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Review

Spinal and supraspinal control of motor function during maximal eccentric muscle contraction: Effects of resistance training

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Abstract

Neuromuscular activity is suppressed during maximal eccentric (ECC) muscle contraction in untrained subjects owing to attenuated levels of central activation and reduced spinal motor neuron (MN) excitability indicated by reduced electromyography signal amplitude, diminished evoked H-reflex responses, increased autogenic MN inhibition, and decreased excitability in descending corticospinal motor pathways. Maximum ECC muscle force recorded during maximal voluntary contraction can be increased by superimposed electrical muscle stimulation only in untrained individuals and not in trained strength athletes, indicating that the suppression in MN activation is modifiable by resistance training. In support of this notion, maximum ECC muscle strength can be increased by use of heavy-load resistance training owing to a removed or diminished suppression in neuromuscular activity. Prolonged (weeks to months) of heavy-load resistance training results in increased H-reflex and V-wave responses during maximal ECC muscle actions along with marked gains in maximal ECC muscle strength, indicating increased excitability of spinal MNs, decreased presynaptic and/or postsynaptic MN inhibition, and elevated descending motor drive. Notably, the use of supramaximal ECC resistance training can lead to selectively elevated V-wave responses during maximal ECC contraction, demonstrating that adaptive changes in spinal circuitry function and/or gains in descending motor drive can be achieved during maximal ECC contraction in response to heavy-load resistance training.

Keywords: Corticospinal excitability; Eccentric muscle contraction; H-reflex, Neuromuscular plasticity, Resistance training; V-wave

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1. Introduction

During eccentric (ECC) muscle contraction, myofibers produce force while simultaneously being lengthened that, for electrically innervated muscle preparations *in vitro*, results in markedly greater ($\geq$60% increased) contractile force and work production compared with that observed during isometric (ISO) or shortening (concentric (CONC)) contraction conditions[1−3] (Figure 1). This phenomenon was first verified (extrapolated backwards) for intact human muscle by Abbott et al.[4] In terms of intact human skeletal muscles, a marked deviation (~50% force deficit) can be observed between the shape of the contractile force−velocity relationship when obtained *in vivo* in untrained subjects during maximal voluntary ECC contraction conditions[5−12] versus that recorded for isolated muscle and myofiber preparations *in situ*[2,3] (Figure 1). Notably, however, highly strength-trained individuals seem to be capable of producing substantially higher ECC muscle forces (larger joint moments) compared with untrained subjects,[10] suggesting that maximal ECC muscle strength capacity is trainable.

ECC contractions play a crucial role in the production and control of movement[13] and have been suggested to be uniquely controlled by the central nervous system,[14−17] typically characterized by a more variable motor output compared with CONC contraction conditions.[18] Suggesting the presence of inhibitory neural mechanism(s), electrical muscle stimulation superimposed onto maximal voluntary contractions has been observed to selectively increase active force production during ECC but not CONC muscle actions,[10,19,20] causing the resulting force−velocity relationship to more closely resemble that observed for isolated muscle or myofiber preparations[21] (Fig. 1).

High levels of ECC muscle strength are required in many types of sports, because this strength provides an enhanced

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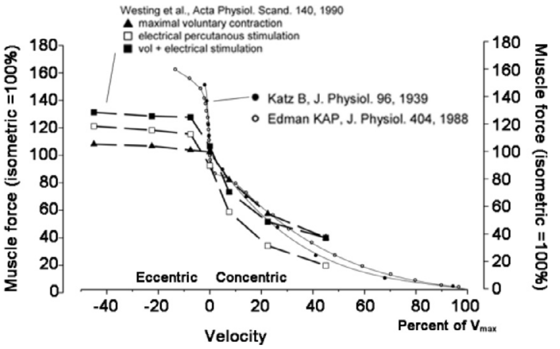

Fig. 1. Contractile force−velocity relationships obtained for shortening (CONC) and lengthening (ECC) contractions in isolated *in vitro* preparations of whole muscle[2] and single muscle fibres[3] obtained from the frog (*Rana Temporaria*, m. sartorious at 11.5°C[2]; anterior tibialis muscle fibers at 1.4°C−1.5°C[3]). On the vertical axis (muscle force) a unit of 100 corresponds with a maximal ISO contraction force *in vitro*. On the velocity axis, 100% corresponds with V_{max}. Positive and negative velocities denote CONC and ECC muscle actions, respectively. Superimposed curves show muscle strength measured *in vivo* during maximal voluntary activation and/or when percutaneous electrical stimulation was applied to the knee extensors.[19] *In vivo* muscle strength was obtained by use of isokinetic dynamometry as the maximal knee extensor torque generated at 60° knee joint angle (0° = full knee extension), during (a) maximal voluntary muscle activation (*triangles*), (b) electrical muscle stimulation (*open boxes*), and (c) electrical stimulation superimposed onto maximal voluntary contraction (*closed boxes*). To scale isokinetic knee joint angular velocity, a maximal angular velocity of 800°/s was assumed for maximal unloaded knee extension[115,116] with a force unit of 100, corresponding with the maximal voluntary ISO strength (MVC). CONC = concentric; ECC = eccentric; ISO = isometric; MVC = maximum voluntary contraction; V_{max} = maximal unloaded contraction velocity. Adapted from Aagaard and Thorstensson[21] with permission.

