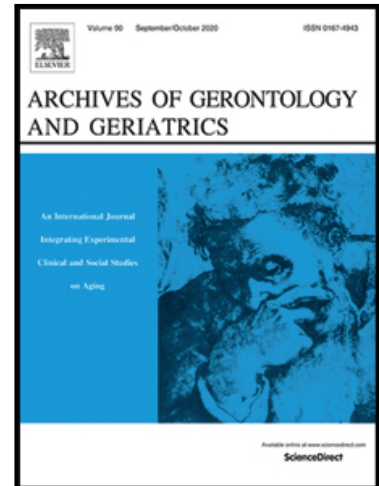


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Neural plasticity is a two-way street: Counteracting age-related neural deterioration with strength training

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Highlights

- Skeletal muscle strength is typically reduced with advancing age
- The nervous system plays a key role in this reduction
- Reductions are evident as decreased efferent neural drive
- Strength training with heavy loads can maintain or improve efferent neural drive
- In turn, skeletal muscle strength can be increased or maintained

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Neural plasticity is a two-way street: Counteracting age-related neural deterioration with strength training

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Running head: Strength Training and Neural Plasticity in Aging

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ABSTRACT

Changes in the nervous system with age are largely responsible for decreased force generating capacity (FGC), i.e., maximal strength and rate of force development. Emphasizing studies applying near-maximal/maximal contractions and stimulation intensity and training intensity as strong evidence, and training intensity above 60% maximal strength, this review uncovered that efferent neural drive, comprising motor unit recruitment and firing frequency, consistently appeared to be a main contributing factor for the decline and subsequent improvement in FGC with age. However, identifying single steps along the efferent neural drive pathway is challenging. Structural changes in the brain and corticospinal excitability alterations may be partly responsible for the reduced FGC, although these are seldom investigated in relation to FGC. Further, methodological constraints associated with measurements of corticospinal excitability challenge firm conclusions. Conduction velocity in the corticospinal tract is slower

with age and intracortical inhibition increases, the latter may be improved following strength training. Peripheral factors – loss of spinal α -motoneurons, reduced spinal α -motoneuron excitability, and reduced conduction velocity – also contribute, albeit without considerable improvements following strength training. Despite methodological constraints associated with corticospinal measurements, we conclude that the efferent neural drive enhancement observed following strength training is likely a result of central nervous system adaptations, as peripheral adaptations appear to be negligible. It therefore seems essential to apply training that specifically targets efferent neural drive enhancement with older age. Heavy loads are imperative for efferent neural drive improvements and should be recommended to maintain or improve efferent neural drive and maximal FGC in older adults.

Key words: older adults, nervous system decline, heavy strength training, efferent neural drive

INTRODUCTION: Age-related decline in force generating capacity

With increasing age, there is a well-established decline in skeletal muscle force generating capacity (FGC), in terms of maximal strength and the ability to produce force rapidly (Lindle et al., 1997; Pearson et al., 2002; Suetta et al., 2019). The latter can be measured as rate of force development (RFD) or power. Both maximal strength and RFD/power have been linked to functional ability (Unhjem et al., 2019), fall risk (Moreland et al., 2004), and mobility limitations (Bean et al., 2003), and are independently associated with risk of all-cause, cardiovascular-, and cancer mortality (Jochem et al., 2019; Ruiz et al., 2008; Schnohr et al., 2025; Volaklis et al., 2015). Importantly, the decline in maximal strength with age is two-five times greater than the reduction in muscle mass (Bruce et al., 1997), showing that other factors than muscle mass play a pivotal role in the loss of FGC with age. As the muscles' ability to produce force is regulated in large part by the nervous system, a thorough examination of the nervous system's role in the age-related deterioration is warranted.

While recent reviews have examined neural determinants of strength decline with ageing (Clark, 2023) and strength training-related neural adaptations (Siddique et al., 2022; Walker, 2021) separately, to the best of our knowledge, there has been no updated review encompassing both themes since that published by Aagaard et al. (2010). This combination may provide unique knowledge of how to combat typical age-related neural deterioration by presenting both perspectives. Moreover, in light of the developments in methodology in recent years, it seems appropriate to provide an updated insight into the neural adaptations that occur with ageing *per se*, as well as in response to strength training. Thus, the aim of the present narrative review was twofold. First, to examine the changes in the nervous system which may be responsible for the reduced FGC with increasing age. Two, to examine the impact of strength training in reversing parts of the age-related nervous system decline and in turn maintain, or even improve, neuromuscular function. Figure 1 represents a conceptual summary of the findings in the present review. Although other modalities of exercise, such as ballistic or skill training, also have the potential to improve neuromuscular function and increase FGC, this was not the focus of the current literature review as we have emphasised strength training (minimum 60 % of 1 repetition maximum (RM) resistance). By emphasising study outcomes from test regimes using near-maximal or maximal contractions and stimulation intensity as strong evidence, this review provides a novel perspective to the existing literature, as these conditions allow for testing of the entire motoneuron pool, most likely a prerequisite to examine strength training-related neural adaptations.

Search strategy and inclusion criteria

A literature search from inception to 20th April 2026 on the PubMed/Medline, CINAHL, Embase and SPORTDiscus databases provided the original articles reviewed. To identify studies reporting data on neural decline which may be associated with strength decrements with age (Part I), searches included the following combination of key words: Strength decline (Including the following MeSH Terms: sarcopenia) OR muscle strength (MeSH Terms: maximal strength, strength) AND older adults (MeSH Terms: ageing, elderly, old, aged). In addition, the following key words were used in combination with the terms above: nervous system OR neural deterioration OR neural OR efferent neural drive OR structural brain changes OR transcranial magnetic stimulation OR H-reflex OR M-wave OR V-wave OR voluntary activation OR electromyography OR firing frequency OR motor unit recruitment. Inclusion criteria included ≥ 1 of the target outcomes; ≥ 60 years of age; comparison with younger age

group or longitudinal study design to identify age-related changes; comparison with relevant age-matched group (e.g., healthy vs. frail) to identify normal aging vs. exacerbated age response. To identify studies reporting data on neural adaptations following strength training with age (Part II), searches included the same key words were used as in Part 1, with additional key words: strength training OR resistance training. Inclusion criteria included ≥ 1 of the target outcomes; ≥ 60 years of age; healthy population (i.e., strength training not for rehabilitation purposes); strength training as the sole intervention; strength training intensity $> 60\%$ 1RM or 15RM for the majority of the training period (McDonagh & Davies, 1984); training period ≥ 2 weeks (also including lifelong strength trained master athletes); bilateral and unilateral (including cross-education paradigms) strength training. Full text articles available in English language were included. We characterize test regimes using $> 60\%$ of maximal contractions and near-maximal/maximal stimulation intensity as strong evidence in the present review. The literature search was performed by authors THT, MFB, and OKB, with relevant studies based on title and abstract collated before inclusion and critical appraisal by all authors. Any duplicated or unrelated articles were excluded. Disagreement between authors regarding inclusion of studies was discussed until consensus between all authors was reached. Reference lists of related reviews and included studies were also searched to detect other relevant articles not previously identified.

