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Different Neural Adjustments Improve Endpoint Accuracy With Practice in Young and Old Adults

Evangelos A. Christou, Brach Poston, Joel A. Enoka, and Roger M. Enoka

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Christou EA, Poston B, Enoka JA, Enoka RM. Different neural adjustments improve endpoint accuracy with practice in young and old adults. *J Neurophysiol* 97: 3340–3350, 2007. First published March 21, 2007; doi:10.1152/jn.01138.2006. The purpose of the study was to determine the practice-induced adjustments in the motor-output variability and the agonist–antagonist activity that accompanied improvements in endpoint accuracy of goal-directed isometric contractions in young and old adults. Young and old adults performed 100 trials that involved accurately matching the peak of a force trajectory (25% maximum) to a target force in 150 ms. Endpoint accuracy was quantified as the absolute difference between the target and the peak force and time-to-peak force. Motor-output variability was expressed as the SDs of the force trajectory, peak force, and time-to-peak force. The force and time errors differed between the two groups initially, but after 35 practice trials the errors were similar for the two groups. Reductions in force endpoint error were predicted by decreases in the variability of the force trajectory for both groups, adaptations in the agonist (first dorsal interosseus) and antagonist (second palmar interosseus) EMG for young adults, and adaptations only for the agonist EMG for old adults. Reductions in time endpoint error were predicted by increases in the SD of time-to-peak force and a longer delay to the peak EMG of the antagonist muscle for young adults, but by decreases in the SDs of time-to-peak force and force trajectory and a shorter delay to the peak EMG of the antagonist muscle for the old adults. The findings indicate that the neural adjustments underlying the improvement in endpoint accuracy with practice differed for young and old adults.

INTRODUCTION

Practice of goal-directed contractions can improve the accuracy of novel motor tasks (Woodworth 1899), whether the task involves isometric contractions (Floyer-Lea and Matthews 2005) or movements (Corcos et al. 1993; Darling and Cooke 1987a; Gottlieb et al. 1988; Muller and Sternad 2004). The greatest improvements in accuracy occur at the beginning of practice and are associated with changes in activity within higher centers (Floyer-Lea and Matthews 2005; Hikosaka et al. 2002; Ungerleider et al. 2002).

The neuromuscular mechanisms responsible for the initial improvements in accuracy with practice may differ for young and old adults. Young adults appear to improve accuracy initially by adjusting the amplitude and timing of the agonist and antagonist muscle activity (Corcos et al. 1989, 1990; Ghez and Gordon 1987; Gordon and Ghez 1987a,b; Gottlieb et al. 1992). Variation in the magnitude of the agonist activity seems to impair peak force accuracy, whereas variations in the duration of the agonist muscle activity and the magnitude of the

antagonist muscle activity produce errors in the time-to-peak force (Ghez and Gordon 1987; Gordon and Ghez 1987a,b). In contrast, the initial neuromuscular adaptations exhibited by old adults may be related to heightened levels of motor-output variability (Christou et al. 2003; Enoka et al. 2003; Sosnoff et al. 2004; Vaillancourt et al. 2004) and coactivation of the agonist and antagonist muscles (Burnett et al. 2000; Laidlaw et al. 2002; Spiegel et al. 1996). There is evidence that old adults increase coactivation to attenuate fluctuations in the movement trajectory (Seidler-Dobrin et al. 1998), which can disrupt the requisite ratio and timing of activation between the agonist and antagonist muscles during goal-directed contractions (Darling et al. 1989).

Numerous experimental studies previously demonstrated that motor-output variability decreases with practice of goal-directed isometric contractions (Floyer-Lea and Matthews 2005; Gordon and Ghez 1987a) and movements (Darling and Cooke 1987b; Muller and Sternad 2004). Although the minimum-variance hypothesis (Harris and Wolpert 1998) suggests that less noisy (variable) trajectories are associated with less endpoint variance and consequently greater accuracy, variability in muscle activation can increase as contractions become more accurate and less variable (Darling and Cooke 1987b; Osu et al. 2004).

The relative contribution of the reduction in motor-output variability to the initial improvement in endpoint accuracy of young and old adults is unclear (Muller and Sternad 2004). Some of this uncertainty can be attributed to the study of tasks in young (Corcos et al. 1989, 1990; Ghez and Gordon 1987; Gordon and Ghez 1984, 1987a,b; Gottlieb et al. 1992) and old adults (Darling et al. 1989; Seidler-Dobrin et al. 1998) that involve multiple agonist and antagonist muscles, which can make it difficult to identify the activation patterns that are responsible for endpoint accuracy and motor-output variability. In the current study, the experimental model was abduction of the index finger, which is controlled predominantly by single agonist (first dorsal interosseus) and antagonist (second palmar interosseus) muscles (Chao et al. 1989; Li et al. 2003). The purpose of the study was to determine the practice-induced adjustments in motor-output variability and the agonist–antagonist activity that accompanied improvements in endpoint accuracy of goal-directed isometric contractions in young and old adults. Motor-output variability was quantified as the variability in force trajectory, peak force, and time-to-peak force, whereas endpoint accuracy was expressed as the absolute error from the targeted force and time coordinates. Pre-

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liminary data were previously presented in abstract form (Christou et al. 2005).

METHODS

Fourteen young adults (seven men; 24.0 ± 2.1 yr) and 14 old adults (seven men; 72.1 ± 3.7 yr) volunteered to participate in the study. All subjects reported being healthy without any known neurological problems and were right-handed (Edinburgh Handedness Inventory; Oldfield 1971). Subjects provided written informed consent before participating in the study and the Human Research Committee at the University of Colorado in Boulder approved the procedures of the study.

Experimental arrangement

Each subject was seated and faced a 17-in. monitor that was located 1 m away at eye level. All subjects affirmed that they could clearly see the information provided on the monitor. The left arm was abducted by 45° and the left elbow was flexed to 90° . The left forearm and hand were maintained in a prone position on a wooden table (Taylor et al. 2003). The forearm and wrist were immobilized by Velcro straps that restrained the subject from exerting a force on the transducer with the elbow flexor muscles. Metal plates were used to restrain the thumb, middle, ring, and fifth fingers of the left hand and there was approximately a right angle between the left index finger and thumb. Only the left index finger was free to move and push against the force transducer. The left index finger was placed in a modified finger orthosis to maintain extension of the middle and distal interphalangeal joints. The left hand was used in this study because there is evidence to suggest that subjects learn a task more slowly with the nondominant hand (Sainburg 2002).

