Chapter 2

The Neuroscience of Behavior

Consider a reaction vessel in which water, nitrogen and carbon dioxide are exposed to an energy flux from an energetic source to a "cold" energy sink. The molecules near the high energy region of the reactive vessel will tend to ionize, while the region near the "cold," low energy sink will tend to precipitate a large variety of complex molecular organizations of the constituent atoms. This process is in fact competitive, where the energy disparity in the reaction vessel explores the combinatoric possibilities and the most stable molecules win. In a famous experiment, Urey and Miller (1953) demonstrated that the earth's raw materials (primordial soup) together with constant electrical discharge, could have spontaneously produced the complex molecules that are the precursors of amino acids! The striking thing about these particular molecules is that they catalyze a sequence of chemical bonding reactions that end up replicating the original molecule. In a competitive chemical reaction, the advantage was dramatically skewed toward these replicating molecules, and this stable organization or "species" was further promoted by reactions which buffered the replicating molecules from competing, destructive reactions. It is possible that when these higher forms of "life" exceeded a threshold density, that it was possible to explore symbiotic, inter-species relationships. Lynn Margulis has postulated that a symbiosis between an anaerobic bacteria (which produced oxygen as a waste product) and an ancestor of mitochondria (which metabolizes oxygen to produce energy) generated a new form of so-called "cellular" organization [15]. The result was an *organism* with a hardened exterior membrane for protection and mechanisms for metabolizing selectively absorbed outside material into its internal structure, all surrounding a nucleus which encoded all the information necessary to build an exact replica of itself.

Somewhere around a billion years ago, aggregates of specialized cells began to organize multicelled organisms. The specialization permitted the construction of tougher outer membranes, sensory structures to warn of complex, multicelled enemies, and motor elements that could be used to elude these enemies. But in order for this colony of symbiotic cells to compose these functions, there had to be a means of intercellular communication. Chemical communication (the transfer of information was accomplished via the secretion of chemical substances) is used by the endocrine system to regulate certain aspects of the human body. Another form of intercellular communication depends on the small accumulation of charge (or *polarization*) on the outer membrane of the cell. A suitable stimulus can cause a depolarization of the cell membrane which can propagate from cell to cell along pathways of connecting cell membranes. Some cells specialized further to depolarize in response to pressure, some to temperature, some signaled incoming electromagnetic energy of specific wavelengths, others measured mechanical strain (or the degree of stretch) in the organism, still others responded to these electrical signals by contracting vigorously.

2.1 The Evolution of the Central Nervous System (CNS)

All vertebrates share a common architecture in the most ancient element of our nervous system. An elongated central *ganglion* (cluster of cells) receives afferents (inputs) from dorsal, somatosensory processes and produces efferents (output) via ventral, motor processes (Figure 2.1). The somatosensory fibers bring information about external stimuli, muscle traction, and tensions in tendons and ligaments to the cord, and the motor fibers conduct stimuli back out to the muscles. A reflex, realized as a mapping from sensory inputs to motor outputs, manages the complex synergy of cell types to produce an observable behavior in the organism.

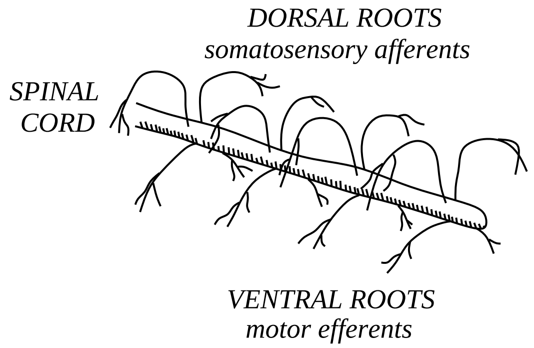

Figure 2.1 *The Afferents/Efferents of the Spinal Cord.*

In time, a dense region of specialized cells began to form at one end of the ganglion. This *brain stem* is organized into the hindbrain, the midbrain, and the forebrain. The specialized structure of the brain stem is also called the *animal* brain (see Figure 2.2) and is present in the brain of contemporary humans. The forebrain was used to process olfactory information; the midbrain processed visual and auditory information; and the hindbrain managed the increasingly complex motor systems. In more advanced animals, the forebrain developed into the largest structure and performed the bulk of early sensory processing (see the Reptilian Brain in Figure 2.2). The mammalian brain displayed further differentiation and specialization. The cerebellum developed in order to manage the increasingly agile mammalian body in an ever increasing repertoire of interactions with a dynamic environment. The cerebral cortex, became a powerful architecture for interpreting and integrating rich sensory systems and for initiating motor behavior.

