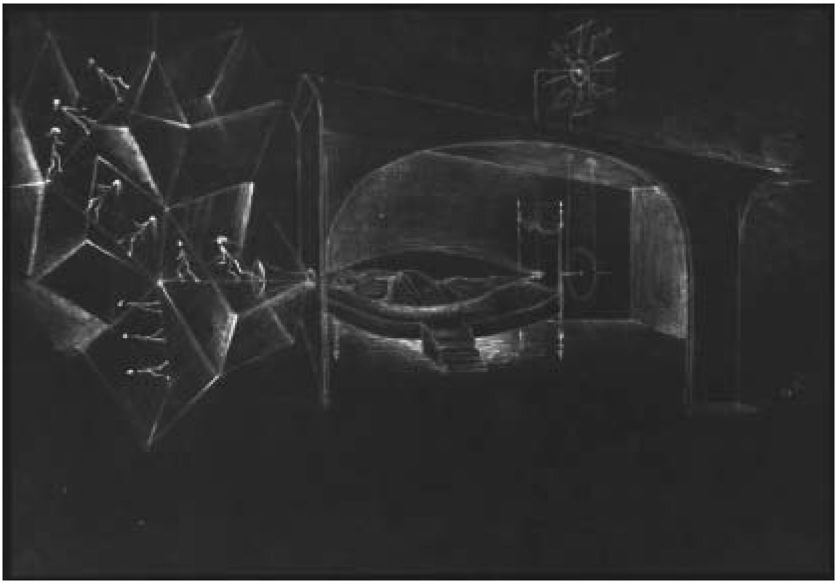
Motor Primacy and the Organization of Neuronal Networks: Thinking as Internalized Movement

A fundamental first step in exploring the nature of mind, from a scientific point of view, is to reject the premise that the mind appeared suddenly as a result of spectacular intervention. The nature of mind must be understood on the basis of its origin, the process of its becoming, by the biological mechanism of trial and error endlessly at work. The mind, or what I shall refer to as the "mindness state," is the product of evolutionary processes that have occurred in the brain as actively moving creatures developed from the primitive to the highly evolved. Therefore, a true examination of the scientific basis for mindness requires a rigorous evolutionary perspective, as it is through this process that mindness came to be. How the mind came to us (or we to it, as we shall see) is a rich and beautiful story that is over 700 million years old—and, like all things biological, is still being written.

A prerequisite for grasping the nature of mind is, first and foremost, the appropriate perspective. Just as Western society, steeped in dualistic thinking, must re-orient in order to grasp the elemental tenets of nondualistic philosophy, so there must be a fundamental reorientation of perspective in order to approach the neurobiological nature of mind. An attempt at such reorienting was the task in the American Alumni Lectures at St. Andrews; this book will proceed in that vein.

Charles Sherrington, in his Gifford Lectures at Edinburgh in 1937, entitled *Man on his Nature* (1941, chapter 12), hinted at the possibility that if human beings ever came face to face with their true natures that knowledge might trigger the demise of human civilization. To him, evidently, humans prefer to consider themselves the lowest of angels rather than the highest of beasts. I am of the opinion that if we were to comprehend fully the awesome nature of mindness, we would, in fact, respect and admire each other all the more.



R. Vario, *Sueño,* 1958. Pencil/paper, 23 × 16 cm.

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Setting Mind to Mind

Mindness, Global Function Brain States, and Sensorimotor Images

There are some basic guidelines to be considered when taking a scientific approach to the mind. Because this book is not supposed to be a detective story, let me offer some demarcating/clarifying definitions of the mind or "mindness state" that will be used here. From my monist's perspective, the brain and the mind are inseparable events. Moreover, the mind, or mindness state, is but one of several global functional states generated by the brain. Mind or the mindness state, is that class of all functional brain states in which sensorimotor images, including self-awareness, are generated. When using the term sensorimotor image, I mean something more than visual imagery. I refer to the conjunction or binding of all relevant sensory input to produce a discreet functional state that ultimately may result in action. For instance, imagine that you have an itch on your back, at a place that you cannot see but which generates an internal "image" giving you a location within the complex geography of your body as well as an attitude to take: SCRATCH! That is a sensorimotor image. The generation of a sensorimotor image is not a simple input/output response, or a reflex, because it occurs within the context of what the animal is presently doing. For obvious reasons, a dog wouldn't want to scratch with one leg while another one is up in the air. So, context is as important as content in the generation of sensorimotor images and premotor formulation.

There are other states that occupy the same space in the brain mass but which may not support awareness. These include being asleep, being drugged or anesthetized, or having a grand mal epileptic seizure. When one's brain is in these states, consciousness is lost; all memories and feelings melt into nothingness; yet the brain continues to function, requiring its normal supply of oxygen and nutrients. During these states, the brain does not generate awareness of any kind, not even of one's own existence (self-awareness). It does not generate our worries, our hopes, or our fears—all is oblivion.

By contrast, I consider the global brain state known as dreaming to be a cognitive state, but not with respect to co-existing external reality because it is not directly modulated by one's senses (Llinás & Pare 1991). Rather, this state draws from the past experiences stored in our brain or from the intrinsic workings of the brain itself. Yet another global brain state would be that known as "lucid dreaming" (LaBerge & Rheingold 1990), where one is actually aware that one is dreaming.

In short then, the brain is more than the one and a half liters of inert grayish matter occasionally seen pickled in a jar atop some dusty laboratory shelf. One should think of the brain as a living entity that generates well-defined electrical activity. This activity could be described perhaps as "self-controlled" electrical storms, or what Charles Sherrington (1941, p. 225), one of the pioneers of neuroscience, refers to as the "enchanted loom." In the wider context of neuronal networks, this activity is the mind.

This mind is co-dimensional with the brain; it occupies all of the brain's nooks and crannies. But as with an electrical storm, the mind does not represent at any given time all possible storms, only those isomorphic with (re-enacting, a transformed recreation of) *the state of the local surrounding world as we observe it* when we are awake. When dreaming, as we are released from the tyranny of our sensory input, the system generates intrinsic storms that create "possible" worlds—perhaps—very much as we do when we think.

Living brains and their electrical storms are descriptors for different aspects of the same thing, namely neuronal function. These days, one hears metaphors for central nervous system function that are derived from the world of computers, such as "the brain is hardware and the mind, software" (see discussion by Block 1995). I think this type of language usage is totally misleading. In the working brain, the "hardware" and the "software" are intertwined in the functional units, the neurons themselves. Neurons are both "the early bird" *and* "the worm," because mindness coincides with functional brain states.

Before returning to our discussion of mindness, think about the itch on your back again, and in particular the moment of the sensorimotor image—before you put into action the motor event of scratching the itch. Can you recognize the sense of future inherent to sensorimotor images, the pulling toward the action to be performed? This is very important, and a very old part of mindness. From the earliest dawning of biological evolution it was this governing, this leading, this pulling by predictive drive, *intention,* that brought sensorimotor images—indeed, the mind itself—to us in the first place.

