

Biological motor control

2.1 Introduction

One of the great challenges of science today is to understand the human brain, and the biological basis of perceiving, learning, action and memory. The problem is, of course, the brain's incredible complexity of structure and subtlety of design. A great deal is known about the lowest levels: the biochemical mechanisms underlying the operation of individual neuron cells. Similarly the operation and interactions of various simple neural circuits in the brain is well understood. But at higher levels our knowledge becomes less detailed. Little is known about how the brain works at a "systems level", in other words how its various parts interact to produce coordinated, adaptive and intelligent behavior¹.

This chapter explains how the control of movement (motor control) is achieved in the brains of humans and other mammals. From an engineering perspective, the motivation for this study is to try and steal some of the good design features of the brain to use in a robot or "artificial life form". Only those parts of the brain concerned with motor control will be described here. Of course there are many other brain systems necessary for an organism's survival, such as sensory, memory and cognitive systems, which would also need to be emulated by a successful automaton. However these other systems will be largely ignored.

The overall structure of the brain is first outlined. Then the motor control system is described from the bottom up: the neurons, muscles, spinal cord, brain stem, cerebellum and motor cortex. This material is relevant in several respects.

- The CMAC and FOX are simple models of the cerebellum (FOX is more realistic in some ways).
- The simple model that will be constructed of the muscles and spinal reflexes will be used in Chapter 7 to achieve low level robot joint control.
- The intelligent controller design principle of multiple interacting behavior-implementing modules gets its biological justification here: the brain is structured in such a manner. The concept of brain-stem modulation of spinal reflexes is a good organizing principle for autonomous robot design and will be used in Chapter 7.
- The eligibility-based reinforcement learning technique gets its biological justification in the description of classical conditioning presented below: the Purkinje cells of the cerebellum implement

¹The brains of lower (and therefore simpler) animals are better understood.

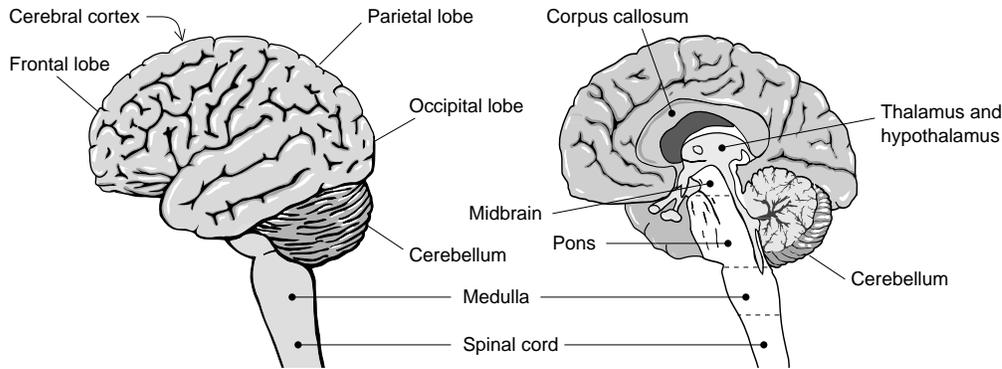


Figure 2.1: The human brain, exterior (left) and interior (right) views.

classical conditioning using a chemical eligibility signal.

There are generally two types of motor control theory: those that are hopelessly naïve from an engineering point of view, and those that are hopelessly naïve from a neurobiological point of view. The biological realism of the CMAC and FOX is not necessary from an engineering perspective, but it is interesting from a biology perspective.

Such a short chapter can not do justice to this huge subject area, so many details are omitted. Despite this, a lot of biological detail is presented, and the uninterested reader may skip to the conclusions at the end of this chapter. Much of the information presented here comes from [59], [53], [1] and [40]². At each level a simplified functional model will be presented which encapsulates the essential features (and fills in some details where there is no supporting biological evidence).

2.2 Overall structure

The brain contains many subsystems specialized to different tasks, much like organs in the body. Human behavior (or that of any animal) arises from the interaction of these systems. The gross anatomy of a human brain is shown in figure 2.1. Figure 2.2 shows the principle structures involved in motor control and the connections between them. The motor systems are arranged in a rough hierarchy. Upper levels of the hierarchy send modulatory commands to the lower levels, and the lower levels in turn send back processed sensory and state information.

The *spinal cord* is the major interface between the brain and the outside world. It contains many bundles of sensory and motor nerves, and also many neural circuits organized to provide reflex behaviors.

The *brain stem* is made up of the medulla, pons, and mid-brain. It contains many distinct nuclei (groups of neurons) which are specialized to various tasks such as maintenance of posture, control of balance and transformation of sensory information. It regulates many of the low level aspects of behavior, and implements basic survival motor programs.

The *cerebellum* helps to coordinate instinctive and learned motor behaviors. It receives information from the motor cortex and from the spinal cord, which it uses to modulate other brain stem areas.

The *thalamus* processes and distributes almost all sensory and motor information going to the cerebral cortex. The *basal ganglia* are an adjunct to the cerebral cortex, they have a role in the coordination of

²Also see [101] and [9] for general information on brain structure and dynamics.

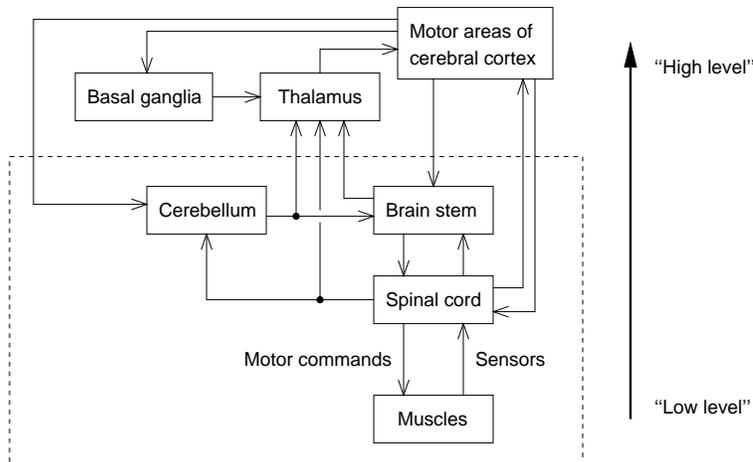


Figure 2.2: *The principle motor control areas of the brain.*

movement and also play a part in cognition. They may be involved in computing the transitions between different movement states [28].

The *cerebral cortex* is a thin folded sheet of neurons which covers the cerebrum. The cerebrum has two hemispheres on either side of the head which are connected together by a thick bundle of nerve fibers called the corpus callosum. The cerebral cortex is concerned with perceptual, cognitive, and higher motor functions, as well as emotion and memory. Complex behavioral responses originate here. It has many areas which are specialized to different cognitive functions, such as vision, language, and planning.

Figure 2.3 shows the motor control areas of the brain in more detail. Not all the nuclei or connections between them are shown, just the most well known. This figure highlights the fact that the brain is very elaborate and has many interacting subsystems.

2.3 Neuron biology

Neuron biology is a complicated subject, and only the barest details will be given here. A neuron is a cell that is specialized to carry electrochemical signals. The signals are represented as voltage differences across the cell membrane. Figure 2.4 shows the basic structure of a neuron. The neuron has many thin projections that connect it to other neurons. These are the *dendrites* which carry inputs to the neuron, and the *axons* which carry the neuron's output to other neurons. Over short distances the static neuron voltage can carry information. Over longer distances signals are transferred along dendrites or axons as a stream of voltage pulses, and information is encoded in the pulse rate (also called the firing rate).

Each pulse transmitted to a neuron is integrated by the cell body until a threshold is reached, whereupon the neuron emits its own pulse and the integration restarts. The interface between any two neurons occurs at a synapse, which is a junction between an axon terminal and a dendrite. The axon terminal can be excitatory or inhibitory by some amount, which means that the synapse modulates the incoming pulse so that it will have a greater or lesser integrating effect on the target neuron, thus increasing or decreasing its firing rate.

