Aging does not affect voluntary activation of the ankle dorsiflexors during isometric, concentric, and eccentric contractions

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Aging does not affect voluntary activation of the ankle dorsiflexors during isometric, concentric, and eccentric contractions. This study examines the age-related deficit in force of the ankle dorsiflexors during isometric (Iso), concentric (Con), and eccentric (Ecc) contractions. More specifically, the contribution of neural and muscular mechanisms to the loss of voluntary force was investigated in men and women. The torque produced by the dorsiflexors and the surface electromyogram (EMG) from the tibialis anterior and the soleus were recorded during maximal Iso contractions and during Con and Ecc contractions performed at constant angular velocities (5–100°/s). Central activation was tested by the superimposed electrical stimulation method during maximal voluntary contraction and by computing the ratio between voluntary average EMG and compound muscle action potential (M wave) induced by electrical stimulation (average EMG/M wave). Contractile properties of the dorsiflexor muscles were investigated by recording the mechanical responses to single and paired maximal stimuli. The results showed that the age-related deficit in force (collapsed across genders and velocities) was greater for Iso (20.5%; \(P < 0.05\)) and Con (38.6%; \(P < 0.001\)) contractions compared with Ecc contractions (6.5%; \(P > 0.05\)). When the torque produced during Con and Ecc contractions was expressed relative to the maximal Iso torque, it was significantly reduced in Con contractions and increased in Ecc contractions with aging, with the latter effect being more pronounced for women. In both genders, voluntary activation was not significantly impaired in elderly adults and did not differ from young subjects. Similarly, coactivation was not changed with aging. In contrast, the mechanical responses to single and paired stimuli showed a general slowing of the muscle contractile kinetics with a slightly greater effect in women. It is concluded that the force deficit during Con and Iso contractions of the ankle dorsiflexors in advanced age cannot be explained by impaired voluntary activation or changes in coactivation. Instead, this age-related adaptation and the mechanisms that preserve force in Ecc contractions appeared to be located at the muscular level.

skeletal muscle; gender; contractile properties

IT IS WELL ESTABLISHED THAT the force produced by a muscle group is reduced with advancing age (for reviews, see Refs. 12, 28, 35). Although similar between genders, the magnitude of this force deficit is related to the task performed by the subject and is less for eccentric (Ecc) contractions compared with isometric (Iso) or concentric (Con) contractions (18, 34–36, 42). The smaller age-related decline in Ecc force appears to be independent of muscle fiber type and size (18), yet the underlying mechanisms remain unclear. A slowing of cross-bridge cycling (10, 17, 25) and changes in muscle-tendon stiffness (32, 41) have been suggested to explain the capacity of elderly adults to better preserve muscle force under Ecc conditions than in Con and Iso contractions.

In addition to a loss of muscle mass (14, 26), impaired voluntary activation may also contribute to the muscle weakness commonly observed in older adults (16, 29, 40). A classical approach to assess the ability of individuals to achieve complete activation of a muscle group is to superimpose a single electrical stimulus (3, 15, 16, 43) or a brief train of stimuli (5, 11, 21, 22, 24, 30, 40) to its motor axons during a maximal voluntary contraction (MVC). When the muscle is fully activated by the voluntary command, no extra force will be elicited by the stimulation. In contrast, the presence of extra force will indicate a submaximal activation of the muscle that can be quantified by different methods (15, 22). Studies that investigated possible age-related alterations in activation during MVC reported conflicting results. Some studies observed a reduced voluntary activation (21, 30, 40), whereas others did not show significant differences between elderly and young subjects (11, 23, 37, 39, 43). Although differences in methodology (40) and the muscle groups tested (21) may explain part of this discrepancy, they do not entirely account for the conflicting results. For example, Jakobi and Rice (21) reported that older adults can achieve similar voluntary activation during Iso contractions, compared with young men, when sufficient attempts are provided. This observation suggests that the lack of practice, rather than impaired capacity of the nervous system to maximally activate muscles, may explain the observed reduction in voluntary activation. An additional factor that can contribute to reduced agonist activation is antagonist coactivation (38). To our knowledge, possible changes in the level of agonist activation and coactivation in elderly adults have been mainly investigated during static contractions. A few studies reported that antagonist activity during maximal Iso contractions is increased with aging (20, 24, 29), a change that could reduce agonist activation, not only by the opposing action of the antagonists but also by reciprocal Ia inhibition (9).