PART ONE: Nervous system alterations associated with the age-related decline in FGC

The aging brain

The brain undergoes a number of structural changes with age, which may have consequences for the ability to produce skeletal muscle force. In fact, maximal strength in the lower limbs is associated with brain aging, using magnetic resonance imaging to calculate brain age (Vaughan et al., 2022). However, of importance, except this study, which did not specify the site at which brain aging occurred, these changes are typically not examined in relation to decline in FGC with age and should therefore be interpreted with caution. Nevertheless, in the two paragraphs below, we discuss potential mechanisms which may provide insight into important alterations that impact FGC, while recognizing that these may represent typical age-related neural deterioration, rather than those specifically related to FGC.

There is evidence of severe shrinking of the cerebral cortex in older adults, particularly to those regions associated with behaviour and movement (Farokhian et al., 2017; Haug & Eggers, 1991), including the motor cortex (Salat et al., 2004). This appears to be primarily due to smaller perikaryon size, rather than loss of neurons (Haug & Eggers, 1991). An interesting notion from Haug and Eggers (1991) was that the shrinkage of neurons in the anterior regions of the brain appeared to coincide with a reduction in activity level of the subjects. In contrast, neurons associated with processing sensory input did not undergo the same shrinkage with age as they are likely activated more consistently throughout the lifespan, leading the authors to conclude that “use it or lose it” was a suitable description of this phenomenon. Moreover, loss of white matter, which decreases by 10% per decade (Marnier et al., 2003), also affects the volume of the cerebral cortex, and has been suggested to be more pronounced than loss of grey matter (Guttmann et al., 1998). Similarly, white matter integrity has been found to be compromised with age (Madden et al., 2004). Decreased plasticity in the motor cortex has also been demonstrated in older compared to young and middle-aged adults (Fathi et al., 2010), which may have consequences for potential training adaptations in response to strength training. Furthermore, for the interested reader, several reviews are available examining common neurochemical changes observed with age are reduced dopamine and serotonin (Morgan et al., 1987), glutamate (Segovia et al., 2001), and gamma-aminobutyric acid (GABA) (Mora et al., 2008) systems.

The cerebellum and basal ganglia receive input from most areas of the cerebral cortex, including the motor cortex, and are of importance for motor control and coordinated movements (Bostan & Strick, 2018). These structures also suffer changes with age which have been associated with muscle weakness and gait slowness (Arleo et al., 2024; Chen et al., 2015). These changes include degradation of neurochemical systems, atrophy, and neuron loss (Hubble, 1998). It may be speculated that these adaptations affect the connectivity within the brain and between the brain and spinal cord, resulting in reduced FGC.

Corticospinal and reticulospinal tract excitability

The corticospinal output is a result of excitatory and inhibitory input to the motoneurons (Krnjević, 1997), which may lead to a voluntary muscle contraction. Thus, decreases in excitability, i.e., increasing the threshold to elicit action potentials within the motor cortex or

along the corticospinal pathway, may impact strength characteristics. Corticospinal excitability is often examined with transcranial magnetic stimulation (TMS) of the motor cortex. The elicited action potentials and subsequent muscle response can be recorded in the target muscle as the size of the motor evoked potential (MEP). However, there are clear methodological constraints related to low stimulation and contraction intensity when using the TMS. Thus, the age effect on corticospinal excitability remains equivocal. Compared to young, older adults have demonstrated lower (Oliviero et al., 2006; Sale & Semmler, 2005; Siddique, Frazer, Tallent, Hayman, Andrushko, et al., 2025; Talelli et al., 2008), similar (Christie & Kamen, 2014; Clark et al., 2015; McGinley et al., 2010; Siddique et al., 2024; Stevens-Lapsley et al., 2013) or even higher (Bernard & Seidler, 2012; Gomez-Guerrero et al., 2024) corticospinal excitability (MEP amplitudes). The highest contraction intensity used to examine corticospinal excitability in older adults is 60 % of maximal voluntary contraction (MVC) (Gomez-Guerrero et al., 2024). Thus, most studies are performed below this contraction intensity, where there may not be a need to recruit all motor units, including the high threshold motor units which are largely responsible for strength performance. Moreover, stimulation intensity to produce a MEP is below the intensity to elicit a maximal muscle response (M_{max}). This combination makes the TMS most appropriate to examine low-force contractions, for instance when investigating fatigue-related responses or dexterity, in contrast to strength-related adaptations. Nevertheless, it does appear that MEP latency is increased with age (Bernard & Seidler, 2012; Eisen & Shtybel, 1990), suggesting there may be a slower conduction velocity in the corticospinal tract compared to young, which may be of particular importance for rapid force development.

Recently, there has been growing interest in the role of the reticulospinal tract in relation to force production, which may also be assessed using TMS. Reticulospinal tract excitability in older adults appears to be similar (Maitland & Baker, 2021; Siddique, Frazer, Tallent, Hayman, Ahtiainen, et al., 2025; Siddique et al., 2026; Siddique, Frazer, Tallent, Hayman, Andrushko, et al., 2025) or lower (Mooney & Celnik, 2025) compared to young when examined in relation to FGC, represented by ipsilateral motor evoked potentials (iMEP) or reaction time using the StartReact Protocol. Reticulospinal tract excitability appears to be related to FGC, as evident from a reduced iMEP along with elbow flexor force decrements (Mooney & Celnik, 2025). In contrast, there was no difference in reticulospinal tract excitability of the elbow flexors, where there also was no apparent force decrement (Mooney & Celnik, 2025; Siddique, Frazer, Tallent, Hayman, Ahtiainen, et al., 2025; Siddique et al., 2026; Siddique, Frazer, Tallent, Hayman,

Andrushko, et al., 2025). Similarly, there was a positive association between reticulospinal tract excitability and force production in the older adults (Maitland & Baker, 2021), albeit performed at low contraction intensity to obtain iMEPS (highest reported 20 % MVC (Mooney & Celnik, 2025)).

