

Differential age-related changes in motor unit properties between elbow flexors and extensors

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Abstract

Aim: Healthy adult ageing of the human neuromuscular system is comprised of changes that include atrophy, weakness and slowed movements with reduced spinal motor neurone output expressed by lower motor unit discharge rates (MUDRs). The latter observation has been obtained mostly from hand and lower limb muscles. The purpose was to determine the extent to which elbow flexor and extensor contractile properties, and MUDRs in six old (83 ± 4 years) and six young (24 ± 1 years) men were affected by age, and whether any adaptations were similar for both muscle groups.

Methods: Maximal isometric voluntary contraction (MVC), voluntary activation, twitch contractile properties, force–frequency relationship and MUDRs from sub-maximal to maximal intensities were assessed in the elbow flexors and extensors.

Results: Both flexor and extensor MVCs were significantly ($P < 0.05$) less ($\sim 42\%$ and $\sim 46\%$ respectively) in the old than in the young. Contractile speeds and the force–frequency relationship did not show any age-related differences ($P > 0.05$). For the elbow flexors contraction duration was ~ 139 ms and for the extensors it was ~ 127 ms for both age groups ($P > 0.05$). The mean MUDRs from 25% MVC to maximum were lower ($\sim 10\%$ to $\sim 36\%$) in the old than in the young ($P < 0.01$). These age-related differences were larger for biceps (Cohen's $d = 8.25$) than triceps (Cohen's $d = 4.79$) brachii.

Conclusion: Thus, at least for proximal upper limb muscles, mean maximal MUDR reductions with healthy adult ageing are muscle specific and not strongly related to contractile speed.

Keywords ageing, humans, motor neurone, motor unit discharge rate.

It is well established that healthy adult ageing is associated with alterations to the neuromuscular system that lead to reductions in strength, power and muscle mass (Rice & Cunningham 2002, Klass *et al.* 2007). For example, the concept of age-related motor unit (MU) remodelling proposes a shift to a greater percentage of type I muscle fibres when compared with young adults (Klass *et al.* 2007). This shift may result from the loss of high-threshold motor neurones – presumably those

innervating fast twitch, or type II fibres – and the existing muscle fibres being re-innervated by viable low-threshold motor neurones supplying slow twitch (type I) muscle fibres (Larsson 2003, Gordon *et al.* 2004). As a result of MU remodelling, it is often reported, although there are exceptions (Roos *et al.* 1999, Dalton *et al.* 2009), that motor unit discharge rates (MUDRs) during sustained [$\geq 50\%$ maximal isometric voluntary contraction (MVC)] (Kamen *et al.* 1995, Connelly *et al.* 1999,

Erim *et al.* 1999, Kamen & Knight 2004) and fast isometric contractions (Klass *et al.* 2008) are lower than those recorded for young adults. The mechanisms responsible for an age-related reduction in MUDRs may involve central nervous system alterations including various anatomical and physiological changes at the cortical (Sjoberg *et al.* 1999, Raz *et al.* 2000, Peinemann *et al.* 2001, Oliviero *et al.* 2006, Rowe *et al.* 2006, Dickstein *et al.* 2007), and spinal (Doherty *et al.* 1993, Eisen *et al.* 1996, Scaglioni *et al.* 2002, Sale & Semmler 2005) levels.

Previous studies on age-related changes in motor neurone output in humans, especially at higher contraction intensities have focused on lower limb muscles (Connelly *et al.* 1999, Kamen & Knight 2004) or hand muscles (Kamen *et al.* 1995, Barry *et al.* 2007). However, lower limb muscles in humans are designed mainly for posture and locomotor tasks whereas hand muscles have unique properties (Katz *et al.* 1993) directed towards grasping and fine motor control. It is well established that basic features such as anatomical location, activity patterns and fibre composition affect not only functional outcomes, but also impose differential age-related changes upon the neuromuscular system (Rice & Cunningham 2002, Klass *et al.* 2007). For example, unique to the elbow flexors and extensors is that whole muscle contractile speeds have been reported not to slow, or slow modestly, with age (Doherty *et al.* 1993, Allman & Rice 2001, Klein *et al.* 2002). Thus, without systematic investigation it should not be assumed that the muscles of the proximal upper limb will demonstrate comparable age-related changes in motor neurone properties as muscles of the lower limb or hand.

The elbow flexors and extensors are a proximal muscle pair with similar function and fibre composition; however, despite their close cortical representation (Penfield & Boldrey 1937), they have a differential strength in corticospinal projections (Palmer & Ashby 1992). It has been suggested that there is a greater cortical preference in activating the biceps brachii in comparison with the triceps brachii (Palmer & Ashby 1992). This differential distribution of corticospinal projections to human motor neurones suggests that lesions of the short latency pathway might result in a specific distribution of weakness, such that the elbow flexors are more affected than the elbow extensors, which has been found in hemiplegic patients (Colebatch *et al.* 1986). It is unknown how healthy ageing may affect these properties, but in this upper limb agonist–antagonist pair, old men exhibit greater difficulty maximally activating the elbow flexors (Jakobi & Rice 2002, Hunter *et al.* 2008) compared with the extensors (Jakobi & Rice 2002), which may be partly related to MUDR (Knight & Kamen 2008). Thus, recording

MUDRs over a range of contraction intensities, including at maximal effort, may give further insight into whether age-related changes in rate coding are differentially altered within an agonist–antagonist pair and emphasize that physiological reductions with healthy adult ageing are muscle specific.