Force measurement

With the index finger abducted about 5° at the metacarpophalangeal joint, the abduction force exerted by the index finger was measured with a force transducer (Model 41, Sensotec) that was aligned with the proximal interphalangeal joint. To maximize the force in the abduction direction and to minimize the involvement of other muscles, subjects pushed against the rigid surface by a low-friction contact point. This was accomplished by mounting a 0.5-cm-diameter thimble (semisphere) on the orthosis. Unless subjects exerted a force perpendicular to the contact point (abduction), the thimble would slip from the rigid surface (Valero-Cuevas 2000). The force was digitized at 1,000 samples/s with a data-acquisition interface power 1401 (Cambridge Electronic Design, Cambridge, UK) and stored on a personal computer.

EMG measurement

Abduction of the index finger is produced almost exclusively by the first dorsal interosseus (FDI) muscle (Chao et al. 1989; Li et al. 2003) and the primary antagonist is second palmar interosseus (SPI) muscle. The EMG activity of these two muscles was measured with intramuscular bipolar electrodes that were inserted percutaneously into each muscle. Each electrode comprised two stainless steel wires (50- μ m diameter) that were insulated with Formvar (California Fine Wire, Grover Beach, CA). The electrodes were inserted into the belly of each muscle using a 30-gauge hypodermic needle. After the insertion of the electrodes, the needle was removed and the wires remained in the muscle belly for the duration of the experiment. Reference electrodes were placed on the styloid process of the ulna for the FDI and on the dorsal surface of the fifth metacarpophalangeal joint for the SPI. The EMG signals were amplified ($\times 1,000$ – $5,000$) and band-pass filtered (100– $5,000$ Hz; Coulbourn Instruments, Allentown, PA). The EMG of both muscles was sampled at 10k samples/s with a data-

acquisition interface power 1401 [Cambridge Electronic Design (CED), Cambridge, UK] and stored on a personal computer.

Experimental procedures

Subjects visited the laboratory for one experimental session that lasted roughly 2 h. At the beginning of the session, subjects completed several questionnaires and were familiarized with the experimental procedures. The familiarization included demonstration of the sub-maximal goal-directed contractions and explanation of the feedback provided on the monitor. After the familiarization, each subject performed the following procedures: 1) maximal voluntary contractions (MVCs) with the FDI (abduction of the index finger) and SPI (adduction of the index finger) muscles; 2) 100 submaximal goal-directed isometric contractions (5 blocks \times 20 contractions); 3) a repeat of the MVC trials with the FDI and SPI muscles to assess the level of fatigue.

MVC TASK. Subjects were instructed to exert maximal abduction (FDI) and adduction (SPI) forces with the index finger in the shortest time possible. The maximal force achieved in 150 ms was used to determine the target force for the goal-directed isometric contractions. Before each MVC, subjects were required to maintain a constant abduction force equal to 0.05 N (roughly 1.5% of the MVC force) for 3–5 s. The MVC task began when force was equal to 0.1 N (roughly 3% of the MVC). Three to five trials were recorded for each muscle, with a nearly 60-s rest between trials. Based on the force–time profiles, the peak force during the contraction and the maximal force achieved during the first 150 ms were recorded. The target force for the goal-directed task corresponded to 25% of the force achieved in the first 150 ms of the MVC task. The EMGs for FDI and SPI were normalized to the peak EMG levels recorded during the MVC task.

ENDPOINT ACCURACY TASK. The task was to match the peak of the abduction force exerted by the index finger to a target that consisted of a thick black line on a white background. The target line was displayed on the bottom half (15 \times 30 cm) of the computer monitor (Fig. 1A). The endpoint of the line had the target coordinates of 150 ms (time target) and 25% of the 150-ms MVC force (force target). The size of the target (0.1 cm²) remained constant. Subjects were instructed to match the endpoint of a force trajectory (peak force) to the endpoint of the line (force and time target).

Before each trial of the goal-directed task, subjects were required to maintain a constant abduction force equal to 1.5% of the MVC force for 3–5 s. The target for the baseline contraction was presented to the subjects in the top half of the monitor as a thin black line and the subject's abduction force was shown as a green line. Subjects were instructed to perform the endpoint accuracy task at their convenience (no reaction was required) after the cue "GO" from one of the experimenters. The endpoint accuracy task was performed 100 times with a 60-s rest every 20 trials and a 5-s rest between trials. Subjects could not see the force exerted during each trial, but did receive visual feedback of the performance 1 s after each trial. The force exerted during the goal-directed contraction was superimposed as a red line on the target template (black line on white background) and was presented to the subjects on the bottom half of the monitor. In addition, one of the investigators provided verbal feedback about the performance by describing it as 1) low force, short time; 2) high force, short time; 3) high force, long time; or 4) low force, long time. The knowledge of results provided by this feedback was intended to improve performance in subsequent trials (Newell 1976).

Data analysis

Data were acquired with Spike2 software (Version 5.07; CED) and analyzed off-line using custom-written programs in Matlab (The MathWorks, Natick, MA).

