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Age-related differences in pre-movement antagonist muscle co-activation and reaction-time performance.

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ABSTRACT

Multiple causes contribute to the prolonged reaction-times (RT) observed in elderly persons. The involvement of antagonist muscle co-activation remains unclear. Here the Mm. Biceps and Triceps Brachii activation in 64 apparently healthy elderly (80±6 years) and 60 young (26±3 years) subjects were studied during a simple RT-test (moving a finger using standardized elbow-extension from one pushbutton to another following a visual stimulus). RT was divided in pre-movement-time (PMT, time for stimulus processing) and movement-time (MT, time for motor response completion). RT-performance was significantly worse in elderly compared to young; the slowing was more pronounced for MT than PMT (respectively 101±10ms and 41±6ms slower, p<0.01). Elderly subjects showed significantly higher (p<0.01) antagonist muscle co-activation during the PMT-phase, which was significantly related to worse MT and RT (p<0.01). During the MT-phase, antagonist muscle co-activation was similar for both groups. It can be concluded that increased antagonist muscle co-activation in elderly persons occurs in an early phase, already before the start of the movement. These findings provide further understanding of the underlying mechanisms of age-related slowing of human motor performance.

KEYWORDS

Antagonist Co-contraction, Electromyography, Ageing, Reaction Time, Skeletal Muscle
1. INTRODUCTION

Skeletal muscle is profoundly affected during aging, a phenomenon defined as sarcopenia and characterized by atrophy and weakness (Rosenberg, 1989). Sarcopenia is partly caused by an age-related loss of motor neurons, especially large motor neurons innervating type II muscle fibers. Consequently, important reductions of maximal strength and explosivity occur at higher age. In addition, alterations in intra- and inter-muscular coordination can be expected due to age-related denervation and reinnervation of muscle fibers. (see (Saini et al., 2009) for review). Another phenomenon is the general slowing of motor performance that occurs during aging. A well known observation is the increase of the reaction time (RT) seen in elderly persons. RT can be divided in a pre-movement time (PMT, the time to process a stimulus and initiate a response), and a movement time (MT, the time to execute the response, involving motor activity) (Roberts and Pallier, 2001). Although age-related decreases in cognitive functioning are known to result in slower processing speed and increase in RT, slowing is also observed in cognitively intact elderly persons (Gorus et al., 2006). Interestingly, the consistently observed increase in MT, contributing for 70% to the total increase in RT (Gorus et al., 2006), points towards important changes in neuro-motor performance.

Higher antagonist co-activation has been reported in elderly persons for both isometric and dynamic contractions (Izquierdo et al., 1999; Klein et al., 2001; Macaluso et al., 2002). It is assumed that this might be a physiologic compensation for age-related muscle weakness in order to increase joint stiffness and maintain joint stability (Hortobagyi and DeVita, 2000). On the other hand, antagonist co-activation will be unfavorable, since it counteracts the agonist action, thus decreasing effective maximal force and power development (Macaluso et al., 2002). However, the extent of age-related changes in antagonist co-activation remains controversial and seems to vary according to muscle and contraction type. To date, the
antagonist co-activation pattern in elderly persons during rapid, open-chain movements without external resistance remains unexplored.

The aim of this study was to investigate the difference in muscle co-activation between elderly and young healthy subjects during a point-to-point RT-test. We hypothesized that increased antagonist co-activation during the MT of the RT-test would be related to longer MT and RT in the elderly compared to the young subjects. Here we report that in the elderly antagonist co-activation starts very early, already during the PMT, thus interfering with the execution of the open-chain movement.

2. METHODS

2.1. Participants

One hundred twenty-four apparently healthy subjects participated in the study, among whom were 60 young subjects (30 male, 30 female, aged 26±3 years) and 64 community-dwelling elderly (32 male, 32 female, aged 80±6 years). Subjects were excluded when presenting functional disability of the dominant upper extremity (paresis/paralysis, tremor or recent surgery), cognitive decline (Mini Mental State Examination (MMSE) score <24/30 (Folstein et al., 1975)), neurologic disorders, acute or uncontrolled conditions, or chronic inflammatory pathology. According to the present guidelines (Ferrucci et al., 2004), stable morbidity was not an exclusion criterion per se for elderly participants. In this way a representative elderly population was obtained. The study was approved by the Medical Ethics Committees of the Universitair Ziekenhuis Brussel (Belgium) and the Erasmus Universitair Medisch Centrum Rotterdam (The Netherlands); and all participants gave written informed consent.