Because daily tasks require not only Iso contractions but also dynamic actions, the question of whether a difference in voluntary activation during movements exists between young and elderly adults appears particularly relevant. This question is interesting because a difference in voluntary activation during Con and Ecc contractions previously has been reported in untrained young subjects (2, 44). The main purpose of this study was to examine the age-related contribution of neural and muscular mechanisms to the force deficit observed during different types of muscle contractions (Iso, Con, Ecc). It was
hypothesized that the deficit in voluntary activation during maximal dynamic contractions compared with Iso contractions would be greater in elderly than in young subjects. Because it has been reported that the force reduction during Ecc actions was greater in men compared with women (18, 27), the hypothesis of a possible gender difference in the adaptation mechanisms was also investigated. The ankle dorsiflexor muscles were selected for investigation based on their role in locomotion.

MATERIALS AND METHODS

Subjects. Twenty young subjects (10 men and 10 women, aged 25.4 ± 1.0 and 25.9 ± 1.4 yr, respectively; means ± SE) and 19 elderly subjects (10 men and 9 women, aged 78.7 ± 1.8 and 74.6 ± 1.9 yr, respectively) participated in the study. All subjects were healthy and without neuromuscular disorders at the time that they participated in this study. Both young and elderly subjects reported moderate physical activity. Elderly persons were living at home and walked daily without the use of an assistive device. All subjects participated in two sessions: once for familiarization and once for data collection. During the familiarization session, subjects practiced the different types of contractions and velocities of movement and also experienced electrical stimulation. Subjects were not engaged in any strenuous locomotor activity for at least 24 h before the experimental session. The University Ethics Committee approved this investigation, and all experimental procedures were performed in accordance with the Declaration of Helsinki. All subjects were volunteers and gave their informed consent before participating in the study.

Ergometric device. A motor-driven, computer-controlled ergometer (type HDX 115C6; Hauser Compax O260M-E2; Offenburg, Germany), adapted for the ankle dorsiflexor muscles, was used in this study. This device, which was equipped with a footplate that was fixed to the rotational axis of the motor, recorded the torque generated in static and dynamic (isokinetic) conditions. The subject was secured on an adjustable seat in a slightly reclined position. The dominant foot was strapped to the plate, so that the axis of rotation of the ankle joint was aligned with that of the motor. In the Iso position, the plate was inclined at an angle of −40° relative to the floor. The subject position was adjusted to obtain a 10° ankle plantarflexion and a 50–60° knee inclination at an angle of 40° relative to the floor. The foot was held in place by a heel block and was tightly attached to the plate by means of two straps. One strap was placed around the foot, 1–2 cm proximal to the metatarsophalangeal joint of the toe, and the second strap was placed around the foot, just below the ankle joint.

Mechanical and electromyographic recordings. The device was equipped with a linear potentiometer and strain-gauge transducers (sensitivity: 0.018 V/N·m; linear range: 0–200 N·m) that were mounted on the rotational axis of the motor. They were used to measure, respectively, the displacement of the ankle attached to the footplate and the torque produced by the dorsiflexor muscles during MVCs and in response to electrical stimulation. The surface electromyographic (EMG) activity was recorded from the tibialis anterior (TA) by means of two silver-disk electrodes (8 mm in diameter). One electrode was positioned over the muscle belly (two-thirds of the distance between the lateral malleolus and the fibular head). The second electrode was placed 2 cm distal to the first one. The ground electrode (2 × 3-cm silver plate) was attached between the stimulating electrodes and the EMG recording electrodes. The EMG signals were amplified (×1,000) and filtered (10 Hz–5 kHz) by a custom-made differential amplifier. To estimate muscle coactivation, the surface EMG of the soleus (Sol) was also recorded. One electrode was positioned over the Sol motor point, and the second electrode was placed 2 cm distal to the first one. The torque, the displacement, and the EMG signals were simultaneously recorded by a computer at a sampling rate of 2,000 Hz and were analyzed offline by using the AcqKnowledge data analysis software (model MP150; Biopac Systems, Santa Barbara, CA).

