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RESEARCH ARTICLE | *Control of Movement*

Maximal strength training: the impact of eccentric overload

Tiril Tøien,[1] Håvard Pedersen Haglo,[1] Runar Unhjem,[2] Jan Hoff,[1,3] and Eivind Wang[1,4,5]
[1]*Department of Circulation and Medical Imaging, Faculty of Medicine, Norwegian University of Science and Technology, Trondheim, Norway;* [2]*Faculty of Professional Studies, Nord University, Bodø, Norway;* [3]*Department of Physical Medicine and Rehabilitation, St. Olav's University Hospital, Trondheim, Norway;* [4]*Department of Health and Social Sciences, Molde University College, Norway; and* [5]*Department of Medicine, University of Utah, Salt Lake City, Utah*

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Tøien T, Pedersen Haglo H, Unhjem R, Hoff J, Wang E. Maximal strength training: the impact of eccentric overload. *J Neurophysiol* 120: 2868–2876, 2018. First published October 17, 2018; doi:10.1152/jn.00609.2018.—The search for the most potent strength training intervention is continuous. Maximal strength training (MST) yields large improvements in force-generating capacity (FGC), largely attributed to efferent neural drive enhancement. However, it remains elusive whether eccentric overload, before the concentric phase, may augment training-induced neuromuscular adaptations. A total of 53 23 ± 3 (SD)-yr-old untrained males were randomized to either a nontraining control group (CG) or one of two training groups performing leg press strength training with linear progression, three times per week for 8 wk. The first training group carried out MST with four sets of four repetitions at ~90% one-repetition maximum (1RM) in both action phases. The second group performed MST with an augmented eccentric load of 150% 1RM (eMST). Measurements were taken of 1RM and rate of force development (RFD), countermovement jump (CMJ) performance, and evoked potentials recordings [V-wave (V) and H-reflex (H) normalized to M-wave (M) in musculus soleus]. 1RM increased from 133 ± 16 to 157 ± 23 kg and 123 ± 18 to 149 ± 22 kg and CMJ by 2.3 ± 3.6 and 2.2 ± 3.7cm for MST and eMST, respectively (all $P < 0.05$). Early, late, and maximal RFD increased in both groups [634–1,501 N/s (MST); 644–2,111 N/s (eMST); $P < 0.05$]. These functional improvements were accompanied by increased V/M-ratio (MST: 0.34 ± 0.11 to 0.42 ± 14; eMST: .36 ± 0.14 to 0.43 ± 13; $P < 0.05$). Resting H/M-ratio remained unchanged. Training-induced improvements did not differ. All increases, except for CMJ, were different from the CG. MST is an enterprise for large gains in FGC and functional performance. Eccentric overload did not induce additional improvements, suggesting firing frequency and motor unit recruitment during MST may be maximal.

NEW & NOTEWORTHY This is the first study to apply evoked potential recordings to investigate effects on efferent neural drive following high-intensity strength training with and without eccentric overload in a functionally relevant lower extremity exercise. We document that eccentric overload does not augment improvements in efferent neural drive or muscle force-generating capacity, suggesting that high-intensity concentric loads may maximally tax firing frequency and motor unit recruitment.

efferent neural drive; evoked potentials recordings; heavy resistance training; rate of force development

INTRODUCTION

In search of the most potent strength training modality, loading intensity has been recognized as a key component (Campos et al. 2002; Heggelund et al. 2013). Additionally, intentional maximal velocity in the execution of movement may enhance the improvements in maximal muscle strength and rate of force development (RFD) (Behm and Sale 1993), collectively referred to as force-generating capacity (FGC). In accordance with these training principles, maximal strength training (MST) typically uses loads up to 95% of maximal strength, few repetitions (3–5), and emphasis on maximal intended velocity in the concentric phase. Compared with conventional strength training with lower intensity (e.g., 70% of maximal strength), more repetitions (8–12), and slower intended velocity, MST has been shown to yield a twofold increase in RFD and ~40% larger increase in maximal strength (Heggelund et al. 2013). MST is tailored to target neural adaptations and specifically tax efferent neural drive (i.e., motor unit recruitment and firing frequency). Indeed, increases in efferent neural drive following MST have been shown in a range of populations (Ekblom 2010; Fimland et al. 2009; Unhjem et al. 2016a).

Since stimulating the efferent neural drive maximally may be essential to yield the largest improvements in FGC, the prospect of increasing intensity more than what may be achieved by high concentric intensity and maximal intended velocity training is intriguing. As the human muscle is stronger during lengthening actions, the eccentric phase offers such a unique opportunity for increased loading and possibly subsequent enhanced efferent neural stimulation in the initial part of the concentric phase. Indeed, acute eccentric overload is documented to increase the force output at the onset of the concentric phase and consequently improve strength performance (Doan et al. 2002; Sheppard and Young 2010). In fact, force output at the start of the concentric phase appears to increase in proportion to the magnitude of the preceding eccentric phase (Takarada et al. 1997). Since produced force is dependent on motor unit recruitment and firing frequency (Enoka and Duchateau 2017), efferent neural drive may be

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Address for reprint requests and other correspondence: T. Tøien, Dept. of Circulation and Medical Imaging, Faculty of Medicine, Norwegian Univ. of Science and Technology, Prinsesse Kristinas gt. 3, 7030 Trondheim, Norway (e-mail: tiril.toien@ntnu.no).

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responsible, at least in part, for higher initial force production in the concentric phase following eccentric overload. However, the longitudinal training responses in FGC remain equivocal (Brandenburg and Docherty 2002; Godard et al. 1998). One reason for this could be that previous studies have typically used a concentric underload to compensate for the additional eccentric overload (Kaminski et al. 1998). This may have attenuated the gains in FGC. To the best of our knowledge, no studies to date have applied eccentric overload in a functionally relevant exercise task of the lower extremity before a high concentric load with maximal intended velocity, where motor unit recruitment and firing frequency are already high (Enoka and Fuglevand 2001).

With the use of evoked recordings (V-wave normalized to M-wave) during maximal muscle contractions and supramaximal electrical stimulation in the lower extremities, the aim of the study was to contrast the effects of MST with or without eccentric overload on efferent neural drive, FGC, and functional performance. Implying that one training group (MST) performed concentric and eccentric action at ~90% of one-repetition maximum (1RM), whereas the other training group (eMST) performed an eccentric phase with ~150% 1RM followed by a concentric phase at ~90% 1RM. It was hypothesized that *1*) MST with eccentric overload would induce larger increases in efferent neural drive than MST, and *2*) MST with eccentric overload would be superior to regular MST in improving leg press maximal strength and RFD.

METHODS

Subjects. A total of 53 healthy, young, nonsmoking males volunteered to participate in the study. The subjects were not familiar with regular strength training of the lower extremities before the study. They were instructed to continue their regular physical activity during the course of the study. Subjects were allocated to one of three groups; one training with MST ($n = 19$), one training MST with an additional eccentric overload (eMST; $n = 19$), and a nontraining control group (CG; $n = 15$). The study was approved by the local ethics committee, and all subjects gave written informed consent before undertaking testing and training. The study was performed according to the Declaration of Helsinki.

Study timeline. Care was taken to ensure the participants performed pre- and posttests within 2 h of the same time of day. Each participant was requested to avoid alcohol 24 h before any testing and training. They were also instructed to eat and drink as they usually would before the pretest and to mimic this routine on the follow-up test. Standardized test procedures were performed on the same day, before and after the training period. After a 10-min treadmill warm up, the subjects performed testing of countermovement jump (CMJ) performance, leg press maximal strength and RFD, and plantar flexion evoked reflexes. Training was conducted three times per week for 8 wk, and a minimum of 20 sessions had to be completed to proceed to the follow-up testing. The CG did not train and served as a time-control from pre- to posttest.