Let us shore up the discussion with a bit more precision. I propose that this mindness state, which may or may not represent external reality (the latter as with imagining or dreaming), has evolved as a goal-oriented device that implements predictive/intentional interactions between a living organism and its environment. Such transactions, to be successful, require an inherited, prewired instrument that generates an internal image of the external world that can then be compared with sensory-transduced information from the external environment. All of this must be supported in real time. The functional comparison of internally generated sensorimotor images with real-time sensory information from an organism's immediate environment is known as perception. Underlying the workings of perception is prediction, that is, the useful expectation of events yet to come. Prediction, with its goal-oriented essence, so very different from reflex, is the very core of brain function.

Why Is Mindness So Mysterious?

Why is mindness so mysterious to us? Why has it always been this way? The processes that generate such states as thinking, consciousness, and dreaming are foreign to us, I fancy, because they always seem to be generated with no apparent relation to the external world. They seem impalpably internal.

At New York University School of Medicine, in a lecture in honor of the late Professor Homer Smith, entitled, "Unity of Organic Design: From Goethe and Geoffrey Chaucer to Homology of Homeotic Complexes in Anthropods and Vertebrates," Stephen J. Gould mentioned the well-known evolutionary hypothesis that we vertebrates may be regarded as crustaceans turned inside out. We are endoskeletal, with an internal skeleton; crustaceans are exoskeletal, with an external skeleton.

This idea led me to consider what would have happened if we had remained exoskeletal? If we had an external skeleton, the concept of how movement is generated might be just as incomprehensible to us as is the concept of thinking or mindness. Having an internal skeleton means that we become quite aware of our muscles from birth. We can see their movement and feel their contractions and clearly understand, in a very intimate way, their relation to the movement of our different body parts. Unfortunately, we do not have such direct knowledge concerning the workings of our brain. Why not? Because from a cerebral mass point of view, we are crustaceans—our brains and spinal cord are covered by exoskeleton! (figure 1.1).

If we could observe or feel the brain at work, it would be immediately obvious that neuronal function is as related to how we see, interpret, and react, as muscle contractions are related to the movements we make. As for our crustacean friends, who lack the luxury of direct knowledge of the relationship of muscle contraction to movement, their movement ability, if they could consider it, *might* seem as inexplicable to them as thinking or mindness is to us. The essential point is that we do understand about muscles and tendons; in fact, we revel in them. We go so far as to hold world competitions for the comparison of symmetrically hypertrophied muscle mass produced by obsessively "pumping iron" (and occasionally popping steroids), even though, as physical strength for size

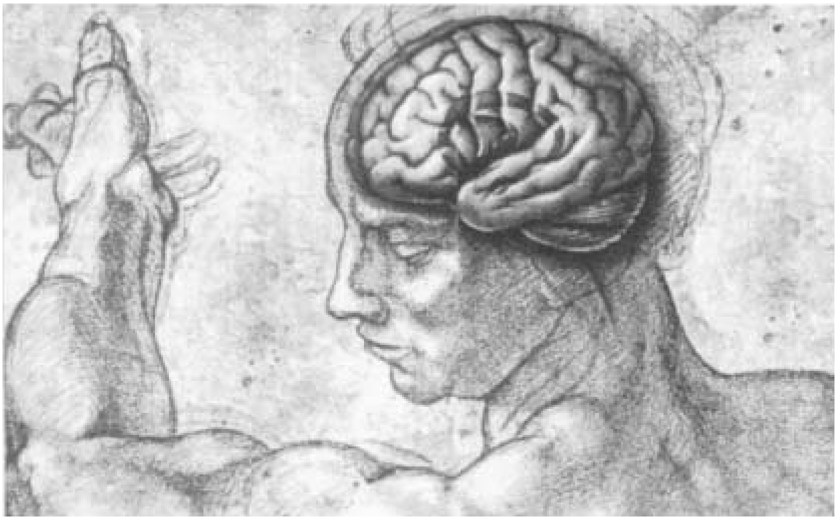


Figure 1.1
Detail showing the upper body and head from a life drawing by Leonardo da Vinci, with an image of the brain superimposed.

goes in the animal kingdom, we are way down near the bottom of the heap. The more analytically probing among us employ measuring tapes, scales, and force transducers in an effort to describe the properties of these precious organs of movement. However, no such paraphernalia are available for directly assessing the working of the brain (IQ tests not withstanding). Perhaps this is why, in the field of neuroscience, such differing concepts have arisen about how the brain is functionally organized.

The central generation of movement and the generation of mindness are deeply related; they are in fact different parts of the same process. In my view, from its very evolutionary inception mindness is the internalization of movement.

Historical Views of Motor Organization in the Brain

Around the turn of this century, there arose two strong opposing views on the subject of the execution of movement. The first, championed by

William James (1890), viewed the working organization of the central nervous system as fundamentally reflexological. From this perspective the brain is essentially a complex input/output system driven by the momentary demands of the environment. Production of movement must be driven by sensation, and the generation of movement is fundamentally a response to a sensory cue. This basic idea was very influential in the groundbreaking studies of Charles Sherrington and his school (1948). It provided the impetus for the study of central reflexes—their function and how they were organized—and ultimately for the study of central synaptic transmission and neuronal integration. All of these have played crucial roles in present-day neuroscience.

A second influential approach was championed by Graham Brown (1911, 1914, 1915). Brown believed that the spinal cord was not organized reflexologically. He viewed this system as organized on a self-referential basis by central neuronal circuits that provided the drive for the electrical pattern generation required for organized movement. This conclusion was based on his studies of locomotion in deafferented animals, that is, animals in which the pathways bringing sensation from the legs to the spinal cord are severed. Under these conditions animals could still produce an organized gait (Brown 1911). This led Brown to propose that movement, even organized movement, is intrinsically generated in the absence of sensory input. He viewed reflex activity as required only for the modulation of, rather than being the driving force for, the production of gait. So, for example, while locomotion (one step after the other) is organized intrinsically, not requiring input from the external world, sensory input (e.g., a slippery spot on the ground) reflexively resets the rhythm so that we don't fall, but it does not generate walking itself.

Brown went on to propose that locomotion is produced in the spinal cord by reciprocal neuronal activity. In very simplified terms, autonomous neuronal networks on one side of the spinal cord activate the muscles of the limb on the same side while preventing activity by the opposite limb. He described this reciprocal organization as "half-paired centers" (Brown 1914), as their mutual interaction generated the left/right limb pacing that is locomotion (see figure 2.5, below).

In this context, the function of the sensory input giving rise to reflex activity during locomotion is there to modulate the ongoing activity of the spinal cord motor network in order to adapt the activity (the output signal) to the irregularities of the terrain over which the animal moves. We now know that such ongoing activity born of the intrinsic electrical activity of neurons in the spinal cord and brain stem forms the basis for both breathing (Feldman et al. 1990) and locomotion (Stein et al. 1986; Cohen 1987; Grillner and Matsushima 1991; Lansner et al. 1998) in vertebrates. A similar dynamic organization, but supported by a quite different anatomical arrangement, is found in invertebrates (Marder 1998). In both vertebrates and invertebrates, the neuronal activity being transmitted and modified between different levels by synaptic connectivity has comparable dynamic properties.

