Age-related decline in rate of torque development is accompanied by lower maximal motor unit discharge frequency during fast contractions
Malgorzata Klass, Stéphane Baudry and Jacques Duchateau


You might find this additional info useful...

This article cites 43 articles, 29 of which can be accessed free at:
http://jap.physiology.org/content/104/3/739.full.html#ref-list-1

This article has been cited by 15 other HighWire hosted articles, the first 5 are:

Discharge properties of motor units during steady isometric contractions performed with the dorsiflexor muscles
Mark Jesunathadas, Malgorzata Klass, Jacques Duchateau and Roger M. Enoka
[Abstract] [Full Text] [PDF]

Neuromuscular Contributions to Age-Related Weakness
David J. Clark and Roger A. Fielding
[Abstract] [Full Text] [PDF]

Dynapenia and Aging: An Update
Todd M. Manini and Brian C. Clark
[Abstract] [Full Text] [PDF]

Dynapenia and Aging: An Update
Todd M. Manini and Brian C. Clark
[Abstract] [Full Text] [PDF]

Neuromuscular Contributions to Age-Related Weakness
David J. Clark and Roger A. Fielding
[Abstract] [Full Text] [PDF]

Updated information and services including high resolution figures, can be found at:
http://jap.physiology.org/content/104/3/739.full.html

Additional material and information about Journal of Applied Physiology can be found at:
http://www.the-aps.org/publications/jappl

This information is current as of June 2, 2012.
Age-related decline in rate of torque development is accompanied by lower maximal motor unit discharge frequency during fast contractions

Malgorzata Klass, Stéphane Baudry, and Jacques Duchateau

Laboratory of Applied Biology, Université Libre de Bruxelles, Brussels, Belgium

Submitted 22 May 2007; accepted in final form 30 December 2007

Klass M, Baudry S, Duchateau J. Age-related decline in rate of torque development is accompanied by lower maximal motor unit discharge frequency during fast contractions. J Appl Physiol 104: 739–746, 2008. First published January 3, 2008; doi:10.1152/japplphysiol.00550.2007.—The aim of this study was to investigate the association between the rate of torque development and maximal motor unit discharge frequency in young and elderly adults as they performed rapid submaximal contractions with the ankle dorsiflexors. Recordings were obtained of the torque exerted by the dorsiflexors during the isometric contractions and the surface and intramuscular electromyograms (EMGs) from the tibialis anterior. The maximal rate of torque development and integrated EMG (percentage of total EMG burst) at peak rate of torque development during fast contractions were lower in elderly than young adults by 48% (P < 0.05) and 16.5% (P < 0.05), respectively. The young adults, but not the elderly adults, exhibited a positive association (r² = 0.33; P < 0.01) between the integrated EMG computed up to the peak rate of torque development and the maximal rate of torque development achieved during the fast contractions. These age-related changes during fast voluntary contractions were accompanied by a decline (P < 0.001) in motor unit discharge frequency (19, 28, and 34% for first 3 interspike intervals, respectively) and in the percentage of units (45%; P < 0.05) that exhibited double discharges (doublets) when a train of three electrical stimuli at 100 Hz is less in elderly adults compared with young adults (5).

The change in the intrinsic properties of the muscle may also be accompanied by impaired voluntary activation that reduces the rate of torque development during fast voluntary contractions. The force produced by a muscle during a voluntary contraction depends on the number of recruited motor units and the rate at which the active units discharge action potentials. The relative contribution of these two mechanisms to the increase in force varies as a function of contraction speed, such as the earlier activation of motor units as contraction speed increases (14, 15). This lowering of the force threshold at which a motor units is recruited is likely due to a more synchronous input to the motoneuron pool that reduces the time to reach activation threshold (2, 42). In tibialis anterior, for example, approximately three times as many motor units are recruited to produce a given peak force during a rapid contraction compared with a slow ramp contraction (14). When this occurs, force gradation above one-third of maximum depends much more on rate coding (14), and, in young adults, it reaches discharge frequencies around 100 Hz (6, 14, 19, 43, 44) that exceed those recorded (30–60 Hz) during slow contractions (14, 23, 32).

