RESEARCH ARTICLE

Precision in isometric precision grip force is reduced in middle-aged adults

Påvel Lindberg · Chrystele Ody · Antoine Feydy · Marc A. Maier

Abstract We investigated age related changes in the control of precision grip in 29 healthy adults spanning early adulthood to middle age (21–67 years). Subjects performed a visually guided, isometric precision grip ramp-and-hold force-tracking task. Target force levels were 3, 6, and 9 N. Precision and performance of force regulation was quantified. Larger errors were made during the ramp than during the hold phase. Age correlated positively with the amount of error at the lowest (3 N) force level in both phases. Force onsets were systematically earlier in middle-aged subjects and the average slope of the force during the ramp decreased with increasing age. The results show that precision during low grip force control decreases already during middle age and those subjects may modify their force generation strategies to compensate for early and subtle degenerative changes in the motor system before decline in grip strength is apparent.

P. Lindberg · C. Ody · A. Feydy · M. A. Maier
Inserm, UMR_S 742, ANiM, 75005 Paris, France

P. Lindberg · C. Ody · A. Feydy · M. A. Maier
UPMC Univ Paris 06, UMR_S 742, ANiM,
75005 Paris, France

M. A. Maier
Université Paris Diderot Paris-7, UMR_S 742, ANiM,
75013 Paris, France

P. Lindberg (✉) · A. Feydy
Service de Radiologie B, APHP, CHU Cochin,
Faculté de Médecine, Université Paris Descartes,
27 rue du Faubourg St. Jacques, 75014 Paris, France
e-mail: pavel.lindberg@cch.aphp.fr

Introduction

The precise control of force between the digits is a necessary pre-requisite for dexterous object manipulation. It is well established that ageing affects grip function (Sosnoff and Newell 2006; Cole 1991) and the capacity for dexterous manipulation (e.g., Smith et al. 1999; Cole et al. 1999). Ageing also leads to increased motor output variability (Laidlaw et al. 2000; Christou and Tracy 2006). Although underlying physiological changes with age have been examined, how they affect grip function remains unclear (Cole et al. 1999; Enoka et al. 2003). For example, it is not clear why motor output variability seems to increase with age more so during rapid discrete isometric contractions than during force maintenance (Christou and Carlton 2001). Physiologically, several components of the motor system change in old age: (1) muscle strength declines (Doherty 2003; Ranganathan et al. 2001) as well as muscle mass (Lexell et al. 1988), (2) there is a loss of spinal motoneurons (Cruz-Sánchez et al. 1998) and the number of motor units decreases (Brown 1973; Campbell et al. 1973), (3) the functional properties of the remaining motor units change, e.g., the size of single motor units increases and their contractile speed decreases (Doherty and Brown 1997). Furthermore, the average firing rate of motor units is reduced and their firing pattern altered (Erim et al. 1999). If age-related behavioral changes occur, it is not clear whether these can be fully attributed to passive, physiological changes in the motor and sensory systems (i.e., directly caused by age-related degeneration) or whether some of these may also be due to an active change in

task-strategy in order to compensate for passive deterioration in the underlying systems (Woollacott and Manchester 1993).

Although many studies indicate quite drastic physiological changes after age 60, they also show *progressive* changes prior to old age (Cruz-Sánchez et al. 1998), and in particular for muscles acting on the thumb and index finger: the number of motor units in the thenar muscles declines with increasing age, with an approximate reduction of 1.2 motor units per year from adolescence to age 60 (Brown 1973). This was not the case for more proximal arm muscle motor units (Galea 1996). Age-related atrophy has also been shown to be greater in thenar than hypothenar muscles (Voermans et al. 2006). Despite the loss of thenar motor units before age 60, strength of these muscles may be maintained, probably by reinnervation of denervated muscle fibers by sprouting of the remaining motor axons (Brown 1973). Given these findings, we hypothesized that on the behavioral level and as a consequence of these progressive physiological alterations, healthy subjects (<60 years) should show (1) a gradual decline in grip force control with age, since there are presumably fewer motor units available for graduation of forces, (2) this effect would be expected to be more pronounced for low forces, and (3) subjects should not show a decline in overall grip strength, since the loss of motor units is presumably compensated for by reinnervation of muscle fibers resulting in increased motor unit twitch tensions (Doherty and Brown 1997).

A variety of tasks have been used to investigate the behavioral effects of ageing on grip function, including the grasp-and-lift task (Cole 1991; Cole et al. 1999; Augurelle et al. 2003) and visuomotor tracking of isometric force (Jagacinski et al. 1995; Vaillancourt and Newell 2003; Voelcker-Rehage and Alberts 2005; Sosnoff and Newell 2006). Few studies have investigated both dynamic and static force tracking profiles during isometric precision grip (Voelcker-Rehage and Alberts 2005) and often sinusoidal tracking was used (Jagacinski et al. 1995; Vaillancourt and Newell 2003; Voelcker-Rehage and Alberts 2005; Sosnoff and Newell 2006), i.e., a continuously changing slope of force. The effect of ageing on grip performance has usually been studied by comparing groups of young (age 20–30) and old (age 60–75) subjects (e.g., Lazarus and Haynes 2000; Vaillancourt and Newell 2003; Voelcker-Rehage and Alberts 2005; Sosnoff and Newell 2006). Together, these studies leave no doubt that grip function changes in old age, however, they do not indicate whether these changes occur abruptly or progressively. Behavioral studies covering the middle-aged population are relatively rare, whereas imaging studies are more common (e.g., Pieperhoff et al. 2008). Despite suggestions that subtle changes in dexterity may occur before age 60 (Smith et al. 1999), there has been, to our knowledge, only one previous study describing

a decrease in grip force control in normal middle-aged subjects (Cole et al. 1999): their results showed that healthy subjects increased their grip force profiles in a grasp-and-lift task already at age 50, presumably reflecting an increased safety margin to prevent the object from slipping.

According to our hypothesis, the aim of this study was, first, to determine whether behavioral age-related changes in force tracking occur already in middle age (working adults <60 years). Second, if this was the case to characterize these changes in terms of task precision at different force levels, i.e., to quantify the degree of accuracy in force tracking (minimizing the tracking error was the instructed goal) (Kurillo et al. 2004). Third, to test whether in this population maximal grip force was independent of age. Finally, based on the suggestion that altered finger force characteristics in older subjects may be adaptive (Shim et al. 2004), we also investigated whether middle-aged subjects might adopt particular task strategies to actively compensate for possible age-related passive degenerative processes. Task performance (i.e., behavioral characteristics not constrained by any instruction) was quantified by measures such as the number of force adjustments, the variation of force, as well as the timing of force onsets and offsets (see "Methods" for details). Finally, we used a visually guided tracking task where subjects matched the isometric force between the thumb and index finger (i.e., precision grip force) to a ramp-and-hold target. This allowed us to separately quantify the precision and characterize the performance during the ramp (period of force increase) and the hold (period of constant force maintenance).