Brown's views remain highly regarded by many of us and have been seminal to our understanding of the intrinsic activity of central neurons (Llinás 1974, 1988; Stein et al. 1984). This conceptual view of spinal cord function may be extended to the workings of the brainstem and areas of higher brain function, such as the thalamus and forebrain—areas where mindness is ultimately generated in our brain.

The Intrinsic Nature of Brain Function

A working hypothesis related to Brown's ideas is that nervous system function may actually operate on its own, intrinsically, and that sensory input modulates rather than informs this intrinsic system (Llinás 1974). Let me hasten to say that being disconnected from sensory input is *not* the normal operational mode of the brain, as we all know from childhood, when first we observed the behavior of a deaf or blind person. But the exact opposite is equally untrue: the brain does not depend on continuous input from the external world to generate perceptions (see *The Last Hippie,* by Oliver Sacks), but only to modulate them contextually. If one accepts this view, it follows that the brain, like the heart, operates as a self-referential, closed system in at least two different senses: one, as something separated from our direct inquiry by implacable bone; and two, as a system that is mostly self-referential, only able to know universals by means of specialized sense organs. Evolution suggests that these sense organs specify internal states that reflect neuronal circuit selection derived from ancestral trial and error. Such circuits become genetically predetermined (for example, we can see color primarily without having to learn to do so). Once we are born, these ancestral circuits (comprising the inherited, functional architecture of the brain) are further enriched by our own experiences as individuals and thus constitute our own particular memories, indeed, our selves.

We can look to the world of neurology for support of the concept that the brain operates as a closed system, a system in which the role of sensory input appears to be weighted more toward the specification of ongoing cognitive states than toward the supply of information—context over content. This is no different than sensory input modulating a pattern of neural activity generated in the spinal cord to produce walking, except that here we are talking of a cognitive state generated by the brain and how sensory input modulates such a state. The principle is the same. For example, prosopagnosia is a condition in which individuals, due to neurological damage, cannot recognize human faces. They can see and recognize the different parts of a face, as well as subtle facial features, but not the face as a whole entity (Damasio et al. 1982; De Renzi and Pellegrino, 1998). Moreover, the people that inhabit the dreams of prosopagnostics are faceless (Llinás and Pare 1991) (we shall return to this issue later in the book).

The significance of sensory cues is expressed mainly by their incorporation into larger, cognitive states or entities. In other words, sensory cues earn representation via their impact upon the pre-existing functional disposition of the brain (Llinás 1974, 1987). This concept, that the significance of incoming sensory information depends on the pre-existing functional disposition of the brain, is a far deeper issue than one gathers at first glance—particularly when we look into questions of the nature of "self."

Intrinsic Electrical Properties of Neurons: Oscillation, Resonance, Rhythmicity, and Coherence

How, then, do central neurons organize and drive bodily movement, create sensorimotor images, and generate our thoughts? Having grown in our knowledge from the days of Brown, we may paraphrase the above question today to read: How do the intrinsic oscillatory properties of central neurons relate to the information-carrying properties of the brain as a whole? Before attempting to answer this question, there are still a few more terms to cover. Let me start by describing what is meant by the intrinsic oscillatory electrical properties of the brain, from a relatively nontechnical point of view. This concept is at the heart of all we shall discuss in this book.

Oscillation

When one thinks of the word “oscillation,” one thinks of a rhythmic back-and-forth event. Pendulums oscillate, as do metronomes; they are periodic oscillators. The sweeping motion of a lamprey’s tail, back and forth, as it swims (Cohen 1987; Grillner and Matsushima 1991) is a wonderful example of an oscillatory movement.

Many of the types of neurons in the nervous system are endowed with particular types of intrinsic electrical activity that imbue them with particular functional properties. Such electrical activity is manifested as variations in the minute voltage across the cell’s enveloping membrane (Llinás 1988). This voltage may oscillate in a manner similar to the traveling, sinusoidal waves that we see as gentle ripples in calm water, and are weakly chaotic (Makarenko and Llinás 1998). As we will see later, this confers a great temporal agility to the system. These oscillations of voltage remain in the local vicinity of the neuron’s body and dendrites, and have frequencies ranging from less than one per second to more than forty per second. On these voltage ripples, and in particular on their crests, much larger electrical events known as action potentials may be evoked; these are powerful and far reaching electrical signals that form the basis for neuron-to-neuron communication. Action potentials are the messages that travel along neuronal axons (conductive fibers that comprise the information pathways of the brain and the peripheral nerves of the body). Upon reaching the target cell, these electrical signals generate small synaptic potentials. Such local changes in the voltage across the membrane of a target cell add or subtract voltage to the intrinsic oscillation of the target cell receiving the signal. Intrinsic oscillatory properties and modifying synaptic potentials are the coinage that a neuron uses to arrive at the generation of its own action potential message, which it will send on to other neurons or to muscle fibers. And so, in the case of muscle, all possible behaviors in us arise from activation of the motor neurons that activate the muscles that ultimately orchestrate our movements. These motor neurons in turn receive messages from other neurons located "up stream" from them (figure 1.2).

The peaks and valleys of the electrical oscillations of neurons can dictate the waxing and waning of a cell's responsiveness to incoming synaptic signals. It may determine at any moment in time whether the cell chooses to "hear" and respond to an incoming electrical signal or ignore it altogether. As will be discussed in more depth in chapter 4, this oscillatory switching of electrical activity is not only very important in neuron-to-neuron communication and whole network function, it is the electrical glue that allows the brain to organize itself functionally and architecturally during development. Indeed, simultaneity of neuronal activity is the most pervasive mode of operation of the brain, and neuronal oscillation provides the means for this simultaneity to occur in a predictable, if not continuous, manner.

Coherence Rhythmicity and Resonance Neurons that display rhythmic oscillatory behavior may entrain to each other via action potentials. The resulting, far-reaching consequence of this is neuronal groups that oscillate in phase—that is, coherently, which supports simultaneity of activity.

Consider the issue of coherence from the perspective of communication, for coherence is what communication rides on. Imagine a soft summer night in a rural setting. Amidst the rich quietude, you hear first one cicada, then another. Soon, there are many chirping. More importantly, they may chirp in rhythmic unison (note that to chirp in unison they must all have a similar internal clock that tells them when to chirp next—such a mechanism is known as an intrinsic oscillator). The first cicada may be calling out to see if there are any kin about. But this unison of many cicadas chirping rhythmically becomes a bonding, literally a conglomerated functional state. In the subtle fluctuations of this rhythmicity comes the transfer of information, at the whole community level, to a vast number of remotely located individuals. Similar events occur in

