

Eccentric contractions require unique activation strategies by the nervous system

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Enoka, Roger M. Eccentric contractions require unique activation strategies by the nervous system. *J. Appl. Physiol.* 81(6): 2339–2346, 1996.—Eccentric contractions occur when activated muscles are forcibly lengthened. This mode of muscle function occurs frequently in the activities of daily living and in athletic competition. This review examines the experimental evidence that provides the foundation for our current understanding of the benefits, consequences, and control of eccentric contractions. Over the past several decades, numerous studies have established that eccentric contractions can maximize the force exerted and the work performed by muscle; that they are associated with a greater mechanical efficiency; that they can attenuate the mechanical effects of impact forces; and that they enhance the tissue damage associated with exercise. More recent evidence adds a new feature to this repertoire by suggesting a new hypothesis: that the neural commands controlling eccentric contractions are unique. Examination of this hypothesis is critical because the existence of such a control scheme would increase substantially the complexity of the strategies that the nervous system must use to control movement.

muscle work; exercise; movement control

HUMAN MOVEMENT IS ACCOMPLISHED by using muscles to exert forces against objects and support surfaces. In Fig. 1A, for example, the elbow flexor muscles can exert a torque to control the rotation of the forearm about the elbow joint and thereby move the load represented by the mass of the forearm, hand, and weight. When the muscle and load torques are equivalent under such conditions, the load does not move, and the elbow flexor muscles perform an isometric (constant length) contraction. However, when the two torques are different, the load is either raised or lowered. When the muscle torque exceeds the load torque, the elbow flexor muscles shorten and perform a concentric contraction to raise the load (Fig. 1B). In contrast, when the muscle torque is less than the load torque, the activated muscle is lengthened and performs an eccentric contraction to lower the load.

Eccentric contractions occur frequently in everyday activities and in athletic competition. They are characterized by the ability to achieve high muscle forces, an enhancement of the tissue damage that is associated with muscle soreness, and perhaps require unique control strategies by the central nervous system. The purpose of this article is to review the experimental evidence that provides the foundation for our current understanding of the benefits, consequences, and neural control of eccentric contractions. The outcome of examining this evidence is a new hypothesis: the

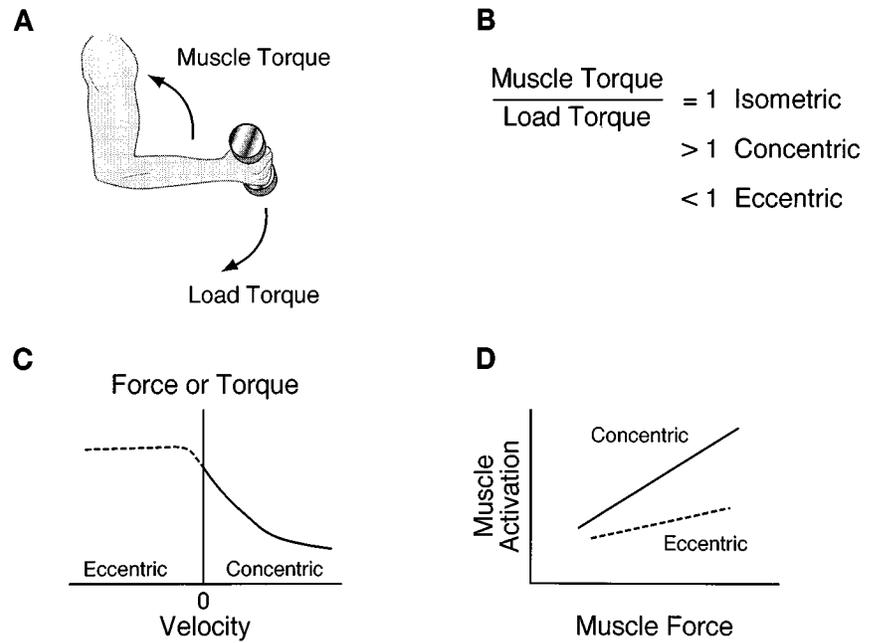
neural commands controlling eccentric contractions are unique.

