

HIGHLIGHTED TOPIC | *Eccentric Exercise*

Insights into the neural control of eccentric contractions

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Duchateau J, Baudry S. Insights into the neural control of eccentric contractions. *J Appl Physiol* 116: 1418–1425, 2013. First published February 21, 2013; doi:10.1152/jappphysiol.00002.2013.—The purpose of this brief review is to examine our current knowledge of the neural control of eccentric contractions. The review focuses on three main issues. The first issue considers the ability of individuals to activate muscles maximally during eccentric contractions. Most studies indicate that, regardless of the experimental approach (surface EMG amplitude, twitch superimposition, and motor unit recordings), it is usually more difficult to achieve full activation of a muscle by voluntary command during eccentric contractions than during concentric and isometric contractions. The second issue is related to the specificity of the control strategy used by the central nervous system during submaximal eccentric contractions. This part underscores that although the central nervous system appears to employ a single size-related strategy to activate motoneurons during the different types of contractions, the discharge rate of motor units is less during eccentric contractions across different loading conditions. The last issue addresses the mechanisms that produce this specific neural activation. This section indicates that neural adjustments at both supraspinal and spinal levels contribute to the specific modulation of voluntary activation during eccentric contractions. Although the available information on the control of eccentric contractions has increased during the last two decades, this review indicates that the exact mechanisms underlying the unique neural modulation observed in this type of contraction at spinal and supraspinal levels remains unknown and their understanding represents, therefore, a major challenge for future research on this topic.

electromyogram; motor unit; voluntary activation; cortical excitability; spinal excitability

AS REVIEWED IN ANOTHER ARTICLE of this *Highlighted Topics* series (31), the force produced by a muscle is influenced by several parameters such as muscle length, contraction velocity, and contraction type. In animal studies, for example, the force produced by whole muscles or single fibers during a maximal contraction is greater during lengthening (eccentric) than shortening (concentric) contractions, at least when measured on the plateau and on the descending limb of the length-tension curve (20, 38, 49). Similarly, maximal torque during electrically induced and voluntary contractions is lower for concentric than eccentric contractions in humans (61, 64, 76), although the electromyogram (EMG) amplitude is either similar or less during maximal eccentric contractions produced by voluntary muscle activation (2, 5, 48, 75). Therefore, both muscular and neural characteristics contribute to the greater mechanical output and efficiency [ratio of work performed to energy expenditure classically reported during eccentric contractions (12); for reviews, see Refs. 1, 16, 21].

This brief review focuses on three main issues: 1) the possible deficit in muscle activation during maximal eccentric contractions, 2) the specificity of the control strategy used by the central nervous system (CNS) during submaximal eccentric contraction, and 3) the potential mechanisms responsible for this “unique” neural activation (21).

VOLUNTARY ACTIVATION DURING MAXIMAL CONTRACTION

A major question in the performance of eccentric contractions is whether the voluntary activation is sufficient to develop the maximal force capacity of the muscle. Three main experimental approaches have been used to probe the maximality of muscle activation during eccentric contractions: 1) surface EMG recordings, 2) twitch interpolation, and 3) motor unit recordings. To avoid the possible feedback-mediated influence of contraction velocity and muscle length across contraction types, most studies have used an isokinetic dynamometer to control limb velocity during maximal anisometric contractions.

EMG recording. The most widely used approach to estimate the activation signal sent to the muscle is to measure the EMG amplitude recorded with surface electrodes. In such experi-

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mental conditions, surface EMG amplitude is often less during maximal eccentric contraction than during maximal concentric and isometric contractions (2, 5, 40, 61, 73, 75). However, some studies have not found any difference in EMG amplitude between eccentric and concentric contractions (6, 8, 18, 19, 47) or between eccentric and isometric contractions (27). This discrepancy across studies may depend on differences in the muscle investigated, the joint angle at which the measurements were made, or the presence of an isometric contraction prior to the anisometric contraction (42). In addition, the interference EMG signal is influenced by amplitude cancellation, especially during high-torque contractions (39), which may differ across contraction types depending on the EMG measurement (mean amplitude of the rectified EMG or root mean square amplitude) and the respective contributions of motor unit recruitment and rate coding to the net muscle force. For example, the greater motor unit discharge rates during concentric contractions (see below) likely involve more EMG amplitude cancellation than during eccentric contractions, reducing thereby the difference in EMG between the two contraction types. Thus caution is necessary when using surface EMG amplitude to estimate differences in voluntary activation between contraction types.

Superimposed electrical stimulation. The maximality of muscle activation can also be assessed by superimposing a single stimulus or a brief train of electrical pulses over the muscle or its motor nerve during the force plateau of a maximal voluntary contraction (MVC). The force increment in response to the electrical stimulus is used to quantify the deficit in voluntary activation (30). Although, this method has some limitations (see Ref. 14), it has revealed a greater deficit during eccentric compared with concentric contractions for the knee extensor muscles (Fig. 1; Refs. 5, 11, 76). For example, Beltman and colleagues (11) found a voluntary activation deficit of 21% during a maximal eccentric contraction with the quadriceps femoris compared with a deficit of only 8% during a maximal concentric contraction both performed at an angular velocity of 60°/s. A similar conclusion was reached with the

application of transcranial magnetic stimulation (TMS; see Ref. 48). The training level of the subjects can also influence the magnitude of the deficit, as Amiridis and colleagues (5) reported that highly trained athletes do not display any deficit in voluntary activation of the quadriceps during eccentric contraction performed at velocities ranging from 15 to 120°/s. Therefore the training status of the subjects could explain inconsistent results on activation deficit for this muscle in a previous study (6). Furthermore, as for isometric contractions (10), the degree of activation deficit during eccentric contractions seems to vary across muscles; it is much greater for the knee extensors than for the dorsiflexor muscles (8, 41).