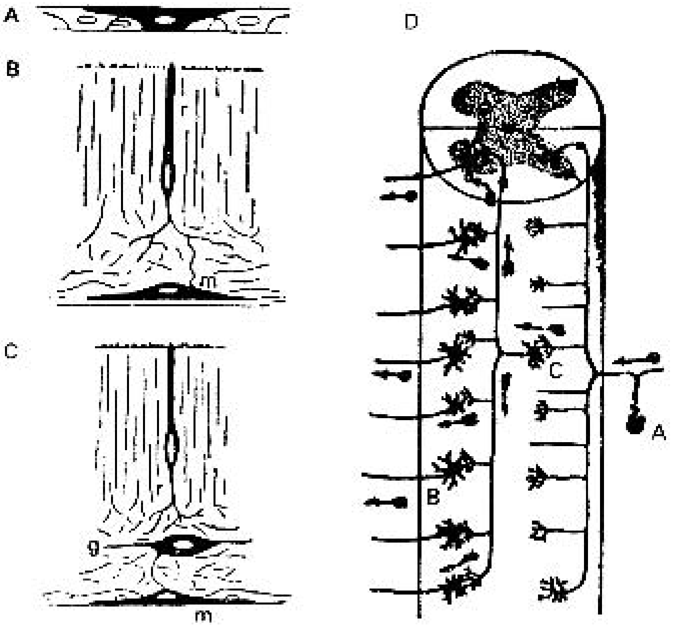


Figure 1.2
Evolution of nervous systems. An interneuron, in the strict sense, is any nerve cell that does not communicate directly with the outside world either as a sensing device (a sensory neuron) or by means of a motor terminal on a muscle (a motor neuron). Interneurons, therefore, receive and send information to other nerve cells exclusively. Their evolution and development represent the basis for the elaboration of the central nervous system. The diagrams above represent stages of development present in early invertebrates. In (*A*), a motile cell (in black) from a primitive organism (a sponge), responds to direct stimulation with a wave of contraction. In (*B*), in more evolved primitive organisms (e.g., the sea anemone), the sensory and contractile functions of the cell in A have been segregated into two elements; "r" is the receptor or sensory cell and "m" is the muscle or contractile element. The sensory cell responds to stimuli and serves as a motor neuron in the sense that it triggers muscle-cell contraction. However, this sensory cell has become specialized so that it is incapable of generating movement (contraction) on its own. Its function at this stage is the reception and transmission of information. In (*C*), a second neuron has been interposed between the sensory element and the muscle (also from a sea anemone). This cell, a motor neuron, serves to activate muscle fibers (m) but responds only to the activation of the sensory cell (r) (Parker 1919). In (*D*), as the evolution of the central nervous system progresses (this example is the vertebrate spinal cord), cells become interposed between the sensory neurons (A) and motor neurons (B). These are the interneurons, which serve to distribute the sensory information (arrow in A) by their many branches (arrows in C) to the motor neurons or to other neurons in the central nervous system. (Adapted from Ramón y Cajal, 1911.)

some types of fireflies, which synchronize their light flash activity and may illuminate trees in a blinking fashion like Christmas tree lights.

This effect of oscillating in phase so that scattered elements may work together as one in an amplified fashion is known as resonance—and neurons do it, too. In fact, a local group of neurons resonating in phase with each other may then resonate with another group of neurons that are quite far from the first group (Llinás 1988; Hutcheon and Yarom 2000). Electrical resonance, a property supported by direct electrical connectivity among cells (as occurs in the heart, allowing it to function as a pump by the simultaneous contraction of all of its component muscle fibers) is perhaps the oldest form of communication among neurons. The delicately detailed nuances of chemical synaptic transmission come later in evolution to enhance and embellish neuronal communication.

Not all neurons resonate at all times. It is the crucial property of neurons to be able to switch in and out of oscillatory modes of electrical activity that allows resonance to occur transiently among differing groups of neurons at different times. If they were not able to do this, they would not be able to represent the ever-changing reality that surrounds us. When differing groups of neurons capable of displaying oscillatory behavior "perceive" or encode different aspects of the same incoming signal, they may join their efforts by resonating in phase with each other. This is known as neuronal oscillatory coherence. Simultaneity of neuronal activity, brought into existence not by chance but by intrinsic oscillatory electrical activity, resonance, and coherence are, as we shall see, at the root of cognition. Indeed, such intrinsic activity forms the very foundation of the notion that there is such a thing called our "selves."

Returning to the original question of intrinsic properties, one may propose the following: that intrinsic electro-responsiveness of the brain's elements, the neurons and the networks they weave together, generate internal representations (connections) that engender functional states. These states are specified in detail, but not in context, by incoming sensory activity. That is, brain function is proposed to have two distinct components. One is the private or "closed" system that we have discussed and that is responsible for qualities such as subjectivity and semantics; the other is an "open" component responsible for sensory-motor transformations dealing with the relations between the private component and the external world (Llinás 1974, 1987). Because the brain operates for the most part as a closed system, it must be regarded as a reality emulator rather than a simple translator.

Acknowledging this, we might go on to say that the intrinsic electrical activity of the brain's elements (its neurons and their complex connectivity) must form an entity, or a functional construct. Furthermore, this entity must efficiently handle the transformation of sensory input arising from the external world into its motor output counterpart. How can we study such a complicated functional construct as this? First we must model it, make some assumptions concerning how the brain may be implementing such transformational properties, and for this we must be very clear about what the brain actually does. If we decide, as a working hypothesis, that this functional brain construct must bestow reality emulating properties, we may then consider what types of models could support such a function.

Let us begin with a simple sensory-motor transformation. The motor aspect is implemented by muscle force (contractile) exercised on bones linked to each other by hinges (joints). In order to study our assumed transformational properties, we may describe the contractile aspect as performing a given movement in space (or in mathematical terms, a vector), and so the set of all muscle contractions contributing to this movement (or any type of behavior) will be enacted in a "vectorial coordinate space." With this approach, the electrical activity patterns that each neuron generates in the formation of a motor pattern, or any other internal pattern in the brain, must be represented in an abstract geometric space. This is the vectorial coordinate space where sensory input and its transformation into a motor output take place (Pellionisz and Llinás 1982). If this sounds a bit like double-talk to you, please read the contents of box 1.1.

How Did the Mind Arise from Evolution?

Let us go back to the very first point made at the beginning of this chapter, that the mind did not just suddenly appear at some point fully formed. With some forethought and a little educated digging, we can find in biological evolution a quite convincing trail of clues as to the brain's

Box 1.1

Abstract Representation of Reality

Let us imagine a cube of electrically conductive material, a gelatin-like substance, held in a spherical glass aquarium. Let's imagine that the surface of the container has small electrical contacts that can allow electricity to pass between one contact and any other through the gelatin. Finally, let's say that the gelatin condenses into thin conductive filaments if current passes between the electrical contacts often, but returns to amorphous gel if no current flows for a while.

If we now pass current among some contacts connected to one or more sensory systems that transform a complex external state (let's say playing soccer) and other contacts related to a motor system, a condensed set of wirelike paths will grow that allows the sensory inputs to activate a motor output. (Keep in mind that these wires do not interact with each other—they are insulated, just as for the most part are the fiber pathways of the brain, and therefore there are no short circuits. These wires can, however, branch to generate a complex connectivity matrix). As we proceed to generate more complex sensory inputs they will in turn generate more complex motor outputs. In short, a jungle of "wires" grows inside the fishbowl, or melts, if stimuli are not repeated for a time. This veritable mess of wires would be the embedding that relates certain sensory inputs (in principle any thing that can be transduced by the senses, what we may call universals) to given motor outputs. As an example, this contraption could be used hypothetically to control a soccer-playing robot (backpropagation algorithms have this general form).