Maximal strength, RFD, and jumping performance. The subjects performed CMJs on a force plate (9287CA; Kistler) sampling at 800 Hz. Subjects started from a standing position and were instructed to perform a CMJ where the aim was to jump as high as possible. They were instructed to use arm swing but no instructions were given regarding range of motion of the knee or hip joint. Bioware software v. 5.3.0.7 (Kistler) was used to calculate jump height; velocity data and the initial displacement were used to compute displacement of the center of mass by performing integration. This computation of displacement is based on velocity being the rate of change of displacement. The highest vertical displacement of the center of mass was recorded as the vertical jump height. The highest of three jumps was used in further analysis.

Maximal strength was obtained as 1RM in a horizontal leg press (Technogym silver line). Following three warm up sets of two to eight repetitions on light loads (<60% of expected 1RM), 1RM was reached within five lifts, separated by 3–4 min of rest, by increasing the load with 5–10 kg until the subjects were unable to complete the lift. The lifts consisted of an eccentric phase (from ~180 to 90° angle in the knee joint) and a concentric phase (from ~90° back to 180° angle in the knee joint). Range of motion was determined visually with the aid of a goniometer. 1RM was taken as the highest load successfully lifted.

After a 3- to 4-min break, dynamic RFD trials were performed in the same leg press apparatus. A standard weight of 70% of pretest 1RM was used, and force was obtained at 800 Hz on a force platform (9286AA; Kistler) mounted on the leg press apparatus with a custom built attachment and the same Bioware software as used to calculate CMJ height. A high intraclass correlation coefficient (ICC; 0.98) has been reported for measurements of CMJ (Markovic et al. 2004). For each 1RM and RFD lift, the participant was instructed to perform the eccentric phase in a slow and controlled manner, before aiming to lift the weight as forcefully and fast as possible. The best of three RFD trials, determined as the steepest force-time curve, was used for data analysis. RFD was calculated as Δforce/Δtime in the time intervals 0–30, 0–50, 0–100, 0–150, and 0–200 ms, where 0 ms denotes the onset of concentric force production, along with maximal RFD in the steepest part of the force-time curve. In leg press 1RM and RFD, an ICC of 0.99 and 0.94, respectively, has been documented (Spiering et al. 2011).

Evoked reflex recordings. As an assessment of efferent neural drive to the lower extremities, H-reflexes and V-waves were evoked in the tibial nerve located in the popliteal fossa of the right leg, while seated in a custom made isometric apparatus (Unhjem et al. 2016b) with the ankle in a neutral position and the knee flexed at 90°. Electric potentials were recorded from musculus soleus, using self-adhesive pairs of bipolar AG/AgCI electrodes (M-00-S/50; Ambu, Ballerup, Denmark) with an interelectrode distance of 25 mm. The skin was carefully shaved, abraded (Nuprep; Weaver, Aurora, CO), and wiped clean with alcohol. The preparation procedure was included to ensure minimal resistance in the skin; the maximal interelectrode impedance level was set to 5 kΩ. After preparation of the skin, the electrodes were placed as recommended by SENIAM (Hermens et al. 2000). Measuring tape and anatomical landmarks were used to identify the appropriate location of electrode placement, and pictures were taken of the relevant leg to ensure identical placement of the electrodes from pre- to posttest. For percutaneous nerve stimulation, a current stimulator (DS7AH; Digitimer, Welwyn Garden City, UK) gave a 1-ms square wave stimulus to the tibial nerve in the popliteal fossa via handheld gel-coated (Lectron 2 conductive gel; Pharmaceutical Innovations, Newark, NJ) bipolar felt pad electrodes, which were 8 mm in diameter and had 25 mm between the tips (Digitimer). These electrodes were placed at the position evoking the largest H-reflex amplitude relative to the M-wave amplitude. EMG data were obtained with Megawin software 700,046 version 3.0, by using the ME6000 Biomonitor (Mega Electronics, Kuopio, Finland) at 2 kHz, common mode rejection ratio of 110 dB. The signals were amplified and band-pass filtered (8–500 Hz).

H-reflex measurements were obtained during 10% of isometric maximal voluntary contraction (MVC) to maintain a stable motoneuron excitability and minimize postsynaptic effects (Knikou 2008). To minimize any conditional effects, testing was done in the same laboratory and performed by the same researcher. First, the optimal site for stimulation was located, before the current intensity was gradually increased by 2–5 mA searching for the maximal H-reflex peak-to-peak amplitude (H_{max}). Importantly, stimulation intensity was carefully monitored to ensure similar M-wave responses during H_{max} between groups and from pre- to posttest [see Table 3; M at H_{max}

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(%M_{max})]. Subsequently, the electrical stimulation current was increased further to elicit the maximal M-wave (M_{max}) obtained during 10% MVC. M_{max} was identified when no further increase in M-wave amplitude was seen, despite increased electrical current. A supramaximal stimulus of 150% of the stimulus needed to evoke M_{max} was given to ensure that the true M_{max} was reached (Aagaard et al. 2002). H_{max} was normalized to M_{max}, both obtained at 10% MVC.

Following the detection of M_{max}, six to eight V-wave recordings were performed. The V-wave responses were evoked by delivering a supramaximal stimulus to the tibial nerve during MVC. Importantly, the subjects were instructed to exert maximal, rapid voluntary muscle force. The subjects were perceived to have reached MVC when a plateau of torque was observed. One-minute rest periods were given between each MVC. V-waves were normalized to the maximal M-waves obtained during MVC (M_{sup}). To be included in analysis, the amplitude of the M-wave had to be ≥95% of M_{sup} and the force had to be ≥90% of MVC. Previous test-retest reliability for the V-wave technique has been shown to be 0.86 (ICC) (Solstad et al. 2011).

Training intervention. The CG did not receive any training during the intervention. The two training groups attended 8 wk of individually supervised strength training, three times per week. All training sessions were carried out in a laboratory setting in the leg press apparatus used in the testing procedures with the testing personnel monitoring each session.

Maximal strength training. The MST training consisted of four sets of four repetitions, and the intensity was set to 90–95% of 1RM in both movement phases. The training followed a linear progression model, which meant that when the participant was able to lift a fifth repetition in a set, the load was increased by 5 kg. If the participant could only lift three repetitions, the load was decreased by 5 kg. The training was, as the testing, initiated with an eccentric phase, at a range of motion starting from 180° angle in the knee joint to 90° knee flexion, followed by a concentric phase back to ~180° knee angle, and finished with a plantar flexion (Fimland et al. 2009). In accordance with previous research, the training was carried out with a controlled eccentric phase, before maximal mobilization of force in the concentric phase, as previously used in our laboratory to facilitate neuromuscular adaptations to resistance training (Hoff et al. 2007; Wang et al. 2017). Three-minute rest periods were applied between each set.

Eccentric maximal strength training. The eMST group followed the same principles as the MST group, including the leg press exercise, movement phases, sets, repetitions, rest periods, and intensity in the concentric phase (90–95% of 1RM). However, the eccentric load was set to 150% of 1RM. This load was chosen based on previous leg press maximal eccentric strength (Hollander et al. 2007). The extra load was added manually in the eccentric phase and removed on the same cue as the participant was given to perform the concentric phase. The same linear progression model was used as for the MST group, and the eccentric load increased relative to the load in the concentric phase. A pilot test including 19 participants confirmed that the load chosen in the eccentric phase was well tolerated by the participants. With the use of the force platform (9286AA; Kistler), this pilot test also revealed that the absolute force in the initial part of the concentric phase was 34 ± 5% higher when an eccentric overload of 150% of 1RM was added compared with equal load in both phases of the action ($P < 0.001$).