2.2. Measurements
2.2.1. Clinical characteristics

Height and weight were measured, and self-reported morbidity and medication use were recorded. All participants completed the Yale Physical Activity Survey (YPAS) questionnaire and the Activity Dimensions Summary score (YPAS-ADS) was calculated, reflecting the subject’s physical activity (vigorous activity, leisure walking, moving, standing, and sitting) over the last month on a scale from 0 (no activity at all) to 177 (maximal activity) (Dipietro et al., 1993). Dependency for basic activities of daily life (bADL) was rated using a 6-item scale (bathing, dressing, transfers, use of toilet, continence, and eating) as described by Katz et al. (Katz et al., 1963), complemented by orientation in time and place. Each item was scored from 1 (completely independent or no problem in orientation) to 4 (completely dependent or completely disoriented). Dependency for instrumental ADL (iADL) was evaluated using a 9-item questionnaire (telephone use, transportation, shopping, food preparation, housekeeping, handy-man work, laundry, medication use, and handling finances) following Lawton et al. (Lawton et al., 1982). Each item was scored from 1 (completely dependent) to 3 (completely independent). Cognitive functioning was assessed using the Mini Mental State Examination (MMSE) (Folstein et al., 1975). MMSE-scores ≥23/30 were considered as normal.

2.2.2. Measurement sequence

First, the subjects performed a maximal isometric voluntary contraction (MVC) test of the elbow flexion and extension. Next, after five minutes recovery, the participants performed the RT-test which was preceded by a familiarization session (consisting in 15 trials).

2.2.3. Maximal isometric voluntary contraction

The subject was seated on a chair with the shoulder of the dominant arm adducted and neutrally rotated, elbow flexed at 90° and forearm in neutral position. The forearm was
stabilized using a custom-made arm rest supporting the proximal third of the ulna, and the distal part (at the processus styloideus) was firmly attached to a strength gauge (Tedea-Huntleigh model 615, Cardiff, United Kingdom, capacity = 200kg, total error <0.02% related load). The subject was instructed to push (elbow extension) or pull (elbow flexion) to the gauge as hard as possible under verbal encouragement and to maintain that effort for five seconds. The highest developed strength plateau out of three consecutive trials was considered as MVC. The signals of the strength gauge were synchronously sampled (at 12500Hz, Butterworth 4th order, low-pass 1Hz and notch-filtered) together with the surface electromyography (sEMG) of the Mm Biceps & Triceps Brachii and stored on a personal computer for further analysis.

2.2.4. Reaction time test

Simple, point-to-point RT was assessed using a modified van Zomeren RT-device as described previously (Gorus et al., 2006). Briefly, the device consists of a control panel (connected to a computer) with a central ready button around which eight pushbuttons (that can be illuminated) are arranged in a semicircle. The subject was positioned in front of a horizontally placed control panel with the trunk stabilized to the chair's back support using a belt (eliminating trunk movement). The elbow rested on an articulating elbow support, thus allowing unrestricted elbow extension movement (in a horizontal plane) and maximally reducing postural activity of Mm. Biceps & Triceps Brachii at rest. The position of the control panel was adjusted in order to obtain 60° abduction in the shoulder and 100° elbow extension (when target pushbutton pressed). Movements of the upper arm and hand were monitored using ADXL202 uniaxial piezo-resistive accelerometers (Analog devices, Breda, The Netherlands, adapted by Temec Instruments, Kerkrade, The Netherlands), attached with adhesive tape on the lateral Epicondyle (one accelerometer, directed towards the target
pushbutton in horizontal plane) and on the Processus Styloideus of the Ulna (three accelerometers, X-axis directed towards the target pushbutton in horizontal plane, Y- and Z-axis perpendicular to respectively X- and Y-axis).

During the RT-test, subjects had to hold down the central ready button to trigger stimulus onset; stimulus offset was attained by pressing the illuminated target button. The RT-assessment protocol in this study consisted in a simple, non-choice RT-test during which always the same target button was used (the fourth or fifth pushbutton for respectively left- and right-handed subjects; 13cm distance between central ready and target button). Participants were instructed to respond as quickly and accurately as possible and, after response offset, to return immediately to the central pushbutton, thereby triggering the stimulus onset for the next trial. Tasks were made self-paced, meaning that the next inter-stimulus interval (randomly fluctuating between 3 to 6 seconds) only started after the participant has returned to the central pushbutton. PMT was defined as the interval between stimulus onset and the moment when the subject releases the central button; and MT as the time needed to move the finger to the peripheral response button (using standardized elbow-extension, involving M. Triceps Brachii contraction). The activity of the central and target pushbuttons were synchronously sampled at 12500Hz, together with the accelerometers’ signals and sEMG of the Mm Biceps & Triceps Brachii (see figure 1), and stored on a personal computer for further analysis.