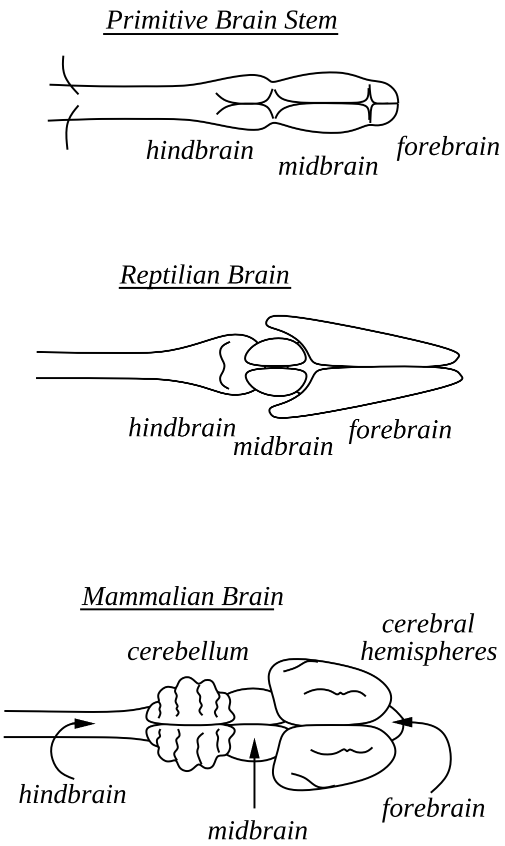

Figure 2.2 *The Evolution of the Mammalian Brain.*

The resulting behavior of the organism became more purposeful — responding to longer term objectives rather than simply responding to immediate stimuli. This developmental trend continued through the early mammals, through the primates, and into the human species (Figure 2.3). Here, the tissue devoted to the cerebral cortex and the cerebellum dramatically overwhelm the underlying animal brain. The value of the increasing information processing capability is significant — justifying the expenditure of up to 20% of a humans resting metabolism.

2.2 The Neuron

The purely reactive motor responses generated by the primitive spinal cord are insufficient for an organism to respond in a *proactive* manner. Local transformations from input stimuli to motor signals (reflexes) do not capture the global properties of survival in a complex environment. In order to improve the prospects of survival, the organism must begin to exploit the utility of additional information in order to further resolve danger and opportunity.

