

Lifelong strength training mitigates the age-related decline in efferent drive

Runar Unhjem,¹ Mona Nygård,¹ Lene T. van den Hoven,¹ Simranjit K. Sidhu,² Jan Hoff,^{1,3}
and Eivind Wang^{1,4,5}

¹Department of Circulation and Medical Imaging, Faculty of Medicine, Norwegian University of Science and Technology, Trondheim, Norway; ²Discipline of Physiology, School of Medicine, The University of Adelaide, Adelaide, Australia;

³Department of Physical Medicine and Rehabilitation, St. Olav's University Hospital, Trondheim, Norway; ⁴Department of Research and Development, St. Olav's University Hospital, Trondheim, Norway; and ⁵Department of Medicine, University of Utah, Salt Lake City, Utah

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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* 121: 415–423, 2016. First published June 23, 2016; doi:10.1152/jappphysiol.00117.2016.—Recently, we documented age-related attenuation of efferent drive to contracting skeletal muscle. It remains elusive if this indication of reduced muscle strength is present with lifelong strength training. For this purpose, we examined evoked potentials in the calf muscles of 11 [71 ± 4 (SD) yr] strength-trained master athletes (MA) contrasted with 10 (71 ± 4 yr) sedentary (SO) and 11 (73 ± 6 yr) recreationally active (AO) old subjects, as well as 9 (22 ± 2 yr) young controls. As expected, MA had higher leg press maximal strength (MA, 185 ± 32 kg; AO, 128 ± 15 kg; SO, 106 ± 11 kg; young, 147 ± 22 kg, $P < 0.01$) and rate of force development (MA, 5,588 ± 2,488 N/s; AO, 2,156 ± 1,100 N/s; SO, 2,011 ± 825 N/s; young, 3,663 ± 1,140 N/s, $P < 0.05$) than the other groups. MA also exhibited higher musculus soleus normalized V waves during maximal voluntary contractions (MVC) [maximal V wave amplitude/maximal M wave during MVC ($V_{\text{sup}}/M_{\text{sup}}$): 0.28 ± 0.15] than AO (0.13 ± 0.06, $P < 0.01$) and SO (0.11 ± 0.05, $P < 0.01$), yet lower than young (0.45 ± 0.12, $P < 0.01$). No differences were apparent between the old groups in H reflex recorded at rest or during MVC [maximal H reflex amplitude/maximal M wave during rest ($H_{\text{max}}/M_{\text{max}}$); maximal H reflex amplitude during MVC/maximal M wave during MVC ($H_{\text{sup}}/M_{\text{sup}}$)], and all were lower ($P < 0.01$) than young. MA (34.4 ± 2.1 ms) had shorter ($P < 0.05$) H reflex latency compared with AO (36.4 ± 3.7 ms) and SO (37.3 ± 3.2 ms), but longer ($P < 0.01$) than young (30.7 ± 2.0 ms). Using interpolated twitch analysis, MA (89 ± 7%) had plantar flexion voluntary activation similar to young (90 ± 6%), and this was higher ($P < 0.05$), or tended to be higher ($P = 0.06$ – 0.09), than SO (83 ± 10%) and AO (84 ± 5%). These observations suggest that lifelong strength training has a protective effect against age-related attenuation of efferent drive. In contrast, no beneficial effect seems to derive from habitual recreational activity, indicating that strength training may be particularly beneficial for counteracting age-related loss of neuromuscular function.

aging; muscle strength; V wave; H reflex; voluntary activation

NEW & NOTEWORTHY

This cross-sectional study shows that efferent drive to contracting muscle is compromised with age. Furthermore, it shows that old subjects involved in long-term strength training mitigate this decline in efferent drive. In contrast, no difference in efferent drive was observed between recreationally active and

sedentary old subjects. This indicates that strength training in particular may be beneficial for counteracting the age-related loss of efferent drive.

THE AGE-RELATED LOSS OF MUSCLE strength is associated with remodeling of the nervous system (2, 26). Contributing to the deleterious effects with age is a gradual loss of motoneurons (2), resulting in lowered spinal and cortical motoneuron excitability (15, 38, 39), reduced motoneuron firing frequency (17), increased presynaptic inhibition (30), and slower nerve conduction velocity (28, 39). In combination, these impairments seem to compromise the efferent drive to the muscle (13, 16, 42), and consequently also the force production of contracting skeletal muscle. Ultimately, the reduction in efferent drive may culminate in a lowered voluntary activation (VA) (10, 31), albeit VA reductions are not always observed with advancing age (34).

Applying evoked reflex recordings in the calf muscles, we recently documented that the efferent drive in old individuals was improved after 8 wk of strength training, evident as a ~70% increase of the normalized V wave response [maximal V wave amplitude/maximal M wave during maximal voluntary contraction (MVC) ($V_{\text{sup}}/M_{\text{sup}}$) ratio] during superimposed MVC, and accompanied by an unaltered resting H reflex response (42). While the H reflex primarily reflects the excitability and inhibition of the peripheral Ia-afferent reflex arc, the V wave is more sensitive to the magnitude of efferent voluntary drive, because motoneuron recruitment and firing frequency will directly influence the size of the reflex that can be recorded in the muscle during superimposed MVC (1, 46). Indeed, improvements in motoneuron recruitment and firing frequency have previously been reported following strength training in the old. Although the completeness of motoneuron recruitment cannot be measured directly (19), improvements reflecting enhanced motoneuron recruitment and/or motoneuron firing frequency have been indicated by measurements of VA estimated by interpolated twitch analysis (39, 41). Also, utilizing needle electromyography (EMG) recordings, improvements in motoneuron firing frequency have been documented after strength training (6, 12). Together these findings suggest that efferent drive, specifically motoneuron firing frequency, and likely also motoneuron recruitment, can be improved by strength training in the old.

Interestingly, despite the observed efferent drive improvements in the Unhjem et al. (42) study, the $V_{\text{sup}}/M_{\text{sup}}$ ratio of the old was still ~60% lower than what was observed in the young. Even the strongest old individuals, with similar muscle strength as the young, exhibited sub-

Address for reprint requests and other correspondence: R. Unhjem, Dept. of Circulation and Medical Imaging, Faculty of Medicine, Norwegian University of Science and Technology, Prinsesse Kristinas gt. 3, 7006 Trondheim, Norway (e-mail: runar.unhjem@gmail.com).

stantial efferent drive deficits. While the $V_{\text{sup}}/M_{\text{sup}}$ ratio appears to improve following strength training in the old, the normalized H reflex response measured at rest has been demonstrated not to change (39, 42). The age-related depression of the resting H reflex (15, 39), in combination with the lack of change following strength training (39, 42), may suggest that spinal neural factors compromise efferent drive in the old and that these deficiencies cannot be recovered by short-term strength training. Alternatively, the lack of strength training-induced changes on the Ia-afferent reflex arc may also be explained by methodological limitations. Specifically, muscle contractions of a certain intensity may be necessary to detect differences. Indeed, in studies with young subjects, strength training is shown to increase H reflex excitability when the reflex is obtained during muscle contractions (1, 8) but not when it is measured at rest (1, 8, 46).

