Chapter 4

Physiological sensory system

The musculoskeletal system is a mechanical system with muscles as actuators. Too often, the feedback system is ignored when the behavior of the system is studied. In comparison, one can not imagine a robot without feedback control. Several types of feedback systems are considered in this chapter (figure 4-1): Visual, vestibulary, tactile, but the focus is on reflexive feedback by the muscle spindles and Golgi Tendon Organs (GTO). Muscle spindles provide feedback about the length and contraction velocity of the muscles. GTOs sense the force that is developed in the muscles. Some pathways in the Central Nervous System are described. In the next chapter, the contribution of length, velocity and force feedback for position control of the neuromusculoskeletal system will be described.
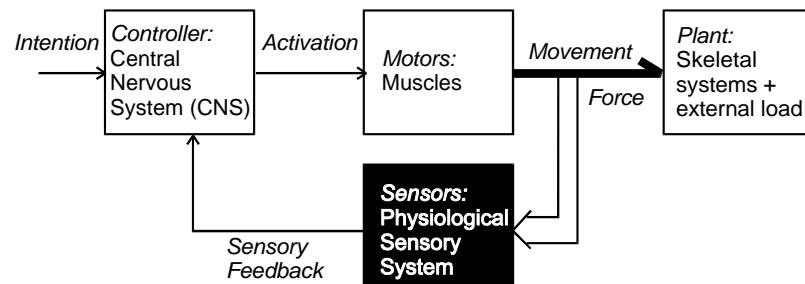

Figure 4-1   Schematic block diagram of the human motor control system. Subject of this chapter is the sensory system.

OBJECTIVES

This chapter will show:
- Musculoskeletal system with proprioceptive feedback
- Sensors and neurons
- Muscle spindles
- Golgi Tendon Organ
- Central Nervous System
    - reflex loops
    - reciprocal inhibition
    - sensory integration

4.1   Introduction

In Figure 4-2A, an open loop musculoskeletal system is shown. The Central Nervous System (CNS) generates a neural input (α-activation) to the muscles, which results in a muscle force that accelerates the skeletal system. The acceleration is twice integrated in order to obtain the position. If the neural input is fine-tuned, a desired position can be reached. However, in presence of (force) disturbances the desired position will presumably not be reached, since there is no way that information about the disturbance is used to adapt the neural input. However, strictly spoken the effect of the
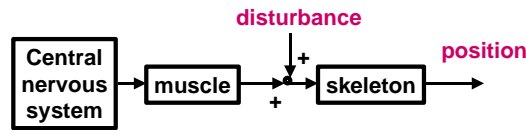
A. Open loop control model
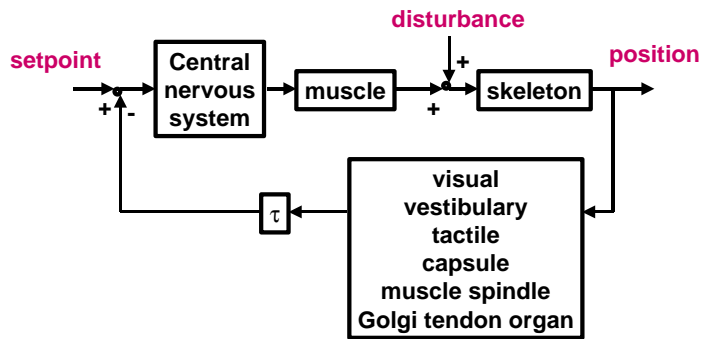
B. Closed loop control model

Figure 4-2:   In the open loop control model, the Central Nervous System
              generates commands to generate motions of the musculoskeletal
              system. If disturbances are present, their effect on the position can
              not be compensated.
              In the closed loop control model the Central Nervous System acts as
              controller. Information from the sensory organs about the position
              of the musculoskeletal system is compared with the desired position
              (setpoint, also generated inside the CNS), and compensatory signals
              are sent to the muscles.

force disturbance will be attenuated by the length and velocity dependence of the
muscular contraction dynamics, i.e. the muscular visco-elasticity.
In Figure 4.2B, a closed loop musculoskeletal system is shown. A number of sensors is
present in the human body, which provide information about the state of the
musculoskeletal system. Some sensors provide information about the whereabouts of
the human body with respect to the outside world (exteroreceptors), other sensors give
information about the state of the inside of the human body (interoreceptors). Important
exteroreceptors are the vestibulary system and the visual system. Interoreceptors are
sensory organs in the joint capsule, muscles and tendon. In the joint ligaments and
capsule sensors are present which can detect the position of the joint, i.e. the joint
angle. However, since most ligaments are only stretched at the utmost joint angles,
there is no neural signal proportional with the joint angle, and it is unlikely that joint
sensors have an important role in the direct control of the joint position.
Muscle spindles are sensors attached to the muscle fibers, which provide information
about the length and contraction velocity of the muscle fibers. Golgi Tendon Organs
are found in the muscle tendons, and result in neural signals proportional to the muscle
force. Muscle spindles and GTOs give continuous signals, and it is very likely that the
joint position can be reconstructed from this signal at any time.
Tactile sensors in the skin are a special category of interoreceptors, since they are
excited by stimuli from outside the body.

4.2   the vestibulary organ

The vestibulary system consists of three perpendicular semi-circular canals and an otolith system in each of the inner ears (Figure 4-3). The semi-circular canals are sensitive to rotational accelerations of the head. Since there are three perpendicular rotational sensors, any rotational movement of the head will be detected. The semi-circular canals are filled with fluid, and sealed off by a membrane (cupula) which prevents the fluid flow around. The excursion of the cupula is sensed and transmitted to the CNS. Through the mass-spring-damper properties of the fluids and the cupula, the semi-circular canals act as rotational velocity sensors for an important range of frequencies, i.e. between 0.1 and 10 Hz (Figure 4-4).

The orientation of the head can only be reconstructed through integration in time of the rotational acceleration. This will result in integration offset. This integration offset can be experienced when rotating with the eyes closed. After several turns, it is difficult to know one's orientation in the room.

Translational accelerations are being detected by the otolith system in the inner ear. The otolith system consists of small bone parts on little hairs. The amount of bending of the hairs gives an indication of the acceleration and weight of the bone parts. The otolith system gives information about the translational accelerations of the head, but the otolith system is also sensitive for gravity.
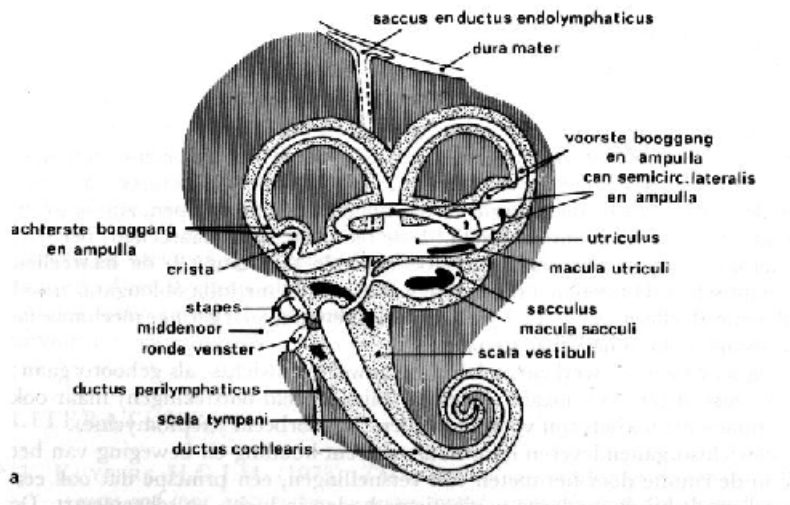

