Motor Control

How Posture and Movements are Governed

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This article is a review of the nature of motor control: the abilities and limitations of the body, the principles of doing and learning, how parts of the nervous system interact, and how information is processed to generate the blend of sensory, perceptive, and motor functions that we call motor control. The relation to physical therapy is stressed: PT is regarded as an emerging applied science of motor control, and motor control is regarded as a basic science of physical therapy.

Key Words: Motor activity, Movement, Physical therapy, Posture.

As a neuroscientist, I am gratified to see the burgeoning interest of physical therapists in the rapidly maturing science of motor control. We can learn much from each other, provided we understand the basics of the two fields. I regard physical therapy as an emerging applied science of motor control and motor control as one of the basic sciences of physical therapy.

In this article, I will survey the nature of motor control—the abilities and limitations of the body, the principles of doing and learning, how parts of the nervous system interact, and how information is processed to generate the blend of sensory, perceptive, and motor functions that we call motor control.

WHAT IS MOTOR CONTROL?

Posture and Movement

Motor control is a field of study covering sensory, perceptive, and motor functions. Motor control is also the name given to the functions of mind and body that combine to govern posture and movement. We are born with only rudimentary motor abilities, and the rest have to be learned by active practice during infancy, childhood, and thereafter. This is demonstrated in the learning of walking, sports, and practical skills. Motivation, attention, and other states of mind are very important because they determine how well we attend to learning a motor task and how well we carry it out. Learning and doing are inevitably intertwined; we learn as we do, and we do as well as we have learned.

All postures—of the limbs, the trunk, and the whole body—are maintained by some muscular antigravity effort. Movements are changes of postures and can be made consciously or as automatic adjustments. A few years ago this distinction usually meant voluntary as opposed to reflex actions, but we shall see in the following sections that these words no longer adequately describe what is meant.

How do we plan movements that we have already learned, such as swinging a golf club and hitting the ball just right (Fig. 1)? How do we arrange that the trunk, legs, and arms act at the correct times in relation to each other? How are the details worked out that make the right forces come on at the right joints at precisely the right times?

Apparently, we visualize the task that we have learned to perform. The present effort is guided by the memory of how the ball will fly when we move in a certain way. The memory is twofold: we remember how it felt to make the effort and what result was achieved by it. Our sense of effort is based on messages from sense organs in and near muscles. Much of this sensing, and the planning based on it, goes on without our awareness. We are assisted by programs that are assembled in the brain. For instance, as adults we know how to use our feet for standing or walking, but we have to learn precise ways to move them for a specific task, be it playing golf or compensating for some physical disability. Swinging a golf club requires that the feet be placed far enough apart and the legs and trunk be braced to support the body when it sways as the center of gravity is shifted. (Bracing means to set muscles at the proper tensions, or tone.) Stance and tone have to be right before the planned swing can be carried out successfully. Simi-
larly, the upper arms have to be placed and braced appropriately for the coming wrist action.

These are important considerations for physical therapy, because in some cases postures of the trunk and limbs can be learned to enable subsequent performance of movements that were not possible before training. Furthermore, it is becoming possible to calculate which movements can substitute for lost abilities while maintaining acceptable body postures. Therapists can then teach patients to make those movements.

Planning and Programs

The integrated parts of the action sequence depicted in Figure 1 can be regarded as an overall motor program that creates smooth, fast, skillful action. Motor programs are communications in the CNS (brain and spinal cord) that are based on past experience and can generate planned postural adjustments and movements. Programs consist of coordinated, learned parts called subprograms that act as motor commands for more automatic routines. Some subprograms can be discerned in Figure 1: the golf swing and stroke are made up of sequences of movements and postures. Like all movements, they involve many joints because the skeleton links many muscles. The mechanical skeletomuscular linkages cause interactions across several joints, which demands muscular coordination. Multijoint movements are called compound movements that perhaps are composed—literally in the brain—of simple movements that only involve one joint. Simple movements are easier to think about in the abstract and may be natural units that the brain uses for calculating compound movements. Simple movements, however, never occur by themselves. Various postural muscles cooperate for the intended movement even when supports are provided for the posture of body and limbs. We will return to this point later.

