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appear to require recruitment of the largest force units, which are characteristically fast contracting but much more susceptible to fatigue. This stereotyped recruitment is often referred to as the size principle because recruitment is generally related to the increasing individual force outputs of motor units that become active. The factors that control motoneuron recruitment are complex and incompletely understood. However, it is clear that they involve interactions between intrinsic motoneuron properties and factors that relate to the organization of their synaptic inputs.

Recruitment patterns appear to be subject to some variation under certain conditions. Movements that require very sudden, forceful contractions ("ballistic" movements) create synchronous activation of the entire motoneuron pool. It may even be possible, under certain special conditions (e.g., in movements that include rapid alternation), for the CNS to activate preferentially the motoneurons that control large, fast-contracting muscle units. This degree of functional flexibility of activation pattern appears to be conferred by differences in the organization of particular synaptic input systems that can be controlled independently by the CNS.

See also Motor Endplate; Muscle Contraction; Muscle Receptors; Neuromuscular Junction; Neuron; Size Principle; Spinal Cord, Ventral Horn

Further reading

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Motor Control

Gerald E. Loeb

The importance of muscular action and coordination to animals in general can best be appreciated by asking any child the difference between animals and plants: animals move and plants do not. Despite a few curious exceptions, it can generally be said that the unique end product of the animal nervous system is controlled motion, whether it be autonomic activity such as respiration and digestion or voluntary activity such as catching food or expressing thoughts.

The motor nervous system is often pictured as the other half of the central nervous system, paralleling the sensory nervous system. This probably stems from the experimental strategy of studying organisms from the outside inward. We study senses upward from their peripheral receptors toward more abstract internal representations of the information content. We study motion backward from its external manifestations toward more abstract internal representations of intent. Somewhere the two must meet. Perhaps it would be more useful to think of motor control as the highest abstraction of perceptual information, in which all the different information sources about external and internal conditions and experience combine to produce an appropriate behavior.

This rather philosophical introduction is intended to shed some light on a conceptual gap between studies of sensory and motor function. The upward study of sensory information processing from the concrete to the abstract forces the investigator to confront the complex, highly distributed computational processes needed to transform information from one representation to another. The backward study of motor control from what appear to be simple movements to their control signals encourages the use of rather simplistic clockwork mechanisms to describe motor programs and feedback of sensory information. Perhaps the most salient discovery of the past decade of motor control research is the absence of the private line pathways from higher to lower motor centers and from local proprioceptors onto motoneurons—circuits explicit in the traditional theories of motor control. Unfortunately, more sophisticated theories are still few and primitive in both their conception and their implications for experimental testing. Consequently, motor control studies are in a state of transition.

Levels of study

Kinesiology. This is the study of visually apparent motion, the end product of the motor control process. Methods include cinephotography, videotape, and various specialized devices for tracking the multidimensional motion of limbs and manipulanda. These are most commonly employed in applied areas such as quantification of movement disorders and athletic performance, where they serve mostly an empirical descriptive function.

Dynamics. This is the study of the forces giving rise to the motion of physical objects. Methods include direct measurement of reaction forces at force plates and manipulanda, direct measurement of internal strains via implanted transducers, and indirect calculation of causative forces from apparent motion (inverse dynamics). These studies give information that is closer than kinesiology to the control signals in the nervous system but still far from the neuromuscular substrate because of the redundancy of muscles acting on any joint and their nonlinear force output in the face of various length, velocity, and joint angle conditions.

Musculoskeletal anatomy. Because of the difficulty of studying the actual function of individual muscles in normally behaving animals, much of our knowledge about the roles of muscles comes from suppositions based on their anatomical arrangements and actions on the skeleton. Given the redundancy of musculature and the complexity of multiarticular muscles and multiaxis joints, it is not surprising that anatomical categories such as extensor and flexor do not correlate well with the functional purposes implied by those terms.

Muscle output. This is usually the study of the electrical signals produced by active muscle (electromyography) to determine the relative timing and amplitude of recruitment of individual muscles (and even individual motor units within muscles). This technique is being used increasingly in both animal and human experiments, and despite some technical caveats, probably provides a fairly good representation of the final output of the motor control circuitry, at least in vertebrate striated twitch muscle.

Central nervous system recording. The study of the electrical signals produced by the motor control circuits themselves, usually recorded as the activity of single neurons or local groups of neurons, is the most direct approach to motor control, but suffers both from technical limitations and from the very narrow view afforded by monitoring only one or two of the vast multiplicity of elements involved in motor control information processing in even the simplest organisms.

Types of movement

There are many categorizations of motor behavior and motor control, generally intended only for phylogenetically or experimentally restricted parts of the spectrum of motor behavior. The following is an attempt to select three fairly independent factors that tend to occur in most such categorizations: complexity, initiation, and modifiability.