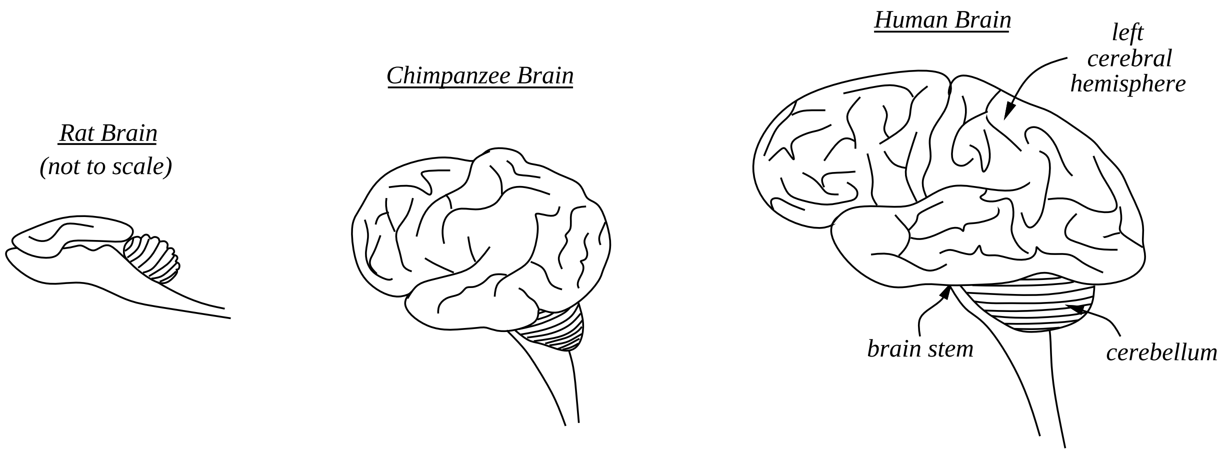

Figure 2.3 *The Evolution of the Human Brain.*

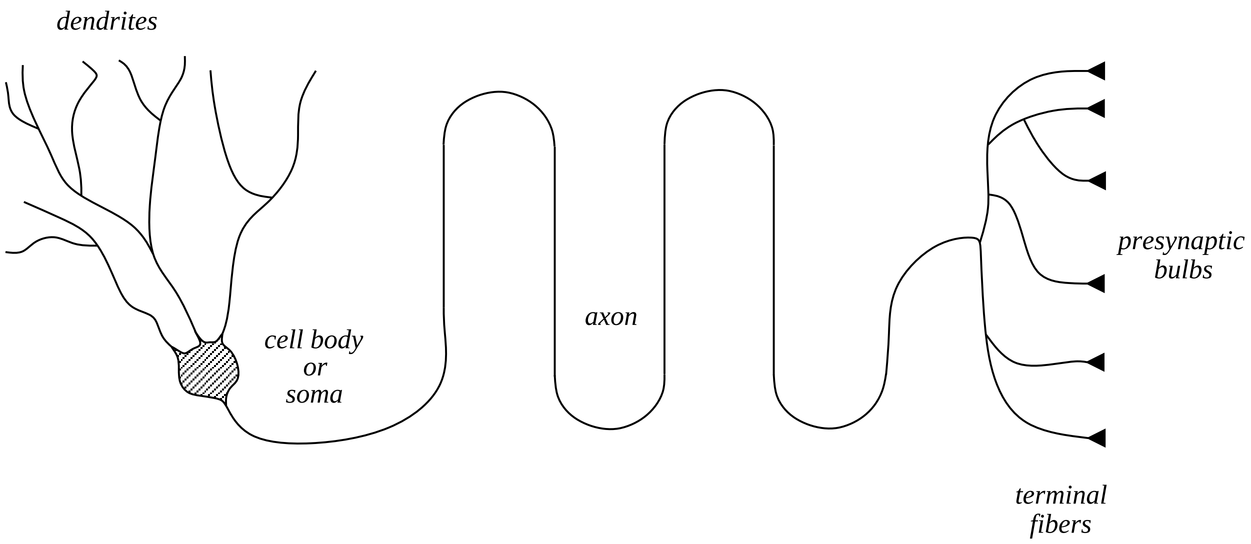

Figure 2.4 *The Neuron: A Single Element of the Electrical Network.*

The cell responsible for activating a particular muscle fiber can make a better decision about when to depolarize if it considers the collective information derived from many sensory cells.

This is possible if the cellular membrane can be brought into contact with a large number of information bearing cells. The mechanism for electrical communication between cells has developed so as to optimize the utility of information.

2.2.1 Structure

Figure 2.4 illustrates how the originally compact cell body has adapted in order to collect more information from its neighbors and how it may in turn distribute its output across many neighbors as well. The so-called *multipolar* neuron illustrated in Figure 2.4 has developed a tree-like structure of *dendrites* for input, and a single *axon* for output. Its structure reflects what appears to be its principle function: the processing of multiple signals from other neurons. The axons of many other neurons make contact with the dendrites of a given neuron, or with the cell body itself. These connections are called *synapses* and collectively, they permit the events across a set of cells to affect the activity of another cell.

The cell membrane contains a very non-uniform distribution of ion pumps. The sodium-potassium pumps exchange cations, K^+ and Na^+ across a selectively permeable membrane. The cytoplasm inside the cell membrane soaks up the positively charged cations with large organic anions. The membrane is much more permeable to K^+ than to any other species, and the sodium-potassium pump elevates the relative concentration of potassium across the semi-permeable membrane. Therefore without stimulation, the selective behavior of the cell membrane generates a concentration gradient in potassium by tending to swap Na^+ for K^+. The potassium ion is pushed upward on the concentration gradient by anionic attraction inside the cell. The attraction force is derived from the electrical potential. The rest potential of the cell is the membrane potential for which the K^+ concentration gradient balances the anionic attraction from inside the cell. A nominal neuron will come to equilibrium at about $-70mv$ — the electromotive potential of about $-70mv$ is required to pull K^+ inside the cell against its concentration gradient. The resting cell, therefore, has a negatively charged interior. A neighborhood of cells will interact by affecting changes in the membrane permeability and thereby modulating the membrane potential.