Electrical stimulation. The dorsiflexor muscles were activated by rectangular electrical pulses of 1 ms delivered by a custom-made stimulator triggered by a digital timer (model 4030; Digitimer, Welwyn Garden City, UK). The stimuli were delivered to the peroneal nerve through two electrodes (silver disks, 8-mm diameter), with the cathode placed over the peroneal nerve close to the fibular head and the anode placed on the opposite side of the leg. To avoid the activation of the peroneal muscles, the nerve was stimulated distal to the branching to these muscles, and the absence of any peroneal muscle activity was assessed by palpation. Maximal stimulus intensity was determined by progressively increasing the intensity until the torque and the compound action potential (M wave) reached a plateau. The level of stimulation was then set 10–20% above maximum. The mechanical response to single and paired (10-ms interval) supramaximal stimuli was recorded. The magnitude of activation during voluntary contractions under Iso, Con, and Ecc conditions was assessed by the superimposed stimulation method (3, 5, 15) using paired (10-ms interval) supramaximal stimuli delivered to the peroneal nerve. During Iso contractions, stimuli were applied during the torque plateau, whereas, during Con and Ecc contractions, stimuli were triggered at the midpoint of the range of motion, corresponding to a constant ankle of 10° plantarflexion for all contractions.

Experimental procedure. The experimental session began with the recording of the mechanical response of the ankle dorsiflexors and the EMG activity (M wave) of the TA in response to three and three paired supramaximal electrical stimuli delivered to the peroneal nerve. Thereafter, the subjects performed three Iso MVCs of the ankle dorsiflexors. During the last two trials, paired electrical stimuli were superimposed on the MVC. This was followed by maximal Con and Ecc contractions, performed at different angular velocities (3, 25, 50, 75, and 100°/s), through a 30° range of motion (between 25° plantar flexion and 5° dorsiflexion). The order for the different contraction types was not randomized because possible muscle damage associated with Ecc contractions may influence the results. For each contraction type, however, movement velocities were imposed in random order. Before the movements, subjects were instructed to produce a maximal Iso torque and to sustain the maximal effort throughout the entire range of motion (Fig. 1). For each velocity, the subjects performed two to three submaximal trials of familiarization and two maximal Ecc and Con contractions. During the second trial at maximal effort, the level of voluntary activation was assessed by the superimposed stimulation method (see above). When submaximal activation was observed, a second trial with superimposed stimuli was performed to retest the subject’s inability to fully activate the dorsiflexor muscles. This was only observed in Ecc contractions and for 37 out of the 195 trials (17 and 20 trials in elderly and young subjects, respectively). The subjects were verbally encouraged during the different efforts, and each contraction was separated by a 3-min pause to avoid fatigue.

Measurements. The peak torque (Pp), contraction time, and time to half relaxation (RT50) were measured from the twitch response to single stimulation. The maximal rates of twitch torque development (+dP/dt) and relaxation (−dP/dt) were obtained from the first derivative of the torque signal. The peak torque (Pp) and the maximal rate of torque development (+dP/dt) of the mechanical response to paired stimuli were also measured. The voluntary torque and the associated average (rectified) EMG activity of the TA and Sol were measured for a 1-s period during the plateau of the Iso MVC. During movements, the average torque and aEMG activity of TA and Sol were measured throughout the entire range of motion (Fig. 1). Voluntary activation during Iso, Con, and Ecc maximal contractions was assessed by the superimposed stimulation method. Because the torque-time curve was linear, at least during 50–100 ms before stimulation (Fig. 1), the MVC torque reached at the time of the superimposed paired stimulation was determined by extrapolation of the slope from the prestimuli measured torque (5). The central
The aEMG activity of the TA during MVC was normalized to the maximal Iso torque, it appeared that the voluntary activation of the dorsiflexor muscles, tested by the superimposed stimulation method, appeared to be maximal or near maximal in both young and elderly adults (Fig. 2, C and D). This age-related effect was more pronounced (P < 0.001) for women (23.1 ± 1.5%; P < 0.001) than men (11 ± 1.4%; P < 0.01).