To our best knowledge, all previous strength-training studies investigating evoked potentials have been of relatively short duration (months), typically involving subjects with little or no strength-training experience. Not only is a short-term training intervention insufficient to reach the strength levels attained by long-term continuous strength training, but also it may be questioned whether a lack of strength training over many decades may have led to irrefutable neuronal loss, which might not be restored if it is first lost. Therefore the aim of the current study was to assess evoked reflex potentials in exceptionally strength-trained master athletes, a testament to long-term high-intensity strength training, and compare these to recreationally active and sedentary old individuals. Specifically, we hypothesized that efferent drive and Ia-afferent reflex arc excitability would be higher in master athletes compared with recreationally active and sedentary old, but not different from young.

METHODS

Subjects

A total of 41, 32 old (≥ 65 yr) and 9 young (18–30 yr), healthy, nonsmoking, nonobese [body mass index (BMI) < 30] male subjects participated in the study. Strength-trained master athletes [MA; $n = 11$; age 71 ± 4 (SD) yr; weight 92.5 ± 12.9 kg; height 178 ± 9 cm] were recruited through strength and weight-lifting clubs. All MA participants reported to have started their strength training before 20 yr of age and that they subsequently had been engaged in continuous lifelong strength training. At the current time they all competed in power and/or weight lifting at the national and/or international level, and the group included two recent world champions, as well as six recent national champions. Strength-training characteristics of the MA are presented in Table 1. Other old subjects were recruited through senior societies and assigned to two groups, sedentary old (SO; $n = 10$; age 71 ± 4 yr; weight 97.4 ± 12.9 kg; height 179 ± 6 cm) or recreationally active old (AO; $n = 11$; age 73 ± 6 yr; weight 87.0 ± 17.6 kg; height 178 ± 8 cm), on the basis of their activity level.

Table 1. *Strength-training characteristics of the strength-trained master athletes*

	Value
Years with strength-training competitions, yr	34 ± 14
Training frequency, sessions/wk	3.4 ± 0.8
Training hours, h/wk	6.0 ± 2.9
Average training intensity, % of 1RM	84 ± 7

Values are means \pm SD. 1RM, one-repetition maximum.

Subjects that reported participation in recreational activities (i.e., hiking, golf, orienteering, cross-country skiing, biking, dancing) 2–4 times a week were allocated to the AO group, while those that reported less than one time per week were allocated to the SO group. Importantly, all subjects in the AO and SO groups reported not engaging in systematic strength training. Young moderately active subjects ($n = 9$; age 22 ± 2 yr; weight 79.3 ± 12.0 kg; height 187 ± 5 cm) were recruited among students at the university. The young subjects reported participation in sports and habitual activities (i.e., cross-country skiing, soccer, hiking, golf) 2–4 times per week, but none engaged in regular strength training or participated competitively in sports. Exclusion criteria were any neuromuscular, pulmonary, or cardiovascular disease or if the participants had any orthopedic restrictions when carrying out the testing procedures. The study was approved by the local ethics committee (Regional Committee for Medical and Health Research Ethics in Central Norway) and conducted in accordance with the latest Declaration of Helsinki. Written informed consent was obtained from all subjects prior to inclusion.

Testing of Physical Fitness

In addition to the self-reported level of recreational activities, as an objective measurement of general fitness level, maximal oxygen consumption ($\dot{V}O_{2\text{max}}$) was tested using an incremental treadmill (Woodway, Weil am Rhein, Germany) protocol. After a 10-min warm-up period, the speed was set to 6 km/h for the three old groups, and then the incline was gradually increased by 2% every minute. For the moderately active young group, to allow running, the inclination was kept constant at 5%, and the speed increased by 1 km/h every minute. All subjects continued their effort until exhaustion, and encouragement was given to the participants toward the end of the test. Oxygen consumption measurements were obtained using the Cortex Metamax II (Cortex Biophysik, Leipzig, Germany), and standardized criteria were applied to determine $\dot{V}O_{2\text{max}}$ in accordance with previous literature (47).

Strength-Testing Experimental Protocol

Participants carried out all strength testing in a single day. The 3-h experimental protocol started with MVC and evoked reflex recordings, continued with VA measurements after 20-min rest, and ended after another 20 min of rest with measurements of one-repetition maximum (1RM) and rate of force development (RFD) in a leg press apparatus. All subjects performed all testing procedures.

Evoked Potentials

Evoked potentials were elicited in the tibial nerve in the right leg in a custom-made, fixed plantar flexion apparatus (Fig. 1A) (42). All reflex recordings were obtained seated with a 90° knee angle and the ankle joint dorsiflexed at 20°. Eyes were fixed on a marked point on the wall, to ensure similar eye and head movement during testing. A 1-ms square-wave stimulus was delivered in the popliteal fossa, using a current stimulator (DS7AH; Digitimer, Welwyn Garden City, UK) and bipolar felt pad electrodes (8 mm in diameter, 25 mm between tips; Digitimer) at the position eliciting the largest H reflex potential with the concomitant smallest M wave. Recordings of evoked potentials were obtained from musculus soleus (SOL), m. gastrocnemius medialis (GM), m. gastrocnemius lateralis (GL), and m. tibialis anterior (TA), through self-adhesive AgCl electrodes (M-00-S/50; Ambu, Ballerup, Denmark). By use of measuring tape and anatomical landmarks, electrodes were placed in accordance with Surface Electromyography for the Non-Invasive Assessment of Muscles (SENIAM) recommendations (11), after a skin preparation procedure including shaving, rubbing with skin prep gel (Nuprep; Weaver, Aurora, CO), and wiping the skin with alcohol, to provide interelectrode impedance < 5 k Ω . Data were obtained using a ME6000 Biomonitor (Mega Electronics, Kuopio, Finland) at 2 kHz with a

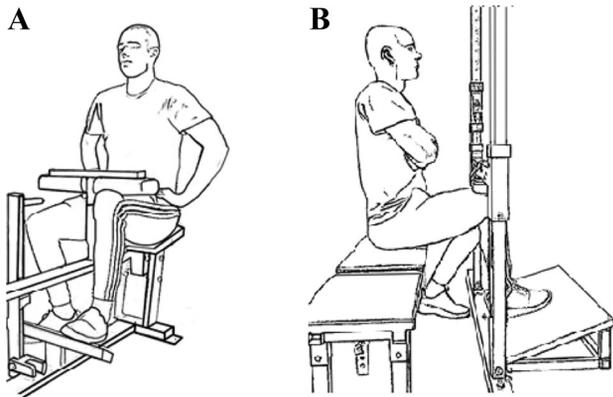


Fig. 1. Testing setup for evoked reflex recordings and plantar flexion torque (A) and voluntary activation measurements (B).

common mode rejection ratio 100 dB, amplified and band-pass filtered (8–500 Hz), mediated through Megawin software 700,046 version 3.0.