The net transfer of ions per unit time across a cellular membrane is a current that spreads across areas of the cell membrane near a focal site. As this current spreads, it interacts with other such spatially and/or temporally distributed current flows. The result of this interaction can serve to depolarize or hyperpolarize the membrane, the former are said to excite and the latter to inhibit the membrane potential.

A depolarization pulse, or *action potential* is generated by a neuron when its input stimulation exceeds a threshold level (Figure 2.5). Each cell has a *refractory period* which limits the frequency at which it can repolarize and generate another action potential (repolarization takes on the order of $1/100^{th}$ of a second, so these cells can fire at up to 100 Hz). Until that rate limitation is reached, increasing input stimulation levels cause an exponentially increasing output rate. An increasing external stimulus will both enlist a greater number of cells to fire and it will increase the firing rate of each individual cell as well.

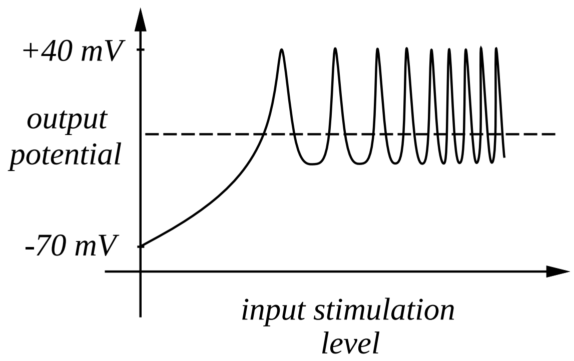

Figure 2.5 *The Electrical Output of a Neuron as a Function of Input Stimulus.*

The mechanisms with which neurons affect other neurons are broadly categorized as electrical and chemical synapes. Electrical synapses occur when current in one cell induces a potential at an adjacent cell (field potential synapse) or when microtubules that transfer Na^+ and K^+ directly between the cytoplasm in neighboring cells (gap junctions). Recently, some theories propose that methods of direct cell-to-cell *electrotonic* couplings have special functional significance in the nervous system.

The chemical synapse is far more prevalent in the CNS. When a depolarization pulse runs down an axon to the presynaptic bulbs, it causes the release of a neurotransmitter into the synapse. The synapse can be either excitatory or inhibitory depending on the specific neurotransmitter present. An inhibitory synapse causes an increase in the membrane potential of the downstream cell. This makes it less likely that this cell will send a depolarization output pulse on its axon. In an excitatory synapse, the downstream cell is depolarized slightly, causing the membrane potential to decrease slightly toward the point where it collapses, generating a depolarization output spike. Since every cell has multiple excitatory and inhibitory inputs, which side wins is a function of the relative numbers of each synapse and their firing rates.

2.2.2 Types of Neurons

The human nervous system can be coarsely divided into two principle components: the Central Nervous System (CNS) and the Peripheral Nervous System (PNS). The CNS consists of the spinal column (composed of the spinal nerves), the brain stem (hindbrain: cranial nerves and cerebellum) the basal ganglia (midbrain), and the two cerebral hemispheres (forebrain). The PNS is responsible for projecting the output signals that activate muscles and for generating sensory signals in response to external stimuli.

The Central Nervous System: Interneurons

The central nervous system is primarily an information processor with afferent and efferent tracts supplying the input and output. The central interneurons come in a wide variety of shapes and sizes that implement different type of input/output transformations. The most common type are multipolar cells similar in structure to Figure 2.4 that have multiple dendritic branches emerging from the cell body. Others have a bipolar structure characterized by a single dendritic input and a single output axon, both of which extend some distance from the cell body and then branch. The degree of dendritic branching varies dramatically. Some regions of the CNS exhibit quite sparse dendritic branching while others (such as the Perkinje cells) have dramatically bushy dendrites. Moreover, the axons of some cells project across the entire brain while others communicate only with their immediate neighborhood in the brain.

The cortex (derived from the latin word for "bark" or the convoluted surface of a tree) exhibits a particularly dense organization of highly interconnected neurons. This structure forms the outer layer of the cerebral hemispheres and is a single large sheet of interneurons. This layer of cells is highly convoluted to maximize the surface area of the layer within the confined volume of the cranium. Most of the computational work of the brain is confined to these areas, the so-called gray matter of the brain. The much larger, internal "white" area of the brain is devoted to metabolic support and contains relatively long axonal projections from one cortical area to another.