As the excitability of the motoneurons are also dependent on intracortical inhibition, it is common to examine the cortical silent period (CSP) and short-interval cortical inhibition (SICI) following a TMS-induced MEP. CSP is thought to represent GABA_B receptor-mediated inhibition whereas SICI is used to measure GABA_A receptor-mediated inhibition, which may also influence corticospinal excitability (Clark et al., 2015). Although not always the case (Plow et al., 2013; Siddique et al., 2024; Siddique, Frazer, Tallent, Hayman, Andrushko, et al., 2025), older adults typically have longer CSPs compared to young (Christie & Kamen, 2014; Clark et al., 2015; Gomez-Guerrero et al., 2024; McGinley et al., 2010), indicating higher levels of inhibitory input, which may decrease the excitability of their motoneurons. Extending these findings, muscle weakness in older adults appear to be associated with longer CSP (Clark et al., 2021). However, as findings have been inconsistent regarding SICI, with higher (McGinley et al., 2010), lower (Peinemann et al., 2001; Siddique, Frazer, Tallent, Hayman, Andrushko, et al., 2025) or similar (Clark et al., 2015; Siddique et al., 2024) response compared to young, the functional significance of GABA_A inhibition in relation to aging is unclear. As TMS is difficult or even impossible to apply during stronger contractions (McNeil et al., 2013), it can be discussed whether this methodology is appropriate to examine strength-related adaptations with age, as they should be examined during strong contractions where important FGC differences occur.

Efferent neural drive

Modulation of force is primarily achieved through two mechanisms, motor unit recruitment and firing frequency to the recruited motor units (Duchateau & Enoka, 2011). Together, these are often termed efferent neural drive (Aagaard et al., 2002), and can be quantified using different methodologies, such as surface- or intramuscular electromyography (EMG), voluntary activation (VA) with the interpolated twitch technique, or the V-wave method. The latter two have their advantage since they apply supramaximal stimulation in conjunction with maximal muscle contractions, appropriate when assessing FGC. The supramaximal electrical stimulation

is applied cutaneously on a peripheral nerve to elicit a maximal motor response in a targeted muscle. The findings related to efferent neural drive is highlighted with a bold arrow in our conceptual figure (Figure 1), as these are considered strong evidence given the test conditions under which they are obtained.

Surface EMG (sEMG) recordings obtained during MVC have yielded inconsistent results. Compared to young, older adults have displayed either similar (Cannon et al., 2007; Klass et al., 2005) or reduced efferent neural drive (Klass et al., 2008; Moritani & deVries, 1980; Tøien, Malmo, et al., 2022). These inconsistencies may be due to methodological constraints inherent to the methodology, resulting in challenges with intergroup comparisons along with sensitivity to detect changes over time (Farina et al., 2014; Vigotsky et al., 2017; Aagaard et al., 2020).

The V-wave method has only recently been applied to detect age-related differences in efferent neural drive between older and younger adults (Tøien, Unhjem, et al., 2022; Unhjem et al., 2015; Unhjem et al., 2016). The V-wave is an electrophysiological variant of the H-reflex, evoked by supramaximal electrical stimulation to a peripheral nerve (commonly the tibial nerve) during a MVC. The V-wave magnitude depends on the removal of antidromic signals caused by the strong electrical stimulus colliding with the voluntary efferent output. A stronger efferent neural drive from spinal and supraspinal centres removes more of the antidromic signals, and in turn results in a higher V-wave amplitude (Aagaard et al., 2002). In conjunction with the H-reflex method, which uses low stimulus intensity and no or low-force contractions to reflect α -motoneuron excitability, the V-wave can be used to indicate descending neural drive from supraspinal centres to spinal α -motoneurons (Vila-Chã et al., 2012; Aagaard et al., 2002), i.e., central nervous system adaptations. Although the V-wave cannot fully distinguish between spinal and supraspinal adaptations with age, it appears to be robust to distinguish between age groups with different FGC, evident as lower efferent neural drive consistently shown in older adults compared to young (Tøien, Unhjem, et al., 2022; Unhjem et al., 2015; Unhjem et al., 2016). Figure 2 exemplifies this finding, with a large difference evident in V-wave normalised to M-wave (V/M-ratio) in older vs. young adults.

To specifically examine motoneuron firing frequency, intramuscular EMG recordings have been applied using a needle or wire inserted into the muscle bed (Duchateau & Baudry, 2014; Duchateau & Enoka, 2011; Kamen, 2005). Older adults are shown to have a 16-64 % lower firing frequency compared to young during maximal contractions (Christie & Kamen, 2010; Kamen & Knight, 2004; Kamen et al., 1995; Klass et al., 2008; Patten et al., 2001; Rubinstein & Kamen, 2005). For instance, Kamen et al. (1995) observed a 64 % lower firing frequency in older adults during MVC (Figure 3). Recent high density sEMG (HDsEMG) results reveal similar findings (Guo et al., 2026), with firing frequency documented as a major predictor of 1-year strength loss in older adults (Hirono et al., 2024). Although these findings may certainly be due to decreased descending neural drive from supraspinal centres to the skeletal muscle, they may also be explained by longer refractory periods, as older adults are shown to have a longer motoneuron hyperpolarization period than young (Christie & Kamen, 2010). In addition, lower proportion and atrophy of type II fibres (Lexell, 1993; Lexell et al., 1988) which have higher firing frequency (Christie & Kamen, 2010), are suggested to be partially responsible for this efferent neural drive reduction.

Also reflecting efferent neural drive, VA can be quantified as a percentage of activation of the muscle by using a supramaxial electrical stimulation to potentially add additional force to a MVC (Allen et al., 1998). If additional force can be added with the electrical stimulation, this indicates that the muscle cannot be fully activated through voluntary efferent neural drive. Comparisons between younger and older adults are also somewhat equivocal when using the interpolated twitch technique to assess VA, potentially due to insensitivity of the method to capture important differences between the age groups. In general, VA typically has a larger range among older adults (70-100 %) (Christie & Kamen, 2010; Harridge et al., 1999; Scaglioni et al., 2002; Stevens et al., 2003; Unhjem et al., 2016; Venturelli et al., 2015), compared to 90-100 % in young adults (Allen et al., 1995; Stevens et al., 2003; Unhjem et al., 2016; Venturelli et al., 2015), and a meta-analysis of VA in older adults reveal an overall reduced capacity to activate their muscles compared to young (Rozand et al., 2019). It has also been noted that the reductions in VA in older adults may vary substantially between muscle groups, as it appears that proximal muscles may be more affected (e.g., knee extensor and elbow flexors) than more distal muscles such as the dorsiflexors (Clark & Taylor, 2011; Klass et al., 2007). Moreover, reduction of VA appears to be more prominent in the oldest age groups (Wrucke et al., 2024)

and may even not be detected until ~80 years of age (Harridge et al., 1999; Scaglioni et al., 2002).