Figure 4-3.   The three semi-circular canals in the vestibulary organ are sensitive to rotational accelerations, due to the mass-spring-damping properties of the fluid and the cupula, which closes the canal. The otolith near the center of the semi-circular canals is sensitive for translational accelerations and for gravitational forces.
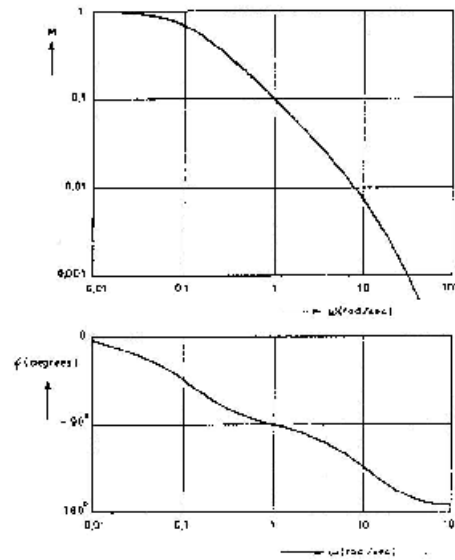
Figure 4-4   *Transfer function in the frequency domain of the semi-circular canals: $H(\omega) = x_{cupula}(\omega) / \alpha(\omega)$, in which $\alpha(\omega)$ are the rotational accelerations. Between 0.1Hz and 10 Hz the transfer function approximates an integrator, and the sensor output is proportional to rotational velocity.*

The perceived integration offset directly points to the role of the visual system, which provides direct position and orientation information of the head position. Humans are capable of deriving velocity information by the visual system (how fast an object is moving), but no acceleration information (changes of the speed of the object). The combination of the visual and vestibulary system provides position, velocity and acceleration information of the head. It is obvious that for the position of the rest of the body in space the relative position of the head with respect to the trunk must be detected by sensors in the neck musculature.

4.3   Tactile sensors

The skin is the boundary between the outside world and the inside body. One important function of the skin is protection against damaging influences from outside, like bacteria and viruses, and chemicals. Another function is the information exchange between the inside body and the direct environment. In the skin, sensory organs are sensitive for touching (mechanoreceptors), heat and cold (thermoreceptors) and pain (nocireceptors).
Tactile sensors in the skin provide information about the external forces, i.e. normal and shear forces at the skin. Humans are capable of sensing the forces under their feet, which is an important cue for postural control while standing. In addition, there are pressure sensors and temperature sensors. The shape of the sensor cells determines if they are more sensitive to certain deformations, and result e.g. in pressure or stretch sensors. The sensors are connected to nerves. Often more than one sensor is firing through the same nerve. The more a sensor is deformed, the higher the firing frequency will be in the nerve. In the hairy body regions, hardly any tactile sensors are present, and most information is detected by sensors around the hair roots. Most sensors are present in the non-hairy regions of the human body, like the hand palms and the foot

soles.

The following sensory organs can be found in the (non-hairy) skin (Figure 4-5):

- *Pacini corpuscles*. These sensors are 2-3 mm big, and are located deep in the skin at the border of the dermis and subdermal layer. These tactile sensors are sensitive for light touching and small deformations.
- *Meisner corpuscles*. These sensors are located in small clusters just under the epidermis, and are therefore typical touch sensors.
- *Golgi-Mazzoni corpuscles*. These sensors are located at the border of dermis and subdermal layer, and are sensitive to large deformation and pressure.
- *Discs of Merkel*. These sensors are located near the skin surface and are specific touch sensors.
- *Ruffini corpuscles* located in the dermis. There are two types of Ruffini corpuscles, one is sensitive for pressure, and the other is sensitive for temperature.
- *Free nerve endings*. These are the final branches of the nerves, and are not connected to sensory organs. They are only stimulated by large deformations, and are thought to be pain sensors.

Tactile sensors are only sensitive to *changes* in the stimuli. For example, after sitting for a long time one is not aware about the pressure at the seat. Only after some movements, the pressure is felt again. In prosthesis design, it has been attempted to use tactile interfaces to inform patients e.g. about the joint angles or contact forces. In order to use tactile stimuli, one must know the observation window which stimuli can still be noticed. The observation window is defined by a horizontal frequency axis, and by a vertical amplitude axis. The combination of frequency and amplitude determines if a certain stimulus can be observed. The threshold is the smallest stimulus amplitude that still can be noticed. The threshold depends on the frequency of the stimulation. The threshold is experimentally determined, and defined as the combination of frequency and stimulus amplitude for which 50% correct observations are made whether the stimulus is present or not.
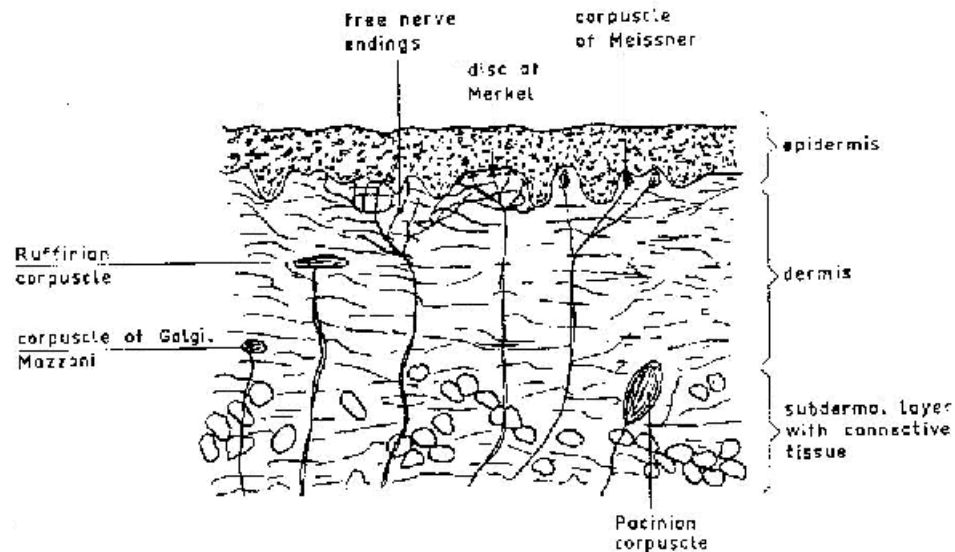

Figure 4-5   Cross-section of the non-hairy skin.

Another important property of an observation window is the Just Noticeable Difference (JND). The JND is the smallest *difference* in amplitude or in frequency that can be noticed. If the JND is very large, larger differences in the stimuli are needed and less information can be coded within the observation range of the sensor.