Materials and methods

Participants

Twenty-nine subjects (14 males, 15 females) ranging in age from 21 to 67 (mean = 41) participated in the study. Age was normally distributed (Shapiro-Wilk W test = 0.95, $P = 0.17$). All subjects were right handed and were students or full time employed. Subjects reported no sensory deficits and all had adequate pressure sense for the task, i.e., 70% or more correct identification of the 0.4 g Semmes–Weinstein monofilament on the finger and thumb pads. Exclusion criteria included: (1) any neuromuscular disorder that may impair precision grip (e.g., arthritis, neck pain or any radiating symptoms, diabetes); (2) any visual impairment or difficulty in watching a computer screen; and (3) any cognitive impairment or difficulty in understanding the task. Subjects, who regularly engaged in activities requiring high dexterity of the dominant hand (e.g., frequent playing of musical instrument or video

games) were also excluded. The procedures of the study complied with the Declaration of Helsinki and subjects provided informed consent.

Data acquisition

Participants were seated in a chair and grasped a manipulandum as shown in Fig. 1a. The forearm was flexed to about 45 degrees, positioned on the table and the wrist was fastened to ensure a steady posture throughout testing. Subjects performed a visuomotor step-tracking task by exerting isometric force between the thumb and index finger. Each fingertip applied force on a force sensitive resistor (FSR, ±2% repeatability, force range 0.07–70 N). The distance between the thumb and index finger transducer was 1 cm. Calibration, i.e., a linear regression, was performed for each transducer separately by applying weights ranging from 50 to 2,000 g. Force transducer output was amplified and then sampled at 1 kHz by a CED Micro1401 (Cambridge Electronic Design®). Spike2 (version 4.24; Cambridge Electronic Design®) was used to display the recorded force in real-time as well as the target force on a 15-in. computer screen. Recorded force was displayed as a small box whose vertical position was a linear function of the summed force. The target force trajectory moved with constant velocity over the screen from right to left (Fig. 1a). The screen displayed 3 s of the target force prior and 3 s after the cursor. This allowed the subject to anticipate the forthcoming ramp-and-hold profile.

Task

Subjects were instructed to perform a visuomotor step-tracking task by following the target force with the cursor as precisely as possible. The task comprised 18 blocks each consisting of 4 ramp-and-hold target force trajectories from 0 N to either 3, 6, or 9 N. Since reduced force control in older adults occurs predominantly during tasks in low force ranges (Galganski et al. 1993; Sosnoff and Newell 2006), we collected data across three force ramp-and-hold profiles at 3, 6 and 9 N, i.e., from about 10–30% MVC. Prior to each ramp, the target remained for 3 s at 0 N. The target force then increased linearly (ramped up) during a 2-s period to reach the steady state force level, i.e., the slope increased from 1.5 to 3 and to 4.5 N/s in the three force targets. The steady-state period lasted 4 s, after which, the target force dropped instantaneously to 0 N. Between blocks there was a 5-s pause with a black screen. Each subject performed a pseudo-randomised order of six blocks at each force level (i.e., 24 trials at each force level and 72 trials). To avoid changes of hand and grip position during testing the subjects were continuously monitored and instructed to maintain the index and thumb on the force transducers throughout the pause periods. Subjects were instructed to minimize the distance (error) between the applied and the target force. All subjects were familiarized with the task before testing. Collection of the 72 trials took approximately 12 min. Since age-related changes in grip function may partly be explained by diminished grip strength (Sosnoff and Newell 2006), all subjects performed three trials of maximal grip force (between thumb and index finger) after the ramp-and-hold trials.

Data analysis

Force data were processed and analyzed using Matlab v6 (The MathWorks, Inc.). Thumb and index finger force were down-sampled to 100 Hz and summed. Trials where the baseline force (from 1.5 to 0.5 s prior to the ramp) exceeded 20% of the target force were discarded. Two periods of 2 s were defined: (1) the ramp-phase (from the start to the end of the target force ramp) and (2) the hold-phase (from 2 to 4 s into the steady state period). The last phase of the steady-state period was chosen in order to
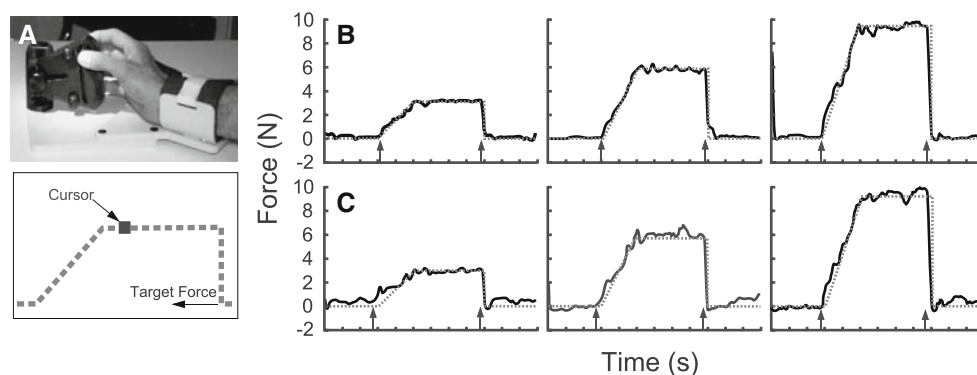

Fig. 1 Precision grip set-up and single trial raw data. **a** The subject applied isometric grip force with his thumb and index finger. The cursor on the screen in front of the subject moved in the vertical direction as a linear function of grip force. The target force scrolled over the screen from right to left. **b** A single 3, 6 and 9 N trial of a younger subject (age 21). **c** A single 3, 6 and 9 N trial of an older subject (age 67). *Dashed line* target force, *solid line* actual grip force. *Arrows* force onset and offset

avoid transient adjustments from the ramp to the steady-state period. A detailed analysis was performed trial-by-trial. First, *precision* was quantified by the following characteristics, which were separately calculated for the ramp and hold phase:

1. Error = the area (or sum over each bin) of the absolute difference between actual force and target force.
2. Positive error (overshoot) = error for periods of actual force > target force.
3. Negative error (undershoot) = error for periods of actual force < target force.

Relative error values, i.e., normalized to the target force, were also calculated. Thus, the term "error" will henceforth implicitly indicate absolute values, whereas the term "relative" will be used explicitly.

Second, *performance*, i.e. the way subjects solved the task, was characterized by:

4. Number of corrective adjustments = the number of times the actual force trace crossed the target force trace.
5. Mean force and coefficient of variation (CV) of the force applied during the hold (within-trial).
6. Mean slope of the applied force (dF/dt, i.e. rate of change of force) and the CV of the slope during the ramp (within-trial).
7. Force onset relative to the ramp onset, defined as the time when the slope crossed a positive threshold, i.e. $dF/dt > 0.2*max_{trial} (dF/dt)$. Onsets were negative if occurring prior to target onset and positive otherwise (Fig. 1b).
8. Force offset, defined as the time when the slope crossed a negative threshold, i.e., $dF/dt < -6$). Offsets were negative if occurring prior to the end of target hold and positive otherwise (Fig. 1b).