Spinal factors

Spinal α -motoneurons remain the final segment of the nervous system before the action potential reaches the muscle to enable a muscle contraction. A spinal α -motoneuron and the muscle fibres it innervates are termed a motor unit. Both anatomical and physiological changes are well-documented in older adults' peripheral nervous system which may affect FGC. For instance, older age appears to be accompanied by gradual loss of spinal α -motoneurons (Mittal & Logmani, 1987). This is believed to pertain particularly to those that innervate type II muscle fibres, resulting in denervation of those fibres (Kelly et al., 2018; Tøien et al., 2023). This may cause reduced number of functional motor units (Piasecki, Ireland, Coulson, et al., 2016; Wu et al., 2020) and larger motor units through neural sprouting, which may result in grouping of muscle fibres (Hepple & Rice, 2016; Kelly et al., 2018; Lexell & Downham, 1991). A reduced number of available motor units appear to be reflected in reduced maximal M-wave amplitude, i.e., the compound muscle action potential during maximal stimulation of a peripheral nerve recorded from surface EMG, with aging (Piasecki, Ireland, Coulson, et al., 2016; Piasecki, Ireland, Stashuk, et al., 2016; Power et al., 2012; Scaglioni et al., 2002; Unhjem et al., 2015; Unhjem et al., 2016), although this is not a universal finding (Tøien, Unhjem, et al., 2022). As the M-wave represents both the number of motor units, the size of the motor unit, and endplate transmission efficacy (Barkhaus et al., 2024), it is unclear which of these factors are predominantly affected. However, using intramuscular EMG recordings to investigate single motor unit potentials, aging is followed by reduced motor unit number, represented by reduced motor unit potential and motor unit estimates along with larger motor units (Hourigan et al., 2015; Piasecki, Ireland, Stashuk, et al., 2016). Notably, sarcopenic and frail individuals have even lower number of motor units compared to healthy older adults (Piasecki et al., 2018; Swiecicka et al., 2019), suggesting that the loss of motor units is exacerbated in individuals with poor age-related health status, likely resulting in a negative spiral with major decrements in FGC.

Deterioration of the neuromuscular junction (NMJ) has also been observed with increasing age (Oda, 1984; Sirago et al., 2023). So too has neuromuscular junction transmission failure or

variability, evident as more near-fibre jiggle obtained via needle EMG recordings (Hourigan et al., 2015). Further, reduced myelination, shorter internodal length, and reduced spinal α -motoneuron axon diameter, which, along with loss of the largest motor axons, may cause slower conduction speed with age (Metter et al., 1998; Mittal & Logmani, 1987; Scaglioni et al., 2002). Physiologically, this may be observed as increased H-reflex latency with age (Scaglioni et al., 2002). Considering that the M-wave latency appears to be unaffected by age, the conduction velocity of the Ia afferent pathway is potentially more affected than the efferent pathway (Scaglioni et al., 2002). However, this may also be due to the very short latency of the M-wave (~ 5 ms), which may mask subtle differences between age groups along the efferent pathway.

Moreover, there are signs of reduced α -motoneuron excitability, i.e., reduced H-reflex amplitude in older adults compared to young (Scaglioni et al., 2002; Tøien, Unhjem, et al., 2022; Unhjem et al., 2015; Unhjem et al., 2016), although this may also be caused by increased pre- and/or postsynaptic inhibition. Persistent inward currents, representing intrinsic α -motoneuron excitability, are also reduced in vastus lateralis (Guo et al., 2024), biceps brachii and triceps brachii (Hassan et al., 2021) as well as soleus and tibialis anterior (Orssatto et al., 2021). Persistent inward currents can amplify synaptic input to the motoneuron up to fivefold and increase the synaptic input time course, which may initiate self-sustained firing of motoneurons (Heckman et al., 2008). As such, it appears to be linked to motoneuron firing frequency and is associated with maximal strength (Hassan et al., 2021). The reduction in motoneuron excitability implies that increased synaptic input from supraspinal and spinal centres is necessary to evoke an efferent motor unit action potential in the peripheral nervous system. However, common synaptic input to the α -motoneurons, i.e., the net excitatory inputs to the motoneuron pool (Hug et al., 2023), has recently been shown to be reduced in older adults compared to young (Guo et al., 2024). Thus, it is conceivable that the combination of lower efferent, descending neural drive, likely resulting in reduced common synaptic input along with reduced α -motoneuron excitability all contribute to reductions in FGC with age.

Afferent response related to maximal strength and RFD may potentially be altered with age. However, to the best of our knowledge we are not aware of any studies that have investigated how a potential attenuation of afferent feedback contributes to the decline in force generating capacity.

PART TWO: Strength training to counteract the neural deterioration with age

It is well-documented that older adults exhibit a great potential to improve FGC by performing strength training (Berg et al., 2018; Fiatarone et al., 1994; Wang et al., 2017). The first line of evidence showing that the nervous system plays a pivotal role in strength training-induced adaptations comes from measurements of muscle mass following strength training. The percentage improvement in FGC is substantially larger than the increase in muscle mass (Fiatarone et al., 1990), indicating a protagonist role of the nervous system. A further testament to nervous system adaptations comes from the notion that unilateral strength training can induce strength increases in the contralateral limb (Tracy et al., 1999; Tøien et al., 2018). This phenomenon can be viewed in Figure 4, where a contralateral increase in MVC and RFD was observed following only three weeks of unilateral strength training. As peripheral adaptations should not be expected without training of the specific limb adaptations are deduced to occur in the central nervous system. Indeed, contralateral strength gains have been documented to be accompanied by increases in efferent neural drive (Tøien et al., 2018). However, there is still uncertainty regarding the origin of the strength-training induced neural adaptations in older adults. Therefore, potential mechanisms are discussed below as well as summarized in Figure 1 based on the findings below. We have also included a supplementary table (S1) summarizing the findings from all relevant papers in this part of the review.