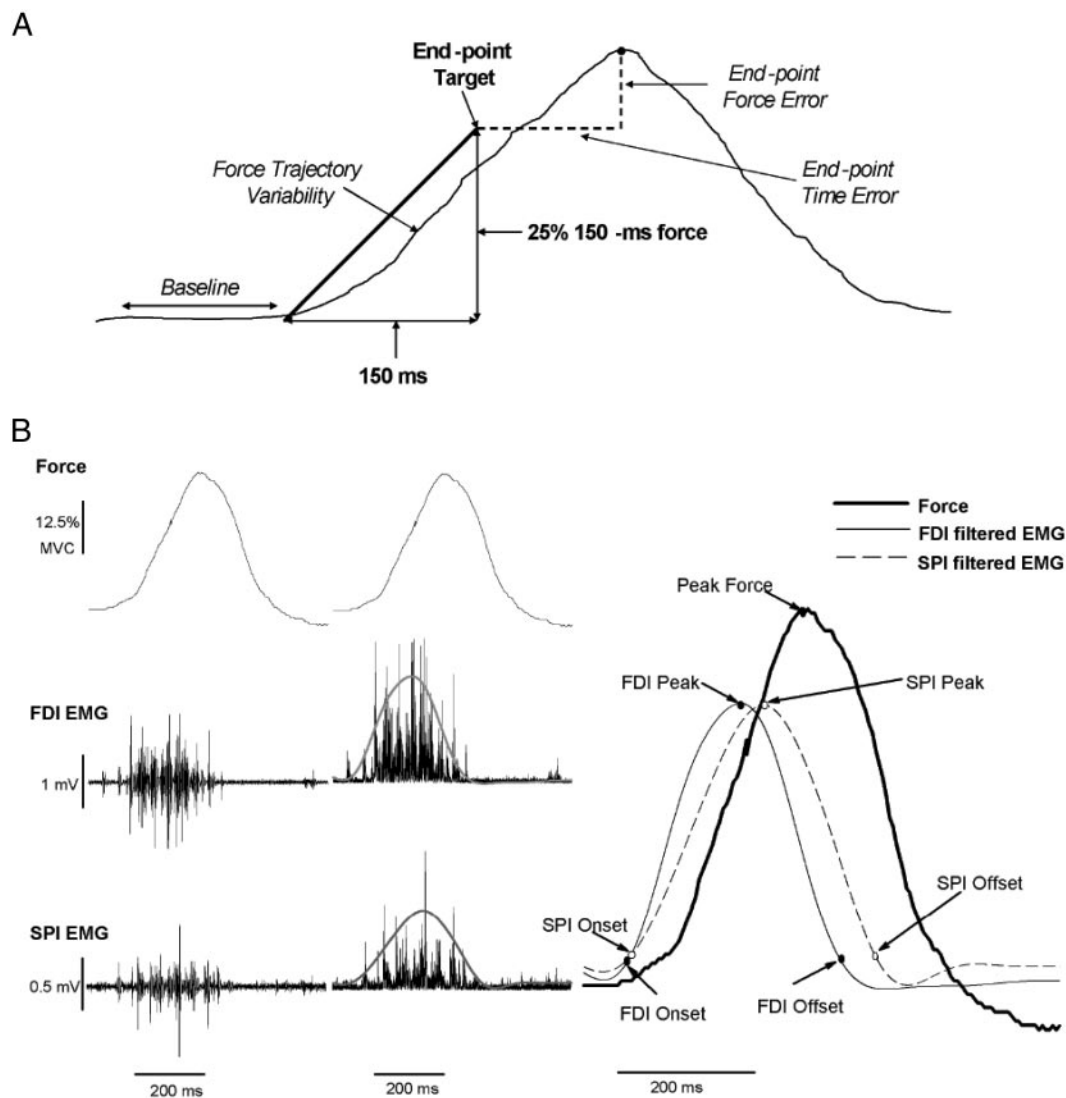


FIG. 1. Goal-directed task and assessment of endpoint accuracy and electromyographic (EMG) activity of the agonist and antagonist muscles. *A*: target was the endpoint of a trajectory displayed as a thick black line on white background. Coordinates of the target included time (x ; equal to 150 ms) and force (y ; equal to 25% of the maximal force achieved in 150 ms). Subjects were instructed to exert an abduction force and match the peak force of the force–time trajectory to the target. Force and time endpoint errors were quantified as the absolute error to the targeted force and time. *B*: interference EMG (left column) of the first dorsal interosseus (FDI, agonist) and second palmar interosseus (SPI, antagonist) muscles was rectified (middle column) and low-pass filtered at 6 Hz (solid line superimposed over rectified EMG). EMG activity was characterized by the following measurements of the low-pass filtered EMG: onset (start), offset (end), peak amplitude, duration, and area under the EMG–time curve (integrated EMG) for each muscle. In addition, measurements were made of the relative EMG amplitude and timing between the 2 muscles and the peak force (see the text for details).

ENDPOINT ACCURACY. Errors were measured between the endpoint of the trial (peak force) and the target in the time (ms) and force (N) domains (Fig. 1*A*). The force endpoint error was the absolute difference between the targeted peak force and the exerted peak force, whereas the time endpoint error was the absolute difference between the targeted time-to-peak force and the exerted time-to-peak force for each trial.

ABDUCTION FORCE. Once the goal-directed abduction force exceeded the threshold (3% of the 150-ms force), it was characterized by the following parameters: 1) peak force; 2) time-to-peak force; 3) variability in peak force: trial-to-trial variability for peak force for every five trials as the average of the square distance of each trial from the mean of five trials for peak force (van Beers et al. 2004); 4) variability in time-to-peak force: trial-to-trial variability for time-to-peak force for every five trials as the average of the square distance of each trial from the mean of five trials for time-to-peak force (van

Beers et al. 2004); and 5) variability in the force trajectory: SD of the detrended force from force onset to peak force.

AGONIST AND ANTAGONIST EMG BURSTS. The interference EMG of the FDI and SPI muscles was rectified and smoothed using a fourth-order Butterworth digital filter with a cutoff frequency of 6 Hz (Fig. 1*B*). This filter was used to identify the overall EMG bursts of the agonist and antagonist muscles. Preliminary analyses indicated that estimation of onset and offset times for the EMG activity was similar with a 40-Hz low-pass filter. The EMG activity was characterized by measuring: 1) onset (start) of EMG: >15% of the peak EMG; 2) offset (end) of EMG: <15% of the peak EMG; 3) Normalized peak EMG amplitude—relative to the maximal MVC value; 4) EMG duration: the time between the onset and offset; 5) EMG-force delay: time between peak EMG amplitude for FDI and SPI and peak force; 6) SPI-to-FDI peak delay: time between peaks in FDI and SPI EMGs; 7) SPI-to-FDI onset delay:

time between onsets in FDI and SPI EMGs; and 8) concurrent activity: percentage overlap of SPI and FDI durations. The trial-to-trial variability of these parameters was quantified as the SD of each parameter for every five trials.

Statistical analysis

To examine the improvement in endpoint accuracy across trials for young and old adults, a two-way ANOVA (age \times 20 blocks of five trials each) with repeated measures on blocks of trials compared the force and time endpoint error and the motor-output variability (force-trajectory variability, peak-force variability, and time-to-peak force variability) across blocks (SPSS version 13.0). Post hoc analysis to locate differences between blocks of trials included one-way ANOVA and Tukey's honestly significant difference test. The differences between the two age groups were identified with independent *t*-tests. The inflection point (change of sign in double differential) of the decreasing force and time error with practice was also used to identify the trial block where practice-induced improvements in endpoint accuracy reached a plateau. Pearson correlations (*r*) were used to determine significant associations between endpoint error, motor-output variability, and EMG variables.