The Peripheral Nervous System: Motor and Sensory Neurons

The peripheral nervous system is composed of the specialized cells which generate the input/output signals. Primary motor neurons are found almost exclusively in the spinal cord. This type of cell projects axons directly onto a muscle cell. The axons of these cells must be quite long at times to connect the spinal cord to peripheral muscles.

A variety of specialized cells have developed in order to measure the state of our musculoskeletal system (proprioceptive sensors) and external stimuli. Some of the cells which project onto the somatosensory cortex are presented in Figure 2.6.

Internal Receptors: Motor control in humans involves control of antagonistic muscle groups which allows the stiffness of each joint to be modulated. The control of these muscle groups requires the acquisition of sensory data which describe both positions and forces. Internal receptors contribute to the sensing of the relative position of the parts of the body, a sense termed proprioception. Four receptors of this type are described below [7, 12].

- Neuromuscular spindles sense the degree of stretch in the muscle fiber. These receptors are to some degree responsible for the reflexive cohesion of the skeleton and provide precise movement control. They come in two varieties: one responds to high frequencies and another responds to low frequencies and DC traction.

- The Golgi tendon organ exhibits a very slow response and contributes to the control of muscular tension by measuring the degree of stretch of the muscle fiber at the tendon-muscle interface.

- The Articular surfaces in the joints of the body produce signals proportional to extreme position, velocity, or ligament tension. These receptors are not analogous to continuous potentiometers, but provide feedback for extreme movement of the joint.

- Ruffini corpuscles are reported to function as thermal receptors and to contribute to the sensing of kinematic forces and accelerations.

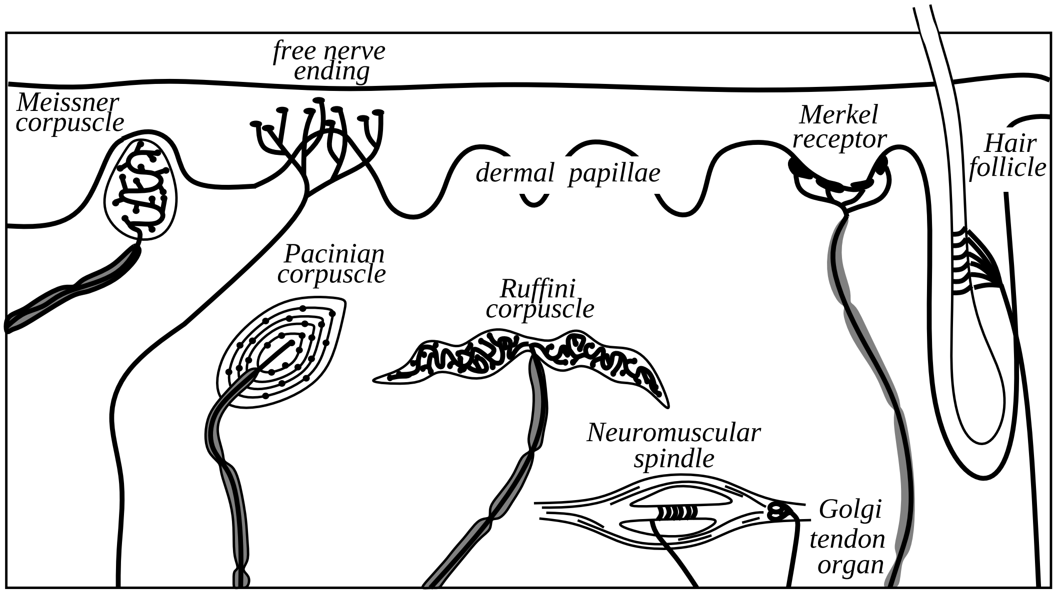

Figure 2.6 *Some of the Sensory Neurons that Project onto the Somatosensory Cortex*

Epidermal Receptors: These receptors, located in the outermost layer of the skin, are distinguished from those above in that they respond to external stimuli. Epidermal receptors provide the most direct indication of general mechanical interactions between the skin surface and an external object. The sensors in the epidermis are characterized by two types of receptors.

- Merkel disks are sensory receptors with a large bandwidth which can respond to both compression and shear stimuli.