Neurons come in many shapes and sizes. For instance, the granule cells of the cerebellar cortex are tiny, star shaped and only have four inputs (synapses) on average. In contrast the Purkinje cells are much larger, tree shaped, and have up to 200,000 inputs each. Neurons vary greatly in their internal dynamics:

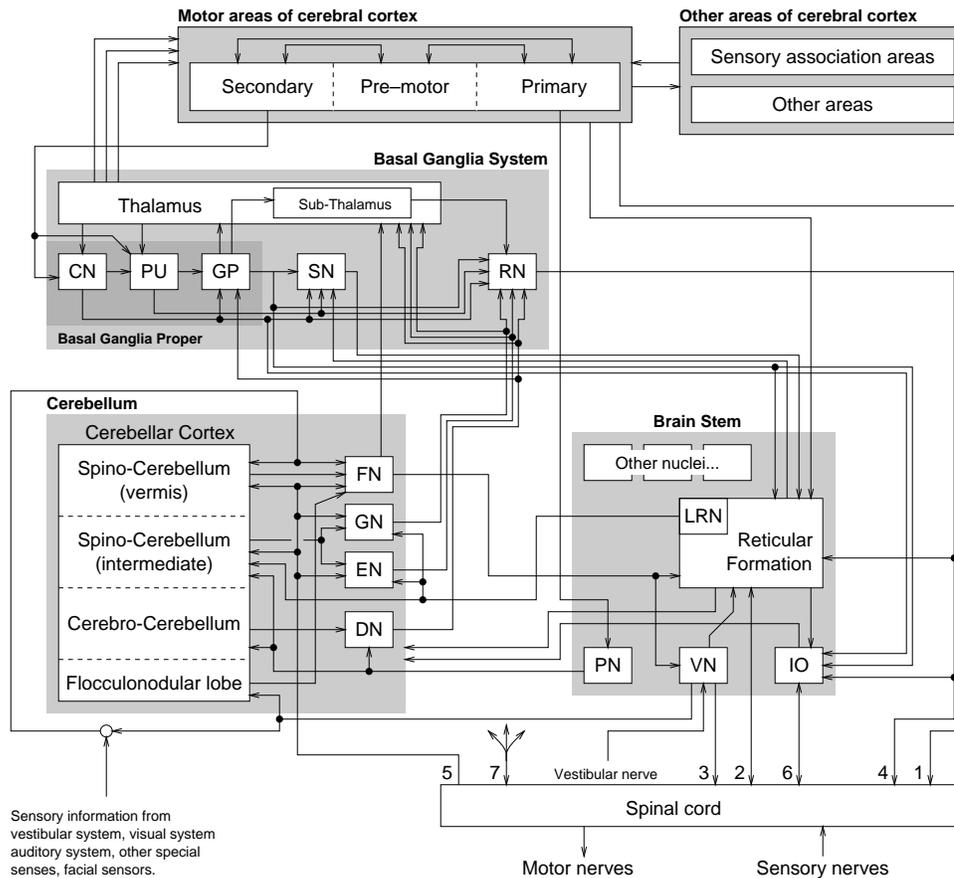


Figure 2.3: The major motor control areas of the brain, in more detail. FN: Fastigial nucleus, GN: Globose nucleus, EN: Emboliform nucleus, DN: Dentate nucleus, RN: Red nucleus, PN: Pontine nuclei, LN: Lateral reticular nucleus, CN: Caudate nucleus, PU: Putamen, GP: Globus Pallidus, SN: Substantia nigra. Spinal cord tracts: 1:cortico-spinal tract, 2:reticulo-spinal, spino-reticular, and various other tracts, 3:vestibulo-spinal tracts, 4:rubro-spinal tract, 5:spino-cerebellar tracts, 6:olivo-spinal and spino-olivary tracts, 7:various other tracts. This picture was assembled from several sources, including [59], [53], [1] and [40].

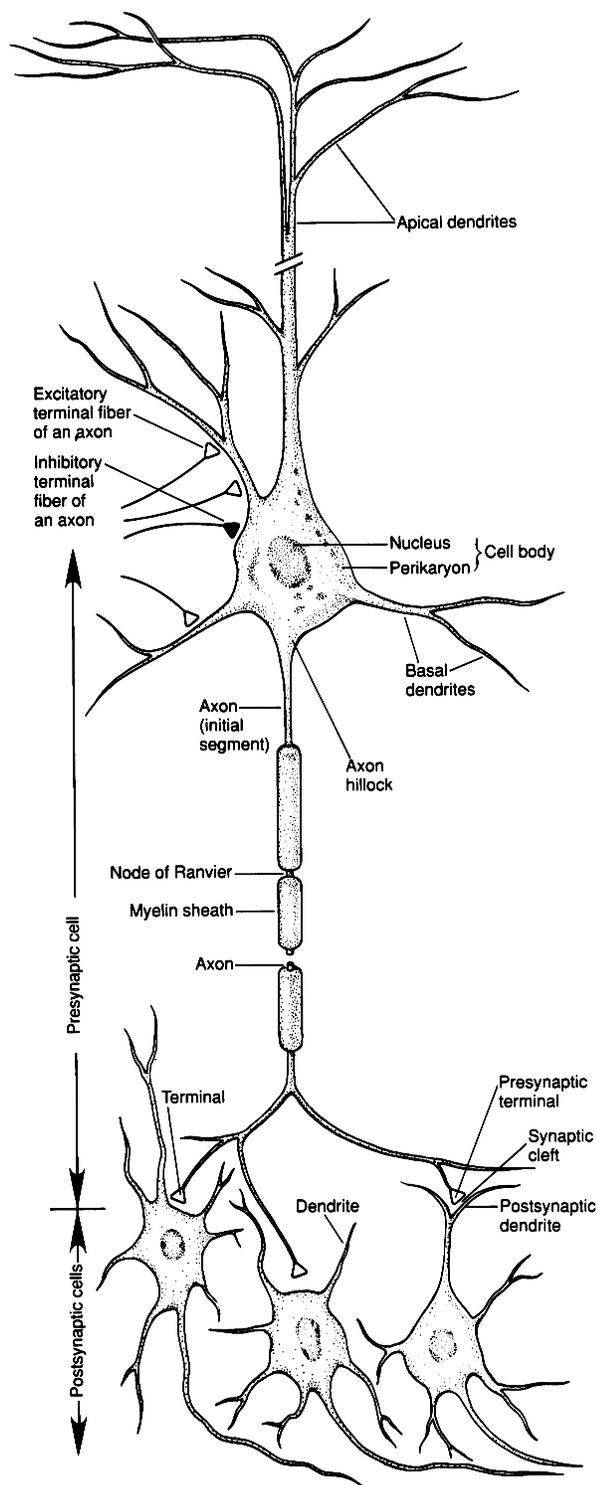


Figure 2.4: The basic features of a typical neuron. From *Principles of Neural Science*, 3rd edition, by E.R. Kandel, J.H. Schwartz and T.M. Jessel, page 19. Copyright ©1991 Appleton & Lange.

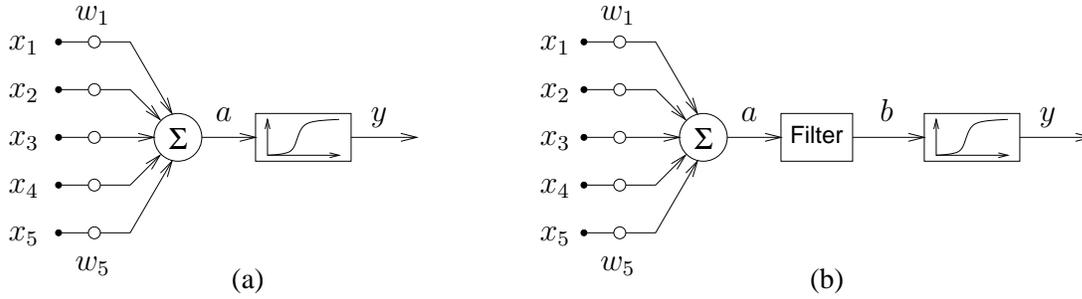


Figure 2.5: Some simple neuron models.

some just act to relay incoming signals, while others can have complicated oscillatory behavior that is modulated by the incoming signals.