Motor unit activity. Another useful approach to assess voluntary activation, but particularly challenging at maximal or near maximal forces, consists of recording single motor unit activity (17). Although this method cannot measure the completeness of motor unit recruitment, it can be used to compare motor unit discharge rate. On the basis of previous work that indicated an upper limit of motor unit recruitment of ~80–90% MVC torque for most limb muscles (44, 74), data on rate coding during MVCs can provide insight on differences in motor output between contraction types. In the only study that performed such recordings, Del Valle and Thomas (15) were able to record the discharge rate of motor units in triceps brachii during maximal eccentric and concentric contractions. They observed lower discharge rate during maximal eccentric contractions compared with concentric contractions. Because in this study surface EMG during the maximal eccentric contractions represented only ~75% of that during maximal concentric contractions, submaximal activation may have been responsible for the lower motor unit discharge rate in the former condition. However, when contraction intensities for the two anisometric contractions were adjusted using surface EMG, motor unit discharge rates during the eccentric contractions were still lower than during concentric contractions (15).

The results obtained with all three techniques (surface EMG amplitude, twitch superimposition, and motor unit recordings) converge on the same conclusion that voluntary activation is often not maximal during eccentric contraction in untrained individuals and may be constrained by mechanisms that establish motor unit discharge rate (see below for the potential mechanisms).

SPECIFICITY OF THE CONTROL STRATEGY DURING SUBMAXIMAL CONTRACTION

Another central question in the field during the last two decades has been whether submaximal eccentric and concentric contractions are controlled with a similar activation strategy (21). Because the activation of motoneurons depends on the interaction between the net synaptic input and the distribution of intrinsic properties across the population of motoneurons (28), the possibility exists for a qualitative difference in the activation signal sent to muscle during the two types of anisometric contractions. This question has been addressed with protocols that involve either of two types of loading modalities: 1) lifting (concentric) and lowering (eccentric) a constant load over a prescribed range of motion and 2) assisting (concentric) and resisting (eccentric) the torque produced by a servomotor device that regulates the angular velocity of the limb. Muscle activation during these studies has mainly

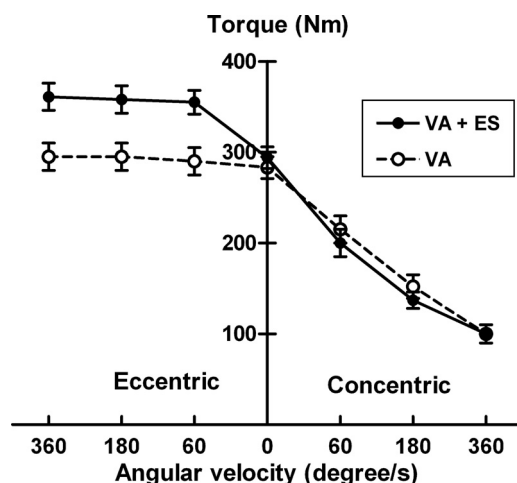


Fig. 1. Torque-velocity relation during maximal contractions. Illustration of the torque-velocity relation of the knee extensor muscles during isometric and anisometric (eccentric and concentric) contractions performed at 3 different angular velocities. Data (means \pm SE) were obtained during maximal voluntary activation alone (VA) and with superimposed electrical stimulation (VA + ES). Note that the 2 relations differ only during the eccentric contractions. Data from Ref. 76.

been investigated with surface EMG and single motor unit recordings.

Surface EMG. Two factors contribute to the lesser EMG amplitude when a submaximal load is displaced during an eccentric contraction. First, fewer motor units are required to reach a given absolute torque during eccentric contractions due to the greater intrinsic force capacity of the muscle fibers when lengthened during the contraction (20, 31, 38, 49). Second, net muscle torque is less than the load torque during contractions, whereas muscle torque must exceed the load torque during concentric contractions. Moreover, the modulation of muscle activation appears to differ during submaximal eccentric contractions when resisting an imposed load, as it is the case with an isokinetic dynamometer, compared with controlling the displacement of an inertial load over a prescribed range of motion at a given velocity. The amplitude of the activation signal varies little during the whole range of motion when resisting an imposed load in contrast to the modulation that occurs when a load is being displaced (16). As already mentioned, however, surface EMG may not be sensitive enough to detect modest differences in motor unit activity during submaximal contractions (see Ref. 50). Therefore, the preferred approach to investigate the specific modulation of the activation signal during submaximal eccentric contractions is to record the discharge of action potentials by single motor units.

Motor unit recruitment order. In contrast to the lack of information on motor unit activity during maximal anisometric contractions, more is known about the differences between

concentric and eccentric contractions at submaximal intensities. In a pioneering study that involved the recording of single motor units during a movement that involved lifting and lowering an inertial load with the plantarflexor muscles to match a prescribed trajectory, Nardone and colleagues (53) observed that high-threshold motor units were selectively activated during eccentric contractions compared with concentric contractions. They reported that 15% and 50% of the motor units recorded in soleus and gastrocnemii, respectively, were only recruited during eccentric contractions. These units had high recruitment thresholds (as measured during isometric contractions) and their activation was accompanied by the derecruitment of other units that were active during the concentric phase of the movement. The selective recruitment of high-threshold motor units during the eccentric contractions occurred most often at faster angular velocities. Nardone and colleagues (53) suggested that a change in motor unit recruitment order might be related to the requirements of the task. Subsequently, Howell et al. (33) also reported the selective recruitment of a few motor units (3 of 21 units) in the first dorsal interosseus when lifting and lowering an inertial load. In this study, however, motor units activated only during the eccentric phase of the movement had low recruitment thresholds, and their activation appeared mainly at the transition from the lifting to the lowering phase of the movement or when oscillations occurred during muscle lengthening.