- Free Ended Nerve Fibers consist simply of nerve fibers with free endings which respond to a variety of stimuli, including temperature and pain. These receptors are classified by their diameter, conduction speed, sensitivity or threshold level, and the presence or absence of a myelin sheath. The performance of these sensors is proportional to the diameter of the nerve fiber. As the diameter increases, the threshold stimulation decreases, the amplitude of output signal increases, the duration of each signal impulse increases, and the velocity of the signal increases. The presence of a myelin sheath induces a somewhat different conduction path in the nerve fiber which increases the velocity of propagation. The types prevalent in the epidermis are the so-called A and C type free ended receptors. Type A has a relatively large diameter and is myelinated while type C is smaller, more numerous and unmyelinated.

frequency response	0 to 400 Hz (+ very high freq)
response range	0 to 100 $grams/mm^2$
sensitivity	approx. 0.2 $grams/mm^2$
spatial resolution	1.8 mm
signal propagation	motor neurons 100 m/sec
	sensory neurons 2 to 80 m/sec
	autonomic neurons 0.5 to 15 m/sec

Table 2.1: Sensory Signal Specifications on the Fingertip

The signal output of any one of these epidermal neural receptors consists of a generated potential, which is proportional to the stimulus level. When the generated potential exceeds a threshold value, an action potential is induced. Action potentials form a series of constant amplitude spikes whose frequency is proportional to the level of stimulation. When the threshold value of the receptor is exceeded, the input stimulation is encoded in the frequency domain. The threshold varies from receptor to receptor so that increased stimulation corresponds to more numerous signal responses.

Dermal Receptors: Beneath the epidermal layer of the skin, the dermis incorporates two types of receptors [7]:

- Meissner corpuscles respond to light touch; they are located beneath the convoluted dermal papillary layer. These structures are ovoid with the major axis perpendicular to the skin surface and contain neural fibers running normal to and tangential to the skin surface. The Meissner corpuscles are specialized high frequency transducers.

- Pacinian corpuscles (as distinguished from an intramuscular pacinian type receptor) respond best to accelerating mechanical displacement rather than constant velocity deformation. These sensors are quite sensitive to pressure but are not sensitive to direction, and respond primarily to vibration stimuli.

Properties of the various sensory receptors are commonly described in relative terms. From the perspective of mechanical design, it is instructive to consider the range of values for these parameters. Table 2.1 has been assembled from a variety of sources (see references at end of chapter) and presents some performance specifications for the sensory apparatus in the human hand.

