottom of the figure. The figure is meant to illustrate the organization of the SSMS associated with a particular muscle, and therefore depicts circuitry on one side of the spinal segment. The schema depicted here has extensive reciprocal connections to other muscle networks. These are illustrated by the right-hand blocks, which represent both synergist and antagonist motor circuits and muscles, some of which are contralateral (within the same vertebra segment) to the left-hand circuit. Interconnections between these blocks and the left-hand muscle circuit are busses of afferent and propriospinal signals.

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[12] Any interneuron with branches reaching more than one spinal segment is called a propriospinal neuron (P-IN). [V.B. Brooks, *The Neural Basis of Motor Control*, NY: Oxford University Press, 1986, pg. 88].
[13] A. Lundberg, "Multisensory control of spinal reflex pathways", *Prog. in Brain Res.* (1979) **50:** 11-28.
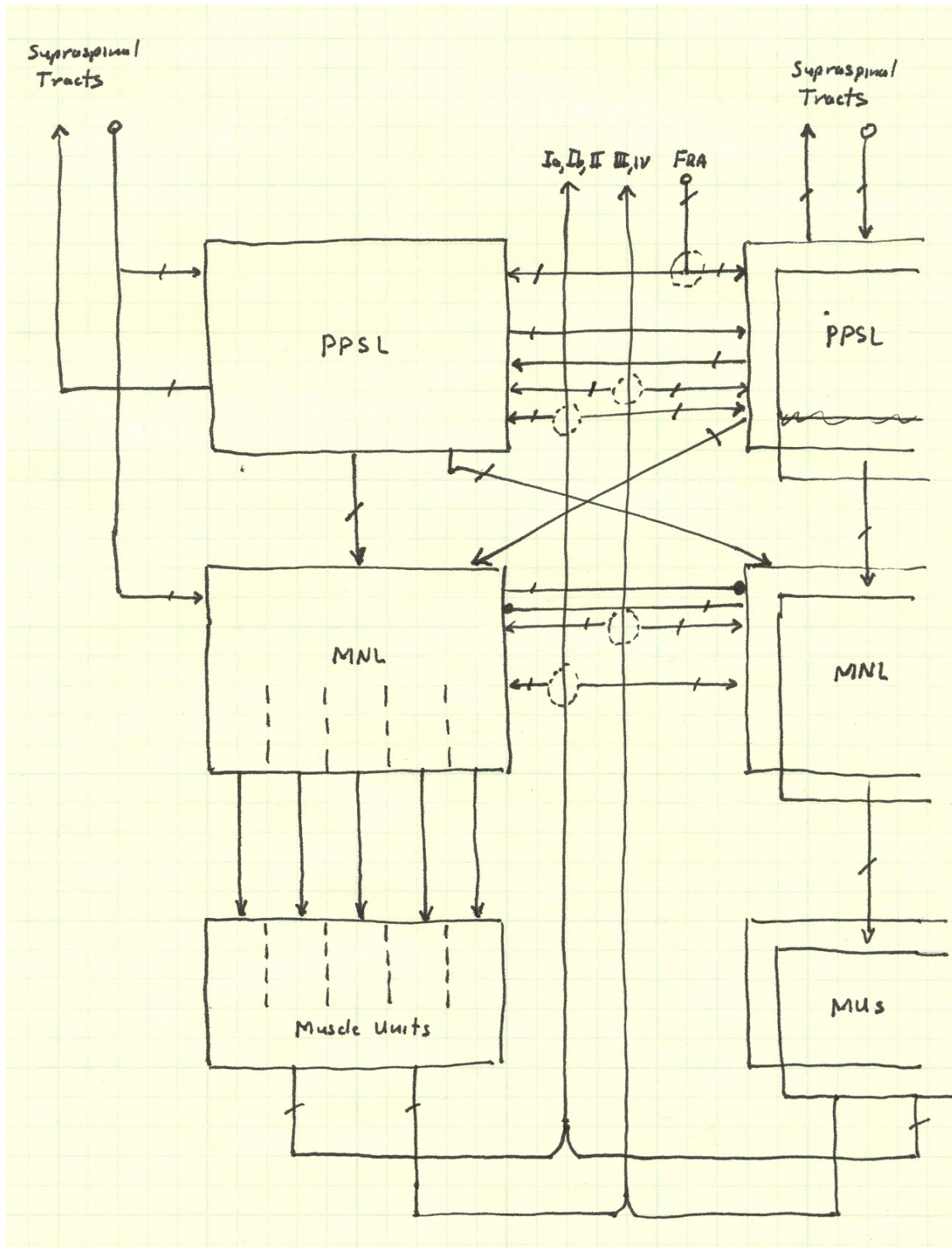
Figure 17: Neural network organization of the SSMS. PPSL = propriospinal level. MNL = motoneuron level. MU = muscle unit. MU outputs consist of the muscle spindle signals (groups Ia, Ib, II) and the groups III and IV nociceptors. Joint afferents and cutaneous afferents are grouped together as FRA (flexor reflex afferents). All supraspinal control and feedback signals are grouped together in the supraspinal tracts. It is known that group Ia afferents make monosynaptic connections to other MNLs. It is less certain whether groups Ib, II, III, or IV afferents make such connections other than through the PPSL. Propriospinal interconnects run between PPSLs and from PPSLs to MNLs.