2.3.1 Neuron models

Despite this complexity it is common to use extremely simple neuron models in artificial neural networks. Figure 2.5a shows a simple stateless neuron model. The input and output values represent firing rates. The weighted inputs are summed and then a “squashing function” $f(\cdot)$ is applied to get the output:

$$y = f\left(\sum_i w_i x_i\right) \quad (2.1)$$

Note that the weights w_i represent the synapses, with $w_i > 0$ being excitatory and $w_i < 0$ being inhibitory. The squashing function is usually bounded above and below and monotonically increasing. A typical example is the sigmoid function:

$$f(a) = \frac{k_1}{1 + e^{-k_2(a-k_3)}} \quad (2.2)$$

where $k_1 \dots k_3$ are arbitrary constants. Figure 2.5b is similar except that the output goes through some kind of differential equation, typically a first order filter:

$$\frac{db}{dt} = \tau(a - b) \quad (2.3)$$

where τ is a time constant. This adds state variables to the system and allows the modeling of more dynamic neural networks. More sophisticated models of neurons and neural groups, and a description of their information processing capabilities are given in [98] and [45].

2.3.2 Models of learning

Learning can be regarded as the neural process of forming internal *representations* of the external world. Different parts of the brain perform different types of learning, using various mechanisms. In most cases learning happens at the level of individual neurons by adjustment of synapses or alteration of a neuron’s dynamics in response to incoming signals.

Classical conditioning is a common mode of associative learning, in which stimuli are associated with an appropriate response. Here is a simple (contrived) example: if a person stubs their toes against

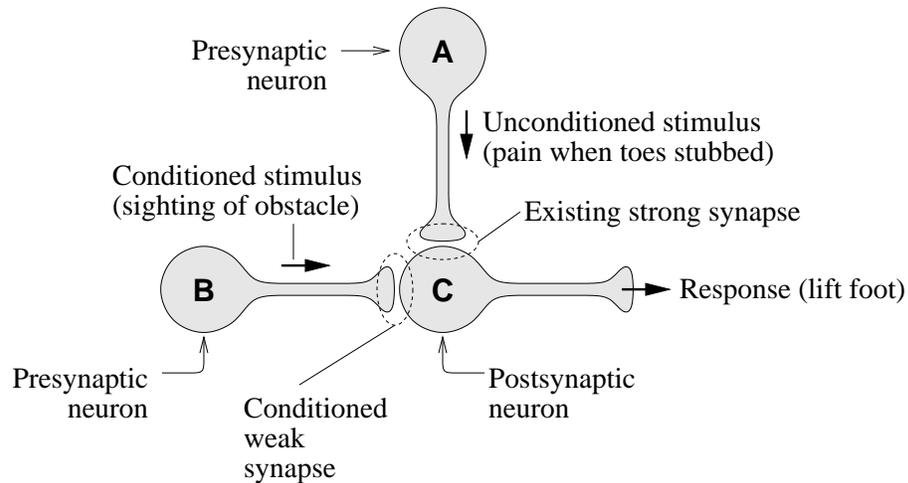


Figure 2.6: *The mechanism of classical conditioning.*

an obstacle while walking, they will withdraw the foot from the obstacle. If the person is able to see the obstacle as well, classical conditioning can associate that sighting with the pain resulting from a collision, and *preemptively* trigger the withdrawal of the foot to avoid the obstacle.

In 1949 Donald Hebb proposed a cellular mechanism for classical conditioning, which is now known as Hebbian learning [44] (figure 2.6). An “unconditioned stimulus” (the pain signal when the toes are stubbed) originates from neuron A. This is able to elicit a strong response in neuron C (which lifts the foot above the obstruction) because of the high-strength synapse coupling the two. A “conditioned stimulus” (the visual sighting of the obstruction) originates from neuron B. It is initially unable to elicit a response because its synapse on to C is weak. However, if B fires *at the same time* as C is firing, then the B-C synapse will be strengthened. Initially C only fires in response to A. If B fires in conjunction with A then B’s synapse will grow stronger and it will also be able to trigger a response in C. In this way the conditioned stimulus is *associated* with the unconditioned stimulus.

The synaptic mechanisms of Hebbian learning have been extensively studied [58]. The way in which the conditioned and unconditioned stimulus are paired in time is significant. They have to be close enough together so that C’s firing is “remembered” by the synapse when B fires. Note that classical Hebbian learning only results in synaptic strengthening. Other (similar) processes allow the synapse to be weakened as well.

Other neuron learning modalities include long and short term potentiation, sensitization and habituation [59]. These all use mechanisms similar to Hebbian learning. These synaptic learning rules are known to occur in the neurons of the cerebral cortex, the cerebellar cortex, and the hippocampus.

2.4 Muscles

The actuators of the motor control system are the skeletal muscles. Every joint in the body has two or more muscles which can apply a torque to the joint by contracting (figure 2.7). A simple muscle model is a spring whose spring constant can be changed by external signals. Muscles are organized in extensor/flexor pairs, so that movement in both directions around a joint can be achieved. Different muscles that work to provide the same mechanical action on a joint are called synergists. Muscles that

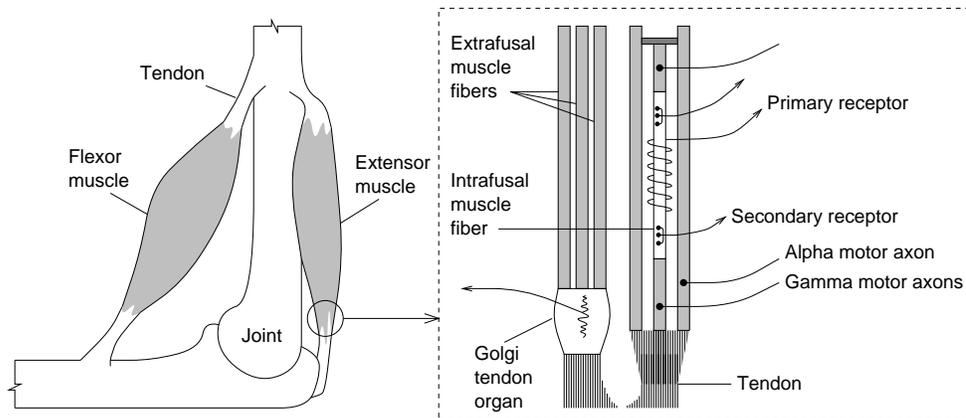


Figure 2.7: *Muscle anatomy and a schematic of the internal fiber arrangement.*

work to provide opposing motions are called antagonists. Different muscles differ in size, speed, and fatigue properties. Muscles are made up of many small cylindrical fibers, of two main types. The large extrafusal fibers provide the main contracting force. The smaller intrafusal fibers act as sensory organs.

2.4.1 Muscle contraction

Extrafusal fibers are innervated by the axons of large alpha motor neurons. The fiber contracts briefly when it receives a pulse from the axon. The alpha motor neurons are contained within the spinal cord. Each one drives from about 10 to 1000 muscle fibers, collectively referred to as a motor unit. The contraction force of a muscle is controlled by modulating the firing rate of the motor axons and by selectively activating more motor units as the desired force increases. As the higher levels of the brain request more muscle force, more motor units are recruited in order from the weakest (but most energy efficient) to the strongest (but least energy efficient). This allows a fine grading of the muscle force at the least metabolic cost.

2.4.2 Muscle spindles

The intrafusal fibers are attached to small gamma motor neurons (figure 2.7). They provide little muscle power—instead they function as sensory organs. The central area of the fiber contains two kinds of sensors. Primary receptors measure the length plus rate of change of length of the central area. Secondary receptors measure the length only. Both receptors send nerve fibers to the spinal cord. These receptors are stimulated whenever the central area is stretched. This happens either when the muscle itself is stretched (because the intrafusal fibers are tied to the extrafusal fibers), or when the intrafusal fiber tries to contract by itself against its attachments. In this way the intrafusal fibers act as comparators. The signals received from the stretch receptors can thus be modulated by the firing rate of the gamma motor neurons.

The stretch dynamics of the intrafusal fibers are complex, nonlinear and subject to both plastic and elastic effects. The dynamics of the spindle receptors are similarly complex, as shown in figure 2.8. The primary receptor responds quickly (under 1ms) to the initiation of any stretch, with a high firing rate. Thereafter its signal is roughly proportional to the length of the central area (plus the derivative of this length). The secondary receptor responds more slowly.