Complexity. Most sense organs are under the control of special muscles whose control is intimately linked with the output of these and other related sense organs. Examples include gain control (iris muscles of the eye, auditory ossicular chain muscles, and intrafusal innervation of muscle spindles), directionality control (extraocular and ear pinna muscles), and intermodality coordination (vestibulo-ocular reflex, vestibulocolic reflex). These processes include most of, if not all, the successful applications of engineering servocontrol theory to physiological motor control.

Some movements are the result of a single command to one or more muscles. Examples include ballistic movements (e.g., hitting an object, and some escape maneuvers) and even some oscillatory behavior in which the cycling is intrinsic to the end organ (e.g., insect flight muscle).

Most mammalian behavior is actually the result of executing temporally programmed sequences of commands to various muscles to generate controlled, smooth trajectories. These include both cyclical acts (e.g., walking and chewing) and nonrepetitive acts (e.g., targeted pointing and speech).

Initiation. Some motor outputs are closely linked with specific sensory stimuli, which may be either necessary or sufficient for their production (e.g., withdrawal from noxious stimuli, scratching a skin irritation). These natural behaviors are often related to but should not be confused with experimentally contrived demonstrations of reflexes, which are usually not natural motor acts but perhaps parts of them.

We have no difficulty assigning certain motor behaviors in higher organisms to a volitional category, but gray areas abound. Is the initiation of a movement programmed at a lower center (e.g., locomotion) voluntary even if it is part of escape from a noxious stimulus? Is a reflex behavior (e.g., yawning) actually volitional if it can be suppressed consciously or even performed at will (e.g., scratching)? Failure to resolve such issues has been a significant obstacle to defining the relationship between upper and lower motor centers.

Modifiability. Some motor behaviors, including complex ones such as rapid pointing and eye movement, are executed without significant online modification of muscle output from sensory feedback. This does not mean that such feedback is not present; it may be used to instruct the control apparatus on the future performance of the movement (e.g., gain resetting in the vestibulo-ocular reflex) or to signal the need for an additional, separate corrective movement (e.g., eye-hand coordination).

Most muscles are equipped with proprioceptive sense organs for length and tension. Frequently the output of these and other mechanically related sense organs in skin and joints and other muscles have strong excitatory and inhibitory effects on the final common pathway of motor control, the motoneurons. These sensory modalities are presumed to provide a continuous source of information about the performance of the motor plant and about unexpected external loads for which compensatory modification of the motor output may be required. (see Fig. 1) Again, gray areas exist regarding the volitional enhancement or suppression of such pathways and the use of such information to trigger new, as opposed to modified, motor behaviors.

Major areas of current research

Study of sensorimotor integration involves the pathways and the rationale for the combination of various sources of sensory information in the initiation and control of motor behavior. It is becoming clear that the sources of sensory information are mostly highly nonlinear sensors of mechanical events that

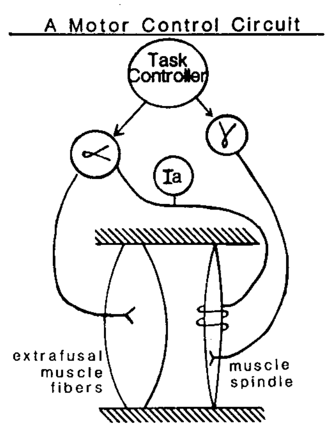

Figure 1. Typical servocontrol circuit proposed for mammalian skeletal muscle using negative feedback from muscle spindles to stabilize length. The muscle spindle (narrow structure at lower right) has its own intrafusal muscle fibers, under the control of gamma motoneurons (γ). Stretch of the center of the spindle causes activity in the afferent fiber (Ia) whether caused by contraction of these intrafusal muscle fibers or by externally applied stretch of the whole muscle. If the muscle is stretched, increased activity in the spindle afferents excites alpha motoneurons (α) as part of the stretch reflex. The tension generated by the extrafusal muscle fibers innervated by these motoneurons (large structure at lower left) acts to oppose the stretch. If the animal wishes to voluntarily shorten the muscle at a controlled rate, simultaneous activation of both alpha and gamma motoneurons (Task Controller) will cause a constant level of excitatory feedback from the muscle spindle afferents only as long as the intrafusal muscle contraction matches the shortening of the muscle as a whole. If external loads cause shortening to occur too slowly, Ia activity increases, increasing muscle contraction to overcome the load; if shortening proceeds too rapidly, the Ia becomes silent, shutting off this source of excitation to the alpha motoneurons. Many variations on this theme have been proposed, and there is much debate about the importance of such circuits even when they have been demonstrated to exist.

are not simply related to basic physical parameters such as angles, lengths, velocities, and forces. Perhaps related to this is the finding that even at the most peripheral levels, the interneuronal circuits almost always carry highly convergent and divergent mixes of signals from different modalities and physical loci. The use of such sensory information in motor control appears to involve processing that is more akin to perception than to servocontrol, even when the processing occurs largely at unconscious, lower nervous system levels.