Multiple linear regression models were used to establish statistical models that could predict the force and time endpoint error (criterion variables) in the first block of trials from the peak-force variability, time-to-peak force variability, force-trajectory variability, and agonist and antagonist muscle activity parameters (predictor variables). Similarly, multiple linear regression models were used to determine statistical models that could predict the change in force and time endpoint error with initial practice (block 1 to block 8; criterion variable) from the change in peak-force variability, time-to-peak force variability, force-trajectory variability, and agonist and antagonist muscle activity parameters (predictor variables). Predictor variables were included in the multiple regression models only when they were significantly associated (bivariate regressions) with the force and time endpoint error (criterion variables).

The goodness-of-fit of the model, which indicates how well the linear combination of the variables predicted the force and time endpoint error, was given by the squared multiple correlation (R^2) and the adjusted squared multiple correlation (adjusted R^2). The adjusted R^2 is reported because the R^2 can overestimate the percentage of the variance in the criterion variable that can be accounted for by the linear combination of the predictor variables, especially when the sample size is small and the number of predictors is large (Green and Salkind 2002). The relative importance of the predictors was estimated with the part correlations (part *r*), which provide the correlation between a predictor and the criterion, partialing out the effects of all other predictors in the regression equation from the predictor but not the criterion (Green and Salkind 2002). A positive sign of the part correlation indicates that the predictor and the criterion are directly related, whereas a negative sign indicates that they are inversely related.

The alpha level for all statistical tests was 0.05. Data are reported as means \pm confidence intervals within the text and figures.

RESULTS

The purpose of the study was achieved by examining the initial adjustments in endpoint accuracy, motor-output variability, and EMG burst activity of the agonist and antagonist muscles as young and old adults practiced the task. Endpoint accuracy was denoted as the error in force and time coordinates of the peak in the force relative to the target force, and motor-output variability corresponded to variability in the force trajectory, peak force, and time-to-peak force (Fig. 1).

Strength

Young and old adults exhibited similar [$t(26) < 0.2, P > 0.2$] peak force (21.4 ± 3.4 vs. 25.7 ± 6.7 N) and time-to-peak force (1.15 ± 0.28 vs. 1.21 ± 0.34 s) during the MVC task. The mean force (5.52 ± 1.42 vs. 6.52 ± 1.89 N) produced during the submaximal task (25%) was also similar [$t(26) < 0.2, P > 0.2$]. Therefore differences in endpoint accuracy between the two groups of subjects were not related to the strength and contraction speed capabilities of the subjects.

Practice and endpoint accuracy

Force [$F(19,557) = 9.0, P < 0.001$; Fig. 2A] and time [$F(19,557) = 4.3, P < 0.001$; Fig. 2B] endpoint error improved with practice. Most of the improvement occurred in the first 40 trials for both age groups and remained relatively constant over the remaining 60 trials (Fig. 2). The largest mean differences in force and time error between the two groups of subjects occurred in the initial block of trials and blocks 8–12 [$F(19,223) = 1.9$ – $5.8, P < 0.001$; Tukey's honestly significant difference: $P < 0.05$]. There was a significant age \times block interaction for both force [$F(19,557) = 1.7, P = 0.03$] and time [$F(19,557) = 1.9, P = 0.01$] endpoint error, which indicated that old adults exhibited greater impairments in endpoint accuracy at the beginning of the protocol. Post hoc analysis of the

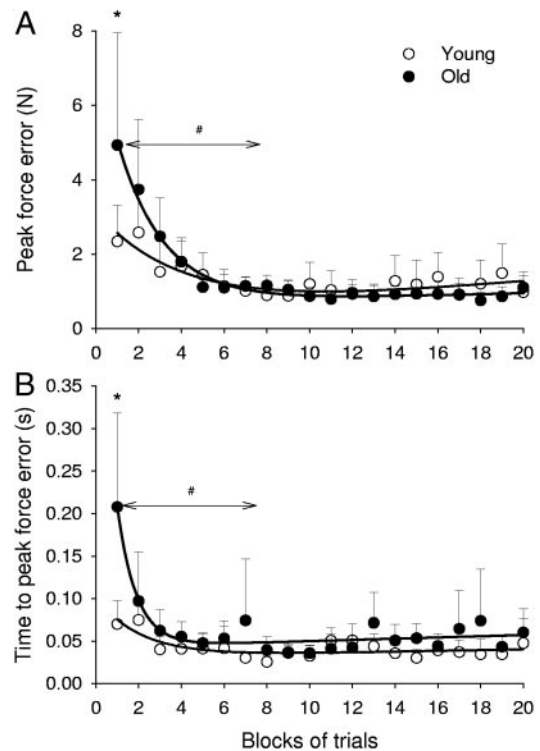


FIG. 2. Average force and time endpoint error for blocks of 5 trials across the 100-trial protocol. A: practice improved (#) force endpoint error in both young (62%) and old (77%) adults in the first 8 blocks of trials (40 trials). B: practice improved (#) time endpoint error in both young (64%) and old (81%) adults in the first 8 blocks of trials (40 trials). Point of inflection for both age groups was around the eighth block, which indicated most of the practice-induced improvements in endpoint error occurred during the first 40 trials, and remained constant for trials 41–100. Old adults exhibited significantly greater (*) force and time endpoint error compared with young adults in the first 2 blocks of trials.

interactions indicated that, although force and time endpoint error decreased significantly ($P < 0.001$) with practice for both age groups in the first eight blocks (force endpoint error: 62 and 77%; time endpoint error: 64 and 81%; young and old adults, respectively), the force [$t(26) = -1.3$, $P < 0.001$] and time [$t(26) = -1.3$, $P < 0.001$] error for old adults was only greater than that for young adults during the first block of trials. The average rate of improvement with practice was thus greater for old adults. The age main effect (average age difference for all 20 blocks) was significant for the time endpoint error [$F(19,557) = 5.37$, $P = 0.02$], but not for the force endpoint error [$F(19,557) = 0.9$, $P = 0.76$].

Practice and motor-output variability

The variability in peak force [$F(19,557) = 9.2$, $P < 0.001$], time-to-peak force ($F = 7.7$, $P < 0.001$), and the force trajectory [$F(19,557) = 6.8$, $P < 0.001$] declined with practice. Similar to the endpoint accuracy measures, most of the improvement occurred in the first 40 trials for both age groups and remained relatively constant over the remaining 60 trials. There was a significant age \times block interaction for peak-force variability [$F(19,557) = 1.6$, $P = 0.04$], time-to-peak force variability ($F = 4.3$, $P = 0.04$), and force-trajectory variability [$F(19,557) = 4.1$, $P = 0.04$] because the old adults exhibited greater motor-output variability at the beginning of the protocol. The age main effect was significant for the time-to-peak force variability [$F(19,557) = 4.3$, $P = 0.04$], but not for the peak-force variability [$F(19,557) = 0.16$, $P = 0.7$] or force-trajectory variability [$F(19,557) = 0.15$, $P = 0.9$].