2.2.5. Surface electromyography and signal processing

Self-adhesive pre-gelled electrodes (Ag/Cl, 10mm diameter, 20mm inter-electrode distance) were placed over the M. Biceps Brachii Caput Breve, M. Triceps Brachii Caput Longum and one reference electrode on the spinal processus of the seventh cervical vertebra (the skin was
cleaned using pure alcohol and shaved when necessary) according to the SENIAM-recommendations (Hermens et al., 2000). sEMG sensors were connected to a universal amplifier (MPAQ, IDEE/Maastricht Instruments, Maastricht, The Netherlands) using shielded wires in order to avoid movement artifacts. All raw sEMG signals were simultaneously sampled at 12500Hz (Butterworth 4th order, band-pass 10-5000Hz and notch-filtered) and stored on a personal computer.

Signal processing was performed using data-acquisition software (IdeeQ version 2.9b3, IDEE/Maastricht Instruments, Maastricht, The Netherlands). Root-mean-square amplitude (RMS) of Mm. Biceps & Triceps Brachii sEMG signals were calculated over 2 seconds corresponding to the highest maximal strength plateau obtained during the MVC for elbow flexion and extension. Antagonist co-activation was calculated as

\[
\text{Antagonist co-activation} = \left( \frac{100 \times \text{RMS}_{\text{Antagonist}}}{\text{RMS}_{\text{MVCagonist}}} \right)
\]

For the RT-test, 28 stimuli were generated by the test device. When errors occurred (i.e. when MT>3 seconds) the system automatically generated a replacement stimulus. Additionally, an observer recorded the wrongly executed trials during the RT-test (e.g. when the subject missed the target pushbutton or made aberrant movements with the arm). The correctly executed trials were confirmed by offline visual inspection of the accelerometer signals. For each participant, at least 23 correctly executed trials (stimuli) were available for data analysis. Median RT, PMT and MT were calculated based on the first available 23 trials, as described previously (Gorus et al., 2006). RMS of Mm. Biceps & Triceps Brachii were calculated over PMT and MT periods of each of the 23 trials, and average muscle activation during PMT and MT was expressed as percentage of activation during MVC, computed as:
Muscle activity during PMT = \[ \frac{100}{23 \cdot RMS_{MVC}} \times \sum_{i=1}^{23} RMS_{PMTi} \]

Muscle activity during MT = \[ \frac{100}{23 \cdot RMS_{MVC}} \times \sum_{i=1}^{23} RMS_{MTi} \]

2.3. Statistical analysis

Statistical analysis was performed using PASW-statistics 17.0.3 (SPSS Inc, Chicago, USA). Differences according to age-groups (young versus old), as well as the interaction with gender, were analyzed for all outcome measures using two-way Analysis Of Variance (ANOVA). Since bADL, iADL and MMSE are expressed on ordinal scales, as well as to reduce potential bias due to possible outliers, Spearman's Rho correlation coefficients were computed to analyze relations of muscle activation with PMT, MT, RT and clinical characteristics. Significance was set a priori at \( p<0.05 \).

3. RESULTS

As expected, the elderly participants showed significantly (\( p<0.01 \)) higher BMI, morbidity and medication use compared to the young ones (see table 1). No significant difference was found in physical activity (based on the YPAS-ADS) between both groups. The MMSE and dependency scores were all optimal in the young (data not shown), and excellent although sometimes sub-maximal in the elderly participants. None of the elderly participants showed problematic MMSE or dependency scores.

As can be seen in Figure 2, M. Biceps Brachii co-activation during maximal isometric extension of the elbow was significantly higher in the elderly participants compared to the young (\( p<0.01 \), no significant interaction with gender). On the other hand, co-activation of the M. Triceps Brachii during elbow flexion was not age-dependent and was comparable in
magnitude to the co-activation of the M Biceps Brachii during elbow extension in the young subjects.

