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Differences in the force/endurance relationship between young and older men

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Abstract The aim of the present study was to ascertain if in six young (23–35 years) and in six older (70–72 years) healthy men matched for comparable absolute and specific maximal force of the dominant elbow flexors, differences in isometric endurance, myoelectrical fatigability, and shortening velocity are still recognizable. To assess the specific force, the muscle cross sectional area (CSA) was determined from magnetic resonance imaging (MRI) scans. The performance of the elbow flexors was studied by assessing the isometric endurance times (ET) at different percentages of maximal isometric contraction (MVC), the average muscle fibre conduction velocity of action potentials (CV), and the median frequency (MDF) of the surface electromyogram (sEMG) of the biceps brachii. Finally, the torque-velocity curve was assessed by means of maximal isokinetic contractions at six fixed angular velocities. All data were expressed as the mean (SD). The results showed that: (1) the ET was longer in the older subjects at the highest levels of isometric contraction, independently from the absolute force; (2) the modifications of muscle fibre CV during isometric effort progressed less rapidly in the older than the younger groups, as did those of MDF; and (3) at the same angular velocity, the older subjects exerted less absolute force than the younger subjects. These results suggest an impairment of the neuromuscular system of older men, which is less powerful and less fatigable than that of young men.

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Introduction

Aging is associated with a progressive decrease in muscular strength and power. Age-induced strength decay has been attributed to the impairment of neural control and/or peripheral factors such as change in muscle fibre composition and reduction of active tissue (Frontera et al. 1991; Kent-Braun and Ng 1999). In assessing the effect of age on muscle strength, the specific force, i.e., the force per unit of muscle area, is one of the most relevant parameters since it can reveal if loss of strength is due to a loss of active tissue or to an intrinsic impairment of the neuromuscular properties. Unfortunately, the results of studies on specific force are conflicting (Kent-Braun and Ng 1999). While a number of investigators have reported a decreased specific force (Davies et al. 1986; Phillips et al. 1993; Vandervoort and McComas 1986) other authors did not find any significant differences in specific force between young and old adults (Hakkinen and Hakkinen 1991; Hakkinen et al. 2001; Kent-Braun and Ng 1999; Overend et al. 1992).

The capability to maintain a given level of force over time, i.e., the capability to endure a specific motor task, is another important determinant of muscle performance. Fatigue has been defined as "any exercise-induced reduction in the ability of a muscle to generate force or power; it has peripheral and central causes" (Gandevia 2001). Focusing on static exercise, older individuals demonstrated more resistance to isometric fatigue than young adults at the same relative force output, a process which is referred to as the "fatigueparadox" (Merletti et al. 1992, 2002; Narici et al. 1991). However, once again the results of research in this field are controversial. Some authors have found lower fatigability in older compared to younger individuals during voluntary contractions (Merletti et al. 1992; Narici et al. 1991), others failed to find any difference in muscle endurance (Larsson and Karlsson 1978; Porter et al. 1995), while others reported a greater fatigability in older subjects in response to electrically elicited contractions (Davies et al. 1986; Lennmarken et al. 1985).

An indirect assessment of muscle fatigability can be obtained by surface electromyography (sEMG); a decline in median frequency (MDF) of the sEMG power spectrum and a decline in muscle fibre conduction velocity (CV) have been considered as early signs of muscle fatigue. In accordance with the fatigue paradox, the rate of decrease of the CV and the MDF is lower in older individuals (Merletti et al. 1992, 2002).

In many of the above-mentioned studies, differences in power and endurance could have been influenced by difference in absolute force, younger individuals being on average stronger than older individuals. The greater velocity and power of the former could be exclusively due to this fact. For example, if the force-velocity curve of older subjects is below that of younger subjects, at any given value of force the older individuals will show a reduced velocity of movement than the younger subjects. Moreover, if the maximum (isometric) force was the same in older and younger individuals, the difference in velocity at a given value of submaximal force can only result from a slowing of the muscle contractile properties in older individuals.

The aim of the present study was to verify which of the two working hypothesis outlined above holds. Thus (1) the absolute and specific force, (2) the isometric endurance, (3) the average muscle conduction velocity of action potentials, (4) the frequency power spectrum of the sEMG, and (5) the force/velocity relationship during dynamic contractions were studied in a transversal comparison between older and younger subjects. The elbow flexors were considered for this research. Two main constraints were carefully observed in the present study: first, the relevant parameters were all determined in the same subject, and second, the subjects were selected so that the older and younger individuals were comparable for their absolute maximal isometric force. In addition, the muscle cross sectional area (CSA) was determined on MRI scans and was used to normalize the MVC (specific force).