The aging human brain, corticospinal and reticulospinal excitability

To the best of the authors knowledge, no study has investigated the structural impact of strength training on motor cortex and associations with FGC in older adults. Due to the uncertainty regarding these structural changes' role in loss of FGC unveiled in Part I, this may not be surprising. However, a few studies have examined other cerebral morphology alterations in response to strength training. Despite an expected improvement in maximal strength and power, as well as in cognitive function, a paradoxical reduction in whole-brain volume was observed in older adults following a one year strength training intervention (Liu-Ambrose et al., 2010). Similarly, following one year of strength training, expected age-related reductions, which were similar to the control group, were observed in total grey matter, hippocampus volume, dorsolateral- or ventrolateral prefrontal cortex volume (Bloch-Ibenfeldt et al., 2025), despite increased maximal strength in the trained legs. Thus, there appears to be limited evidence to

support altered structural brain changes in response to strength training with age. However, in contrast, several studies indicate a protective effect of strength training in older adults on white matter degeneration, or even a regression (Best et al., 2015; Bolandzadeh et al., 2015; Suo et al., 2016), which may indicate a positive effect on myelination of axons and signal transmission in the brain as a result of strength training. In addition to muscle hypertrophy and strength gains, leg press strength training promoted an increase in grey matter in older adults (Fontes et al., 2017), implying changes that are relevant to motor control. Although not measuring structural changes, a similar strength training intervention demonstrated a protective effect against loss of neurochemical markers, such as glutamate complex and myo-inositol (a marker of glial cell activation) relative to total creatine, indicative of neuronal density and neurotransmission, and a positive association between gains in knee extension/flexion peak torque and these neurochemical markers of brain health in older adults (Sheoran et al., 2023).

While TMS is commonly applied to examine strength training-induced adaptations in young adults, it is seldom used in older adults. The methodological constraints of TMS are substantial in the context of high-force contractions. The TMS methodology does not allow test conditions with optimal, i.e., near-maximal/maximal contraction or stimulation intensity, making the method unsuitable for strength training-related adaptations. Thus, the following results should be interpreted with caution. TMS-induced reduced cortical inhibition, i.e., reduced inhibition of GABA_B receptor mediated inhibition (measured as decreased CSP) has been documented following bilateral (Christie & Kamen, 2014) and unilateral strength training promoting contralateral (opposite side) (Siddique, Frazer, Tallent, Hayman, Ahtiainen, et al., 2025) and ipsilateral (same side) strength gain (Siddique et al., 2026). However, as this did not have an impact on corticospinal excitability (evident as unchanged MEP amplitude measured during 10-50 % MVC), the functional significance of this adaptation is unclear. In contrast, a recent study found that corticospinal excitability (MEP amplitude measured during 20 % and 60 % MVC) decreased in older adults without concomitant alteration in silent period duration, following seven weeks of strength training (Gomez-Guerrero et al., 2024). Of note, older adults had higher corticospinal excitability before training, thus the decrease following strength training normalized older adults to young. Although 50-60 % MVC are of the highest contraction intensities used when examining corticospinal excitability in older adults this may yet be insufficient to detect strength training-related adaptations, which are highly dependent on alterations during the highest contraction intensities. MEP amplitude appears to increase

until ~60-75 % MVC (Škarabot et al., 2019), and in fact decrease from 75 % MVC to MVC (Martin et al., 2006). Therefore, assessing alterations following strength training with the TMS method seems counterintuitive, as the method fails to detect changes occurring at the highest contraction level. In this review, we therefore emphasize results from studies applying an experimental design using near-maximal/maximal contraction and stimulation intensity as strong evidence, as this may be a prerequisite to examine neural adaptations associated with fast twitch motor units following strength training in older adults, such as the interpolated twitch technique and the V-wave method.

Interestingly, Siddique et al. (2025; 2026) found increased reticulospinal tract excitability (measured using the Start React Protocol) to accompany ipsilateral and contralateral strength gain following unilateral strength training. This may suggest that the subcortical brainstem pathways play a significant role in FGC adaptations in older adults.

Efferent neural drive

One of the main adaptations to strength training in older adults appears to be efferent neural drive enhancement, from motor cortex to motor units. These consistent findings of increased efferent neural drive are emphasised in Figure 1 with bold, double arrows, as it can be viewed as a major contributor to enhanced FGC after strength training in older adults. Using sEMG during MVC, efferent neural drive has been shown to increase after strength training (Cannon et al., 2007; Correa et al., 2012; Häkkinen et al., 1998; Moritani & deVries, 1980; Silva Correa et al., 2014; Simoneau et al., 2007; Tracy et al., 2004; Walker & Hakkinen, 2014). In addition to the increase in motor unit recruitment and/or firing frequency, this may also indicate an increased motor unit synchronization (Yao et al., 2000). Increased motor unit firing frequency following strength training has also been confirmed applying invasive intramuscular needle EMG (Christie & Kamen, 2010; Kamen & Knight, 2004; Patten et al., 2001). In fact, maximal motor unit firing frequency in the knee extensors may even be restored to the level of young (Kamen & Knight, 2004). Notably, these increases appear to be particularly pronounced in the initial phase of strength training, i.e., within the first two weeks. Higher firing frequency during MVC has also been demonstrated in older strength trained master athletes compared to older untrained (Leong et al., 1999), highlighting the importance of firing frequency as a key contributor to strength training adaptations with age.

Using the interpolated twitch technique, increased VA has also been observed following strength training in older adults (Hvid et al., 2016; Knight & Kamen, 2001; Scaglioni et al., 2002; Siddique, Frazer, Tallent, Hayman, Ahtiainen, et al., 2025; Siddique et al., 2026; Suetta et al., 2009; Tøien et al., 2018). However, this is not a universal finding (Cannon et al., 2007; Harridge et al., 1999; Unhjem et al., 2021). These contrasting observations may be related to limitations inherent with the methodology, including insensitivity and a ceiling effect along with insufficient stimulus to recruit the fastest motor units in the hierarchy, in accordance with Henneman's size principle (Henneman, 1957), due to only using a single or double pulse.