capacity to decelerate movements in very short time and thereby perform fast stretch−shortening cycle actions (e.g., rapid jumping),[22] while also allowing rapid shifts in movement direction (e.g., fast side-cutting movements).[23] Furthermore, high ECC strength in antagonist muscles provides an enhanced capacity to decelerate and break movements at the end of the range of motion, thereby potentially protecting against injury to ligaments (e.g., the anterior cruciate ligament [ACL]) and joint capsule structures.[6,24] High ECC strength in specific antagonist muscles also plays an important role for performing rapid limb deceleration at end of the range of motion in fast ballistic movements, thereby yielding a longer time for limb acceleration and thus allowing the attainment of higher movement speeds.[25] Finally, high levels of ECC muscle strength may be desirable in older individuals to decrease the risk of falls during stair descent.

Signs of nonuniform muscle activation typically can be observed during maximal voluntary ECC muscle contractions in untrained subjects (Fig. 2),[7,26] and it has been suggested that such neural strategies may serve as a protective mechanism against cytoskeletal damage induced by repetitive ECC muscle actions,[7,27] which typically is observed when more uniform patterns of myofiber recruitment are evoked by means of electrical percutaneous or motor nerve stimulation.[28,29]

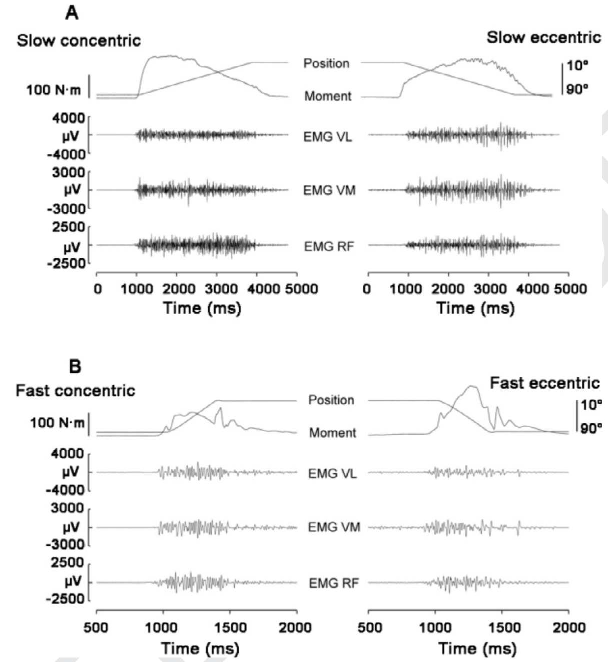

Fig. 2. Raw tracings of isokinetic knee joint moment and (EMG signals obtained in an untrained male subject during maximal CONC (*left*) and ECC (*right*) knee extensor contraction during joint movements performed at slow (A) and fast (B) joint angular speeds (30°/s and 240°/s, respectively). Range of joint motion was from 90° to 10° during CONC contraction and from 10° to 90° during ECC contraction (0° = full knee extension). Note the appearance of large EMG amplitude spikes separated by short interspike periods of no or low neuromuscular activity during ECC contraction conditions, indicating a more nonuniform pattern of muscle activation during maximal ECC compared with CONC muscle actions in untrained individuals. CONC = concentric; ECC = eccentric; EMG = electromyography. Adapted from Aagaard et al.[7] With permission.

2. Mechanical muscle function during ECC muscle actions of maximal voluntary effort

Untrained individuals typically demonstrate a levelling off (plateauing) in maximal muscle strength during slow CONC or ECC muscle actions, whereas strength-trained individuals do not.[5,6] Notably, this plateauing in maximal muscle strength can be removed in response to heavy-load resistance training (HLRT).[5,30,31] Furthermore, no plateauing seems to be present in highly resistance-trained athletes exposed to years of HLRT.[6,9] Conversely, resistance training using low external loads and high contraction speeds seems to have no effect on the plateauing phenomenon,[5] suggesting that heavy-load resistance exercise (>80% 1 repetition maximum) should be used to diminish or fully remove the influence of this force-inhibiting mechanism. HLRT (i.e., resistance training using exercise loads ~80%−85% 1 repetition maximum) consistently has been reported to result in marked gains in maximal ECC muscle strength.[5,12,26,31−43] Moreover, resistance training using maximal ECC muscle contractions or coupled ECC−CONC contractions (i.e., involving stretch−shortening cycle muscle actions) seems to evoke greater gains in maximal ECC muscle strength than CONC training alone.[32−35,42,44] In contrast, maximal ECC muscle strength seems to remain unaffected in response to low-load resistance training,[5,33,41,45] suggesting

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