Previous but limited data from humans (Connelly *et al.* 1999, Roos *et al.* 1999) suggest that the age-related slowing of whole muscle contractile properties is related to its constitutive MUDRs with one recent exception (Dalton *et al.* 2009), but whole muscle contractile speeds do not slow with age in the elbow flexors and extensors (Doherty *et al.* 1993, Allman & Rice 2001, Klein *et al.* 2002). Furthermore, testing the force–frequency relationships provides a comprehensive assessment of muscle contractile properties, but none have been published for the elbow flexors and extensors in relation to adult ageing. Thus, the purpose of this study was to compare elbow flexor and extensor contractile properties and MUDRs in young and old men to determine whether these elements of the MU, in a proximal pair of upper limb muscles, are modified in parallel. Based on previous findings (Doherty *et al.* 1993, Kamen *et al.* 1995, Connelly *et al.* 1999, Klein *et al.* 2002), it was hypothesized that MUDRs would be lower for both muscle groups of the old compared with young men, despite a limited slowing in contractile properties.

Methods

In the same subjects, contractile properties and MUDRs were measured in the elbow flexors and extensors. Six old (83 ± 4 years) and six young (24 ± 1 years) men volunteered for the study. The groups differed in age by ~ 60 years, but were similar with respect to body weight (old: 80 ± 5 kg; young: 77 ± 11 kg) and height (old: 170 ± 9 cm; young: 173 ± 6 cm). All subjects were considered healthy and recreationally active. Exclusion criteria for participation included: diabetes, alcoholism, hypertension, angina, or known neurological, or upper limb orthopaedic pathologies, and extensive upper body resistance training. Each subject gave written and oral informed consent according to the guidelines established by the local university review board.

Experimental arrangement

In the non-dominant limb, elbow flexor and extensor contractile properties were assessed in a supine position, on a modified padded examination table (Klein *et al.* 2001). The subjects' legs were elevated for comfort and stability, and to minimize the potential effects of extraneous movements in the lower body which might influence upper body positioning and force generation.

The chest and shoulders were secured to the table with inelastic straps to prevent extraneous shoulder and trunk movements. A custom-built dynamometer was fastened to a small platform attached to the side of the table. An opening (12.5 × 27.5 cm) in the platform allowed access to the elbow extensor muscles. The arm rested beside the body on the platform and the elbow joint was flexed to 90° for all elbow flexion and extension measurements. The wrist was supinated for elbow flexion, but placed in a neutral position for elbow extension because supination during extension was uncomfortable and hindered the production of a maximal effort. In both positions, the hand and wrist were wrapped with tensor bandages in order to prevent wrist flexion and finger movements. For each subject, detailed measures were made of all positions and straps in order to standardize the set-up between sessions. Forces were measured by a strain gauge (SST-700-100A; AS Technology, Haliburton, ON, Canada), which was attached to the wrist plate of the dynamometer. The strain gauge was calibrated with known weights to confirm linearity and to convert volts to Newtons of force (N). Force output was amplified and sampled at 500 Hz, and displayed in real-time on an oscilloscope for visual feedback. The force signal was converted from analog to digital format by a 12-bit A/D converter (model 1401 Plus; Cambridge Electronic Design, Cambridge, UK) and stored on computer for off-line analysis.

Contractile properties

Elbow flexor and extensor contractile properties were each measured during two sessions. To avoid an experimental order effect the muscle group tested first was randomized between sessions and subjects. Voluntary and electrically stimulated measures for both muscle groups were tested in an identical sequence. Electrical stimulation of the elbow flexor and extensor muscle groups was applied percutaneously through carbon rubber stimulation electrodes, which were tightly bandaged over the muscle group being tested. For the elbow flexors, the anode electrode (4 × 4.5 cm) was placed diagonally across the motor point of the biceps brachii ~12 cm distal to the acromion process and the cathode electrode (4 × 4.5 cm) was located over the distal tendon ~2 cm proximal to the cubital fossa. For stimulation of the elbow extensors the anode electrode (4 × 4.5 cm) was placed diagonally across the proximal posterolateral portion of the long and lateral heads of the triceps brachii while the cathode electrode (4 × 4.5 cm) was placed over the triceps brachii tendon ~4.5 cm proximal to the olecranon process.