Looking at the fishbowl we can understand that there, somewhere in the complex geometry of wires, are the rules for playing soccer, but in a very different geometry from the playing of soccer itself. One cannot understand by direct inspection that the particular wiring represents such a thing. "Soccer" is being represented in a different geometry from that of soccer in external reality, and in an abstract geometry at that—no legs or referees or soccer balls, only wires. So the system is isomorphic (can enact soccer playing) although not homomorphic with soccer playing (does not look like soccer playing). This is analogous to the tape inside a videocassette, which despite close inspection offers no clues as to the details of the movie embedded in its magnetic code. Here we have a representation of the external world in which intrinsic coordinate systems operate to transform an input (a sensory event) into the appropriate output (a motor response) using the dynamic elements of the sensory organs and motor "plant," the set of all muscles and joints, or their equivalent. This sensory-motor transformation is the core of brain function, that is, what the brain does for a living.

origin. If one agrees that the mind and brain are one, then the evolution of this unique mindness function must certainly have coincided with the evolution of the nervous system itself. It should also be obvious that the forces driving the evolution of the nervous system shaped and determined the emergence of mind as well. The questions to ask here are clear. How and why did the nervous system evolve? What critical choices did nature have to make along the way?

It Began at a Critical Time

The first issue is whether a nervous system is actually necessary for all organized life beyond that of a single cell. The answer is no. Living organisms that do not move actively, including sessile organisms such as plants, have evolved quite successfully without a nervous system. And so we have landed our first clue: a nervous system is only necessary for multicellular creatures (not cell colonies) that can orchestrate and express active movement—a biological property known as "motricity." It is interesting to note that plants, which have well-organized circulatory systems but no hearts, appeared slightly later in evolution than did most primitive animals; it is as if sessile organisms had, in effect, chosen not to have a nervous system. Although this seems a rather strange statement to make, the facts are quite irrefutable—the Venus Flytrap, Mimosa, and other locally moving plants not withstanding.

Where does the story begin? What type of creature can we look to for support of this important connection between the early glimmerings of a nervous system and the actively moving, versus sessile, organism? A good place to begin is with the primitive *Ascidiacea,* tunicates or "sea squirts," which represent a fascinating juncture in our own early chordate (true backbone) ancestry (figure 1.3).

The adult form of this creature is sessile, rooted by its pedicle to a stable object in the sea (figure 1.4, left) (Romer 1969; Millar 1971; Cloney 1982). The sea squirt carries out two basic functions in its life: it feeds by filtering seawater, and it reproduces by budding. The larval form is briefly free-swimming (usually a day or less) and is equipped with a brainlike ganglion containing approximately 300 cells (Romer 1969; Millar 1971; Cloney 1992). This primitive nervous system receives sensory information about the surrounding environment through a statocyst

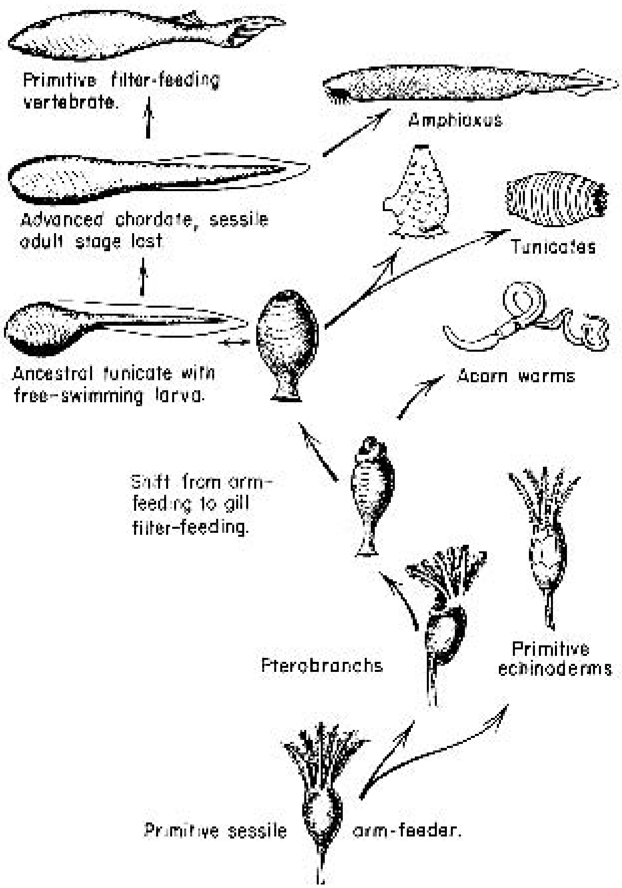


Figure 1.3
A simplified diagram of chordate evolution. The tunicates, or sea squirts (*Ascidiaceae;* see figure 1.4) represents a stage in which the gill apparatus has become highly evolved in the sessile adult, while the larval stage in some species is free-swimming, exhibiting the advanced features of a notochord and nerve cord associated with the motile behavior. See text for more details. (Adapted from Romer, 1969, p. 30.)