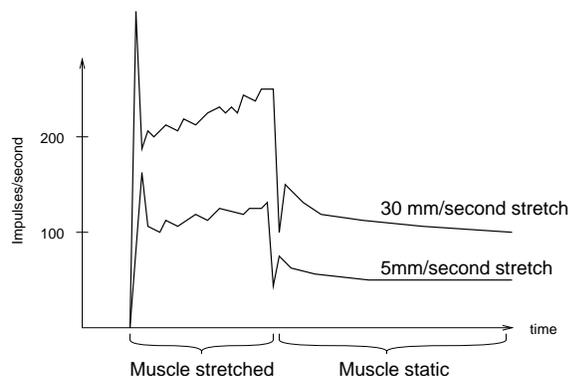


Figure 2.8: *Approximate primary receptor response for different muscle stretch rates (From [59] page 569).*

There are two types of gamma motor neuron, static and dynamic, which connect to intrafusal fibers with different dynamic properties. Activation of the static gamma system increases the steady state primary receptor response and the secondary receptor response. Activation of the dynamic gamma system increases the transient primary receptor response. The static and dynamic gamma activity (that is, the gain of the static and dynamic elements of the primary receptor response) is varied by higher level brain centers according to the current behavior. Both types of activity increase with the speed and difficulty of the movement. Static (but not dynamic) gamma activity is required for steady postures such as sitting or standing. Dynamic gamma activity is required for faster movements, such as walking, running, or difficult balancing tasks.

When the muscle contracts, the intrafusal fibers don't just go slack. Instead the gamma system is activated concurrently to shorten them and maintain tension. This alpha-gamma co-activation is controlled by the spinal cord.

2.4.3 Golgi tendon organs

Golgi tendon organs occur at the interface between the tendon and the body of the muscle (figure 2.7). Each of these organs is in series with about 10–15 muscle fibers. They measure tension in the muscle. Their receptor response is similar to that of the primary receptors in the muscle spindles, except that the quantity measured is muscle tension, not intrafusal fiber stretch.

2.5 Spinal cord

The anatomy of the spine and spinal cord is shown in figure 2.9. Almost all of the body's peripheral sensory and motor nerves connect to the spinal cord at some point. Sensory nerves (from various sense organs in the muscles, skin, and other places) enter the spinal cord through the sensory roots. Motor nerves to the muscles originate from spinal cord neurons and leave through the motor roots.

The white matter of the spinal cord contains many tracts of nerve fibers. These tracts convey ascending and descending fibers to other spine segments, and between spine segments and the upper brain. For example, the corticospinal tract contains fibers which connect motor neurons directly to the cerebral cortex. But the spinal cord is not just a passive cable. Its gray matter contains neural circuits which

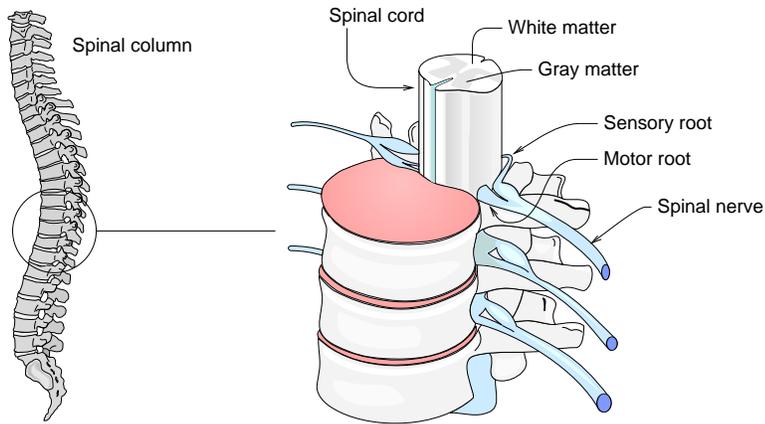


Figure 2.9: *Anatomy of the spine and spinal cord.*

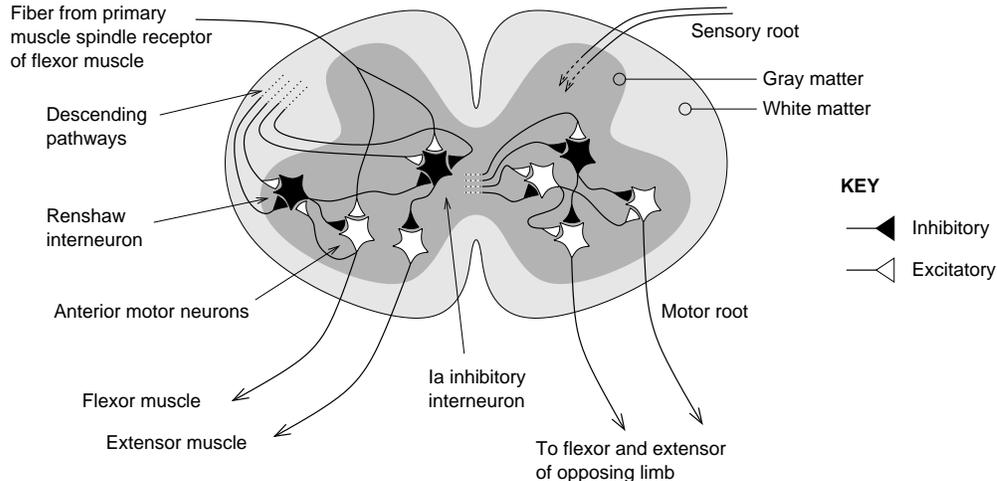


Figure 2.10: *Some basic spinal cord circuits.*

implement many of the reflexes that are required for the low level control of movement. “Reflexes” in this context are typically fast stereotyped responses that are triggered by environmental stimuli.

There are two main classes of spinal cord neurons: large anterior motor neurons and small internuncial cells (figure 2.10). All motor root nerves originate from the anterior motor neurons. The internuncial cells are much more numerous than the motor neurons. They are interconnected in complex patterns and they implement many simple (and not-so-simple) reflexes. Most incoming sensory signals connect to the internuncial cells and are able to trigger various reflexes. Figure 2.10 shows a few of the basic spinal cord neural circuits.

Most of the spinal cord reflex circuits are modulated by higher brain centers via the descending tracts. This modulation is very important, as coordinated movement can only be achieved by selectively sensitizing appropriate reflexes and suppressing others, depending on the situation.

2.5.1 Stretch reflex

The simplest (and arguably most important) spinal reflex is the stretch reflex. This reflex opposes the stretching of a muscle beyond its present length. It is implemented by having the primary muscle spindle receptors send excitatory signals directly to the anterior motor neurons for synergist muscles (figure 2.10). When a muscle stretches, the primary spindle receptors respond immediately, exciting the motor neurons and causing the muscle to contract. Because the stretch reflex operates in all muscles, any movement of the joint will be opposed.

The negative stretch reflex opposes shortening of the muscle in a similar manner. All muscles have a small resting tension, so the primary receptors are always active when the muscles are holding a static position. When the muscle is shortened, the primary receptor response drops, and this causes excitation of the antagonist muscles.

The effectiveness of the stretch reflex can be modulated by signals from the descending pathways. This is obviously necessary, because if the stretch reflex was always fully active the body would be frozen in a static posture. This modulation may occur through “pre-synaptic modulation”, where a synapse from a descending axon directly inhibits the synapse from the spindle primary receptor to the anterior motor neuron. This modulation allows higher brain centers to achieve fine control of movement. The stretch reflex gain can also be altered by changing the activity of the gamma motor neurons.

The gamma fibers in conjunction with the stretch reflex function as a kind of servo system. When gamma neurons are excited the ends of the intrafusal fibers contract, causing the primary receptors to be excited. This excites the stretch reflex and causes contraction of the muscle until the central area of the intrafusal fibers are no longer stretched. The muscles contract to a length predetermined by the gamma fiber activation. The dynamics of this contraction can be altered by changing the amount of static gamma versus dynamic gamma activation. This servo system is controlled by higher brain centers, principally the cerebellum, motor cortex and the basal ganglia, via the brain stem nuclei.

Alternatively, when the gamma system is inactive, the intrafusal fibers are flaccid and the alpha system is the main source of muscle contraction. The alpha mechanism is a direct muscle drive with no limits on the extent of movement. However, during fast muscle contractions both the alpha and gamma neurons can be excited together so that muscle spindle feedback does not disrupt the movement.

Muscle tone is the static tension in a muscle, and is present even when the muscle is at rest. Muscle tone is caused partially by the intrinsic elasticity of the muscle and partially by the stretch reflex.