Although not observed in all studies (see Ref. 38), it has been shown that maximal and submaximal discharge frequencies are reduced in elderly adults during sustained and slow ramp contractions above 50% maximal voluntary contraction (MVC) (3, 12, 22, 23, 39). Because of the concurrent slowing of the contractile properties of the muscle, however, the decrease in discharge rate does not seem to limit the maximal force developed during an MVC (12). Nonetheless, motor units do not achieve maximal discharge frequencies during sustained and slow ramp contractions (6, 14, 42) because some mechanisms likely constrain discharge rate to a level that does not exceed the frequency required for sufficient tetanic fusion (7, 12, 23). In contrast, maximal discharge frequency can be reached at the onset of a voluntary contraction performed as fast as possible (see Refs. 14, 43) because the regulatory mechanisms have not had an opportunity to influence discharge rate. The high initial rates can also include interspike intervals of ~5 ms (doublet discharge; Ref. 19), which likely arise as a result of delayed depolarization (9) and reflect the intrinsic properties of the motoneuron (11). Because the increase in the maximal rate of torque development during a fast contraction after a training program is accompanied by an increase in motor unit discharge rate and the number of doublet discharges (44), we hypothesized that some of the age-related reduction in the maximal rate of torque development could be due to the converse changes. Accordingly, we recorded the discharge of motor units in the tibialis anterior muscle during fast contractions as young and elderly adults produced a range of torques with the dorsiflexor muscles.

MATERIALS AND METHODS

Five young adults (mean ± SD: 20.2 ± 1.6 yr; range: 18–22 yr) and five elderly adults (75.6 ± 5.7; range: 71–84 yr) with equal costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
number of women (3) and men (2) in each group participated in the study. All subjects were familiarized with the experimental procedures during a first session, and they were tested thereafter in at least 2–3 different occasions for a total of 38 experimental sessions. Subjects were not engaged in any strenuous locomotor activity for at least 24 h before the experimental session. All subjects were healthy and without neuromuscular disorders at the time of participation in the investigation. Elderly subjects were living at home and walked daily without the use of an assistive device. The local Ethics Committee approved this study, and the subjects gave informed consent prior to participation in the investigation. All the experimental procedures were performed in accordance with the Declaration of Helsinki.

Experimental apparatus. The subject sat on a chair in a slightly inclined position during the experiment with the foot of the right leg strapped to a footplate. The plate was inclined at an angle of 45° to the reclined position during the experiment with the foot of the right leg. The knee and ankle were strapped to a footplate. The plate was inclined at an angle of 45° to the reclined position during the experiment with the foot of the right leg. The knee and ankle were strapped to a footplate. The plate was inclined at an angle of 45° to the reclined position during the experiment with the foot of the right leg.

Experimental procedure. Before single motor units were recorded, the torque exerted by the dorsiflexor and plantar flexor muscles during an MVC was determined. The subject was required to reach maximal torque in ~1-s and to maintain this level for ~3-s. Two to three MVCs were performed, each separated by 2–3 min of rest. At each recording site, motor units were first identified during slow isometric contractions performed at different torque levels. Once a motor unit action potential had been clearly identified, subjects performed two to three isometric ramp contractions at 10% MVC/cm up to the maximum force. Thereafter, they were asked to produce fast voluntary (isometric) contractions around three target torques: 25, 50, and 75% MVC. In a random order, subjects were requested to perform ~10 contractions around each of these torque levels but were not required to reach the torque target accurately. Throughout the experiment, subjects received visual feedback of the torque and an auditory signal that indicated the moment to perform the contraction. Each fast contraction was separated by at least 3–5 s, and 3–5 min of rest was allowed between motor unit recordings from different electrode locations.