Note that the subject was provided with a real-time visual feedback on precision, but had no such feedback on performance measures. For each subject, precision and performance criteria were averaged over all trials of a given force condition, i.e. for 3, 6 and 9 N. Finally, as age-related force fluctuations may occur during steady-state maintenance of force (Christou et al. 2004) we identified the frequency components during the hold period using the discrete Fourier transform. Power spectra of force between 1 and 15 Hz were analyzed for any age effects.

Statistical analysis

Differences in error and number of corrective adjustments were analyzed using a general linear model repeated measures ANOVA with two within subjects factors: PHASE (ramp and hold) and FORCE level (3, 6, and 9 N).

To study the effects of error type (positive or negative) an additional factor (ERROR TYPE) was used in the ANOVA analysis. Differences in the slope during the ramp, in the force during the hold, and in the timing (onsets and offsets) were analyzed with one within subject factor: FORCE level (3, 6, and 9 N). Post hoc contrasts were used for *post hoc* testing of group differences. The relation between age and precision or performance criteria, as well as the relation between maximal force, steadiness during hold phase and age were examined using Pearson correlations. Statistical analysis was performed using Statistica 7 (StatSoft, Inc.) and the level of significance set to $P < 0.05$.

Results

Figure 1b and c show single trial raw data of the visually guided force tracking task for the 3, 6 and 9 N target force levels. The force trajectory clearly showed fluctuations around the target force (dashed line). The force trajectories were analyzed in terms of task-parameters and as a function of age.

Precision of isometric force tracking (whole group results)

We first quantified the precision in the tracking task. Figure 2a shows that the grand average of the error increased (linearly) as a function of the increasing target force [$F(2,56) = 203.6$, $P < 0.001$, $\eta_p^2 = 0.88$] during the ramp as well as during the hold. However, the error increased more during the ramp, with a significant interaction between phase and force level [$F(2,56) = 21.4$, $P < 0.001$, $\eta_p^2 = 0.43$]. At all three target force levels, the grand average of the error was higher during the ramp than the hold phase [$F(1,28) = 57.6$, $P < 0.001$, $\eta_p^2 = 0.67$]. Figure 2b shows that the positive error (overshoot), increased as a function of target force during the ramp but not during the hold, whereas the negative error (undershoot) increased as a function of target force during both the ramp and the hold (i.e., an interaction between FORCE, PHASE, ERROR TYPE: $F(2,56) = 100.5$, $P < 0.001$, $\eta_p^2 = 0.78$).

Figure 2c and d illustrate the precision as relative error, i.e. normalized to the target force. The relative error was also higher during the ramp than the hold [Fig. 2c, $F(1,28) = 20.5$, $P < 0.001$, $\eta_p^2 = 0.42$]. In contrast to the (absolute) error, the relative error decreased as a function of target force [$F(2,56) = 88.6$, $P < 0.001$, $\eta_p^2 = 0.76$], which is explained by the fact that the absolute error increased with a slope < unity, i.e. it was not twice as large when the target force doubled.

Relative positive error (overshoot) or negative error (undershoot) was found to interact with both task phase

Fig. 2 Precision measures as a function of target force. **a** Grand average and SD of the error during the ramp (*solid line*) and the hold period (*dashed line*). Y axis in 10^{-2} N s (Newton seconds). **b** Grand average and SD of the positive and the negative error during the ramp and the hold period. **c** Grand average and SD of the relative error during the ramp and the hold period. Relative error is absolute error/target force). **d** Grand average and SD of the positive and the negative relative error during the ramp and the hold period
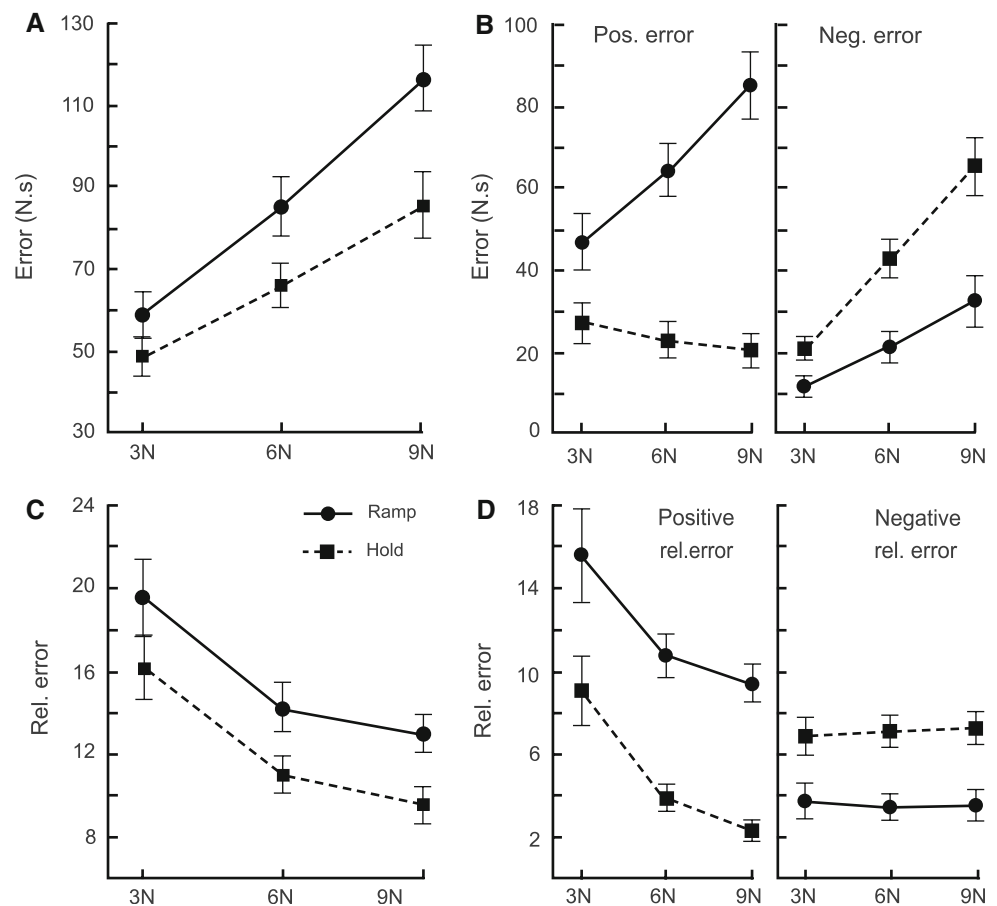
$[F(1,28) = 150.0, \quad P < 0.001, \quad \eta_p^2 = 0.84]$ and force $[F(2,56) = 47.3, P < 0.001, \eta_p^2 = 0.63]$. Figure 2d shows that the relative positive error decreases as a function of target force, both for the ramp and the hold phase. Furthermore, at all three target levels, the relative positive error was higher during the ramp than the hold. In contrast, the relative negative error did not vary as a function of target force and was higher during the hold than the ramp.

Performance of isometric force tracking (whole group results)

We used several quantitative performance criteria to characterize the tracking behavior. First, the number of force adjustments, quantified by the number of crossings between the actual and target force, was evaluated. The number of adjustments was found to increase with increasing force level $[F(2,56) = 4.9, P = 0.01, \eta_p^2 = 0.15]$. However, *post hoc* analysis revealed no difference at 3 compared to 6 and 9 N during ramp or hold ($P > 0.1$) except for fewer adjustments made during hold 3 N than hold 6 N ($P = 0.03$).