Subprograms then are planned units of action that can have various degrees of complexity. The steady holding posture of the arms in the first outline of Figure 1 could be considered a subprogram. It contains smaller units, however; one example would be the controls of tensions in each arm. These units in turn have even smaller units, the subprograms for tension control at the shoulder, elbow, wrist, and finger joints. In the second outline of Figure 1, in which the club is lifted, we can also identify particular movement subprograms, such as the flexion of the right arm. This intended movement changes the previously maintained intended posture and does it with planned speed and force.

How detailed is the planning of intended movements by programs and their subprograms? Can all the necessary instructions be fed forward from brain to spinal cord to muscles? Yes, they can be for all-out "bang-bang" ballistic movements such as whacking the golf ball as hard as possible (sixth outline in Fig. 1).

Programs and Feedback

Intended movements may be programmed to various levels, but they depend to some degree on sensory information that is fed back from the peripheral sense organs to the spinal cord and brain. At the very least, sensory feedback probably contributes to movement preparation before the programmed relaxation of postural tensions at a joint, which precedes actual motion. Figure 2 shows that a planned simple movement begins with relaxation of the opposing (antagonist) muscle, both for the fastest speed shown (skilled ballistic movements) and those of moderate speed (continuous movements). Agonist postural tension can also be relaxed before movement onset (not illustrated).

The timing of force application is planned in all programmed movements, as expressed for fast movements by the burst of the propelling (agonist) muscle. Timing of force termination is also planned in programmed movements, as demonstrated by appropriately timed bursts of EMG activity in antagonist
skilled ballistic (very fast) and continuous movements (of moderate speed) are programmed, whereas slow, discontinuous movements are not. Note the inhibition of the antagonist muscle as the first sign of impending programmed action, preceding onset of the agonist muscle (both marked by arrows). Also note lack of antagonist action in discontinuous movement. Movement durations are indicated by vertical broken lines. Initial and final positions (zero velocity) are determined by tonic EMG levels. These levels create tonic length-tension relations as plotted in Fig. 6, and phasic EMG pulses create force pulses (hills) plotted in Fig. 7.

Learning, Memory, and Motor Skill

Natural movements commonly contain programmed, simple movements of moderate speed that are called continuous because they reach their endpoint without interruption. Their velocity profiles present only a single peak (Fig. 2). Programmed movements ordinarily use sensory feedback for adjustments of their path, as will be explained below, but they can manage without it if the need arises. This is not true for nonlearned, feedback-dependent movements that are not programmed (as labeled in Fig. 2) or are, at any rate, least programmed. We use such movements when we are not certain how to proceed. A novice golfer might move his arms that way when moving the club slowly back and forth (Fig. 1) during his first lesson on how to get a measure of the distance between club and ball before swinging. The analogy with the flight of piloted rocket ships is appropriate not only for lift-off and prearranged soft landings but also for course corrections, when we also use sensory feedback. It can be used in conjunction with feedforward steering, because our brains remember our body image (much as an on-board gyroscope retains map-coordinate references) and compute as well as correct flight path and landing according to the map references. The relevant parts of the brain are identified in Fig. 4.
I judges where he stands and how he swings by reference to where he sees the ball and to the visual impression of the landscape that it will fly over and land on. Also important are the reports from the inner ear about head position in relation to gravity and to head movement (vestibular inputs). The most important body sense is proprioception. Sensory organs in the tendons that anchor muscles to the bones signal how hard the muscles are pulling, and the sense organs within the muscles signal how much the muscles are stretched (Fig. 5). This is known as proprioceptive feedback, which assists the CNS in calculating, for instance, how much the triceps brachii muscle is stretched when the biceps brachii muscle contracts to flex the elbow. In addition, we use kinesthetic input from receptors in the joints, and somatic input from skin sensors for touch, temperature, or pain.