In Figure 4-6 the observation window or transfer function of the tactile sensors to mechanical vibrations of the skin (imposed by an air chamber at the skin) is shown. The threshold has the shape of an integrator (slope = -1 in the frequency-amplitude plot). In other words, the stimulus must contain a certain power in order to elicit a response in the sensory organs. The Just Noticeable Difference (JND) is large for the mechanical sensibility. Hence, only a very limited amount of information can be coded into the stimuli.
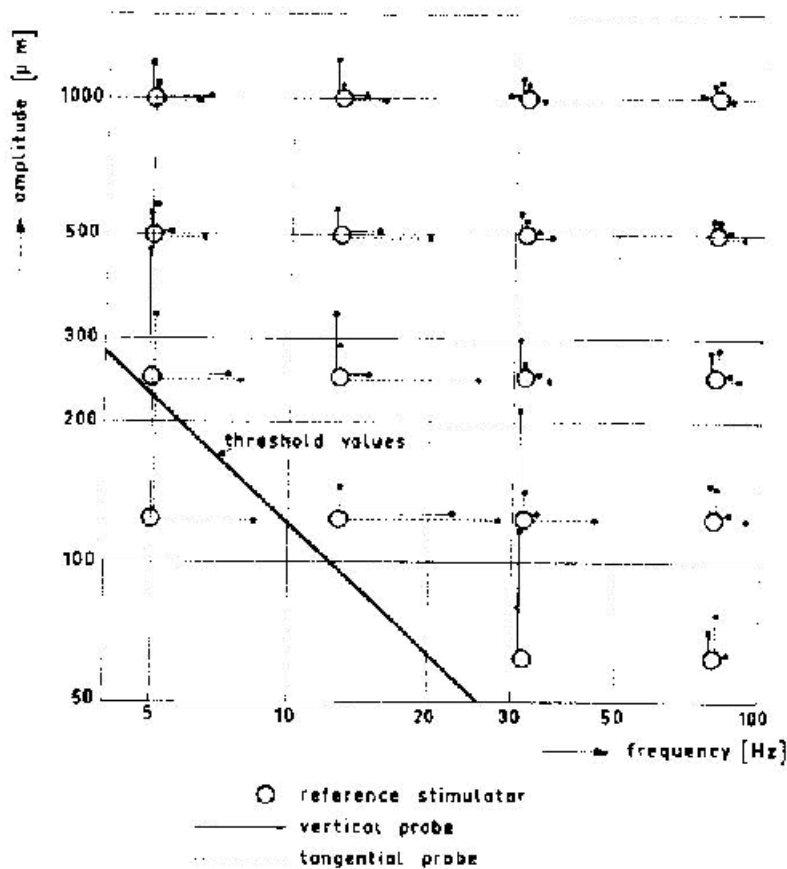

Figure 4-6   *Observation window of the tactile sensors for mechanical stimuli. The threshold value has the shape of an integrator, showing that a certain power is needed to stimulate the sensors. The just noticeable difference is quite large, especially near the threshold value.*

4.3.1   PAIN

Pain is psychosomatic and by definition subjective. How the pain sensation arises is unknown. There are two competing theories. One theory tells that there are specific pain receptors, the free nerve endings. If these pain receptors are stimulated by large deformations or extreme temperature, they send a signal to the CNS that is interpreted as pain. The second theory states that pain is the result of a malformed pattern of afferent signals, which is interpreted as pain. The skin with its many sensors is very sensitive to pain. However, the pain is felt by the neurons in the CNS, whereas the damage is in the periphery. Pain relieving medication takes advantage of this fact, and alleviates the pain sensation by the CNS without taking away the trauma.
Electrical stimulation of the skin can cause a touch sensation, but also a pain sensation. Electrical stimulation poses high requirements on the equipment used. The signal amplitude that causes severe pain is only a factor four higher than the threshold amplitude that is just above the sensation level. This has prevented the widespread use of electrical signals for transferring information through the skin. However, recently the use of electrical signals has been revived. The use of bi-phasic signals has been shown to cause less painful sensations in contrast to the mono-phasic signals as used before.

4.3.2   APPLICATIONS

Tactile information is very important for use in daily life, for the upper extremities as well as for the lower extremities. For example, information about slip when holding a cup provides feedback for muscle co-contraction necessary to hold the cup. The importance of tactile information can be appreciated if a patient with a hand prosthesis is observed. These patients have many difficulties in holding delicate objects like a plastic cup, an egg or a banana. They have to rely completely on the visual system that only provides position information and no force information.
The pressure between the prosthesis socket and the stump is often a very important source of information about the weight of an object, or the forces applied. Patients with an above-knee prosthesis need this type of information as the first indication if the prosthesis knee is stretched or not.

4.4   The neural system

4.4.1   NEURONS

The Central Nervous System consists of the brain inside of the skull, and the spinal cord inside the spinal column. The peripheral nervous system consists of afferent nerve fibers, transporting information from sensors towards the CNS, and efferent nerve fibers, transporting information from the CNS towards the muscles. In addition, there is the autonomous neural system that innervates organs like the bladder or the intestines. A typical nerve fiber (or neuron) has dendrites through which signals from other neurons or sensors are received, and axons that stimulate other neurons or muscle fibers (Figure 4-7). A signal is transmitted from a stimulating neuron to a receiving neuron through a synapse (see Figure 4-8). When a neural signal arrives at a synapse, some neurotransmitter is released inside the synapse gap. The neurotransmitter is taken up through the membrane of the receiving neuron. There are excitatory and inhibitory neurons. The neurotransmitters of excitatory neurons will result in an increase of the potential of the receiving neuron. On the contrary, the neurotransmitters of inhibitory neurons will result in a decrease of the potential of the receiving neuron. If the potential of the receiving neuron exceeds a certain threshold, the neuron will start firing.
Efferent neurons, i.e. the motor neurons, are activated in the spinal cord and will transmit the information to the muscles. These cells can be longer than 1 m! Between
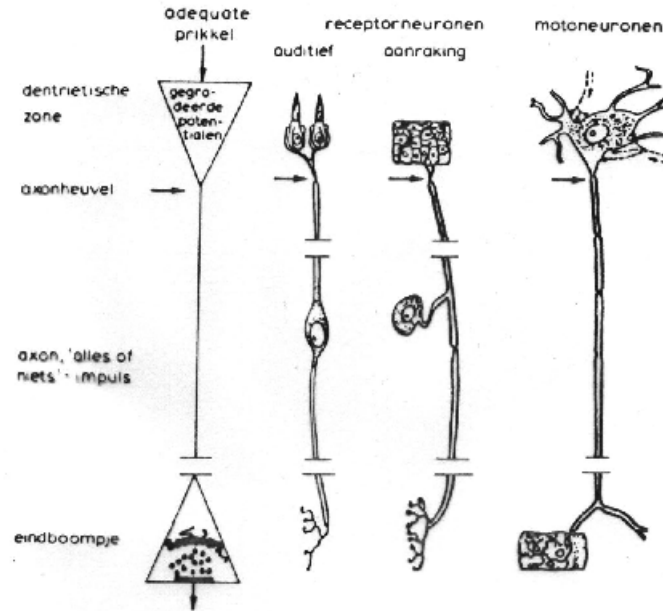
*Figure 4-7   Neurons consists of dendrites, a nucleus and axons. The dendrites are
              stimulated e.g. by other neurons or by sensory organ. If the neuron is
              activated, nerve pulses are transmitted along the axon towards the
              endnode. Here, another neuron or e.g. a muscle can be stimulated.*

the motor neuron and the muscle, there is also a synapse, the motor endplate. Here, a
potential at the muscle membrane is generated which will propagate along the muscle
fibers. Ultimately, this muscle potential will stimulate the calcium release from the
sarcoplasmatic reticulum, and the muscle will start to contract.

