Plantar flexor activation capacity and H reflex in older adults: adaptations to strength training

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Plantar flexor activation capacity and H reflex in older adults: adaptations to strength training. J Appl Physiol 92: 2292–2302, 2002. First published February 8, 2002; 10.1152/japplphysiol.00367.2001.—The purpose of this study was to investigate whether the voluntary neural drive and the excitability of the reflex arc could be modulated by training, even in old age. To this aim, the effects of a 16-wk strengthening program on plantar flexor voluntary activation (VA) and on the maximum Hoffman reflex (Hmax)-to-maximum M wave (Mmax) ratio were investigated in 14 elderly men (65–80 yr). After training, isometric maximum voluntary contraction (MVC) increased by 18% (P < 0.05) and weight-lifting ability by 24% (P < 0.001). Twitch contraction time decreased by 8% (P < 0.01), but no changes in half relaxation time and in peak twitch were observed. The VA, assessed by twitch interpolation, increased from 95 to 98% (P < 0.05). Pretraining VA, also evaluated from the expected MVC for total twitch occlusion, was 7% higher (P < 0.01) than MVC. This discrepancy persisted after training. The interpolated twitch torque-voluntary torque relationship was fitted by a nonlinear model and was found to deviate from linearity for torque levels >65% MVC. Compared with younger men (24–35 yr), the Hmax- to Mmax ratio and nerve conduction velocity (H index) of the older group were significantly lower (42%, P < 0.05; and 29%, P < 0.001, respectively) and were not modulated by training. In conclusion, older men seem to preserve a high VA of plantar flexors. However, the impaired functionality of the reflex pathway with aging and the lack of modulation with exercise suggest that the decrease in the Hmax- to Mmax ratio and H index may be related to degenerative phenomena.

twitch interpolation; triceps surae; aging; exercise

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ences in their general pattern of use (39). Thus it seems plausible that age-related adaptations in maximal neural activation may vary in relation to the specific involvement of different muscles in daily physical activities. Hence, there is the expectation that, even in old age, adaptations of neural drive to prolonged periods of strength training might be achieved.

Given that regulation of motoneuron activity is obtained through supraspinal as well as spinal inputs, it may also be of interest to investigate age-related changes in excitability at the peripheral level, namely in the spinal reflex pathway, and whether these can be modulated by regular physical activity during aging.

The quantitative evaluation of the neuromuscular excitability may be appraised by measuring the electromyographic (EMG) responses evoked by an electrical stimulus applied on a peripheral nerve. It is accepted that a submaximal stimulation produces a characteristic reflex response (H wave), which is the result of the motoneuron discharge evoked by the activation of the Ia fibers from the muscle spindles, whereas increasing the stimulus intensity results in the direct depolarization of the α-motoneurons’ axons. The ratio between the amplitudes of the maximum reflex response (Hmax) and maximum direct motor wave (Mmax) is commonly used as an index for estimating the level of reflex excitability of the motor pool (Hmax-to-Mmax ratio) (31). However, because this, in turn, depends on the facilitation of the transmission between the Ia fibers and the α-motoneurons (44), we cannot neglect the role of presynaptic inhibitions and possibly oligosynaptic contributions in modulating the reflex response. It is noteworthy that, as a consequence of the natural changes occurring in the central nervous system with senescence, aging has been associated with a decrease in motoneuron excitability and thus in nerve conduction velocity (13, 18, 40, 46), but it has also been observed that physically active older adults have preserved an efficient neuromuscular performance with a faster reflex response compared with their sedentary counterparts (23). It remains, therefore, to elucidate whether physical deconditioning rather than just degenerative phenomena may be involved in the age-related adaptations of the spinal reflex pathway. The Hmax-to-Mmax ratio has been shown to display a certain degree of plasticity to regular physical exercise in young subjects (10, 35, 43); nevertheless, whether a similar adaptation also occurs in older adults remains presently unknown.

In light of these considerations, the present study was designed to investigate whether the voluntary neural drive to the muscle and the excitability of the reflex arc could be modulated by training, even in old age. To this aim, the effects of a 16-wk strengthening program on PF activation capacity and on the Hmax-to-Mmax ratio were investigated in a population of 14 elderly men.

METHODS

The experiments here described are part of a comprehensive training study designed to provide an overall conditioning stimulus, involving both the upper and lower limbs. However, this particular paper shall deal with the neural adaptations of the PF muscles to strength training in aging.

Subjects

Fourteen men (aged 68 yr, range 65–80 yr; mass 80 kg, range 65–98 kg; height 172 cm, range 163–194 cm) agreed to participate in the study after being fully informed about the investigation and the possible related risks and discomfort. All subjects underwent a series of medical examinations, including a complete blood test, urine analysis, chest-X ray, rest and stress electrocardiogram, blood pressure, and detailed anamnesis focusing on the individual physical and leisure activities. For each subject, a profile, based on the past and present physical activities, was defined, taking into account the type and number of hours of exercise per week. Only healthy (free from neurological, cardiovascular, metabolic, inflammatory diseases) and moderately active subjects were admitted to the study. People were considered moderately active who were taking part in recreational, noncompetitive, physical activities with a frequency of no more than twice a week, not including regular strength training or high-intensity muscular efforts. During the 16-wk program, the subjects maintained their habitual leisure activities.