CONTRIBUTIONS TO PERFORMANCE

The actual force that a muscle can exert is not solely a function of the activation level produced by a voluntary command but also depends on the speed at which the muscle changes its length: the so-called “force-velocity relationship” of muscle (Fig. 1C) (20, 50). The faster a muscle shortens during a concentric contraction, the less the maximum force it can exert. Conversely, the maximum force that a muscle can achieve during a voluntary eccentric contraction is largely unaffected by changes in the speed of lengthening, at least beyond an initial limit. In highly motivated subjects, the greatest forces occur during eccentric contractions (Fig. 1C). Furthermore, eccentric contractions require lower levels of voluntary activation by the nervous system (as indicated by the electromyogram) to achieve a given muscle force (Fig. 1D) (4).

Although concentric contractions provide the propulsive force necessary for such movements as running, jumping, throwing, and lifting, a common human-movement strategy is to combine eccentric and concentric contractions into a sequence known as the stretch-shorten cycle (26). The prevalence of this movement strategy can probably be attributed to several factors, such as its ability to maximize performance, to enhance

Fig. 1. Mechanical and activation characteristics of eccentric contractions. *A*: movement depends on ratio of muscle and load torques. *B*: ratios of muscle and load torques that produce isometric (no change in muscle length), concentric (shortening), and eccentric (lengthening) contractions. *C*: variation in maximum muscle force as a function of muscle velocity. *D*: differences between concentric and eccentric contractions in required muscle activation (EMG) to achieve a given muscle force.



mechanical efficiency, and to attenuate impact forces (27, 43). The stretch-shorten cycle involves an initial eccentric contraction (typically a small-amplitude stretch at a moderate-to-fast velocity) that is followed immediately by a concentric contraction (Fig. 2). Although inclusion of the stretch-shorten cycle in a movement can require substantial training (e.g., the movement known as the “clean” in Olympic weightlift-

ing), it appears in most movements without the need for specialized training.

The most commonly recognized attribute of the stretch-shorten cycle is its ability to maximize the work done by the muscle (6). This effect is accomplished by the initial eccentric contraction producing a greater muscle force at the beginning of the concentric contraction, compared with a movement that involves only a concentric contraction. In the example shown in Fig. 2, where the goal was to jump as high as possible, the Achilles tendon force is plotted against muscle velocity for two jumps; one jump (upper line) included a stretch-shorten cycle, whereas the other jump involved only a concentric contraction. For these two jumps, the Achilles tendon force at the beginning of the concentric contraction (*y*-intercept) was greater for the jump that included the stretch-shorten cycle. As a result, the area under the concentric part of the force-velocity curve, which represents the work done by the muscles during the propulsive phase of the jump, was greater for the jump that used the stretch-shorten cycle. Use of the stretch-shorten strategy can increase the vertical-jump height of athletes by ~6 cm (28).

The inclusion of eccentric contractions in human movements, however, is not limited to the stretch-shorten cycle. For example, consider the task of raising and lowering the load shown in Fig. 1A. The lowering phase of this movement, which is accomplished by an eccentric contraction of the elbow flexor muscles, differs from the eccentric contraction in a stretch-shorten cycle in the magnitude of the displacement experienced by the muscle fibers. When the stretch-shorten cycle is used to maximize the power produced by a muscle, the increase in muscle length during the eccentric contraction is relatively small compared with that required during the controlled lowering of a load. Such observations suggest that there are at least two other reasons