In contrast, most subsequent studies have not found any difference in motor unit recruitment between eccentric and

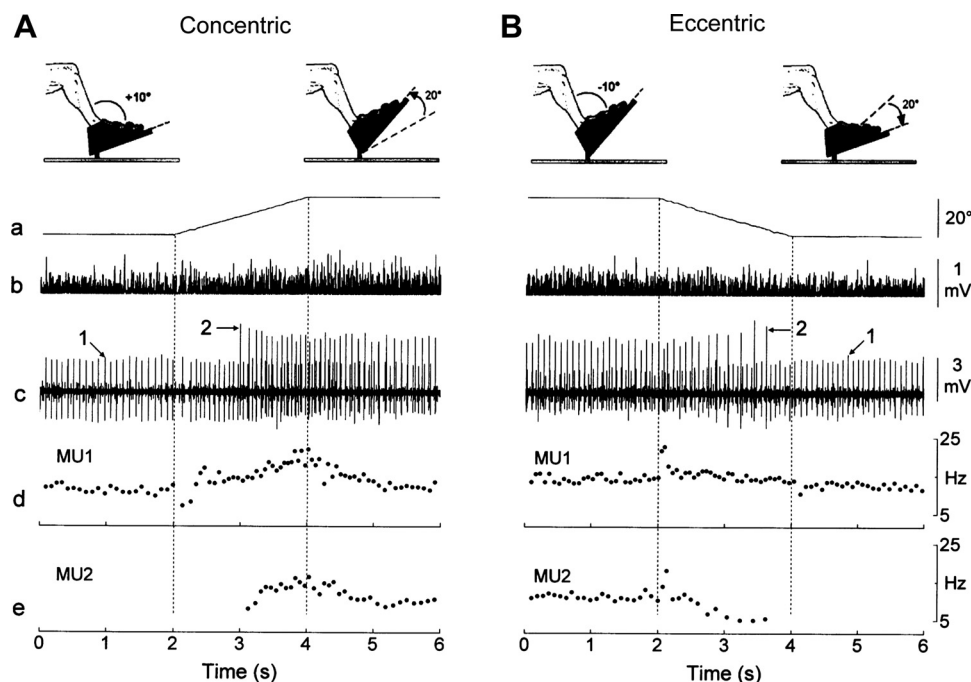


Fig. 2. Modulation of motor unit discharge rate during submaximal concentric and eccentric contractions. Discharge and recruitment of 2 motor units (MU1 and MU2) in tibialis anterior during an initial isometric contraction and subsequent concentric (A) and eccentric (B) contractions with the dorsiflexor muscles. Vertical dotted lines indicate the beginning and end of each movement. Traces indicate angular ankle displacement (a), rectified surface (b), and intramuscular (c) EMG of the tibialis anterior and instantaneous discharge rate of MU1 (d) and MU2 (e). MU2 (# 2 on trace c) was recruited during the concentric contraction at an ankle angle of 1° of dorsiflexion and derecruited during the eccentric contraction at a more extended ankle joint angle (8° plantarflexion) whereas MU1 (# 1) was continuously activated during the three contraction types. At the transition from the initial isometric contraction to the anisometric contraction there was either a transient decrease (concentric contraction) or increase (eccentric contraction) in discharge rate due to an unloading reflex or stretch reflex, respectively (d–e). Subsequently, there was greater modulation of discharge rate for both motor units during the concentric contraction than during the eccentric contraction. [Adapted with permission from (56). Copyright © 2006, John Wiley and Sons.]

concentric contractions when lifting and lowering an inertial load (9, 24, 46, 68–70) or resisting a torque motor (4, 56, 70). Furthermore, it has been shown that when individuals performed slow concentric and eccentric dorsiflexion contractions with similar changes in fascicle length of the tibialis anterior, the eccentric contractions displayed a progressive derecruitment of motor units compared with concentric contractions (Fig. 2; Ref. 56). This derecruitment involved the highest threshold motor units as observed during a progressive reduction in torque during an isometric contraction, in agreement with the size principle (29).

A parsimonious interpretation of these findings is that the recruitment order of motor units is usually similar during eccentric and concentric contractions but that it may vary when the task requires the individual to perform a relatively fast eccentric contraction that matches a prescribed trajectory (16). However, stretches due to small oscillations in muscle length during the braking phase (lengthening phase) or a slight change in joint position at the transition between the concentric and eccentric phases may contribute to the recruitment/derecruitment of some motor units (70). A slight shift in posture may also change either the force vector within the muscle and activate motor units from different muscular compartments (72), particularly in two-joint muscles such as the gastrocnemii

(52), or modify the relative contribution of synergist muscles (51, 53).

Motor unit discharge rate. In addition to motor unit recruitment, the discharge characteristics of motor units modulate the activation signal sent to the muscle (28). As the net muscle torque must exceed the load torque during concentric contractions and be less than the load torque during eccentric contraction, most studies have reported that in addition to unit derecruitment, discharge rate declines when lowering an inertial load compared with lifting the load (15, 37, 46, 67, 69–71). A similar behavior was observed when resisting a torque motor for a comparable change in absolute torque and fascicle length for both eccentric and concentric contractions (Fig. 2; Ref. 56) or when the two anisometric contractions were performed at a same relative torque level (4). Together, these findings indicate that rate coding is modulated differently between concentric and eccentric contractions.