Methods

Subjects

After signing an informed written consent, approved by the local ethic committee, six young men [mean age 28.3 (4.8) years, range 23–35 years; stature 1.77 (0.04) m; body mass 69.6 (7.3) kg] and six older men [mean age 71.3 (0.81) years, range 70–72 years; stature 1.72 (0.04) m; body mass 74.6 (8.2) kg] volunteered for this study. As proposed by Greig and colleagues (Greig et al. 1994), participants were selected according to exclusion

criteria to define "medically stable" older subjects for exercise studies. All individuals reported a moderate level of physical activity but they were not involved in any kind of systematic training.

General procedures

Torque, force, angular velocity and sEMG were collected during isometric and dynamic contractions using a dynamometer (Kin Com, Chattanooga, Tenn., USA). The subject's positioning was assessed individually. For the the isometric tests, the elbow angle was fixed at 90° with the upper arm parallel to the trunk and the forearm in a neutral position (halfway between pronation and supination). During isokinetic contractions, subjects were instructed to exert maximal effort over the whole range of motion. The force trace was always displayed on a PC screen to provide participants with visual feedback.

After abrading and cleaning the skin with ethyl alcohol, a 16-silver bar electrode (10×1 mm; interelectrode distance 10 mm) linear array (LISiN, Turin, Italy) was placed over the longitudinal axis of the biceps brachii. A ground electrode was placed around the wrist. The sEMG signal was detected in a single differential mode using the configuration described by Farina et al. (2000). Briefly, four consecutive electrodes of the 16, corresponding to three single differential signals (a triplet of single differential signals), were selected for EMG parameter estimation. The triplet was selected as being the one showing the highest correlation coefficients between the two double differential sEMG signals. These double differentials were computed off-line and used for the calculation of the CV as described more in depth in the following paragraphs.

All signals were amplified (\times 1,000), band-pass filtered (10–450 Hz; LISiN EMG 16, Turin, Italy), A/D sampled at 2,048 points per second at 12-bit resolution (DAQ card AI-16XE-50, National Instruments, Tex., USA) and stored on the computer disk.

MRI

Before the experimental sessions, serial images in the axial plane were acquired by MRI using a 20-cm diameter extremity coil (CP Flex Coil, Siemens Medical, Erlangen, Germany) in a 1.5 T whole body magnet and 64 MHz scanner (Siemens Vision System, Siemens Medical). Subjects were supine with the right elbow extended and adjacent to the trunk and the forearm in a neutral position. A soft pad was placed under the arm so it rested parallel to the gantry and the elbow extensors were not compressed. Using the software, a grid of 20–25 slices (according to the muscle length) was centred on a coronal scout image so the slices were perpendicular to the arm. In order to differentiate muscle, fat and connective tissue several parameters were selected: a repetition time of 1,000 ms, an echo time of 14 ms, a

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single acquisition, a 256×160 matrix, a 20×20 cm field of view, and a slice thickness of 7 mm. The same investigator analysed all of the images. The cross sectional area of the muscle, the humerus and the non-contractile tissue were determined for each image of the arm by manual tracing. The software package then displayed an intensity histogram. Everything in the regions above a selected intensity threshold (Kent-Braun et al. 2000) was considered non-contractile tissue and was subtracted from the muscle cross sectional area (CSA). For each subject, the image with the greatest CSA was selected to calculate the mean CSA of the two groups of subjects.

Experimental protocol

After a preliminary session to familiarize the participants with the experimental procedures, each individual participated in four experimental sessions on 4 different days. In each experimental session, the MVC was assessed as detailed below.

MVC task

After a practice session and warm-up trial at submaximal intensity, participants were required to rapidly increase the force exerted by the elbow flexors to a maximum. A target line was set on the computer screen at a value 20% higher than the best MVC, with the exception of the first trial. Subjects followed their performance on the computer screen and were verbally encouraged to achieve a maximum in an attempt to exceed the target force, and to maintain it for at least 2-3 s before relaxing. A minimum of three maximal attempts were performed, separated by 3 min to recover from fatigue, and the best performance was chosen for further analysis. Subjects were asked to make further attempts if the MVC of their last trial exceeded that of previous trials by at least 5%, as suggested by Baratta and colleagues (Baratta et al. 1998).