The MVC torque was determined from the trial that yielded the largest value and the average rectified EMG (aEMG) amplitude was measured for a 1-s period during the plateau of the MVC. Each fast contraction was characterized by its peak torque, time to peak torque, and peak rate of torque development, measured from the first derivative of the torque signal (Fig. 1). The peak torque was identified when the derivative crossed zero. The aEMG amplitude of the total EMG burst of the tibialis anterior during the fast contractions was also measured and expressed as a percentage of the maximal aEMG amplitude during the MVC. The rate of EMG rise during the fast contraction was quantified by computing the integral of the rectified surface EMG (integrated EMG) from its onset: 1) to the first 25 and 50 ms, 2) to the time at which the peak rate of torque development was attained (~75 ms), and 3) to the end of the EMG burst. The EMG activity of the soleus (antagonist) during the different contractions was integrated during the same periods and quantified as the ratio between soleus and tibialis anterior aEMG of the EMG burst.

Motor unit discrimination was accomplished with a computerized, spike-sorting algorithm (Spoke 2, version 5, Cambridge Electronic Design). Single motor unit action potentials were identified on the basis of amplitude, duration, and waveform shape. During ramp and fast contractions, each motor unit was analyzed on a spike-by-spike basis, and only units that were clearly identified were included in the analysis. Motor unit recruitment threshold was measured during the isometric ramp contractions and expressed as a percentage of the MVC torque when the action potential of the selected unit first appeared in the EMG trace. Motor unit discharge frequency was measured at the onset of the fast contractions, and the duration of the first three interspike intervals was measured (43, 44). The analysis was limited to the first three interspike intervals because few motor units discharged more than four times, and the recording was not contaminated by movement artifact. Instantaneous discharge frequency was expressed as the reciprocal of the interval between two successive spikes of the same motor unit.

The peak torque and contraction time of the evoked contractions were measured from the mechanical response to the single electrical stimulus. The maximal rate of torque development was obtained from the first derivative of the torque signal.

Statistics. The mechanical and EMG data recorded during MVC and fast contractions in young and elderly subjects were compared by the Student’s t-test or the nonparametric Kolmogorov-Smirnov two-
RESULTS

The mean MVC torque produced during dorsiflexion was significantly greater (28%) in young compared with elderly adults (46.4 ± 9.8 vs. 33.2 ± 7.9 N·m; P < 0.05). In contrast, the corresponding aEMG activity of the tibialis anterior during the MVC did not differ significantly between the two groups (386 ± 144 vs. 419 ± 146 μV; P = 0.63).

Comparison of fast contractions in young and elderly adults. Regardless of the torque achieved, the contractile properties of the five fastest contractions for each subject and the corresponding EMG activities were compared between elderly and young subjects. Although the average absolute peak torque achieved during the fast contractions was greater in young adults than elderly adults (34.7 ± 7.1 vs. 25.2 ± 5.6 N·m; P < 0.05), there was no difference (P = 0.38) between the two groups when peak torques were expressed relative to the respective MVC torques (76.9 ± 11.4 vs. 71.6 ± 5.6% MVC). The average time to peak torque during the fast contractions was 26% longer (P < 0.01) in elderly adults (210 ± 24 vs. 166 ± 23 ms). As illustrated in Fig. 1, the slower contraction was accompanied by a 48% decrease in the absolute peak rate of torque development (228 ± 50 vs. 440 ± 114 N·m/s; P < 0.01) and by a 33% decrease in the relative peak rate of torque development (647 ± 49 vs. 962 ± 146% MVC/s; P < 0.01).

The peak rate of torque development was linearly related to the peak torque achieved during the fast contractions produced at different torque levels in both young and elderly groups (Fig. 2). The difference in the slope of the regression lines indicates that regardless of the torque achieved during the fast contraction, the peak rate of torque development was significantly (P < 0.01) lower in elderly adults, and the difference between groups was augmented with increased peak torque.

