Review

Stretching the limits of maximal voluntary eccentric force production in vivo

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Abstract

During eccentric contractions, muscular force production capacity is enhanced compared to isometric contractions. Although this is well accepted in terms of muscle mechanics, maximal voluntary eccentric contractions are associated with neural inhibition that prevents increased force production of in vivo human muscles. However, because it was shown that maximal voluntary eccentric forces can exceed maximum isometric forces by a factor of 1.2–1.4, this review focuses on the question of whether the absent eccentric force enhancement, as observed in many studies, can unambiguously be attributed to an inherent neural inhibition. First, we demonstrate that participant familiarization, preload, and fascicle behavior are crucial factors influencing maximal voluntary eccentric force production. Second, we show that muscle mechanics such as muscle length, lengthening velocity, and stretch amplitude interact when it comes to maximal voluntary eccentric force production. Finally, we discuss the diverging findings on neural inhibition during maximal voluntary eccentric contractions. Because there was no inhibition of the major motor pathways in the presence of enhanced maximal voluntary eccentric forces, further research is needed to test the concept of neural inhibition and to understand why maximal voluntary force production is reduced compared to the force capacity of isolated muscle preparations.

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1. Introduction

The most fundamental property of skeletal muscle during a contraction is actively to produce force, and when an active muscle is lengthened this is referred to as a stretch or an eccentric contraction. In experiments with isolated muscle preparations, or human muscles activated by electrical stimulation, the muscular force production capacity during such eccentric contractions is increased by 1.2–2.4 times that of isometric contractions at the same muscle length. Furthermore, this increase in force capacity is largely unaffected by the lengthening velocity of the muscle, at least beyond a critical velocity.1–4

The majority of experiments on maximal voluntary eccentric contractions, however, have failed to reproduce the findings reported from studies testing isolated muscle preparations or in situ human muscles activated by electrical stimulation. This especially refers to the observation that during maximal voluntary eccentric contractions humans cannot achieve forces or net joint torques that exceed the corresponding isometric reference force. Because this failure in force production was accompanied by reduced muscle activity, as measured by electromyography, maximal voluntary eccentric contractions were associated with neural inhibition.5–8

On the other hand, a number of studies have reported mean maximal voluntary eccentric forces or torques that exceeded the corresponding isometric reference forces by a factor of 1.2–1.4, whereas single participants produced eccentric forces in the range of 1.5–1.8 times that of maximal voluntary isometric contractions (MVICs) (Fig. 1) (Walter Herzog, pers. comm.). Therefore maximal voluntary eccentric forces fall within the range of eccentric forces reported for isolated muscle preparations or electrically stimulated muscles, albeit mostly at the lower end.9–12 Furthermore, electromyography during maximal voluntary eccentric contractions is not necessarily reduced but can also be increased compared to isometric contractions.13,14

Finally, there is ample evidence of residual force enhancement after maximal voluntary eccentric
contractions,15 which can only occur when the eccentric forces exceed their corresponding isometric maximum.

Accordingly, knowledge concerning muscular force production capacity during maximal voluntary eccentric contractions is controversial. This situation implies that one must consider with caution the conclusion that an inherent neural inhibition is the reason for low voluntary eccentric forces or torques. Thus, the first aim of this paper is to stretch the limits of maximal voluntary eccentric force production by highlighting important factors that should be taken into account when conducting research on in vivo eccentric muscle function. The second part of the paper will discuss whether modulations of neural measures can be attributed unambiguously to neural inhibition.

2. Enhanced eccentric forces in vivo—inhibited or undetected?

2.1. Familiarization

Usually, experiments on in vivo eccentric contractions are conducted using motor-driven dynamometers, where participants have to maximally resist the motor that stretches their muscle by extending or flexing the joint under investigation. Being tested in such a constraint itself is unfamiliar, but non-specific participants are rarely used to performing maximal voluntary eccentric contractions. Accordingly, the question is whether the absence of increased forces during maximal voluntary eccentric contractions is due to inherent neural inhibition or the inability to perform the task. In a study by Amiridis et al.,16 maximal voluntary eccentric torque of highly skilled subjects (national- and international-level high jumpers) exceeded the corresponding maximal isometric torque; however, the same did not occur with sedentary participants. Furthermore, the highly skilled subjects showed no signs of neural inhibition while the opposite was the case for the sedentary subjects. Similarly, it has been shown that heavy resistance training diminishes neural inhibition17 and that non-specific training of only 6 weeks’ duration enables participants to produce eccentric forces above the isometric level.18