Isometric endurance task

Endurance tests at 30% or 50% or 80%MVC were performed on different days. The order of the trials was randomized. A horizontal target band was displayed on a PC monitor. Participants were requested to match the target and to hold the force as long as possible (until voluntary exhaustion). The end of the exercise was anticipated if the torque value dropped more than 10% below the target for 3 s. Trials were also interrupted if participants reported any pain or discomfort.

Dynamic task

The torque-velocity curve was assessed for each subject on a separate day. Angular velocity values were fixed at 15, 30, 60, 90, 120, $150^{\circ} \text{ s}^{-1}$ and the subjects were

requested to flex the elbow joint as fast as possible. The range of motion was 80° (from 50° to 130° being 0° the full extension). The maximal torque was assessed for each angular velocity value.

Data analysis

All sEMG data collected during the isometric endurance task were analysed off-line (LabVIEW 6.0.2 software, National Instruments, USA). The sEMG variables of interest were the MDF, and the CV of the motor unit action potentials. All variables were computed during the whole duration of the contraction starting from the point at which, after reaching the target force, the force showed a steady trace to the chosen endpoint, according to the criteria described above. Care was taken to avoid the transient phases. The CV was estimated according to Merletti and Lo Conte (1995), from the two double differentials of a triplet of adjacent signals using the EMG cross-correlation (CC) function which assumes that the time delay between two similar signals is the amount of time shift that must be applied to one signal to minimize the mean square error with the other and to maximizes the CC between the two signals (Naeije and Zorn 1983). Estimates of CV were accepted only if the CC values were higher than 0.8. The MDF was computed from the central single differential signal of the selected triplet over non-overlapped adjacent epochs of 500 ms.

A linear regression was applied to the scattered MDF and CV data. The rate of change of the sEMG variables $(\%s^{-1})$ was defined as the percentage ratio between the slopes of these regression lines and their initial values at t_0 . The value at t_0 was calculated as the mean of the first 3 s (Sbriccoli et al. 2003). In this manuscript the results of this ratio will be referred to as "normalized slopes" and reported in absolute values. Thus, they appear as positive values while in fact they are negative since both MDF and CV decrease over time.

The following force parameters were analysed for the MVC task: the maximum value of force (MVC), and the ratio between the MVC and CSA (specific force). The endurance time (ET) of each contraction was also recorded following the criteria used for the sEMG analysis. During the dynamic task, values of peak torque were used to obtain torque-velocity relationships. Peak torque was preferred to isoangular torque for the reasons extensively discussed by Ferri and colleagues (Ferri et al. 2003).

Statistical analysis

Regression lines for individual data sets of ET versus %MVC, torque versus angular velocity and CV slope versus ET were computed using the least squares method. A univariate analysis of variance [between factor: age (young vs. older); within factors: intensity of

contraction (30% vs. 50% vs. 80%)] was used to compare the dependent variables (ET, the normalized slopes of MDF, and CV). T -tests with the Bonferroni correction were implemented when appropriate. Data are expressed as means (SD) in the text, tables and figures. Statistical significance was accepted if the *P* value was < 0.05.

Results

MVC-CSA

The CSA was roughly related to the body mass both in the young and older subjects. Mean values of CSA are shown in Table 1. No relevant differences were observed between the two subject groups for their intra-muscular connective and fat tissue areas (P = 0.08). The absolute MVC values are shown in Table 1. While the MVC was slightly different in the older group with respect to the younger subjects, this difference was reduced when the MVC values were normalized to the body mass index (BMI) and to the CSA. None of the differences between the younger and older subjects were significant.

ET-torque

As shown in Table 2, the ET was significantly longer in the older group compared to the younger group at 50% MVC (P < 0.01) and 80% MVC (P < 0.05). At 30% MVC the ET was also longer for the older subjects, although this difference did not reach statistical significance probably due to the high standard deviation associated with the mean values.