These mechanical impairments were not associated with significant changes in the total EMG burst during the fast contractions around each of 3 torque levels (25, 50, and 75% MVC) were performed with the ankle dorsiflexors in young and elderly adults. The 5 fastest contractions for each subject and the corresponding EMG activities were compared between elderly and young subjects. Although the average absolute peak torque achieved during the fast contractions was greater in young adults than elderly adults (34.7 ± 7.1 vs. 25.2 ± 5.6 N·m; P < 0.05), there was no difference (P = 0.38) between the two groups when peak torques were expressed relative to the respective MVC torques (76.9 ± 11.4 vs. 71.6 ± 5.6% MVC). The average time to peak torque during the fast contractions was 26% longer (P < 0.01) in elderly adults (210 ± 24 vs. 166 ± 23 ms). As illustrated in Fig. 1, the slower contraction was accompanied by a 48% decrease in the absolute peak rate of torque development (228 ± 50 vs. 440 ± 114 N·m/s; P < 0.01) and by a 33% decrease in the relative peak rate of torque development (647 ± 49 vs. 962 ± 146% MVC/s; P < 0.01).

The peak rate of torque development was linearly related to the peak torque achieved during the fast contractions produced at different torque levels in both young and elderly groups (Fig. 2). The difference in the slope of the regression lines indicates that regardless of the torque achieved during the fast contraction, the peak rate of torque development was significantly (P < 0.01) lower in elderly adults, and the difference between groups was augmented with increased peak torque.

These mechanical impairments were not associated with significant changes in the total EMG burst during the fast contractions around each of 3 torque levels (25, 50, and 75% MVC) were performed with the ankle dorsiflexors in young and elderly adults. The 5 fastest contractions for each subject and the corresponding EMG activities were compared between elderly and young subjects. Although the average absolute peak torque achieved during the fast contractions was greater in young adults than elderly adults (34.7 ± 7.1 vs. 25.2 ± 5.6 N·m; P < 0.05), there was no difference (P = 0.38) between the two groups when peak torques were expressed relative to the respective MVC torques (76.9 ± 11.4 vs. 71.6 ± 5.6% MVC). The average time to peak torque during the fast contractions was 26% longer (P < 0.01) in elderly adults (210 ± 24 vs. 166 ± 23 ms). As illustrated in Fig. 1, the slower contraction was accompanied by a 48% decrease in the absolute peak rate of torque development (228 ± 50 vs. 440 ± 114 N·m/s; P < 0.01) and by a 33% decrease in the relative peak rate of torque development (647 ± 49 vs. 962 ± 146% MVC/s; P < 0.01).
subjects during the fast contractions. Although the aEMG of the tibialis anterior represented a greater percentage of the maximal aEMG during an MVC in elderly adults (94.2 ± 11.9 vs. 75.5 ± 14.7%), the difference was not significant (P = 0.10). A comparable level of activation at the beginning of the fast contraction was also observed for both groups, because the integrated EMG during the first 25 and 50 ms comprised a similar percentage of the total EMG burst (Fig. 3A). In contrast, the EMG integral up to the time at which the peak rate of torque development occurred (78 ± 8 and 75 ± 12 ms in elderly and young adults, respectively) was greater (P < 0.05) for the young subjects (Fig. 3A). There was a positive linear association between the maximal rate of torque development and the EMG integral (percentage of the total EMG burst) up to the peak rate of torque development for the two groups of subjects combined (r² = 0.50, P < 0.001; Fig. 4) and for young subjects (r² = 0.33; P < 0.01) but not for elderly adults (r² = 0.06; P = 0.26).

Similar associations to those of the tibialis anterior were observed for the antagonist soleus muscle (Fig. 3B). The ratio between soleus and tibialis anterior aEMG activities were 0.08 ± 0.02 and 0.09 ± 0.03, respectively, in elderly and young subjects (P = 0.45), indicating that the coactivation of soleus did not differ significantly between the two groups of subjects during the fast contractions.

Motor unit activation pattern during fast contractions. A total of 248 motor units in the five young adults and 118 motor units in the five elderly adults were successfully discriminated during the fast contractions. The fewer motor units recorded in elderly adults is due to their reduced ability to meet performance criteria for the different tasks during the entire experimental session and to the age-related reduction in motor unit number in the tibialis anterior (30). The recruitment threshold of these units during ramp contractions ranged from 1 to 90.2% MVC (median: 26.3%; skewness: 0.641; kurtosis: −0.491) for young adults and from 0.4 to 64% MVC (median: 15.6%; skewness: 1.093; kurtosis: 0.781) for elderly adults. The two distributions differed significantly (P < 0.001).