More consistently, efferent neural drive increases have been documented when applying the V-wave method, both following strength training of short (< three weeks) and longer duration (eight weeks) in older adults (Tøien et al., 2018; Unhjem et al., 2015; Unhjem et al., 2021). Figure 5 illustrates improvements in efferent neural drive, using the V-wave method, following three weeks of maximal strength training (MST) (Unhjem et al., 2021). Importantly, Figure 5 also illustrates that the increase in efferent neural drive was only observable when performing strength training with near-maximal loads, whereas ballistic, unloaded training, i.e., performed in a strength training exercise with maximal speed of movement but no external load, did not result in increased efferent neural drive. Moreover, strength trained master athletes (<70 years) are also documented to display higher efferent neural drive compared with sedentary and recreationally active older adults (Tøien, Unhjem, et al., 2022; Unhjem et al., 2016). In fact, no differences were observed between the two latter groups, suggesting that maintenance of efferent neural drive with age requires external loading of a magnitude which recreational activity is unable to fulfil. The lack of increase in efferent neural drive following ballistic, unloaded training, strengthens the confidence with which we can assume that external heavy loading is necessary to increase or maintain efferent neural drive with advancing age (Unhjem et al., 2021).

Interestingly, the strength training-induced increases in efferent neural drive are typically observed without changes in α -motoneuron excitability (H-reflex amplitude). These adaptations may thus occur at the corticospinal level, as increased descending neural drive from supraspinal centres to spinal α -motoneurons. This is further supported by increased efferent neural drive

(increased V-wave amplitude) in the untrained limb following unilateral training (Tøien et al., 2018). In this case, peripheral adaptations cannot explain the enhancement in FGC and efferent neural drive observed in an untrained limb. Moreover, in highly trained older individuals, it was recently documented that efferent neural drive (V-wave) was similar between strength trained and endurance trained master athletes, which was elevated compared to untrained older adults (Tøien, Unhjem, et al., 2022). However, this was achieved through different neural pathways (See figure 4 in Tøien, Unhjem, et al. (2022)). Specifically, in endurance trained athletes the high efferent neural drive was achieved *through a high α -motoneuron excitability* (high H-reflex excitability). In contrast, in strength trained athletes this was achieved *despite a low α -motoneuron excitability*, suggesting that high corticospinal descending neural drive was responsible for the high efferent neural drive.

Spinal factors

Peripheral spinal factors appear to be largely unaffected by strength training, as viewed from Figure 1 as largely unchanged in response to training, despite documented age-related deterioration of these factors. A loss of spinal α -motoneurons can directly impact muscle fibre distribution through neural sprouting. It is possible to elucidate the impact of strength training by examining grouping of muscle fibres. A recent study documented that grouping of muscle fibres did not change following strength training in older adults (Kraková et al., 2023). However, this finding should be interpreted with caution, as the authors did not observe the expected difference in grouping between young and older adults before the training intervention (Kelly et al., 2018; Sonjak et al., 2019). In contrast, strength trained master athletes were recently documented to exhibit less grouping of muscle fibres and preserved type II fibre count compared to endurance trained and untrained older adults (Tøien et al., 2023). Taken together, and represented in Figure 1 as no change in number of spinal α -motoneurons, number of motor units and number of motor unit size, these results indicate that continuous strength training throughout life may be necessary to maintain type II fibres and potentially the spinal α -motoneurons innervating these fibres, whereas it may be irreversible if the spinal α -motoneurons are already lost.

Strength training does not appear to increase spinal α -motoneuron excitability, assessed as an H-reflex, during low-force contractions or rest (Christie & Kamen, 2014; Scaglioni et al., 2002;

Tøien et al., 2018; Unhjem et al., 2015; Unhjem et al., 2021). However, this measure has been observed to be elevated in strength trained master athletes when obtained during a MVC (Tøien, Unhjem, et al., 2022). A similar result has also been observed following short term strength training in young adults (Aagaard et al., 2002). These findings may indicate that the introduction of voluntary descending neural drive during a MVC may increase the α -motoneuron excitability in strength trained individuals (Aagaard et al., 2002). Along this line, persistent inward currents, also reflecting α -motoneuron excitability have recently been shown to increase following strength (Orssatto et al., 2023). Interestingly, this adaptation appeared to be related to increased motoneuron firing frequency (Casolo et al., 2026) suggesting that intrinsic motoneuron properties may be important to modulate force through firing frequency adjustment. Of note, these results were obtained using low-force contractions (up to 40 % MVC). However, importantly, there was a stronger correlation between persistent inward currents obtained during the heavier contraction intensity (40 % MVC) and maximal strength (both leg press and plantar flexion maximal strength) (Orssatto et al., 2023), implying that the heavier contraction intensities may be more suitable to examine force-related adaptations. Extending these findings, Orssatto et al. (2025) recently revealed that master athletes had higher persistent inward currents than age-matched healthy and sarcopenic older adults, especially at high contraction intensities.

The attenuated conduction velocity observed in older adults (longer H-reflex latency) does not appear to be improved following three to eight weeks of strength training (Scaglioni et al., 2002; Unhjem et al., 2015; Unhjem et al., 2021). Similarly, even chronically strength trained master athletes appear to have reduced conduction velocity compared to young (Tøien, Unhjem, et al., 2022; Unhjem et al., 2016). Nonetheless, compared to untrained and recreationally active older adults, H-reflex latency is documented to be less attenuated in strength trained master athletes (Unhjem et al., 2016), although not always observed (Tøien, Unhjem, et al., 2022). Thus, reduced conduction velocity may be an inevitable characteristic of aging, albeit it is unclear whether lifelong strength training may mitigate this reduction. Moreover, full recruitment of the motor unit pool, assessed as M-wave amplitude, does not appear to change in response to strength training (Christie & Kamen, 2014; Scaglioni et al., 2002; Siddique, Frazer, Tallent, Hayman, Ahtiainen, et al., 2025; Siddique et al., 2026; Tøien et al., 2018; Unhjem et al., 2015; Unhjem et al., 2021), possibly because the loss of motor units with age is irreversible (Hepple & Rice, 2016). It is also unclear whether the NMJ instability observed with age can be

ameliorated. An acute bout of strength training appeared to downregulate the gene expression for several acetylcholine receptor subunits, which may be of importance for NMJ stability (Soendenbroe et al., 2020). However, the chronic response of the NMJ to strength training remains unknown.