Prediction of endpoint error in the first block of trials

On average, old adults exhibited greater force and time endpoint error in the first block of trials compared with young adults. Therefore multiple linear regression models were used to determine the following: 1) the contribution of motor-output variability (variability in peak force, time-to-peak force, and force trajectory) to the force and time endpoint error in the first block of trials; and 2) the agonist and antagonist EMG parameters that contributed to the force and time endpoint error in the first block of trials.

The force endpoint error in the first block of trials was strongly predicted (Fig. 3A) by the force-trajectory variability ($R^2 = 0.96$; adjusted $R^2 = 0.95$; $P < 0.001$), whereas the time endpoint error in the first block of trials was moderately predicted ($R^2 = 0.67$; adjusted $R^2 = 0.64$; $P < 0.001$) by equal contributions from the force-trajectory variability (part $r = 0.59$) and time-to-peak force variability (part $r = 0.57$; Fig. 3B). These findings suggest that the less-accurate performance of the old adults in the initial trials was associated with greater motor-output variability.

The correlation matrix for the endpoint accuracy and motor-output variability measures is presented in Table 1. The individual correlations suggest that force-trajectory variability (within-trial measure) and peak-force variability (across-trial measure) were strongly associated ($r = 0.75$, $P < 0.001$). In contrast, force-trajectory variability (within-trial measure) and time-to-peak force variability (across-trial measure) were not significantly associated and may be a consequence of different physiological mechanisms.

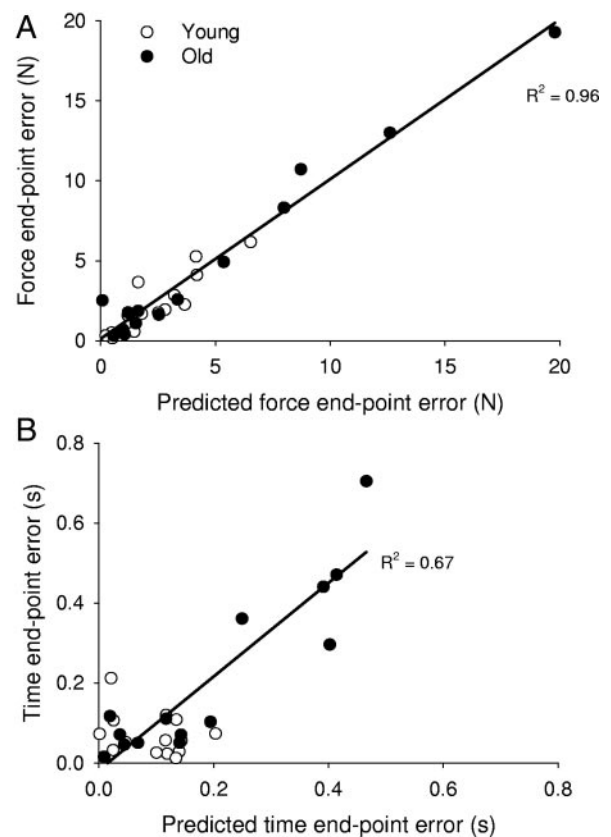


FIG. 3. Prediction of force and time endpoint error for the first 5 trials from motor-output variability. A: stepwise, multiple linear regression analysis indicated that force endpoint error (both age groups) was strongly predicted ($R^2 = 0.96$, $P < 0.001$) from the force-trajectory variability. B: stepwise, multiple linear regression analysis indicated that time endpoint error (both age groups) was moderately predicted ($R^2 = 0.67$, $P < 0.001$) from the force-trajectory variability (part $r = 0.59$) and time-to-peak force variability (part $r = 0.57$).

The force endpoint error during the first block of trials was predicted ($R^2 = 0.3$, adjusted $R^2 = 0.24$; $P < 0.01$; Fig. 4A) by a multiple-regression model that included the FDI peak EMG (part $r = 0.28$) and the SD of FDI EMG duration (part $r = 0.29$). This regression model suggests that the initial endpoint error in force was associated with greater amplitude of the agonist EMG and greater variability of the agonist EMG duration. The time endpoint error during the first block of trials was predicted ($R^2 = 0.80$, adjusted $R^2 = 0.79$; $P < 0.001$; Fig. 4B) by a multiple-regression model that included the FDI peak EMG (part $r = 0.24$) and the SD of the delay between the peak FDI EMG and peak force (part $r = 0.63$). This regression model suggests that the initial endpoint error in time was associated with greater amplitude of the agonist EMG and greater variability in the timing between the agonist peak EMG and peak force. Although these EMG burst variables best predicted the endpoint errors in force and time, other EMG variables were also individually associated with these measures of endpoint accuracy (Table 2).

Predicting the change in endpoint error with practice

The young and old adults exhibited different rates of improvement in force (62 vs. 77%, respectively) and time (64 vs. 81%, respectively) endpoint error during the first 40 trials (Fig.

TABLE 1. Correlation matrix for the initial (block 1) measures of end-point accuracy and motor-output variability

| | Force Error | Time Error | SD Force Trajectory | SD Peak Force | SD Time to Peak Force |
|-----------------------|-------------|--------------|---------------------|---------------|-----------------------|
| Force error | 1.000 | 0.598 | 0.978 | 0.734 | 0.018 |
| Time error | | 1.000 | 0.585 | 0.394 | 0.567 |
| SD force trajectory | | | 1.000 | 0.745 | -0.004 |
| SD peak force | | | | 1.000 | 0.018 |
| SD time to peak force | | | | | 1.000 |

Bold numbers indicate significant Pearson correlation ($P < 0.05$).

2). Multiple regression models were used to determine the following adaptations with initial practice (blocks 1 to 8) for each age group: 1) the contribution of the change in motor-output variability (peak force variability, time-to-peak force variability, and force trajectory variability) to the improvements in force and time endpoint error; and 2) the agonist and antagonist EMG burst parameters that contributed to the improvements in force and time endpoint error.