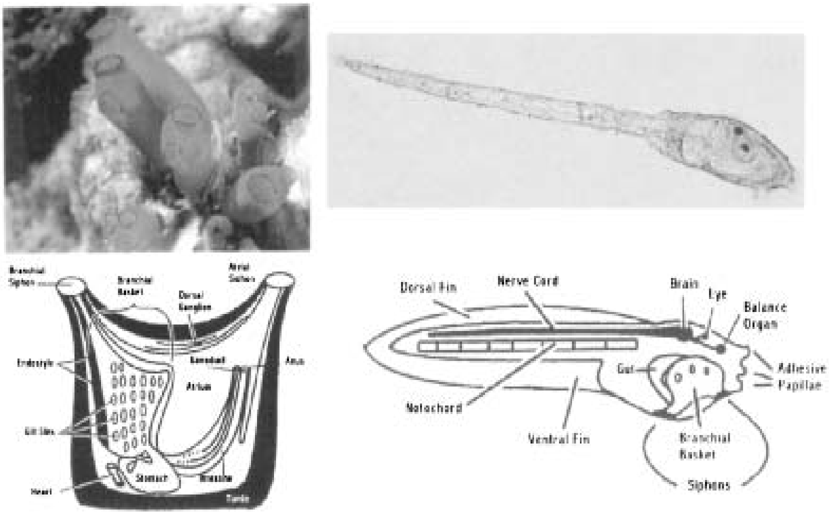
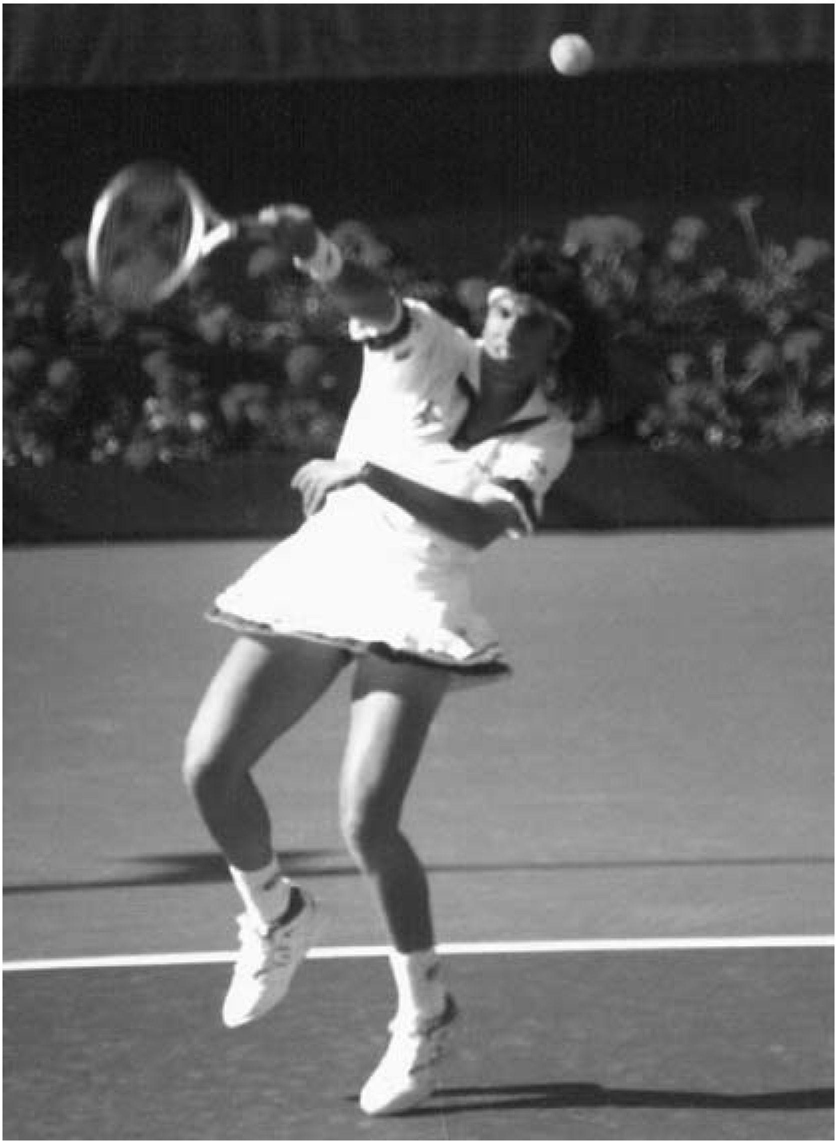


Figure 1.4
Sea squirts (*Ascidiaceae*) or tunicates, which have a sessile, filter-feeding adult stage attached to the substratum (*left*), and in many cases a brief free-swimming larval stage (*right*). (*Bottom left*) Diagram of a generalized adult solitary sea squirt. The black outer portion is its protective "tunic." (*Bottom right*) Diagram of a typical free-swimming sea squirt larva or tadpole. A gut, gills and branchial structure are present, but are neither functional nor open. See text for details. (From website www.animalnetwork.com/fish/aqfm/1997/)

(organ of balance), a rudimentary, light-sensitive patch of skin, and a notochord (primitive spinal cord) (figure 1.4, right). These features allow this tadpole-like creature to handle the vicissitudes of the ever-changing world within which it swims. Upon finding a suitable substrate (Svane and Young 1989; Young 1989; Stoner 1994), the larva proceeds to bury its head into the selected location and becomes sessile once again (Cloney 1982; Svane and Young 1989; Young 1989). Once reattached to a stationary object the larva absorbs—literally digests—most of its own brain, including its notochord. It also digests its tail and tail musculature, thereupon regressing to the rather primitive adult stage: sessile and lacking a true nervous system other than that required for activation of the simple filtering activity (Romer 1969; Millar 1971; Cloney 1982). The lesson here is quite clear: the evolutionary development of a nervous system is an exclusive property of actively moving creatures.

We have now derived a basic concept—namely, that brains are an evolutionary prerequisite for guided movement in primitive animals—and the reason for this becomes obvious. Clearly, active movement is dangerous in the absence of an internal plan subject to sensory modulation. Try walking any distance, even in a well-protected, uncluttered hallway, with your eyes closed. How far can you go before opening your eyes becomes irresistible? The nervous system has evolved to provide a plan, one composed of goal-oriented, mostly short-lived predictions verified by moment-to-moment sensory input. This allows a creature to move actively in a direction according to an internal reckoning—a transient sensorimotor image—of what may be outside. The next question in our pursuit of the evolution of mind should now be clear. How did the nervous system evolve to be able to perform the sophisticated task of prediction?



Tennis pro Gabriella Sabatini returns a shot. Photo reprinted courtesy of Alan Cook, alcook@sprintmail.com, http://alancook.50mpegs.com.

2

Prediction Is the Ultimate Function of the Brain

Why Must the Brain Predict?

In chapter 1, we argued that a nervous system is only necessary for living creatures that move actively. If so, how has a nervous system contributed to their evolutionary success? Clearly, such creatures must move intelligently in order to survive, to procure food and shelter, and to avoid becoming food for someone else. I use the word "intelligently" to imply that a creature must employ a rudimentary strategy, or at the very least rely upon a set of tactical rules regarding the basic properties of the external world through which it moves. Otherwise, movement would be purposeless and necessarily dangerous. The creature must anticipate the outcome of a given movement on the basis of incoming sensory stimuli. A change in its immediate environment must evoke a movement (or lack of it) in response to ensure survival. The capacity to predict the outcome of future events—critical to successful movement—is, most likely, the ultimate and most common of all global brain functions.

Before proceeding, it is important to have a clear sense of what is meant by "prediction." Prediction is a forecast of what is likely to occur. For example, we predict common outcomes—such as walking barefooted on the hot pavement will hurt, or that not turning the car when approaching a dead-end will result in something probably harmful to you and the car. When one runs to hit a tennis ball, one must predict where in time and space the ball and the face of one's racket can successfully meet.

Consider two mountain rams squaring to fight. As they eye one another, they slowly rise onto their hind legs and look for the tiniest of clues that will provide a hint of when the other is about to shift its weight forward and charge. Because even a half-step lead in momentum can change the outcome of the contest, a ram (or any creature for that matter) must be able to anticipate the attack in order to counter strike, that is, it must be able to predict that a blow is coming before it arrives.

The ability to predict is critical in the animal kingdom—a creature's life often depends upon it. Still, the mechanism of prediction is far more ubiquitous in the brain's control of body function than the examples so far described. Consider the simple act of reaching for a carton of milk in the refrigerator. Without giving much focused thought to our action, we must predict the carton's weight, its slipperiness, its degree of fullness, and, finally, the compensatory balance we must apply for a successfully smooth trajectory of the carton to our glass. Once movement is initiated, we adjust our movement and the compensatory balance as we receive direct sensory information coming in. However, before even reaching, we have made a ballpark, premotor prediction of what will be involved.