The H-reflex and M-wave measurements at baseline were compared with those obtained in young, moderately active adults (10 men, aged 29 yr, range 24–35 yr; mass 81 kg, range 72–100 kg; height 178 cm, range 165–184 cm), previously tested in our laboratory with the same technique. All of them signed a declaration of informed consent. The study was approved by the Ethics Committee of the S. Maugeri Foundation (Institute of Occupational Medicine and Rehabilitation, Pavia, Italy), where the investigation was carried out.

Strength Training Protocol

The subjects participated in a 16-wk strength-training program. Each training session, carried out on commercially available strengthening machines (Technogym), consisted of six different exercises involving the main muscle groups of the upper and lower limbs. The training frequency was three times per week, every other day, except the weekend. During the first five sessions, before the beginning of the study, subjects were familiarized with the equipment and with the exercise technique. The training of the lower limb muscles involved bilateral, closed kinetic chain movements, performed on a leg-press machine for the knee extensors and PF and on a sitting calf-rise machine specifically for the PF. In the leg press, leg extension was performed from a knee angle of 95° to −5° from full extension, to prevent knee-joint damage. For the calf-rise exercise, subjects plantar flexed from a position of −20° of dorsiflexion to maximum plantar flexion (−30°). The subjects were instructed to perform the lifting of the weight (concentric action) in ~2 s and, immediately after, the lowering of the weight (eccentric action) in ~3 s. This timing was achieved through the use of a visual display of the load excursion featured in the Technogym training machines used in this study. The training protocol consisted, for the first 3 mo, of one set of 10 repetitions with an initial load of 50% of one repetition maximum (1 RM: the maximum load that can be lifted once only) and was increased within 4 wk of training to 80% 1 RM. In the last month, an extra set of 10 repetitions was added, and the two sets were interspaced by a 2-min rest. For safety reasons, the 1 RM in each subject was estimated by measuring the three repetitions maximum (3 RM: maximum load that can be lifted 3 times only) with the use of the load-repetitions curve obtained by Sale and Mac-
Dougall (42). According to this relationship, a 3 RM corresponds to ~93% of 1 RM. The training load was updated every 2 wk to match it, as close as possible, to 80% of 1 RM. Each training session was preceded by 10-min warm-up exercise on a cycle ergometer at a heart rate corresponding to 50% peak O2 uptake (previously measured) and by one set of 15 repetitions at 20% of 1 RM on each training machine, followed by 10 min of stretching exercises. Subjects were individually supervised during training sessions at all times.

**Measurements**

All measurements were carried out on the dominant leg. The assessment of H- and M-wave amplitudes was conducted at baseline and after 10 and 16 wk. Voluntary activation (VA) capacity and muscle contractile properties were evaluated before and at the end of the training program.

Maximal voluntary contraction, VA, and contractile properties. The PF isometric maximal voluntary contraction (MVC) and the evoked twitch torque were determined in the supine position with the foot dorsiflexed at 20° (with 0° being the perpendicularity of the dynamometer footplate to the tibia). Such position was maintained throughout the experimental session. The pelvis was firmly fixed to the examination table to prevent movements during efforts. A strap was placed around the foot to secure it sturdily to the strain gauge of the dynamometer (Cybex Norm, Cybex Ronkonkoma) used to measure the force produced during evoked and voluntary contractions. Torque measurements were sampled at 200 Hz, amplified by five, band-pass filtered (10 Hz–1 kHz) by using an analog-to-digital board (Biopac, MP100), and hence stored on the hard disk of a desktop computer (Power Macintosh 8600/200).

A percutaneous constant-voltage electrical stimulator, developed by the European Space Agency, was used to deliver square-wave stimuli of 50 μs in duration to the triceps surae via two large surface electrodes (VersaStim, ConMed). The anode (12.5 × 7.5 cm) was placed over the belly of the gastrocnemius muscle, and the cathode (9 × 3.5 cm) over the soleus muscle, after cleaning of the skin with alcohol pads. The stimulus intensity was progressively increased until a further increase in current resulted in no further increment in twitch amplitude; this current was then regarded as supramaximal and the corresponding twitch as maximum.