The change in force endpoint error with practice for young adults was strongly predicted ($R^2 = 0.81$; adjusted $R^2 = 0.80$; $P < 0.001$; Fig. 5A) from the change in force-trajectory variability, whereas the change in time

endpoint error was weakly predicted from the change in the variability of time-to-peak force ($R^2 = 0.25$; adjusted $R^2 = 0.25$; $P = 0.03$; Fig. 5B). The change in force endpoint error with practice for old adults was strongly predicted ($R^2 = 0.96$; adjusted $R^2 = 0.96$; $P < 0.001$; Fig. 5C) from the change in force-trajectory variability, whereas the change in time endpoint error was strongly predicted ($R^2 = 0.74$; adjusted $R^2 = 0.69$; $P < 0.001$) from the change in force-trajectory variability (part $r = 0.67$) and change in time-to-peak force variability (part $r = 0.52$; Fig. 5D). This analysis indicates that the improvement in force endpoint accuracy with 35 practice trials for both young and old adults was associated with a decrease in the force-trajectory variability. However, the improvement in time endpoint accuracy for old adults was associated with a decrease in force-trajectory variability and time-to-peak force variability, but an increase in the time-to-peak force variability for young adults ($r = -0.5$, $P = 0.02$; Figs. 5B and 6). The individual associations between the change in endpoint accuracy and motor-output variability measures are reported in Table 3.

A similar analysis examined the adjustments in the agonist-antagonist EMG activity that accompanied improvements in accuracy with practice for young and old adults. The change in force endpoint error with 35 practice trials for young adults was predicted ($R^2 = 0.82$, adjusted $R^2 = 0.76$; $P < 0.001$; Fig. 7A) by the change in peak FDI EMG (part $r = 0.21$), SD of peak SPI EMG (part $r = 0.53$), and the delay in the SPI-to-FDI peak EMG (part $r = -0.33$). The change in force endpoint

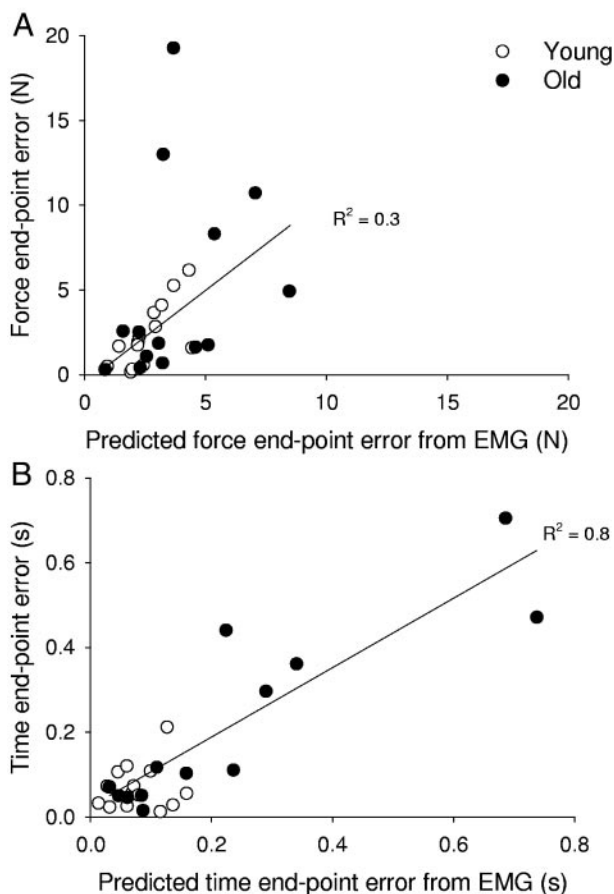


FIG. 4. Prediction of force and time endpoint error for the first 5 trials from the agonist-antagonist EMG. A: stepwise, multiple linear regression analysis indicated that the force endpoint error was predicted ($R^2 = 0.3$, $P < 0.001$) by the FDI peak EMG (part $r = 0.28$) and the SD of the FDI EMG duration (part $r = 0.29$). B: stepwise, multiple linear regression analysis indicated that the force endpoint error was strongly predicted ($R^2 = 0.8$, $P < 0.001$) by the FDI peak EMG (part $r = 0.24$) and the SD of the delay between FDI peak EMG and peak force (part $r = 0.63$).

TABLE 2. Pearson correlations between the EMG burst parameters and measures of end-point accuracy

| Initial EMG Burst Variable | Force Error | Time Error |
|------------------------------|--------------|---------------|
| Peak FDI, % | 0.526 | 0.619 |
| Peak FDI to peak force, s | -0.167 | -0.808 |
| FDI duration, s | 0.347 | 0.307 |
| Peak SPI, % | 0.235 | 0.104 |
| Peak SPI to peak force, s | 0.347 | 0.621 |
| SPI duration, s | 0.015 | 0.056 |
| SPI peak to FDI peak, s | 0.398 | 0.797 |
| SPI onset to FDI onset, s | 0.287 | 0.722 |
| Concurrent activity, % | -0.099 | -0.006 |
| SD peak FDI, % | 0.346 | 0.108 |
| SD peak FDI to peak force, s | 0.312 | 0.851 |
| SD FDI duration, s | 0.485 | 0.481 |
| SD peak SPI, % | 0.343 | 0.210 |
| SD peak SPI to peak force, s | 0.153 | 0.349 |
| SD SPI duration, s | 0.071 | -0.096 |
| SD SPI peak to FDI peak, s | 0.403 | 0.355 |
| SD SPI onset to FDI onset, s | 0.341 | 0.334 |

Bold numbers indicate significant Pearson correlation ($P < 0.05$). Concurrent activity was defined as the percentage overlap of SPI and FDI durations.