2.5.2 Reciprocal inhibition reflex

Whenever synergist muscles contract, the antagonist muscles must relax for the joint to move. To accomplish this, all neural circuits which excite a motor neuron also send signals to internuncial type-Ia inhibitory interneurons. These interneurons send inhibitory signals to the motor neurons for antagonist muscles. Thus opposing muscles groups will cooperate to achieve movement. The reciprocal inhibition circuitry for the stretch reflex is shown in figure 2.10, where the primary muscle spindle receptors also send branches to the inhibitory interneurons.

Commands from higher centers can regulate the joint stiffness by controlling the degree to which the inhibitory interneurons are effective. For example, inhibition of an inhibitory interneuron will result in less motor neuron inhibition and thus more joint stiffness as antagonist muscles work against each other.

2.5.3 Tendon reflexes

Axons from the Golgi tendon organs synapse directly on to the anterior motor neurons for synergist muscles, implementing something similar to the stretch reflex.

Golgi organ excitation can also cause *inhibition* of the corresponding motor neurons, via inhibitory internuncial cells. This is organized so that extreme muscle tension causes inhibition and therefore muscle relaxation. This is a protective reflex to prevent tearing of the muscles and tendons during exertion.

The tendon reflex is a feedback circuit that can maintain muscle tension at a certain value. The set-point for this reflex is controlled by higher brain centers. This is useful for tasks that need a constant muscle force, not a constant muscle length. This reflex is required because a muscle's force dynamics are quite nonlinear (the force exerted for a given excitation depends nonlinearly on the muscle's length).

2.5.4 More complex reflexes, and central pattern generators

More complicated reflexes involve multiple interneurons and coordinated groups of muscles. In these reflex circuits, some interneurons act as "gates" which allow higher centers to modulate reflexes. These either use pre-synaptic modulation (effectively a synapse on a synapse) or direct inhibition of neurons in reflex circuits.

Central Pattern Generators (CPGs) are oscillatory neural circuits which control rhythmic movements such as scratching and walking. Many CPGs work because of reciprocal inhibition and reflex rebound. Reciprocal inhibition means that groups of neural circuits in the CPG associated with different muscles inhibit each other. Reflex rebound means that after a reflex has been triggered it can become harder to trigger for a given time thereafter, but the corresponding opposing reflex becomes easier to trigger.

Many CPGs rely on the complicated internal dynamics of individual neurons. For example, a neuron can increase its firing threshold with extended excitation (this is called adaptation). Similarly, a neuron's threshold can increase as a result of past inhibition (this is called rebound). Some CPGs use pacemaker cells which have an oscillating output, i.e. they repeatedly generate short bursts of pulses.

2.5.5 Postural and locomotion reflexes

Complex groups of internuncial cells are organized to provide reflexes that are useful for maintaining postural equilibrium, and in walking. Multiple spinal cord segments communicate via the spinal cord tracts, to coordinate multi-segment reflexes which involve large parts of the body. These reflexes have been experimentally isolated in quadrupeds, particularly cats and dogs [40].

Many locomotion reflexes are controlled by CPGs. The CPGs cause alternating movement of muscles on opposite sides of the body. There are independent CPGs for each limb, which are coupled together to achieve coordinated whole-body behavior.

The *posture supportive* reaction causes a limb to extend against pressure applied to a footpad. This reaction allows a quadruped to stand statically.

The *magnet* reaction causes a foot to move in the direction from which pressure is applied to the edge of a footpad. This is useful for keeping balance.

Stepping reflexes cause oscillations of the limbs in appropriate walking patterns. For example, the reciprocal stepping response in quadrupeds causes adjacent legs to go forwards and backwards rhythmically. The diagonal stepping response causes coordinated stepping movements in all four legs. Galloping movements can be triggered by simultaneous stimulus on the front or back paws, as would be felt during normal galloping. These reflexes result mainly from reciprocal inhibition and rebound effects.

Spinal *righting reflexes* in decerebrate cats and dogs cause them to make movements appropriate to standing up when they are placed on their side.

The *scratch reflex* is particularly sophisticated. In quadrupeds it is triggered by skin irritation and it causes a leg to find and rhythmically scratch the irritated site.

2.5.6 Other spinal reflexes

Transient changes in motor neuron output are opposed by recurrent inhibition with *Renshaw interneurons*. Renshaw interneurons are excited by a motor neuron. They inhibit that same motor neuron and the inhibitory interneurons for the antagonist muscles (figure 2.10). This effectively limits the speed at which the motor neuron output can change. Thus Renshaw cells act as a low pass filter for all motor commands [110]. The effect is distributed to muscles around a joint by type-Ia interneurons. Renshaw cells are modulated by higher centers to change the effective “excitability” of a muscle’s motor units.

Group Ib inhibitory interneurons have many excitatory and inhibitory inputs from other internuncial neurons. They inhibit the anterior motor neurons. These neurons mediate the tendon reflex, the withdrawal reflex, and many others.

The *withdrawal reflex* (“flexor” reflex) makes the limb withdraw from a painful skin stimulus. A complex circuit of internuncial cells is involved, and the stimulus is distributed to many muscles. The response is maintained for some seconds after the stimulus.

The *crossed extensor reflex* occurs 0.2–0.5 seconds after a stimulus triggers the withdrawal response. This causes the opposing limb to extend, pushing the body away from the stimulus.

Autonomic reflexes control other body functions like sweating, vascular tone, motor functions of the gut, and so on. These will not be considered further.

2.5.7 Spinal motor model

What are the variables of low level muscle control? In other words, what are the “joint commands” that descend from the high level systems to instruct the joints? At the very lowest level it could be said that the variables of muscle control are simply the alpha motor neuron activations which produce joint torque directly. But more convenient variables can be found.

Latash [65] has suggested that the set-point of the stretch reflex is an appropriate control variable. This conclusion is drawn from Merton’s servo hypothesis, which is that the main function of the stretch reflex is compensation of the influence of load upon muscle length, i.e. that it is a length regulating mechanism. This leads to the low level joint controller model shown in figure 2.11. This model is a simple proportional-derivative controller that tries to get the joint angle θ equal to a reference θ_r by applying an appropriate joint torque. The constants k_p and k_d set the “spring constant” and amount of damping in the controller. They are equivalent to the static and dynamic gamma motor neuron activations. A torque output filter performs a role equivalent to the Renshaw cells by limiting the rate of change of torque. The parameter τ adjusts the filter’s time constant.

Specifying θ instead of the torque simplifies the control of movement, because even with static parameters it can provide joint movements with reasonably good dynamics. It allows complex movements to be “played out” in θ coordinates by higher level centers, effectively giving those centers less to think about.

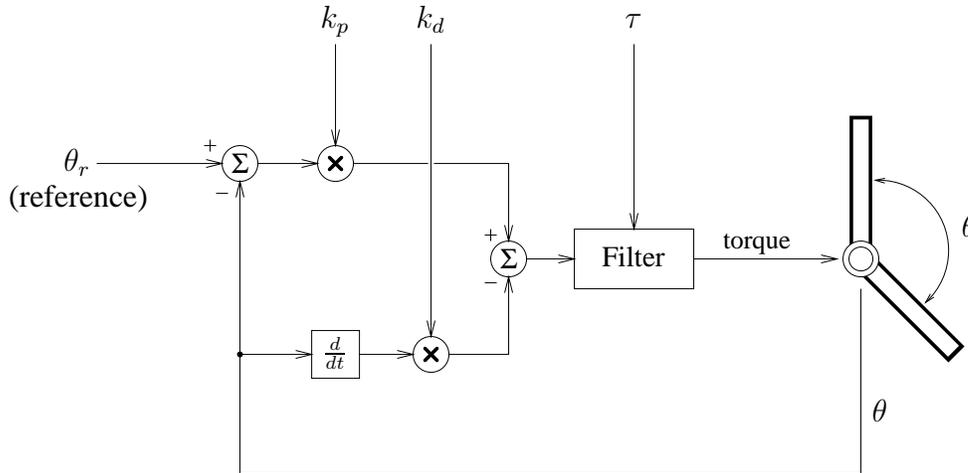


Figure 2.11: *Low level joint controller.*

2.6 Brain Stem

The brain stem is a complex extension of the spinal cord. The basic principle of multiple interconnected modulated reflexes is also implemented in the brain stem, but highly elaborated to handle more complex situations, and to use past experience to improve performance.