Statistical analyses. IBM SPSS statistics software version 23 (Chicago, IL) was used for statistical analyses, and GraphPad Prism 6 (San Diego, CA) was used for graphic illustrations. The data were assessed for normality with Q-Q plots and Shapiro-Wilk's test for normality, and all the main variables (1RM, RFD, CMJ, and V/M-ratio) exhibited a normal distribution, and as such parametric tests were applied. To detect within group differences following training, paired samples *t*-tests were used. Independent sampled *t*-tests were used to detect between-group differences. The Pearson test for linear regression was used to evaluate associations between absolute increases in variables. Statistical analysis of training data was performed with *session 1* as first time point and *session 20* as the last time point, as all subjects included in analysis completed 20 sessions. Data are presented as means ± SD in the tables and text and as means ± SE in figures. $P \leq 0.05$ was considered statistically significant.

RESULTS

Adherence. Two subjects in the MST group withdrew; one due to injury unrelated to the study and one due to groin pain likely associated with the training. Additionally, one subject withdrew from the eMST group due to back pain likely related to the training and one participant withdrew from the CG without providing a reason. Furthermore, two subjects in eMST were excluded from all data analysis, one due to low training compliance (14 sessions), whereas one subject was unable to plantar flex during training, leaving $n = 16$ in eMST, $n = 17$ in MST, and $n = 14$ in the CG. Moreover, one result from eMST and one from CG were excluded from V-wave analysis, as the participants were unable to contract maximally during V-wave trials at posttest (<90% MVC in all trials). The remaining participants completed 23 ± 1 of the 24 planned sessions (both groups), and there was no difference in compliance between training groups ($P = 0.624$). One subject was asked to perform one repetition of both training regimes to give a visual representation of the training. The result is presented in Fig. 1.

Subject characteristics. Subject characteristics are presented in Table 1. A slight but significant body mass increase of ~2% was observed within the eMST group from pre- to posttraining [$t_{15} = -3.350$; 95% confidence interval (CI) = −2.19, −0.49; $P = 0.004$; Table 1], whereas no such increase was observed in MST ($t_{15} = -0.935$; 95% CI = −1.25, 0.49; $P = 0.365$) or CG ($t_{13} = -0.737$; 95% CI = −0.72, 1.46; $P = 0.474$). This pre- to posttest difference in eMST was significantly different from the CG ($t_{28} = 2.689$; 95% CI = 0.41, 3.01; $P = 0.012$), but no between-group difference was evident between the two training groups ($t_{30} = 1.675$; 95% CI = −0.21, 2.12; $P = 0.104$).

Training data. Concentric training load increased from *session 1* to *session 20* in both training groups (eMST:

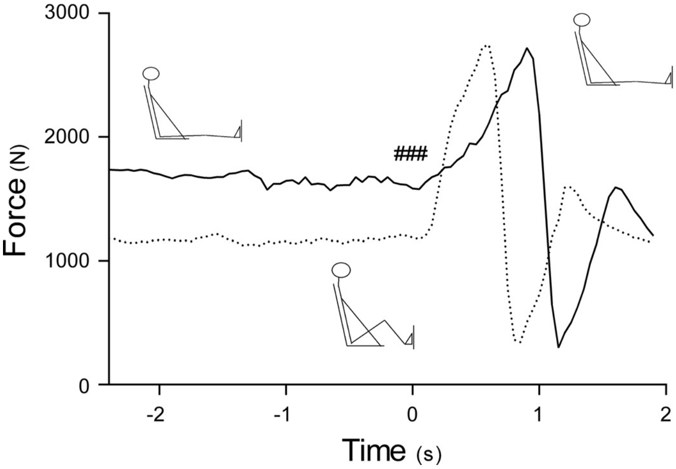

Fig. 1. A visual presentation of one of four repetitions during a training session in the dynamic leg press with (whole line) and without (dotted line) eccentric overload performed by a representative subject. Time 0 denotes the onset of concentric force production. ###$P < 0.001$, force at the start of the concentric phase between groups.

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Table 1. *Descriptive characteristics*

	eMST		MST		CG	
	Pre	Post	Pre	Post	Pre	Post
Age, yr	22 ± 3		24 ± 2		23 ± 4	
Stature, cm	181 ± 8		181 ± 6		183 ± 7	
Body mass, kg	73.4 ± 8.5	74.7 ± 8.2*†	77.5 ± 8.7	77.9 ± 8.4	79.7 ± 9.1	79.3 ± 8.1

Data are presented as means ± SD. eMST, maximal strength training with eccentric overload; MST, maximal strength training; CG, control group. $^*P < 0.05$, significantly different from corresponding pretraining value. $^\dagger P < 0.05$, significant pre- to posttraining between-group difference (eMST vs. CG).

$t_{15} = -14.421$; 95% CI = −44.84, 33.29; $P < 0.001$; MST: $t_{16} = -11.199$; 95% CI = −39.88, −27.18; $P < 0.001$; Fig. 2). No difference in concentric training load was detected between the two training groups in the increase in training load from session one to 20 ($t_{31} = 1.365$, 95% CI = −2.73, 13.80; $P = 0.182$; Fig. 2).

Maximal strength, RFD, and jumping performance. 1RM increased by 21 ± 9% (123 ± 18 to 149 ± 22 kg; $t_{15} = -9.586$; 95% CI = −30.94, −19.68; $P < 0.001$) in eMST and 18 ± 10% (133 ± 16 to 157 ± 23 kg; $t_{15} = -7.592$; 95% CI = −30.82, −17.31; $P < 0.001$) in MST from pre- to posttest (Fig. 3). No pre- to posttest difference in 1RM was detected in CG ($t_{13} = -0.201$; 95% CI = −4.19, 3.48; $P = 0.844$). No between-group difference in 1RM increase was detected between eMST and MST ($t_{30} = 0.303$; 95% CI = −7.18, 9.68; $P = 0.764$). Between-group difference was observed between eMST and CG ($t_{28} = 7.613$; 95% CI = 18.24, 31.67; $P < 0.001$) and MST and CG ($t_{23.244} = 6.526$; 95% CI = 16.20, 31.22; $P < 0.001$). Maximal strength normalized to body mass (1RM/m_b) increased significantly in eMST (1.68 ± 0.21 1RM/m_b to 1.99 ± 0.24 1RM/m_b; $t_{15} = -9.762$; 95% CI = −0.37, −0.24; $P < 0.001$) and MST (1.72 ± 0.26 1RM/m_b to 2.03 ± 0.36 1RM/m_b; $t_{15} = -6.801$; 95% CI = −0.40, −0.21; $P < 0.001$). No pre-to posttest difference in 1RM/m_b was detected in CG ($t_{13} = -0.881$; 95% CI = −0.06, 0.02; $P = 0.394$). No between-group difference in 1RM/ m_b increase was detected between eMST and MST ($t_{30} = 0.168$; 95% CI = −0.11, 0.12; $P = 0.916$). Between-group difference in the increase was observed between eMST and CG ($t_{23.671} = 8.007$; 95% CI = 0.21, 0.36; $P < 0.001$) and MST and CG ($t_{19.845} = 5.956$; 95% CI = 0.19, 0.39; $P < 0.001$).

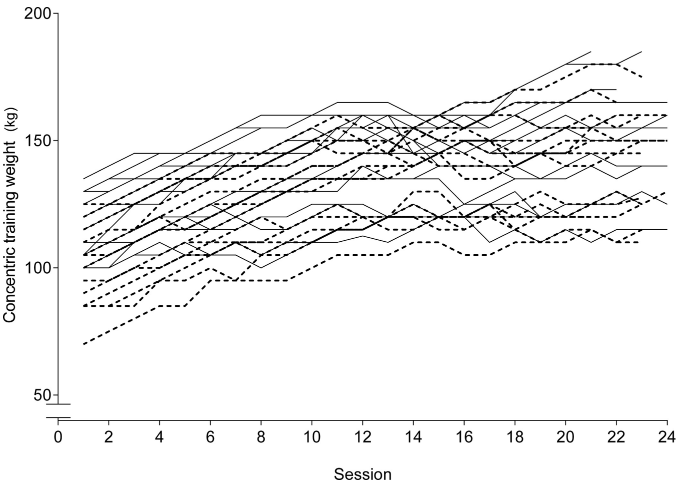

Fig. 2. Concentric training weight for one repetition in a set in each session for all individuals for maximal strength training with eccentric overload (dotted lines) and maximal strength training (whole lines).