Once movements are launched, the CNS monitors their progress not only through sensory peripheral feedback as described above but also through internal feedback from brain and cord. Some spinal connecting neurons, for example, can signal changes of posture because they receive input from several joints. Information about movement progress is fed back to various brain parts for comparison with the commands previously issued for the intended movement. The use of error-detection for negative feedback to steer according to a program is an important principle (Fig. 3). If there is a mismatch between the intended program (or model) and the actual movements, appropriate corrections can be made by the CNS, even without conscious decisions. The better the programs have been learned, the fewer the corrections that are needed. As a consequence, movements become continuous as in Figure 2. They are faster and smoother; in other words, they are more skillful. Motor skill, the optimal use of programmed movements, is further improved by adjusting muscle tensions to make ac-
Fig. 5. Block diagram of muscle control system. Muscle and its load are regulated by two feedback pathways, one signaling length and velocity through spindle receptors (in parallel with muscle) and the other signaling muscular force through tendon organs (in series with muscle). The CNS initiates movement and modifies feedback by sending three sorts of control signals to various neurons in the spinal cord. Gamma bias edits feedback from spindles. Responses of tendon organs are not edited and therefore report actual muscular force. Messages from both spindles and tendon organs project to spinal neurons as shown in the diagram, as well as further centrally into the brain (not shown). Excitation and inhibition are denoted by + or −. (Reproduced, with permission, slightly modified, from Houk JC: Feedback control of muscle: A synthesis of the peripheral mechanisms. In Mountcastle VB (ed): Medical Physiology, ed 13. St. Louis, MO, The CV Mosby Co, 1974, p 670)

accurately programmed movements with the greatest economy. The adapted tension adjustments become part of the motor subprograms.

Movements are learned from past experience if success has been recognized. How is such reinforced experience converted into motor memory? This is the same as asking how neurons can be adapted so that they are more likely to respond to previously useful inputs or how to make neural centers generate subprograms. This is not understood, but it is assumed that useful motor behavior is recognized when successful and this recognition is somehow fed back from higher to lower centers in the CNS. Learning from previous experience thus depends on sensing and moving, not just on sensing, and it is facilitated by unceasing communication between the sensory and motor systems. One instance where this is of great importance is “active touch,” or handling objects. Their shapes and textures are perceived better when the objects are actively explored than when they are passed over the passive hands or fingers.

Retention and improvement of skill depend on continued use of appropriately adjusted programs. Maxims such as “try, try, try again” and “practice makes perfect” express the common knowledge that continued practice improves learned movements. Another maxim, “use it or lose it,” reminds us that the most skillful, optimal use of motor programs tends to fade unless it is actively refreshed. It is conceivable that most of our movements and postures, no matter how casual, contain many programmed components because we develop good sensory images of our bodies and of their motor capabilities. Spinal motoneurons know the muscles to which they are connected, and more generally, the brain knows the body that it lives in. After all, they grew up together. This is not just a quip; it reflects the clinical finding that slowly growing brain lesions do not necessarily betray their presence by early signs of dysfunction, because the brain learns to adapt and to compensate. The suddenly inflicted lesion is what can produce immediate, catastrophic consequences.

An urgent problem for physical therapists is to learn how to assist the patient to replace motor programs that have been lost after brain damage, for instance by a stroke. The inactive tissue disconnects remaining cortex and subcortical centers from their programmed inputs. Consequently, the capacity to make voluntary learned movements is impaired. Unwanted, disabling postures are “released” and take over as the remaining inputs become predominantly inappropriate. New, unwanted influences are probably also created by invading new neural connections. These pathological influences will generate unwanted programs leading to abnormal postures and to limited movement capability. They could be thwarted by early acquisition of more desirable programs through physical therapy.
WHAT STRUCTURES IMPLEMENT MOTOR CONTROL?