Practical implications

Maintenance of efferent neural drive from motor cortex to maximally contracting musculature with age does not appear to occur in response to recreational physical activity (Unhjem et al., 2016) or following ballistic (fast) contractions performed in a typical strength training exercise *without* external load (Unhjem et al., 2021). Applying heavy loading appears to be necessary, likely due to the use of fast twitch musculature. Notably, in older adults, the efferent neural drive is closely linked to the ability to produce force rapidly (Maffiuletti et al., 2016). RFD/power appears to become increasingly important with older age to maintain rapid muscle performance and physical function, and has been suggested to be more sensitive to capture the risk of future or current mobility limitations than maximal strength (Lomborg et al., 2022; Reid & Fielding, 2012). One example of a strength training protocol adhering to the principles of using heavy loads is MST, designed to specifically target efferent neural drive adaptations (Tøien et al., 2025). In turn, large improvements in maximal strength and RFD have been documented in older adults (Berg et al., 2018; Tøien et al., 2018; Unhjem et al., 2021; Wang et al., 2017). This is due to a combination of heavy loads (~90 % of maximal strength), few repetitions (3-5) and application of maximal intended velocity in the concentric phase to stimulate the neural system maximally. This combination likely recruits all available motor units, including the crucial high threshold motor units, with high firing frequency from contraction onset. As MST uses a slow, controlled eccentric phase, this type of strength training is shown to be simple, safe and feasible even in fragile populations such as patients with rheumatic disease (Haglo et al., 2022), women with osteoporosis and osteopenia (Mosti et al., 2013), and chronic obstructive pulmonary disease (Hoff et al., 2007).

Summary

The age-related decline in FGC can be largely attributed to nervous system attenuation, encompassing central and peripheral nervous system changes. These appear to include both

structural and functional changes, ultimately resulting in reductions in efferent neural drive. As such, the entire efferent neural pathway from the motor cortex in the brain to the contracting skeletal muscle, may be affected, although the research pertaining to structural brain changes should be interpreted with caution as there is uncertainty regarding the role of these changes relating to reductions in FGC. Moreover, while it seems plausible that corticospinal excitability plays a role in efferent neural drive decline with age, the methodological constraints related to low contraction and stimulation intensity does not allow for firm conclusions. In the peripheral nervous system several factors affect FGC with age, including loss of spinal α -motoneurons, resulting in fewer and larger motor units with more type I muscle fibres; reduced spinal α -motoneuron excitability and/or increased pre-/postsynaptic inhibition; and reduced conduction velocity. Importantly, strong evidence suggests that as FGC capacity is regulated mainly through efferent neural drive, i.e., motor unit recruitment and/or firing frequency to the recruited motor units, these underlying peripheral mechanisms may play a role in the observed reduction in efferent neural drive with age. For instance, although speculative, the loss of the largest spinal α -motoneurons is likely to be reflected in reduced firing frequency as these require higher firing frequency.

Fortunately, some of these detrimental neural alterations with age are reversible, at least in part, allowing FGC to be maintained or even improved with strength training using heavy loading. Compelling evidence suggests overall efferent neural drive is consistently observed to improve with strength training, applying appropriate methodology to examine strength training-related adaptations, i.e., maximal contraction and stimulation intensity. Albeit efferent neural drive is not restored to the level of young, despite a rejuvenation of FGC. Components in the central nervous system are, at least in part, responsible for the strength training-induced improvement. Importantly, improvements in efferent neural drive appear to be dependent on the use of heavy training loads, to maximally activate the highest-threshold motor units with a high firing frequency. Consequently, strength training targeting the nervous system should be of utmost importance to improve FGC, physical function, and ultimately longevity at older age.

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FIGURE LEGENDS

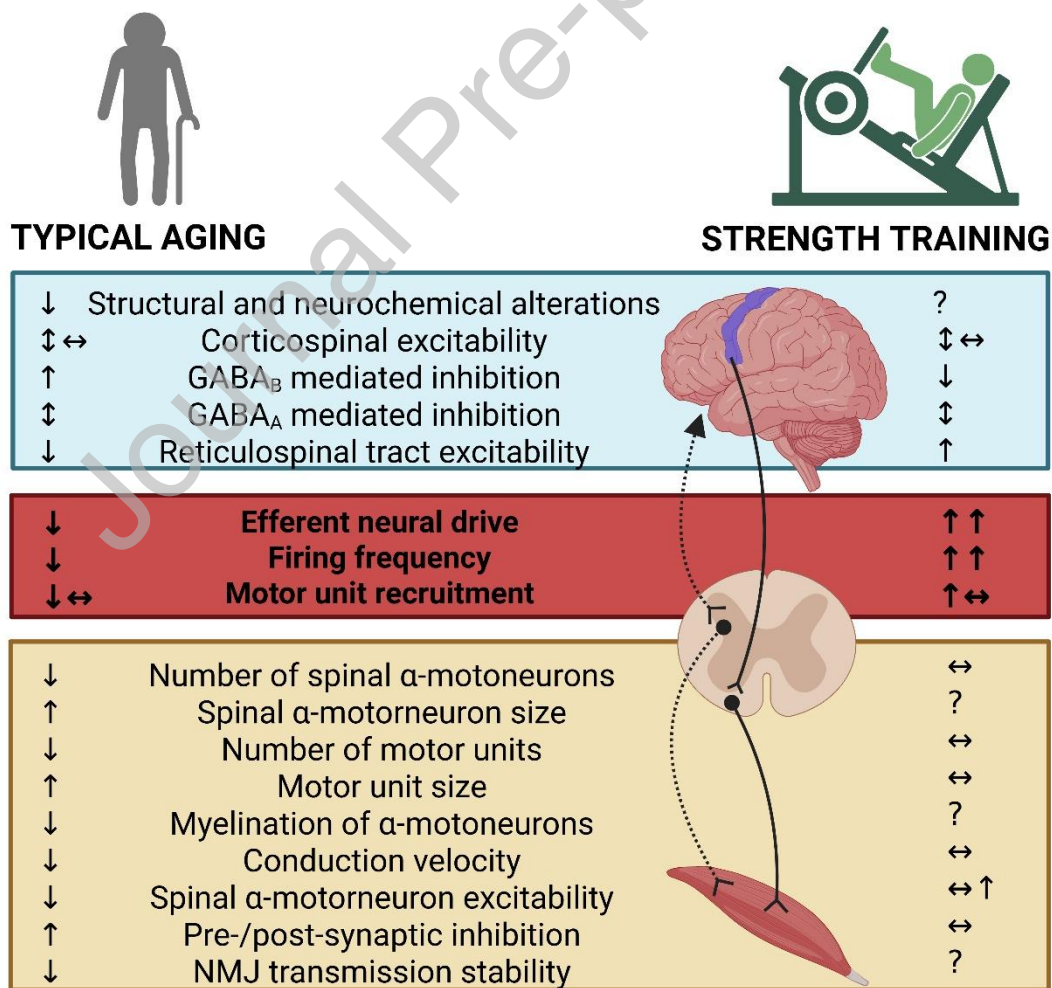


Figure 1 summarising potential mechanisms responsible for strength decline with age along with possible mechanisms allowing increased force generating capacity following strength training in older adults. Arrows pointing up or down represent increase or decrease, horizontal arrows represent no change, whereas question marks represent uncertainty. The data included in the figure is extracted from all papers included in the text of the present review. Figure is made with Biorender.com.