The term motor programming encompasses the acquisition, storage, selection, and read-out of complex temporal-spatial sequences of motor command signals. The motor physiology literature is full of pattern generators for mastication, locomotion, targeted pointing, speech, etc. These are usually presented as black boxes whose contents and even whereabouts are mostly unknown.

The actual relationship of motor control circuitry to motor behavior has received relatively little study, primarily as a result of methodological limitations. Most existing motor control principles are based on physiological and anatomical experiments on reduced, often paralyzed preparations. This has permitted physiologists to pursue rather narrow views of motor performance which incorporate little of the work and cooperativity among muscles that characterize natural behavior, as studied by kinesiologists interested in sports performance or rehabilitation. For example, the different mechanical output properties of muscle and the types of proprioceptive feedback needed to control them during isometric, actively shortening, or actively lengthening (as controlled springs) behaviors are just beginning to be addressed. Motor control theories regarding these real operating modes will also find application in the fields of robotics (where the limitations of simple servocontrol engineering are being felt acutely) and in functional neuromuscular stimulation, where prosthetically applied electrical stimulation is being used to reanimate paralyzed but physically intact limbs (e.g., spinal cord injury and stroke patients).

See also Control Systems; Muscle Afferent Innervation; Muscle Contraction; Reflex Control

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Motor Control, Hierarchies of

John C. Fentress

Hierarchies of motor control imply the ability of nervous systems to articulate separable properties of movement that are in turn combined into functionally coherent patterns. The first definition of hierarchical organization is descriptive. Motor actions are dissected into their component aspects, which are then arranged into more broadly defined functional groups. Thus, the movements used to tie one's shoes can be separated, but it is only through the spatiotemporal combination of these actions that shoe tying is accomplished. Similarly, in human speech the combined articulations of phonemes produce words that in turn produce phrases, sentences, and so on. From these descriptive statements formal rules of motor organization can often be derived, such as for the sequencing, relative priorities, and clustering of movement properties. Finally, these rules can lead to a search for nervous system structures that may participate more or less selectively in different aspects of motor control. For example, in both invertebrate and vertebrate species, command, pattern generation, and feedback functions are differentially represented in different neuronal populations. These various functions may vary in their specificity, and ultimately they must be brought together for integrated motor performance. The concept of motor hierarchies, then, refers to an ordered nonequivalence of abstracted elements in motor performance and its control. This complex multidimensionality of movement has led to the search for basic units of action and their rules of connection in space, time, and across complementary levels of organization.

Elementary motor units and their limits

For vertebrate species, motor units are normally defined in terms of individual motor neurons and the muscle fibers that they activate. Thus, each mature mammalian skeletal muscle fiber is innervated by only one motor neuron. Since individual action potentials can lead to a contraction in the population of muscle fibers, this population of muscle fibers and its motor neuron provide a convenient unit of action. However, there are limits to simple unit concepts in intact behaving organisms. Motor neurons typically have a diversity of excitatory and inhibitory inputs mediated by a complex of descending pathways, and motor neurons that contact a given muscle often exhibit a number of collective properties. This combined activity may summate in a nonlinear fashion, as the properties of individually defined motor units are not always fully independent of one another. As a result, both finer separations and larger groups of motor activity are possible than would be anticipated by the study of single motor units in isolation. There are also certain elements (e.g., Ia inhibitory fibers) that may be thought of as either sensory or motor depending upon one's descriptive or analytical perspective. The same abstracted element within a circuit can additionally be used for several different functions, depending upon the dynamics of the system as a whole. In brief, motor units and units of movement are not easily related, and motor units themselves exhibit a number of collective relational and dynamic properties.

At the next level of abstraction is the reflex unit, viewed by Sherrington and most contemporary workers as a "convenient fiction." These reflexes can vary over a wide range in their complexity, from the simple monosynaptic stretch reflex (mediated by muscle spindles and alpha motor neurons of the same muscle) through intricate patterns of reciprocal innervation. In the intact animal, reflexes are normally interwoven together into higher order patterns of action, and their detailed functions can be modulated by a number of descending influences. Muscles connecting with a single joint necessarily influence one another, and most organized movement is best viewed as involving multijoint synergies. To produce effective and flexible motor sequences, mammalian nervous systems activate