**Voluntary activation.** The voluntary activation of the dorsiflexor muscles, tested by the superimposed stimulation method, appeared to be maximal or near maximal in both young and elderly adults, regardless of the type or velocity of contractions (Fig. 3). For velocities between 50 and 100°/s in Ecc contractions, a small deficit in activation was observed for a few (2–3) subjects in both the young and elderly groups (Fig. 3). Regardless of gender or age, the median of voluntary activation was supported by the EMG results (Fig. 4). In the Iso condition and for all velocities in the Con and Ecc contractions, the aEMG of the TA did not differ significantly between young and elderly adults (P > 0.05; data not shown). The M wave, recorded in response to a single maximal electrical stimulation, showed a slight decrease in peak-to-peak amplitude with aging (Table 1), which was statistically significant (P < 0.05) only in men.

**RESULTS**

**Torque-velocity relationship.** Regardless of type or speed of contractions, women were significantly (P < 0.001) weaker than men in both the young and elderly groups (Fig. 2, A and B). In both genders, the age-related deficit in torque was greater in Iso and Con contractions compared with Ecc contractions (Fig. 2). Although the difference in absolute torque between elderly and young adults was statistically significant for Iso (19.3 and 22.4% in women and men, respectively; P < 0.05) and Con (39.7 and 37.4%; P < 0.001; data collapsed across velocities) contractions for both genders, this was only the case in elderly men for Ecc contractions (10.5%; P < 0.05; Fig. 2B). For women, the absolute torque during Ecc contractions was similar (P > 0.05) in elderly and young groups (Fig. 2A).

When the torque produced during Con and Ecc contractions was normalized to the maximal Iso torque, it appeared that the Con torque was reduced with aging (Fig. 2, C and D). The mean reduction in relative torque during Con contractions, computed across velocities, was 24.9 ± 1.4% (P < 0.001) for women and 18.8 ± 3.1% (P < 0.001) for men, but the difference between genders was not statistically different (P = 0.09). In contrast, elderly adults performed higher relative torque during Ecc conditions, compared with young adults (Fig. 2, C and D). This age-related effect was more pronounced (P < 0.001) for women (23.1 ± 1.5%; P < 0.001) than men (11 ± 1.4%; P < 0.01).

The absence of age-related changes in muscle activation was supported by the EMG results (Fig. 4). In the Iso condition and for all velocities in the Con and Ecc contractions, the aEMG of the TA did not differ significantly between young and elderly adults (P > 0.05; data not shown). The M wave, recorded in response to a single maximal electrical stimulation, showed a slight decrease in peak-to-peak amplitude with aging (Table 1), which was statistically significant (P < 0.05) only in men.
However, when voluntary aEMG of the TA was normalized to its corresponding M-wave amplitude, the ratio did not differ \((P > 0.05)\) between young and elderly subjects, regardless of gender or velocity of movement (Fig. 4).

EMG activity of the Sol during the activation of the dorsiflexors was present in both young and elderly adults. Regardless of the type or velocity of contractions, the level of coactivation, tested by the Sol aEMG-to-TA aEMG ratio, was very similar \((P > 0.10\%)\) in both elderly (range: 9.3–11.9\%) and young (range: 8.2–11.6\%) adults. Because antagonist activity was only recorded in five elderly subjects (4 women and 1 man), it was not possible to test gender differences in coactivation.