During the first part of the experimental session, subjects were asked to perform three, 5-s-long MVCs of the PF. During each contraction, subjects were verbally encouraged to deliver maximal performance, and the highest torque generated was considered as the MVC. At least a 10-min rest period was introduced after the MVCs to minimize twitch potentiation in the successive test. Three supramaximal single stimuli, separated by a 1-min pause, were then delivered to the relaxed muscle to obtain a mean control twitch. The control twitch recordings enabled the determination of the peak twitch torque (Pt), twitch contraction time (CT), half relaxation time (HRT), and, as a consequence, the Pt-to-MVC ratio (Pt/MVC), as well as Pt-to-CT ratio (Pt/CT), which may be considered as an index of the mean velocity of contraction. Subsequently, the subjects performed, in randomized order, voluntary contractions at five target levels: 20, 40, 60, 80, and 100% of the previously determined MVC. The target efforts and the exerted torque were displayed, in real time, on the computer monitor as visual feedback to the subject. When the torque performed was considered to match the reference, two supramaximal single twitches, at 1 Hz, were interpolated. Especially for the higher contraction levels, the torque developed by the subjects did not always match precisely the target line, but the mechanical recordings allowed accurate determination of the value of voluntary torque at which the stimulus was triggered. To avoid interference due to fatigue, 2 min of rest were given between trials.

Because superimposed stimulation is presumed to activate motor units not recruited by the voluntary effort, the ratio of the extra torque (Pta) generated by each supramaximal superimposed stimulus during MVCs, over the amplitude of the evoked torque at rest (Pt), was used to calculate the VA, where 100% represents full motor unit recruitment [%VA = (1 − Pta/Pt) × 100]. For each subject, the highest over four VA scores was considered as the VA.

**Analysis of the Pta-voluntary torque relationship.** Because the Pta appeared to decline in a nonlinear fashion as contraction intensity (%MVC) increased (Fig. 1), the analysis of this relationship posed some problems in terms of regression equation, which had to satisfy the following requirements: 1) both the linear and curvilinear portions of the relationship have to be described and 2) curve and axes must intersect at relevant points, namely at MVC = 0% [representing the extrapolated “control twitch” (Pt.exp)] and at Pta = 0 [representing the extrapolated maximum intensity contraction (MVC.exp), Fig. 1]. To fulfill these constraints, the following equation was obtained

\[
\%\text{MVC} = a\left[1 - b^{C_{\text{t}}/d}\right] + b\left(1 - P_{\text{t}}/d\right)
\]

This equation contains curvilinear (exponential) and linear components, weighted by the coefficient b. The curvature of the nonlinear portion of the function is described by c. The coefficient d represents a prediction of P_{\text{t, exp}}, whereas a is an estimate of MVC.exp (Table 1). The four coefficients have been estimated for each subject by feeding a nonlinear regression equation was obtained.
Table 1. Coefficient values of Eq. 1

<table>
<thead>
<tr>
<th></th>
<th>a (MVC_exp)</th>
<th>b</th>
<th>c</th>
<th>d (P_ex)</th>
<th>N·m</th>
<th>P_ex/MVC_exp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pretraining</td>
<td>107.1 ± 10.9</td>
<td>0.81 ± 0.17</td>
<td>-0.39 ± 0.40</td>
<td>19.8 ± 4.4</td>
<td>0.19 ± 0.03</td>
<td></td>
</tr>
<tr>
<td>Posttraining</td>
<td>105.1 ± 4.8</td>
<td>0.76 ± 0.14</td>
<td>-1.59 ± 3.8</td>
<td>21.6 ± 4.6</td>
<td>0.18 ± 0.03</td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SD before starting (pretraining) and at the end of the strength training program (posttraining); n = 14 a, b, c, d: coefficients (see METHODS for descriptions); MVC, maximal voluntary contraction; MVC_exp, extrapolated MVC; P_t, peak twitch torque; P_ex, extrapolated P_t. *Pre- vs. posttraining is statistically different, P < 0.01.

software package (SYSTAT 5.2.1 for Macintosh) with individual (P_t, %MVC) data.

To evaluate the contraction intensity at which the relationship with P_t changed from linear to curvilinear, a threshold in the curve slope was introduced as parameter k. The k was set to 1.5 because it corresponds to the value that minimizes the %MVC variance at which the procedure found the linear part. By substituting P_t obtained from individual (P_t, %MVC) data.

Statistics

A one-way factor ANOVA with repeated measures was used to determine the effects of the training program. Subsequently, the Newman-Keuls (post hoc) test was performed to locate differences between means, if present. The pre- and posttraining comparisons were conducted by applying Student’s t-test, unless the data did not meet the criteria of normality (P < 0.05), in which case a nonparametric Wilcoxon matched pairs test was applied. Linear regression analysis (Pearson product-moment correlation) was used to compare the degree of association between variables, whereas the individual relationship between P_t and voluntary isometric torque was analyzed by applying a nonlinear correlation test. The one-sample Student’s t-test was employed to evaluate the difference between the VA and 100%. Reproducibility of the measurements of VA and of H_max and M_max amplitudes was quantified, in consecutive days, during the familiarization period before training, with the intraclass correlation coefficient (ICC), by using a two-way random effect model. The latter measurements were repeated over 4 separate days for the VA and over 3 separate days for the H_max and M_max. The accepted level of significance of all statistical tests was set at 5%. The data are presented as means ± SD.