There was an increase in each RFD time interval in both training groups, whereas no pre-to posttraining difference was detected in CG (see Table 2). The time intervals 0–30 ms, 0–50, 0–100, 0–150, and 0–200 ms and maximal RFD in the eMST group increased by 39 ± 25% ($t_{14} = -5.440$; 95% CI = −897.70, −390,04), 57 ± 35% ($t_{14} = -7.048$; 95% CI = −1,496.97, −798.44), 62 ± 38% ($t_{14} = -10.007$; 95% CI = −2,184.52, −1,413.38), 49 ± 34% ($t_{14} = -10.171$; 95% CI = −1874.67, −1221.71), 39 ± 20% ($t_{14} = -10.027$; 95% CI = −1,499.38, −970.96), and 37 ± 27% ($t_{14} = -5.189$; 95% CI = −2,983.96, −1,238.74), respectively. Similarly, in the MST group RFD intervals increased by 43 ± 36% ($t_{14} = -5.540$; 95% CI = −876.10, −391.17), 51 ± 47% ($t_{14} = -5.594$; 95% CI = −1,194.87, −538.17), 53 ± 44% ($t_{14} = -5.632$; 95% CI = −1,838.79, −833.03), 38 ± 27% ($t_{14} = -6.753$; 95% CI = −1,621.89, −846.87), 29 ± 18% ($t_{14} = -6.534$; 95% CI = −1,314.90, 670.72), and 27 ± 18% ($t_{14} = -6.928$; 95% CI = −1,960.01, −1041.52), respectively. No between-group differences in the training-induced increase were detected between the training groups for either RFD interval (Table 2). Both training groups increased RFD in each time interval significantly compared with CG (Table 2).

CMJ height increased by 4 ± 7 and 4 ± 6% in eMST ($t_{14} = -2.355$; 95% CI = −4.25, −0.20; $P = 0.034$) and MST ($t_{15} = -2.494$; 95% CI = −4.17, −0.33; $P = 0.025$), respectively (Fig. 4). No pre- to posttest difference was detected in CG ($t_{13} = -0.861$; 95% CI = −3.33, 1.43; $P = 0.405$). No between-group difference in CMJ increase was detected between eMST and MST ($t_{29} = -0.021$; 95% CI = −0.03, 1.30; $P = 0.983$). No between-group difference in CMJ increase was detected between eMST and CG ($t_{27} = 0.880$; 95% CI = 1.27, 1.44; $P = 0.386$) or MST and CG ($t_{28} = 0.921$; 95% CI = 1.30, 1.41; $P = 0.365$).

Evoked reflex recordings. Strength training significantly increased the soleus V/M-ratio by 32 ± 9% in eMST ($t_{14} = -3.516$; 95% CI = −0.12, −0.03; $P = 0.003$) and 27 ± 8% in MST ($t_{16} = -3.787$; 95% CI = −0.12, −0.03; $P = 0.002$; Fig. 5). A significant decrease in M_{sup} ($t_{12} = 2.571$; 95% CI = 166.06, 2,12.06; $P = 0.025$) and maximal V-wave amplitude (V_{max}; $t_{12} = 2.409$; 95% CI = 51.19, 1,019.96; $P = 0.033$) was detected in the CG from pre- to posttest, but no pre-to posttest difference was detected in V/M-ratio in CG ($t_{12} = -0.02$; 95% CI = −0.02, 0.06; $P = 0.324$). No between-group difference was detected between eMST and MST in V/M-ratio increase ($t_{30} = -0.139$; 95% CI = −0.06, 0.06; $P = 0.891$). Between-group difference in V/M-ratio increase was observed between eMST and CG ($t_{26} = 3.273$; 95% CI = 0.03, 0.15; $P = 0.003$) and MST and CG ($t_{28} = 3.394$;

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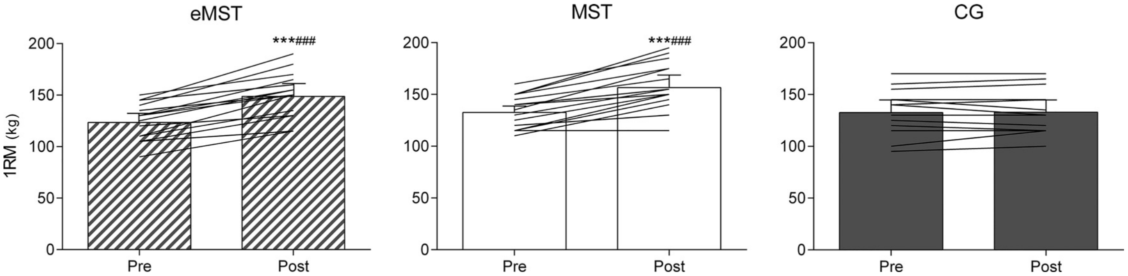

Fig. 3. Maximal strength before and after 8 wk of strength training. Data are presented as means ± SE and individual responses. eMST, maximal strength training with eccentric overload; MST, maximal strength training; CG, control group; 1RM, one repetition maximum. $***P < 0.001$, within group from pre- to posttest, $\#\#\#P < 0.001$, MST and eMST vs. CG.

95% CI = 0.04, 0.16; $P = 0.002$). The absolute increase in V/M-ratio for all groups collapsed was associated with the increase in 1RM ($P = 0.026$, r = 0.335). No other significant associations were observed. No difference was observed in the soleus H/M-ratio from pre- to posttraining in eMST ($t_{12} = 0.375$; 95% CI = −0.06, 0.09; $P = 0.714$), MST ($t_{15} = 1.288$; 95% CI = −0.03, 0.12; $P = 0.217$), or CG ($t_{12} = -0.783$; 95% CI = −0.10, 0.05; $P = 0.449$; Table 3).

DISCUSSION

MST performed with maximal intended velocity in the concentric phase of the movement stimulates neural firing frequency and motor unit recruitment (Toien et al. 2018), and yields effective improvements in muscle FGC (Heggelund et al. 2013). The present study aimed to investigate if applying an eccentric overload would enhance neural stimulation and, in turn, augment FGC adaptations. The main finding was that MST with and without eccentric overload resulted in similar increases in FGC, functional performance, and efferent neural drive to maximally contracting musculature. To the best of our knowledge, the current study is the first to compare neural responses in high-intensity strength training with and without an eccentric overload, and the results indicate that efferent neural drive may already be maximally stimulated during constant load MST. Since MST without eccentric overload has a lower muscular tension and thus likely a lower risk of injuries and is easier to carry out, conventional MST should be advocated as an effective means to increase muscle FGC and functional performance.