In order to elicit twitches at rest, 50 μs single pulses at a frequency of 1 Hz were applied to either the elbow

flexors or extensors. During each visit, two series of 8–10 pulses were elicited and each series was separated by ~2 min of rest. To determine the intensity of the pulses, the current was adjusted in incremental steps (DS7AH; Digitimer, Hertfordshire, UK) until a level was attained which activated as much of the muscle as possible without interference from antagonists. Palpation, noticeable contraction of antagonists or a decrement in force with an increase in current were used to assess activity of antagonist muscles. Off-line quantification of the twitch responses consisted of measures of peak twitch tension (PT), time to peak tension (TPT), half relaxation time (HRT), and contraction duration (CD), which is the sum of TPT and HRT. Values reported for each subject were an average of ~16 twitches. Force–frequency relations of the elbow flexors and extensors were recorded from a 1-s train of pulses delivered at 1, 2, 5, 8, 10, 12, 15, 20, 30, 40, 50, 80 and 100 Hz. Stimulus current was adjusted until the 50 Hz train (50 μs pulse width) was ~20% of MVC. The order in which the trains were delivered was randomized between subjects. Each stimulus frequency was applied twice, separated by 2–3 s. The highest force response is reported.

To measure the MVC, subjects were instructed to either flex, or extend their elbow joint as hard and as fast as possible, and to sustain this effort for ~5 s. Subjects performed three to four MVCs per muscle group during each session with 3–5 min rest between each contraction. If the peak forces varied by more than 5% among the first three MVCs another MVC was performed to ensure consistency. The measure taken as the MVC force corresponded to the greatest peak force achieved among the three to four MVCs. Visual feedback and strong verbal encouragement were given during the MVCs. The modified twitch interpolation technique (Hales & Gandevia 1988) was used to assess voluntary activation during the MVCs for each muscle group. This technique consisted of applying a series of paired electrical pulses (two pulses at 100 Hz) to the muscle during and following the attempted MVC. Stimulation current for the double pulse was set at a tolerable level, without current spread to the antagonists. Voluntary activation was estimated from a ratio of the amplitude of the interpolated paired response (T_s) to the amplitude of the post-MVC paired pulse response (T_r): % activation = $(1 - T_s/T_r) \times 100$. The measure of voluntary activation was taken from the MVC with the highest peak force.

Motor unit properties

Subjects participated in four to seven sessions for the recording of MUDRs in the biceps brachii and visited the laboratory another four to seven times for MUDR

recordings in the triceps brachii, over a period of 4 weeks for each muscle group, on non-consecutive days. The biceps brachii MU recordings were performed 7–12 months prior to the triceps brachii experiments and the same exclusion criteria were applied for each testing regime. Although seated upright, for the biceps brachii MU tests, the elbow angle (90°) and wrist positions were the same as for the supine dynamometer. In either situation, to record MUDRs during steady state voluntary contractions custom-made tungsten microelectrodes (125 µm in diameter; 3–5 cm in length) (Connelly *et al.* 1999, Roos *et al.* 1999) were inserted, one into the long, and one into the short heads of the biceps brachii, or one each into the long and lateral heads of the triceps brachii. When recording from biceps or triceps brachii one common reference electrode was attached over the lateral epicondyle of the humerus. Before insertion of the microelectrodes, the skin area was cleansed thoroughly with 70% ethanol. During the brief (5–10 s) voluntary efforts at the five predetermined forces (10%, 25%, 50%, 75% and 100% MVC), the microelectrodes were slowly advanced through the muscle (<0.5 cm per contraction) to record from as many different MUs as possible. Despite these small electrode movements, this method has shown that active MU trains can be identified for brief durations during steady state contractions. Thus, because of the movement of the electrode to record from many different MUs and the challenge to follow a train of MU potentials during high intensity contractions, MUDRs were calculated from trains containing varying numbers of potentials, but none fewer than six (see below). This technique allows a large sample of units to be extracted per subject and thus per group, especially during high intensity contractions including MVC. It has been previously demonstrated that the probability of sampling from the same MU is very low using this technique (Rich *et al.* 1998).

Recording from two separate heads in each muscle group and from many needle insertion angles, areas and depths enabled a comprehensive sample of average MUDRs. The five target forces were randomly assigned during each test session to avoid the effects of fatigue on MUDRs. To further protect against fatigue, 1–5 min rest was given between contractions, and the 75% and 100% MVC contractions were limited to less than 6 s duration. During all contractions visual feedback and verbal encouragement were provided. Separate visual and auditory feedback was provided to the operators to help detect discrete action potential trains.