The Knowing and the Emotive Brain

As discussed at the beginning of the article, the mind and the senses control posture and movement. This is accomplished through cooperation of the knowing part and the emotive part of the CNS. The knowing part consists of the sensory, motor, and associative systems, and the emotive part consists of the limbic system. The emotive part is an old part of the brain and is located centrally, near the midline with other old structures. (The limbic cortex is part of the mesial rim around the corpus callosum.) The knowing brain deals with sensations, perceptions, and motor functions, whereas the emotive brain deals with emotional behavior based on basic biological drives. These drives are feeding, drinking, reproduction, and other life-preserving activities that center on the hypothalamus, which regulates them through the autonomic nervous system and the neuroendocrine pituitary system. The hypothalamus receives reports from senses basic to these drives and feedback from the limbic nuclei (Fig. 4). It is common experience that motivation and the emotional state of mind influence learning and performance of any task, including movement programming to acquire motor skill. The balky child or the disinterested adult do not improve easily. This may hinge on ineffective assistance by the limbic system of sensorimotor processing in the brain stem (Fig. 4). Motivating the patient can be of great assistance to the therapist.

Task-related Systems Contain Higher and Lower CNS Parts

Tasks of different complexities can have similar overall flows of information within the framework of the scheme in Figure 4. Yet, parts of the CNS interact in many different ways, depending on conditions such as the nature of the task, the emotions, and the experience of the subject. As a practical example, we know that a novice must form a general scheme in his mind before he can make sense out of particular instructions. A general scheme also has to come first in motor behavior, leaving the details for subsequent action to subordinate routines. For instance, the decision to begin an action probably hinges on limbic support of the basal ganglia, which opens "gates" for the ability to begin. (The immobile patient with Parkinson's disease may be an example of deficient "gating".) The decision to perform a task in a certain way, such as using a particular golf swing in a given situation, is a choice of strategy based on understanding and association of many factors, including where the ball is located, the lay of the land, and the wind.

Such associations are thought to be made in the association areas of the cerebral cortex that receive and assess diverse sensory inputs and relate them to progress reports from the motor system. Furthermore, some brainstem systems gate the cortex to let data be processed consciously or unconsciously. The association cortex thus operates at high levels of forming perceptions and motor strategies.

The motor cortex, in contrast, operates at a lower level—how to carry out the movements needed for a given strategy. The motor cortex receives instructions from the association cortex, the cerebellum, and the basal ganglia and issues tactical commands to the spinal cord. High and low centers do not operate as a rigid hierarchy, with orders going only from the top downwards, because most structures are connected through various feedback loops for messages going up and down. This forms interactive motor centers at various levels (Fig. 4). For instance, a program formed in the cerebral cortex (one depending on discharge of cortical neurons) can be "put on hold" by a not-ready signal from the spinal cord until the whole system is ready to go. The interlinked powers of go and not-ready decisions are distributed within the system. The intermediate motor centers (eg, motor cortex, cerebellum, basal ganglia) deal with the tactics of movement execution. They coordinate the head, trunk, and limbs and translate such items as movement direction and force into patterns of muscle action. We should note that instructions to the spinal cord for most postural muscles are mediated by different paths from those for fine control for finger movements, that is, by the pyramidal tract. (The descending tracts are not drawn separately in Fig. 4.)

By making general decisions first and leaving details to be fitted into the circumstances of the movement later, we are able to produce the same effect over and over again without ever doing it exactly the same way twice. The golfer in Figure 1 provides an example. As another example, think of how we sign our name and how similar it is even when signed on paper or on the blackboard. Yet, we use entirely different sets of muscles in the two cases. The act is accomplished by overall commands that are parcelled out by intermediate centers to the spinal output stages, consisting of motoneurons and their associated interneurons. These output stages, which are the lowest motor centers, specify intensity and duration of action for particular muscles, but even they never act in isolation. The muscles are coordinated by connecting systems of spinal interneurons and by paths to and from cerebral cortex, cerebellum, and brainstem (Fig. 4).