Strength training, eccentric overload, and muscle FGC. As expected, 8 wk of high-intensity strength training increased FGC. The improvements in maximal strength and RFD following MST were in accordance with what has previously been reported in young individuals (Fimland et al. 2009; Heggelund et al. 2013). However, despite eccentric actions being known to acutely influence concentric force output and strength performance (Doan et al. 2002; Sheppard and Young 2010; Takarada et al. 1997), eccentric overload before the high-intensity concentric phase during MST did not enhance training adaptations in the current study. Although consistent with one previous study (Godard et al. 1998), the present results contrast to several studies reporting enhanced strength-training induced improvements when an eccentric overload is applied (Brandenburg and Docherty 2002; Hortobágyi et al. 2001; Kaminski et al. 1998; Walker et al. 2016). However, only one of these studies reported differences between training groups in concentric strength improvements (Brandenburg and Docherty 2002). Albeit, in the latter study, the larger increase in concentric maximal strength following eccentric overload training was only seen in elbow flexors and not elbow extensors, indicating that adaptations to eccentric overload training may be muscle group specific. As the current study did not include groups training eccentric and concentric training in isolation, it is difficult to assess the relative importance of each phase in concentric strength improvement. However, since the two phases are mutually influential, the effects of separate eccentric and concentric training may not necessarily translate directly into their relative contribution during combined muscle action. A meta-analysis by Roig et al. (2009) revealed that concentric and eccentric training yielded concentric effects that were not different. Albeit, several studies have documented that concentric training is superior compared with eccentric training for concentric strength improvements (Blazevich et al. 2007; Seger and Thorstensson 2005; Tomberlin et al. 1991). One reason that concentric and eccentric training may yield similar effects when compared is that the total work has to be higher during eccentric training if the intensity level is aimed to be the same. As intensity is a key component for strength training-

Table 2. *Dynamic leg press rate of force development*

	eMST			MST			CG			Between-Group		
	Pre	Post	*P*	Pre	Post	*P*	Pre	Post	*P*	*P*	*P*	*P*
0–30 ms	1,912 ± 605	2,568 ± 616	<0.001*	1,564 ± 487	2,198 ± 757	<0.001*	1,942 ± 733	1,906 ± 635	0.886*	0.951†	0.023‡	0.025§
0–50 ms	2,346 ± 850	3,505 ± 945	<0.001*	2,091 ± 919	2,957 ± 978	<0.001*	2,417 ± 677	2,247 ± 819	0.517*	0.221†	<0.001‡	0.001§
0–100 ms	3,296 ± 1,024	5,136 ± 1,048	<0.001*	3,001 ± 1,169	4,337 ± 1,402	<0.001*	3,508 ± 651	3,403 ± 855	0.732*	0.138†	<0.001‡	0.001§
0–150 ms	3,567 ± 889	5,163 ± 808	<0.001*	3,501 ± 999	4,736 ± 1,344	<0.001*	3,793 ± 477	3,822 ± 816	0.916*	0.204†	<0.001‡	0.001§
0–200 ms	3,355 ± 705	4,629 ± 675	<0.001*	3,492 ± 832	4,484 ± 1,196	<0.001*	3,547 ± 404	3,618 ± 707	0.740*	0.233†	<0.001‡	0.001§
Max	6,132 ± 1,203	8,344 ± 1,608	<0.001*	5,810 ± 1,639	7,311 ± 1,924	<0.001*	6,188 ± 807	5,992 ± 1,178	0.667*	0.199†	0.001‡	0.001§

Data (in N/s) are presented as means ± SD; eMST, maximal strength training with eccentric overload; MST, maximal strength training; CG, control group. *P, from corresponding pretraining value. †P, between-group eMST and MST. ‡P, between-group eMST and CG. §P, between-group MST and CG.

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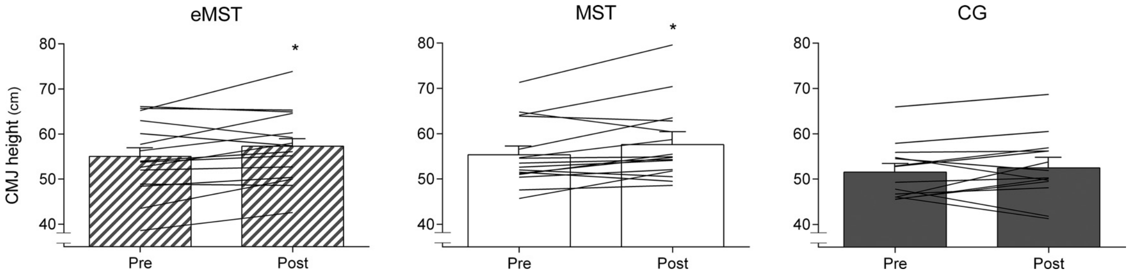

Fig. 4. Countermovement jump (CMJ) height before and after 8 wk of strength training. Data are presented as means ± SE and individual responses. eMST, maximal strength training with eccentric overload; MST, maximal strength training, CG; control group. $*P < 0.05$, within group from pre- to posttest.

induced improvements (Heggelund et al. 2013), a higher intensity will be more effective. This may also result in relatively larger eccentric contribution to total strength (combined eccentric and concentric strength) improvement, as evident in the Roig et al. (2009) meta-analysis.

Other studies using inertia to apply eccentric overload via a flywheel (Norrbrand et al. 2008) are difficult to compare with the present study, as it is challenging to quantifying the intensity applied with the flywheel compared with the present study. However, it should be noted that a recent meta-analysis concluded that flywheel resistance training was not superior to constant load strength training for increases in strength (Vicens-Bordas et al. 2018), which is in line with the present results. In the present study, leg press was chosen because of its functional relevance and previously well-documented FGC improvements (Fimland et al. 2009; Unhjem et al. 2015), and particular care was taken to ensure a progressive increase in concentric intensity (~90% of 1RM) throughout the training period, by adding more resistance when the participants could lift more than the intended four repetitions. Importantly, previous studies have documented that short (Fimland et al. 2009) and long-term (Unhjem et al. 2016b) leg press/squat strength training appears to be mirrored in the plantar flexors, likely because adaptations in the central motor pathway are manifested throughout the lower extremities. Of note, since the initial phase of the concentric movement with high firing frequency and motor unit recruitment is argued to be very important for the efferent neural drive training response, the later phase of the movement (including the plantar flexion muscle action) may be of less importance. Albeit, we cannot exclude that the late phase was a contributor for the training-induced neurophysiological adaptations.

The similar CMJ height increase after eMST and MST underpin the functional relevance of the increase in concentric FGC and augmented the confidence with which we could interpret the similarity between the two training groups. The increases in CMJ height were in line with previous studies following MST (Helgerud et al. 2011; Hoff et al. 2001). It is important to consider the functional benefit of the strength training-induced increases in FGC. Although eccentric strength plays a role in absorbing force, concentric strength directly enhances the propulsive phase in, e.g., jumping and running, in accordance with Newton's second law of motion. Moreover, since the muscle is stronger eccentrically than concentrically, the concentric strength sets the upper limit in many sporting actions. Thus eccentric overload did not enhance the concentric strength and in turn CMJ performance more than regular MST.

Strength training, eccentric overload, and efferent neural drive. In accordance with previous findings, functional leg press strength training resulted in a marked increase in efferent neural drive to the muscles of the lower extremities (Fimland et al. 2009). An increase in V/M-ratio to maximally contracting musculature has commonly been attributed to alterations in corticospinal factors (Fimland et al. 2009; Unhjem et al. 2016b), advocated to reflect enhanced descending input to the spinal motoneuron pool. Albeit, different recruitment of afferents and motoneurons, as well as spinal reflex pathways, may also be of influence (Aagaard et al. 2002). A slight decrease in absolute V_{max} and M_{sup} was observed in the CG. This may have been due to electrode placement or a change in interelectrode impedance. This observation highlights the importance of normalizing to H- and V-waves to an M-wave, as methodological error may occur, but which will affect V_{max} and the concurrent M_{sup} similarly and consequently give a representative V/M-ratio.