Muscle mechanical properties. The effects of aging on the mechanical properties of the dorsiflexor muscles are reported in Table 1. For both genders, \(P_t\) and \(P_d\) did not show significant differences between young and elderly subjects. The data also indicated a slowing of the contractile kinetics in elderly adults, as indicated by the twitch contraction time, which was prolonged by 23\% \((P < 0.05)\) and 33\% \((P < 0.01)\) in elderly women and men, respectively. A similar tendency was observed for \(R_{1/2}\), but these differences did not reach statistical significance. In accordance with the slowing of the twitch time course, \(+ dP_t / dt\) and \(+ dP_d / dt\) were reduced with aging, but the data only reached statistical significance for the paired stimulation \(+ dP_d / dt\). Interestingly, this decreased rate of torque development was more pronounced \((P < 0.05)\) in elderly women (32 and 43\% for \(+ dP_t / dt\) and \(+ dP_d / dt\), respectively) compared with elderly men (15 and 26\% for \(+ dP_t / dt\) and \(+ dP_d / dt\), respectively). No age-related difference was observed for the rate of torque relaxation \((- dP / dt)\), either for women or for men (Table 1).

DISCUSSION

The present study shows that maximal torque deficits of the ankle dorsiflexor muscles with advancing age are less pronounced during Ecc contractions compared with Iso and Con contractions. The main finding is that these force deficits are not attributable to impaired voluntary command in elderly adults. This conclusion is supported by the absence of differences in voluntary activation between young and elderly subjects when tested either by the superimposed stimulation method or by the voluntary aEMG-to-M wave ratio. Consequently, the reduced performance of the ankle dorsiflexors with aging is likely located at the muscular level.

The greater torque decrement during Iso and Con contractions compared with Ecc actions in advanced age is in agreement with other works (18, 27, 34–36, 42). For Iso contractions, we observed a ~20\% loss of force, a percentage that was very similar for the two genders (19 and 22\% for elderly women and men, respectively). Surprisingly, the deficit in torque was not related to the speed of movement, because a similar decline was observed at all velocities in both Con and Ecc contractions. These results contrast with those of Pousson.
et al. (36) and may be due to the relatively narrow range of velocities (from $-100$ to $+100^\circ$/s) tested in the present study.

The literature regarding the capacity of elderly adults to fully activate their muscles includes conflicting results. Some studies reported lower voluntary activation in elderly compared with young adults (21, 30, 40), whereas others did not observe a difference (8, 11, 23, 24, 43). Moreover, most studies have investigated voluntary activation during Iso contractions, which do not represent the only type of muscle actions in activities of daily life. To our knowledge, only the study of White and Harridge (45) has tested possible age-related alterations in voluntary activation during dynamic actions in the elderly population. Their results showed, by comparing maximal voluntary and electrically induced contractions, that the activation of the triceps surae during Con (isokinetic) movements at angular velocities up to $240^\circ$/s did not differ between young and elderly men. In the present study, the activation of the ankle dorsiflexors, quantified by the superimposed stimulation method, was maximal or near maximal in both genders during Iso, Con, and Ecc contractions. Submaximal activation was observed in a very few trials during Ecc contractions. This was only observed for the highest velocities and in a similar proportion for elderly and young adults. Although the use of voluntary EMG as an index of voluntary activation can be misleading (13), the voluntary aEMG-to-M-wave ratio for the TA also was similar in elderly and young adults, regardless of the type or velocity of contractions. The results of the two methods indicated that, similar to young subjects, elderly adults are able to fully activate their ankle dorsiflexors during all types of contractions performed at angular velocities up to $100^\circ$/s.

Various factors could explain the lack of difference in voluntary activation between elderly and young subjects. First, both groups were moderately active and did not differ too

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**Fig. 3.** Comparison of muscle activation, assessed by the superimposed stimulation method, in elderly and young women (A) and in elderly and young men (B) during the different types of contractions and velocities of movement. Voluntary activation was calculated according to the following equation, MVC torque/(MVC torque + superimposed torque) (22), and expressed as a percentage of maximum. Individual values are presented on each graph, but not all data points can be seen, as many are superimposed. Regardless of velocity, the median of muscle activation for each group was equal to 100%.