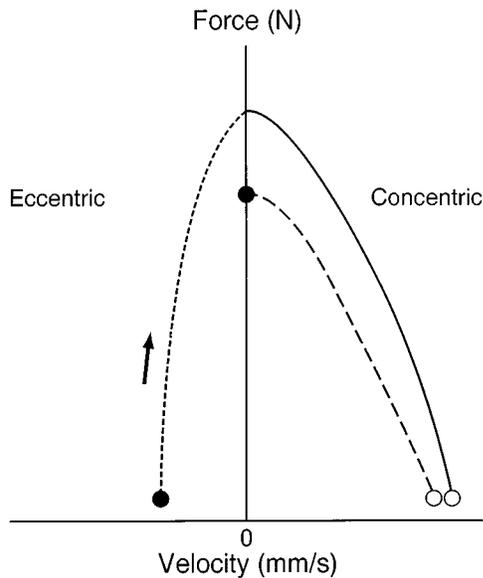


Fig. 2. Idealized force-velocity relationship for calf muscles (soleus and gastrocnemius) during 2 jumps to reach maximum height (see Refs. 7, 16, 21). In one jump (dashed-solid line), muscles performed a stretch-shorten cycle. In other jump (dashed line), muscles performed only a concentric contraction. Each jump began (based on ground reaction force) at solid circle and concluded with takeoff at open circle. Maximum force (measured at tendon), greater positive work (area under force-velocity curve for velocity >0), and highest jump were achieved with stretch-shorten cycle.

why eccentric contractions are included in a movement: the greater mechanical efficiency and the energy dissipation that can be achieved with eccentric contractions. Komi (27; see also Ref. 48), for example, reported that the mechanical efficiency (ratio of work performed to energy expenditure) of a stretch-shorten movement performed by the legs on an inclined-sled apparatus was ~40% compared with the conventionally cited 20–25% for concentric contractions. This comparison suggests that it is more economical to perform a given amount of work with a movement that involves a stretch-shorten cycle than with one involving only a concentric contraction. Furthermore, the ability of muscle to absorb energy during an eccentric contraction can be used to brake a movement and probably serves to protect less compliant elements (e.g., bone, cartilage, ligament) of the neuromuscular system from damage due to high-impact forces and repetitive low-level forces (27, 51). These considerations suggest that the reasons for including an eccentric contraction in a movement may vary across tasks but that the net effect is an enhancement of performance.

CONSEQUENCES OF ECCENTRIC CONTRACTIONS

Based on the cross-bridge theory of muscle contraction, the force exerted by muscle is generated by the interaction of actin and myosin, which results in the myofibrillar proteins translating relative to one another. However, when the muscle fibers are lengthened in an eccentric contraction, the actomyosin bonds are probably disrupted mechanically rather than undergo an ATP-dependent detachment (15). This loading profile undoubtedly places high stresses and strains on the involved structures and may contribute to the tissue damage that occurs with eccentric contractions. Numerous structural abnormalities are evident in muscle after exercise, especially exercise that involves eccentric contractions. These abnormalities include sarcolemmal disruption, dilation of the transverse tubule system, distortion of myofibrillar components, fragmentation of the sarcoplasmic reticulum, lesions of the plasma membrane, cytoskeletal damage, changes in the extracellular myofiber matrix, and swollen mitochondria (16, 43).

Accompanying these changes, there can be a gradual increase in the soreness of the involved muscles that peaks 24–48 h after the exercise. This effect is known as delayed-onset muscle soreness. It occurs frequently after the performance of unfamiliar exercises that include eccentric contractions and is attenuated as the exercises are repeated in subsequent sessions (8, 13). Although some investigators have attempted to establish an association between delayed-onset muscle soreness and the exercise-induced remodeling of musculo-tendinous tissues (7, 43), two observations suggest an alternative explanation. First, delayed-onset muscle soreness appears to be related temporally more to an inflammatory response than to the appearance of structural damage (42). Second, gains in muscle strength that result from eccentric contractions appear to be achieved by changes in the neural activation of muscle

rather than by an enhancement of the hypertrophic response (9, 14). Although the role of neural mechanisms in strength gains is not unique to eccentric contractions, the relative significance of these mechanisms seems greater for this type of activity. These findings suggest that the short- and long-term consequences of including eccentric contractions in an exercise program can be to induce structural adaptations in muscle, to activate an inflammatory response, and to modify the neural commands used to control the movement. Whereas these adaptations can also be induced by other types of contractions, they seem to be maximized by eccentric contractions.