The unprocessed electromyographic (EMG) data recorded from each of the microelectrode channels in the biceps and triceps brachii were amplified ($\times 100$ –5000) and wide band filtered (between 10 Hz and 10 kHz) using a Neurolog NL824 (Digitimer) pre-

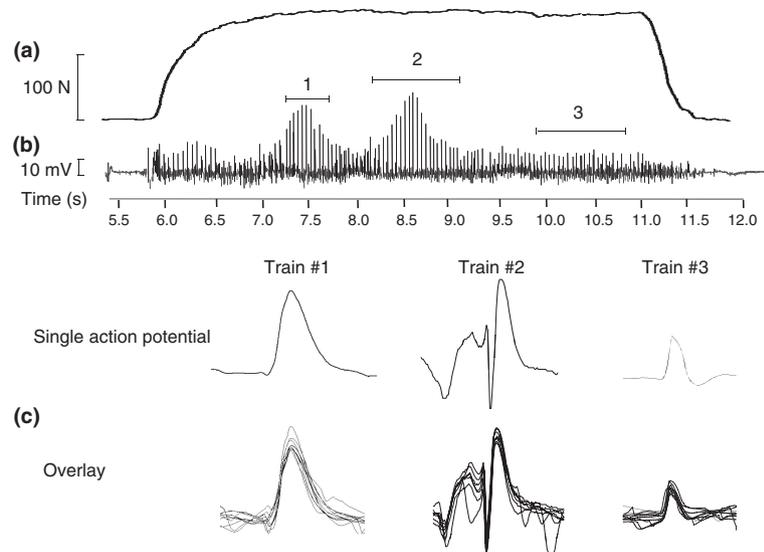
amplifier, amplifier and filter. After amplification and filtering the signal was converted from analog to digital format by a 12-bit A/D converter (CED Model 1401 Plus; Cambridge Electronic Design). The unprocessed EMG data were sampled online at 12 kHz. Subjects targeted the five force levels with force feedback from an oscilloscope positioned in their line of sight.

After data acquisition, off line analysis was conducted with a customized software package (Spike2; Cambridge Electronic Design). The unprocessed EMG from each microelectrode was analysed by comparing and overlaying individual sequential action potentials with respect to their shapes and amplitudes (Fig. 1). Although software is required to overlay action potentials and calculate interspike interval statistics, the ultimate comparison of the shape and amplitude of the action potential was performed visually by one experienced operator and often checked independently by another. Beyond the criteria of shape and amplitude, a minimum of six contiguous MU spikes were required for analysis, and the accepted MU discharge variability for a train was $\leq 30\%$. These criteria were previously discussed in greater detail (Connelly *et al.* 1999, Roos *et al.* 1999). Because the occurrence of doublet discharges (<10 ms) is very low ($\sim 0.04\%$) during steady state contractions (Barry *et al.* 2007), this MU behaviour was not assessed. In order to make statistical comparisons between age and muscle groups, the MU trains were grouped into five bins based on the targeted force levels. The 10% bin contained MU trains recorded at forces <12.5% MVC; a 25% bin was 12.5–37.5%; a 50% bin was 37.5–62.5%; a 75% bin was 62.5–87.5%; and a 100% bin contained forces >87.5%. Additionally, the highest MVC force generated during MU recording (i.e. with inserted electrodes) was taken as the 100% MVC value and all other force levels achieved were normalized to this peak value for each subject.

Statistical analysis

Data were analyzed using SPSS version 10 (SPSS, Chicago, IL, USA). The four dependent variables of twitches recorded at rest (PT, TPT, HRT, CD), MVC and voluntary activation were compared with a 2×2 (age group \times muscle group) analysis of variance. Age-related comparisons in mean MUDRs at the five target levels were assessed with a $2 \times 2 \times 5$ (age group \times muscle group \times force level) mixed analysis of variance. The critical value for statistical significance was set at $P < 0.05$. Tukey's *post hoc* tests were used to identify differences when statistical interactions or main effects were found. To explore whether the expected age-related differences in MUDRs were greater in one muscle group vs. the other, effect sizes (Cohen's *d*) were calculated. Regression analyses (R^2) were used to

Figure 1 Example of a typical motor unit (MU) action potential train from the triceps brachii of an 80-year-old man. (a) A MVC force record (168 N). (b) An unprocessed EMG signal recorded through a tungsten microelectrode inserted into the muscle belly. (c) Example of an action potential shape and overlay of all action potentials from three identified MU trains. Train 1 is an overlay of 10 action potentials discharging at 22 Hz. Train 2 is an overlay of 23 action potentials discharging at 21 Hz, whereas train 3 is an overlay of 19 action potentials discharging at 25 Hz.



determine relationships between force and MUDRs for each age and muscle group. All data are presented as means and standard error of the mean (SE).