The PPSL does not consist of a single network. Rather, it is comprised of a large number of interconnected subnetworks, each of which implements a task-related interneuron subpopulation. These subnetworks include circuitry in both the dorsal and ventral horns, but the MNL consists only of ventral horn circuits. We will define the "depth" of a neural network as the number of layers of neurons interposed between afferent signals and the motoneurons in the MNL. We will use "width" to describe the number of neurons in a particular layer at the same synaptic level. Using this terminology, **the biological evidence suggests that PPS networks have shallow depths, probably only one to two neurons deep from afferent input to the motoneuron synapse**. This is implied by the fact that most afferents entering the PPS level make di- or tri-synaptic connection with motoneurons (see pg. 19). However, there also seems to be evidence that polysynaptic connections of order greater than three are sometimes made. This can be easily accommodated if we assume that some signal paths travel laterally through the PPS subnetwork before descending to the motoneurons.

The biological evidence also shows that subnetworks in the PPSL exhibit mutual lateral inhibition. This means that activity in one subnetwork tends to inhibit activity in other subnetworks, particularly those whose activity is directed at antagonist muscle units. (Recall that flexor and extensor motoneurons frequently reside in the same lateral horn). We can see an illustration of this in figure 15 in the pathway running from the medial division afferent through interneuron INT, Islet cell IC, stalk cell SC, and terminating on the marginal cell MC. This example only illustrates lateral inhibition in one direction, but we should keep in mind that other medial afferents making a similar connection to a different dorsal horn circuit can supply lateral inhibition back to an MC that projects to the same motor unit associated with the dorsal circuit shown in the figure.

One of the critical functions that is almost certainly performed at the PPS level is central pattern generation (CPG). CPG circuits are thought to be responsible for producing timed sequences of motoneuron excitation during voluntary movement involving synergist muscles. Leg and ankle control in the left and right legs during walking is one example of such movement. So far as I know, the specific neurons comprising a central pattern generator in spinal cord segments has not yet been identified. However, there is compelling indirect biological evidence that points to the existence of such circuits in the PPSL. There are three principal CPG schemes that are thought to be likely in biological neural networks. These are illustrated in Figure 18. The most popular hypothesis for CPG in spinal circuits is the half-center model, which we will discuss in more detail in Part II. Here it will suffice to say that the CPG network has mutual lateral inhibition with other FRA-pathway networks in the PPSL (not shown in the figure). This lateral inhibition de-activates CPG during normal flexor reflexes, and allows the CPG network to take over the lower reflex circuitry during voluntary movement. It is also thought that synergistic muscle movements involve multiple "local" CPG networks that are synchronized through propriospinal signals and through PPSL signals from the lateral side of the vertebra segment.

Another important function believed to be carried out by PPSL networks is the coordination of α-MN and fusimotor neuron (β- and γ-motoneuron) firing. It is known that motoneuron control during voluntary movement depends on limb and joint positions. This has led to the concept of "task groups" to control the MNs according to the needs of the task effort[14]. This is schematically illustrated in Figure 19. Different descending MN excitation signals are determined according to FRA and supraspinal control inputs coordinated through reciprocal connections among different PPSL circuits.

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[14] G.E. Loeb, "The control and responses of mammalian muscle spindles during normally executed motor tasks", *Exercise Sports Sci. Rev.* (1984) **12:** 157-204.