NEURAL CONTROL OF ECCENTRIC CONTRACTIONS

In contrast to the decades of research on performance-related aspects of eccentric contractions, it is only in the last decade that much attention has been focused on the control of eccentric contractions by the nervous system. The fundamental issue can be identified by asking the question, Does the nervous system issue a specific command for an eccentric contraction? The most conservative answer is that the nervous system simply grades the amount of muscle activation, and hence the muscle torque, so that when the muscle torque is less than the load torque, the result is an eccentric contraction (Fig. 1*B*). In this scheme, activation of the motoneurons innervating the muscle is independent of the contraction type (*viz.* isometric, concentric, eccentric), and only the activation intensity is modulated in accordance with the desired muscle torque. This scheme would enable the nervous system to employ a single strategy, such as the size principle (10), to activate the involved motoneurons in the different types of muscle contractions. Alternatively, if the activation sequence of motoneurons is different for an eccentric contraction, as suggested by Nardone et al. (33), then the response to the question must be that the nervous system does indeed command an eccentric contraction, as distinct from a concentric or an isometric contraction.

A separate control strategy for eccentric contractions, however, would complicate the task of the nervous system to control movement. For example, this would mean that for movements involving both concentric and eccentric contractions (e.g., Fig. 1*A*) there must be change in the control strategy at the transition between the two types of contractions. Consistent with this possibility, we have found that older adults have greater difficulty than younger individuals in smoothly grading the force exerted by a hand muscle at the transition from a concentric to an eccentric contraction as they raise and lower a submaximal load (30).

Given the possibility that the control of eccentric contractions may be different, we examine the evidence underlying the hypothesis that the neural commands used to control eccentric contractions are unique. The experimental evidence that addresses this hypothesis has been gleaned from a number of protocols, such as those involving studies of maximum voluntary contrac-

tions, motor unit behavior, motor-evoked potentials and reflex testing, and muscle fatigue.

Maximum voluntary contractions. The most common experimental technique used to assess the maximality of a voluntary contraction is to superimpose electric shocks on the muscle during the contraction. The magnitude of the extra force varies among individuals and the muscles that are tested. For example, Allen et al. (3) found for the elbow flexor muscles that subjects were, on average, able to achieve the maximum force in ~25% of their isometric contractions, with the average magnitude varying between 90 and 100% of maximum across the five subjects. For eccentric contractions, however, it appears to be difficult to achieve even 90% of the maximum force by voluntary commands. When subjects performed eccentric contractions with the knee extensor muscles using an exercise machine that maintained a constant angular velocity during the task (isokinetic contraction), the torque exerted by these muscles was much less (~20%) during the maximum voluntary contraction, compared with the torque obtained when electrical stimulation of the quadriceps femoris muscle was superimposed on the voluntary contraction (Fig. 3A) (50).

Furthermore, the magnitude of the muscle activation [as indicated by the electromyogram (EMG)] during a maximum eccentric contraction is often much less than that recorded during a maximum concentric contraction (Fig. 3B). This limitation was evident in the EMG of knee extensor muscles before the onset of movement associated with concentric and eccentric contractions (17). In this experiment, subjects performed either maximum concentric or eccentric contractions with the knee extensor muscles on an isokinetic device (30°/s), and the maximum EMG was compared for the two conditions. For the vastus lateralis muscle, the EMG during the eccentric contraction averaged 84 ± 41 (SD)% of the value for the concentric condition. However, when the subjects ($n = 14$) expected to perform a maximum concentric contraction, but the device forced

an eccentric contraction, the magnitude of the initial EMG for the unexpected eccentric contraction averaged $104 \pm 40\%$ of that recorded in the maximum concentric contraction. These data demonstrate that the initial level of EMG, which preceded the movement, was significantly greater for an expected concentric contraction, whether the subsequent movement involved an expected shortening (concentric) or an unexpected lengthening (eccentric) of the knee extensor muscles.

While young subjects have found it difficult to maximally activate a muscle by voluntary commands during a maximum eccentric contraction, this limitation may vary as a function of age. Numerous reports have indicated that muscle strength (isometric contraction) declines after the age of ~60 yr (32), at a rate of ~10–15% per decade (12). When the maximum force capability of muscle is assessed with nonisometric contractions, there is less of a decline with age in force for eccentric contractions compared with concentric contractions (23, 37). Because the shape of the torque-velocity relationship of the knee extensor muscles during voluntary contractions on an isokinetic device does not appear to change with age (23), it is likely that the relative preservation of maximum force for eccentric contractions represents an age-related adaptation in the neural activation of muscle during concentric and eccentric contractions.