The importance of familiarization is further supported by our own pilot data (n = 6) for participants who attended 4 test sessions that included 3 MVICs and 3 maximal voluntary eccentric contractions of the dominant leg’s quadriceps femoris muscle; the contralateral leg was tested during Sessions 1 and 4 only. Results showed that the ratio of eccentric to isometric torque increased significantly to 1.29 ± 0.09 and 1.30 ± 0.12 during the last session for the dominant and the contralateral legs, respectively (Fig. 1, unpublished data). Maximal voluntary isometric torque; voluntary activation (VA) during MVICs, which was measured by the interpolation twitch technique;19 and resting twitches remained unchanged, indicating that participants learned how to perform proper maximal voluntary eccentric contractions. Nevertheless, most studies do not report or include familiarization, and studies that used a familiarization period typically showed increased eccentric forces.10,11,13,14

2.2. Preload

Eccentric forces or torques are typically evaluated in relation to the maximal voluntary isometric force or torque at the same joint angle, and thus the same muscle length. It takes a typical subject approximately 300 to 500 ms to reach a maximal steady-state force20—the time required to fully activate the muscle and to take up the compliance of the muscle—tendon unit.21 Linnamo et al.9 demonstrated that maximal voluntary eccentric forces exceeded their corresponding isometric reference only when participants preactivated their muscles to ±5% of the MVICs before the onset of the eccentric contractions. This was confirmed by our own data, where eccentric forces increased above the isometric reference when the eccentric contraction was manually triggered as participants reached at least 95% of their MVICs (i.e., full activation at the starting length before the muscle stretch) (Fig. 2C, unpublished data). In many studies that could not find enhanced eccentric forces, eccentric contractions started at rest or from a low preload. This condition also applies to the seminal work of Westing et al.,5 who introduced the idea of neural inhibition during maximal voluntary eccentric contractions. Therefore the question arises about whether the
interpretation of their results can be fully accepted. Further justification for questioning their results is provided by data from an ongoing study showing that the maximal voluntary eccentric torques do not exceed the maximal voluntary isometric torque when started from 30% or 70% MVICs. However, if the same eccentric torques are not related to the maximal isometric torque but rather to the time-matched isometric torque (i.e., the isometric torque produced at the same time after the onset of the contraction), they exceed the corresponding isometric reference force (Fig. 2A, B, unpublished data). Thus, when comparing eccentric and isometric forces, the level of activation and the time available for activation should be taken into account.

2.3. Fascicle behavior

In studies on eccentric force production in vivo, it is widely assumed that the eccentric contraction begins as soon as the dynamometer triggers joint rotation. However, considering that an eccentric contraction is defined as muscle lengthening (i.e., a lengthening of the contractile elements), due to the effects of preload and muscle–tendon unit compliance, an eccentric contraction may not begin with the start of joint rotation. This is the case because at the start of a contraction fascicles take up tendon compliance, which may result in initial fascicle shortening. This means that contractions from rest contain an initial concentric phase, irrespective of whether or not joint rotation lengthens the entire muscle tendon unit. Therefore, when comparing maximal voluntary isometric steady-state forces with forces from so-called eccentric contractions that started from rest or from a submaximal preactivation, the isometric forces are actually compared to concentric forces (Fig. 2, unpublished data). According to the force–velocity relation, it is therefore not surprising that many studies could not find enhanced eccentric forces.

Furthermore, comparisons between eccentric and isometric forces are usually done at identical joint angles; however, again due to the compliance of the muscle–tendon unit, identical joint angles guarantee only identical muscle–tendon unit lengths, not
identical fascicle lengths. Because fascicle length represents the length of the contractile elements and therefore defines the active force-generating capacity of a muscle, this can also bias the comparison of in vivo eccentric and isometric forces.