Second, we evaluated force generation during the ramp. As expected (and imposed by the task), the mean slope during the ramp increased as a function of target force.

Unexpectedly, we also found that the relative (normalized) slope also increased with target force $[F(2,56) = 15.8, P < 0.001, \eta_p^2 = 0.36]$ (Fig. 3a). This is related to the fact that the positive error during the ramp increased with target force. The CV of the slope, i.e. the variation of the slope during the ramp, was higher at lower forces $[F(2,56) = 99.3, P < 0.001, \eta_p^2 = 0.78]$ and decreased as a function of target force (Fig. 3b).

Third, we quantified the maintenance of force during the hold. The relative mean force level decreased with increasing force during the hold (Fig. 3c), $[F(2,56) = 76.4, P < 0.001, \eta_p^2 = 0.73]$, indicating that subjects maintained force farther away from the target force at 3 N compared to 6 and 9 N ($P < 0.001$). The variation of the force during the hold period (i.e. the CV of force) also decreased with increasing force $[F(2,56) = 31.1, P < 0.001, \eta_p^2 = 0.53]$ (Fig. 3d).

Fourth, we evaluated the timing of force changes about the target force on- and offset. The average time of force onset varied between −307 and 91 ms, but did not depend on target force level $[F(2,56) = 1.6, P = 0.2, \eta_p^2 = 0.05]$. Average offset time, i.e., force release, varied between −185 and 101 ms and was earlier with increasing force $[F(2,56) = 23.1, P < 0.001, \eta_p^2 = 0.45]$.

Fig. 3 Performance measures as a function of target force: **a** Grand average and SD of the relative mean slope of applied force during the ramp. **b** Grand average and SD of the Coefficient of variation of the slope as a function of target force. **c** Grand average and SD of the relative mean force during the hold. *Y-axis* Rel. mean force of 1 equals the target level. **d** Grand average and SD of the Coefficient of variation of the force during the hold
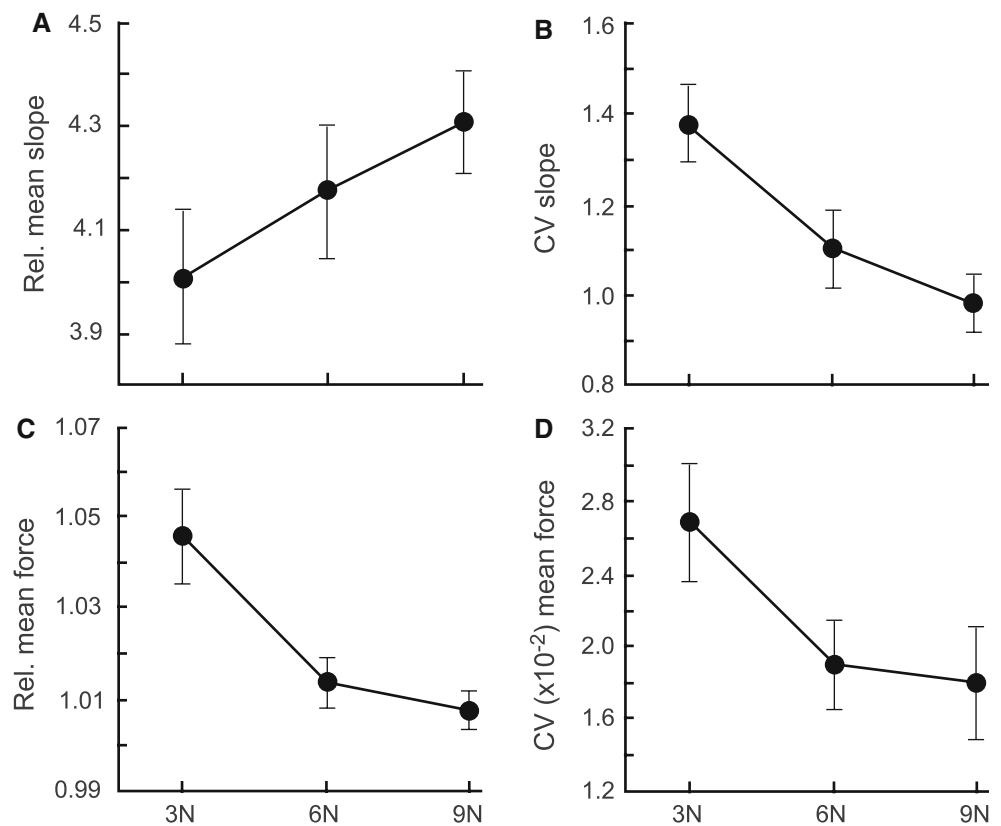
Relation between precision of isometric force tracking and age

The relation between task precision and age was quantified by Pearson correlations. The error increased with age at 3 N during the ramp (Fig. 4a, $r = 0.58$, $P = 0.001$) and the hold (Fig. 4b, $r = 0.46$, $P = 0.01$). However, no relation between error and age was found at 6 and 9 N (Fig. 4).

Examination of error type during the ramp revealed that the positive error increased with age at 3 N ($r = 0.47$, $P = 0.01$). A similar relation was found at 6 N ($r = 0.41$, $P = 0.03$) and no relation was found at 9 N ($P > 0.2$). Negative error did not correlate with age at any force level during the ramp.

During the hold, positive error also increased with age ($r = 0.43$, $P = 0.02$; $r = 0.59$, $P = 0.001$; $r = 0.51$, $P = 0.005$, at 3, 6, and 9 N, respectively). Similar to the ramp, negative error did not correlate with age at any force level during the hold.

Relation between performance of isometric force tracking and age

The relation between task performance and age was quantified by Pearson correlations. First, the number of force adjustments made during the ramp correlated

negatively with age at 3 and 6 N, i.e., middle-aged subjects made fewer adjustments (Fig. 5, $r = -0.47$, $P = 0.009$; $r = -0.50$, $P = 0.006$, respectively). No age effect was found with the number of adjustments made during the hold.

Second, force generation during the ramp was also age-dependent: the relative mean slope decreased with increasing age across all force levels (Fig. 6a, $r = -0.46$, $P = 0.01$; $r = -0.65$, $P < 0.001$; $r = -0.53$, $P = 0.003$). An increasing CV of the slope with age was found at 3 N ($r = 0.40$, $P = 0.03$). However, no relation was found at 6 and 9 N ($P > 0.2$).

Third, force maintenance was only partially dependent on age (Fig. 6b): during hold, the relative mean force increased with increasing age at 3 N ($r = 0.51$, $P = 0.005$). A trend for similar relationships was found at 6 and 9 N ($r = 0.4$, $P = 0.03$; $r = 0.38$, $P = 0.04$, respectively). No relation was found between age and CV of force at any force level ($P > 0.12$).