The relationship between torque and ET for the old and young groups is shown in Fig. 1. Exponential relationships for the younger and older groups have the form:

 $ET_{Y} = 188 - 163.1 \ln \% MVC$ (1)

and

Table 1

 $ET_{O} = 206 - 153.3 \ln\% MVC$ (2)

Torque/velocity relationship

The results of the torque versus angular velocity measurements are shown in Fig. 2. The data for both the young and older groups were normalized to the values obtained during the MVC test. The data for both groups were well fitted by an exponential curve. The equations have the form:

Torque%
$$_{\rm Y} = 100e^{-0.0029av}$$
 (3)

and

Torque%
$$_{\rm O} = 100e^{-0.0071av}$$
 (4)

where av is angular velocity.

As shown in Fig. 2, the normalized torque values were significantly higher (P < 0.05) in the young group than in the older group at the angular velocities of 60, 90, 120 and 150° s⁻¹. For the older group, the exponent av was more than double that of the younger group, and this made the two curves diverge at higher angular velocity values.

Conduction velocity

During the isometric contraction the CV decreased progressively at all %MVC values until the force break point was reached. Thereafter, the CV remained at a constant level while the force continuously decreased. This was observed in all subjects at all force levels. A typical example obtained during an endurance test (80%MVC) is shown in Fig. 3 for younger and older subjects. The initial CV values showed no difference between the older and the younger subjects at all force levels. Figure 4 shows the average values of the normalized CV slopes for the old and young groups at 30%, 50% and 80%MVC. The CV slope increased as a function of force in both groups. The normalized CV slope increased significantly when passing from 30% MVC to 50% MVC (*P* < 0.05), and from 50% MVC to 80% MVC in both groups (P < 0.05). In spite of the similar behaviour of the CV slopes for both groups at 30% and 50% MVC, at 80% MVC a few differences were observed between the two groups. Firstly, it is notable that the increase of the normalized CV slope during the shift from 50% MVC to 80% MVC was greater in the vounger group (from 0.21 to 0.89) compared to the older group (from 0.14 to 0.54). Secondly, the normalized CV slope at 80%MVC obtained for the young group was significantly higher than that observed in the older group (0.89 vs. 0.54, P < 0.05), possibly indicating a more pronounced fatigability in the young group at the highest force level.

Table 1 Mean values of maximal voluntary contraction (<i>MVC</i>) and cross sectional area		MVC (N)		CSA (cm ²)		$\frac{\text{MVC BMI}^{-1}}{(\text{N.m}^2.\text{kg}^{-1})}$		MVC CSA ⁻¹ (N.cm ⁻²)	
(CSA) for the young and old groups. The MVC values		Mean	SD	Mean	SD	Mean	SD	Mean	SD
normalized to either body mass index (<i>BMI</i>) or CSA are also given	Young Old <i>P</i> value	559 639 NS	97 155	17.5 18.4 NS	1.0 3.6	25.8 25.7 NS	6 5.34	32 34.7 NS	6.4 7.4

Table 2 Endurance times (*ET*)at different percentages of MVCin the young and old groups

	ET (s) at 30%MVC		ET (s) at 50%	% MVC	ET (s) at 80% MVC		
	Mean	SD	Mean	SD	Mean	SD	
Young Old <i>P</i> value	193 202.3 NS	19.7 41.3	62.2 108 <i>P</i> < 0.01	13.6 32.1	17.2 31.5 <i>P</i> < 0.05	6.5 13.3	



Fig. 1 Endurance time versus force in the younger (*black bars*) and older (*grey bars*) groups. Force is expressed as a percentage of the maximal voluntary force (MVC). Data are reported as mean values (SD). Best fitting curves were computed on individual data points. $r^2_{\rm Y} = 0.93$, $r^2_{\rm O} = 0.82$. The data for older group is represented by a *solid line*, that of the younger group by a *dashed line*. *: P < 0.05

MDF

Similarly to the CV, the MDF declined steadily as long as the required force level was maintained. After the