3. Influence of contraction conditions on eccentric force production in vivo

3.1. Lengthening velocity

Based on the results from experiments using muscle preparations, it is well accepted that eccentric force production is largely unaffected by lengthening velocity, at least beyond a certain velocity. This result was also found for in vivo human muscles. For example, for the elbow flexors, eccentric forces were lower for an angular velocity of 1 rad/s compared with 2 rad/s and 4 rad/s, but no difference was found between the 2 fast velocities.9 Similarly, during stretch of the quadriceps femoris (QF) group, eccentric torques increased up to an angular velocity of 30˚/s but did not change further with increasing lengthening velocity.16 However, these results are not without exception. For example, Finni et al.25 found that maximal voluntary eccentric forces of QF increased from 60˚/s to 120˚/s angular velocity, but decreased when the QF was stretched at 180˚/s. Furthermore, for a leg press task, eccentric net knee joint torque was independent of angular velocity for joint angles less than or equal to the optimal joint angle, whereas eccentric torque varied with angular velocity for knee joint angles greater than the optimal joint angle.26 In accordance with the work of Finni et al.,25 knee joint torques decreased at high angular velocity for Hahn et al.26 The reason for these different findings for lengthening velocity and voluntary eccentric force remains unclear and requires further research.

3.2. Muscle length and stretch amplitude

Enhanced force production during eccentric contractions is usually associated with increased cross-bridge forces27 and passive forces caused by stretch of the adjustable molecular spring titin.28 Due to inappropriate cross-bridge attachment at short muscle lengths,23 a decrease of the myofilament lattice spacing at long muscle lengths,29 and an increase in titin force with long muscle length,30 eccentric forces normalized to their isometric reference are expected to be higher at long compared to short muscle lengths. The results of the few human in vivo studies on the influence of muscle length on voluntary eccentric force production are controversial. Maximal voluntary eccentric torque of QF during a leg press task increased above MVIC torque at long muscle lengths only,26 but Doguet et al.31 found the exact opposite and Linnamo et al.9 did not find an influence of muscle length on eccentric force production of the elbow flexors. However, these results may be biased by stretch amplitude. Initial data from an ongoing study suggest that eccentric force potentiation of QF is larger at long compared to short muscle length when stretch amplitude is matched (Fig. 3A, B, unpublished data). This result agrees with studies on isolated muscle preparations but requires systematic confirmation. Note, however, that matched joint angular rotation does not necessarily result in the same amount of fascicle lengthening at short and long muscle lengths (Fig. 3C, unpublished data). Summarizing, future studies should consider whether there is an interaction of lengthening velocity, stretch amplitude, and muscle length on voluntary eccentric force production.26,32

4. Neural control of maximal voluntary eccentric contractions—truly unique?

Under well-controlled experimental conditions, maximal voluntary eccentric forces can exceed their corresponding isometric maximum. In contrast to this assertion, in most studies
aimed at investigating the neural control of voluntary eccentric contractions, enhanced voluntary eccentric force was not found. Therefore, the common interpretation that eccentric contractions are associated with neural inhibition should be questioned, and methods used to evaluate potential neural inhibition must be carefully taken into account.

4.1. Voluntary activation as a measure of neural inhibition

Voluntary activation is usually assessed by the interpolation twitch technique or the central activation ratio. Although the relationship between force production and VA is highly nonlinear, both methods use linear formulas to calculate VA. Moreover, both approaches are relatively insensitive at high force levels, which are the 2 main reasons why these techniques should be used as semiquantitative measures only. Also, the techniques are designed for isometric but not eccentric (or concentric) contractions. Applying the interpolation twitch technique for dynamic contractions (eccentric and concentric) has the limitation that the amount of superimposed torque cannot be measured directly but has to be estimated instead.