Where, in all these reentrant, interactive loops, are the locations of motor programs that are a form of ready-to-use memory? One current theory holds that most parts of the CNS contain synapses that can be
altered permanently by inputs of special significance, such as feedback from higher centers about success. Therefore, one might guess that the products of modifiable synapses, very small subprograms, are also distributed in the CNS. The answer appears to be that programs do not live in tight nuclei but instead are formed by subprograms that are distributed in the CNS. The size of the distributed system is determined by the number of CNS centers that participate in the programmed task.

**Task Systems Have Parts for Various Levels of Generality**

Task systems can include practically the entire CNS for various phases of complex events, or they can be restricted to relatively few active centers for specific episodes of compound or simple movements. The term task system is meant to describe the assembly of centers that is most actively involved in a task at any given time. The systems' involvement is likely to be always a mixture of feedforward commands and feedback adjustments.

An arm movement, as in Figure 1, provides a good example of the operation of intermediate centers as a task system. Movement direction is thought to be programmed by the association cortex and the motor cortex, with special monitoring of relevant events by the association cortex. Appropriate muscles and their relative forces are specified by the thalamocortical system, particularly the motor cortex. The endpoints of movements are also arranged in the motor cortex, by setting the angles and mechanical stiffness of the joints. (Stiffness is the angular force needed to move the joint through a given angle.) Stiffness is determined with assistance of the basal ganglia and the cerebellum, by the degree of cocontraction of muscles acting in opposition to each other on that joint (Fig. 6). The motor cortex, however, can only function through cooperation of the basal ganglia and the cerebellum. Onset of intended movements is triggered by cerebellar prompting of the cerebral cortex as well as of the spinal cord. Movement speed depends on the force of the initial impulse of the propelling agonist muscle (Fig. 2). In a learned movement, the initial impulse, as well as the arresting antagonist impulse, is programmed, again with a trigger from the cerebellum. This oversimplified sketch indicates that no part ever works in isolation. Yet, local lesions can degrade performance through major influences on particular functions, as with the stroke victim with speech impairment and patients with cerebellar damage who correctly appreciate their environment and plan their movements correctly but can neither govern the correct execution of intended movements nor their adaptation to changing conditions.

Let us take a look at an even more limited task as an example: the spinal reflexes (Fig. 5) that operate in the golfer's arm during the swing. This may seem to be a purely spinal-task system, but it is more than that; the cerebellum, brainstem, basal ganglia, and cerebral cortex are also involved. What vary are the degrees and times of involvement relative to the movement. For the whole swing of the arm, as in Figure 1, we must include all of the above centers. For the more limited task of in-flight management of arm muscles, after movement onset and before termination, spinal reflexes can compensate to some degree for unexpected perturbations (labeled external forces in Fig. 5). But even spinal reflexes send reference copies of incoming and outgoing signals up to the brainstem, cerebellum, and cortex for comparison with the expected course signaled by reference copies from higher centers (Fig. 4). These copies can guide the arm to the intended endpoint (like the computer and rocket gyroscope referred to earlier), provided the joint around which the movement revolves is kept at the same position relative to the body as when the command was issued. Another look at Figure 1 shows right away, however, that the brain has to calculate...
a lot of successive commands “on the fly,” because many joints are moving. The sensorimotor system sketched in Figure 4 serves as gyroscope and computer, with the cerebellar circuit acting as the chief comparator and adaptive adjustor. (The same function is presumably served for the limbic system by the hypothalamic circuit.) How the cerebellar adjustor adapts to changing circumstances is taken up in the next section.