RESULTS

MVC and 1 RM

The 16-wk strength-training program resulted in significant improvements in maximum voluntary isometric torque and weight-lifting capacity of the PF. At the end of the 16th wk, MVC increased by 17.8%, from 103.3 ± 31.4 to 115.7 ± 25.3 N·m (P = 0.02), and the 1 RM (mean of extrapolated values from the 3 RM) increased by 23.7%, from 47.8 ± 11.6 to 57.0 ± 8.8 kg (P < 0.001).

Contractile Properties

Values of P_t, CT, HRT, and P_t/MVC for the triceps surae are presented in Table 2. As can be observed, CT
Table 2. Effects of strength training on contractile properties of the triceps surae muscle at rest.

<table>
<thead>
<tr>
<th></th>
<th>P₁, N·m</th>
<th>P₁/MVC</th>
<th>CT, ms</th>
<th>P₁/CT, N·m·ms⁻¹</th>
<th>HRT, ms</th>
<th>P₁/HRT, N·m·ms⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pretraining</td>
<td>18.6±3.9</td>
<td>0.19±0.03</td>
<td>146.5±14.7</td>
<td>0.14±0.02</td>
<td>104.4±11.1</td>
<td>0.20±0.04</td>
</tr>
<tr>
<td>Posttraining</td>
<td>19.1±4.1</td>
<td>0.17±0.03</td>
<td>134.9±13.9</td>
<td>0.15±0.01*</td>
<td>107.4±9.9</td>
<td>0.19±0.03</td>
</tr>
</tbody>
</table>

Values are means ± SD before and after 16 wk of training; n = 14. CT, contraction time; HRT, half relaxation time; P₁/MVC, P₁/CT, and P₁/HRT, ratios of twitch contraction at rest. Pre- vs. posttraining is statistically different: *P < 0.05; †P < 0.01.

was significantly reduced by training (−7.7 ± 5.5%; P = 0.002) as was P₁/MVC (−10.3 ± 14.2%, P = 0.014). On the other hand, P₁/CT increased by 10.3 ± 14.2% (P = 0.023), whereas HRT, P₁/HRT, and P₁ did not show significant changes at the end of the strengthening program.

VA

Individual data for the measurements pre- and post-training are illustrated in Fig. 2. The mean VA value was 94.8 ± 6.7% at baseline and 97.7 ± 2.1% at the end of the 16 wk, thus showing a slight (+3.7 ± 9.5%, P = 0.03) but significant relative increase [(%VA posttraining − %VA pretraining)/%VA pretraining]·100, with a concomitant tendency for a decline in variability as training progressed. Even excluding the two different outliers pre- and posttraining (indicated in Fig. 2 with asterisks), the increase in VA still remained significant (P = 0.02). The one-sample t-test revealed that VA at pretraining was significantly different from 100% (P = 0.015) and remained significantly lower (P = 0.002) posttraining. This would indicate, in both cases, a relatively high, but still incomplete, activation level. A negative correlation (r² = 0.812, P < 0.001) was also observed between the baseline activation and the training effect (%VA increase), excepting for the subject who presented a slight decrease in VA after the 16 wk and obviously the outlier with the larger gain (Fig. 3). This suggests that the greatest deficit of activation before the conditioning period corresponds to the greatest increase after training. The ICC of the measurements of VA repeated over 4 consecutive days was 0.88, indicating good reproducibility of these measurements.

P₁a-Voluntary Torque Relationship

The relationship between extra force produced by the interpolated twitch and levels of voluntary isometric torque appears with inverted variables in Eq. 1, because the function fulfilling the imposed constraints (see METHODS) could not be reversed due to the lack of a unique solution. As a consequence, the regression analysis estimates the coefficients by minimizing the horizontal distances between the experimental data and the equation (in the graph shown in Fig. 1, for example), rather than the vertical ones. However, the very high correlation coefficient of individual regressions (0.99 < r² < 0.94; P < 0.001) suggests that such an approximation should be considered as negligible.

The studied P₁a-torque relationship appears to be nonlinear. More specifically, amplitude of the P₁a de-
creases almost linearly with torque in the submaximal torque range, but this effect is progressively lower, with a trend to even out, when the voluntary isometric contraction approaches 100%. The regression, which was found to fit the whole range of torque values, was a composite equation, with a curvilinear (exponential) and a linear component. The individual fitting by Eq. 1 enabled estimation of the expected value of MVC (MVC\textsuperscript{exp}) for zero P\textsubscript{ta} (Fig. 1 and Table 1), i.e., the maximal voluntary isometric torque that the subject would be able to produce when attaining whole muscle activation. This parameter (MVC\textsuperscript{exp} expressed as a percentage of the MVC observed) did not show any significant difference between the pre- (107.1 ± 10.9%; P = 0.008 pre, and P = 0.002 post, Fig. 4). Furthermore, a significant increase in the absolute values of MVC\textsuperscript{exp} was observed subsequent to the strengthening program (109.6 ± 33.6 vs. 122.3 ± 30.4 N\textperiodcentered m, P = 0.04), which is quite in line with the improvement in MVC observed (15.8 vs. 17.8%).