The brain's ability to predict is not only generated from our awareness of its operation; prediction is a far older evolutionary function than that. Consider this: have you ever found yourself blinking just before a bug lands in your eye? You did not see the bug, at least not on a conscious level, yet you anticipated the event and blinked appropriately to ward off its entry into your eye. Prediction is at the heart of this basic protective mechanism. Prediction, almost continually operative at conscious and reflex levels, is pervasive throughout most, if not all, levels of brain function.

In the beginning of this book, I mentioned that the mindness state, which may or may not necessarily represent external reality, has evolved as a goal-oriented device to guide the interactions between a living organism and its environment. Success in a goal-oriented, moving system is enhanced by an innate mechanism for prediction. Furthermore, we can assume that prediction must be grounded, that there can be only one predictive organ. It would make little sense if the head predicted one thing and the tail another. Predictive functions must be centralized.

Prediction and the Origin of "Self"

Although prediction is localized in the brain, it does not occur at only one site in the brain. These predictive functions must be brought together into a single understanding or construct; otherwise, the end result would be no different than if prediction were grounded in any number of different organs. What pulls these functions together? What is the repository of predictive function? I believe the answer lies in what we call the self: *self is the centralization of prediction.* The self is not born out of the realm of consciousness, only the noticing of it is (i.e., self-awareness). According to this view, the self can exist without awareness of its own existence. Even in we as self-aware individuals, self-awareness is not continuously present. In the middle of a difficult challenge, such as swimming away from a shark, you will try to get to shore and be quite aware of what is happening, but you will probably not be thinking to yourself, "Here I am swimming away from a shark." You will think about it only when you get to shore and safety.

The concept of self-awareness will be discussed in later chapters, but I wanted to point to the issue of self now. Understanding that the brain performs prediction on the basis of an assumed self "entity" will lead us to how the brain generates the mindness state.

Why this predictive ability arose is clear: it is critical to survival, guiding it at the level of both the single animal (moment-to-moment) and the species (in fact, of all actively moving species throughout evolution). How did the ability to predict arise from evolution? The answer can be found with a little thoughtful digging. First, however, we must understand how the nervous system actually performs prediction; once we know that, we will find the answer to how nature evolved this amazing function.

As we will see later in this chapter, for the nervous system to predict, it must perform a rapid comparison of the sensory-referred properties of the external world with a separate internal sensorimotor representation of those properties. For the prediction to be useful, the nervous system must then transform or utilize this premotor solution into finely timed and executed movement. Once a pattern of neural activity acquires internal significance (sensory content gains internal context), the brain generates a strategy of what to do next—another pattern of neural activity. This strategy can be considered an internal representation of what is to come. Such premotor patterns of neural activity must then be transformed into the neuronal activity that sets into motion the appropriate bodily movement: These transformations require an internal representation of what is to come, in order for them to become actualized in the external world context (figure 2.1).

Prediction Saves Time and Effort Prediction is crucial to brain function not only for the successful execution of goal-oriented, active movement, but also as a basic functional operation in order to conserve time and energy. This may sound a bit strange, since the nervous system—particularly the human nervous system—being the most sophisticated and capable "processor" yet known, might be expected to be above such trivial considerations. Nevertheless, when the brain deals with the vicissitudes of the external world (and the internal as well) its activity does not parallel reality in its continuity; it just feels that way to us. In real life the brain operates in a discontinuous manner from a processing perspective. It is not possible to take in all of the information available to our senses from the external world and then arrive at the correct decision quickly in a continuous fashion. Neurons are fast, but they are not that fast. Note, I am still only speaking of the premotor phase of processing. Remember that a successful interaction with the external world also necessitates the subsequent timely execution of the brain's given decision through movement.

It seems that the brain must compartmentalize incoming information and implement its attention on a need to know basis in order to fuel its momentary decision-making ability without overloading. The brain must leave itself enough time to implement a movement decision so that it remains in step with what is happening in the external world at a given moment. It must also be able to skip to the next moment's need for processing without being encumbered by the previous moment's processing. In other words, the brain cannot be stuck doing one thing when it needs to move on to the next task. This mode of operation derives from what is known as a look ahead function, which is an inherent property of

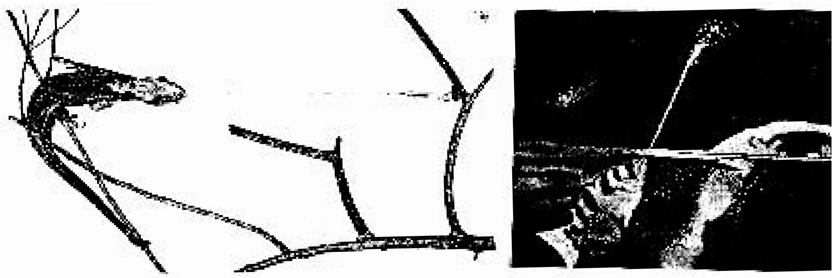


Figure 2.1
Two examples of the ability of animals to plan motor execution by predicting events to come. (*Left*) A chameleon midway in the process of extending and withdrawing its sticky-tipped tongue to capture an insect. (*Right*) The archer fish of the East Indies, so named because it rapidly and accurately shoots drops of water to stun and capture insects or spiders near the water's surface. (Photographs courtesy of the New York Zoological Society. Adapted from Romer, 1969, pp. 68 and 167.)

neuronal circuits. Indeed, prediction begins at the single neuron level. We can address this issue with an example: the control of movement.

Prediction and the Control of Movement

Because the ability to predict evolved in tandem with increasingly complex movement strategies, we must look at movement control in order to understand prediction. Let us return to the refrigerator for a carton of milk. The appropriate pattern of contraction must be specified for an extension/grasping sequence to be executed properly (add to this the correct use of postural muscles for support of the body while bending over during the reach). Now consider what the brain must do to pull off this simple movement sequence. Each muscle provides a direction of pull (a vector). Each muscle vector is composed of individual muscle fibers that are operated in pre-established groups based on their common innervation by the same motor neuron. This is called a motor unit (a single motor neuron innervates tens to hundreds of muscle fibers). A given muscle may be composed of hundreds of such individual motor units. The number of muscles multiplied by the number of motor units may then be viewed as the total number of degrees of freedom for any given movement. A movement such as reaching into the refrigerator is considered a simple one (as compared to, say, a good tennis return). However, from a functional perspective, even a simple movement often engages most of the body's muscles, resulting in an astronomical number of possible simultaneous and/or sequential muscle contractions and degrees of freedom. With the milk carton example, your arm may be brought toward the carton from any number of initial positions and postures (maybe your back hurts today and so you bend into your reach from a stilted, atypical stance).

All of this potential complexity exists before the load is actually placed on your arm and body; you have yet to pick up the carton and can only guess its weight during your initial reaching motion.

So this simple movement is not simple when we break it down and try to understand how the brain handles it all. However, the dimensionality of the problem of motor control does not derive solely from the number of muscles involved, the differing degrees of pull force and angle, and so forth. The real dimensionality of the problem stems from the complicated interaction between the possible directions of muscle pull and their sequence of activation in time.