Fig. 2 Torque versus angular velocity in the young (*black symbols*) and old (*grey symbols*) groups. Torque was normalized to the maximum torque obtained during the MVC test. Best fitting curves were computed on individual data points. $r^2_{\rm Y} = 0.68$, $r^2_{\rm O} = 0.80$. Data enclosed in *frame* are different (P < 0.05) between the younger and older groups at any angular velocity considered

force breakpoint, the normalized MDF slope levelled and this was observed in all subjects (see Fig. 3 for an example in young and old subjects). The normalized MDF slope was force-dependent as above described for the normalized CV slope (see Fig. 5). For the younger group, the normalized MDF slope increased significantly across all force levels (P < 0.05), whilst in the older group this difference was significant only between 50% and 80% MVC (P < 0.05). No difference was found in the initial MDF values between the groups. The normalized MDF slope obtained at 50% MVC were significantly greater (P < 0.05) in the younger group [0.37 (0.14)] compared to the older group [0.19 (0.07)]. The same result was obtained at 80% MVC, whereas the



Fig. 3 Conduction velocity (*CV*, *closed squares*), median frequency (*MDF*, *open squares*) and force data (*triangles*) during the endurance test (80% MVC) in two subjects. *Y* Young, *O* older. Force is normalized and expressed as a percentage of the maximal voluntary force



Fig. 4 Conduction velocity (*CV*) slopes at different MVC levels in the younger (*black bars*) and older groups (*grey bars*). CV data are normalized to the initial CV value obtained during the MVC test. Data are reported as mean values (SD). *: P < 0.05

normalized MDF slopes were greater in the young group [1.46 (0.36)] than in the older group [0.73 (0.54)], and this difference was significant (P < 0.05). These results are in accordance with those reported for the normalized CV slope and further suggest an increased fatigability in the young group at intermediate (50%MVC) and higher force levels (80%MVC).

CV slope/ET

The relationship between the normalized CV slope and the ET in both groups is shown in Fig. 6. The equations describing the best fitting curves of the two groups were very similar:

$$\text{CVnorm slope}_{V} = 29.308 \text{ ET}^{-1.2642}$$
 (5)



Fig. 5 Median frequency (*MDF*) slopes at different MVC levels in the younger (*black bars*) and older groups (*grey bars*). Data are reported as mean values (SD). *: P < 0.05



Fig. 6 Conduction velocity (*CV*) slopes versus endurance time (*ET*) in the younger (*black symbols*) and older (*grey symbols*) groups at 30% MVC (*circles*), 50% MVC (*triangles*) and 80% MVC (*squares*). Best fitting curves were computed on individual data points. $r^2_{\rm Y} = 0.80$, $r^2_{\rm O} = 0.62$. Data are reported as mean values (SD). The data for the older group is represented by the *solid line*, that of the younger group by the *dashed line*

and

$$CVnorm \ slope_{O} = 31.649ET - 1.2458$$
 (6)

1 0 1 50

Discussion

As mentioned in the introduction, our subjects were selected on the basis of having a comparable absolute force level. This fact does not imply that their muscle CSA was also comparable, depending on the extent of the muscular areas of the two groups. The published results of studies on specific force are conflicting, since some authors have reported a lower specific force in older individuals (Davies et al. 1986; Phillips et al. 1993; Macaluso et al. 2002; Vandervoort and McComas 1986) and others have reported no differences between old and young subjects (Hakkinen and Hakkinen 1991; Hakkinen et al. 2001; Kent-Braun and Ng 1999; Overend et al. 1992). An increased amount of intramuscular non-contractile tissue has been found in older subjects (Klein et al. 2001). The majority of authors noted that the fat-free CSA was lower in older compared to younger subjects (Hakkinen and Hakkinen 1991; Hakkinen et al. 2001; Jubrias et al. 1997; Kent-Braun and Ng 1999; Overend et al. 1992; Young et al. 1984, 1985). Our results are in agreement with the findings of Kent-Braun and Ng (Kent-Braun and Ng 1999); the force per unit of muscular area of the elbow flexors is the same in both groups. Furthermore, a small percentage of non-contractile tissue, with respect to the total CSA, was observed in both the old and young groups, and this can be attributed to the good level of physical condition in the older group.

The torque versus angular velocity relationship was comparable in the older and younger groups at the lowest angular velocity. As the torque diminished the young subjects became progressively faster. Our data are consistent with those of Pousson and colleagues (Pousson et al. 2001) who demonstrated that angular velocity is a function of torque in both old and young individuals. The same authors have also demonstrated that the torque values achieved by older subjects were significantly lower than those achieved by younger individuals at higher angular velocity values. According to the working hypotheses presented in the Introduction, this suggests that the reduced speed of movement in the elbow flexors of the older group is due to a slowing of their muscle contractile properties.