It was also possible to estimate the expected P\textsubscript{ta} (P\textsubscript{ta}\textsuperscript{exp}) for MVC = 0%. The comparison with the observed mean P\textsubscript{ta} (P\textsubscript{ta}\textsubscript{obs}) value highlighted a significant gap. It has been observed that the P\textsubscript{ta}\textsuperscript{exp} was higher than the P\textsubscript{ta}\textsubscript{obs} for either pre- (+6.0 ± 9.1%, P = 0.008) or posttraining (+13.9 ± 15.0%, P = 0.001) evaluations (Tables 1 and 2).

P\textsubscript{ta}\textsuperscript{exp}/MVC\textsuperscript{exp}, consequently derived, did not show any statistically significant modifications with training (Table 1), as opposed to P\textsubscript{ta}/MVC (Table 2).

The %MVC, at which the relationship with P\textsubscript{ta} changes from linear to curvilinear, was presented as a mean value in 9 subjects for the evaluation before training and in 11 subjects for the evaluation after training, because the other subjects showed a linear P\textsubscript{ta}-voluntary isometric torque relationship. This suggests that the descriptive ability of the chosen function incorporates both curvilinear and linear relationships; in the latter case, coefficients b and c are equal to 1 and 0, respectively. Finally, it appears that the departure from linearity for k = 1.5 (see METHODS) occurred at a similar %MVC, when pre- and posttraining conditions are compared (64.0 ± 15.2 and 65.2 ± 3.2% MVC, respectively), as illustrated in Fig. 5.

**H Reflex and M Wave**

In the investigated senior group, it was found that the Hoffmann reflex could be elicited only in 11 out of 14 subjects. The results were compared with those obtained in young adults formerly tested in our laboratory. It was found that the H\textsubscript{max}-to-M\textsubscript{max} was 42% lower (P = 0.02) in the elderly compared with the younger group. This difference is due to a larger depression of the H\textsubscript{max} (~64%, P = 0.005) compared with M\textsubscript{max} peak-to-peak amplitude (~44%, P = 0.007, Table 3) with aging.

Furthermore, regular resistance training in old age did not induce adaptive changes in the excitability of

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**Fig. 4.** Comparison of the MVC (open bars) and MCV\textsuperscript{exp} (solid bars) presented as absolute values before and after the training program. Values are means ± SD. *Pre- vs. posttraining is statistically different, P < 0.05. **MVC vs. MVC\textsuperscript{exp} is statistically different, P < 0.01.

**Fig. 5.** Point at which the relationship between extra force and maximal isometric torque change from linear to exponential. The fraction of P\textsubscript{ta}, at which the curvature deviates >1.5 times from the linear slope was calculated from the first derivative of Eq. 1. The corresponding contraction intensity is obtained from Eq. 1 by substituting the P\textsubscript{ta} value (see METHODS). Small circles, individual data points (pretraining n = 9, posttraining n = 11); large circles, means ± SD; ○, pretraining; ●, posttraining.
the H-reflex loop. As a matter of fact, no statistically significant differences were found in \( H_{\text{max}} \) and \( M_{\text{max}} \) amplitudes or in the \( H_{\text{max}} \)-to-\( M_{\text{max}} \) during the course of the 16-wk strength training. Anyway, it has to be taken into account that the absence of significant modifications might also be related to the great intersubject variability of the reflex response, as observed in our elderly population (see Table 3). The ICC of measurements repeated over 3 consecutive days before training was 0.74 for \( H_{\text{max}} \) and 0.79 for \( M_{\text{max}} \), indicating quite a high reliability of both evaluations.

The mean latency time of the two responses was measured to detect possible changes in the signal conduction velocity through the reflex and the direct motor pathway. At baseline, older participants presented a longer mean H conduction time than the younger counterparts (+11%, \( P = 0.004 \)), whereas no difference of M latency was observed. Even in this case, measurements were not significantly modified by the exercise. The linear relationship between the body height and the H-M interval, observed by Guiheneuc and Bathien (19) in adults, was maintained in our older population \( (r = 0.7; P = 0.01) \). Such correlation enabled the estimation of the H index for each subject. The mean value showed at pretraining was 75.2 ± 10.4, considering that the equation to assess the H index has been drawn so as to obtain a value close to 100 in healthy young subject (19), as confirmed by the value obtained from our younger population (105.8 ± 13.1). The significant difference between the two groups \( (29\%, \ P < 0.001) \) confirms the reduction in nerve conduction velocity with aging, which, furthermore, does not appear to be modified by exercise, because no significant variation was observed over the course of the training period (Table 3).