The spinal output stage and its connections (Fig. 5) not only refer information to the brain as discussed above but also receive control signals from the brain for adjustments of reflex thresholds or of their gain. The threshold is the level at which reflex correction, of muscle length, for example, is set to begin. An analogy might be the temperature at which the thermostat turns on the furnace. Gain is how much reflex correction is supplied for a particular level of muscle stretch. In the furnace analogy, gain would be the intensity of heating that the furnace puts out, once it has been switched on at threshold.

Another example of reflex property under descending controls is reciprocal inhibition of opposing muscles. Strong reciprocal inhibition allows the limb to swing loose, that is, to be compliant. We saw in Figure 2 that joints are made more compliant before the onset of a planned movement. Weak reciprocal inhibition, in contrast, permits cocontraction of opposing muscles, which makes the joint stiff. The golfer holds his arms fairly stiff during the hold before the swing, but they are compliant during the swing and then stiffen again before the impact. Central reflex connections were the reason for the warning earlier against too rigid a distinction between reflex and voluntary actions. Therapists can increase or decrease unwanted actions through appropriate touch, pressure, or imposed postures. Repetition of these movements and understanding by the patient of what is wanted can help involve larger task systems and can thus build new, voluntary capabilities on the initial changes produced by the therapist.

WHAT INFORMATION IS PROCESSED IN MOTOR CONTROL?

The codes of receptors and of muscles are reasonably easily unraveled, as are those of neurons connected directly to them. Messages of more centrally located neurons are harder to decode unless there is some readily available reference system. Greater strides have been made in understanding information processing in the visual pathway than in the motor system, for instance. Nevertheless, it seems assured that discharges of central neurons in a programmed task system help to re-create an intended, expected motor event. Central sensorimotor codes will become more understandable when we have gained a better grasp of the operating principles of the CNS. This understanding will be important for the rationalization of physical therapy and for generation of innovative therapeutic procedures.

Sensory Models (Perceptions) Are Based on Edited Versions of Sensory Reports

Sensorimotor integration is the key to motor control. Therapists know, however, that sensory perceptions do not necessarily reflect the quality or the intensity of sensory inputs. Instead, perceptions are based on edited versions of that input. For example, city dwellers become unaware of constant noise if it holds no meaning for them. Such habituation is caused by synaptic block at various levels in the CNS, perhaps with guidance by the hippocampus. Another example is failure to recognize people when we meet them out of the usual context. Conversely, patients who know they have lost a limb still refer the pain from the severed nerve endings to the phantom limb. This impresses on us that our sensory perceptions (sensory models) are context-oriented. Knowing this is useful because motor decisions are made on the basis of such perceptions, that is, within the sensorimotor context of greatest relevance. Another form of subconscious editing affects brainward ascent of proprioceptive and somatic sensory inputs; they are modulated by descending motor paths. In these cases, sensations are accentuated or diminished in the context of planned or ongoing movements. An analogy could be drawn to executive decision making where detailed attention to important matters is vital, but indiscriminate consideration of all possible factors may be too slow and therefore futile. These thoughts highlight the possibilities inherent in carefully selected biofeedback.

The best-known example of central editing of peripheral information is the control by gamma motorneurons of the sensitivity of muscle spindles (Fig. 5). The gamma bias tends to keep spindles sufficiently stretched, through contraction of the intrafusal muscles they are attached to, to maintain their sensitivity during shortening of the main muscle with which they lie in parallel. This is called servo control and operates during all but the quickest contractions. One current theory holds that for intended movements, the brain programs gamma as well as alpha spinal motorneurons and that the sensitivity of the spindles is modulated according to the program (Fig. 5).