Although recordings were obtained from all three plantar flexors (SOL, GM, and GL), stimulation intensity was consistently adjusted to optimize SOL reflex recordings throughout the testing. After performing two plantar flexion MVCs, resting maximal H reflex amplitude (H_{\max}) was determined by gradually increasing the current intensity with 2-mA increments until a plateau or a decline in H reflex amplitude was observed with further increasing current intensity. After resting H reflex recordings were obtained, the subjects were instructed to perform MVC, while the electrical stimulus was applied during MVC to determine the SOL maximal superimposed H reflex amplitude (H_{sup}). The current stimulator was initially set to the intensity needed to evoke resting H_{\max} and was further increased with 2-mA increments until a plateau or a decline in reflex amplitude was observed with further increasing current intensity. Each contraction lasted ~ 2 s, and the stimuli were given after a plateau of torque was observed. Two-minute rest periods were given between each trial, and H_{sup} was achieved within four to six trials. The highest recorded reflex potentials during MVC in GM and GL are also referred to as H_{sup} . Maximal M wave amplitude during rest (M_{\max}) was then determined by increasing the current intensity by 5–10 mA, until no further increase in M wave amplitude was observed. To ensure that a true M_{\max} was obtained, two supramaximal stimuli at 150% of the intensity needed to evoke M_{\max} were given. After a 10-min rest period, six V waves were recorded by delivering a supramaximal stimulus during MVC (1). EMG_{rms} was determined from the best MVC trial, and the recordings between ± 100 ms of peak force were converted to the root mean square (rms) and normalized to the maximal peak-to-peak amplitude M wave obtained during MVC (M_{sup}).

VA Assessment Using Interpolated Twitch Method

Plantar flexion VA was determined by interpolated twitch, with the ankle in a $\sim 20^\circ$ dorsiflexed position. Six plantar flexion MVCs were performed, in which a single square-wave supramaximal stimulus (150% of the stimulus intensity needed to evoke M_{\max}) was delivered to the tibial nerve when a plateau of force was reached. Three seconds after the MVC another supramaximal stimulus was given to determine potentiated resting twitch. Two-minute rest was given between each trial. Force data were recorded at 2 kHz through a force platform (Fig. 1B) (model 9286AA; Kistler, Winterthur, Switzerland).

Strength Testing

Plantar flexion MVC was obtained prior to the evoked potential recordings, in the same custom-made plantar flexion apparatus (Fig. 1A). Each subject was given two trials, and the highest torque attained

was recorded as MVC. A 2-min rest period was given between each trial, and subjects were instructed to perform the contraction as fast and forcefully as possible. Finally, after the evoked potentials and VA assessments for plantar flexion, as a measurement of performance-associated strength, maximal dynamic muscle strength in the lower extremities was measured as 1RM using a seated horizontal leg press apparatus (Technogym, Gambettola, Italy). Knee joint angle in the lower position was set to 90° . After three warm-up sets of six to eight repetitions, the load was gradually increased by 10 kg until failure. 1RM was typically achieved within three to five trials. Rest periods between each trial were 3–5 min. RFD was recorded in the same leg press apparatus, through a force platform (model 9286AA; Kistler) at 2 kHz. The load was set to the closest 10-kg increment above the subject's body weight (32), and the lift was performed from a 90° knee joint angle. Subjects were instructed to move slowly down to a 90° knee angle, hold the position for 1 s, and then perform the concentric phase of the movement as fast and forcefully as possible. Each subject was given three attempts, of which only the best trial was considered for analysis.

Leg Muscle Volume

Leg muscle volume of the right thigh and lower leg was estimated through anthropometrical measurements, utilizing measuring tape and skin fold caliper (Holtain, Crosswell, UK). Thigh length was measured from the lateral femoral epicondyle to the greater trochanter, while lower leg length was measured from the lateral malleolus to the head of fibula. Thigh circumferences were measured at the midpoint and 10 cm proximal and distal to the midpoint, while lower leg circumferences were measured below the fibular head, at the midpoint, and above the lateral malleolus. Skin fold measurements were taken at three sites at the midpoint for both thigh (medial, anterior, and lateral) and lower leg (medial, posterior, and lateral). The method has previously been found valid with acceptable accuracy compared with proton magnetic resonance imaging ($^1\text{H-MRI}$) (22).

Data Analysis

Only the V wave trials in which the torque was $\geq 90\%$ of MVC and the M wave was $\geq 95\%$ M_{sup} were used for analysis. Reflex potentials obtained during rest (H_{\max}) were normalized to M_{\max} , while reflex recordings obtained during MVC (H_{sup} , V_{sup}) were normalized to the maximal M wave amplitude obtained during MVC (M_{sup}). Latency of the H reflex was determined as the time interval between the electrical stimulus to the first detection of the reflex volley. Because stimulation intensity was optimized for SOL, the percentage of M_{\max}/M_{sup} elicited at H_{\max}/H_{sup} was analyzed only for this muscle. VA was calculated, using Bioware software v.3.06 (Kistler), as $[1 - (\text{superimposed twitch}/\text{resting peak twitch})] \times 100$, and expressed as a percentage (3). RFD, both for dynamic leg press and isometric plantar flexion, was calculated as $\Delta\text{force}/\Delta\text{time}$ between 10 and 90% of peak force (32). Isometric plantar flexion RFD was normalized to MVC to express relative plantar flexion RFD. Furthermore, to account for potential differences in body mass, leg press 1RM was expressed in absolute values, relative to body weight (kg^{-1}), and relative to allometrically scaled body weight ($\text{kg}^{-0.67}$). Leg muscle volume was calculated using the following equation: $V = (L/12\pi) \cdot (C1^2 + C2^2 + C3^2) - [(S - 0.4)/2] \cdot L \cdot [(C1 + C2 + C3)/3]$, where L refers to length, C1, C2, and C3 refer to proximal, middle, and distal circumferences, respectively, and S refers to skin fold thickness (22), and divided by length to express leg cross-sectional area.