In the current study, the magnitude of efferent neural drive to the lower extremities increased similarly following constant load and eccentric overload MST. Although this may be somewhat surprising, given the higher intensity at the onset of concentric muscle action in the eMST group, where the presence of doublet discharges and very high motor unit discharge rate can be assumed (Maffiuletti et al. 2016), it subsequently

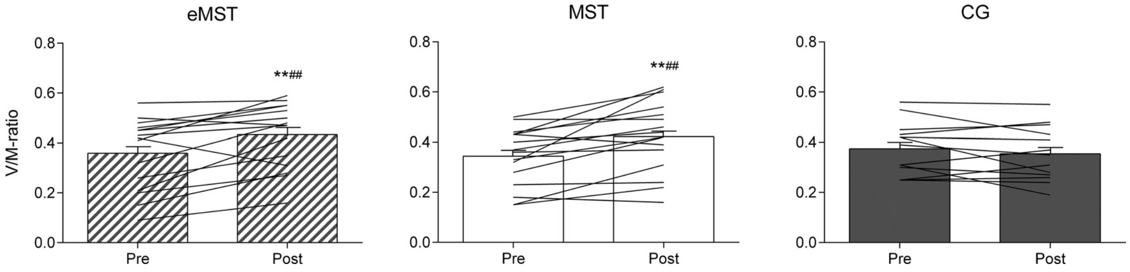

Fig. 5. Soleus V/M-ratio before and after 8 wk of strength training. Data are presented as means ± SE and individual responses. eMST, maximal strength training with eccentric overload; MST, maximal strength training; CG, control group; V/M-ratio, maximal V-wave amplitude/maximal M-wave amplitude. $**P < 0.01$, within group from pre- to posttest; $\#\#P < 0.01$, MST and eMST vs. CG.

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Table 3. *Absolute amplitudes and normalized evoked peak-to-peak amplitude potentials of the soleus muscle*

	eMST		MST		CG	
	Pre	Post	Pre	Post	Pre	Post
M_{max}	6,653 ± 1873	6,846 ± 2411	5,951 ± 2040	6,067 ± 2477	7,031 ± 1617	6,363 ± 1,685
H_{max}	3,551 ± 1647	3,451 ± 1781	3,127 ± 1726	2,646 ± 1093	3,398 ± 927	3,203 ± 1,208
H/M-ratio	0.52 ± 0.19	0.51 ± 0.17	0.52 ± 0.16	0.47 ± 0.17	0.50 ± 0.15	0.53 ± 0.19
M at H_{max} (%M_{max})	27 ± 12	26 ± 15	23 ± 10	26 ± 17	23 ± 7	25 ± 13
M_{sup}	7,350 ± 2,082	6,509 ± 2,261	6,099 ± 2,107	6,195 ± 2,281	7,401 ± 1,947	6,312 ± 1,981*
V_{max}	2,706 ± 1,405	2,895 ± 1,489	2,191 ± 1,138	2,694 ± 1,536	2,878 ± 1,389	2,342 ± 1,225*

Data (in μV) are presented as means ± SD. eMST, maximal strength training with eccentric overload; MST, maximal strength training; CG, control group; M_{max}, maximal M-wave (muscle wave) during 10% maximal voluntary contraction; H_{max}, maximal H-reflex during 10% maximal voluntary contraction,; H/M-ratio, maximal H-reflex amplitude/maximal M-wave amplitude; M_{sup}, maximal M-wave amplitude during maximal voluntary contraction; V_{max}, maximal V-wave amplitude. *$P < 0.05$, significantly different from corresponding pretraining value.

also appeared to result in a slower concentric RFD when executing the training (Fig. 1). Recognizing that the motor unit discharge rate is relatively constant during lengthening contractions and increases progressively to a higher level during shortening contractions, the training stimulation may have been blunted throughout the concentric action in the eMST group. Thus the eccentric overloading appeared to result in a differential stimulation for adaptations to training (onset of force vs. development of force). This may explain the lack of differences between the eMST and MST groups. Moreover, the average force production in the concentric phase in the eMST group appeared to be similar to the MST group (Fig. 1), which may result in similar strength-training induced adaptations. Another explanation for the similar improvements in the training groups may be that firing frequency and motor unit recruitment were maximal for the MST group with constant loading because the repetitions were carried out with an intentional maximal RFD. Indeed, previous literature provides evidence that it is the maximal intentional RFD, rather than the applied training load, that yields the most effective adaptations (Hoff et al. 2007; Maffiuletti et al. 2016).

The V-wave peak-to-peak amplitude, an electrophysiological variant of the H-reflex, is determined by the removal of antidromic impulses, which allows the reflex volley to propagate to the muscle (Aagaard et al. 2002; Duclay and Martin 2005). As such, an increased V/M-ratio has been interpreted as increased transmission of efferent impulses, i.e., increased motor unit recruitment and/or firing frequency (Aagaard et al. 2002). Since motor unit recruitment in healthy, young individuals is usually, at least close to, complete (>90–95%) (Goodall et al. 2009), firing frequency was likely a major adaptation in response to strength training in the present study. Increased firing frequency has been shown to accompany strength training improvements (Christie and Kamen 2010; Kamen and Knight 2004; Patten et al. 2001). In fact, by rearranging a mathematical equation from Upton et al. (1971), Aagaard et al. (2002) postulated that the increase in V/M-ratio following a similar strength training intervention as used in the present study was due to increased motoneuron firing frequency. Increased number of doublets, motor unit firing rates with very brief interspike intervals, also appears to be improved in response to ballistic training, particularly relevant for RFD improvements (Van Cutsem et al. 1998). As such, maximal intentional RFD, as used in the present study, was likely of importance to increase motor unit discharge rates.

Although maximal eccentric strength has commonly been demonstrated to exceed maximal concentric strength, and it may be conceivable that the amount of afferent feedback was higher during eccentric overload (Enoka and Duchateau 2017), similar V/M-ratios have been observed for both contraction types (Duclay and Martin 2005; Duclay et al. 2008; Ekblom 2010). Thus enhanced eccentric strength does not seem to be a result of higher efferent neural drive, when compared with concentric strength. Furthermore, following a training period of purely eccentric muscle actions (Duclay et al. 2008) or eccentric overload (Ekblom 2010), V/M-ratios have increased similarly during concentric, isometric, and eccentric contractions. Thus, although motor efferent output is somewhat dependent on sensory afferent feedback from the muscle (Aagaard et al. 2000), adding an additional load on the muscle in the eccentric phase does not appear to induce higher efferent neural drive than what can already be achieved in the concentric phase with high intensity. Although the lower limit of eccentric load seems unclear, incorporating both eccentric and concentric actions appears to be critical for strength training adaptations (Dudley et al. 1991).

The training-induced improvement in muscle FGC in the current study was likely not only the result of neural adaptations but an interaction between neural and muscular factors. Although not the scope of this paper, the training may have led to a faster muscle phenotype contributing to the early and late phase RFD and maximal strength increase. Indeed, an increase in area and percentage of type II fibers has recently been documented after MST (Wang et al. 2017), and an increase in type II myosin heavy chain percentage was found to be associated with an increase in RFD (Harridge et al. 1996; Hvid et al. 2010). The increase in body mass observed only in the eMST group suggests there may have been an effect on muscle size specifically in this group. More detailed measurements of morphological characteristics would have been preferable to precisely determine this effect. However, an increase in body mass was somewhat unsurprising, as eccentric actions performed at high intensity have typically been shown to induce larger increases in hypertrophy compared with concentric actions (Roig et al. 2009). Although this may translate to higher eccentric strength, it is interesting that this eccentric-related hypertrophy appears not to influence concentric strength (Roig et al. 2009). Indeed, the similar strength training effects seen in the current study are in support of this notion. Since the effects on efferent neural drive were similar after MST with and without eccentric overload, this may also have led to a similar

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synergistic interaction with muscular factors. Accordingly, the strength training carried out in the present study may have reduced the recruitment threshold of fast motor units, increased calcium release, cross-bridge coupling, and sodium channel density (Maffiuletti et al. 2016).