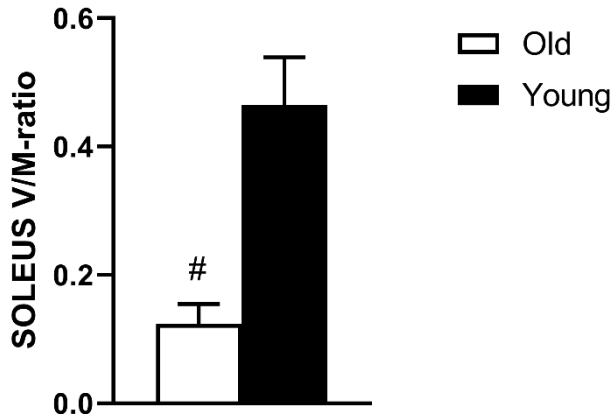


Figure 2 showing the difference in efferent neural drive (V/M-ratio) in older (open bars) versus younger adults (closed bars). Data displayed at mean \pm SE. Figure is amended using GraphPad Prism 10 from that originally published in Unhjem et al. (2015) Strength training-induced responses in older adults: attenuation of descending neural drive with age. *AGE* 37, 47 (2015), by permission of Springer Nature

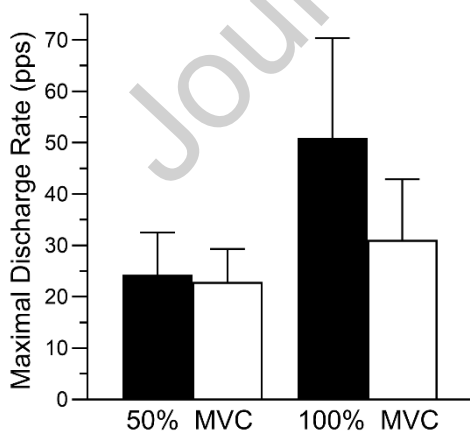


Figure 3 showing maximal firing frequency presented in pulses per second (pps) for first dorsal interosseus muscle in young (closed bars) and older adults (open bars). Firing frequency obtained during 50 % of maximal voluntary contraction (MVC) was not different between

groups, whereas firing frequency during 100 % MVC was 64 % lower in older adults (31.1 ± 11.8 pps vs. 50.9 ± 19.5 pps). The figure was recreated in using GraphPad Prism 10 using data from Kamen et al. (1995) Motor unit discharge behavior in older adults during maximal-effort contractions. *J Appl Physiol* (1985). 1995 Dec;79(6):1908-13, by permission of the American Physiological Society.

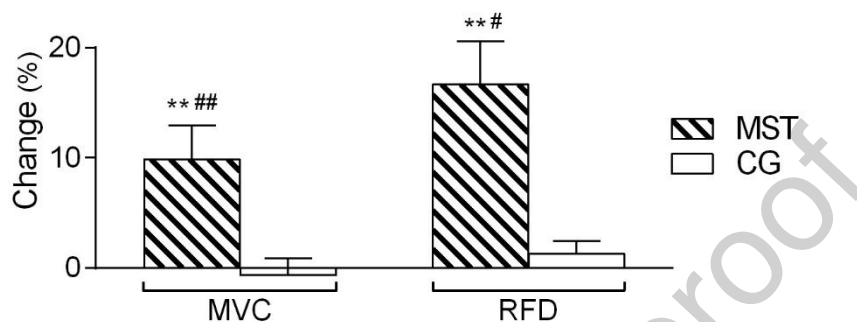


Figure 4 showing percentage change in maximal voluntary contraction (MVC) and rate of force development (RFD) in the contralateral limb following three weeks of unilateral maximal strength training (MST) in older adults (>70 years). The contralateral strength gain following unilateral strength training illustrates the role of the nervous system to facilitate strength adaptations. CG: control group, data displayed at mean \pm SE. Tøien et al. (2018) Neural Plasticity with Age: Unilateral Maximal Strength Training Augments Efferent Neural Drive to the Contralateral Limb in Older Adults. *J Gerontol A Biol Sci Med Sci*, 73, 596-602, by permission of Oxford University Press.

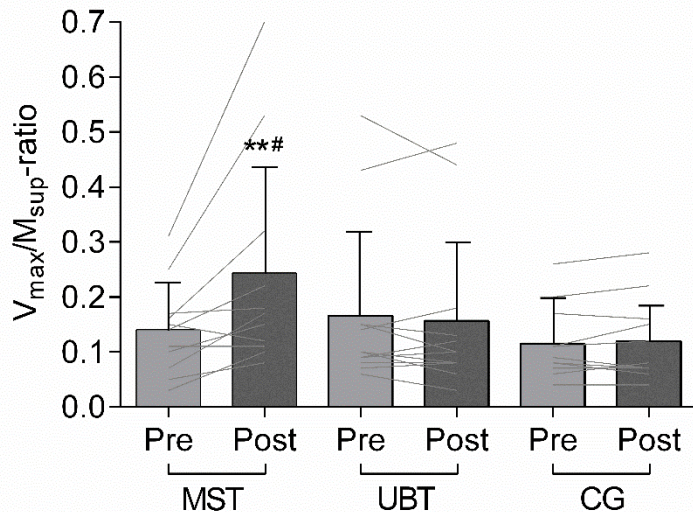


Figure 5 displaying increased efferent neural drive (V_{max}/M_{sup} -ratio) following maximal strength training (MST) in older adults (<70 years). There was no increase in efferent neural drive in the group that trained with unloaded ballistic contractions (UBT) or in the control group (CG), highlighting the role of heavy loading to increase efferent neural drive. Data displayed at mean \pm SD and with individual values. Unhjem et al. (2021) External Resistance Is Imperative for Training-Induced Efferent Neural Drive Enhancement in Older Adults. *J Gerontol A Biol Sci Med Sci*, 76, 224-232, by permission of Oxford University Press.

Declaration of interest statement

The authors declare no conflict of interest.

Ethics declaration

The authors have nothing to report

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Declaration of interest statement

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