**DISCUSSION**

**MVC and Weight-lifting Capacity**

The present study confirms that older adults, aged between 65 and 80 yr, positively respond to a high-resistance training program in terms of increments in maximal isometric torque and weight-lifting capacity of the PF. One noteworthy observation is the lack of a significant difference between the increase in extrapolated 1 RM (24%) and MVC (18%). This finding contrasts with the majority of studies in young adults (41), as emphasized by the results of Jones and Rutherford (25), of a 250% improvement in weight-lift capacity but just a 15% increase in MVC after a 12-wk strengthening program. A general explanation for the larger increase in 1 RM, compared with the static measurement, is that increments in strength after training may be limited to specific movement patterns. Therefore, it is not the first time that a lower degree of specificity in the training response has been observed in the aged (compare Ref. 37). It seems that, at least for the PF, dynamic strength training in older adults may lead to smaller improvements in the ability to coordinate synergist muscle and fixator muscle function (39). Nevertheless, this explanation will need to be borne out by further investigations, given the present lack of consensus, with several studies upholding the validity of the principle of specificity of training even in the elderly (8).

**Contractile Properties**

The contractile characteristics of our older group, before training, present the typical traits of elderly muscle, with slower contraction kinetics compared with literature values for young adults (21, 47). One noteworthy finding, after strength training, was the significant decrease in CT with a concomitant increase in \( P_{t}/CT \), despite the fact that there were no changes in HRT and \( P_{t} \). These reports are in agreement with results obtained by Duchateau and Hainaut (15) after 16 wk of dynamic strength training in young adults but differ from some of the results obtained from senile muscle. In fact, Rice et al. (37) reported an increase in CT of the triceps brachii, whereas Brown et al. (8) observed a significant increment in HRT on the elbow flexors, after dynamic strength training in older subjects.

Key factors that may be held responsible for faster CT and greater \( P_{t}/CT \) could be related to changes in the excitation-contraction coupling process, to an increased shortening velocity of muscle fibers, and, possibly, to modifications in myotendinous stiffness (37). Several studies have provided experimental evidence that changes in CT may be associated with quantitative as well as qualitative modifications of the sarco-
plasmic reticulum (volume, density, and calcium release and recapture kinetics) and correlated with myosin ATPase activity (4). Because similar adaptations have been observed after strength training in aged lower mammals (29), it could be speculated that a prolonged period of increased loading might induce an enhancement in ATPase activity and calcium kinetics (15). Yet the reduction of CT after training may also be related to changes in the spread of excitation through the transverse tubular system. Even if EMG were not recorded during the percutaneous muscle stimulation, an additional analysis of the maximal M wave recorded from the soleus muscle, before and after training, showed no differences in terms of amplitude (see Table from the soleus muscle, before and after training, an additional analysis of the maximal M wave recorded during the percutaneous muscle stimulation, the transverse tubular system. Even if EMG were not related to changes in the spread of excitation through the transverse tubular system. Even if EMG were not recorded during the percutaneous muscle stimulation, an additional analysis of the maximal M wave recorded from the soleus muscle, before and after training, showed no differences in terms of amplitude (see Table 3) but also in terms of conduction time (M wave peak-to-peak duration: 3.2 ± 1.0 ms pretraining vs. 3.1 ± 0.9 ms posttraining). Thus these observations suggest that the acceleration of the twitch time course is not associated, in this case, with a faster electrical propagation due to an enhancement in muscle membrane excitability. It has to be added that the shorter CT might account for the lack of increase in P_t, despite the improvement in maximal voluntary torque. Indeed, the reduced CT would decrease the time available to the contractile elements to stretch the series elastic component (SEC) and, consequently, result in a smaller P_t.

VA and Expected MVC

In the present study, the capacity of older adults to employ all available motor units was evaluated by using the twitch interpolation technique (2, 3). This technique has for long been regarded has the “gold standard” for the assessment of activation capacity (2, 7, 8, 22, 36, 46, 48), and several authors reported no difference when comparing single twitches, doublets, quadruplets, and quintuplets (3, 6, 24). On the other hand, more recent studies indicate that the use of pulse-train stimulation may be more reliable than single pulses, because this technique may enable assessment of both recruitment and activation (5, 12, 28, 32, 45, 49). However, tetanic stimulation is undoubtedly painful. Therefore, in view of these unsettled opinions regarding the choice of single or multiple pulses and to minimize discomfort in older individuals, we opted for the more frequently used method to detect muscle activation deficit in older individuals, based on single pulses (2, 7, 8, 22, 36, 46, 48).