Afferent neurons, i.e. the sensory neurons are stimulated when the sensor at the
peripheral end of the neuron is triggered by a specific trigger to that sensor. The signal
is transported towards the CNS, and will be transmitted through synapses to other
neurons in the CNS. Also the sensory neurons are one big nerve cell between sensor
and CNS. The cell nucleus of sensory neurons is located just outside the spinal cord,
whereas the cell nucleus of motor neurons is located inside the spinal cord. When a
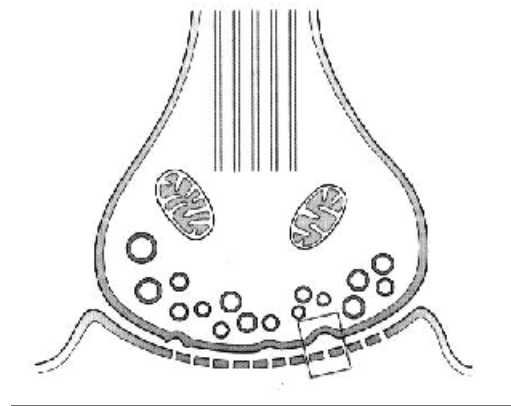

*Figure 4-8   In a synapse gap between two neurons, neurotransmitter is released by a
              particle that passes the cell membrane. The neurotransmitter passes
              through the membrane of the receiving neuron, and increases (excitatory
              synapse) or decreases (inhibitory synapse) the cell potential.*

peripheral nerve is dissected, the sensory neurons can not be distinguished from the motor neurons. However, inside the vertebral column, very near to the spinal cord, the nerve splits into a motor part which enters the spinal cord at the frontal side, and a sensory part which enters the spinal cord at the back side. Here it is possible to denervate solely the sensory nerves, which is done in case of animal experiments or for patients with spastic paralysis or severe pain complaints.

Interneurons are stimulated by neurons, and themselves stimulate other neurons through synapses. Interneurons are only found in the CNS: All sensory signals from the periphery are first transported to the CNS, processed and motor signals are sent back to the periphery. It is estimated that there are 10^{11} interneurons in the human CNS. On average each interneuron has about 10000 synapses with other interneurons, so in total there are 10^{15} synapses. In comparison, massive parallel computer systems have 'only' up to 128000 parallel chips! Very much in contrast to a computer chip, the information processing is parallel and asynchronous processed. One can imagine the enormous computing potential of the human brain, in many ways unequalled by the current computer systems. Any model of the CNS is just a very big simplification of the complex structure and function of the CNS.

4.4.2   SIGNAL TRANSMISSION ALONG THE NERVES

In the resting situation, there is a potential of -70 µV between the interior of the neuron and the exterior. If this potential decreases to -50 µV, e.g. due to excitation by another neuron or triggering of a sensor, a transport mechanism becomes active, which transports K^+, Na^+ and Cl^- ions through the membrane, resulting in a reversal of the cell potential to +20 µV. Shortly after this depolarization the resting situation will be restored. This is called a twitch or a spike at the neuron. After the spike there is a short refractory period, in which the cell potential is even below -70 µV, and the neuron is more difficult to stimulate. This limits the number of spikes that can pass to about 400 spikes/sec. At a higher potential at the dendrites, more spikes will be generated. The information is so to say frequency encoded: The number of spikes per second is an indication of the activation of the dendrites. Neural spikes have a very discontinuous
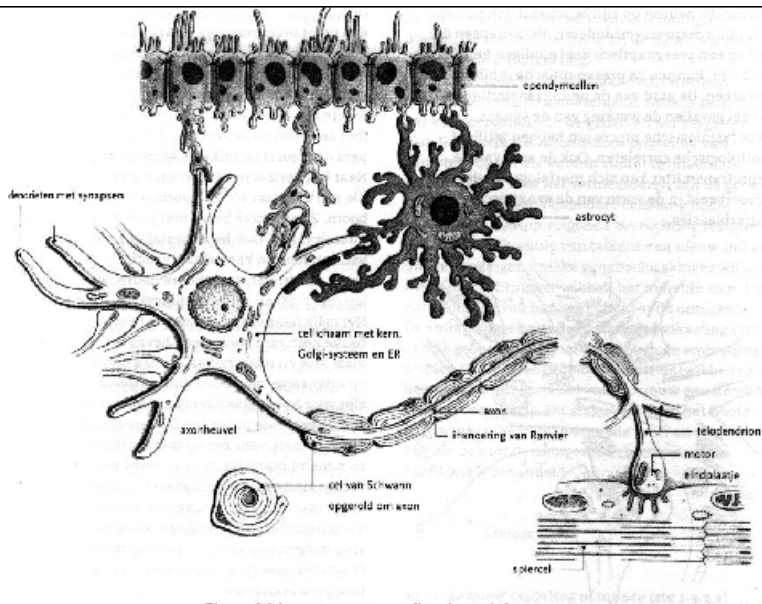

Figure 4-9   Motor nerve cell with dendrites receiving stimuli from other neurons. The spikes are transmitted along the long axon, isolated by myelin for faster transmission speeds. The myelin sheaths show the typical Nodes of Ranvier, through which small current loops come into existence.

character. For calculations, mostly the quantity 'spikes/sec' is used as a continuous variable to describe the activation. The number of spikes per second can be calculated from the interval between two spikes.

A depolarization at a certain point at the nerve cell membrane will result in a change of the potential nearby, which will also result in a depolarization. In this way, the spike will propagate along the nerve cell. This is a relatively slow mechanism, about 2-4 m/sec. There is another mechanism to increase the transmission speed. The nerve cells are 'isolated' by myelin sheaths. At certain distances the myelin sheaths are interrupted by the so-called 'nodes of Ranvier' (see Figure 4-9). The myelin sheaths help to prevent potential leakage from the cell interior to the cell exterior, and an electrical current can pass through the cell interior, with a certain drop of potential. However, if at the next node of Ranvier the potential is still above the threshold potential of -50 μV, then an active depolarization will take place, and the cell potential is actively amplified! This can increase the transmission speed up to about 100 m/sec. If the myelin sheaths are larger (i.e. the nerve is thicker), there will be less leakage and the nodes of Ranvier can be at greater distances of each other. Hence, thicker nerves have larger transmission speeds. However, the maximal transmission speed of 100 m/sec is still a factor three slower than the speed of sound, and we will see in the remainder of this chapter that the time-delays due to the neural transmission speed, and also neural processing, play an important role in the control of motion. For larger animals, this limited transmission speed may become a real hassle for motor control. Therefore, it is thought that e.g. dinosaurs had a second brain located at the down end of the spinal cord, at the pelvic girdle.

4.4.3   ORGANIZATION OF THE HUMAN CENTRAL NERVOUS SYSTEM

The human CNS can be divided in four areas, the cerebrum (major brain), the cerebrum (minor brain), brain stem and the spinal cord. In the CNS, the axons show up as white material and the cell nucleus with the dendrites is gray matter.

In the spinal cord, there are many pathways in vertical direction, transporting information up and down. These pathways are located in the central part of the spinal cord. Around these central areas, gray matter is located, made up by interneurons that can process information at this level. For instance, reflexes are generated at the spinal level. The pathways in the spinal cord can go up straight to parts of the cerebellum, or via indirect pathways with additional processing e.g. at the cerebrum or at the thalamus. Unraveling all these pathways is an enormous task, and one can imagine that only very small parts of the brain are analyzed in detail. Deriving the functional role of these pathways is even more difficult, since a working brain can not be dissected, and a dissected brain does not function any more. Most information is obtain by scanning the electrical signals at the skull (EEG) or the blood flow to certain brain areas using magnetic fields (PET scans). However, this information is about larger clusters of neurons.

In the brain stem, many upward and downward pathways have connections with the interneurons. It is thought that the brain stem has an important role in the generation of motion on a functional level. The Purkinje cells in the cerebrum have an enormous amount of dendrites and axons, and are thought to have a key role in comparing sensory and motor information, in order to adapt the motor output, but presumably also in order to learn from the proprioceptive information.