The distribution of the first three interspike intervals for the elderly adults was shifted to lower frequencies compared with young adults. When doublets of <5 ms were not considered, the median value for motor units discharge frequency during the first three intervals was 71.9, 56.3, and 53.9 Hz, respectively, for the young, and it was 58.5, 40.4, and 35.5 Hz, respectively, for the elderly. Discharge frequencies were significantly lower (P < 0.001) for the second interspike interval compared with the first (Fig. 5) for both groups of subjects. However, discharge frequencies were significantly lower (P < 0.05) for the third interspike interval compared with the second only for the elderly adults. The age-related decline in discharge frequency was statistically significant (P < 0.001; Kolmogorov-Smirnov 2-sample test) for the three interspike intervals and tended to be larger for the third (34%) than for the second (28%) and first (19%) interspike intervals. Figure 6 illustrates the typical behavior of single motor units of similar recruitment threshold during a fast contraction performed by one subject from each group. In addition to a lower maximal discharge frequency for each interspike interval in the elderly adults, they also exhibited a greater decline in the instantaneous discharge frequency during the first four motor unit discharges of the fast contraction.

A few of the motor units discharged with doublets (interspike interval <5 ms) at the onset of the EMG burst in both groups of subjects. The percentage of motor units that dis-

---

**Fig. 3.** A: EMG activity of the tibialis anterior at the onset of fast contractions with the ankle dorsiflexors by young and elderly adults. The EMG activity has been integrated from its onset to the first 25 and 50 ms, and to the time at which the peak rate of torque development (peak RTD) was attained. All values (means ± SE) are expressed as percentage of the total integrated EMG burst. B: EMG activity of soleus at the onset of fast contractions of the ankle dorsiflexors integrated for the same periods of time as for agonist activation and expressed as percentage of the total integrated EMG activity during soleus activation. *Significant difference between young and elderly adults, P < 0.05.
charged such doublets during the first three interspike intervals was significantly greater \((P < 0.05)\) for young (8.4%) than for elderly (4.6%) adults. The doublets were only observed during the first and second interspike intervals in both groups and appeared more frequently during the first (5.7 and 3.8%) compared with the second (2.7 and 0.8%) interval.

**Muscle mechanical properties.** In three subjects of both groups, the mechanical properties of the dorsiflexor muscles were tested by a single electrical stimulation. The elderly adults had a reduced twitch amplitude \((1.84 \pm 1.12 \text{ N} \cdot \text{m} \text{ vs. } 2.34 \pm 1.16 \text{ N} \cdot \text{m})\), a 23% longer contraction time \((97.5 \pm 10.9 \text{ vs. } 74.9 \pm 10.6 \text{ ms})\), and a 41% decrease in the maximal rate of torque development \((34.3 \pm 20.3 \text{ vs. } 57.7 \pm 21.1 \text{ N} \cdot \text{m/s})\). The maximal rate of torque development during the fast voluntary contractions in these subjects was reduced by 51% in elderly adults \((249 \pm 62 \text{ N} \cdot \text{m/s})\) compared with the young adults \((511 \pm 34 \text{ N} \cdot \text{m/s})\).

**DISCUSSION**

The main finding of this study was that older adults exhibited a slower maximal rate of torque development during a fast contraction of the ankle dorsiflexor muscles that was accompanied by a reduction in motor unit discharge frequency and number of doublet discharges. The decrease in motor unit discharge frequency with aging tended to be more pronounced for the second and third interspike intervals than for the first interval. These results indicate that healthy aging involves neural impairments that likely limit the maximal capacity of motoneurons to discharge at very high rates.

**Age-related change in the rate of torque development.** The maximal rate of torque development during a fast contraction was significantly lower, and the time to peak torque was longer, in elderly adults compared with young adults. The impairment in the rate of torque development increased with the amplitude of the peak torque achieved during the submaximal contractions (see Fig. 2). Aging affected the maximal rate of torque development to a greater extent than the maximal torque produced during an MVC \((48 \text{ vs. } 28\%)\). This observation is consistent with previous studies performed during fast voluntary isometric contractions \((4, 21)\).