The similar recruitment order of motor units during concentric and eccentric contractions in most studies implies that the CNS employs a single size-related strategy to activate the involved motoneurons in the different types of contractions. However, additional investigations are needed to demonstrate unambiguously whether the changes in recruitment order observed occasionally during eccentric contraction in some con-

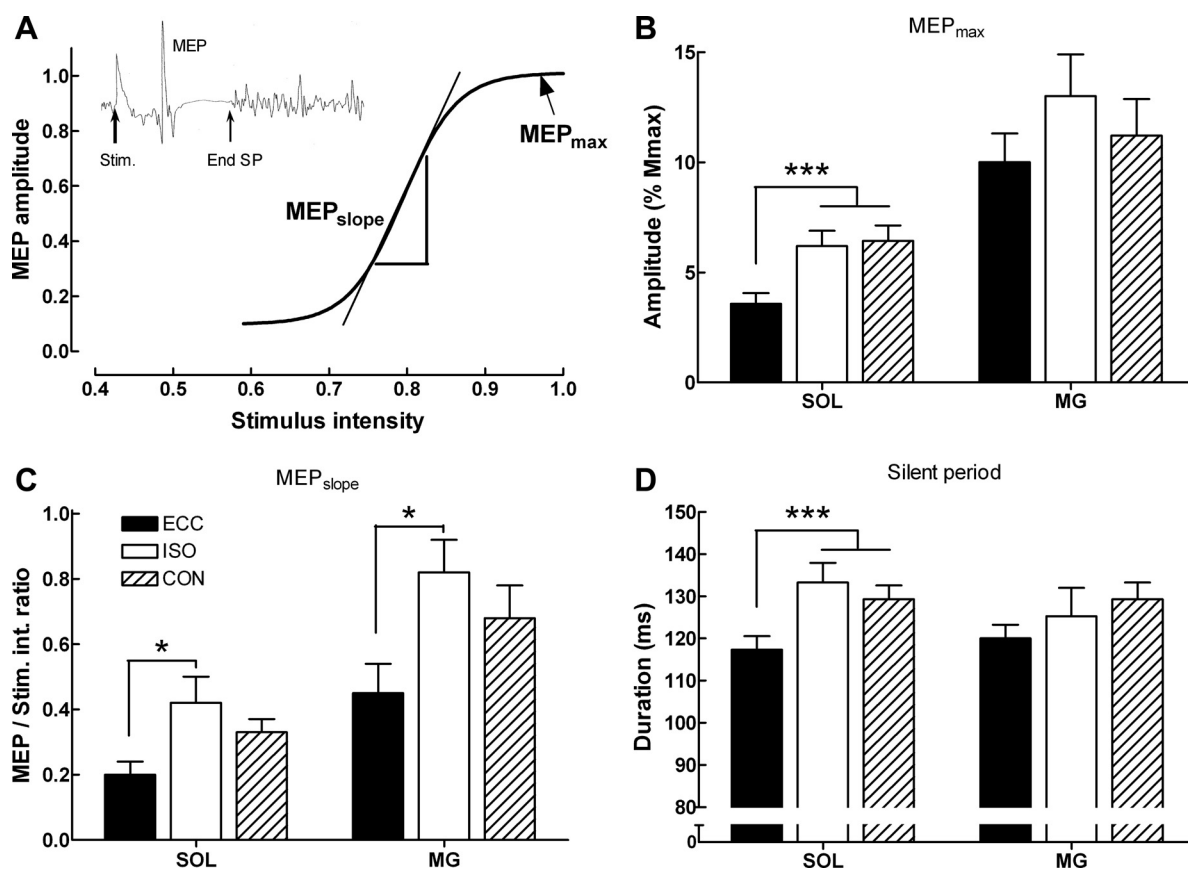


Fig. 3. Modulation of corticospinal excitability during maximal eccentric, isometric, and concentric contractions. A motor evoked potential (MEP) and silent period (SP) evoked in soleus by transcranial magnetic stimulation (TMS) and the associated input-output relation for one subject (A). Graph displays the amplitude of the MEP expressed relative to stimulus intensity. Main parameters are maximal MEP amplitude (MEP_{max}), the slope of the steeper part of the input-output relation (MEP_{slope}), and the duration of the silent period recorded for the greatest stimulus intensity as measured from the stimulus artifact (Stim.) to the end of the SP. Modulations of MEP_{max} (B), MEP_{slope} (C), and the duration of the silent period (D) during eccentric, isometric, and concentric MVCs are shown. Data are means \pm SE for a group of 12 subjects in both soleus (SOL) and medial gastrocnemius (MG) muscles. *Significant difference at $P < 0.05$; eccentric vs. isometric. ***Significant difference at $P < 0.001$; eccentric vs. isometric and concentric. Data from Ref. 19.

ditions are due to a specific strategy related to the task being performed or simply the result of the mechanical conditions encountered by the muscle during its contraction. In contrast, the reduced discharge rate of motor units during eccentric contractions is a common finding regardless of load type (inertial load or resisting a torque motor) and indicates that the activation signal sent to the muscle is less during eccentric contraction.

POTENTIAL MECHANISMS FOR THE SPECIFIC ACTIVATION IN ECCENTRIC CONTRACTION

The reductions in EMG amplitude and submaximal voluntary activation usually observed during eccentric contractions led to the suggestion that motor unit recruitment and discharge rates during maximal eccentric contractions may be limited to protect against muscle damage (2, 5, 15, 64, 75). The proponents of this tension-limiting hypothesis suggest that inhibitory feedback from sensory receptors, especially the Golgi tendon organs, depresses the responsiveness of the motoneuron pool to incoming descending inputs (2, 75). When normalized to the isometric torque, however, the torque-velocity relations are similar during maximal and submaximal (30% of maximal effort) eccentric contraction in the soleus muscle, which suggests that the reduced activation observed during eccentric contractions in untrained individuals may not be explained by a tension-related feedback mechanism (61). Moreover, the observation that a depression in EMG amplitude is already present during a maximal isometric contraction that precedes a subsequent eccentric contraction (25) is consistent with this conclusion. Together, these observations suggest that other mechanisms located at both spinal and supraspinal levels should be involved in the specific neural adjustments associated with eccentric contractions.

Cortical mechanisms. Several electrophysiological methods have been used to investigate the contribution of cortical mechanisms to the control of eccentric contractions. These include recording the motor evoked potential (MEP) in response to TMS and electrical stimulation of the motor cortex (TES) or spinal cord at the cervicomedullary junction (CMEP). The first method assesses the responsiveness of the corticospinal tract, whereas the two other methods test motoneuron responsiveness because they both bypass cortical neurons (63) and their axons are not subjected to presynaptic inhibition (54).