In the cerebrum and cerebellum by far the most interneurons are located. The sensory and motor part of the brain is located about halfway between the front and backside of the brain, and is more or less topographically organized according to the part of the body that it is connected to. In the cerebellum, intentions are generated which can be transformed into motions. Functions are located in a distributed manner, i.e. a certain function will be performed by the elicitation of a part of the brain which may also be

(partly) active when another function is performed. So it is impossible to say that one neuron has one function.

There are many philosophical and religious theories about the nature of the human consciousness and 'soul'. From a mechanistic point of view, everything that happens boils down to signals transported along neurons and passed trough excitatory and inhibitory synapses. One can wonder how information is stored in the brain, e.g. how does the memory work or how is information retrieved. Since there is no 'hold-circuit' in which electrical or magnetic information is stored, the information must be stored in the structure of the system, i.e. the connectivity between the interneurons and the strength of the synapses. The strength of a synapse determines how much the potential of the receiving neuron is raised or lowered due to one spike of the stimulating neuron. It has been shown that the strength of synapses can change very rapidly, in the order of seconds, which will alter the function of the whole system.

4.4.4   PERIPHERAL NERVOUS SYSTEM

The peripheral nervous system consists of nerves outside the central nervous system, going to and from muscles, sensors and organs. The autonomous nervous system innervates the internal organs like the bladder, arteries, etc., and will not be discussed further in this chapter. Afferent nerves transport information from the peripheral sensors towards the CNS, and efferent nerves transport information from the CNS to the muscles. Efferent nerves leave the CNS at the ventral side (front side) of the spinal cord; afferent nerves enter the CNS at the dorsal side (backside) of the spinal cord. A few centimeters from the spinal cord the efferent and afferent nerves merge and can not be distinguished from each other. The peripheral nerves pass through small openings in the spinal columns. At this stage, they are called the nerve roots. Spinal roots are names after the vertebrae between they leave the spinal column. There are 8 cervical roots (C1 - C8), 12 thoracic roots (T1 - T12), 5 lumber roots (L1 - L5) and 5 sacral roots (S1 - S5). Spinal roots innervate more or less sensors and muscles in 'horizontal' segments if one assumes the arms and legs stretched out horizontally (which is obviously difficult for the legs!). Especially at the arm and leg segments, many sensors and muscles are innervated. At these segments the spinal roots enter a nerve network (the plexus brachialis and plexus lumbrosacralis, respectively). At the distal side peripheral nerves leave the plexus. The peripheral nerves consist of motor and sensory neurons that originate at several spinal roots. The peripheral nerves split into branches that innervate individual muscles and e.g. parts of the skin. The neurons innervating muscles most often originate from multiple spinal roots. In general, one can state that the proximal muscles (closer to the center of the body) originate from higher spinal roots than more distal muscles (further away from the center of the body). For instance, the shoulder muscles are innervated by spinal roots C5 and C6, the elbow muscles by C6 and C7, the forearm and hand muscles by C7 to T1.

4.4.5   NERVE LESIONS

As stated before, motor and sensory neurons are very large cells, which run from the spinal cord to the peripheral structures. In case of lesions of the nerve cells, the part that is not connected any more with the cell nucleus will die. The cell nuclei of the motor neurons are located in the ventral part of the spinal cord; the cell nuclei of the sensory neurons are located in small 'bags' (ganglions) just *outside* the spinal column.

Most often nerve lesions are due to stretch trauma (fast elongation, e.g. after a fall on the arm) and more seldom due to direct trauma as cuts or shot wounds. The severity of nerve lesions can be different, because of the magnitude of the impact. In case of an edema due to an impact, the signal transmission is blocked while the nerve itself is intact. Function will return after a few days when the edema is away. If the axon is interrupted, the peripheral part that is not in connection with the cell nucleus will die. If

the myelin sheaths are intact, the nerve will start to grow from the central part. The growing speed is about 1 mm per day. So to innervate the upper arm muscles again after a trauma near the neck, it takes almost a year before any function will return. The myelin sheaths will guide the axons to the muscles and sensors that were innervated by the same neurons before. A proper return of function is then expected. If the myelin sheaths are also interrupted but the collagen fibers around the nerve fibers are intact, the axons may also start to grow, but motor neurons might end at sensors, and sensory nerves at the muscles, which will not result in any function. On average 25% of the nerves will be connected to a proper site. For instance, motor neurons will innervate a great deal more muscle fibers after the trauma (giant motor units). The coordination after such a trauma can sometimes be very difficult, and only part of the function will return (e.g. 'weak' muscles).

Due to the speed of nerve growth (1 mm per day), it may take up to two years after trauma to restore function. If after two years no function did return, it is very unlikely that it will ever return. Then, surgical action or conservative treatment is indicated. Conservative treatment will aim at the improvement of function through orthotic and prosthetic devices, or through training and physical therapy. Surgical treatment can consist of orthopedic surgery, e.g. tendon transfers, or neurosurgery, aiming to reconnect the nerves. A dilemma is that the best time for neurosurgery is about 2 months after trauma. After six months, post-trauma neurosurgery does not provide very good results any more. However, after two months natural recovery might still occur! Hence, a good diagnosis is essential, and often surgery is attempted to see if any reconstruction can be made.

When the nerve is not in continuity any more after trauma, or scar tissue prevents nerve growth, no return of function is to be expected. Then, neurosurgery is indicated. During neurosurgery bad parts with scar tissue of the nerves will be removed, and replaced by nerve grafts. A nerve graft is a part of a nerve taken away from another part of the body. Usually sensory nerves innervating skin areas in the lower leg are used as nerve grafts. The nerve grafts is sutured to the healthy central part of the nerve, and to the peripheral part. The nerve graft functions as a tubing system, guiding axons towards the peripheral part of the nerve. As before, only 25% of the nerves is expected to end at a proper site. The return of function depends on the length of the graft (which can be up to 10 cm.), the distance between the central part and the muscle or sensor (hand function will seldom return), and the quality of the connection between the original nerve parts and the graft.

Spinal cord lesions occur after severe trauma, often fractures, of the spinal column. These are mostly stretch injuries. Very often, the cause of the nerve injury itself is due to the edema, which can cause a great pressure inside the spinal column. Complete and partial lesions can occur after trauma. Partial lesions might improve over time, and complete lesions can turn out to be partial lesion. However, if the nerves are not continuous no return of function is to be expected, since nerve growth passed the lesion site has never been detected in spinal cord lesions. If after a few months after trauma no return of function is seen, further improvement due to nerve recovery is unlikely. Neurosurgical repair of spinal cord lesions has been unsuccessful until now.

4.5   Proprioceptive sensors

4.5.1   INTRODUCTION

Inside the human body, sensors are present in the joint capsule, ligaments and muscles in order to provide information about the position of the limbs. Without looking, one is complete aware about the locations the limbs. It will be shown in the next chapters that for accurate control of the limb motions, this sensor information is essential. Information from several sensors is combined to obtain the most accurate information about the state of the body: Sensory Integration. For instance, the interpretation of the
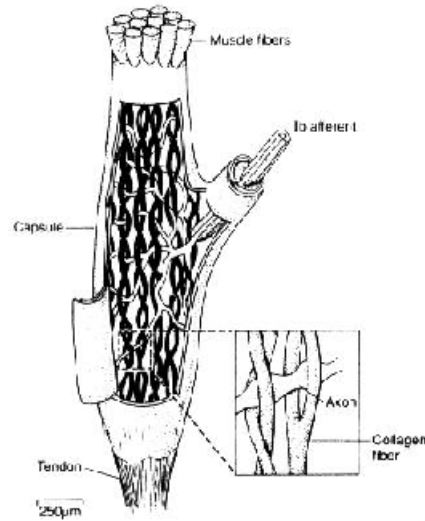
Figure 4-10   The Golgi tendon organ consists of a nerve ending intertwingled with the tendon fibers. The Golgi tendon organ is sensitive to the muscle force exerted through the tendon.

vestibulary information is only useful when the neck muscle provide information about the orientation of the head.