Our results provide evidence that VA achieved before training was incomplete (94.8%). This conclusion also appears to be supported by the estimated MVC values. Indeed, both pre- and posttraining, the higher values of the expected vs. the observed MVC (Fig. 1) indicate that there is a discrepancy between what can be voluntarily performed and what might be achieved for total twitch occlusion. Belanger and McComas (7) observed that young adults had similar difficulty in reaching full motor unit activation during MVCs. It has been proposed that this suboptimal activation capacity may be a muscle-specific limitation to force generation, rather than a consequence of age-related disuse. As a matter of fact, Dowling et al. (14) suggested that certain muscles could not be fully activated during voluntary efforts, thereby limiting the expression of maximal force production. In this context, it seems noteworthy that the present group of moderately active older men has preserved an almost maximal VA capacity of the PF. This contrasts with the observations of Harridge et al. (22) and Winegard et al. (48), indicating an ~20% reduction in activation capacity of the quadriceps femoris and PF muscles in octogenarian men. It is plausible that the lower activation level, observed by these authors, may partially depend on the higher mean age of their experimental groups (88 and 81 yr, respectively). This appears to be in line with the observation that the eldest subject in our study (80 yr) showed, pretraining, the greatest deficit in VA and the largest increase after the conditioning period (71.9 vs. 98.5%), whereas the “youngest” volunteer (65 yr) showed no modification (99.3 vs. 99.2%), suggesting a presumable age-related effect on activation capacity. More generally, given the negative correlation (r² = 0.812, P < 0.001) between the training effect (%VA increase) and the baseline activation, it appears that the greatest deficit of VA at baseline corresponds to the greatest increase after training (Fig. 3). On the other hand, the preserved activation capacity of the dorsiflexors observed in very old subjects by Winegard et al. (48) suggests that the discrepancy in central activation among muscles is probably associated with differences in their patterns of use.

Conversely, it is also plausible that disuse, as well as physical deconditioning, may justify the significant increase in VA (3.7%) after training. However, it should be pointed out that even a 5% increase in activation may not have an effect on MVC (12) and, as such, the functional significance of this increase in VA should be viewed with caution. In fact, De Serres and Enoka (12) argued that, in the interpolation technique, the signal-to-noise ratio is too low to make definitive conclusions about such small changes. Yet the fact that the relative MVCexp (%MVC observed) did not increase significantly with exercise argues against an improvement in motor unit activation. Thus, according to these observations and given the greater reliability of this alternative approach, we may conclude that the increase in VA is probably not a training effect.

Surprisingly, P_t/MVC decreased after training (Table 2), which could indicate the presence of neural adaptations. However, taking into account that the shorter CT might justify the lack of increase in P_t, it follows that the contribution of muscular factors cannot be excluded. Therefore, the widely held view that a major portion of the strength gain, induced by training older adults, is due to changes in neural drive (17, 20) seems partly challenged by the results of this study. Also, measurements of PF cross-sectional area performed in these subjects showed an increase of 9% after training, thus suggesting that hypertrophy, or intrinsic changes of the contractile tissue, exerted a greater
contribution to the gain in torque than did neural factors (34).

**P*<sub>ta</sub>-Voluntary Torque Relationship**

As previously observed in young adults, the relationship between the extra force produced by the interpolated twitch and the levels of voluntary isometric torque is nonlinear, thus indicating a near-maximal activation capacity for a submaximal voluntary torque (3, 7, 9, 12, 14, 36, 39). Moreover, the shape of this relationship seems to be muscle specific, as is also the capacity of attaining complete motor unit activation (7). Using the best curve-fitting procedure, previous authors have fitted the experimental points with an exponential (14) or a third-order polynomial function (12). However, in both cases, the regression line often did not intersect the x-axis, and, as a result, prediction of the MVC corresponding to complete muscle activation was not always possible. This drawback was overcome by Phillips et al. (36) with a procedure involving linearization of the evoked force, preserving a reasonable least squares fit of the data. In the present investigation, care was taken to preserve the method of the best fitted regression to identify a function that satisfied the requirements for intersection of the axis at relevant points, allowing us to estimate a MVC<sub>exp</sub> and a P<sub>t exp</sub>. At the same time, we were able to describe a linear plus curvilinear data set and, consequently, locate the contraction intensity at the transition point. The departing from linearity may be caused by several factors, including an increasing mechanical contribution of synergistic muscles at high-torque levels of voluntary plantar flexion, as well as a modification of motor unit activation pattern (recruitment vs. rate coding). It has, in fact, been shown that, for certain muscles, the majority of the motor units are recruited for submaximal levels of effort (11). The departure from linearity could also be attributed to the progressive stretching of the SEC. Because of the viscoelastic properties of this component, damping of the twitch would be higher at low-force levels (when the SEC is more slack) but would be very low when the SEC is fully stretched, i.e., at high-force levels. It is likely that the higher value of the P<sub>t exp</sub> compared with the observed measure could be attributable to the fact that the model proposed in the present study does not take into account the tensile properties of the SEC. It seems, in fact, that, for the weaker levels of efforts, the relationship between extra force and voluntary torque may not be strictly linear (7, 9) because of the slack of the SEC. On the other hand, above ~20% MVC, a considerable part of the slack is taken up by the contractile component, and the SEC are probably stretched enough so that the muscle could reach true isometric conditions earlier in time and thus, presumably, at a length closer to optimum muscle length. Accordingly, with this assumption, we may hypothesize that the extrapolation technique enables determination of a P<sub>t</sub> response as if it were evoked in the same conditions of the P<sub>ta</sub>, thus justifying the relevance in P<sub>t exp</sub>/MVC<sub>exp</sub>. Again, the absence of neural adaptations was suggested by the fact that, differently from P<sub>t</sub>/MVC (see previous session), the expected ratio was not modulated by training.