A. HALF-CENTER MODEL   **B. CLOSED-LOOP MODEL**   **C. PACEMAKER MODEL**
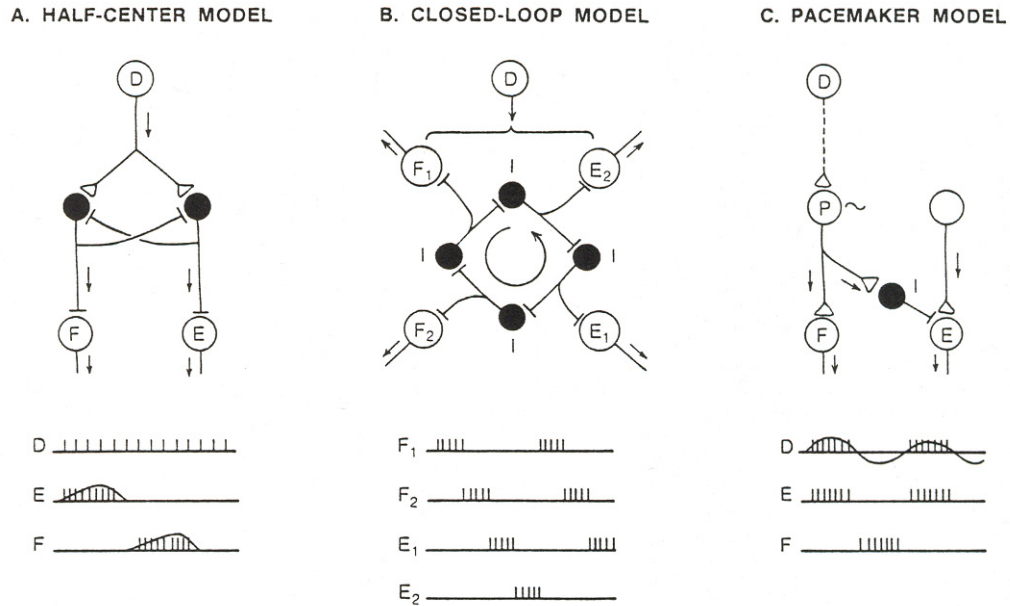
Figure 18: Simplified schematics of CPG circuit schemes. The diagrams depict the minimum number of neurons required and their connections for each type of CPG. Solid-black neurons depict neurons with inhibitory action; open circles represent neurons with excitatory action. D = driver cell; F = flexor motoneuron; E = extensor motoneuron; P = pacemaker cell; I = interneuron. Sequences of spike firing or graded potentials are shown in the idealized "recordings" at the bottom of the figure. The driver cell in the closed-loop model provides excitation to all the motoneurons and interneurons.
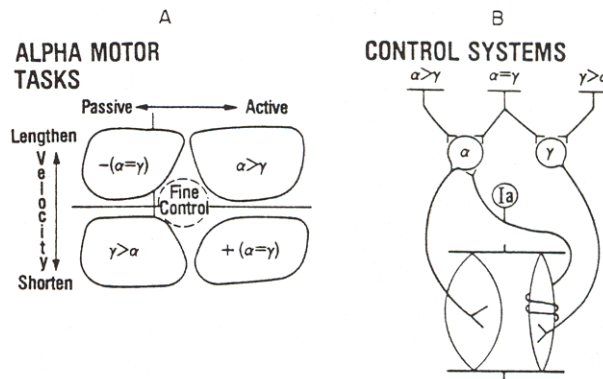

Figure 19: The concept of task-group coordination of motoneurons. The A figure illustrates how PPSL neurons "encode" for a particular task according to the velocity and length of the muscle and whether the muscle stretch is active or passive. This encoding defines four quadrants of required excitation for α- and γ-motoneurons. The encoded quadrant determines the descending pathway control of the motoneurons, illustrated in the B figure. Either MN can be independently excited or can be co-excited, depending on which descending pathway is activated. The left-hand muscle fiber at the bottom of the figure represents an extrafusal muscle group; the right-hand muscle fiber represents a fusimotor (intrafusal) muscle group. The β-MNs are not illustrated in the figure, but since β-MNs are small α-MNs, we can regard them as being implied in the α-MN connections.

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Unfortunately, relatively little is known about the circuit details in the PPSL networks that control these and other muscle coordination tasks. What I have given in this tech brief is a description of some "network-level" characteristics and constraints known to be characteristic of these circuits. But as we add more and more "muscles and bones" to a bipedal locomotion platform, the complexity of the interconnects among PPSL subnetworks, as well as the number of these networks and the specialized tasks each performs, will naturally quickly grow in complexity. In the absence of definitive data from neurobiology, we will most likely have to evolve these networks and their connections.

This concludes Part I of this tech brief. In Part II the more specific known details of SSMS neural circuits will be discussed. This will include what is known of the synaptic connection scheme in the MNL, known properties of the PPSL, and what is known of the types of neurons involved and their relative synaptic weights in their connections.