Statistical Analysis

Statistical analyses were performed using the software package SPSS 21.0 (Chicago, IL), while figures were made using GraphPad Prism 5 (San Diego, CA). Normality of data was confirmed by quantile-quantile plots. One-way ANOVAs were applied to detect

Table 2. Muscle strength characteristics, muscle cross-sectional area, and maximal oxygen consumption

	Old			
	Sedentary	Active	Master Athletes	Young
Leg press 1RM				
kg	106 ± 11	128 ± 15 ^c	185 ± 32 ^d	147 ± 22 ^b
kg m _b ⁻¹	1.10 ± 0.17	1.52 ± 0.19 ^c	1.98 ± 0.27 ^b	1.88 ± 0.33 ^b
kg m _b ^{-0.67}	5.0 ± 0.2	6.6 ± 0.2 ^c	9.0 ± 0.4 ^d	8.0 ± 0.4 ^b
Leg press RFD, N/s	2,011 ± 825	2,156 ± 1,100	5,588 ± 2,488 ^d	3,663 ± 1,140 ^{bb}
Plantar flexion MVC, N/m	107 ± 26	109 ± 23	141 ± 37 ^b	153 ± 26 ^{bb}
Plantar flexion RFD, N/m/s	189 ± 21	196 ± 44	366 ± 165 ^{bb}	363 ± 103 ^{bb}
Relative RFD, MVC/s	1.84 ± 0.35	1.85 ± 0.50	2.53 ± 0.75 ^{bb}	2.37 ± 0.51 ^{bb}
Thigh fat-free CSA, cm ²	187 ± 20	175 ± 25	213 ± 28 ^d	187 ± 25
Calf fat-free CSA, cm ²	73 ± 8	68 ± 12	73 ± 9	68 ± 7
$\dot{V}O_{2max}$, ml·kg ⁻¹ ·min ⁻¹	26.7 ± 5.0	34.4 ± 7.0 ^{cc}	31.5 ± 4.2 ^c	54.8 ± 4.4 ^{aa}

Values are means ± SD. 1RM, one-repetition maximum; m_b, body mass; MVC, maximal voluntary contraction; RFD, rate of force development; CSA, cross-sectional area; ^a*P* < 0.05, ^{aa}*P* < 0.01 significant difference from master athletes, old active, and old sedentary; ^b*P* < 0.05, ^{bb}*P* < 0.01 significant difference from old active and old sedentary; ^c*P* < 0.05, ^{cc}*P* < 0.01 significant difference from old sedentary; ^d*P* < 0.05, ^{dd}*P* < 0.01 significant difference from old active, old sedentary, and young.

differences between groups and were followed up using Tukey post hoc analysis, when appropriate. The Pearson test for linear regression was used to assess correlation between variables. The level of statistical significance was set to *P* < 0.05. All data are presented as means ± SD, unless otherwise noted.

RESULTS

All 41 subjects completed all the testing procedures, without any circumstances advocating subject exclusion. The four groups were not different with respect to height and weight, and the three old groups were not different from each other with regard to age, but all were naturally significantly different from the age of the young (*P* < 0.01). $\dot{V}O_{2max}$ measurements confirmed the reported activity level of the old subjects, as both AO (26%) and the MA (19%) exhibited higher $\dot{V}O_{2max}$ compared with SO (*P* < 0.05). Furthermore, all the old groups had a lower $\dot{V}O_{2max}$ compared with young (*P* < 0.01).

Muscle Strength

As expected, the MA exhibited superior performance in all measured strength variables compared with AO and SO (Table 2). 1RM was 45% higher than AO, 75% higher than SO, and even 26% higher than the moderately active young controls (*P*

< 0.01). Similarly, dynamic leg press RFD was 159% faster than AO, 178% faster than SO (*P* < 0.01), and 53% faster than young (*P* < 0.05). Also for the plantar flexion MVC, MA was 28 and 24% stronger than AO and SO, respectively (*P* < 0.05), but with no difference from the young controls. Isometric plantar flexion RFD was 93 and 87%, respectively, faster in MA compared with SO and AO (*P* < 0.01). Also when expressed relative to MVC, the MA had faster RFD than SO (38%) and AO (37%) (*P* < 0.01). Thigh muscle volume was 22, 14, and 14%, respectively, higher in the MA compared with AO, SO, and young (*P* < 0.05).

Evoked Potentials

MA had 53 and 60% higher (*P* < 0.01) SOL V_{sup}/M_{sup} ratios compared with AO and SO, respectively (Table 3). Yet SOL V_{sup}/M_{sup} ratio of all three old groups was lower (*P* < 0.01) compared with young (Fig. 2). No difference was observed in SOL V_{sup}/M_{sup} ratio between AO and SO. SOL V_{sup}/M_{sup} ratio correlated positively with MVC (*r* = 0.30, *P* < 0.05), VA (*r* = 0.45, *P* < 0.01), and RFD (*r* = 0.34, *P* < 0.05).

In contrast, SOL H_{max}/M_{max} ratio and SOL H_{sup}/M_{sup} ratio were not different between any of the old groups, but again all the old groups were lower (*P* < 0.01) compared with young

Table 3. Absolute amplitudes and normalized potentials in *m. soleus*

	Old			
	Sedentary	Active	Master Athletes	Young
M_{max}	3,742 ± 1,327	3,139 ± 1,166	4,782 ± 1,866 ^b	6,526 ± 2,763 ^{bb}
M_{sup}	4,080 ± 1,392	3,667 ± 2,029	4,724 ± 1,694	8,082 ± 2,352 ^{aa}
H_{max}	1,203 ± 452	907 ± 679	1,432 ± 973	3,396 ± 1,820 ^{aa}
H_{max}/M_{max}	0.29 ± 0.10	0.28 ± 0.15	0.31 ± 0.22	0.53 ± 0.15 ^{aa}
% of M_{max} at H_{max}	28 ± 8	32 ± 12	14 ± 7 ^{bb}	13 ± 6 ^{bb}
H_{sup}	1,503 ± 579	1,457 ± 745	2,086 ± 1,217	5,031 ± 2,178 ^{aa}
H_{sup}/M_{sup}	0.39 ± 0.18	0.39 ± 0.12	0.43 ± 0.16	0.61 ± 0.10 ^{aa}
% of M_{sup} at H_{sup}	30 ± 8	32 ± 8	32 ± 6	27 ± 9
V_{sup}	499 ± 316	508 ± 347	1,427 ± 1,112 ^{bb}	3,586 ± 1,475 ^{aa}
V_{sup}/M_{sup}	0.11 ± 0.05	0.13 ± 0.06	0.28 ± 0.15 ^{bb}	0.45 ± 0.12 ^{aa}
H reflex latency, ms	36.44 ± 3.68	37.25 ± 3.20	34.54 ± 2.14 ^b	30.72 ± 2.04 ^{aa}