Programmed spindles of muscles acting on a joint can in this way detect mismatches between the actual and the expected movement. Central control of spinal gamma motorneurons is an example of a subprogram. Its particular function is to impress “models” of the intended movement on the spindles to make them act as error detectors. The spinal alpha motorneurons respond to mismatch information by adjusting the length of the main muscle. As already discussed,
mismatch messages from the spindles are also relayed for reference to the cerebrocerebellar circuit, including the brainstem (Fig. 4). This circuit assembly is essential for adjusting motor output as required by changes in external circumstances. It functions therefore as an adaptive controller, and the gamma-driven spindles assist servo control by operating as model reference detectors. According to the servo-assistance theory, outlined above, progress of programmed movements is monitored by muscle spindles that signal departure from the program (model) being impressed on them by centrally modulated gamma bias.

The CNS “knows” whether its planned movement is proceeding according to plan or not, but how does it know what the muscles are actually doing? This information is supplied in two ways: by the reference copy of the editing instructions (gamma bias) and by the unedited muscle output (the force generated). Figure 5 shows that the CNS can compute adjustments of force when needed, because it receives feedback information from tendon organs, in series with the main muscle, on how much force is actually being exerted.

**Spinal Motor Output Relies Heavily on Information About Muscles**

The meaning of spinal output (discharges of alpha motoneurons) has been deciphered in considerable detail because it can be related directly to muscle force. As discussed earlier, simple movements may be components of compound movements. This can be rephrased now to say that compound movements are a higher form of planning and that the components, constituent simple movements, might be delegated for execution to lower centers. Supraspinal systems are thus probably relieved from having to calculate in terms of properties of particular muscles; that calculation is the task of the spinal cord. Spinal output stages address specific individual muscles to determine their tensions for postures and for movements. Limbs are held in desired postures by the steady tensions of muscles acting on particular joints. Movements are produced by joint rotations from one posture to another. If speed is unimportant, this movement can be achieved by simple step changes of steady tensions, that is, of muscle tone, maintained by asynchronous contractions and relaxations of motor units. (Agonist step changes are not illustrated in Fig. 2, but the antagonist comes close to demonstrating step changes in the discontinuous movement shown.) Usually, changes of muscle tensions are tonic as well as phasic. The velocities of the resultant position changes of the limb are governed by the rates of force allowing for contraction and relaxation times of muscles and for the properties of the joints.

Muscle tissue is elastic, that is, it springs back when stretched. The restorative spring force, consisting of passive tissue elasticity and active contractile force, depends on the length to which the muscle has been stretched. These relations can be expressed as muscle length-tension curves. When muscle length is regulated by stretch reflexes, greater tensions are obtained. During maintenance of weak tonic stretch reflex, motor units are activated asynchronously and at low rates that allow muscle fibers to contract and relax before being reactivated. The resultant steady tension (muscle tone) is related to muscle length approximately in the same manner as non-neural muscle tissue tension. Figure 6 presents length-tension curves for opposing, nonmoving muscles at two levels of tone. (The curves for non-innervated muscle tissue have not been drawn in below the tonic curves.) At equal levels of tension, the curves of opposing muscles cross, marking the balance of agonist and antagonist to maintain a steady joint angle.

How much opposing muscles cocontract is thus also defined as a property of that limb posture. Much cocontraction enables the joint to resist imposed loads. (As stated earlier, high resistance means a stiff joint, low resistance a compliant joint.) The limb postures marked in Figure 6 by the filled square and filled circle have different joint stiffnesses at the same joint angle, because the tone of both muscles has increased equally. When the tone of opposing muscles is unequal, one muscle shortens and the other is stretched, rotating the joint to a new angle where their tensions are equal. This has occurred in the posture defined by the open circle, when only agonist tone increased. It is believed that limb postures at the ends of movements are programmed by the CNS in terms of appropriate length-tension (tone) relations of opposing muscles acting on a joint. This is achieved by spinal output stages setting the thresholds and gains of tonic stretch reflexes (Fig. 5).