The reduced maximal rate of torque development of elderly adults can be explained, in part, by a slowing of the intrinsic contractile properties of the muscle. This decline in performance has been shown for electrically induced tetanic \((50–100 \text{ Hz})\) contractions \((25, 38)\) and confirmed by our previous studies on the same muscle group \((5, 26)\). In the present study,
the contractile kinetics of the dorsiflexors were studied in three subjects of both groups and the data indicate, in agreement with previous studies (5, 25, 26, 38), an age-related slowing of the muscle twitch. This impairment may be attributed to a slowing of type I and type II muscle fibers (13), greater atrophy of type II fibers (28), and increased tendon compliance (34).

Evidence for neural impairments. Although there is only a moderate relation for the rate of torque development between a fast voluntary contraction and an electrically evoked twitch (1), the slightly greater slowing (~10%) observed during the fast voluntary contractions suggests that a decreased neural activation partly contributed to reduce the rate at which force is produced in aged subjects. This conclusion is also supported by the age-related changes in EMG and discharge pattern of single motor units at the onset of fast voluntary contractions.

As shown by the intramuscular EMG recordings, the average instantaneous discharge frequency of single motor units decreased significantly during the first three interspike intervals. The instantaneous discharge frequency of these successive interspike intervals during a fast contraction was not uniformly reduced in the elderly adults; it declined by 19, 28, and 34% for the first three interspike intervals, respectively. The progressive reduction indicates that, in addition to a decrease in the maximal discharge rate at the onset of a fast contraction, the decline in motor units discharge rate during the successive discharges was greater for elderly than young adults. In addition, aging was associated with a reduced percentage of motor units that discharged with doublets, as was also observed during ramp contractions performed at different speeds (11). The reduced number of doublet discharges in elderly adults (8.4% vs. 4.6%), in combination with the decrease in motor unit discharge frequency, likely explain part of the age-related slowing of fast contractions. It has been shown, for example, that the rate of torque development is related to the maximal discharge rate of motor units (2, 19, 42, 43) and their ability to keep such high rate during the successive discharges at the onset of the activation phase (44).

Comparison of the absolute surface EMG activity between elderly and young adults is risky because of differences in the thickness of the subcutaneous tissues and the distribution of motor unit territories in the muscle. Furthermore, the greater size and longer duration of motor unit action potentials in elderly adults (29) can influence the nonlinear summation of motor unit action potentials in the surface EMG signal (24) and thereby limit the comparison of the data with young adults. To partially control for these confounding factors, we normalized the aEMG during the fast contraction to each individual aEMG during the MVC. Although slightly greater in elderly subjects, the normalized aEMG activity during the fast contraction did not differ significantly between groups. However, there was a positive association between the EMG integral up to peak rate of torque development (% of the total EMG burst) and the maximal rate of torque development for the young adults but not the elderly adults.

Analysis of the normalized EMG integral during a fast contraction indicated some differences in the pattern of muscle activation between young and elderly adults. Whereas the two groups displayed a similar relative activation during the first 50 ms of the fast contractions, young subjects exhibited a greater relative activation at the peak rate of torque development. Consistent with the motor unit data, this observation indicates that elderly adults cannot sustain the activation as well as young adults. There was some discordance, however, between the time course of change in surface EMG and the motor unit data. Because motor unit discharge rate was already lower during the first two interspike intervals in the elderly adults, the normalized EMG should have also been reduced in the first 50 ms. Such divergence between surface and intramuscular EMG has already been reported (33), indicating that changes in motor unit discharge rate are not always detected by surface EMG or are not linearly related with surface EMG (42). Furthermore, the similar amount of EMG activity generated by the elderly adults may indicate the recording or the recruitment of more motor units, which would reduce the likelihood of detecting modest changes in motor unit frequency in the interference signal. Despite this discrepancy, the results suggest a change in the activation pattern of motor units between the two groups of subjects.