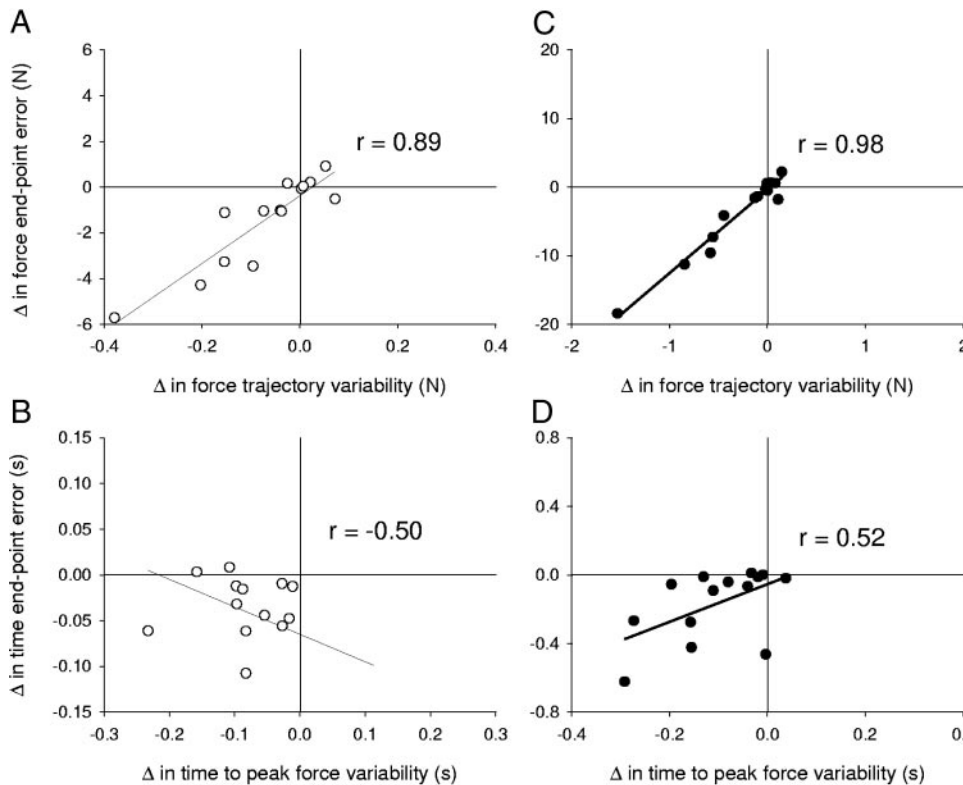


FIG. 5. Association between the change in force and time endpoint error with 35 practice trials and the change in force-trajectory variability and peak-force variability for young (A and B) and old (C and D) adults. A and C: decrease in force endpoint error with practice was strongly associated with the decrease in force-trajectory variability for young ($r = 0.89$, $P < 0.001$) and old adults ($r = 0.98$, $P < 0.001$). B and D: decrease in time endpoint error with practice was associated with an increase in the time-to-peak force variability ($r = -0.50$, $P = 0.03$) for young adults, but a decrease in time-to-peak force variability for old adults ($r = 0.52$, $P < 0.001$).

error with 35 practice trials for old adults was predicted ($R^2 = 0.44$, adjusted $R^2 = 0.40$; $P = 0.009$; Fig. 7B) by the change in the SD of FDI EMG duration (part $r = 0.67$). This analysis indicates that improvements in force endpoint accuracy for young adults were associated with decreased amplitude for the agonist EMG, decreased variability in the amplitude of the antagonist EMG, and a shorter delay between the peak of the antagonist EMG to the agonist EMG, whereas the improvements for the old adults were associated with decreased variability in the duration of the agonist EMG.

The change in time endpoint error with 35 practice trials for young adults was predicted ($R^2 = 0.71$, adjusted $R^2 = 0.69$;

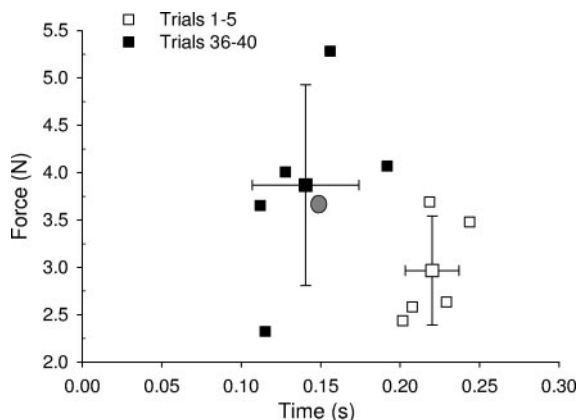


FIG. 6. Data from a single young subject to show the improvement in accuracy from trials 1–5 (open circles) to trials 36–40 (filled squares). Each data point indicates the time and force coordinates of the peak in the force trajectory for one subject in the 2 sets of trials. Target is denoted by the gray circle. On average, trials 36–40 (filled square with SD bars) were closer to the target compared with trials 1–5 (open square with SD bars). Reduction in force and time endpoint error was inversely related to the peak force and time-to-peak force variability.

$P < 0.001$; Fig. 8A) by the change in the delay between the SPI-to-FDI peak EMGs (part $r = -0.84$). Similarly, the change in time endpoint error with 35 practice trials for old adults was predicted ($R^2 = 0.44$, adjusted $R^2 = 0.40$; $P < 0.001$; Fig. 8B) by the change in the delay between the SPI-to-FDI peak EMGs (part $r = 0.67$). The improvements in time endpoint accuracy for young adults were associated with a longer delay between the peak of the antagonist EMG relative to the agonist EMG, whereas the improvements for old adults were associated with a shorter delay between the peak of the antagonist relative to the agonist EMG. However, changes in other EMG variables were also individually associated with the change in force and time endpoint accuracy (Table 4).

DISCUSSION

The purpose of the study was to determine the practice-induced adjustments in motor-output variability and the agonist–antagonist activity that accompanied improvements in force and time endpoint accuracy of goal-directed isometric contractions in young and old adults. The findings suggest that old adults were less accurate than young adults in the force and

TABLE 3. Pearson correlations between the change in end-point accuracy and the change in motor-output variability with practice in young and old adults

| Δ in Motor Output Variability | Young Force Error | Young Time Error | Old Force Error | Old Time Error |
|-------------------------------|-------------------|------------------|-----------------|----------------|
| SD force trajectory | 0.901 | 0.262 | 0.980 | 0.685 |
| SD peak force | 0.192 | 0.228 | 0.783 | 0.470 |
| SD time to peak force | -0.174 | -0.496 | 0.035 | 0.541 |

Bold numbers indicate significant Pearson correlation ($P < 0.05$).