Values are means ± SD; absolute amplitudes are given in μ V. MVC, maximal voluntary contraction; M_{max} , maximal M wave during rest; M_{sup} , maximal M wave during MVC; H_{max} , maximal H reflex amplitude during rest; H_{sup} , maximal H reflex amplitude during MVC; V_{sup} , maximal V wave amplitude. ^a*P* < 0.05, ^{aa}*P* < 0.01 significant difference from master athletes, old active, and old sedentary; ^b*P* < 0.05, ^{bb}*P* < 0.01 significant difference from old active and old sedentary.

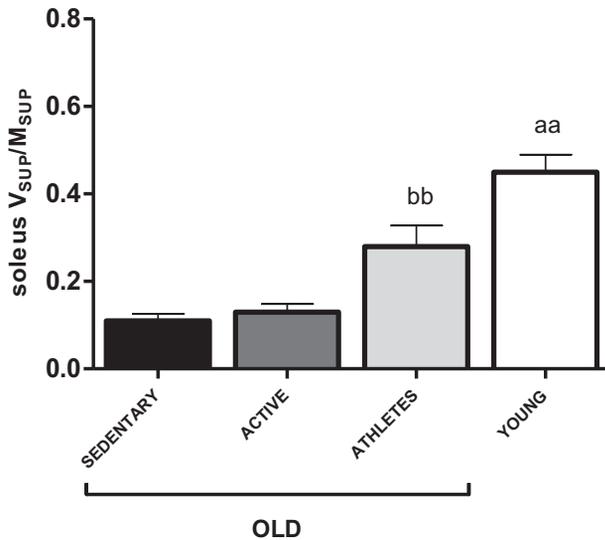


Fig. 2. Soleus V_{sup}/M_{sup} ratio. Data are presented as means \pm SE. ^{aa} $P < 0.01$ significant difference from master athletes, old active, and old sedentary; ^{bb} $P < 0.01$ significant difference from old active and old sedentary.

(Fig. 3). SOL H reflex latency was 7 and 5% shorter ($P < 0.05$) in MA compared with AO and SO, respectively, with no difference observed between AO and SO. The young group exhibited SOL H reflex latency shorter ($P < 0.05$) than all three old groups. The relative M response (% of M_{max}) elicited during resting H_{max} was lower in MA compared with AO ($P < 0.01$) and SO ($P < 0.01$), but not different from the young (Table 3). There was a negative correlation between SOL H_{max}/M_{max} ratio and SOL H reflex latency ($r = -0.63$, $P < 0.01$), while the relative M response elicited at resting H_{max} correlated negatively with 1RM ($r = -0.43$, $P < 0.01$) and RFD ($r = -0.55$, $P < 0.01$). A positive correlation was observed between SOL H_{sup} and SOL V_{sup} ($r = 0.52$, $P < 0.01$).

Similar to what was observed in SOL, GM V_{sup}/M_{sup} ratio was higher ($P < 0.05$) in MA compared with both AO (75%) and SO (110%) (Table 4). However, MA had a 51% lower ($P < 0.01$) V_{sup}/M_{sup} ratio compared with young. Additionally, no difference in GM V_{sup}/M_{sup} ratio was observed between AO and SO. Furthermore, there was no difference in H/M ratio between any of the three old groups, neither at rest nor during MVC. However, all three old groups were lower compared

with young, both at rest (GM H_{max}/M_{max} , $P < 0.01$) and during MVC (GM H_{sup}/M_{sup} , $P < 0.01$). GM latency was shorter in MA compared with AO (12%, $P < 0.05$) and SO (9%, $P < 0.05$), while young exhibited shorter latency in GM compared with all the old groups ($P < 0.05$). Correlations revealed that GM V_{sup}/M_{sup} ratio was associated with MVC ($r = 0.41$, $P < 0.01$) and VA ($r = 0.33$, $P < 0.05$). Finally, similar to SOL, a positive correlation was observed between GM H_{sup} and GM V_{sup} ($r = 0.77$, $P < 0.01$).

Adding support to the notion that evoked potentials are not muscle dependent, recordings in GL revealed a pattern similar to those evoked in SOL and GM (Table 5). While GL V_{sup}/M_{sup} ratio was higher in the MA compared with AO and SO (50%, $P < 0.05$), no difference was observed between the old groups in GL H/M ratio, neither at rest (H_{max}/M_{max}) nor during MVC (H_{sup}/M_{sup}). GL V_{sup}/M_{sup} ratio, GL H_{sup}/M_{sup} ratio, and GL H_{max}/M_{max} ratio were all lower ($P < 0.01$) in the three old groups compared with young. GL V_{sup}/M_{sup} ratio correlated with MVC ($r = 0.30$, $P < 0.05$) and VA ($r = 0.55$, $P < 0.05$). Similar to that in SOL and GM, there was a positive correlation between the GL H_{sup} and GL V_{sup} ($r = 0.63$, $P < 0.01$).

Mirroring the V_{sup}/M_{sup} ratios, VA exhibited a tendency to be higher in MA ($89 \pm 7\%$) compared with AO ($84 \pm 5\%$, $P = 0.09$) and SO ($83 \pm 10\%$, $P = 0.06$), but with no difference compared with the young ($90 \pm 6\%$) (Fig. 4). In contrast, the young group had higher VA compared with AO ($P < 0.05$) and tended to be higher than SO ($P = 0.06$). No differences were observed between any of the four groups in EMG_{rms} for either agonist (SOL, GM, and GL) or antagonist (TA) muscles. VA correlated with the V_{sup}/M_{sup} ratios in all three plantar flexor muscles (SOL, GM, and GL) as well as MVC ($r = 0.55$, $P < 0.01$).