RT performance was significantly worse in the elderly subjects compared to the young (p<0.01 for RT, PMT and MT; no significant interaction with gender, see figure 3). On average, RT was 145±13ms longer in the elderly persons. The slowing was more pronounced for MT (101±10ms slower than young subjects) than PMT (41±6ms slower than young subjects). During PMT, M. Biceps Brachii activity (acting as an antagonist during the RT-task) was significantly higher in the old subjects compared to the young (p<0.01, no significant interaction with gender, see figure 4) whereas M. Triceps Brachii activity (acting as an agonist during the RT-task) was equal in both groups. Higher levels of M. Biceps Brachii activity during PMT were significantly related to longer MT (r=0.33, p=0.0002 and r=0.29, p=0.019 respectively for all subjects and for the elderly separately) and longer total RT (r=0.29, p=0.001 for all subjects). In contrast, higher M. Triceps Brachii activity during PMT was significantly related to shorter PMT (r=-0.19, p=0.031 in all subjects combined, r=-0.26, p=0.044 in the young separately) and shorter total RT (r=-0.28, p=0.032 for young subjects).

In the young participants M. Triceps Brachii activity during MT was significantly higher than in the elderly (p<0.05, no significant interaction with gender, see figure 4); for M. Biceps Brachii activity no significant difference was found. Higher activation of M. Triceps Brachii during MT related significantly to shorter MT and total RT in young (respectively r=-0.40, p=0.002 and r=-0.42, p=0.0008) as well as in all subjects combined (respectively r=-0.26, p=0.003 and r=-0.30, p=0.0008).
For RT, PMT, and MT and muscle activity (during PMT and MT) no significant relationships were found with cognition (MMSE-score), dependency (bADL and iADL), physical activity (YPAS-ADS), morbidity or medication use; neither in the elderly nor in the young participants separately.

4. DISCUSSION

In our experiments we have used a simple point-to-point RT-test allowing for the distinction of PMT and MT. In accordance with previous reports from our laboratory (Gorus et al., 2006), the total RT was significantly longer (+32%) in the elderly subjects compared to the young ones. Also, the difference between young and old participants was 2.4-fold higher for MT compared to PMT; thus confirming our previous findings (Gorus et al., 2006) that the slowing in healthy elderly is most pronounced during the movement phase of the RT-task. An unexpected finding was the more pronounced antagonist co-activation in the elderly persons during the pre-movement phase, which influenced negatively the RT performance.

Initially, we hypothesized that in elderly persons the co-activation of the M. Biceps Brachii (acting as an antagonist during the RT-test) would be higher during the MT-phase compared to the young subjects (as one of the causes for the longer MT). When analyzing the normalized sEMG signals of the Mm. Biceps & Triceps Brachii muscles over the PMT- and MT-phases, we found that the elderly persons showed significantly (p<0.01) higher activation of the M. Biceps Brachii already during the PMT-phase compared to the young ones, whereas M. Triceps Brachii activity was equal in both groups. During the MT-phase, M. Triceps Brachii activity was significantly higher in the young than in the elderly (p<0.05); for M. Biceps Brachii activity no significant difference was found. This is in contrast with our initial hypothesis and means that the increased antagonist co-activation in elderly persons occurs in
an early phase during the RT-test, already before the start of the movement. This higher antagonist co-activation was significantly related to a longer MT (p=0.0002 and p=0.019 respectively for all subjects and for the elderly separately) and longer total RT (p=0.001 for all subjects). These results demonstrate that the longer RT we observed in our elderly participants is related to a higher early co-activation of the antagonist, before the start of the movement. It can be assumed that consequently, the resistance encountered by the agonist muscle will be higher, thus increasing the time necessary to complete the movement task. In addition, the negative effect of this phenomenon will be amplified by the lower agonist activity during the MT-phase observed in the elderly. In the young subjects, antagonist activity during PMT was not significantly related to worse RT-performance. This finding strengthens the hypothesis that age-related factors are (at least partly) involved in the relationship between increased antagonist activity (during the PMT-phase) and RT-performance; and that this finding is probably not biased by inter-individual differences occurring at young age. In this context, it is to be expected that the relationships disappear when making a sub-analysis in a young “narrow age cohort” population (Hofer and Sliwinski, 2001), consisting here in young healthy adults aged 26±3 years (min-max=18-32 years; i.e. without relevant age-difference between the subjects). The fact that the correlation between antagonist muscle activity during the PMT-phase and MT was statistically significant in the elderly subgroup, is probably due to the fact that the age-range in our elderly participants was slightly higher (aged 80±6 years, min-max=70-90 years) and that the age-related changes influencing the relationship between antagonist co-activation and reaction-time might be more important in subjects aged >70 years. Higher M. Triceps Brachii activity during the MT-phase was significantly related to better MT and RT, in young as well as in all subjects combined (p<0.01). Similarly, these results indicate that in young subjects an overall higher activity of the agonist muscle during the PMT and MT-phases is related to shorter RT-performance.
The higher antagonist muscle co-activation in the early phase of the RT-test in our elderly participants is possibly due to age-related deficits in the central nervous system. In this context, Mattay et al. measured the activation pattern of brain areas with fMRI during a simple RT-task in healthy young and healthy older adults (mean age 30 and 59 years respectively) (Mattay et al., 2002). The older persons showed a greater extent of activation in brain regions compared to the younger ones, as well as activation in areas that young subjects did not recruit (including the ipsilateral sensorimotor cortex, putamen and contralateral cerebellum). This phenomenon is probably a compensation strategy in order to maintain high performance, since larger brain region recruitment was significantly related to better RT-test performance in the older group (Mattay et al., 2002). It can not be excluded that elderly persons show disturbed motor program pathways, thus leading to less efficient muscle recruitment and higher antagonist co-activation when performing rapid movements. Since the elderly subjects in our study were on average 20 years older than those in the Mattay et al. study (Mattay et al., 2002), they are even more likely to show different activation patterns. However, our measurements do not allow distinguishing central and peripheral underlying mechanisms.