Several studies have reported specific modulation of the output from the brain during eccentric contractions. First, the duration of the silent period in the ongoing soleus EMG recorded after an MEP, which is usually taken as an index of intracortical inhibition when longer than 100 ms (36), is shorter during eccentric compared with concentric contractions of the plantarflexors (Fig. 3D; Ref. 19). Another method to probe changes in inhibitory and facilitatory circuitries of the motor cortex is to use paired-pulse TMS. When the second pulse (test pulse) follows a subthreshold pulse (conditioning pulse) at interstimulus interval of 1–5 ms the test response is inhibited (short-interval intracortical inhibition), whereas it is facilitated at interstimulus interval of 7–20 ms (intracortical facilitation; see Ref. 43). Using this approach, Howatson and colleagues (32) found that short-interval intracortical inhibition was significantly reduced and intracortical facilitation was increased in the ipsilateral motor cortex during eccentric contractions, but

not during concentric contractions. These observations suggest that, compared with concentric contractions, cortical excitability is enhanced in both contralateral and ipsilateral motor cortex during eccentric contractions and that the modulation of networks involved in intracortical and interhemispheric connections varies with the contraction type.

These recent observations support an earlier finding by Fang and colleagues (22) of a greater amplitude for the movement-related cortical potential recorded by electroencephalography (EEG) during the lowering phase relative to the lifting phase of a movement in which the elbow flexors muscles displaced a submaximal load (10% of body wt). A similar difference was observed when subjects performed constant-velocity anisometric MVCs (isokinetic dynamometer) with the same muscle group (23). Together, these data indicate that a greater brain area is involved in control of eccentric contractions regardless of load type (inertial load or torque motor). Although this interpretation contrasts with the findings of Hahn and colleagues (27) for the soleus muscle, it is consistent with those of Gruber and colleagues (26) who concluded that there is greater cortical excitability (increase in the MEP-to-CMEP ratio) during eccentric contractions compared with isometric contractions for the elbow flexor muscles. Even if the increase in motor cortical excitability has been suggested by Gruber and colleagues (26) as an extra excitatory descending drive during eccentric contractions to compensate for spinal inhibition (26), it does not exclude that this contraction-specific modulation may be due to the activation of different cortical areas during eccentric and concentric contractions as shown by functional MRI (45).

Spinal mechanisms. The size of the MEP in response to TMS is reduced for many muscles during eccentric contractions compared with concentric or isometric contractions (Fig. 3). Such observations have been reported either when resisting an imposed torque at a constant velocity (19, 26) or lowering an inertial load even when the background EMG activity was matched in both anisometric contractions in elbow flexor (3,

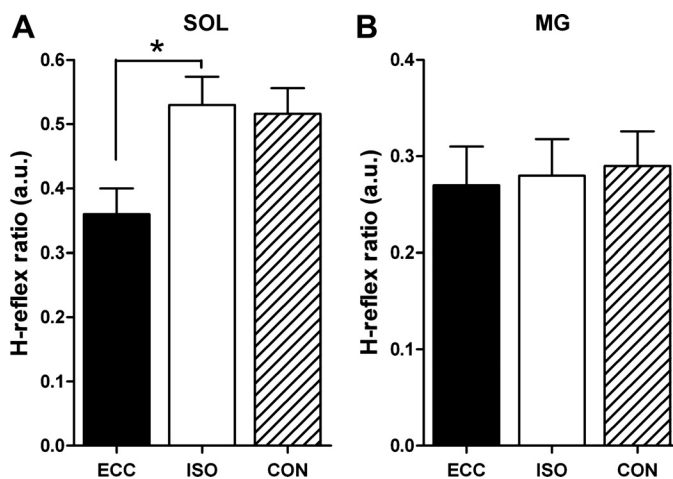


Fig. 4. Modulation of spinal excitability during maximal eccentric, isometric, and concentric contractions. Maximal amplitude of the Hoffmann reflex (H-reflex) normalized to the corresponding maximal M-wave for the SOL (A) and MG (B) muscles during maximal eccentric, isometric, and concentric contractions elicited at the same ankle joint angle (neutral position). Data are means \pm SE for a group of 12 subjects. *Significant difference at $P < 0.001$: eccentric vs. isometric and concentric. Data from Ref. 19.

66) and soleus (65) muscles. Because the MEP amplitude during eccentric contractions was found to be reduced for both TMS and TES (3) or TMS and cervicomedullary junction stimulation (26), the decrease of these responses has been attributed to mechanisms that influence the input and the output at the motoneuron level.

Several mechanisms located at both pre- and postsynaptic sides of the motoneuron may contribute to this reduced responsiveness. A classic method used in humans to assess the modulation of spinal pathways under different conditions is to record the Hoffmann reflex (H reflex; Ref. 58). This electrophysiological response, induced by the electrical stimulation of the Ia afferents originating from muscle spindles, can be modulated by changes in the effectiveness of Ia synaptic input and excitability of the motoneurons. Depression of H-reflex amplitude during eccentric contractions has been reported frequently for different load types (inertial load and torque motor) during both submaximal (3, 55, 62, 65) and maximal (18, 19) contractions (Fig. 4). Because H-reflex amplitude is depressed during passive lengthening (18, 19, 55, 60) and voluntary eccentric contractions are accompanied by an increase in the amount of feedback from muscle spindles (13, 34), some of the spinal modulation during eccentric contractions has been attributed to presynaptic inhibition of the Ia afferents (3, 18, 19, 62) but not always (57). Another potential presynaptic mechanism that may depress H-reflex amplitude is the reduction in transmitter release by the Ia fiber terminals at the synapse with the motoneuron (homosynaptic postactivation depression; Ref. 35), although this mechanism is more evident during passive lengthening than during muscle contractions (60). Nonetheless, the depression of H-reflex amplitude suggests a reduction in the level of excitability (disfacilitation) of the motoneuron pool during eccentric contractions, but the effect seems to differ, for example in soleus and medial gastrocnemius during maximal plantarflexor contractions (Fig. 4B; Ref. 19).