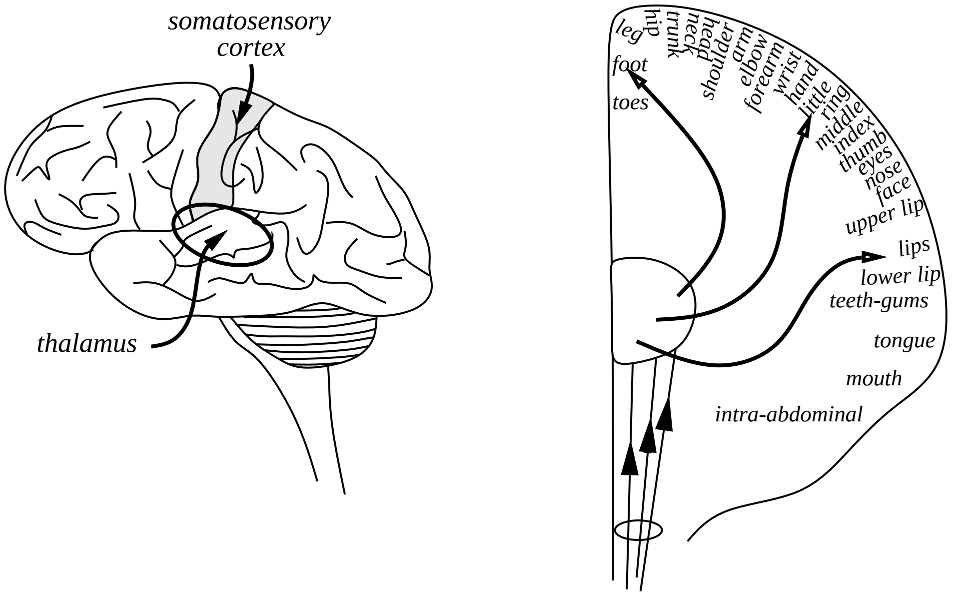

Figure 2.7 *The Sensory Homunculus [adapted from (Kandel and Schwartz 1981)]*

2.3 Sensorimotor Projections in the Brain

2.3.1 The Somatosensory Homunculus

The sensory neurons presented in Section 2.2.2 enter the spinal cord via the dorsal roots (Figure 2.1) where they synapse with the neurons of the cord. From here the information is conducted up the spinal cord to the thalamus (part of the basal ganglia) in the midbrain. The thalamus is thought to have a role in the selection of relevant signals from among the multitude of signals generated by the sensory apparatus. From here the sensory information is projected onto the cerebral hemispheres in a region called the *somatosensory cortex* (Figure 2.7). The somatosensory cortex is a *topographic* map of the body — areas that are adjacent on the body are roughly adjacent on the cortex. Each hemisphere of the cortex maps to the opposite side of the body, that is the left hemisphere contains the sensory map for the right side of the body and vice versa. The relative area of the cortex devoted to various body parts provides some intuition about the relative importance of sensory information from those regions of the body (notice that the hands and digestive tract are over-represented geometrically).

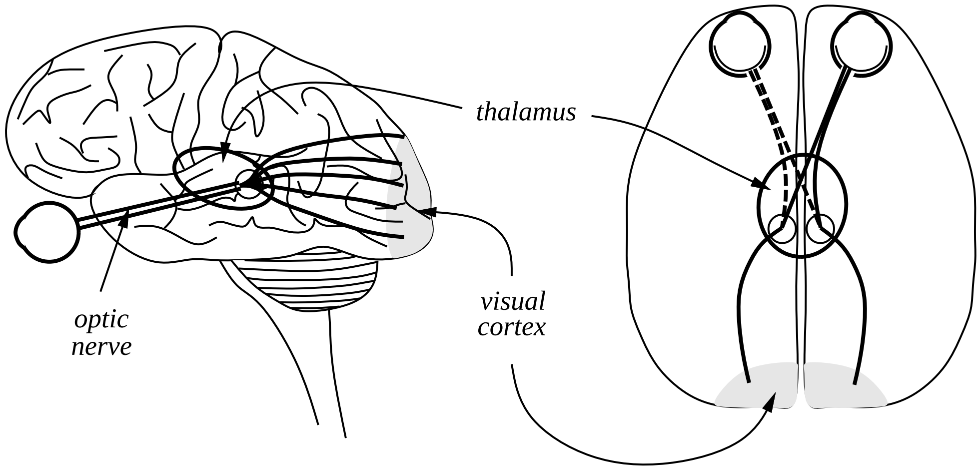

Figure 2.8 *The Visual Cortex*

2.3.2 The Visual Cortex

The rods and cones of the retina project immediately onto an interconnected layer of neurons that preprocess the visual information. These computations are local to relatively small neighborhoods of associated retinal cells. After this preprocessing, the information is passed to elongated ganglion cells which are bundled together and exit the retina as the optic nerve. The optic nerve projects to a cortical nucleus (a region of interconnected cell bodies) at the rear of the thalamus. The cells here also represent a topographic map of the visual field which is distorted in a manner which reflects the relative importance of the visual field. In this case, the fovea or optical center of the retina in over-represented geometrically. From here, visual information is projected onto the visual cortex (Figure 2.8). Populations of cortical and precortical (preprocessor) neurons are highly specialized experts at extracting important kinds of information from a visual scene. Some are proficient at isolating edges (or sharp intensity variations) oriented in certain directions. Others detect motion in the receptive field or are specialized to interpret the disparities between left and right images as depth in the visual scene. Visual processing in the brain provides striking evidence that there exists a hierarchical abstraction of the visual information, up to the level of objects in the scene.

2.3.3 The Motor Cortex

In a similar manner to the somatosensory cortex, the motor cortex is a topographic map of the musculoskeletal system (Figure 2.9). The motor cortex initiates motor commands by projecting