4.5.2   JOINT CAPSULE

The range of motion of a joint is determined by the capsule and ligaments, which stretch and pressure sensors are located. The ligaments are strings of connective tissue strengthening the joint capsule. Often, only at the end of the range of motion the ligaments are stretched. Hence, these sensors are not firing at the mid range of motion, therefore it is not likely that they play a major role in the control of movement. On the other hand, information about the boundaries of the joint motion is necessary to learn to move within these boundaries, in order to prevent damage.

4.5.3   MUSCLE SENSORS

Inside each muscle two types of sensors are present: Muscle spindles provide information about muscle length and contraction velocity, and Golgi tendon organs give information about the force transmitted through the muscle tendon.

5.5.3.1   GOLGI TENDON ORGANS

The Golgi tendon organs (GTO) are located in the muscle tendons. About 50 GTOs are located in a major tendon. The GTOs consist of nerve endings that are intertwingled with the collagen fibers of the tendon (Figure 4-10). When the tendon is stretched, the nerve endings are 'squeezed'. The denervation of these nerve endings results in a spike train along the afferent nerve to the CNS. This afferent nerve is called the Ib afferent
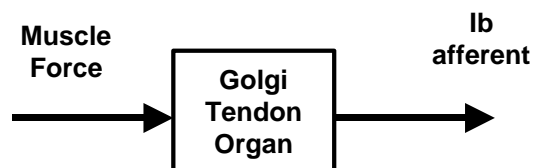

Figure 4-11   Block scheme of a Golgi tendon organ. The only input is muscle force, and the Ib afferent nerve signal is output which has a static and linear relation with the muscle force.
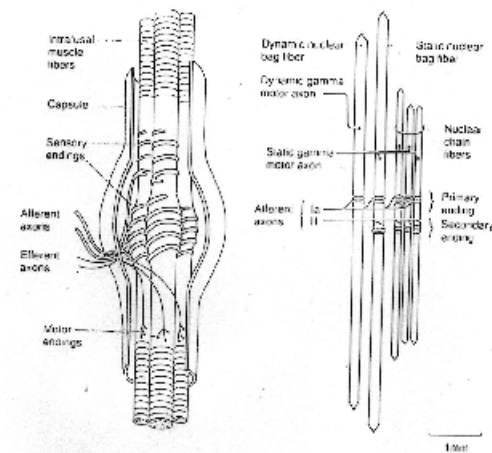
Figure 4-12   A muscle spindle unit consists of 3-5 nuclear chain fibers and 1-2 nuclear bag fibers

nerve fiber. The deformation of the tendon is in accordance with the muscle force exerted along the tendon. Therefore, the Golgi tendon organs provide information about the muscle force.

In the earlier days, experiments in which the whole muscle was stretched resulted in little activity of the GTO. Therefore, it was thought that the function of the GTO was not in the fine motor control, but merely to detect large forces in the tendons and protect the tendon against damage. This theory was also in accordance with the fact that the GTO are connected to the α-motor neuron through an inhibitory interneuron, i.e. when the tendon was stretched, the GTO caused the α-motor neuron to cease firing. However, this theory has been abandoned for two reasons. In the first place, if the α-motor neurons cease firing while the large external force is still stretching the muscle, the muscle will be stretched rapidly, and presumably the muscle fibers will be damaged. Secondly, more recent experiments showed that the Golgi tendon organs are especially sensitive to the forces exerted by the *active* muscle fibers, more than to the passive forces transmitted though endomysium and perimysium (the connective tissue around the muscle fibers).

The GTO is a sensor inside a force feedback loop, in which the muscle force is fed back to the CNS. Forces down to a few μN can be sensed by the GTO. In addition, the Ib afferent fibers are among the fastest transmitting sensory fibers in the peripheral nervous system. It will be shown in the next chapter that the force feedback loop is an important inner loop of the velocity and position feedback loops. Inside the GTO, there

Figure 4-13   Photo of the sensory part of the muscle spindle, in which the nerve ending is wrapped around the nuclear chain and nuclear bag fibers. In addition, the emergence of the sensory nerve towards the CNS can be seen at the left side
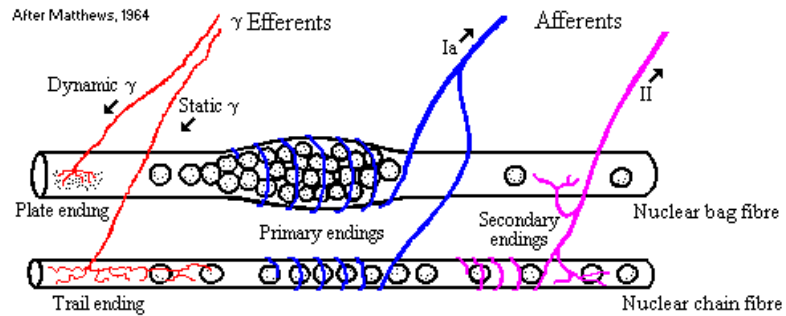
Figure 4-14   A muscle spindle has two efferent nerve inputs (γ_d to the nuclear bag muscle fiber and γ_s to the nuclear chain muscle fiber) and two afferent nerve outputs (Ia from both the nuclear bag and nuclear chain sensory parts, and II mainly from the nuclear chain sensory part).

are no dynamic effects, i.e. the Ib afferent nerve output is always proportional to the muscle force. Hence, there is a static (no time-history) and linear relation between the muscle force and the afferent nerve (Figure 4-11).

4.5.3.2   MUSCLE SPINDLES

In contrast to the Golgi tendon organs, muscle spindles are very complex sensory units. A muscle spindle is a unit consisting of about 3-5 nuclear chain fibers, and 1-2 nuclear bag fibers (Figure 4-12). A muscle spindle has a length of about 8 mm and is located parallel to the muscle fibers. The muscle spindle endings are attached to the muscle fibers, and hence the spindles are lengthened and shortened together with the muscle fibers. Hence, the length and velocity of a muscle spindle are always proportional to the length and contraction velocity of the muscle fibers.

The nuclear bag and nuclear chain fibers contain multiple cell nuclei. As the naming suggest, in the nuclear bag fibers the cell nuclei are located in a bag-formed area in the middle of the fiber, and in the nuclear chain fiber the nuclei are located in a chain along the whole length of the fiber. Both the nuclear chain and nuclear bag fibers consists of two small muscles at the endings, and a sensory part in the middle. A nerve ending is wrapped around the sensory part, and essentially is sensitive to the stretch of the sensory part (figure 4-13). The small muscles inside the muscle spindle are called 'intrafusal' muscles (intrafusal means 'inside the spindle'). Hence, the normal muscle fibers outside the muscle spindle are called the extrafusal muscle fibers. The intrafusal muscle spindles are innervated by a separate motor neuron, the γ-motor neuron, which is an *efferent* innervation to the muscle spindle (carrying signals from the CNS to the periphery).