Much of motor control occurs in real time, "on-line," as it were. Our movements seldom take place under stimulus-free conditions. Consider the following scenarios: running down a steep, winding forest path; steering your car while holding a cup of coffee; jumping up and stretching to return a serve in tennis. The combination of muscles one contracts at any given moment is often determined as a movement sequence and executed in response to teleceptive stimuli (stimuli at a distance taken in mainly through the senses of hearing and vision), kinesthetic feedback (the feeling of one's body moving), or thought.

It is generally assumed that the optimal controller is one that produces the smoothest possible movement. This idea implies the continuous monitoring (that is to say, a sampling rate of every millisecond or faster) of feed-forward and feedback influences on the selected activation sequences in order to minimize the accelerative transients that produce jerkiness in movement. Although this sounds right, we need to evaluate whether it is computationally plausible for the brain to control movement in such a continuous, on-line manner.

From the heuristic formula described above, and, given that there are 50 or so key muscles in the hand, arm, and shoulder that one uses to reach for the milk carton, over 10^{15} combinations of muscle contractions are possible—a staggering number to say the least. If during every millisecond of this reaching/grasping sequence the single best of the 10^{15} combinations is chosen after an evaluation of all of the possibilities, then 10^{18} decisions would have to be made every second. This would mean that the brain, if it were a computer, would need a 1-exahertz (1 million gigahertz) processor to choose the correct muscle combinations to execute appropriately this relatively simple reaching/grasping sequence. In reality, even the above scenario is an over simplification (Welsh et al. 1995). The dimensionality of the problem of motor control is increased many orders of magnitude when one also considers that there is a bare minimum of 100 motor units for every muscle, and that each muscle pull may, and most likely will, involve differing sets of motor neurons.

The brain does not seem to have evolved to deal with the control of movement in this fashion—especially when one considers that there are on the order of 10^{11} neurons in the entire brain. Of these, only a fraction are in the cerebellum, the area of brain where most of the movement control processing would take place for the movement sequence we have been discussing (Llinás and Simpson 1981).

An alternative solution for the continuous control of movement might be a scheme where each muscle in the body is somehow controlled independently through time. Metaphorically, the motor system could be considered a bank of discrete representations (or parallel processors, with one for each muscle). This set-up would significantly ease the functional burden for the control of any single muscle, and render trivial the problem of how to control a highly artificial and rare movement involving only one or two muscles. This scenario presents significant difficulties for the control of complicated muscle synergies, however. A muscle synergy is a set of muscles working in tandem to bring about a given movement. This synergy operates on the stretch reflex, that is, the relation between flexors and extensors (figure 2.2). For instance, our reaching for the milk carton sequence is a muscle synergy, as are the associated muscles involved in the ensuing grasping movement of our hand and the reflex properties of the spinal cord circuits. As the number of muscles involved in a movement sequence increases, there would be a greater reliance on an absolutely precise and infallible synchronizing element to ensure that the muscle activations occur cohesively in time.

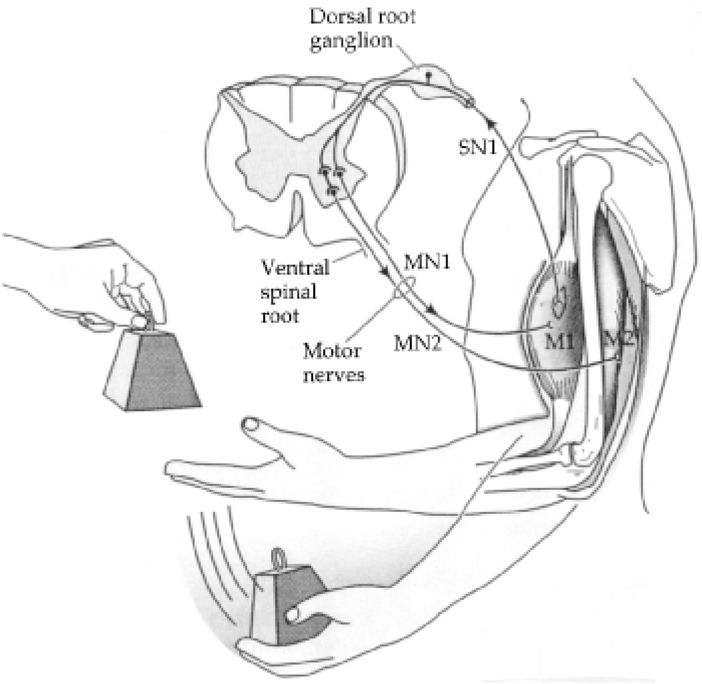


Figure 2.2
Example of the stretch reflex circuit. When a load is placed in the hand, the stretch receptor in the biceps flexor muscle sends a signal to the spinal cord that triggers the stimulation of the biceps muscle and the inhibition of its opposing extensor, the triceps muscle. The result is maintenance or recovery of arm position with the added weight. The entire reflex circuit is contained within the spinal cord and periphery. (From Rosenzweig et al. 1999, figure 11.10.)

This solution seems more fitting for a digital computer than a nervous system. However, unlike the elements of a digital system, neurons are analog: they have nonlinear response properties, and do not fire their action potentials with sufficient temporal precision to control continuously in time such parallel processing machinery.

At this point it should be clear that the continuous control of movement through time demands an extremely high computational overhead. This is true whether the movement is controlled by regulating the activity of every muscle discretely in parallel, or by choosing and implementing combinations of muscles. We do, of course, make complicated movements, and quite often. To delve further into this issue, we must ask the following:

1. How might the dimensionality problem of motor control, this incredible functional overhead for the brain, be reduced without significantly degrading the quality of movement sequences?
2. Which well-established aspects of brain function can provide clues for how to solve this problem?

The Discontinuous Nature of Movement

A relatively straightforward approach to reducing the dimensionality of motor control for the brain is to decrease the temporal resolution of the controlling system, that is, remove it from the burden of being continuously on-line and processing. This can be accomplished by breaking up the time line of the motor task into a series of smaller units over which the controller must operate. Control would be discontinuous in time and thus the operations of such a system would occur at discrete intervals of a "dt" (literally, intervals of a discrete passage of time). We must here consider an important consequence, that movements controlled by this type of pulsatile system would not be executed continuously, demonstrating obligatorily smooth kinematics, but rather would be executed in a discontinuous fashion as a linked series of muscle twitches. Motor physiologists have known this fact for over a century: movements are not executed continuously, but are discontinuous in nature. E. A. Schafer surmised this as early as 1886:

> The curve of a voluntary muscular contraction . . . invariably shows, both at the commencement of the contraction and during its continuance, a series of undulations that succeed one another with almost exact regularity, and can, as it would seem, only be interpreted to indicate the rhythm of the muscular response to the voluntary stimuli which provoke the contraction. . . . The undulations . . . are plainly visible and are sufficiently regular in size and succession to leave no doubt in the mind of any person who has seen a graphic record of muscular tetanic contraction produced by exciting the nerve about 10 times in the second, that the curve . . . is that of a similar contraction. (9)

A tetanic contraction, or tetanus, is the maximum force that a muscle can generate when activated at high frequency. Schafer realized that a clearly defined rhythmicity in the range of 8–12 Hz exists in volitional

[... Rest of ch. discusses brain rhythms and relation to muscle tremors, etc.]