Endurance

The observation that older subjects have a greater endurance time than younger individuals has been already documented in the literature (Bilodeau et al. 2001; Hicks and McCartney 1996). This fact has been attributed to a prevalence of type I muscle fibres versus type II fibres in older muscle (Faulkner and Brooks 1995; Monemi et al. 1999). Merletti and colleagues (Merletti et al. 2002) confirmed the lower fatigability of older individuals; these authors also attributed this difference to the coexistence of different proportions of type I and type II fibres in older and younger individuals. An exponential relationship between fatigability and force was obtained by Mannion and Dolan (1996) in the quadriceps muscle, and by Hagberg (1981) in the elbow flexors. Our results were consistent with those of Hagberg (1981). At 30% MVC both groups had a comparable endurance time, whereas at the highest %MVC levels (50% and 80%MVC) the endurance time became progressively longer in the older group. Our results are also in agreement with Henneman's size principle (Henneman et al. 1965). Following this principle, it may be speculated that at low levels of force demand, the motor units (MU) recruited (slow twitch, low threshold) are the same in both younger and older people. Differences between younger and older subjects become apparent as MU recruitment becomes complete. The fast twitch, rapidly fatiguing fibres, being the later recruited MUs, are those more affected by the ageing process. This is in good agreement with the hypothesis that in younger individuals fast twitch MUs are prevalent while in older individuals, type I fibres are predominant (D'Antona et al. 2003).

This interpretation is further reinforced by the relationship we showed between the ET and the CV. Endurance is inversely correlated with the CV slope, i.e., the ET shortens as the CV decay becomes steeper. The CV decay has been related to the percentage of fast MUs that became unable to participate in force production (Merletti et al. 2002; Sbriccoli et al. 2001). Thus it was hypothesized that the greater is the recruitment of powerful MUs, due to a high force demand, the faster are the MDF and CV decays (Merletti et al. 2002; Merletti and Roy 1996). The most fatigable muscle is probably the muscle with a greater percentage of type II MUs, which are the first to be fatigued. The MDF behaves coherently with this hypothesis.

A possible criticism of the above scenario can be raised from the fact that initial values of CV were the same at all %MVC in both subject groups. This is an issue still under debate; however, in this respect our results are coherent with experimental (Merletti et al. 2002; Merletti and Roy 1996) and simulation (Farina et al. 2002) studies. These authors showed that in general the recruitment of a large MU that either is deep or has a wide innervation zone may generate MU action potentials of long duration that can cause a decrease in MDF associated with an increase in torque and estimated CV. The recruitment of a very deep MU may increase torque with no significant change in either the MDF or CV estimates.

The major relevance of the present study is that data were collected in the same subjects within the same experimental design. In synthesis, our results demonstrated that the most relevant difference in muscular physiology between younger and older individuals is not the force but the velocity. This is the reason for the decreased power of older individuals, which is the agerelated muscular impairment with the greatest impact on the older person's daily activities. The fact that the maximum voluntary force, scaled for unit of muscular area (which approximately represents the sarcomere density) is the same in young and old individuals suggests that MU recruitment is the same in both groups. Thus, reduced MU recruitment is an unlikely candidate (De Serres and Enoka 1998) for the reduced power generation capacity of older muscles, while a prevalent role for a modification of muscle fibre type composition with aging should be involved. In fact, a central inability to recruit fast twitch MUs cannot be excluded, but in this case, we must admit that some MUs remain silent even during the most strenuous effort. At the same level of specific force, fewer MUs would be recruited in older subjects than in younger ones, meaning that older MUs ought to be stronger and this seems unlikely. Kamen et al (1995) showed that the MU discharge rate during maximal muscle activation was lower in older than in younger subjects. Our results do not conflict with this evidence: in our experiments the MVC was equal in both groups, and a tetanic contraction was achieved in both groups. If the discharge rate was lower in the older subjects, this means that slow twitch MUs (with a lower fusion frequency) predominate. In conclusion, the main results of the present study can be summarized as follows: the isometric endurance is longer in older than in younger individuals, independently of the absolute force of the subjects; the modifications of muscle fibre CV during isometric effort progress less rapidly in older than younger individuals, as do those of the MDF; the shortening velocity of the elbow flexors is lower in older than in younger individuals, thus the power of the older individual is reduced accordingly.

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