The nuclear bag fibers are sensitive to the stretch velocity, and the nuclear chain fibers are sensitive to the stretch length. There are two types of *afferent* nerves, Ia and II sensory nerves. The Ia sensory nerve receives branches from the sensors of both the nuclear bag and nuclear chain fibers, and thus contains length and velocity information. The II sensory nerve receives only branches from the nuclear chain fibers, and contains only length information. According to the specific sensitivity of the nuclear bag and

Figure 4-15   A block scheme showing the two mechanical inputs (length and velocity) and two neural inputs (γ_d and γ_s motor neurons), and two neural outputs (Ia and II afferent nerves) of the muscle spindle.
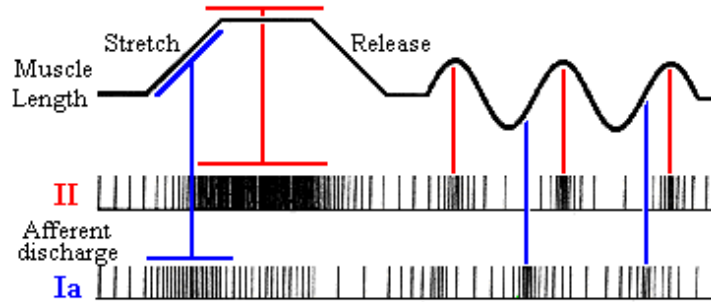
*Figure 4-16   Response of the muscle spindle to a regime of stretch and release. From
              the spike trains in the afferent nerves it can be seen that the II afferent
              nerve is mainly sensitive to length, and the Ia afferent nerve is sensitive to
              lengthening velocity. During release, the Ia afferent nerve is almost silent.*

nuclear chain fibers, the innervating γ-motor neurons are called γ_d (dynamic) and γ_s (static) motor neurons. In Figure 4-14 all efferent and afferent nerves connected to the muscle spindle are shown.

Figure 4-15 contains a block scheme in which all inputs and outputs of the muscle spindle are depicted. The muscle spindle has two mechanical inputs (length and contraction velocity) and two neural inputs (γ_d and γ_s motor neurons), and two neural outputs (Ia and II sensory nerves). Hence, the muscle spindle is a multi-variable system in which there is a non-linear interaction between the inputs.

As stated before, the muscle spindle is sensitive to length and contraction velocity. The resulting spike trains in the Ia and II afferent nerves are shown in figure 4.16. This figure shows that the muscle spindle is primarily sensitive to muscle *stretch* and *stretching velocity* (note that the stretch of the muscle spindle is proportional to the stretch of the extrafusal muscle fibers). During the release, the spike trains almost disappear, especially in the Ia afferent fibers. The II afferent fibers are mainly length dependent, and show their highest activity at the length peaks (shown with red lines). The Ia afferent fibers have their highest activity at the highest lengthening velocity.

The response of the muscle spindle to stretch depends also on the visco-elastic properties of the intrafusal muscle fibers. Figure 4-17 shows that if the intrafusal muscle fibers would have only elastic properties, the sensor is a length sensor. If the intrafusal muscle fibers would have only viscous properties, the sensor is a velocity sensor. If the intrafusal muscle fibers combine elastic and viscous properties, the sensor is sensitive to both length and velocity. In figure 4-18A the theoretical response of a Ia afferent nerve to a length ramp is shown, decomposed in a length, a velocity and an acceleration contribution. In figure 4-18B the actual response is shown, showing the
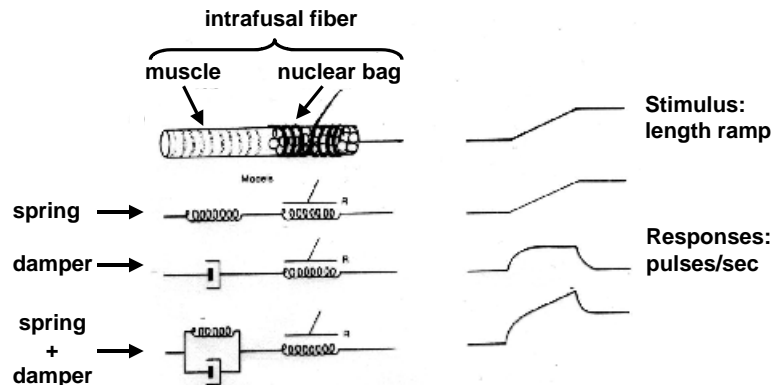

*Figure 4-17   The stretch of the sensory part, and hence the afferent neural output,
              depends on the visco-elastic properties of the intrafusal muscle fibers.*

summation of the length and velocity input. The peak at the start of the lengthening ramp would suggest that also accelerations could be detected. However, experiments have shown that this peak is due to a stiction property in the intrafusal muscle fibers. If the spindle is stretched, the crossbridges in the intrafusal muscle fibers take up the majority of the force for being stretched. Only when the stretch is larger than 1 mm (equivalent to about 5 degrees of joint rotations!), the crossbridges are released and a new equilibrium will result. The initial sticton of the crossbridges results that most of the stretch is taken up by the sensory part, which shows a huge initial peak. The fact that there is no peak at the end of the lengthening ramp shows that it is no acceleration effect, but a stiction effect.

The visco-elastic properties of the intrafusal muscle fibers are further elaborated in figure 4.19. If the ratio of stiffness and viscosity is the same for the sensory part as for the muscle part, then a proportional part of the lengthening will be taken up by the sensory part, and the muscle spindle acts as a position sensor. This is the case for the nuclear chain fibers. The intrafusal muscle fibers in the nuclear bags have very high viscous properties. Hence, if the lengthening velocity becomes higher, the sensory part is stretched more and a higher sensory output results.
The visco-elastic properties of the intrafusal muscle fibers as well as the neural output are changed when the muscle fibers are activated by the γ-motor neurons. As a direct effect when the intrafusal muscle force increases, the sensory part is stretched. As a secondary effect the stiffness and viscosity increases, and the sensor becomes more sensitive: A relatively more compliant sensory part means that more of the stretch is taken up by the sensory part. Here, an important role of the γ-motor neurons arises: They can keep the muscle spindle in the most sensitive region even for the extreme range of lengthening and shortening of the muscle. However, it also implies that for the correct interpretation of the afferent output in terms of length and velocity, also the efferent input to the muscle spindle must be known.
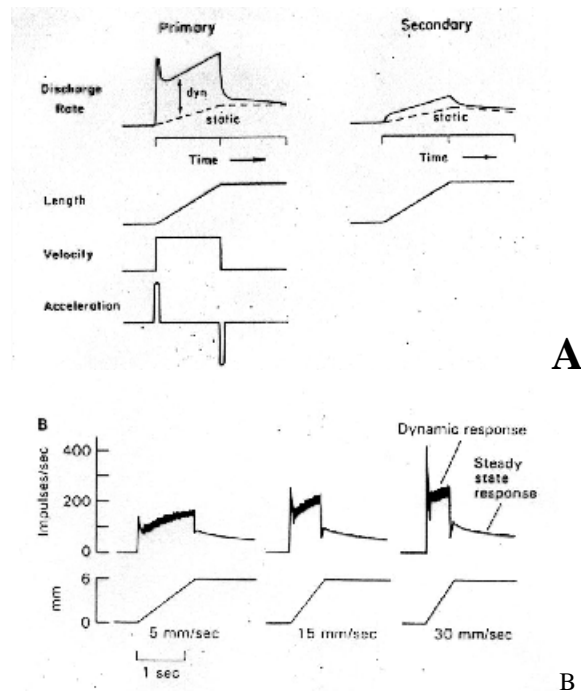

Figure 4-18   A: Theoretical response showing the length, velocity and acceleration contribution. B: Actual experimental results showing the dynamical respons. The absence of a peak during release shows that the latest dynamic effect is due to stiction, instead of an acceleration effect

Some theories about the function of the γ-motor neurons state that they function as a setpoint for the muscle length, since the afferent neural output of the muscle spindles is directly connected to the α-motor neuron activity through a mono-synaptic connection in the spinal cord. Because of the increased sensory output, the α-motor neuron activity increases and the muscle shortens. Then, the muscle and proprioceptive feedback would function like a servo-unit. However, it is easily shown that this theory can not be true, since the afferent neural output will never cease firing when the γ-motor neurons are active, because γ-motor neurons results in a force (not a length!), and a force will always stretch the sensory part.