These findings indicate that, although the peak force exerted by highly motivated subjects during an eccentric contraction is greater than that achieved with isometric and concentric contractions, it is extremely difficult for subjects to achieve the maximum force during an eccentric contraction. This limitation seems to be caused by a reduced activation (EMG) of muscles during an eccentric contraction. These associations, however, probably change with age, because older adults experience less of a decline in the maximum force obtained with eccentric contractions.

Motor unit behavior. The reduced EMG observed during a maximum eccentric contraction suggests an

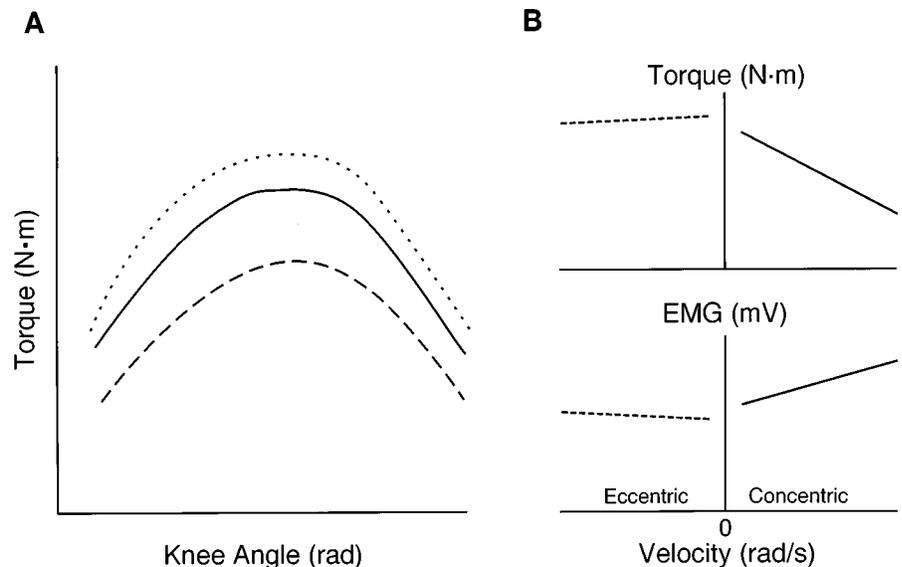


Fig. 3. Evidence of incomplete muscle activation despite a maximum voluntary effort during eccentric contractions (see Refs. 41, 42). *A*: variation in torque exerted by knee extensor muscles on an isokinetic device during a maximum concentric contraction (dashed line), eccentric contraction (solid line), and an eccentric contraction with superimposed supra-maximal electric shocks (dotted line). *B*: although maximum torque is greater during an eccentric contraction, amplitude of EMG (muscle activation) was greater during concentric contraction and increased with velocity.

incomplete activation of the motoneurons that innervate the muscle. This might take the form of a lower level of activation distributed across the entire population of motoneurons or the activation of only a subset of the entire population. Because of the technical limitations of conventional electrophysiological methods, it has not been possible to distinguish between these possibilities. However, magnetic resonance imaging does offer the opportunity to determine the distribution of activation among muscle fibers by quantifying exercise-induced changes in spin-spin (T2) relaxation time (2). With this technique, it is possible to assess the spatial homogeneity of the postexercise changes in T2 and thereby determine whether maximum eccentric contractions involve a lower intensity of activation or whether some regions of a muscle are not activated at all. Initial studies with this technology suggest that brief sequences of submaximal concentric-eccentric contractions against an elastic load do not involve homogeneous activation of an involved muscle (31).

In contrast to the absence of information on motor unit behavior during maximum contractions (25), there is some evidence to indicate that there are differences for submaximal contractions. These differences involve the recruitment order, discharge rate, and recruitment threshold of motor units during the different types of muscle contractions. In a seminal study, Nardone et al. (33) found that high-threshold motor units in the gastrocnemius muscle were selectively activated when the plantar flexor muscles performed eccentric contractions compared with concentric contractions at moderate-to-fast speeds (see also Ref. 24). Furthermore, the rate at which the motoneurons discharged action potentials was lower during the eccentric contractions compared with concentric contractions, and only a few action potentials were discharged at a time, rather than prolonged trains of action potentials (Fig. 4). The observation that the recruitment order of motor units is altered during eccentric contractions provides evidence that the neural commands for these contractions are unique.