The brain stem contains many nuclei (groups of neurons) with specialized functions. It also contains the more diffuse “reticular formation”, which controls many discrete motor activities, such as the control of equilibrium, the support of the body against gravity, and high level reactions to prevent the body from falling.

Many stereotyped movements are controlled by the brain stem. In humans these include standing still, sitting up, turning, head tracking movements, chewing, swallowing, yawning, sucking the fingers, and so on. All of these behaviors are necessary for survival, which is why they are “hard wired” into the brain and not learnt.

2.6.1 Posture and equilibrium

Maintenance of postural equilibrium is dependent on muscle sensors, the vestibular system, and vision. The overall postural response depends on experience, because the correct reaction to maintain equilibrium is highly dependent on the body state and the environment.

The vestibular system helps to maintain the body’s balance with a set of “righting reflexes”. These reflexes move the limbs appropriately to compensate for falling off balance. The sensors of the vestibular system are the semi-circular canals and utricle of the inner ear. The three semi-circular canals detect angular accelerations of the head in three planes. The utricle detects linear accelerations of the head and the head’s orientation with respect to gravity. The output of the vestibular sensors connects to the vestibular nuclei, various other brain stem regions, and the cerebellum. Neck muscle sensors are integrated with vestibular information to determine the whole-body configuration.

2.7 Cerebellum

The cerebellum's task is to regulate the motor activity occurring in other brain areas such as the spinal cord, brain stem, basal ganglia and motor cortex (figure 2.3). The cerebellum is essential for the coordination, dexterity and timing of almost all body movements, especially high speed movements. Signals originating from the cerebellum modulate the extent of movement, initiate and terminate movement, and precisely control the timing of the many events within coordinated sequences of movement. In conjunction with the vestibular system it also helps to ensure correct balance. It can convert "clumsy" movement commands originating in the motor cortex into smooth, fluid actions.

The cerebellum makes up only 10% of the brain volume, but it contains more than half of all the neurons [59, p. 627]. The exterior of the cerebellum is its cortex, a thin sheet of neurons that is folded in on itself many times to pack as much surface area as possible into the small space (about 500 cm²). Surrounded by the cortex are three pairs of nuclei which serve to relay information from the cortex to the rest of the brain (figure 2.3).

The cerebellum is one of the principle adaptive components of the motor system. Its goal is to modulate motor commands so that *actual* movements match *desired* movements. To achieve this it is continuously being trained to anticipate disturbances and preemptively correct for them.

2.7.1 Cerebellar cortex: Anatomy

The cerebellum is one of the best studied regions in the brain [1, p. 194], so a great deal is known about its structure and operation. Figure 2.12 shows a slice of the cerebellar cortex. The cortex has three layers of neurons which contain five different cell types (the "white matter" layer in the figure contains only axons).

The mossy fibers originate in other brain stem and spinal cord nuclei. They are the major inputs, encoding all of the sensory information that the cerebellum needs. The mossy fibers terminate on granule cells. The granule cells are tiny and very numerous (there are about 10¹⁰–10¹¹ of them). Each one takes on average four mossy fiber inputs. Their axons are called "parallel fibers" because they run up in to the molecular layer, split into two and run parallel to each other up and down the cortex.

The Purkinje cells are much larger than the granule cells, and there are only about 15 million of them. They have extensive dendritic trees which collect inputs from up to 200,000 parallel fibers [59]. The Purkinje cell axons are the cortex output. They inhibit neurons in the cerebellar nuclei.

The climbing fibers originate from the "inferior olive", a nucleus in the brain stem. They carry training information to the Purkinje cell synapses by wrapping around the Purkinje cell dendritic tree. Training signals on the climbing fibers change the strength of the Purkinje cell synapses.

The Golgi, stellate and basket cells take parallel fiber inputs and serve to regulate the firing rates of the other cortex neurons by inhibition. The Golgi cells inhibit the granule cells, and the stellate and basket cells inhibit the Purkinje cells.

Different areas of the cerebellar cortex serve different functions. The vestibulo-cerebellum governs eye movement and body equilibrium. The spino-cerebellum controls detailed motor actions. It takes most of its input from the spinal cord. It contains somatosensory maps of the body, which means it is divided into regions that are specific to different body parts. The cerebro-cerebellum connects to the motor cortex via the thalamus and various nuclei. It is thought to aid the planning and initiation of movement.

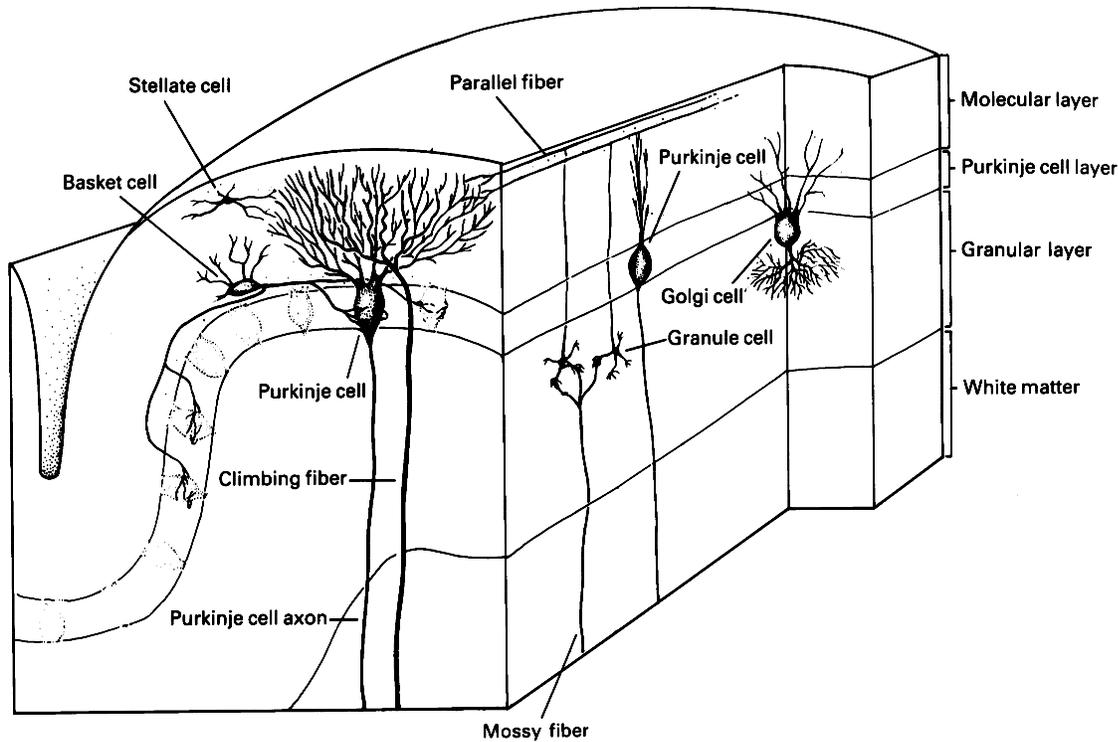


Figure 2.12: *The cortex of the cerebellum, which has three layers and contains five kinds of neurons. From Principles of Neural Science, 3rd edition, by E.R. Kandel, J.H. Schwartz and T.M. Jessel, page 630. Copyright ©1991 Appleton & Lange.*

2.7.2 Cerebellar cortex: Operation

Figure 2.13 shows a schematic of the neurons and connections within the cerebellar cortex and related nuclei. The inputs to the cerebellum are mossy fiber signals which contain sensory information. Some inputs are processed sensory information from high level visual, auditory and motor cortex areas. Other inputs come from low level spinal and brain stem areas. The cerebellum's own motor commands also re-enter the cortex via the lateral reticular nucleus. The area of the cortex that controls a muscle group has inputs from the motor cortex area controlling the same group, and also from the corresponding spinal sensors.

The Purkinje cell outputs modulate the spinal cord reflexes and motor neurons through the cerebellar nuclear cells. Thus the cerebellum is able to control the extent, speed, stiffness and timing of movements.