It is more logical to assume that the γ-motor neuron activation has a two-fold function: Maintaining the muscle spindle in the most sensitive region, and adjusting the gain of the muscle spindle and thereby affecting the loop gain of the length and velocity feedback. The gain of the muscle spindle is the magnitude of sensory output compared to the length or velocity input. In that respect, increasing the spindle sensitivity and the spindle gain is the same action, though functionally interpreted in a different way.

The transmission speed of the sensory nerves depends on the thickness of the myelin sheaths. In Table 4.1, it can be seen that the tactile sensors and free nerve endings have a very slow transmission. The fastest transmission speeds are found for the Ia and Ib afferents. These sensory nerves are part of the inner loop of a feedback system. A pure time-delay causes a phase lag in the open-loop transfer function, which limits the bandwidth of the system. Especially the inner loops (force and velocity) need to be very fast, in order to enable higher feedback gains in the outer loop (position feedback). For a position-controlled system, a higher loop gain will result in a higher admittance, i.e. less sensitivity to force perturbations.

A typical non-linear phenomenon occurs in the Ia afferent nerve at the junction of the branch originating from the nuclear bag fiber, and the branch from the nuclear chain fiber. The spike trains from both nerve branches do not simply add, and continue with the summed spike frequency. Whenever a spike arrives at the junction, it will split into two directions: Towards the CNS but also in the opposite direction along the other branch. Whenever another spike is met at this branch, both spikes will extinct each other. Hence, the spike train with the highest frequency will completely extinct all spikes from the other branch: The *winner takes all* principle, or a *max-operation* between length and velocity. Only when the spike trains have about the same frequency they will enforce each other and the summed frequency will be about 110% of the original common frequency. In other words, when the velocity signal is dominant over the length signal, i.e. during movements, the CNS receives *only velocity* information. When the length signal is dominant over the velocity information, i.e. during postural tasks, the CNS receives *only length* information. Apparently, the CNS can cope with this phenomenon that it does not know whether the afferent information contains length or velocity information. The function and implications of this phenomenon is not known yet.

	Diameter (μm)	Transmission speed (m/s)	Type of sensor	Stimulus
Ia	12 - 20	70 – 100	Muscle spindle	Length & velocity
Ib	12 - 20	70 – 100	GTO	Force
II	6 - 12	35 - 70	Muscle spindle	Length
	2 - 5	12 – 30	Pacini corpuscle	Pressure
	0.5 - 2	3 - 12	Free nerve ending	Nociceptive

Table 4.1: Diameter and transmission speed of some of the proprioceptive sensors in the body.

4.5.3.3   CONNECTIONS BETWEEN THE PROPRIOCEPTIVE SENSORS AND THE CNS

In figure 4-19, the connections between the Ia, Ib (Golgi) and II afferent sensory nerves and the CNS are shown. Multiple pathways of the sensory information through the CNS exist. The simplest path is the monosynaptic connection of the spindle information: The stretch reflex. If the muscle is stretched (e.g. by a hit on the knee tendon), the muscle spindle will fire and consequently the α-motor neuron will be excited and the muscle will contract: The well known knee tendon reflex. Less well known is the reciprocal inhibition. At the same time that the α-motor neuron of the agonist is excited, the antagonist is inhibited which will increase the effect of the stretch reflex. The stretch reflex is also called the short latency reflex. The latencies of this reflex loop are about 25 msec for shoulder muscles to about 50 msec for lower leg muscles.

The stretch reflex is a local reflex, only the muscles that are stretched are involved. In this respect, the muscle with monosynaptic reflex can be regarded as a 'reflexive muscle unit', in which much of the dynamic behavior results from the reflex. One important property is that the (apparent) stiffness and viscosity of the reflexive muscle unit increase far above the intrinsic muscle visco-elasticity that is beneficial especially for postural tasks. The input to the reflexive muscle unit is supra-spinal neural inputs originating from higher CNS levels.

In addition to the stretch reflex, reflexes that are more co-ordinated exist, involving higher levels of the CNS. Coordination at the joint level occurs presumably within one segment level in the spinal cord. At this level, an adequate response can be generated. For example, if the biceps muscle is stretched due to a pronation motion of the forearm, the stretch reflex will result in a supination motion, but also in an elbow flexion. However, a medium latency reflex (with latencies between 70 and 110 msec) will occur in the biceps, but also in the triceps muscle. The triceps activity will generate an extending moment that counteracts the flexion moment of the biceps, and only the pronation motion will be counterbalanced by the biceps activity. The triceps was initially not stretched by the pronation motion, and received its sensory input from the muscle spindles of the biceps!

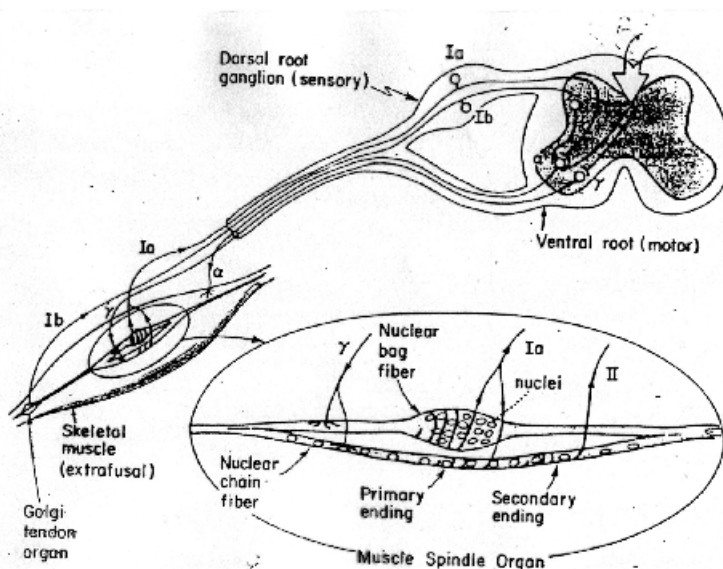For coordination at a limb level, it is likely that more spinal levels are involved. These

Figure 4-19   The Ia and II sensory nerves are directly connected through a excitatory to the α-motor neuron. The Ib sensory nerve is connected through an inhibitory interneuron to the α-motor neuron

are called long latency reflexes, with latencies from 110 msec and up. Examples of these long latency reflexes are the withdrawing reflex when the hand touches a hot object. The sensory input originates from the skin sensors, not from muscle sensors, but a coordinated response will occur.

Sensory information is also important for adaptation of the internal representation of the environment. This internal representation, or internal model, is used as anticipation (feedforward control) to disturbance, which are going to occur. Using a feedforward control, faster and more appropriate reactions can be generated. An even more sophisticated use of sensory information is the learning of new motions.