Another feature of motor unit behavior affected by the type of muscle contraction is the force at which a

motor unit is recruited. This is known as the recruitment threshold and it is depicted in Fig. 4 as the force level at which each motor unit discharged its first action potential. For a given motor unit, the recruitment threshold is lower during nonisometric (concentric and eccentric) contractions compared with isometric contractions (45, 47). Because this reduction in threshold was evident even at very slow limb velocities (1.5°/s), it is probably not caused by the mechanical properties of muscle, as expressed in the force-velocity relationship (45). Furthermore, the decline in threshold does not appear to depend on sensory feedback, as it was not observed during contractions that the subjects intended to be isometric but which the investigators allowed to be nonisometric (44). These findings suggest that the change in the recruitment threshold of motor units during nonisometric contractions is mediated by descending signals from the brain.

The neural commands associated with eccentric contractions not only alter the recruitment order, discharge rate, and thresholds of motor units within a muscle but also influence the relative activity of motor units among synergist muscles (39). For example, Nakazawa et al. (32) found that the EMG activity in brachioradialis relative to biceps brachii during concentric contractions was greater than that during eccentric contractions at longer muscle lengths (more extended elbow joint). As a result, the ratio of EMGs in brachioradialis and biceps brachii changed as a function of elbow joint angle for eccentric but not concentric contractions. Nardone and Schieppati (34) observed a similar interaction between soleus and lateral gastrocnemius for the task shown in Fig. 4. The selective recruitment of the fast-twitch muscle lateral gastrocnemius over the slow-twitch soleus has been reported previously for the paw-shake response performed by the cat hindlimb (40). This is a rapid movement that involves all segments of the leg and requires significant eccentric contractions to control the intersegmental dynamics (41). Perhaps the selective recruitment of lateral gastrocnemius is necessary because of the need to involve eccentric contractions. On the basis of these differences, the neural commands for eccentric contractions

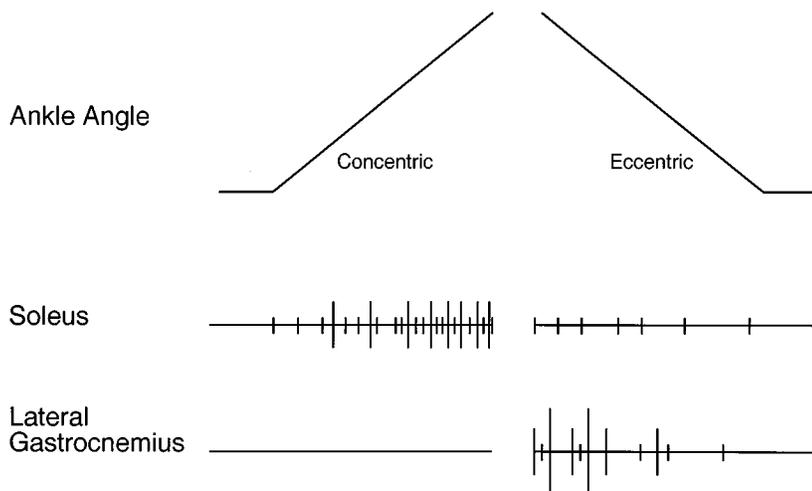


Fig. 4. Motor unit activity (idealized action potentials) in soleus and lateral gastrocnemius muscles of a human volunteer as ankle angle increased (concentric contraction) and decreased (eccentric contraction) to raise and lower a load. Eccentric contractions involved activation of high-threshold motor units with large-amplitude action potentials (see Ref. 31).

appear to be unique because they specify which motor units should be activated, how much they should be activated, when they should be activated, and how this activity should be distributed within a group of muscles.