In the context of neural inhibition and reduced VA during maximal voluntary eccentric contractions, 2 studies are frequently cited. In the first study, VA of QF during maximal voluntary eccentric contractions was 88% ± 2% compared with 95% ± 1% during MVICs; the second study reported VA of 76% ± 12% and 90% ± 9% during eccentric and isometric contractions, respectively. However, in neither study were participants familiarized with the eccentric contractions nor did they produce eccentric torques that exceeded the torque during MVICs, although there is evidence that eccentric QF torques can increase 20%–30% above their isometric maximum. Therefore, the question arises whether the reduced VA, as reported in the literature, is due to an inherent neural inhibition or is caused by the experimental conditions (no familiarization, no preload). Considering that eccentric force production is partly due to passive forces in stretched cross-bridges and titin that do not require activation, it is not surprising that eccentric contractions require less VA to produce the same amount of torque as measured for MVICs. In this context, a recent study found maximal voluntary eccentric torques of QF to be enhanced by 30% above MVICs with similar VA during eccentric and isometric contractions. In contrast, when VA was reduced during eccentric contractions compared to MVIC, torques did not exceed or only slightly (6%) exceeded the isometric maximum.

4.2. Cortical and spinal excitability

In addition to the studies in which surface electromyography or measures of VA were used to investigate potential neural inhibition during maximal voluntary eccentric contractions, a number of studies have analyzed specific neural modulations during eccentric contractions. These experiments mainly used transcranial magnetic stimulation (TMS) of the motor cortex, stimulation of the spinal tract at the cervicomedullary junction, and peripheral nerve stimulation to elicit H-reflex and/or V-wave responses. The findings from these studies were summarized and discussed in a recent review paper, with the conclusion being that cortical and spinal excitability are reduced during eccentric contractions, and inhibition mainly takes place at the spinal level. However, in the review paper, it was not always stated whether eccentric contractions were compared with concentric or isometric contractions. In order to understand the limits of eccentric force production, we will focus only on studies that compared maximal voluntary eccentric contractions with the corresponding isometric contractions.

To the best of our knowledge, only a limited number of studies have looked at specific sites of potential neural modulations when comparing maximal voluntary eccentric contractions to MVICs. One study investigated biceps brachii and brachialis, 3 studies investigated soleus and medial gastrocnemius, and 1 study investigated the vastus lateralis. For the elbow flexors, Gruber et al. found smaller motor-evoked potentials (MEPs) after TMS, as well as smaller cervicomedullary motor-evoked potentials (CMEPs) after electrical stimulation of the spinal tract during eccentric contractions compared to isometric contractions. Because CMEPs decreased more than MEPs, it was concluded that an increased cortical excitability counteracts spinal inhibition at the motoneuron level. Similarly, Duclay et al. observed reduced MEP amplitudes and shorter silent periods after TMS for soleus, which was interpreted as a reduced responsiveness of the corticospinal pathway and as an increased cortical excitability. Because H-reflex amplitudes were reduced as well, inhibition was associated with mechanisms at the spinal level. For the vastus lateralis, smaller MEPs and shorter silent periods were reported for intermediate muscle lengths but not for long ones.

As pointed out before, though, it is possible to achieve maximal voluntary eccentric forces that exceed the corresponding isometric maximum under well-controlled experimental conditions. Despite this, in none of the studies reported above were such enhanced eccentric forces observed. Accordingly, the question arises again if the smaller evoked potentials observed in these studies reported above can be unambiguously attributed to neural inhibition. In this context, the study of Hahn et al. is the only one in which MEPs, CMEPs, and V-waves during maximal voluntary eccentric contractions were measured in the presence of enhanced torques (17% ± 8% above isometric). In contrast to the findings in the other studies, Hahn et al. could not find any modulations of MEPs, CMEPs, and V-waves during maximal voluntary eccentric contractions. This suggests that the major voluntary motor pathways are not subject to substantial inhibition; however, the question remains: Why is the eccentric force enhancement still reduced in most in vivo studies compared to studies using muscle preparations? Because Hahn et al. did not record H-reflex responses, modulations at the spinal level—at the presynaptic and postsynaptic sides of the motoneurons—might be responsible for the reduced force enhancement during maximal voluntary eccentric contractions.

5. Conclusion

It is widely accepted that force production during maximal voluntary eccentric contractions is inhibited by the nervous
eccentric force production with regard to the influence of contraction conditions on eccentric forces beyond those obtained with MVICs. Next, concerning the experimental conditions necessary to achieve MVIC. In the first part of this review, we discussed aspects participants to achieve voluntary eccentric forces as high as 1.8

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Competing interests

The author declares that he has no competing interests.

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