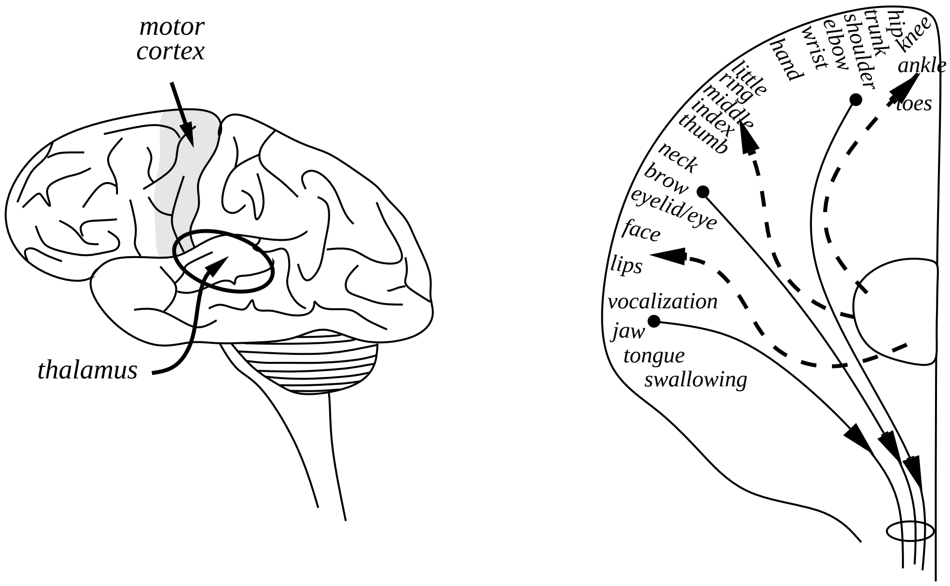

Figure 2.9 *The Motor Cortex*

through the thalamus, into the spinal cord, and eventually to the primary motor neurons which activate muscle cells. This is a major oversimplification however, since the complexity of this projection is enormous. A single voluntary movement actually involves large scale synergies of muscle activity which are sensitive to dynamic and geometric constraints, as well as the context of the task. As a consequence, the motor cortex is highly interconnected with the cerebellum and the basal ganglia and receives reciprocal projections as well. Some of the output generated in the motor cortex does pass almost directly to the spinal cord, such as the fine motions of individual finger movements, but the primary role of the motor cortex appears to be to exert a cognitive and sensory "bias" to lower level motor subsystems. The motor cortex is not, therefore, responsible for motor control but is instead one of the higher centers of motor organization which extends from low level reflex arcs to cognitive, long term plans.

2.4 Internal Signal Flow

The human brain receives signals from its own musculoskeletal system as well as the external environment, and it controls autonomic functions, limb movements, and the environment around it. The macroscopic operation of the brain can be understood as a process of strategically focusing sensory information in the context of the current state and goals of the individual and the mapping of motor responses back out to muscle synergies which are appropriate for the situation — a compression of information coupled to a fanning-out of control.

Figure 2.10 is a very coarse illustration of the information flow from cortical sensory areas. Information moves from the sensory apparatus into the primary cortical-sensory areas where it is continually transformed, passing through the secondary cortical-sensory regions and eventually combined with information from other sources in the so-called association areas of the cortex. These association areas are not well understood. It may be here that our emotions, perseverence and capacity for planning long term action affects the mechanisms we possess for manipulating the environment. The model of brain function that this discussion supports is not one in which modular sensory systems interpret the world and transmit its salient features to a modular motor controller, but rather one in which information derived from the environment (and memories of information gathered in the past) interacts in a highly coupled manner with a dramatically flexible mechanism for altering the state of the internal and external environment. It is clear from this model that an abstraction hierarchy is present which influences how information is gathered and its relative importance in the current and future circumstances, and which also influences how motor actions are selected to achieve immediate and long term goals. The brain may be viewed as a dynamic resource allocator, which determines how to enlist both the computational and mechanical resources at its disposal to solve problems in an environment.

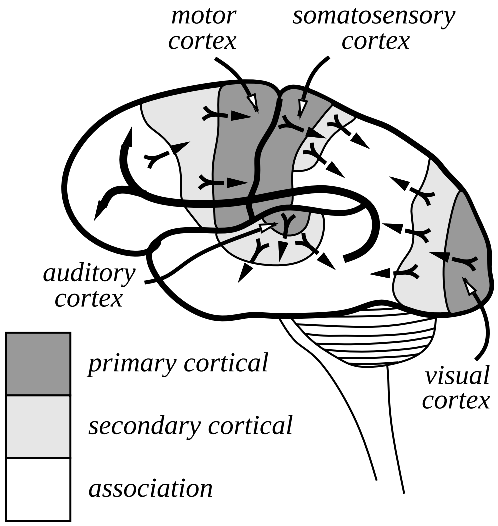

Figure 2.10 *The Flow of Information and Control from Sensory to Motor Areas of the Brain*