Fourth, time of force onset was a function of age: force onset was earlier with increasing age for all three target force levels (Fig. 7, $r = -0.43$, $P = 0.02$; $r = -0.50$, $P = 0.006$; $r = -0.55$, $P = 0.002$, at 3, 6, and 9 N, respectively). Time of offsets did not correlate with age at any force level ($P > 0.6$). Figure 1c gives a single trial example of earlier onsets (arrows) in a middle-aged subject compared to a younger subject (Fig. 1b).
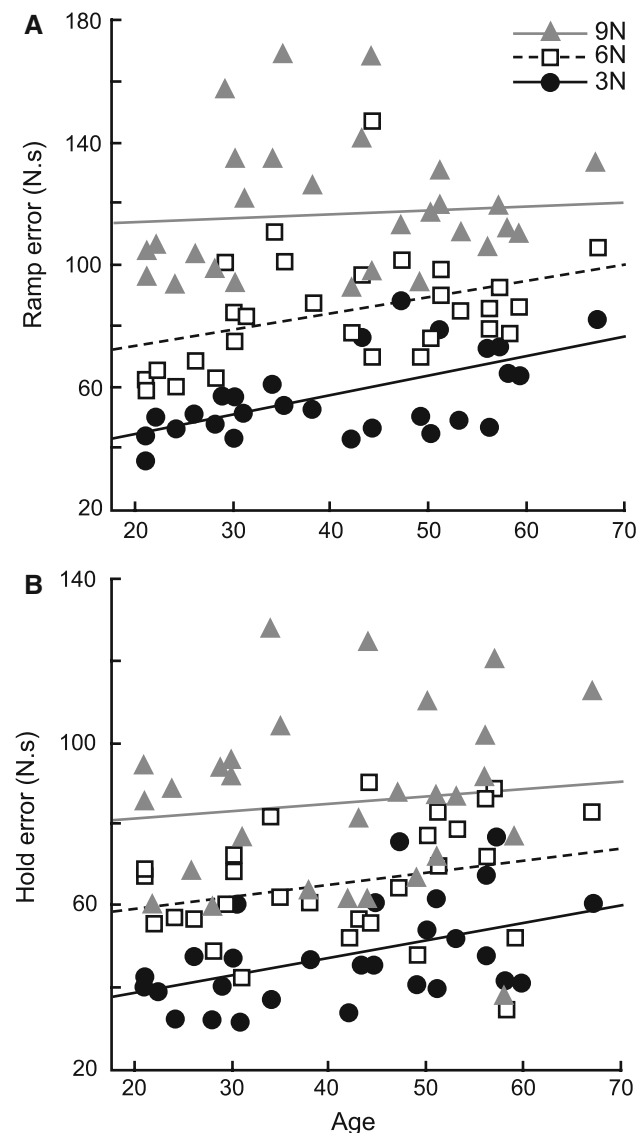
Fig. 4 Precision measures as a function of age. **a** Ramp error as a function of age for each target level. Each *symbol* represents the average ramp error of a single subject across all trials of a given target force (*circle*, *square* and *triangle* depict, respectively, 3, 6 and 9 N target force). *Oblique lines* indicate the linear regression. **b** Hold error as a function of age for each target level. *Symbols* as in **a**
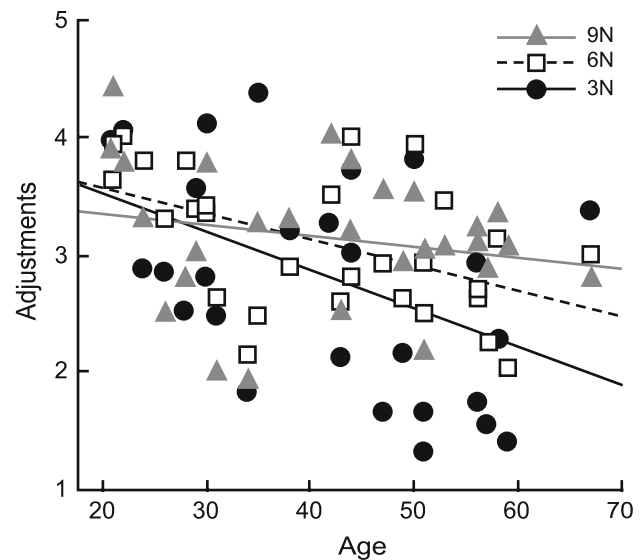

Fig. 5 Performance measure as a function of age. Mean number of force adjustments during the ramp period as a function of age for each target level. Each *symbol* represents the average number of force adjustments of a single subject across all trials of a given target force. *Oblique lines* indicate the linear regression. *Symbols* as in Fig. 4

Relation between maximal force, steadiness during hold phase and age

Maximal force ranged from 22.9 to 39.5 N (mean = 32.5, SD = 4.8 N). Maximal voluntary contraction (grip) force was not correlated to and did not decrease with age ($r = 0.34$, $P = 0.07$). The force power spectra during the hold peaked at 1 Hz independent of the force level. The mean power spectral density of the 1 Hz peak increased as a function of force (1.63, 5.04, and 8.8 at 3, 6, and 9 N levels). However, the force power spectra (from 1 to

15 Hz) during the hold period showed no difference between younger and middle-aged subjects.

Relation between precision and performance characteristics

Since task precision may depend on performance characteristics, we attempted to correlate these two sets of parameters, first for the ramp period and second for the hold period. Table 1 summarizes the results. During the ramp, clearly, the more adjustments (target crossings) were made the smaller the error (negative correlations). Intuitively, this makes sense, since subjects with many crossings tend to be close to the target and thus tend to have small errors. In contrast, large variations of the slope (CV) produced larger errors. Neither the force onset nor the mean slope correlated with error. However, a *post hoc* within-subject analysis across individual trials was performed in order to evaluate whether subjects matched the slope of the force generated with the onset times during the ramp. A positive correlation was found in all subjects (r values ranged from 0.38 to 0.76, mean 0.6), i.e., subjects produced more force (steeper slope) the later the onset.

During the hold, the number of adjustments did not correlate with the error. The mean force correlated with the error at the 3 N level only, while the variation of the force (CV) correlated with error at 3 and 9 N levels.
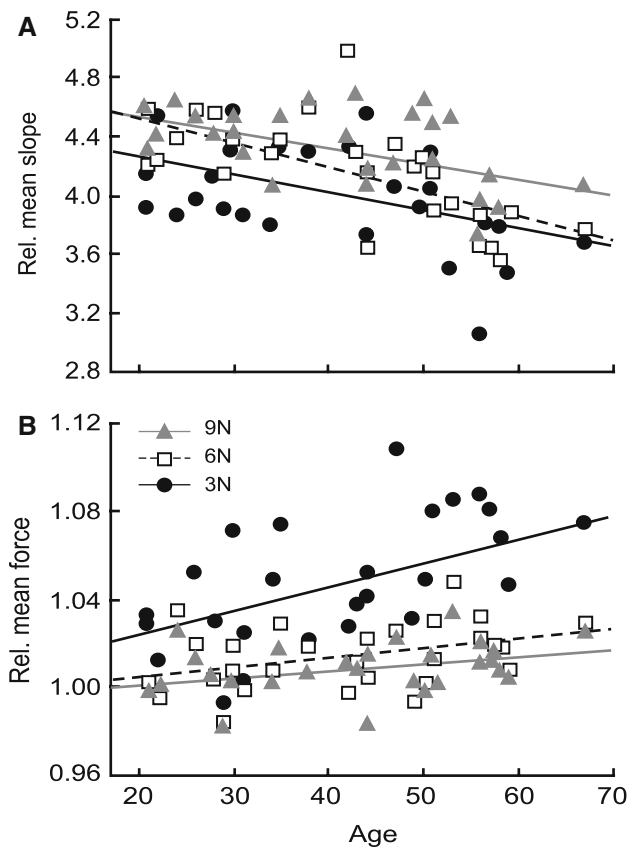
A