The present study, therefore, confirms the nonlinearity of the relationship between the extra force and voluntary torque for older subjects, as previously observed for young adults. However, it would be interesting if further studies could investigate whether age contributes to the departure from linearity of this curve. For instance, given the marked reduction in motor unit discharge rate in old age (26), a later deviation from linearity in the elderly compared with young adults could be hypothesized.

**H Reflex and M Wave**

Our results provide further evidence of the progressive age-related impairment of the neuromuscular system at the peripheral and spinal level as reported in the literature (1, 13, 18, 30, 33, 38, 40, 46). The attenuation of the H<sub>max</sub>-to-M<sub>max</sub> ratio in this older group, compared with a population of younger adults, points to a decrease in the proportion of the available motor units reflexively recruited. The mechanisms responsible for the age-related decrease in reflex excitability may be associated with changes affecting interneurons, as well as both the afferent and efferent pathways, inducing an increased temporal dispersion of impulses. This may result in an increased presynaptic inhibition of I<sub>a</sub> afferent fibers (33) and in random degenerative changes in both sensory and motor axons (1, 30), leading to progressive loss of spinal motoneurons and of the number of functioning motor units with aging (38, 47). The significantly longer reflex latency exhibited by the older adults, together with the maintained direct motor time, suggest specific alterations at the afferent level. This may be associated with a modified conduction velocity of I<sub>a</sub> afferents and/or a decreased synaptic transmission efficacy. On the other hand, the functionality of the neuromuscular junction and efferent conduction speed seems to be maintained.

Several studies in young subjects have addressed the differences in the H<sub>max</sub>-to-M<sub>max</sub> ratio among sedentary and/or differently trained athletes (10, 35), thus suggesting that habitual physical activity may influence the excitability of the spinal reflex pathway. In young adults, strength training and overloading in particular have been shown to influence neural factors such as nerve conduction velocity (27), motoneuron excitability (43), and nerve fiber diameter (16). Thus the hypothesis was put forward that, even in old age, remodeling of neural structures involved in the reflex arc might occur in response to training to mitigate the decline in excitability (13, 40, 46). Had this occurred, a facilitation of the H-reflex recruitment would have been expected, but our results showed that neuromuscular excitability and nerve conduction velocity were not modified by a 16-wk strength-training program. The lack of modifications in the H<sub>max</sub>-to-M<sub>max</sub> ratio and in the H index suggests that regular training in the elderly does not
induce adaptations in afferent and efferent fibers, interneuronal structures, or modulation in synaptic transmission efficacy, as well as in neuromuscular junction function. In other words, the whole inhibitory and excitatory effects that may influence the α-motoneuron pool efficacy do not seem to be influenced by a prolonged period of resistive loading. The absence of adaptive responses seems to indicate that the decrease in the H\textsubscript{max}-to-M\textsubscript{max} ratio and nerve conduction velocity with age could be mainly due to degenerative phenomena rather than disuse. However, it cannot be excluded that the lack of modulation of the H reflex may be due to the rather short period of physical intervention of the present study, because adaptations of the reflex arc have been observed after very long periods of habitual physical activity (35).

Conclusions

This study has shown that muscle activation capacity of the PF is well preserved in fairly active older men aged 65–80 yr. Conversely, a lower H\textsubscript{max}-to-M\textsubscript{max} ratio and a slower nerve conduction velocity were found compared with a younger group of adults, with no modulation after training. These findings confirm an impaired functionality of the peripheral neuromuscular system in old age. Hence, regular resistive exercise does not seem to influence the peripheral segment reflex loop. The absence of adaptive responses suggests that the depression in reflex amplitude in old age could be mostly due to degenerative phenomena.

In older individuals, as already demonstrated in young subjects, the PF motor unit recruitment proceeds in a nonlinear fashion. This suggests that, at high contraction intensities, a substantial contribution of 1) other neural factors, such as the rate coding, 2) a more efficient force transmission due to stretching of the SEC, and 3) an increased mechanical contribution of synergistic muscles may occur.

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