Because the MEPs elicited by electrical stimulation of the motor cortex (3) and the spinal cord (26) are reduced during eccentric contractions, postsynaptic mechanisms may also contribute to the reduction in motor output during eccentric contractions. Potential postsynaptic mechanisms include Ib inhibition (Golgi tendon organ), reciprocal inhibition, and recurrent (Renshaw) inhibition (58). The similar depression of muscle activation at low and high forces suggests that inhibition by Ib afferents likely does not contribute to spinal inhibition during eccentric contractions (61). Although not yet tested with appropriate techniques (see Ref. 58), reciprocal inhibition does not seem to be involved. Indeed, when reciprocal inhibition was indirectly inferred from the level of antagonist muscle coactivation, no substantial difference was reported during eccentric and concentric contractions (2, 5, 19, 56, 59). In contrast, recurrent inhibition, which can limit motor unit discharge rate (7, 77), might increase spinal inhibition during eccentric contractions, in agreement with the lower motor unit discharge rate observed during eccentric contractions (15, 46, 56, 67, 69–71). Experimental data supporting a role for recurrent inhibition in reducing motor units discharge rate during eccentric contractions, however, are still lacking.

CONCLUSION

By considering the voluntary activation of muscle during maximal eccentric contractions and the specificity of the control strategies used by the CNS during submaximal eccentric contractions, this brief review summarizes the potential mechanisms that may be used to control eccentric contractions. Several mechanisms at both supraspinal and spinal levels have been proposed to be responsible for such specific activation. The challenge for the future, however, is to understand the interaction among the different mechanisms that underlie the modulation of muscle activation during eccentric contractions.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: J.D. and S.B. prepared figures; J.D. and S.B. drafted manuscript; J.D. and S.B. edited and revised manuscript; J.D. and S.B. approved final version of manuscript.

REFERENCES

1. Aagaard P. Training-induced changes in neural function. *Exerc Sport Sci Rev* 31: 61–67, 2003.
2. Aagaard P, Simonsen EB, Andersen JL, Magnusson SP, Halkjaer-Kristensen J, Dyhre-Poulsen P. Neural inhibition during maximal eccentric and concentric quadriceps contraction: effects of resistance training. *J Appl Physiol* 89: 2249–2257, 2000.
3. Abbuzzese G, Morena M, Spadavecchia L, Schieppati M. Response of arm flexor muscles to magnetic and electrical and brain stimulation during shortening and lengthening tasks in man. *J Physiol* 481: 499–507, 1994.
4. Altenburg TM, de Ruiter CJ, Verdijk PW, van Mechelen W, de Haan A. Vastus lateralis surface and single motor unit electromyography during shortening, lengthening and isometric contractions corrected for mode-dependent differences in force-generating capacity. *Acta Physiol (Oxf)* 196: 315–328, 2009.
5. Amiridis IG, Martin A, Morlon B, Martin L, Cometti G, Pousson M, van Hoecke J. Co-activation and tension-regulating phenomena during isokinetic knee extension in sedentary and highly skilled humans. *Eur J Appl Physiol* 73: 149–156, 1996.
6. Babault N, Pousson M, Ballay Y, Van Hoecke J. Activation of human quadriceps femoris during isometric, concentric, and eccentric contractions. *J Appl Physiol* 91: 2628–2634, 2001.
7. Baldissera E, Hultborn H, Illert M. Integration in spinal neuronal systems. In: *Handbook of Physiology. The Nervous System. Motor Control*. Bethesda, MD: American Physiological Society, section I, vol. II, 1981, p. 508–595.
8. Baudry S, Klass M, Pasquet B, Duchateau J. Age-related fatigability of the ankle dorsiflexor muscles during concentric and eccentric contractions. *Eur J Appl Physiol* 100: 515–525, 2007.
9. Bawa P, Jones KE. Do lengthening contractions represent a case of reversal in recruitment order? *Prog Brain Res* 123: 215–220, 1999.
10. Behm DG, Whittle J, Button D, Power K. Intermuscle differences in activation. *Muscle Nerve* 25: 236–243, 2002.
11. Beltman JGM, Sargeant AJ, van Mechelen W, de Haan A. Voluntary activation level and muscle fiber recruitment of human quadriceps during lengthening contractions. *J Appl Physiol* 97: 619–626, 2004.
12. Bigland-Ritchie B, Woods JJ. Integrated electromyogram and oxygen uptake during positive and negative work. *J Physiol* 260: 267–277, 1976.