B

Fig. 6 Performance measure as a function of target force. **a** Relative mean slope of applied force during the ramp as a function of age for each target level. Each *symbol* represents the average slope of a single subject across all trials of a given target force. *Oblique lines* indicate the linear regression. **b** Relative mean force during the hold as a function of age during each target level. *Symbols as in Fig. 4*
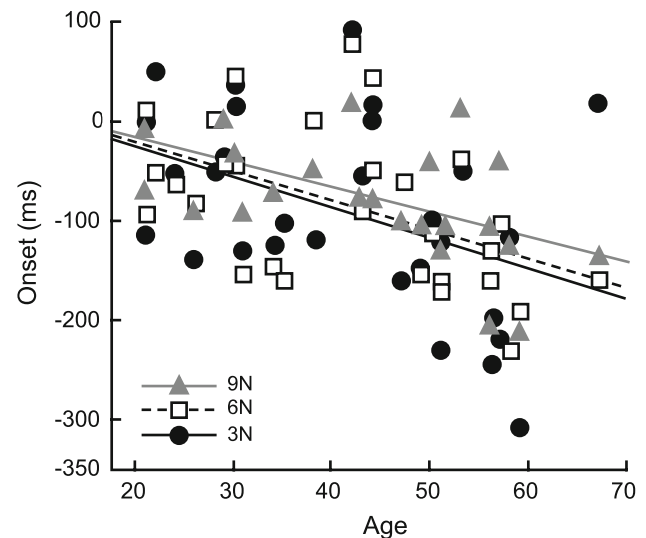

Fig. 7 Performance measure as a function of age. Mean latency of the force onset as a function of age for each target level. Each *symbol* represents the mean force onset time of a single subject across all trials of a given target force. *Oblique lines* indicate the linear regression. Symbols as in Fig. 4

Table 1 Correlations between precision (total error) and performance characteristics

	3 N Total error	6 N Total error	9 N Total error
Ramp			
Adjustments	−0.68***	−0.59***	−0.36*
Mean slope	0.00	−0.18	−0.05
CV of slope	0.51**	0.52**	0.59***
Force onset	−0.36	−0.05	0.08
Hold			
Adjustments	−0.28	−0.19	−0.17
Mean force	0.76***	0.35	−0.08
CV of force	0.61***	0.28	0.52***

Pearson correlation coefficients shown

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Discussion

We examined whether age-related changes in precision grip force tracking occur already in middle age (working adults <60 years). We characterized these changes in terms of *precision* (tracking accuracy) and *performance* (the way the task was achieved). For the visuomotor ramp-and-hold force tracking, we showed that in terms of *precision*, larger errors were made during the ramp than during the hold and this was independent of age (Figs. 2, 3), whereas age mainly affected the precision at the lowest (3 N) but not at higher (6 and 9 N) force levels (Figs. 4, 5). This supports our hypothesis that a gradual decline in grip force control occurs from adulthood to middle age, specifically for force control at low forces. In contrast, but in accordance with our second hypothesis, maximal grip force did not vary with age. In terms of *performance*, the latency (onset of force increase) was systematically earlier in middle-aged subjects (Fig. 7) and the average slope of the force during the ramp systematically decreased with age (Fig. 6). These

latter findings suggest that middle-aged subjects adopt a strategy to compensate for degenerative age-related processes (discussed below).

Precision compromised in visuomotor tracking tasks with age

Our visuomotor force-tracking task was divided into a ramp and a hold phase. Independent of age, the error (whether absolute or relative) was higher during the ramp than the hold phase, indicating that the steady generation (increase) of force is a more difficult task than the maintenance of force. This finding is in agreement with

Vaillancourt and Newell (2003) who found that the precision is lower during dynamic (sine wave tracking) than during constant force tracking, even though the slope of the ramp was constant in our study. Whole group analysis (independent of age) also revealed that visuomotor tracking was more demanding at low forces, as indicated by higher relative error and coefficient of variation. Precision at the 3 N target force was age-dependent with poorer precision with advancing age. Whereas previous findings showed reduced control during submaximal contractions in the elderly (Galganski et al. 1993; Enoka et al. 2003; Sosnoff and Newell, 2006), we found a similar tendency in middle-aged subjects, particularly so for force control at low forces. Poorer precision with increasing age was found both during the generation and maintenance phases of the tracking at 3 N.

Performance: compensatory strategies in middle-aged subjects

The way subjects performed the task was a function of age: both the ramp and the hold period were affected. During the ramp middle-aged subjects showed earlier force onsets than younger subjects. This was true for the ramps of all three target force levels. Two of our findings suggest that this relation reflects an active and systematic (but most likely unconscious) strategy undertaken by middle-aged subjects rather than an age-related general decline in timing: (1) Within-subject analysis revealed positive correlations between time of onset and slope of force in all subjects. Thus, an early onset meant a small slope of force generation, whereas a late onset meant a steeper slope of force generation. This association between onset timing and slope, which assures that the steady-state target force level will be attained at the end of the ramp even if the slope is lower than the target slope, was intact in middle-aged subjects. This association did not vary with age. However, in order to make this strategy work, subjects need to anticipate future force trajectories, which was feasible in our task. (2) No age-dependent difference was found in the timing of force offsets (the release of force at the end of the hold phase). This finding speaks against a general decline in timing with increasing age, since a general decline should also affect the timing of force offset, which was not the case.

During the hold, middle-aged subjects showed a steady and systematic overshoot of force during the force maintenance phase at the 3 N target level, as indicated by the positive correlation between positive error and age. This is similar to the excessive force profile found in middle-aged (Cole et al. 1999) and older (Gilles and Wing 2003) individuals performing a precision grip-and-lift task.

The middle-aged subject's systematic use of these two strategies suggests a behavioral compensation in order to comply with the task requirements and possibly to improve precision. Similar use of compensatory strategies has been reported during reaching, where older subjects slow down the later part of the movement in order to improve accuracy (Goggin and Meeuwsen 1992), and in standing, where they use different muscles in the leg to maintain postural stability while moving the arms (Bleuse et al. 2006). The presence of such behavioral strategies suggests a certain cognitive involvement. Since even simple movements can be regarded as complex cognitive tasks (Hausdorff et al. 2005) our visuomotor force tracking task undoubtedly requires a cognitive effort, and may be more so for middle-aged than younger subjects. This would be in line with (1) behavioral dual-task paradigms that showed a stronger interrelation between cognitive tasks and force control in older subjects (Voelcker-Rehage et al. 2006) and (2) with brain imaging studies, where older subjects showed greater movement-related brain activity in sensory-motor and attentional cortical networks (Heuninckx et al. 2005; Ward and Frackowiak 2003; Mattay et al. 2002). Thus, in terms of a functional implication, it seems possible that middle-aged subjects already deploy additional cognitive resources to counterbalance subtle deteriorating motor performance, as do older subjects with impaired motor performance (Lindenberger et al. 2000).