**Muscle Properties Shape Motor Actions**

During contractions maintained by stronger tonic stretch reflexes, muscles are reactivated before they have had time to fully relax (ie, tetanic fusion begins). This superimposes a force hump on the length-tension curves, which at high tension levels become indistinguishable from curves depicting phasic, synchronous contractions. Such a curve, for one particular moment in time, is illustrated in Figure 7A. Typical time courses are illustrated in Figure 2. Build-up of force depends on the rate of length change, that is, the velocity (Fig. 7B). Strong forces can be reached while the muscle is being stretched at various velocities. This would apply to the elbow extensor, the triceps brachii muscle, when it cocontracts during elbow flexion, that is, during a stiff flexion. Phasic force falls off rapidly when the muscle shortens at increasing speeds. This would be the case for the elbow flexor,
the biceps brachii muscle, during elbow flexions at various rates. Figure 7B is a three-dimensional description of response properties of a single muscle at a particular moment. Neural excitation of the muscle defines length-tension-velocity relationships in that muscle. At a single length this relationship is described as a force-velocity curve, and at a single velocity it is a length-tension curve. For length and velocity at some moment, instantaneous force is marked by the intersection of two such curves. Figure 7C combines two families of such curves and describes the state of the muscle at one particular level of activation for one particular moment. The force "hill" of the nerve-driven, phasically active muscle rises above the sloped length-tension (force) sheet of the tonic state. Phasic tension could be lower or higher than that shown, depending on the intensities of neural drive and of the consequent initial EMG pulses, as drawn in Figure 2. As explained above, phasic tension depends on both length and velocity. When a limb is perturbed from its course by external forces, as in Figure 5, reflex action restores the original force-velocity-length relation, returning the limb to its original path at the right speed trajectory. It is believed that force and speed of limb movements are programmed by the CNS in terms of the phasic as well as the tonic intensities of opposing muscles.

Muscles can only maneuver on the force hill of Figure 7C in those ways that combine compatible muscle properties. Movements require these conditions for all muscles acting on all joints. The spinal cord and some supraspinal centers handle this information and are the final arbiters, or task system, that determine exactly how muscle force is to be applied. Movements call for more complicated computations than are required for postures. The CNS must now manipulate all three factors of the muscle hills for all muscles acting on the joint, including the fourth factor, timing (stressed in Fig. 2). If we imagine the force hills of individual muscles combined into one resultant hill for the joint, then simple movements, just like skiers, choose their paths on the slopes according to what speed they can manage with what force at their particular stage of exhaustion or control. Muscle properties thus provide the variables for the most elementary machine language—force—in the computation of posture and movement.

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SUGGESTED READING

There are two particularly useful books for readers who wish to do further reading about motor control. An undergraduate text is Neurobiology by GM Shepherd, published in 1983 by Oxford University Press. An equally readable text, focused more for medical students, is Principles of Neural Science, edited by ER Kandel and JH Schwartz, published in 1981 by Elsevier/North Holland. Both books teach with great clarity and lead the reader to relevant reviews and research reports.

Fig. 7. A. Length-tension curves of a muscle at a particular moment in time. The lower line defines tonic tension levels maintained by asynchronous nerve activity, at various muscle lengths. The upper line defines phasic levels, produced by synchronous nerve volleys. B. A three-dimensional description of response properties of a muscle at a particular moment. Excitation of the muscle determines length-tension-velocity relationships in that muscle. At a single length this relationship is described as a force-velocity curve, and at a single velocity it is a length-tension curve. For length and velocity at some moment, instantaneous force is marked by the intersection of two such curves. C. Three-dimensional diagram of the relations between muscle length, tension (force), and velocity. The curved sheet represents tonic length-tension relations. The force hill above the tonic level represents force-velocity curves for contractions while the muscle is being lengthened or shortened, at a particular moment and at a particular level of excitation of the force hill. (Reproduced, slightly modified, from Partridge DL, Benton LA: Muscle, the Motor. In Brooks VB (ed): Motor Control (Handbook of Physiology, section 1, vol 2). Bethesda, MD, The American Physiological Society, p 70)