Recently, Renaud et al. have demonstrated that both PMT and MT during a simple, upper-limb RT-test were significantly better in elderly with high cardio-respiratory fitness compared to unfit subjects (Renaud et al., 2010). Also, resistance training can reduce the higher antagonist co-activation in elderly persons (Simoneau et al., 2006). Further studies comparing different exercise regimens are necessary in order to identify the optimal training intervention in order to improve RT-performance as well as the underlying mechanisms.
In order to allow normalization of the sEMG signals measured during the RT-test, the participants performed an isometric MVC for elbow flexion and extension prior to the RT-test. In the elderly subjects we observed a significantly higher M. Biceps Brachii co-activation during maximal isometric extension of the elbow compared to the young ones (8±3% higher, p<0.01). Also Klein et al. reported a +/-5% higher M. Biceps Brachii co-activation in elderly compared to young subjects during maximal isometric elbow extension (Klein et al., 2001). They also reported a similar increase in M. Triceps Brachii co-activation during elbow flexion in their elderly participants (Klein et al., 2001). Contrary to their findings, in our study the co-activation of the M. Triceps Brachii during elbow flexion was equal in both groups and comparable to the co-activation level of the M Biceps Brachii during elbow extension in the young subjects. However, also Pousson et al. failed to demonstrate higher M. Triceps Brachii co-activation in elderly persons during maximal isometric elbow flexion (Pousson et al., 2001). Interestingly, our results are analogous to the findings of Macaluso et al., who found significantly higher co-activation of the M. Biceps Femoris during isometric knee extension in elderly subjects, but no differences in co-activation of the M. Vastus Lateralis during isometric knee flexion compared to young subjects (Macaluso et al., 2002). However, the exact origin of differences in age-related changes of antagonist co-activation between flexor and extensor muscles remains to be elucidated.

One of the strengths of this study is the relatively high number of subjects involved (64 elderly and 60 young participants). In fact, in elderly persons a higher variability is often observed, which necessitates a higher number of participants in order to attain statistical significances. Although morbidity was not an exclusion criterion per se, subjects presenting any clinical condition that could potentially interfere with RT-performance were excluded. Furthermore, all elderly participants in our study were living independently in the community.
and showed excellent cognitive functioning (mean MMSE-score = 29±2 /30). The submaximal MMSE and dependency scores can be considered as normal for a healthy and well-functioning population aged 70 years and over. The relatively high mean age (80±5 years) of our elderly participants allows us to hypothesize that age-related changes in the neuromuscular system have taken place. In this context it is important to notice that the average physical activity pattern was similar between young and old participants, indicating that our findings were not biased by disuse. Moreover, no significant relationships were found for RT and antagonist co-activation with cognition, dependency, physical activity, morbidity or medication use; consequently, the alterations in antagonist muscle activation we observed are probably mainly due to age-related phenomena. On the other hand, although not fully exempt from morbidity, our elderly participants can be considered as high-functioning community-dwelling persons who might perform better than independently-living elderly persons in general.

5. CONCLUSIONS

We can conclude that elderly persons show a higher antagonist co-activation during the early phase of a point-to-point RT-test, already before the start of the movement, which is related to longer RT. These findings provide a new insight into the underlying mechanisms of age-related slowing of human motor performance. Consequently, antagonist co-activation might become a target for new intervention strategies.