DISCUSSION

Efferent drive to contracting muscle has been documented to decline with age. However, since it is not known if this consequence of advancing age may be blunted by continuous long-term strength training, we assessed evoked reflex recordings in exceptionally strength-trained master athletes and contrasted them to sedentary and recreationally active age-matched individuals, as well as a young reference group. The main finding was that the MA had twofold higher V_{sup}/M_{sup} ratios compared with the other two old groups, indicating higher efferent drive among the MA. Second, no difference in

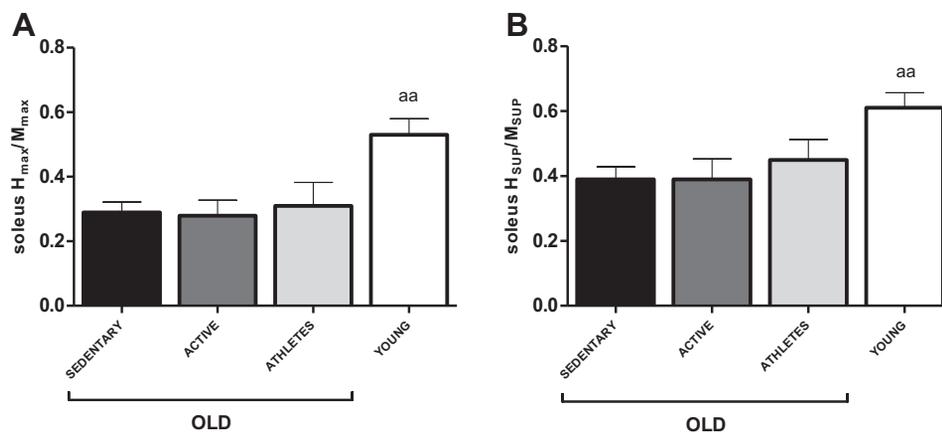


Fig. 3. A: soleus H_{max}/M_{max} ratio at rest. B: soleus H_{sup}/M_{sup} ratio during maximal voluntary contraction. Data are presented as means \pm SE. ^{aa} $P < 0.01$ significant difference from master athletes, old active, and old sedentary.

Table 4. Absolute amplitudes and normalized potentials in *m. gastrocnemius medialis*

	Old			
	Sedentary	Active	Master Athletes	Young
M _{max}	6,203 ± 2,290	5,449 ± 1,798	6,318 ± 1,283	7,601 ± 1,855 ^b
M _{sup}	6,522 ± 2,110	6,233 ± 1,555	7,013 ± 1,004	8,905 ± 3,279 ^{aa}
H _{max}	686 ± 360	658 ± 507	851 ± 452	2,368 ± 1,606 ^{aa}
H _{max} /M _{max}	0.12 ± 0.07	0.12 ± 0.10	0.14 ± 0.07	0.34 ± 0.20 ^{aa}
H _{sup}	1,258 ± 262	1,354 ± 487	1,754 ± 613	3,947 ± 1,390 ^{aa}
H _{sup} /M _{sup}	0.20 ± 0.08	0.24 ± 0.12	0.25 ± 0.09	0.44 ± 0.12 ^{aa}
V _{sup}	576 ± 324	684 ± 423	1,447 ± 677 ^{bb}	3,721 ± 1,786 ^{aa}
V _{sup} /M _{sup}	0.10 ± 0.06	0.12 ± 0.07	0.21 ± 0.10 ^b	0.43 ± 0.18 ^{aa}
H reflex latency, ms	36.04 ± 2.51	37.59 ± 2.98	32.71 ± 1.82 ^b	30.29 ± 0.97 ^a

Values are means ± SD; absolute amplitudes are given in μV . MVC, maximal voluntary contraction; M_{max}, maximal M wave during rest; M_{sup}, maximal M wave during MVC; H_{max}, maximal H reflex amplitude; H_{sup}, maximal H reflex amplitude during MVC; V_{sup}, maximal V wave amplitude. ^a*P* < 0.05, ^{aa}*P* < 0.01 significant difference from master athletes, old active, and old sedentary; ^b*P* < 0.05, ^{bb}*P* < 0.01 significant difference from old active and old sedentary.

V_{sup}/M_{sup} ratio was observed between AO and SO, indicating that recreational activity is not a sufficient stimulus to maintain efferent drive. Finally, despite the elevated efferent drive of the MA over the other old groups, their V_{sup}/M_{sup} ratio was lower compared with young. This apparent inevitable impairment may, at least in part, rely on deterioration of the Ia-afferent reflex arc since MA had an elevated V wave, but not H reflex response compared with AO and SO. In combination, these findings imply that strength training in particular is necessary for efferent drive preservation with age.

Evoked Reflex Potentials and Age

The elevated V_{sup}/M_{sup} ratios observed in strength-trained MA in this study were present in all three plantar flexor muscle groups, suggesting that lifelong strength training has a systematically protective effect on the efferent drive with advancing age. Although the 0.28 ± 0.15 ratio in this group of exceptionally trained old individuals is somewhat lower than the 0.3–0.5 ratio that has typically been observed in young men (1, 9, 42), it was twofold higher than what was observed in sedentary and recreationally active counterparts in the current study. Interestingly, the V wave response, reflecting the magnitude of efferent neural drive, was similar in AO and SO. This suggests that high-intensity strength training in particular may be necessary to preserve efferent neural drive and that physical activity per se is not sufficient to induce any efferent drive maintenance. Thus, in light of this, both SO and AO may be referred to as untrained. The results in these two untrained

groups are in agreement with V_{sup}/M_{sup} ratios reported in moderately active ~70-yr-old men in a previous study (42). In contrast to the V_{sup}/M_{sup} ratio, the H/M ratio did not reveal any difference between the MA and untrained old, either at rest or during MVC. Thus the decline in both resting and superimposed H/M ratio appears to be inevitable with aging per se (15, 39). Previous short-term training interventions with old participants have also documented that the resting H_{max}/M_{max} ratio does not demonstrate plasticity (39, 42). In combination, these findings suggest that a decrease of the H/M ratio with age (i.e., deterioration of the Ia-afferent reflex arc) is independent of training status and training duration. Importantly, although the H reflex and the V wave rely on the same Ia-afferent pathways, the V wave recruits a broader motoneuron pool, because of stronger electrical stimuli and greater supraspinal input during MVC, bringing more motoneurons closer to their firing threshold (27). In light of this, the characteristics of the V wave relate more to high-threshold, faster motor units than does the H reflex response, which is mainly constituted by slow twitch motor unit action potentials. Thus the elevated V_{sup}/M_{sup} ratio of the MA, together with the declined H/M ratios, may suggest that strength training has the most prominent neuroprotective effect on the high-threshold fast twitch motor units.