13. **Burke D, Hagbarth KE, Löfstedt L.** Muscle spindle activity in man during shortening and lengthening contractions. *J Physiol* 277: 131–142, 1978.
14. **de Haan A, Gerrits KH, de Ruiter CJ.** Counterpoint: the interpolated twitch does not provide a valid measure of the voluntary activation of muscle. *J Appl Physiol* 107: 355–357, 2009.
15. **Del Valle A, Thomas CK.** Firing rates of motor units during strong dynamic contractions. *Muscle Nerve* 32: 316–325, 2005.
16. **Duchateau J, Enoka RM.** Neural control of shortening and lengthening contractions: influence of task constraints. *J Physiol* 586: 5853–5864, 2008.
17. **Duchateau J, Enoka RM.** Human motor unit recordings: origins and insight into the integrated system. *Brain Res* 1409: 42–61, 2011.
18. **Ducloy J, Martin A.** Evoked H-reflex and V-wave responses during maximal isometric, concentric, and eccentric muscle contraction. *J Neurophysiol* 94: 3555–3562, 2005.
19. **Ducloy J, Pasquet B, Martin A, Duchateau J.** Specific modulation of corticospinal and spinal excitabilities during maximal voluntary isometric, shortening and lengthening contractions in synergist muscles. *J Physiol* 589: 2901–2916, 2011.
20. **Edman KA, Elzinga G, Noble MI.** Enhancement of mechanical performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres. *J Physiol* 281: 139–155, 1978.
21. **Enoka RM.** Eccentric contractions require unique activation strategies by the nervous system. *J Appl Physiol* 81: 2339–2346, 1996.
22. **Fang Y, Siemionow V, Sahgal V, Xiong F, Yue GH.** Greater movement-related cortical potential during human eccentric versus concentric muscle contractions. *J Neurophysiol* 86: 1764–1772, 2001.
23. **Fang Y, Siemionow V, Sahgal V, Xiong F, Yue GH.** Distinct brain activation patterns for human maximal voluntary eccentric and concentric muscle actions. *Brain Res* 1023: 200–212, 2004.
24. **Garland SJ, Cooke JD, Miller KJ, Ohtsuki T, Ivanova T.** Motor unit activity during human single joint movements. *J Neurophysiol* 76: 1982–1990, 1996.
25. **Grabner MD, Owings TM.** EMG differences between concentric and eccentric maximum voluntary contractions are evident prior to movement speed. *Exp Brain Res* 145: 505–511, 2002.
26. **Gruber M, Linnamo V, Strojnik V, Rantalainen T, Avela J.** Excitability at the motoneuron pool and motor cortex is specifically modulated in lengthening compared to isometric contractions. *J Neurophysiol* 101: 2030–2040, 2009.
27. **Hahn D, Hoffman BW, Carroll TJ, Cresswell AG.** Cortical and spinal excitability during and after lengthening contractions of the human plantar flexor muscles performed with maximal voluntary effort. *PLoS One* 7: e49907, 2012.
28. **Heckman CJ, Enoka RM.** Motor unit. *Compr Physiol* 2: 2629–2682, 2012.
29. **Henneman E.** Relation between size of neurons and their susceptibility to discharge. *Science* 126: 1345–1347, 1957.
30. **Herbert RD, Gandevia SC.** Twitch interpolation in human muscles: mechanisms and implications for measurement of voluntary activation. *J Neurophysiol* 82: 2271–2283, 1999.
31. **Herzog W.** Eccentric exercise: mechanisms of enhanced force production in lengthening contractions. *J Appl Physiol*; doi:10.1152/jappphysiol.00069.2013.
32. **Howatson G, Taylor MB, Rider P, Motawar BR, McNally MP, Solnik S, DeVita P, Hortobágyi T.** Ipsilateral motor cortical responses to TMS during lengthening and shortening of the contralateral wrist flexors. *Eur J Neurosci* 33: 978–990, 2011.
33. **Howell JN, Fuglevand AJ, Walsh ML, Bigland-Ritchie B.** Motor unit activity during isometric and concentric-eccentric contractions of the human first dorsal interosseus muscle. *J Neurophysiol* 74: 901–904, 1995.
34. **Hulliger M, Nordh E, Vallbo AB.** Discharge in muscle spindle afferents related to direction of slow precision movements. *J Physiol* 362: 437–453, 1985.
35. **Hultborn H, Meunier S, Morin C, Pierrot-Deseilligny E.** Assessing changes in presynaptic inhibition of Ia fibres: a study in man and the cat. *J Physiol* 389: 729–756, 1987.
36. **Inghilleri M, Berardelli A, Cruccu G, Manfredi M.** Silent period evoked by transcranial stimulation of the human cortex and cervicomedullary junction. *J Physiol* 466: 521–534, 1993.
37. **Kallio J, Søgaard K, Avela J, Komi PV, Seläne H, Linnamo V.** Motor unit firing rate behaviour of soleus muscle in isometric and dynamic contractions. *PLoS One* 8: e53425, 2013.
38. **Katz B.** The relation between force, and speed in muscular contraction. *J Physiol* 96: 45–64, 1939.
39. **Keenan KG, Farina D, Maluf KS, Merletti R, Enoka RM.** Influence of amplitude cancellation on the simulated surface electromyogram. *J Appl Physiol* 98: 120–131, 2005.
40. **Kellis E, Baltzopoulos V.** Muscle activation differences between eccentric and concentric isokinetic exercise. *Med Sci Sports Exerc* 30: 1616–1623, 1998.
41. **Klass M, Baudry S, Duchateau J.** Aging does not affect voluntary activation of the ankle dorsiflexors during isometric, concentric, and eccentric contractions. *J Appl Physiol* 99: 31–38, 2005.
42. **Komi PV, Linnamo V, Silventoinen P, Sillanpää M.** Force and EMG power spectrum during eccentric and concentric actions. *Med Sci Sports Exerc* 32: 1757–1762, 2000.
43. **Kujirai T, Caramia MD, Rothwell JC, Day BL, Thompson PD, Ferbert A, Wroe S, Asselman P, Marsden CD.** Corticocortical inhibition in human cortex. *J Physiol* 471: 501–519, 1993.
44. **Kukulka CG, Clamann HP.** Comparison of the recruitment and discharge properties of motor units in human brachial biceps and adductor pollicis during isometric contractions. *Brain Res* 219: 45–55, 1981.
45. **Kwon YH, Park JW.** Different cortical activation patterns during voluntary eccentric and concentric muscle contractions: an fMRI study. *Neuro Rehab* 29: 253–259, 2011.
46. **Laidlaw DH, Bilodeau M, Enoka RM.** Steadiness is reduced and motor unit discharge is more variable in old adults. *Muscle Nerve* 23: 600–612, 2000.
47. **Linnamo V, Moritani T, Nicol C, Komi PV.** Motor unit activation patterns during isometric, concentric and eccentric actions at different force levels. *J Electromyogr Kinesiol* 13: 93–101, 2003.
48. **Löscher WN, Nordlund MM.** Central fatigue and motor cortical excitability during repeated shortening and lengthening actions. *Muscle Nerve* 25: 864–872, 2002.
49. **Morgan DL, Whitehead NP, Wise AK, Gregory JE, Proske U.** Tension changes in the cat soleus muscle following slow stretch or shortening of the contracting muscle. *J Physiol* 522: 503–513, 2000.
50. **Mottram CJ, Christou EA, Meyer FG, Enoka RM.** Frequency modulation of motor unit discharge has task-dependent effects on fluctuations in motor output. *J Neurophysiol* 94: 2878–2887, 2005.
51. **Nakazawa K, Kawakami Y, Fukunaga T, Yano H, Miyashita M.** Differences in activation patterns in elbow flexor muscles during isometric, concentric and eccentric contractions. *Eur J Appl Physiol* 66: 214–220, 1993.
52. **Nardone A, Schieppati M.** Shift of activity from slow to fast muscle during voluntary lengthening contractions of the triceps surae muscles in humans. *J Physiol* 395: 363–381, 1988.
53. **Nardone A, Romanò C, Schieppati M.** Selective recruitment of high-threshold human motor units during voluntary isotonic lengthening of active muscles. *J Physiol* 409: 451–471, 1989.
54. **Nielsen J, Petersen N.** Is presynaptic inhibition distributed to corticospinal fibres in man? *J Physiol* 477: 47–58, 1994.
55. **Nordlund MM, Thorstensson A, Cresswell AG.** Variations in the soleus H-reflex as a function of activation during controlled lengthening and shortening actions. *Brain Res* 952: 301–307, 2002.
56. **Pasquet B, Carpentier A, Duchateau J.** Specific modulation of motor unit discharge for a similar change in fascicle length during shortening and lengthening contractions in humans. *J Physiol* 577: 753–765, 2006.
57. **Petersen NT, Butler JE, Carpenter MG, Cresswell AG.** Ia-afferent input to motoneurons during shortening and lengthening muscle contractions in humans. *J Appl Physiol* 102: 144–148, 2007.
58. **Pierrot-Deseilligny E, Burke D.** *The Circuitry of the Human Spinal Cord. Spinal and Corticospinal Mechanisms of Movement.* Cambridge, UK: Cambridge University Press, 2012.
59. **Pinniger GJ, Steele JR, Cresswell AG.** The force-velocity relationship of the human soleus muscle during submaximal voluntary lengthening actions. *Eur J Appl Physiol* 90: 191–198, 2003.
60. **Pinniger GJ, Nordlund M, Steele JR, Cresswell AG.** H-reflex modulation during passive lengthening and shortening of the human triceps surae. *J Physiol* 534: 913–923, 2001.
61. **Pinniger GJ, Steele JR, Thorstensson A, Cresswell AG.** Tension regulation during lengthening and shortening actions of the human soleus muscle. *Eur J Appl Physiol* 81: 375–383, 2000.
62. **Romanò C, Schieppati M.** Reflex excitability of human soleus motoneurons during voluntary shortening or lengthening contractions. *J Physiol* 390: 271–284, 1987.