**Fig. 4.** Comparison of voluntary activation, assessed by the average EMG (aEMG)-to-M-wave ratio, in elderly and young women (A) and in elderly and young men (B) during the different types of contractions and velocities of movement. Values are means ± SE. For all velocities and genders, data did not differ significantly between elderly and young subjects.
Table 1. Electromechanical properties of the ankle dorsiflexors in response to single and paired electrical stimuli in elderly and young women and men

<table>
<thead>
<tr>
<th></th>
<th>Young Women</th>
<th>Elderly Women</th>
<th>Young Men</th>
<th>Elderly Men</th>
</tr>
</thead>
<tbody>
<tr>
<td>M wave Amplitude, mV</td>
<td>3.16±0.33</td>
<td>2.79±0.38</td>
<td>4.54±0.58</td>
<td>3.03±0.24*</td>
</tr>
<tr>
<td>Twitch</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P, N·m</td>
<td>2.0±0.3</td>
<td>1.6±0.2</td>
<td>2.4±0.3</td>
<td>2.6±0.4</td>
</tr>
<tr>
<td>CT, ms</td>
<td>74±3</td>
<td>91±4*</td>
<td>73±5</td>
<td>97±6*</td>
</tr>
<tr>
<td>RT1/2, ms</td>
<td>71±5</td>
<td>77±4</td>
<td>69±6</td>
<td>79±8</td>
</tr>
<tr>
<td>+ dP/dt, N·m/s</td>
<td>49.3±5.4</td>
<td>33.7±4.5</td>
<td>62.4±4.7</td>
<td>52.7±6.7</td>
</tr>
<tr>
<td>− dP/dt, N·m/s</td>
<td>22.3±2.2</td>
<td>18.5±1.5</td>
<td>29.3±4.2</td>
<td>26.5±2.5</td>
</tr>
<tr>
<td>Pa, N·m</td>
<td>7.4±0.9</td>
<td>5.2±0.5</td>
<td>8.2±0.6</td>
<td>7.4±0.8</td>
</tr>
<tr>
<td>+ dP/dt, N·m/s</td>
<td>162.7±13.8</td>
<td>92.7±10.9†</td>
<td>176.9±11.4</td>
<td>130.2±13.2*</td>
</tr>
</tbody>
</table>

Values are means ± SE. M wave, peak-to-peak amplitude of the muscle compound action potential; P, twitch torque; CT, contraction time; RT1/2, half-relaxation time, + dP/dt and − dP/dt, maximal rate of twitch torque development and relaxation to single stimulus, respectively; Pa and + dP/dt, torque and maximal rate of torque development to paired stimuli, respectively. Significant difference between young and elderly subjects: *P < 0.05; †P < 0.01.

much in their physical activity level. Second, the ability to voluntarily activate the ankle dorsiflexor muscles during Iso MVC is usually higher (43) than in other muscles (3, 15, 16). Therefore, we cannot rule out the possibility that a difference in voluntary activation between elderly and young subjects would have been observed for muscle groups that are more difficult to fully activate. Third, to quantify voluntary activation, we used the central activation ratio proposed by Kent-Braun and Le Blanc (22) rather than the superimposed twitch relative to a control twitch evoked at rest (see Refs. 3, 15, 30). We chose the first method because, in a pilot study, a force increment due to the superimposed electrical stimulation was rarely observed during the different types and velocities of contraction. Thus, to avoid fatigue, especially in elderly subjects, we did not induce a doublet when the limb was passively moved through the range of motion at the different velocities. Although the method we used could have overestimated the level of voluntary activation, it must be mentioned that a deficit in activation was only observed in a very few subjects and exclusively for Ecc contractions at velocities >25–50°/s. Furthermore, in a complementary study, performed on four young subjects, that presented an activation deficit in Ecc contractions, we found that both methods gave very similar results (~1% difference) in our experimental conditions. Therefore, and even if the sensitivity of the superimposed doublet stimulation to detect a true voluntary activation deficit has been questioned (22, 40), the main conclusion of our study that aging does not affect voluntary activation of the ankle dorsiflexors remains valid.