Results

Contractile properties

Results for elbow flexor and extensor MVCs, voluntary activation and contractile properties are presented in Table 1. Voluntary and stimulated force did not differ between the elbow flexors and extensors when compared within an age group. The elbow flexor MVC was ~42% lower ($P < 0.05$) and PT was ~64% lower ($P < 0.05$) in the old with similar age-related differences ($P < 0.05$) for the extensors (MVC: ~46%; PT: ~62%; Table 1). There were no differences in voluntary activation between muscles or age groups (94–98%; Table 1). Also, there were no differences ($P > 0.05$) in twitch TPT, HRT and CD between age groups for either

the elbow flexors or extensors (Table 1), and thus no evidence of whole muscle contractile slowing. Furthermore, when the normalized stimulated force–frequency relationship of the biceps and triceps brachii were compared between old and young men there were no differences in relative force output for stimulation frequencies ranging between 1 Hz and 100 Hz ($P = 0.80$; Fig. 2). There were few differences in evoked contractile speeds when comparisons were made within an age group. In the old men, TPT was slower ($P < 0.05$) for the elbow flexors than extensors, but no muscle difference in TPT for the young men, and CD was ~9% longer ($P < 0.05$) in the elbow flexors than in the extensors, regardless of age group (Table 1).

Motor unit properties

There were 1269 and 1189 MU spike trains identified from the biceps brachii of the old and young men respectively. For the triceps brachii, 1071 and 1081 MU

Table 1 Voluntary force and stimulated contractile properties in the elbow flexors and extensors

	EF young	EF old	EE young	EE old
MVC (N)	357 ± 12	207 ± 17*	321 ± 21	173 ± 8*
Voluntary activation (%)	97 ± 1	94 ± 4	97 ± 1	98 ± 1
Peak twitch tension (N)	28 ± 3	10 ± 2*	26 ± 4	10 ± 1*
Time to peak tensions (ms)	73 ± 2	75 ± 3	65 ± 3	63 ± 3†
Half relaxation time (ms)	67 ± 3	63 ± 4	63 ± 4	63 ± 3
Contraction duration (ms)	140 ± 2	138 ± 5	128 ± 4†	126 ± 2†

Values are means ± standard error of the mean. Probability of significant differences set at $P < 0.05$. MVC, maximal isometric voluntary contraction; EF, elbow flexors; EE, elbow extensors.

*Significant difference between old and young men within a muscle group.

†Significant difference between elbow flexor and elbow extensor muscles within an age group.

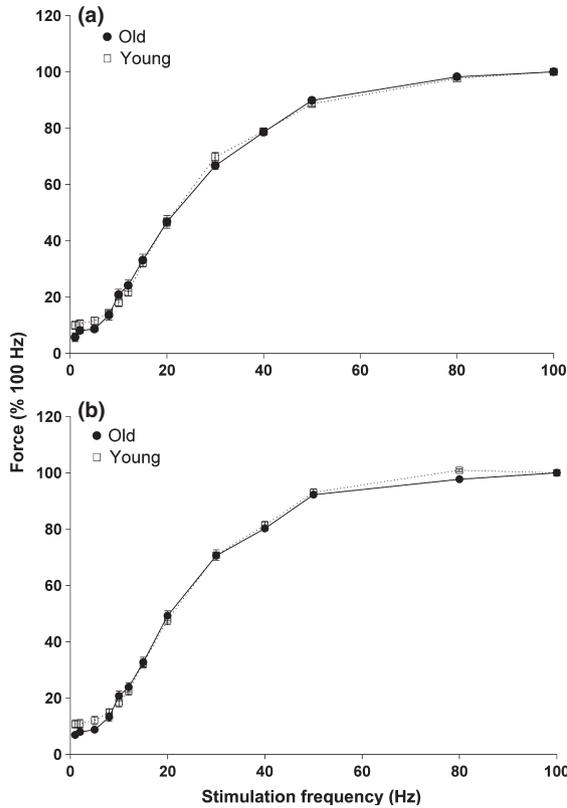


Figure 2 Stimulation frequency (Hz) plotted against normalized force for biceps (a) and triceps (b) brachii for old and young men. Group mean relative force levels were similar between age ($P = 0.80$) and muscle groups ($P = 0.42$). Values are means \pm SE.

spike trains were identified in the old and young men respectively. For each muscle and age group, the greatest number of MU trains were identified at 25%

MVC (~ 400) while the fewest were identified at 100% MVC (~ 100). At 10%, 50% and 75% MVC, approximate numbers of trains were 125, 265 and 215 respectively. There was a range of interspike intervals per MU train (range: 5–89), which were used to calculate the MUDR, but at each force level the average number of intervals did not differ between the two muscles or age groups. The mean number of interspike intervals for 10% MVC was 10.9 ± 2.4 , 25% MVC was 10.5 ± 2.1 , 50% MVC was 8.0 ± 1.8 , 75% MVC was 7.0 ± 1.3 and 100% MVC was 6.5 ± 1.0 .