Evoked Reflex Potentials Mechanisms

The supramaximal electrical stimulus applied during a MVC evokes an antidromic volley in the efferent axons (in addition to an afferent reflex volley and a M wave). At rest the H reflex

Table 5. Absolute amplitudes and normalized potentials in *m. gastrocnemius lateralis*

	Old			
	Sedentary	Active	Master Athletes	Young
M _{max}	8,144 ± 1,806	7,605 ± 2,440	8,191 ± 2,348	7,899 ± 1,855
M _{sup}	8,103 ± 934	7,742 ± 1,848	8,457 ± 1,241	7,847 ± 3,279
H _{max}	928 ± 889	664 ± 488	901 ± 497	1,651 ± 1,606 ^{aa}
H _{max} /M _{max}	0.13 ± 0.13	0.12 ± 0.09	0.13 ± 0.09	0.34 ± 0.20 ^a
H _{sup}	1,323 ± 719	1,536 ± 643	1,695 ± 614	2,897 ± 1,390 ^{aa}
H _{sup} /M _{sup}	0.17 ± 0.11	0.22 ± 0.14	0.18 ± 0.07	0.38 ± 0.12 ^{aa}
V _{sup}	545 ± 320	815 ± 400	1,744 ± 1,022 ^b	2,937 ± 1,786 ^{aa}
V _{sup} /M _{sup}	0.11 ± 0.13	0.11 ± 0.06	0.22 ± 0.17 ^b	0.38 ± 0.18 ^{aa}
H reflex latency, ms	36.24 ± 3.10	36.75 ± 3.34	34.40 ± 2.37	30.16 ± 1.46 ^{aa}

Values are means ± SD; absolute amplitudes are given in μV . MVC, maximal voluntary contraction; M_{max}, maximal M wave during rest; M_{sup}, maximal M wave during MVC; H_{max}, maximal H reflex amplitude; H_{sup}, maximal H reflex amplitude during MVC; V_{sup}, maximal V wave amplitude. ^a*P* < 0.05, ^{aa}*P* < 0.01 significant difference from master athletes, old active, and old sedentary; ^b*P* < 0.05, ^{bb}*P* < 0.01 significant difference from old active and old sedentary.

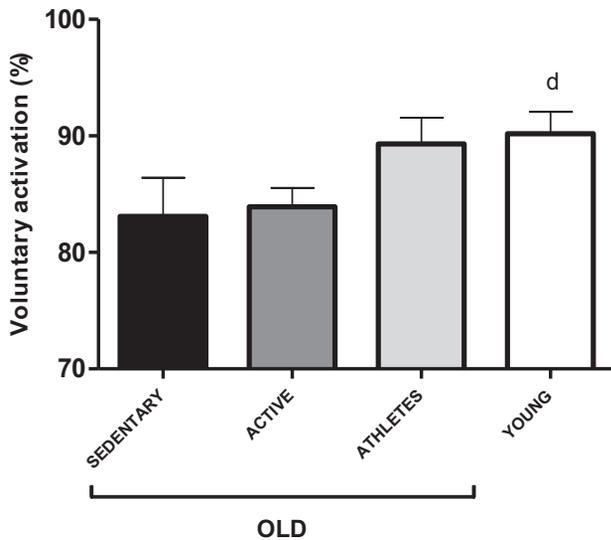


Fig. 4. Plantar flexion voluntary activation. Data are presented as means \pm SE. ^d $P < 0.05$ significant difference from old active.

is completely abolished by collisions with these antidromic potentials, but during MVC the V wave arises because of removal of antidromic potentials by voluntary efferent output, leaving the motoneurons open for transmission of the reflex volley (1, 43). On this basis, the V wave, in combination with the H reflex, has been used to express the magnitude of efferent drive to the muscle. Importantly, as emphasized by Aagaard et al. (1), the V wave should be interpreted in conjunction with the maximal H reflex volley evocable during MVC (H_{sup}). This is because H reflex measurements obtained during MVC more accurately reflect the motoneuron excitability and amount of presynaptic/postsynaptic inhibition during a contraction (1) and thus also the actual reflex volley traveling the reflex arc during a V wave trial. In fact, in this scenario, the term “H reflex” may also be somewhat inappropriate, i.e., because a stronger electrical stimulus is needed to evoke the maximal reflex volley during MVC, which may suggest the activation of higher threshold motoneurons (as with the V wave), while the resting H reflex involves mainly the activation of lower threshold motoneurons.

V wave interpretation. Since the H reflex response did not differ between any of the old groups, this implies that the elevated V_{sup}/M_{sup} ratio of the MA may not be explained by the size of the reflex volley (i.e., differences in motoneuron excitability and/or presynaptic/postsynaptic inhibition). In previous literature (1, 7, 46), alterations in V_{sup}/M_{sup} ratio have been partly ascribed to changes in supraspinal activation of the motoneuron pool. Although this explanation is certainly also germane for the disparate V_{sup}/M_{sup} ratios in the current study, caution should be observed in elucidating the origin of such a change in efferent drive, since different recruitment of afferents and motoneurons, as well as spinal reflex pathways, may influence the efferent drive during MVC (4, 24). In general, the V wave response as a measure of the magnitude of efferent neural drive to myofibers is sensitive to changes in motoneuron firing frequency and motoneuron recruitment (1). Previous studies have indeed shown that strength training is accompanied by marked increases in maximal motoneuron firing frequency, both in old and young subjects (6, 12). Accordingly,

strength-trained MA are shown to possess $\sim 20\%$ higher maximal firing rates, compared with untrained old (23). Such a difference may indeed account for some of the observed differences in efferent drive in our study. However, based on the original equation put forward by Upton et al. (43), a $\sim 20\%$ maximal firing frequency difference cannot alone explain the twofold larger V_{sup}/M_{sup} ratio in the current study. This suggests that in addition to elevated firing frequency, motoneuron recruitment is likely also more complete in strength-trained master athletes (1).

H reflex interpretation. The interpretation of the similar H/M ratio in the three old groups in this study is challenging because, regardless of age, participants in explosive sports have previously been documented to exhibit lower H/M ratios compared with untrained individuals (5). This is because explosive athletes typically have a high proportion of fast twitch type II muscle fibers, whereas the H reflex primarily manifests itself in the slower twitch type I fibers (5). Since the strength-trained MA in the current study should be considered “explosive athletes,” the H/M ratios similar to the untrained old may actually represent some maintenance of the reflex arc, since a lower reflex response among athletes would be expected in general. In support of this notion, the H reflex latency was found to be shorter in the MA compared with the two untrained old groups. Indeed, this finding suggests superior maintenance of the Ia-afferent reflex arc of the old MA. The shorter reflex latency in the MA may be due to denser myelination and shorter internodal length in both afferent and efferent fibers (2, 28, 39, 42) but may also reflect a lower dropout of the largest axonal fibers, which possess the highest conduction velocity (2). Interestingly, our results revealed that MA had relative M waves accompanying the resting H_{max} similar to the young. This indicates that the most excitable largest Ia-afferent fibers may be preserved. In contrast, the untrained old had larger relative M waves associated with their resting H_{max} . In turn, this suggests a closer excitability threshold between afferent and efferent fibers, possibly due to a loss of the largest Ia-afferent fibers (40). Notably, no difference in the relative M waves accompanying H_{sup} was observed during MVC.