Possible mechanisms underlying neural impairments. Although not observed consistently (24, 41), it is sometimes

Fig. 6. Behavior of single motor units from the tibialis anterior of young (A) and elderly (B) adults during a fast isometric contraction. Both the recruitment threshold (2–3% MVC) and the peak torque (~50% of MVC) were similar for the 2 motor units. The traces correspond to the torque (a) and intramuscular EMG plotted at slow (b) and fast (c) time bases. The maximal rate of torque development was lower in the elderly subject (480% MVC/s) compared with the young subject (784% MVC/s). The EMG traces illustrate the typical discharge pattern of a single motor unit. The instantaneous discharge rate during the first 3 interspike intervals were 78, 71, and 61 Hz, respectively, for the young adult; and they were 63, 40, and 34 Hz, respectively, for the elderly adult. The asterisks indicate the discharge of the same motor unit and their traces are superimposed with an extended display (d).
reported that the level of coactivation during an MVC is increased with aging (27). It has been proposed that this adaptation might reduce the performance of agonist muscles during the task, both through the opposing mechanical action of the antagonist muscles and by reciprocal inhibition. However, the absence of age-related changes in coactivation of the plantar flexor muscles, either during MVCs (26, 41) or fast contractions (present study) with the ankle dorsiflexors muscles, negates a role for reciprocal inhibitory mechanisms in reducing the maximal motor unit discharge frequency. Consequently, other physiological mechanisms must account for this lower rate of muscle activation.

Potential mechanisms that may explain the age-related decrease in the rate of torque development during fast contractions should be mainly located along the corticospinal pathway. A change in the excitability of the corticospinal tract by using transcranial magnetic stimulation has been reported in aged subjects. Although there is no effect in the dominant hand (40), it appears that the motor-evoked potential is reduced (16, 40) and that higher stimulation intensities are required to achieve the same maximal output of the motor cortex in elderly adults (37). However, the age-related decline in activation during voluntary contractions can be due to decreases in the descending drive and the excitability of the motoneuron pool. Because doublet discharges at short interspike intervals (<5 ms) seem to depend on the time course of the delayed depolarization of motoneurons (9, 19) and a greater descending drive is required for doublet discharges in elderly adults (11), it is possible that motoneuron excitability declines with aging. This proposition is consistent with a recent paper showing an age-related increase in the duration of motoneuron afterhyperpolarization in the human biceps brachii (36).

Although a suboptimal cortical drive cannot be discounted, the progressive decline in the instantaneous motor unit discharge frequency during the successive discharges at the onset of a fast contraction is consistent with the hypothesis of an age-related alteration in the intrinsic properties of motoneurons (17, 31). This early decline in motoneuron discharge rate when the cell is activated by constant-current injection, which is known as spike frequency adaptation (8, 20), could be modified by aging as it seems to be the case with chronic changes in physical activity levels (18). Another possible mechanism that may contribute to lower maximal discharge frequency and incidence of doublet discharge during fast contractions in elderly adults is recurrent inhibition. The involvement of this pathway is unlikely, however, because it has been shown that elderly adults have similar, or even lower, levels of recurrent inhibition than young adults (10). Together, these observations suggest that changes in the properties of the motoneurons are probably the main factor responsible for the age-related decline in maximal discharge frequency during fast contraction.

In conclusion, the results of this study indicate that the age-related reduction in the maximal rate of torque development of a fast contraction is not only due to a slowing of the contractile properties of the muscle but also to a decrease in the maximal discharge frequency of motor units. Although reduced motor unit discharge frequency does not seem to impair the dorsiflexion torque produced during an MVC (12), it likely limits the maximal rate of torque development.

ACKNOWLEDGMENTS

The authors are particularly grateful to Dr. C. Mottram and Prof. R. M. Enoka for helpful comments on a previous version of this manuscript.

GRANTS

This study was supported by a grant of the European Commission (Framework Program V; Better-Ageing project, QLK6-CT-2001-00323) and the Fonds National de la Recherche Scientifique of Belgium.

REFERENCES