Motor-evoked potentials. The hypothesis that the neural commands for eccentric contractions are unique is underscored by the observation that the potentials evoked in muscle by transcranial stimulation differ for concentric and eccentric contractions (1). When subjects exerted forces or lifted loads that required comparable levels of EMG, the area (expressed in $\text{mV} \cdot \text{ms}$) of the motor-evoked potential in brachioradialis was greater for concentric contractions compared with isometric contractions. In contrast, the size of the motor-evoked potentials was less in both brachioradialis and biceps brachii during eccentric contractions compared with isometric contractions. Furthermore, the amplitude of the Hoffmann (H) reflex evoked in brachioradialis by electrical stimulation of the radial nerve was modulated in a similar manner, such that it was greatest during concentric contractions and least during eccentric contractions (see also Ref. 38).

Because the variation in the evoked potentials across the contraction types was similar for the cortical (transcranial) and peripheral (H reflex via the radial nerve) stimuli, it is likely that the effect was mediated by a mechanism located in the spinal cord. Abbruzzese et al. (1) proposed that subtle changes in cortical excitability may modulate the response of the motoneurons to synaptic input and thereby produce changes in motor unit behavior. For example, the descending signals associated with an eccentric contraction may include a component that modifies the excitability of the motoneurons so that an input signal directed to the motoneuron pool causes different members of the population to be activated. Perhaps eccentric contractions involve a reduced excitability of smaller motoneurons (1).

Muscle fatigue. One functional consequence of the specificity in neural commands for the different types of muscle contractions is the effect on muscle fatigue [for issues related to strength training, see reports by Hortobágyi et al. (21, 22)]. Most studies have found that the decline in muscle force is less during fatiguing protocols involving voluntary eccentric contractions compared with concentric contractions. For example, Tesch et al. (46) had subjects perform three sets of 32 maximal contractions with the knee extensor muscles on an isokinetic device and reported that the decline in force was negligible when the task involved only eccentric contractions but decreased by 34–47% in each set for concentric contractions (Fig. 5). Furthermore, the EMG for the vastus lateralis and rectus femoris muscles, which was lower for the eccentric contractions, increased in each set of maximal contractions for both the concentric and eccentric conditions (Fig. 5). This effect appears to be robust over a range of speeds (30–180°/s) and ranges of motion (70–90°) for the knee extensor muscles on an isokinetic device (11, 18, 36) but not for the leg-press task (29).

The significance of the neural commands in the observed behavior during voluntary fatiguing contrac-

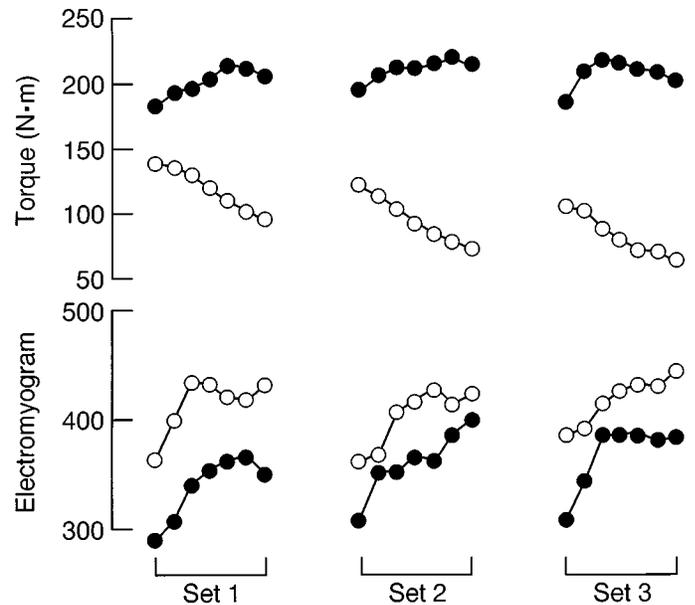


Fig. 5. Torque exerted by knee extensor muscles and EMG recorded in vastus lateralis muscle during 3 sets of 32 maximal contractions performed on an isokinetic device (see Ref. 44). ●, Eccentric contractions; ○, concentric contractions.