Compensatory strategies: possible mechanisms

Why do middle-aged subjects have systematically earlier force onsets prior to the ramp and why do they apply more force during the maintenance phase (at 3 N) than young subjects? Previous studies suggested that a gradual deterioration of tactile or visual processing with age (Kaneko et al. 2005) may cause subjects to alter their strategies (Cole et al. 1999; Lazarus and Haynes 2000; Warabi et al. 1986). However, several observations in the present study suggest that the change of strategy was not due to a deterioration of sensory processing or due to a general slowing of processing: (1) it seems unlikely that a general slowing of visual processing would affect the force onset (earlier in middle-aged subjects) but not the force offset (no age-related difference). (2) As our error-feedback was visual, it seems unlikely that the earlier force onsets in middle-aged subjects were due to subtle tactile impairments (Kaneko et al. 2005). (3) The findings are also inconsistent with the notion of general motor slowing with age (Jagacinski et al. 1995; Smith et al. 1999), since middle-aged subjects showed earlier, not later, onsets and no difference in offset timing.

About the excessive force during the maintenance phase, it has been shown that older subjects increase their

"safety margin" during object manipulation, either in lifting tasks (Johansson and Westling 1987; Cole 1991; Cole et al. 1999) or when manipulating an object under varying external load conditions (Danion et al. 2007). Our results can be similarly interpreted as reflecting an increase in "safety margin" with respect to a possible undershoot during the hold. Cole et al. (1999) suggested that the increased force in older subjects was due to a reduced tactile sensibility implicated in encoding frictional information from the index finger and thumb. Indeed, excessive grip and lift forces have also been found in healthy subjects who undergo anesthesia (Augurelle et al. 2003) and in patients with sensory loss (Hermsdörfer et al. 2004). However, in our study, middle-aged subjects did not have pressure perception thresholds different from younger subjects, corresponding to observations that show a decline in pressure perception mainly after age 60 (Cole et al. 1999; Kaneko et al. 2005). These findings suggest that something other than reduced sensory processing or general slowing is causing the early onsets and the increased force levels seen in this study.

Our data are compatible with the suggestion that particular degenerative changes in the motor system cause subjects to adopt new and active strategies (Shim et al. 2004). Such degenerative changes include reduced subcortical white matter volume along the corticospinal tract (Pieperhoff et al. 2008) as well as reduced corticospinal excitability (Oliviero et al. 2006). At the level of the motor units, several changes have been observed: loss of motor units (Brown 1973; Campbell et al. 1973; Doherty 2003) along with a reduction of their contractile speed (Doherty and Brown 1997), altered firing patterns (Erim et al. 1999; Vaillancourt et al. 2003), reduced and more variable firing rates (Kamen and Knight 2004), especially at low forces (Laidlaw et al. 2000; Tracy et al. 2005). Altered muscle fiber structure, remodeling of motor axons, as well as altered muscle physiology leads to greater force being exerted by single motor units with increasing age (Galganski et al. 1993; Doherty and Brown 1997; Knight and Kamen 2007). Together these degenerative changes likely lead to poorer regulation of isometric precision grip force (Vaillancourt et al. 2003; Kamen and Knight 2004; Kornatz et al. 2005).

Although it is not possible in this study to pinpoint the mechanism causing poorer force tracking in middle-aged subjects, it seems likely that *progressive* age-related degenerative changes occur (Doherty and Brown 1997) that lead to behavioral consequences as we have hypothesized. Reduced force regulation at low forces without decreased grip strength is fully compatible with progressive physiologic alterations, in particular with loss of motor units (Brown 1973; Doherty 2003), larger motor unit twitch tension and slower contraction speed (Doherty and Brown

1997). During the *ramp*, the middle-aged subjects may start producing force earlier to compensate for slowed force production secondary to these degenerative changes. This compensatory strategy would explain why an age-related difference in timing was only found for onsets and not for offsets and why it occurs systematically across all target force levels. This strategy allows more time to generate force but may reduce precision in tasks requiring high temporal accuracy, as indicated by the correlation between onset timing and precision at the 3 N target level. The systematic use of early anticipation has been documented in older people: they anticipate body weight shifts earlier and take more protective steps than younger people take during postural perturbations (Jonsson et al. 2007; Pai et al. 1998). Thus, middle-aged subjects are likely to anticipate movement onsets in a variety of everyday tasks to compensate for degenerative slowness within the motor system. However, this type of compensatory strategy is only applicable in tasks that allow for prediction and sufficient time for action planning: older subjects show slowed reaction times for hand movements in tasks where anticipation is ruled out (Warabi et al. 1986). Similarly, excessive *maintenance* of force at the 3 N target level may also be secondary to degenerative changes in the motor system. In particular, two processes might have lead middle-aged subjects to adopt a compensatory strategy that favored an overshoot: remodeling of motor units and increased firing variability. Both processes would make it more difficult to maintain a low and steady grip force as required in our task. A similar interpretation was offered by Hermsdörfer et al. (2004) for excessive grip forces in subjects without sensory impairments. However, the influence on steady force seems to be moderate, since our middle-aged subjects did not show altered frequency components in the force trace, as found in older subjects (Christou et al. 2004). To conclude, our data show that precision during low grip force control declines already during middle age and suggest that middle-aged subjects adapt their force generation strategies to possibly compensate for early and subtle degenerative changes in the motor system before decline in grip strength is apparent.

References

Augurelle AS, Smith AM, Lejeune T et al (2003) Importance of cutaneous feedback in maintaining a secure grip during manipulation of hand-held objects. J Neurophysiol 89(2):665–671

Bleuse S, Cassim F, Blatt JL et al (2006) Effect of age on anticipatory postural adjustments in unilateral arm movement. Gait Posture 24(2):203–210

Brown WF (1973) Functional compensation of human motor units in health and disease. J Neurol Sci 20(2):199–209

Campbell MJ, McComas AJ, Petito F (1973) Physiological changes in ageing muscles. J Neurol Neurosurg Psychiatry 36(2):174–182

Christou EA, Carlton LG (2001) Old adults exhibit greater motor output variability than young adults only during rapid discrete isometric contractions. J Gerontol A Biol Sci Med Sci 56(12):524–532

Christou EA, Tracy BL (2006) Aging and variability in motor output. In: Davids K, Bennett S, Newell KM (eds) Movement system variability, pp 199–215

Christou EA, Jakobi JM, Critchlow A et al (2004) The 1- to 2-Hz oscillations in muscle force are exacerbated by stress, especially in older adults. J Appl Physiol 97(1):225–235