Practical application. If the purpose is to improve neural adaptations and muscle FGC, MST performed with constant load, high intensity (~90% 1RM), and maximal intended velocity in the concentric phase should be advocated as the strength training of choice over eMST. There are several reasons for this recommendation. First, eccentric actions are associated with more muscle soreness and microdamage to the muscle (Ratamess et al. 2009), which may increase the risk of injury (Baumert et al. 2016) and require longer recovery time (Linnamo et al. 2000). As such, eccentric overload may in fact have a negative effect on other training performed. Albeit, in the current study, muscle soreness appeared to not be an issue for any of the groups, possibly due to the relatively few repetitions in each training set. Second, particularly relevant for weight-bearing endurance activities such as running, the added eccentric load may induce more hypertrophy, since eccentric actions previously have been associated with more hypertrophy (Tesch and Larsson 1982). In fact, MST has been used successfully to improve endurance performance and has a well-documented effect on work economy (Heggelund et al. 2013; Hoff et al. 2002). Third, from a purely practical standpoint, MST is simpler to administer since no or extra personnel or special equipment is required to add and remove the excess weight in the eccentric phase. Finally, of clinical importance, MST has been documented to be feasible and safe to carry out in elderly and a wide range of frail patient populations (Hoff et al. 2007; Toien et al. 2018; Unhjem et al. 2015, 2016a; Wang et al. 2017) and contribute to improved function and ability to maintain independence in daily activities (Unhjem et al. 2017).

Conclusion. The current study showed that eccentric overload does not augment strength training-induced increases in FGC and efferent neural drive if the strength training is performed with high intensity and maximal intended velocity in the concentric phase. Thus, if the purpose is to tailor the most effective training for improvements in RFD, maximal strength, and functional performance, an eccentric overload can be avoided. Rather, MST, which is well established as a highly effective strength training modality, may be recommended in previously untrained young, old, and frail patient populations.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

T.T., H.P.H., and E.W. conceived and designed the research; T.T. and H.P.H. performed experiments; T.T. and H.P.H. analyzed data; T.T., H.P.H., R.J.U., and E.W. interpreted results of experiments; T.T. prepared figures; T.T. and H.P.H. drafted manuscript; T.T., H.P.H., R.J.U., J.H., and E.W. edited and revised manuscript; T.T., H.P.H., R.J.U., J.H., and E.W. approved final version of manuscript.

REFERENCES

Aagaard P, Simonsen EB, Andersen JL, Magnusson P, Dyhre-Poulsen P. Neural adaptation to resistance training: changes in evoked V-wave and H-reflex responses. *J Appl Physiol (1985)* 92: 2309–2318, 2002. doi:10.1152/japplphysiol.01185.2001.

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 (1985)* 89: 2249–2257, 2000. doi:10.1152/jappl.2000.89.6.2249.

Baumert P, Lake MJ, Stewart CE, Drust B, Erskine RM. Genetic variation and exercise-induced muscle damage: implications for athletic performance, injury and ageing. *Eur J Appl Physiol* 116: 1595–1625, 2016. doi:10.1007/s00421-016-3411-1.

Behm DG, Sale DG. Intended rather than actual movement velocity determines velocity-specific training response. *J Appl Physiol (1985)* 74: 359–368, 1993. doi:10.1152/jappl.1993.74.1.359.

Blazevich AJ, Cannavan D, Coleman DR, Horne S. Influence of concentric and eccentric resistance training on architectural adaptation in human quadriceps muscles. *J Appl Physiol (1985)* 103: 1565–1575, 2007. doi:10.1152/japplphysiol.00578.2007.

Brandenburg JP, Docherty D. The effects of accentuated eccentric loading on strength, muscle hypertrophy, and neural adaptations in trained individuals. *J Strength Cond Res* 16: 25–32, 2002.

Campos GE, Luecke TJ, Wendeln HK, Toma K, Hagerman FC, Murray TF, Ragg KE, Ratamess NA, Kraemer WJ, Staron RS. Muscular adaptations in response to three different resistance-training regimens: specificity of repetition maximum training zones. *Eur J Appl Physiol* 88: 50–60, 2002. doi:10.1007/s00421-002-0681-6.

Christie A, Kamen G. Short-term training adaptations in maximal motor unit firing rates and afterhyperpolarization duration. *Muscle Nerve* 41: 651–660, 2010. doi:10.1002/mus.21539.

Doan BK, Newton RU, Marsit JL, Triplett-McBride NT, Koziris LP, Fry AC, Kraemer WJ. Effects of increased eccentric loading on bench press 1RM. *J Strength Cond Res* 16: 9–13, 2002.

Duclay J, Martin A. Evoked H-reflex and V-wave responses during maximal isometric, concentric, and eccentric muscle contraction. *J Neurophysiol* 94: 3555–3562, 2005. doi:10.1152/jn.00348.2005.

Duclay J, Martin A, Robbe A, Pousson M. Spinal reflex plasticity during maximal dynamic contractions after eccentric training. *Med Sci Sports Exerc* 40: 722–734, 2008. doi:10.1249/MSS.0b013e31816184dc.

Dudley GA, Tesch PA, Miller BJ, Buchanan P. Importance of eccentric actions in performance adaptations to resistance training. *Aviat Space Environ Med* 62: 543–550, 1991.

Ekblom MM. Improvements in dynamic plantar flexor strength after resistance training are associated with increased voluntary activation and V-to-M ratio. *J Appl Physiol (1985)* 109: 19–26, 2010. doi:10.1152/japplphysiol.01307.2009.

Enoka RM, Duchateau J. Rate coding and the control of muscle force. *Cold Spring Harb Perspect Med* 7: a029702, 2017. doi:10.1101/cshperspect.a029702.

Enoka RM, Fuglevand AJ. Motor unit physiology: some unresolved issues. *Muscle Nerve* 24: 4–17, 2001. doi:10.1002/1097-4598(200101)24:1<4::AID-MUS13>3.0.CO;2-F.

Fimland MS, Helgerud J, Gruber M, Leivseth G, Hoff J. Functional maximal strength training induces neural transfer to single-joint tasks. *Eur J Appl Physiol* 107: 21–29, 2009. doi:10.1007/s00421-009-1096-4.

Godard MP, Wygand JW, Carpinelli RN, Catalano S, Otto RM. Effects of accentuated eccentric resistance training on concentric knee extensor strength. *J Strength Cond Res* 12: 26–29, 1998.

Goodall S, Romer LM, Ross EZ. Voluntary activation of human knee extensors measured using transcranial magnetic stimulation. *Exp Physiol* 94: 995–1004, 2009. doi:10.1113/expphysiol.2009.047902.

Harridge SD, Bottinelli R, Canepari M, Pellegrino MA, Reggiani C, Esbjörnsson M, Saltin B. Whole-muscle and single-fibre contractile properties and myosin heavy chain isoforms in humans. *Pflugers Arch* 432: 913–920, 1996. doi:10.1007/s004240050215.

Heggelund J, Fimland MS, Helgerud J, Hoff J. Maximal strength training improves work economy, rate of force development and maximal strength more than conventional strength training. *Eur J Appl Physiol* 113: 1565–1573, 2013. doi:10.1007/s00421-013-2586-y.

Helgerud J, Rodas G, Kemi OJ, Hoff J. Strength and endurance in elite football players. *Int J Sports Med* 32: 677–682, 2011. doi:10.1055/s-0031-1275742.

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Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G. Development of recommendations for SEMG sensors and sensor placement procedures. *J Electromyogr Kinesiol* 10: 361–374, 2000. doi:10.1016/S1050-6411(00)00027-4.

Hoff J, Berdahl GO, Bråten S. Jumping height development and body weight considerations in ski jumping. In: *Science and Skiing*, edited by Muller E, Schwameder H, Raschner C, Lindinger S, Komexl E. Hamburg, Germany: Kovac, 2001, p. 403–412.

Hoff J, Gran A, Helgerud J. Maximal strength training improves aerobic endurance performance. *Scand J Med Sci Sports* 12: 288–295, 2002. doi:10.1034/j.1600-0838.2002.01140.x.

Hoff J, Tjønna AE, Steinshamn S, Høydal M, Richardson RS, Helgerud J. Maximal strength training of the legs in COPD: a therapy for mechanical inefficiency. *Med Sci Sports Exerc* 39: 220–226, 2007. doi:10.1249/01.mss.0000246989.48729.39.