6. FUNDING

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7. ACKNOWLEDGEMENTS

The authors have no conflicts of interest to disclose.

8. ABBREVIATIONS

ADL = Activities of Daily Life
bADL = Dependency for basic activities of daily life
iADL = Dependency for instrumental activities of daily life
ADS = Activity Dimensions Summary score
MMSE = Mini Mental State Examination
MVC = Maximal Isometric Voluntary Contraction
MT = Movement Time
PMT = Pre-movement time
RMS = Root Mean Square

\[ RMS_{\text{Agonist}(MVC\text{Agonist})} \] = RMS of the antagonist muscle during MVC of the agonist

\[ RMS_{\text{Antagonist}(MVC\text{Antagonist})} \] = RMS of antagonist muscle during MVC of the antagonist

\[ RMS_{\text{MVC}} \] = RMS of the muscle during MVC

\[ RMS_{\text{PMT}} \] = RMS of the muscle during the \( i \)-th PMT period

\[ RMS_{\text{MT}} \] = RMS of the muscle during the \( i \)-th MT period

RT = Reaction Time

YPAS = Yale Physical Activity Scale
9. REFERENCES


10. TABLES

Table 1. Participants' characteristics.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Young subjects (N=60)</th>
<th>Old subjects (N=64)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Female</strong></td>
<td>50%</td>
<td>50%</td>
</tr>
<tr>
<td>Age (years)*</td>
<td>26.0 ± 3.0</td>
<td>79.6 ± 4.5</td>
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<tr>
<td>Body Mass Index (kg/m²)*</td>
<td>23.2 ± 2.7</td>
<td>24.9 ± 3.3</td>
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<tr>
<td>MMSE (score 0-30)</td>
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<td>28.6 ± 1.5</td>
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<tr>
<td>bADL-dependency (score 8-32)</td>
<td>-</td>
<td>8.3 ± 0.6</td>
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<tr>
<td>iADL-dependency (score 9-27)</td>
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<td>26.0 ± 1.8</td>
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<tr>
<td>Morbidity (number)*</td>
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<td>1.6 ± 1.5</td>
</tr>
<tr>
<td>Medication use (number)*</td>
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<td>2.6 ± 2.5</td>
</tr>
<tr>
<td>YPAS-ADS (score 0-177)</td>
<td>55.1 ± 20.5</td>
<td>49.6 ± 32.8</td>
</tr>
</tbody>
</table>

Mean ± SD. *significant difference between young and old subjects (p<0.01, two-way ANOVA, no significant interaction with gender); MMSE=Mini-Mental-State examination; bADL & iADL=respectively basic and instrumental activities of daily life; YPAS-
11. LEGEND TO THE FIGURES

Figure 1. Signal plot during RT. Representative plot of synchronously sampled sEMG of Mm. Biceps & Triceps Brachii (for illustrative purposes full-wave rectified and RMS-smoothed over 2ms) and signals of the pushbuttons during a single RT-stimulus in a female participant aged 83 years. PMT=pre-movement time, MT=movement time, T1=illumination of target pushbutton (visual stimulus, start of PMT), T2=release of the central ready pushbutton (end of PMT and start of MT), T3=pressing the target pushbutton (end of MT), T4=return to the central ready pushbutton (ready position for a new stimulus).

Figure 2. Antagonist co-activation during maximal voluntary isometric contraction. *significant difference in antagonist co-activation between young and old subjects (p<0.01; two-way ANOVA, no significant interaction with gender); bars represent mean ± SE; MVC=Maximal Voluntary Contraction; %RMS= Root-Mean-Square amplitude of muscle sEMG activity expressed as percentage of activity during agonistic MVC.

Figure 3. Reaction-time performance. *significant difference between young and old subjects (p<0.01; two-way ANOVA, no significant interaction with gender); bars represent mean ± SE; PMT= Pre-movement Time; MT= Movement Time; RT= Total Reaction Time.

Figure 4. Muscle activity during point-to-point reaction time test. Significant difference between young and old subjects *p<0.01; §p<0.05 (two-way ANOVA, no significant interaction with gender); bars represent mean ± SE; PMT= Pre-movement Time; MT= Movement Time; %RMS= Root-Mean-Square amplitude of muscle sEMG activity expressed as percentage of activity during agonistic maximal voluntary contraction.
12. FIGURES

Figure 1.
Figure 2.
Figure 3
Figure 4.