The range of MUDRs for the triceps brachii across all force levels tested was 4–70 and 5–70 Hz in the old and young men respectively. In the biceps brachii, MUDRs ranged from 4 to 60 Hz for the old and 4 to 65 Hz for the young men. To compare the relationship between MUDRs and normalized force, the data set for each age and muscle group were fit by linear regression (Fig. 3). In order to investigate the mean MUDR–force relationship, MUs were grouped around the five target levels normalized to the MVC (see Methods). The three-way interaction (age group \times muscle group \times force level) was non-significant ($P = 0.57$) and the muscle group by force level interaction was not significant ($P = 0.13$). The significant main effect of force ($P < 0.01$) indicated in both muscle groups that the mean MUDRs were greater at each successive force level from 10% to 100% MVC for the old and young men (Fig. 4). The force \times age interaction was significant ($P < 0.01$) and mean MUDRs were less in the old compared with the young men at force levels of 25%, 50%, 75% and 100% MVC for both muscle groups, but not at 10% MVC (Fig. 4). The muscle \times age interaction ($P < 0.05$) was significant. Mean MUDRs were less in the old compared with the young men for both muscle groups.

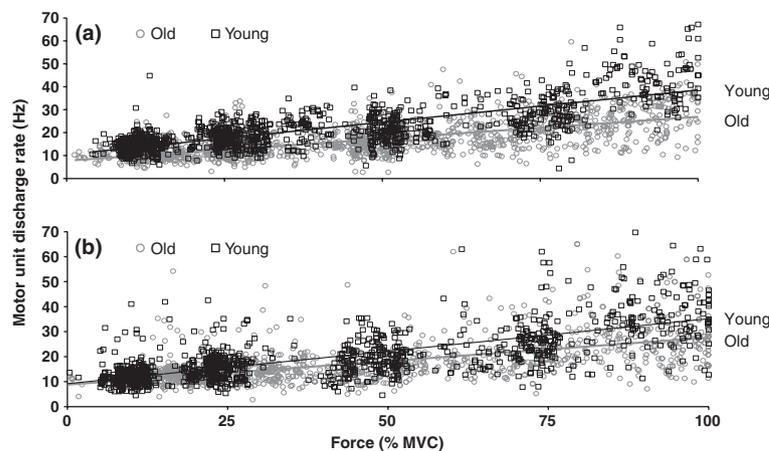


Figure 3 Relationship between force and motor unit discharge rate (MUDR). (a) Scatter plot of all biceps brachii MUDRs relative to their normalized force levels. Linear regression equations are: $\text{frequency}_{(\text{Hz})}(\text{old}) = 0.20 \times \text{force}_{(\% \text{MVC})} + 7.89$, $R^2 = 0.44$ ($P < 0.05$); and $\text{frequency}_{(\text{Hz})}(\text{young}) = 0.31 \times \text{torque}_{(\% \text{MVC})} + 9.34$, $R^2 = 0.61$ ($P < 0.05$). (b) Scatter plot of all triceps brachii MUDRs relative to their normalized force levels. Linear regression equations are: $\text{frequency}_{(\text{Hz})}(\text{old}) = 0.19 \times \text{torque}_{(\% \text{MVC})} + 8.81$, $R^2 = 0.34$ ($P < 0.05$); and $\text{frequency}_{(\text{Hz})}(\text{young}) = 0.26 \times \text{torque}_{(\% \text{MVC})} + 9.22$, $R^2 = 0.49$ ($P < 0.05$).

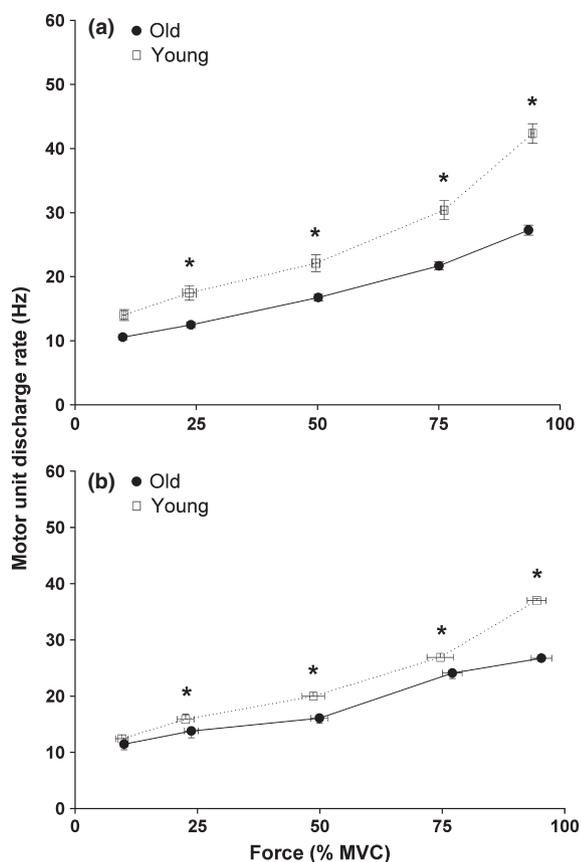


Figure 4 Motor unit discharge rates (MUDRs) recorded at each of the five target force levels for the biceps (a) and triceps (b) brachii for old and young men. The old men had lower MUDRs than the young ($*P \leq 0.05$). The MUDRs were greater at higher force levels ($P < 0.05$). Values are means \pm SE.