One hypothesis of cerebellum operation is that it functions as an array of adjustable pattern generators [86, p. 301]. Figure 2.13 shows that cerebellar nuclei (CN) cells, red nucleus (RN) cells and lateral reticular nucleus (LRN) cells are connected in rings with excitatory synapses. It was proposed that these rings function as bistable devices which can be switched on and off by the Purkinje cell inhibition. Multiple interacting bistable rings would form a "state machine" which is responsible for the execution of a motor program. This state machine would be modulated by the Purkinje cells but is otherwise self sustaining. This is an attractive idea, but it is probably not the whole story. Other studies [23] have shown the importance of the cerebellum in the *timing* of motor responses.

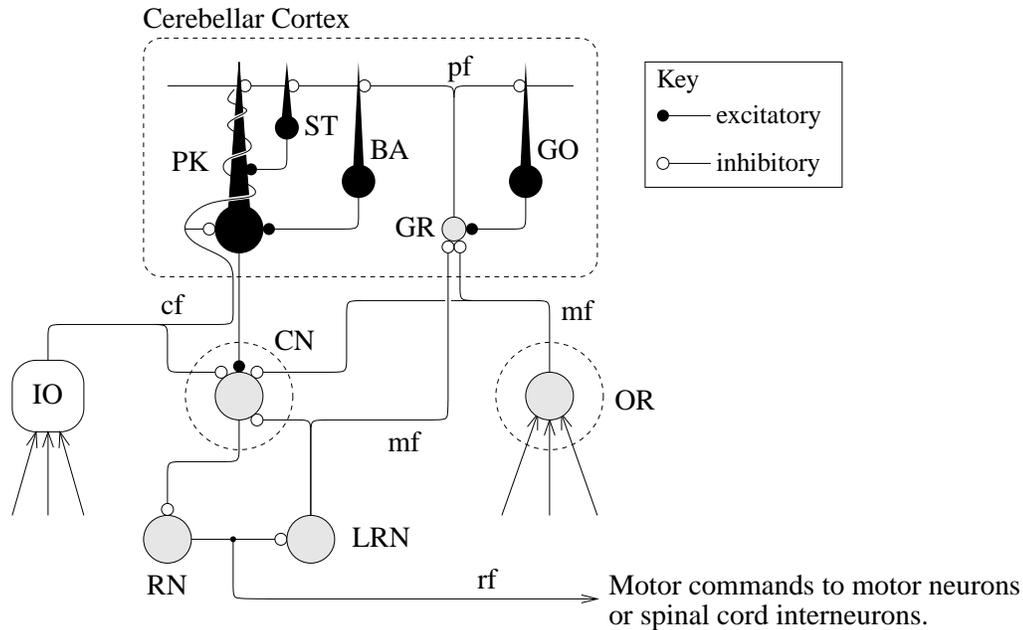


Figure 2.13: Schematic of the neurons and connections within the cerebellar cortex and related nuclei. Key: Purkinje cell (PK), stellate cell (ST), basket cell (BA), granule cell (GR), Golgi cell (GO), originating cell (OR), cerebellar nucleus cell (CN), inferior olive (IO), red nucleus cell (RN), lateral reticular nucleus (LRN), mossy fiber (mf), parallel fiber (pf), climbing fiber (cf), rubrospinal fiber (rf).

Figure 2.14 shows a simple mathematical model of the cerebellar cortex, which represents the two most important cell types: the granule cells and the Purkinje cells. The Purkinje cells just perform a weighted sum of their granule cell inputs.

In this model the granule cells are arranged so that the synapses of the Purkinje cells are used most effectively. Each granule cell forms a logical AND of its inputs (so it only fires when all of its inputs are above a certain threshold). This allows pre-wired associations to be formed among groups of sensor inputs. For example, in figure 2.14, if only one of A and B can fire at once (similarly for C and D) then the granule cells G1...G4 represent all possible input combinations. This gives the Purkinje cells maximum flexibility, because they can have a different response for every possible input (each response is determined by a different synapse).

A fundamental requirement is that the granule cell outputs can distinguish between different body configurations. In the best case the granule cells are configured so that any cerebellar input triggers only a small percentage of them, and as the input changes the active granule cell group also changes. This gives the Purkinje cells the maximum power to discriminate between different inputs. It also maximizes the effectiveness of training, because Purkinje cell learning in one input configuration will not degrade the information stored in another area if there is no overlap in the corresponding granule cell activations.

Remember that the Golgi cells inhibit groups of granule cells. It has been hypothesized that the role of the Golgi cells is to keep the firing rate of the granule cells constant [46]. It is further hypothesized here that the reason Golgi cell inhibition allows only a small number of granule cells to be active at any one time is to force them to compute the logical AND of their inputs (or something similar). This is supported by studies such as [23] which show that Golgi cell feedback acts to limit granule cell activation.

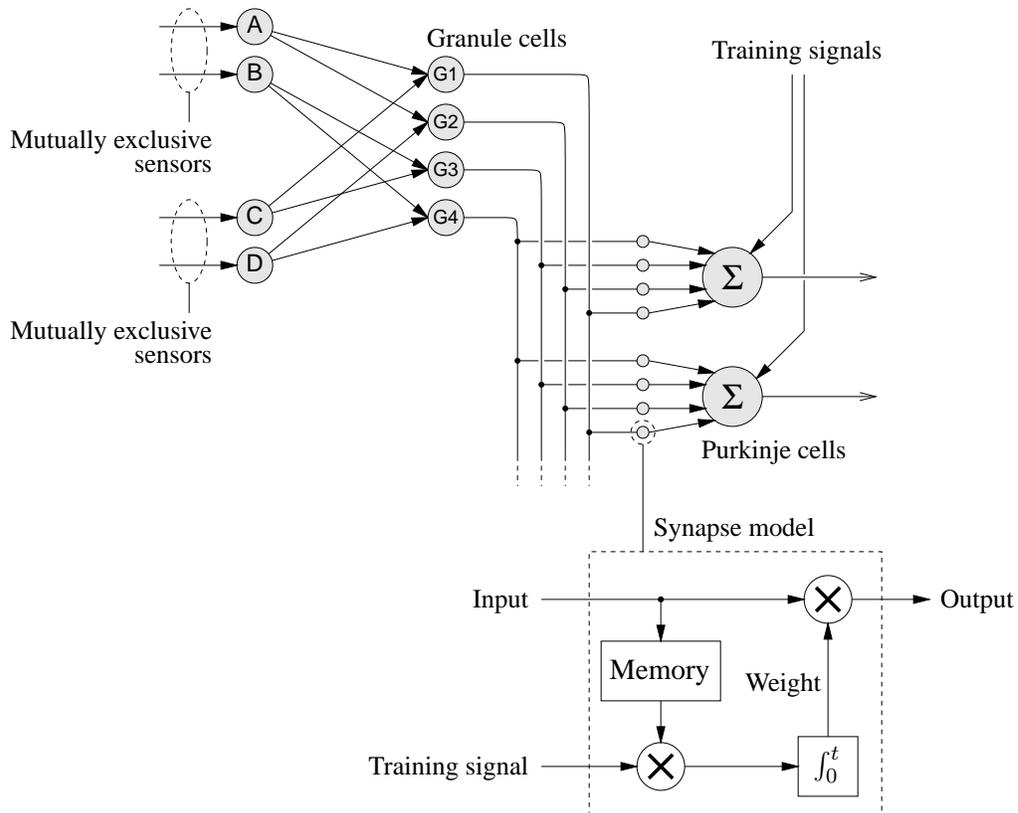


Figure 2.14: A model of the cerebellar cortex, incorporating the granule and Purkinje cells. This model also implicitly incorporates the Golgi cells, as each granule cell computes the logical AND of its inputs. Each Purkinje cell computes a weighted sum of its inputs.

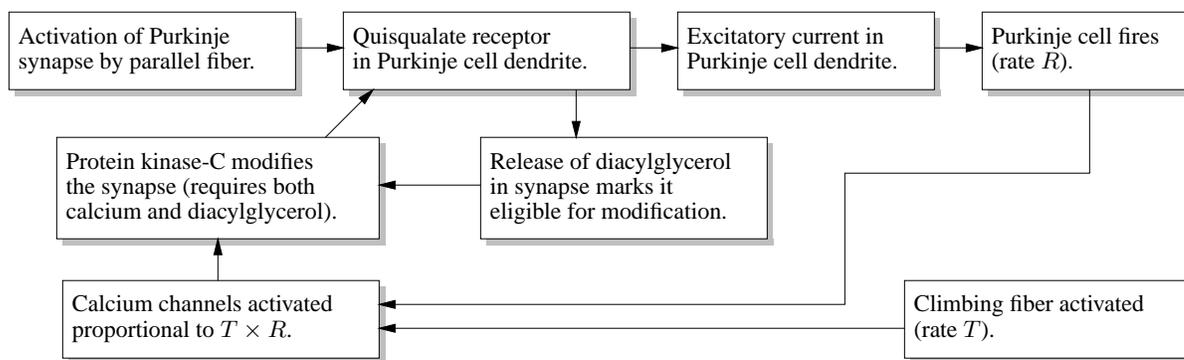


Figure 2.15: The biochemical process by which Purkinje cell synapses are trained (from [86]).