The level of coactivation during a MVC is usually used to estimate the intensity of the neural drive to the antagonist muscles (38). In our study, the level of coactivation, quantified by the Sol aEMG-to-TA aEMGTA ratio, was similar between elderly and young subjects (~10%), regardless of the type or velocity of contractions. This observation suggests that there was no age-related difference in coactivation for the ankle dorsiflexor muscles. Similar results have been reported for upper and lower leg muscles during Iso and Con contractions (30, 32, 36, 41). In contrast, other studies have observed an age-related change in the level of coactivation, which was different between muscle groups and contraction types. For example, Burnett et al. (6) observed an increased antagonist activity during Con and Ecc contractions, but not during Iso contractions, in the first dorsal interosseous muscle. Macaluso and coworkers (29) reported increased coactivation during maximal knee extensions but not during knee flexions. Because the net torque at a joint is equal to the torque difference of agonist and antagonist muscles (7), greater coactivation could reduce the performance of agonist muscles, both through the opposing mechanical action of the antagonist muscles and also by reciprocal inhibition (9). The absence of age-related changes in voluntary agonist activation is consistent with a comparable level of coactivation in elderly and young adults. It should be mentioned, however, that a small increase (5%) in coactivation with aging was not correlated with the reduction of normalized force in elbow flexors and extensors (24). This finding indicates that modest fluctuations in coactivation do not have a large effect on the torque produced by the agonist muscles.

Our experimental results confirm the previously reported slowing of muscle contractile kinetics with aging (4, 25, 37, 43, 46). Such adaptations are usually attributed to a slowing of the contractile properties of both type I and type II muscle fibers (10) and to the greater atrophy of type II fibers compared with type I fibers (26). Among the underlying mechanisms, alterations in excitation-contraction coupling (19, 33) and the speed of cross-bridge cycling (17) have been suggested. The trend toward a slower relaxation time (RT1/2) and rate of torque relaxation in our study is consistent with possible alteration of Ca2+–related mechanisms and sarcoplasmic reticulum function (19, 33). Another change that could contribute to the slowing of the twitch time course with aging is increased tendon compliance. This was recently reported by Narici et al. (31) in the human gastrocnemius muscle. However, such adaptation should have also contributed to reduce the torque produced during the twitch (4). Because twitch torque was not significantly modified with aging, despite the ~20% decrease in maximal force-generating capacity of the muscle, our results suggest that the slowing of the muscle contractile kinetics cannot be mainly attributed to the increased tendon compliance. In contrast, the slowing of the contractile mechanisms should play a major role (10, 17, 25).

As discussed above, the smaller reduction in Ecc torque compared with Iso and Con contractions during aging cannot be explained by a difference in muscle activation or coactivation and, therefore, are likely related to alterations within the
musculotendon complex. The slowing of cross-bridge cycling (17, 25) observed with advanced age may help minimize the loss of force during Ecc contractions by increasing the force developed per cross bridge. Pousson et al. (36) have also suggested that the increase in muscle collagen (1) might enhance the number of attachments between tendon and sarcomeres that would contribute to an increase in passive torque during Ecc actions. Furthermore, an increased antagonist muscle-tendon and joint stiffness in elderly adults could have contributed to the reduction in net muscle torque to a greater extent in Con compared with Ecc contractions. This possibility cannot completely be ruled out, but its contribution should be of little importance because the movement imposed to the ankle joint was performed through an intermediate range of motion, and it has been reported that passive stiffness did not change for such limited range of motion with aging (32, 46).

Despite the uncertainty regarding the mechanisms, it appeared clearly that, although the relative Ecc torque was better preserved than Con contractions in both genders with aging, women showed a greater effect than men. Such observation, also reported by Hortobágyi et al. (18) and Lindle et al. (27), is consistent with a greater slowing of the muscle contractile properties in elderly women compared with men.

In conclusion, the results of the present study showed that the age-related force deficit is greater during Con and Iso contractions compared with Ecc contractions. The results further indicate that elderly adults of both genders remain able to voluntarily activate their ankle dorsiflexors as efficiently as young adults during the different contraction types and movement velocities. It is, therefore, concluded that the force deficit with aging does not appear to result from impaired neural drive to the muscle, but rather from muscular alterations.

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