63. Rothwell JC. Techniques and mechanisms of action of transcranial stimulation of the human motor cortex. *J Neurosci Methods* 74: 113–122, 1997.
64. Seger JY, Thorstensson A. Electrically evoked eccentric and concentric torque-velocity relationships in human knee extensor muscles. *Acta Physiol Scand* 169: 63–69, 2000.
65. Sekiguchi H, Nakazawa K, Suzuki S. Differences in recruitment properties of the corticospinal pathway between lengthening and shortening contractions in human soleus muscle. *Brain Res* 977: 169–179, 2003.
66. Sekiguchi H, Kimura T, Yamanaka K, Nakazawa K. Lower excitability of the corticospinal tract to transcranial magnetic stimulation during lengthening contractions in human elbow flexors. *Neurosci Lett* 312: 83–86, 2001.
67. Semmler JG, Kornatz KW, Dinunno DV, Zhou S, Enoka RM. Motor unit synchronisation is enhanced during slow lengthening contractions of a hand muscle. *J Physiol* 545: 681–695, 2002.
68. Søgaard K. Motor unit recruitment pattern during low-level static and dynamic contractions. *Muscle Nerve* 18: 292–300, 1995.
69. Søgaard K, Christensen H, Jensen BR, Finsen L, Sjøgaard G. Motor control and kinetics during low level concentric and eccentric contractions in man. *Electroencephalogr Clin Neurophysiol* 101: 453–460, 1996.
70. Stotz PJ, Bawa P. Motor unit recruitment during lengthening contractions of human wrist flexors. *Muscle Nerve* 24: 1535–1541, 2001.
71. Tax AA, Denier van der Gon JJ, Gielen CC, van den Tempel CM. Differences in the activation of m. biceps brachii in the control of slow isotonic movements and isometric contractions. *Exp Brain Res* 76: 55–63, 1989.
72. ter Haar Romeny BM, Denier van der Gon JJ, Gielen CC. Changes in recruitment order of motor units in the human biceps muscle. *Exp Neurol* 78: 360–368, 1982.
73. Tesch PA, Dudley GA, Duvoisin MR, Hather BM, Harris RT. Force and EMG signal patterns during repeated bouts of concentric and eccentric muscle actions. *Acta Physiol Scand* 138: 263–271, 1990.
74. Van Cutsem M, Feiereisen P, Duchateau J, Hainaut K. Mechanical properties and behaviour of motor units in the tibialis anterior during voluntary contractions. *Can J Appl Physiol* 22: 585–597, 1997.
75. Westing SH, Cresswell AG, Thorstensson A. Muscle activation during maximal voluntary eccentric and concentric knee extension. *Eur J Appl Physiol* 62: 104–108, 1991.
76. Westing SH, Seger JY, Thorstensson A. Effects of electrical stimulation on eccentric and concentric torque-velocity relationships during knee extension in man. *Acta Physiol Scand* 140: 17–22, 1990.
77. Windhorst U. Muscle proprioceptive feedback and spinal networks. *Brain Res Bull* 73: 155–202, 2007.