To explore whether age-related differences in MUDRs were larger for the biceps than for the triceps brachii, effect sizes were calculated. MUDRs from all force levels were combined for each muscle and age group, and the effect size was greater in the biceps (9.12 Hz, Cohen's d 8.25) than the triceps brachii (5.09 Hz, Cohen's d 4.79).

Discussion

This study compared the age-related differences in both contractile and MU properties in an agonist–antagonist pair of proximal upper limb muscles in the same subjects. Although both the triceps and biceps brachii muscles from the old men had lower relative MUDRs across the range of force levels compared with the young, albeit to differing degrees, neither muscle group demonstrated age-related contractile slowing. Collectively, these findings support our hypothesis and reveal a disproportionate age-related difference between changes in the contractile and neural parameters of the MU in the elbow flexors and extensors, which

corroborates a recent study in the soleus (Dalton *et al.* 2009). However, the present findings do not support previous interpretations (Connelly *et al.* 1999, Roos *et al.* 1999) that suggested changes in contractile function were aligned with changes in MUDRs. Ultimately, the apparent lack of matching of changes in MU and contractile properties and the relatively greater age-related difference in MUDRs in the biceps compared with the triceps brachii may relate to impaired motor control in the upper limb (Barry *et al.* 2005) of aged humans. Our results highlight an often overlooked concept that muscles and more specifically the components of the MU are not affected equally by adult ageing.

Strength, voluntary activation and contractile properties

The elbow flexors and extensors of the old men were $\sim 44\%$ and $\sim 63\%$ weaker than the young for voluntary and involuntary force respectively. Age-related reductions in strength have previously been attributed to decreases in the number of functional MUs (Doherty *et al.* 1993), greater coactivation (Klein *et al.* 2001), changes in muscle architecture (Narici & Maganaris 2007), decrease in contractile cross-sectional area (Klein *et al.* 2001) and a decrease in fibre-specific tension (Frontera *et al.* 2000). Despite weaker voluntary and involuntary strength in the old men compared with the young in this study, which is typical in these muscle groups (Klein *et al.* 2001, Jakobi & Rice 2002), there were no differences in voluntary activation (94–98%) and contractile properties were not slower in the elbow flexors and extensors in the old men compared with the young in this study.

Whole muscle contractile properties reportedly are slower in distal lower (Connelly *et al.* 1999, Dalton *et al.* 2009) and distal upper limb muscles (Narici *et al.* 1991, Doherty & Brown 1997), and modestly slower in proximal lower limb muscles (Roos *et al.* 1999) with increased age. Yet, the present study, in agreement with previous reports on the elbow flexors (Doherty *et al.* 1993, Allman & Rice 2001) and extensors (Klein *et al.* 2002), indicates that the proximal arm muscles do not slow, or only modestly, with healthy ageing. Factors related to location, neuroanatomy and function could account for these differences. For example, when comparing the upper and lower proximal limb muscles, strength (Hughes *et al.* 2001) and type II muscle fibre composition (Lexell *et al.* 1988, Klein *et al.* 2003) are less affected by ageing in the upper limb. Although age-related remodelling (Gordon *et al.* 2004) would suggest that type II MUs are preferentially reduced with ageing, limited reports for proximal upper limb muscles suggest that fibre proportions in the biceps brachii are not altered (Klein *et al.* 2003), although no studies have explored the triceps brachii. Because contractile speeds

are related to fibre composition (Yu *et al.* 2007) this may explain the lack of difference in the normalized force–frequency relationship and twitch contractile durations between old and young subjects.

Motor unit discharge rates

Despite the lack of difference in contractile speeds, it seems that ageing does indeed affect neural output of the constitutive MUs of biceps and triceps brachii muscles. Although the range of MUDRs sampled was not different between the old and young biceps or triceps brachii (Fig. 3), which suggests there is not a selective age-related loss in one type of MU, the mean MUDRs at most force levels were less in the old compared with the young men (Fig. 4). The majority of previous reports as well as the present study found that old subjects exhibit lower MUDRs compared with the young, with the difference exacerbated at higher contraction intensities (Kamen *et al.* 1995, Connelly *et al.* 1999, Kamen & Knight 2004, Barry *et al.* 2007).

In addition to various age-related alterations at the cortical level (Sjoberg *et al.* 1999, Raz *et al.* 2000, Peinemann *et al.* 2001, Oliviero *et al.* 2006, Rowe *et al.* 2006, Dickstein *et al.* 2007), the lower MUDRs in the old men compared with the young may have resulted from morphological changes in the neuromuscular system, such as a loss of motor neurones (Doherty *et al.* 1993) or demyelination of remaining motor neurones, as well as changes in motor neurone excitability. Demyelination (Van Asseldonk *et al.* 2003), which results in a greater outward K⁺ current, could effectively lower MUDRs because it induces a greater hyperpolarization (Kuwabara *et al.* 2000). Thus, the slower duration of motor neurone after-hyperpolarization times (Engelhardt *et al.* 1989, Piotrkiewicz *et al.* 2007) imposes a lower limit on maximal MUDRs in old adults compared with the young. Alternatively, age-related changes in afferent feedback could contribute to a decrease in motor neurone excitability that would inevitably result in lower MUDRs in old adults. For example, with old age there is a decrease in reciprocal post-synaptic inhibition, heteronymous Ia facilitation and oligosynaptic reflexes (Morita *et al.* 1995, Kido *et al.* 2004), and pre-synaptic inhibition is altered (Morita *et al.* 1995, Earles *et al.* 2001, Kido *et al.* 2004).