V wave and H reflex relationship. A direct comparison of the V_{sup}/M_{sup} ratio between subjects with very different H reflex responses may be difficult, i.e., because the size of the evoked H reflex response will directly influence the size of the concomitant V wave. Indeed, a relationship between H_{sup} and V_{sup} was indicated by strong correlations between the two variables for all three plantar flexors in this study. For example, an old subject with a small reflex response will need more efferent drive to achieve the same V_{sup}/M_{sup} ratio compared with a young subject with a larger reflex response. While comparison of the V_{sup}/M_{sup} ratio between the three old groups in the current study is fairly straightforward because their H reflex responses were similar, comparison to the young is challenging since their H_{sup}/M_{sup} ratios were larger. To account for this difference, the maximal V wave amplitude and the maximal H reflex amplitude obtained during MVC may be seen in relation to each other when comparing the efferent drive in subjects with H reflex differences. In fact, in the current study it implies that the master athletes’ efferent drive may actually be closer to the young than what is first observed when the V_{sup}/M_{sup} ratio is considered alone. Discrepancies in the relationship between V_{sup} and H_{sup} may however also imply that different M-H

recruitment curves exist at MVC between the groups. Because aging is characterized by a loss of the largest axonal fibers (2), it may become more difficult to selectively activate Ia-afferents without also recruiting motor axons; hence antidromic collisions may occur already at lower stimulus intensity in the old, decreasing the maximal amplitude of the H reflex. Importantly, although this feature hampers the comparison of V_{sup} and H_{sup} across different age groups, it may advocate better preservation of the largest axonal fibers in the MA compared with the untrained old.

Voluntary Activation

As assessed by interpolated twitch (3), VA was similar between MA and young. MA also exhibited a clear tendency to have a higher VA than the untrained old groups. Although interpolated twitch techniques have been widely used to assess VA differences between young and old, the findings with regard to this measure remain equivocal. Some studies have reported a very high or complete VA in the old (34, 45), while others have documented an incomplete activation (10, 31, 48). Our results endorse the latter, advocating that a reduced efferent drive in untrained old is manifested in a reduced ability to fully activate skeletal muscle. While changes in the $V_{\text{sup}}/M_{\text{sup}}$ ratio often have been ascribed to changes in motoneuron firing frequency (1), interpolated twitch measurements performed with a single stimulus (i.e., for measurements of VA) may be more sensitive to differences in motoneuron recruitment. This is because a single supramaximal nerve stimulation is likely to recruit all available motoneurons simultaneously, yet a single stimulus has very limited potential to detect changes in discharge frequency (29). Recognizing the corresponding differences in both interpolated twitch and $V_{\text{sup}}/M_{\text{sup}}$ ratio, it appeared that the old MA exhibited greater capacity for both motoneuron recruitment and firing frequency compared with the untrained old. Indeed, this difference in efferent drive may be the main contributing factor to the differences in force production between the groups.

Reduced Efferent Drive and Skeletal Muscle Strength

While previous studies with strength-trained master athletes have demonstrated that they possess maximal muscle strength similar to what is typically seen in 20-yr-old individuals (20, 33), the findings in the current study strengthen this assertion, presenting evidence that 70-yr-old athletes can be considerably stronger than young. Our careful selection of highly trained master athletes certainly is an example of exceptionally successful aging and likely represents close to a muscle strength ceiling relative to their age. Not only was the MA maximal strength superior compared with what was observed in the young, but also the functionally important dynamic leg press RFD was ~50% faster than the young controls, and more than 150% faster than the two untrained old groups. Similarly, the isometric plantar flexion RFD, both expressed in absolute values and relative to MVC, was higher (~90 and ~40%, respectively) compared with the untrained old. The RFD is documented to largely rely on neuromuscular factors, reflect maximal motoneuron firing frequency, and decrease with age (6, 12, 13). Also, strength training-induced gains in RFD seem to closely relate to increases in maximal motoneuron firing frequency (6, 12), particularly during the initial phase (<75

ms) of contraction (16, 25, 44). As a consequence, the RFD characteristics of the MA in the current study likely reflect a high efferent neural drive during rapid muscle contractions.

Importantly, none of the investigated characteristics of the neuromuscular system in our study displayed any differences between sedentary and recreationally active old participants. This is somewhat surprising but may suggest that high-intensity strength training in particular, and not physical activity per se, may be essential to preserve the neuromuscular function with age. Although assessed by indirect estimates and animal studies, it has been proposed that lifelong physical training may selectively mitigate the loss of motoneurons, as motoneuron preservation seems to manifest itself primarily in the motor units directly associated with the physical strain (14, 37). Albeit investigated in endurance athletes, the estimated number of motor units in the tibialis anterior muscle was higher in lifelong runners compared with age-matched sedentary individuals (35, 36). In contrast, the estimated number of motor units in the biceps brachii muscle, which is not directly involved in running, was not different between the two groups. Since the age-related loss of motoneurons is suggested to primarily affect the fast twitch motor units (2, 18, 21), it may be that high-intensity strength training, targeting the fast twitch motor units, could be particularly beneficial for counteracting the age-related loss of neuromuscular function. Indeed, the elevated V wave response of the MA, along with the declined H reflex response, is in accordance with this assumption.

Conclusion

Although some deterioration of the Hoffman reflex circuit seem inevitable, the current study demonstrated that exceptionally strength-trained master athletes showed mitigated age-related attenuation in the magnitude of efferent neural drive to maximally contracting skeletal muscle. In contrast, recreationally active old individuals did not exhibit any of this advantage for healthy aging, suggesting that strength training in particular may be necessary for efferent drive maintenance.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

R.J.U. and E.W. conception and design of research; R.J.U., M.N., L.T. v.d.H., and E.W. performed experiments; R.J.U. and M.N. analyzed data; R.J.U., S.K.S., J.H., and E.W. interpreted results of experiments; R.J.U. prepared figures; R.J.U. drafted manuscript; R.J.U., S.K.S., J.H., and E.W. edited and revised manuscript; R.J.U., M.N., L.T. v.d.H., S.K.S., J.H., and E.W. approved final version of manuscript.

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