tions is underscored by a comparison with the performance when the muscles are activated by percutaneous electrical stimulation. Binder-Macleod and Lee (5) examined the fatigability of the quadriceps femoris muscles during evoked concentric and eccentric contractions performed on an isokinetic device. For both conditions, the stimulator output (10 pulses at ~14 Hz)

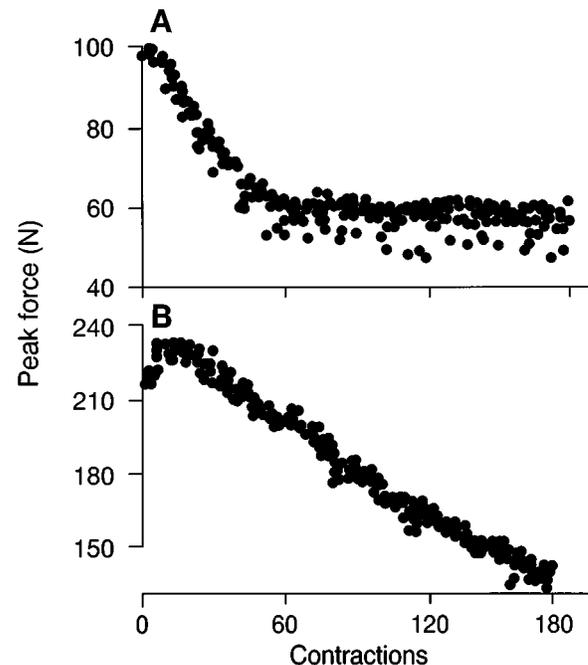


Fig. 6. Decline in force during concentric (A) and eccentric (B) contractions performed by quadriceps femoris muscle. Muscle was activated by percutaneous electrical stimulation, and contractions were performed on an isokinetic dynamometer. [Redrawn from Binder-Macleod and Lee (5)]

was set to elicit a force that was ~20% of the maximum force that could be exerted during a voluntary isometric contraction. The protocol involved 180 contractions, each performed at a rate of 100°/s over a 70° range of motion about the knee joint. The force exerted by the quadriceps femoris declined during both the concentric and eccentric contractions (Fig. 6). For the concentric contractions, the force decreased by ~40% during the first 40 contractions and then remained constant. In contrast, the force declined linearly by about the same amount during the eccentric contraction protocol. Thus a muscle can experience fatigue during an eccentric contraction provided there is sufficient activation.

The difference in the neural commands for eccentric and concentric contractions is further demonstrated by the effect on a limb that does not participate in the fatigue test. Owings and Grabiner (36) had subjects perform a single-leg protocol in which the knee extensor muscles performed maximal eccentric or concentric contractions on an isokinetic device (30°/s). Before and after the fatiguing contractions, the subjects performed maximal contractions with the uninvolved leg. For the subjects who performed concentric contractions, the force exerted by the uninvolved knee extensors during a maximum concentric contraction was not altered by the fatigue task. In contrast, the subjects who performed the eccentric contractions experienced an 11% increase in the maximum force exerted by the uninvolved knee extensors during an eccentric contraction immediately after the fatigue task. This finding suggests that the series of eccentric contractions was associated with a facilitation of the neuronal circuitry, perhaps at the spinal level, that controls the homologous muscles in the uninvolved leg. A similar effect was not observed during the concentric contractions.

Conclusion. Compared with isometric and concentric contractions, eccentric contractions appear to require unique activation strategies by the nervous system. The experimental evidence supporting this hypothesis includes the reduced activation of muscle during maximum eccentric contractions, an altered recruitment order of motor units during submaximal eccentric contractions, a decrease in the size of the potentials evoked in muscle by transcranial and peripheral nerve stimulation during eccentric contractions, and a greater resistance to fatigue (decline in force) during repeated contractions. Variation in the neural strategy may be accomplished by modulation of the relative excitability within the populations of motoneurons innervating a muscle, its synergists, and the contralateral homologous muscle. The principal functional outcome of the unique activation scheme may be to maximize the activity and thereby preserve the health of high-threshold motor units. These motor units are used minimally during daily activities but are essential for intense athletic competition and for emergency movements that require high levels of muscle power.

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