Regardless of the specific mechanism(s), it has been suggested that MUDRs are matched with the contractile speeds of a muscle group (Bellemare *et al.* 1983) and despite the limited number of studies, it has been reported that this relationship may be maintained into old age (Connelly *et al.* 1999, Roos *et al.* 1999). The slower contractile durations of older muscles compared

with the young seem to be matched to the lower MUDRs to take advantage of the leftward shift in the force–frequency curve (Narici *et al.* 1991, Allman & Rice 2004), thereby allowing MU twitches to fuse at lower discharge rates. This in turn would allow for smooth motor control and force production in older adults. However, in the present study MUDRs were indeed lower in the old men compared with the young for the biceps and triceps brachii, albeit to varying degrees, but whole muscle contractile properties were not different between the old and young men. These observations, together with a recent report in the soleus (Dalton *et al.* 2009), challenge the assumed relationship between overall contractile function and MUDRs as they pertain to the concept of age-related remodelling. Either it is too simplistic to suggest that whole muscle contractile properties are strongly related to average constitutive MUDRs as obtained in humans, or that with ageing this functional relationship may be disturbed depending on the anatomical location or muscle group. Furthermore, age-related alterations in the tendon (Narici & Maganaris 2007) and synergistic muscles are other factors that may have contributed to these diverse findings. Additional studies are needed to determine the effects of these unique age-related alterations on motor control strategies.

One factor not addressed in the current study is that of MU recruitment. It has been reported that recruitment thresholds are shifted towards lower force levels with age (Erim *et al.* 1999), and although this is an important parameter of MU function it is unlikely to have a direct bearing on differences in discharge rates (Duchateau *et al.* 2006). Indeed there is no consensus on the distribution of minimal and maximal discharge rates across MU populations (Duchateau *et al.* 2006). For example, disagreement exists as to whether average or peak MUDRs are positively (Barry *et al.* 2007, Oya *et al.* 2009), negatively (De Luca *et al.* 1982, Erim *et al.* 1999) or not at all (Oya *et al.* 2009) related to recruitment thresholds. The technique in this study depends on large population sampling at all force levels and is not designed to follow individual MUDRs from recruitment to high forces or to determine initial recruitment of a MU. Those techniques that are able to follow individual units necessarily have lower yields and may be limited to something less than MVC force levels. However, despite these technical differences most studies seem to agree that MUDRs generally are reduced with ageing, especially at forces greater than 50% MVC (Klass *et al.* 2007).

It is unclear why MUDRs would be lower to varying extents in two muscle groups (~9 Hz less in the biceps and ~5 Hz less in triceps brachii) used often as a functional agonist–antagonist pair, but these findings

support the concept that each muscle is uniquely influenced by the ageing process (Thornell *et al.* 2003). This disparity may be related to the different patterns of projections of corticospinal neurons (Palmer & Ashby 1992) and group I afferents (Cavallari & Katz 1989) innervating both muscle groups that could be differently affected by ageing. Furthermore, it is unknown how the habitual activity of these muscles is affected by age, but disuse (Duchateau & Hainaut 1990, Seki *et al.* 2007) and training (Kamen & Knight 2004) alter maximal MUDRs. Nevertheless, the greater age-related disparity in maximal MUDRs in the elbow flexors compared with the extensors seems to corroborate previous reports noting a limitation in voluntary activation of the elbow flexors (Yue *et al.* 1999, Klein *et al.* 2001) because suboptimal MUDRs have been attributed as a possible factor in low voluntary activation (Knight & Kamen 2008). Conversely, for the elbow extensors, both old and young adults are capable of near-maximal voluntary activation (Klein *et al.* 2001, Jakobi & Rice 2002). Despite similar voluntary activation in the present study, it has been shown that there is greater variability in attempts to achieve high voluntary activation for the elbow flexors compared with the extensors in old men (Jakobi & Rice 2002). Furthermore, maximal MUDRs may be a more sensitive measure of central drive compared with voluntary activation (Taylor 2009) due to the inherent limitations of the interpolated twitch technique, especially at contraction intensities above 90% MVC. Thus, these previous reports in conjunction with our present data suggest that maximal neural drive is impaired to a greater extent in the elbow flexors than for the extensors in old adults, which may contribute to the reduced motor control reported in the upper limb (Barry *et al.* 2005).

Conflict of interest

The authors declare no conflict of interest.

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