Hollander DB, Kraemer RR, Kilpatrick MW, Ramadan ZG, Reeves GV, Francois M, Hebert EP, Tryniecki JL. Maximal eccentric and concentric strength discrepancies between young men and women for dynamic resistance exercise. *J Strength Cond Res* 21: 34–40, 2007. doi:10.1519/00124278-200702000-00007.

Hortobágyi T, Devita P, Money J, Barrier J. Effects of standard and eccentric overload strength training in young women. *Med Sci Sports Exerc* 33: 1206–1212, 2001. doi:10.1097/00005768-200107000-00020.

Hvid L, Aagaard P, Justesen L, Bayer ML, Andersen JL, Ørtenblad N, Kjaer M, Suetta C. Effects of aging on muscle mechanical function and muscle fiber morphology during short-term immobilization and subsequent retraining. *J Appl Physiol (1985)* 109: 1628–1634, 2010. doi:10.1152/japplphysiol.00637.2010.

Kamen G, Knight CA. Training-related adaptations in motor unit discharge rate in young and older adults. *J Gerontol A Biol Sci Med Sci* 59: 1334–1338, 2004. doi:10.1093/gerona/59.12.1334.

Kaminski TW, Wabbersen CV, Murphy RM. Concentric versus enhanced eccentric hamstring strength training: clinical implications. *J Athl Train* 33: 216–221, 1998.

Knikou M. The H-reflex as a probe: pathways and pitfalls. *J Neurosci Methods* 171: 1–12, 2008. doi:10.1016/j.jneumeth.2008.02.012.

Linnamo V, Bottas R, Komi PV. Force and EMG power spectrum during and after eccentric and concentric fatigue. *J Electromyogr Kinesiol* 10: 293–300, 2000. doi:10.1016/S1050-6411(00)00021-3.

Maffiuletti NA, Aagaard P, Blazevich AJ, Folland J, Tillin N, Duchateau J. Rate of force development: physiological and methodological considerations. *Eur J Appl Physiol* 116: 1091–1116, 2016. doi:10.1007/s00421-016-3346-6.

Markovic G, Dizdar D, Jukic I, Cardinale M. Reliability and factorial validity of squat and countermovement jump tests. *J Strength Cond Res* 18: 551–555, 2004. doi:10.1519/1533-4287(2004)18<551:RAFVOS>2.0.CO;2.

Norrbrand L, Fluckey JD, Pozzo M, Tesch PA. Resistance training using eccentric overload induces early adaptations in skeletal muscle size. *Eur J Appl Physiol* 102: 271–281, 2008. doi:10.1007/s00421-007-0583-8.

Patten C, Kamen G, Rowland DM. Adaptations in maximal motor unit discharge rate to strength training in young and older adults. *Muscle Nerve* 24: 542–550, 2001. doi:10.1002/mus.1038.

Ratamess N, Alvar B, Evetoch T, Housh T, Kibler W, Kraemer W; American College of Sports Medicine. American College of Sports Medicine position stand. Progression models in resistance training for healthy adults [ACSM position stand]. *Med Sci Sports Exerc* 41: 687–708, 2009. doi:10.1249/MSS.0b013e3181915670.

Roig M, O'Brien K, Kirk G, Murray R, McKinnon P, Shadgan B, Reid WD. The effects of eccentric versus concentric resistance training on muscle strength and mass in healthy adults: a systematic review with meta-analysis. *Br J Sports Med* 43: 556–568, 2009. doi:10.1136/bjsm.2008.051417.

Seger JY, Thorstensson A. Effects of eccentric versus concentric training on thigh muscle strength and EMG. *Int J Sports Med* 26: 45–52, 2005. doi:10.1055/s-2004-817892.

Sheppard JM, Young K. Using additional eccentric loads to increase concentric performance in the bench throw. *J Strength Cond Res* 24: 2853–2856, 2010. doi:10.1519/JSC.0b013e3181e2731b.

Solstad GM, Fimland MS, Helgerud J, Iversen VM, Hoff J. Test-retest reliability of v-wave responses in the soleus and gastrocnemius medialis. *J Clin Neurophysiol* 28: 217–221, 2011. doi:10.1097/WNP.0b013e31821215cf.

Spiering BA, Lee SM, Mulavara AP, Bentley JR, Buxton RE, Lawrence EL, Sinka J, Guilliams ME, Ploutz-Snyder LL, Bloomberg JJ. Test battery designed to quickly and safely assess diverse indices of neuromuscular function after unweighting. *J Strength Cond Res* 25: 545–555, 2011. doi:10.1519/JSC.0b013e3181f56780.

Takarada Y, Hirano Y, Ishige Y, Ishii N. Stretch-induced enhancement of mechanical power output in human multijoint exercise with countermovement. *J Appl Physiol* 83: 1749, 1997. doi:10.1152/jappl.1997.83.5.1749.

Tesch PA, Larsson L. Muscle hypertrophy in bodybuilders. *Eur J Appl Physiol Occup Physiol* 49: 301–306, 1982. doi:10.1007/BF00441291.

Toien T, Unhjem R, Oren TS, Kvellestad ACG, Hoff J, Wang E. 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, 2018. doi:10.1093/gerona/glx218.

Tomberlin JP, Basford JR, Schwen EE, Orte PA, Scott SC, Laughman RK, Ilstrup DM. Comparative study of isokinetic eccentric and concentric quadriceps training. *J Orthop Sports Phys Ther* 14: 31–36, 1991. doi:10.2519/jospt.1991.14.1.31.

Unhjem R, Flemmen G, Hoff J, Wang E. Maximal strength training as physical rehabilitation for patients with substance use disorder; a randomized controlled trial. *BMC Sports Sci Med Rehabil* 8: 7, 2016a. doi:10.1186/s13102-016-0032-2.

Unhjem R, Lundestad R, Fimland MS, Mosti MP, Wang E. Strength training-induced responses in older adults: attenuation of descending neural drive with age. *Age (Dordr)* 37: 9784, 2015. doi:10.1007/s11357-015-9784-y.

Unhjem R, Nygård M, van den Hoven LT, Sidhu SK, Hoff J, Wang E. Lifelong strength training mitigates the age-related decline in efferent drive. *J Appl Physiol (1985)* 121: 415–423, 2016b. doi:10.1152/japplphysiol.00117.2016.

Unhjem R, van den Hoven LT, Nygård M, Hoff J, Wang E. Functional performance with age: the role of long-term strength training. *J Geriatr Phys Ther* 1, 2017. doi:10.1519/JPT.0000000000000141.

Upton AR, McComas AJ, Sica RE. Potentiation of "late" responses evoked in muscles during effort. *J Neurol Neurosurg Psychiatry* 34: 699–711, 1971. doi:10.1136/jnnp.34.6.699.

Van Cutsem M, Duchateau J, Hainaut K. Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. *J Physiol* 513: 295–305, 1998. doi:10.1111/j.1469-7793.1998.295by.x.

Vicens-Bordas J, Esteve E, Fort-Vanmeerhaeghe A, Bandholm T, Thorborg K. Is inertial flywheel resistance training superior to gravity-dependent resistance training in improving muscle strength? A systematic review with meta-analyses. *J Sci Med Sport* 21: 75–83, 2018. doi:10.1016/j.jsams.2017.10.006.

Walker S, Blazevich AJ, Haff GG, Tufano JJ, Newton RU, Häkkinen K. Greater strength gains after training with accentuated eccentric than traditional isoinertial loads in already strength-trained men. *Front Physiol* 7: 149, 2016. doi:10.3389/fphys.2016.00149.

Wang E, Nyberg SK, Hoff J, Zhao J, Leivseth G, Tørhaug T, Husby OS, Helgerud J, Richardson RS. Impact of maximal strength training on work efficiency and muscle fiber type in the elderly: Implications for physical function and fall prevention. *Exp Gerontol* 91: 64–71, 2017. doi:10.1016/j.exger.2017.02.071.

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