It is possible that the “command” inputs from the motor cortex are also ANDed with the other cerebellar inputs to allow the motor cortex to select different motor commands or motor programs.

2.7.3 Cerebellar cortex: Training

The purpose of cerebellar training is to correct mismatches between intended movements and the results achieved. The synapses of Purkinje cells undergo classical conditioning via a variant of the Hebbian learning mechanism. The parallel fibers transmit the conditioned stimulus, and the climbing fibers transmit the unconditioned stimulus. The climbing fibers have strong synapses on to the Purkinje cells, i.e. they are easily able to trigger a response. Climbing fiber signals convey information about unexpected events, or alternatively they have the meaning “do more (or less) of this in the future”. For example, if a limb bumps into an unexpected obstacle during a motion, climbing fiber signals will be generated to move the limb away from the obstacle. Climbing fiber signals come (though the inferior olive) from various brain stem nuclei which determine when a movement has not been executed successfully.

When a climbing fiber signal arrives, only those Purkinje cell synapses that were active during the movement will be modified. Thus for similar movements in the future (where similar groups of granule cells are active) the correct response will be *anticipated* by the cerebellum. In this way the correct reflex modulation for a particular movement is learnt.

Figure 2.15 shows some of the biochemical details of the hebbian learning mechanism (from [86]). The important point to note is that when a Purkinje synapse is activated by a parallel fiber a chemical trace (diacylglycerol) is released to mark that synapse eligible for modification. When the climbing fiber is activated and the Purkinje cell fires, only the eligible synapses are modified. The chemical trace dissipates each time the climbing fiber fires. Even when there is no training signal the climbing fiber still fires approximately once per second. Note that synaptic modification does not occur if the Purkinje cell fires without a climbing fiber signal, because then the calcium channel activation will not occur.

This behavior is copied in the model of figure 2.14, except for one difference: the training signal only modifies the synapses, it does not activate the Purkinje cell. The effect of synapse eligibility is represented in the block labeled “memory”, and the weight value is accumulated in the integrator block (\int_0^t).

Note that other studies [88] have suggested that synaptic plasticity occurs in the granule cell synapses. This is not a widely held belief but it has been used in some computational studies as a mechanism for the self-organization of the granule cell layer [46].

2.8 Motor cortex

The highest levels of the motor control hierarchy are the motor areas of the cerebral cortex. The mechanisms used by the cortex are not very well understood, but its role can be illustrated by the behavior that results from its absence. For example, removal of the cerebral cortex in cats impairs only certain types of motor function [40]. It does not interfere with the animal's ability to walk, eat, fight, and avoid obstacles in its path—these are all functions controlled at a lower level. But the animal lacks purposefulness in its movement, and it will sit very still for hours at a time. Thus the cerebral cortex adds a voluntary component to behaviors that would otherwise only be elicited by specific stimuli.

In general, the higher (evolutionarily speaking) an animal is, the more the higher levels of motor control subsume the functions of the lower levels. This is called the process of “encephalization”. For example, decortication of the cat leaves it still able to respond adequately to its environment, but decortication of man causes a complete loss of all purposeful motion. This is because in the human brain the lower levels *rely* more on commands descending from the higher levels.

The *primary motor cortex* is divided into areas specific to different body parts, proportional to the amount of dexterity required in each (so the hands and face get more cortex area than the legs or feet). These areas receive input from the sensory cortex and directly from spinal cord sensors corresponding to the body part. Many of the outputs go directly to the spinal cord. This allows the motor cortex to control fine movements, which is especially useful for the hands of primates. Groups of cortical neurons within each functional region can initiate a movement of a related group of muscles to move a limb to a fixed point in space. Any one group of neurons is only active for some behaviors and not others (for example, picking up a cup of coffee but not juggling a ball), even though the behaviors may involve the same muscles. Thus the primary motor cortex is said to perform selection of motor programs.

The *pre-motor cortex* is tightly interwoven with the primary motor cortex. It is involved in the detailed planning of sequences of movements. Neurons in this area become active several hundred milliseconds before a complex movement takes place.

2.9 Biological realism

Many existing robots and automatons are biologically realistic (or biologically inspired) in some way. This is sometimes because researchers want an injection of new ideas into their designs, and sometimes because they want to model biological systems to help understand them better. For example, in [32] the body and spinal cord of the Lamprey (an eel-like fish) were simulated. It was shown that the coupled oscillators in the spinal cord could (in conjunction with sensory feedback) produce the correctly timed muscle contractions necessary for swimming. Other Lamprey studies [90, 91] explored brain stem control models and learning schemes to acquire the appropriate CPG parameters for correct swimming. Other examples are [31] and [11] which model insect walking in a neural network simulation which controls a six legged robot. Realistic inter-leg coordination mechanisms are used and it is shown that interactions between the controlling network, the robot and the environment are important.

There have been many studies of legged locomotion driven by networks of coupled oscillators. For example, [120] investigates a simple network of six neural oscillators for driving biped locomotion. With careful adjustment of the coupling parameters, simulated gaits (walking and running) can be produced on an idealized 2D mechanical model. [26] shows how CPGs made up of coupled oscillators can produce outputs for quadrupedal gaits (walking, trotting and bounding). A driving signal can be varied to generate transitions between the different gaits. [27] uses six phase-locked oscillators to drive the legs of a hexapod robot. It is shown how transitions between gaits are actually symmetry breaking bifurcations

in the coupled system dynamics. [66] has used genetic algorithms to synthesize gait-producing pattern generators in a hexapod robot.

Several groups have attempted to model the brain at a much higher level. For example, [46] describes a quasi-realistic cerebellum model used to control a robot manipulator. It contains a self organizing granule cell layer and a Purkinje layer which uses Hebb learning rules. The “Darwin” system [105] is an ambitious attempt to create a complete artificial brain for various automatons. Based on Edelman’s theory of neuronal group selection, it has realistic cell and synaptic modification dynamics, and various realistic sensory and motor systems. The Darwin-III system contains 50 interconnected networks with some 50,000 cells and 620,000 synaptic junctions.

Many authors have created design paradigms based on biological principles. Crawford [30, 29] suggests a hierarchical controller using radial basis function networks for systems with many degrees of freedom, made up of a network of the simple single-joint controllers. This approach was used to control a simulated human platform diver. Altman [4] presents a distributed decision making model for insects, based on a neural equivalent of Brooks’ subsumption architecture model. Kalveram [57] suggests that robot arm movements can be controlled by CPGs and reflex-like processes which allow high level centers to specify only the kinematics (not the dynamics) of movement. Hallam [41] gives a neuroethological approach for controlling a mobile robot using a neural network with quasi-realistic synapse modification.

2.10 Conclusion

The basic principles of neural control have been described, and it has been shown that the brain is a complex neural machine with many specialized components. The most fundamental behaviors are implemented by the spinal cord. These include the stretch reflex and its associated reflexes, which act as a servo mechanism to regulate muscle length. A model of this servo mechanism is used to achieve low level robot joint control in Chapter 7.

At a higher level the brain stem implements more complex behaviors, which operate through modulation of the lower levels. This “modulation principle” has been found by the author and others to be a useful guideline when designing intelligent controllers.

The cerebellum is the major adaptive component for learned motor behavior. The CMAC, which is described in the next chapter, is based on the cerebellar model of figure 2.14, although biological modeling is sacrificed to engineering implementation details to achieve a practical neural network. The FOX controller, described in Chapter 5, is an even better cerebellar model as its weights have associated eligibility values which are similar (in some respects) to the chemical eligibility trace of the cerebellar Purkinje cells.