Cole KJ (1991) Grasp force control in older adults. J Mot Behav 23(4):251–258

Cole KJ, Rotella DL, Harper JG (1999) Mechanisms for age-related changes of fingertip forces during precision gripping and lifting in adults. J Neurosci 19(8):3238–3247

Cruz-Sánchez FF, Moral A, Tolosa E et al (1998) Evaluation of neuronal loss, astrocytosis and abnormalities of cytoskeletal components of large motor neurons in the human anterior horn in aging. J Neural Transm 105(6–7):689–701

Danion F, Descoins M, Bootsma RJ (2007) Aging affects the predictive control of grip force during object manipulation. Exp Brain Res 180(1):123–137

Doherty TJ (2003) Invited review: aging and sarcopenia. J Appl Physiol 95(4):1717–1727

Doherty TJ, Brown WF (1997) Age-related changes in the twitch contractile properties of human thenar motor units. J Appl Physiol 82(1):93–101

Enoka RM, Christou EA, Hunter SK et al (2003) Mechanisms that contribute to differences in motor performance between young and old adults. J Electromyogr Kinesiol 13(1):1–12

Erim Z, Beg MF, Burke DT et al (1999) Effects of aging on motor unit control properties. J Neurophysiol 82(5):2081–2091

Galea V (1996) Changes in motor unit estimates with aging. J Clin Neurophysiol 13(3):253–260

Galganski ME, Fuglevand AJ, Enoka RM (1993) Reduced control of motor output in a human hand muscle of elderly subjects during submaximal contractions. J Neurophysiol 69(6):2108–2115

Gilles MA, Wing AM (2003) Age-related changes in grip force and dynamics of hand movement. J Mot Behav 35(1):79–85

Goggin NL, Meeuwsen HJ (1992) Age-related differences in the control of spatial aiming movements. Res Q Exerc Sport 63(4):366–372

Hausdorff JM, Yogev G, Springer S et al (2005) Walking is more like catching than tapping: gait in the elderly as a complex cognitive task. Exp Brain Res 164(4):541–548

Hermsdörfer J, Hagl E, Nowak DA (2004) Deficits of anticipatory grip force control after damage to peripheral and central sensorimotor systems. Hum Mov Sci 23(5):643–662

Heuninckx S, Wenderoth N, Debaere F et al (2005) Neural basis of aging: the penetration of cognition into action control. J Neurosci 25(29):6787–6796

Jagacinski RJ, Liao MJ, Fayyad EA (1995) Generalized slowing in sinusoidal tracking by older adults. Psychol Aging 10(1):8–19

Johansson RS, Westling G (1987) Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. Exp Brain Res 66(1):141–154

Jonsson E, Henriksson M, Hirschfeld H (2007) Age-related differences in postural adjustments in connection with different tasks involving weight transfer while standing. Gait Posture 26(4):508–515

Kamen G, Knight CA (2004) Training-related adaptations in motor unit discharge rate in young and older adults. J Gerontol A Biol Sci Med Sci 59(12):1334–1338

Kaneko A, Asai N, Kanda T (2005) The influence of age on pressure perception of static and moving two-point discrimination in normal subjects. J Hand Ther 18(4):421–424

Knight CA, Kamen G (2007) Modulation of motor unit firing rates during a complex sinusoidal force task in young and older adults. J Appl Physiol 102(1):122–129

Kornatz KW, Christou EA, Enoka RM (2005) Practice reduces motor unit discharge variability in a hand muscle and improves manual dexterity in old adults. J Appl Physiol 98(6):2072–2080

Kurillo G, Zupan A, Bajd T (2004) Force tracking system for the assessment of grip force control in patients with neuromuscular diseases. Clin Biomech 19(10):1014–1021

Laidlaw DH, Bilodeau M, Enoka RM (2000) Steadiness is reduced and motor unit discharge is more variable in old adults. Muscle Nerve 23(4):600–612

Lazarus JA, Haynes JM (2000) Isometric pinch force control and learning in older adults. Exp Aging Res 23(2):179–199

Lexell J, Taylor CC, Sjöström M (1988) What is the cause of the ageing atrophy? Total number, size and proportion of different fiber types studied in whole vastus lateralis muscle from 15- to 83-year-old men. J Neurol Sci 84(2–3):275–294

Lindenberger U, Markise M, Baltes PB (2000) Memorizing while walking: increase in dual-task costs from young adulthood to old age. Psychol Aging 15:417–436

Mattay VS, Fera F, Tessitore A et al (2002) Neurophysiological correlates of age-related changes in human motor function. Neurology 58(4):630–635

Oliviero A, Profice P, Tonali PA et al (2006) Effects of aging on motor cortex excitability. Neurosci Res 55(1):74–77

Pai YC, Rogers MW, Patton J et al (1998) Static versus dynamic predictions of protective stepping following waist-pull perturbations in young and older adults. J Biomech 31(12):1111–1118

Pieperhoff P, Hömke L, Schneider F et al (2008) Deformation field morphometry reveals age-related structural differences between the brains of adults up to 51 years. J Neurosci 28(4):828–842

Ranganathan VK, Siemionow V, Sahgal V et al (2001) Effects of aging on hand function. J Am Geriatr Soc 49(11):1478–1484

Shim JK, Lay BS, Zatsiorsky VM et al (2004) Age-related changes in finger coordination in static prehension tasks. J Appl Physiol 97(1):213–224

Smith CD, Umberger GH, Manning EL et al (1999) Critical decline in fine motor hand movements in human aging. Neurology 53(7):1458–1461

Sosnoff JJ, Newell KM (2006) Are age-related increases in force variability due to decrements in strength? Exp Brain Res 174(1):86–94

Tracy BL, Maluf KS, Stephenson JL et al (2005) Variability of motor unit discharge and force fluctuations across a range of muscle forces in older adults. Muscle Nerve 32(4):533–540

Vaillancourt DE, Newell KM (2003) Aging and the time and frequency structure of force output variability. J Appl Physiol 94(3):903–912

Vaillancourt DE, Larsson L, Newell KM (2003) Effects of aging on force variability, single motor unit discharge patterns, and the structure of 10, 20, and 40 Hz EMG activity. Neurobiol Aging 24(1):25–35

Voelcker-Rehage C, Alberts JL (2005) Age-related changes in grasping force modulation. Exp Brain Res 166(1):61–70

Voelcker-Rehage C, Stronge AJ, Alberts JL (2006) Age-related differences in working memory and force control under dual-task conditions. Neuropsychol Dev Cogn B Aging Neuropsychol Cogn 13(3–4):366–384

Voermans NC, Schelhaas HJ, Munneke M et al (2006) Dissociated small hand muscle atrophy in aging: the 'senile hand' is a split hand. Eur J Neurol 13(12):1381–1384

Warabi T, Noda H, Kato T (1986) Effect of aging on sensorimotor functions of eye and hand movements. Exp Neurol 92(3):686–697

Ward NS, Frackowiak RS (2003) Age-related changes in the neural correlates of motor performance. Brain 126:873–888

Woollacott MH, Manchester DL (1993) Anticipatory postural adjustments in older adults: are changes in response characteristics due to changes in strategy? J Gerontol 48(2):64–70