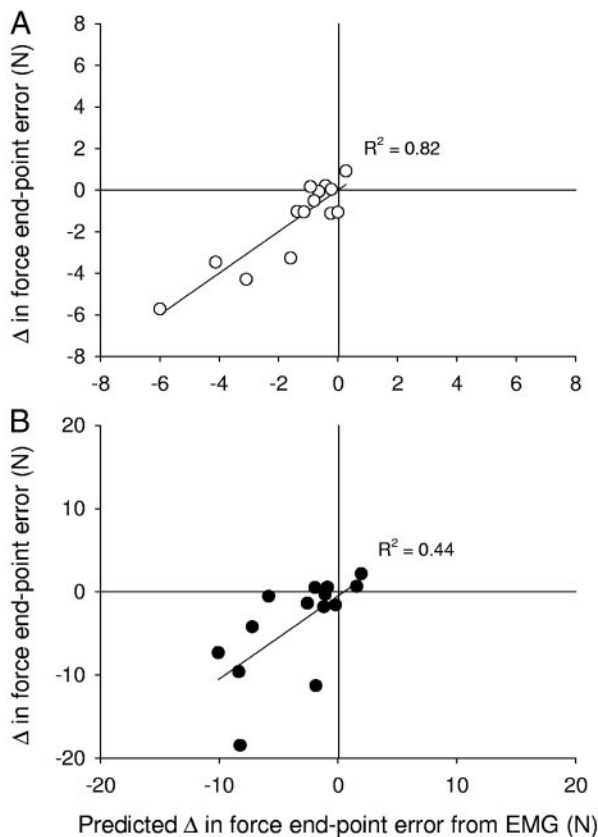


FIG. 7. Prediction of the change in force endpoint error with 35 practice trials from changes in the agonist-antagonist EMG. *A*: stepwise, multiple linear regression analysis indicated that the decrease in force endpoint error with practice for young adults was predicted ($R^2 = 0.88$, $P < 0.001$) by a decrease in the amplitude of the FDI EMG (part $r = 0.21$), a decrease in the variability of the SPI EMG amplitude (part $r = 0.53$), and an increase in the delay between the peak SPI and peak FDI EMGs (part $r = -0.33$). *B*: a stepwise, multiple linear regression analysis indicated that the decrease in force endpoint error with practice for old adults was predicted ($R^2 = 0.44$, $P < 0.001$) from a decrease in the variability of the FDI EMG duration (part $r = 0.67$).

time domains during the initial trials of the task as a result of altered agonist activity and greater motor-output variability. Thirty-five practice trials improved force and time endpoint accuracy for both age groups and old adults became as accurate as young adults. Nonetheless, the adjustments in motor-output variability and muscle activity associated with the initial improvements in endpoint accuracy differed for young and old adults.

Initial practice and endpoint accuracy

Independent of age, 35 practice trials improved force and time endpoint accuracy and lowered motor-output variability. These findings are consistent with previous observations during isometric contractions (Floyer-Lea and Matthews 2005) and movements (Corcos et al. 1993; Darling and Cooke 1987b; Gottlieb et al. 1988; Muller and Sternad 2004). These large, rapid improvements in accuracy must have been caused by changes in the preprogrammed descending command for two reasons: First, the speed of the goal-directed contractions was 150 ms, which does not allow sufficient time for processing of sensory feedback (no visual feedback) and adjustments in the

descending input to influence the motor output (Cordo et al. 1994). Second, large initial improvements in skill acquisition are associated with changes in CNS activity, independent of contraction speed. For example, Floyer-Lea and Matthews (2005) showed that initial learning of an isometric task was associated with decreases in activity in the prefrontal cortex, parietal cortex, and cerebellar cortex, and increases in the cerebellar dentate nucleus, putamen, and thalamus. In contrast, long-term learning of a motor task was associated with adaptations in the contralateral somatosensory and motor cortex and the putamen. Hikosaka et al. (2002) interpret these initial practiced-induced adaptations in higher centers to be associated with the process of learning a new motor task explicitly, which involves spatial improvements (initial learning) followed by fine-tuning of the motor system to further improve motor performance (long-term implicit learning).

The findings of the current study are consistent with the idea that initial practice primarily promotes improvement in the spatial characteristics of the task. Both age groups undershot the targeted force and overshot the targeted time in the first five trials, but the errors in force and time were dramatically reduced (>60%) with 35 practice trials of the task. The improvements in force endpoint accuracy for both age groups were associated with timing adaptations of the agonist and antagonist EMG activity. This adjustment may be associated with increased activation of the putamen, which was previously implicated during initial learning (Floyer-Lea and Mat-

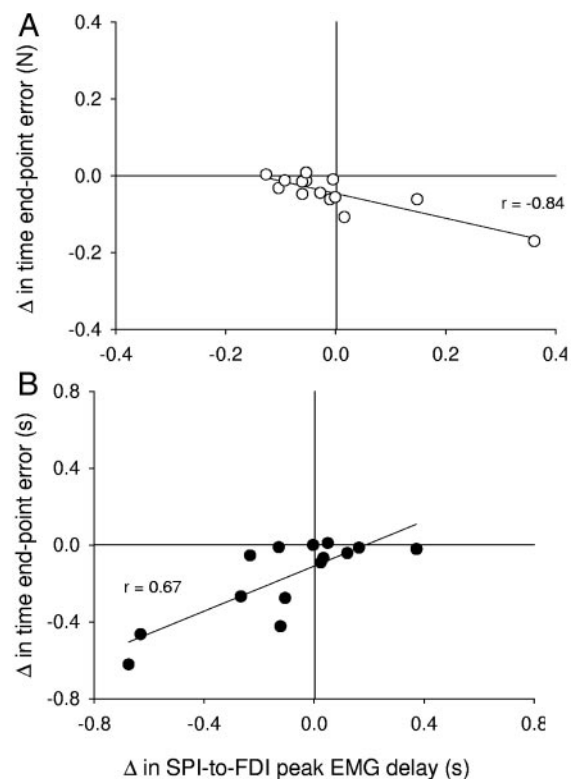


FIG. 8. Association between the change in time endpoint error with 35 practice trials and the change in the timing of the agonist-antagonist peak EMG for young and old adults. Decrease of the time endpoint error with practice for young adults was associated with lengthening of the delay between the SPI-to-FDI peak EMGs ($r = -0.84$; *A*), whereas the decrease of time endpoint error in old adults was associated with shortening of the delay between the SPI-to-FDI peak EMGs ($r = 0.67$; *B*).

TABLE 4. Pearson correlations between the change in EMG burst parameters and change in end-point accuracy with practice in young and old adults

| Δ in EMG Burst Variable | Young Force Error | Young Time Error | Old Force Error | Old Time Error |
|--------------------------------|-------------------|------------------|-----------------|----------------|
| Peak FDI, % | 0.717 | 0.497 | 0.133 | 0.685 |
| Peak FDI to peak force, s | -0.178 | -0.610 | -0.238 | -0.756 |
| FDI duration, s | 0.029 | 0.315 | 0.537 | 0.463 |
| Peak SPI, % | 0.661 | 0.523 | 0.147 | 0.096 |
| Peak SPI to peak force, s | -0.440 | -0.825 | 0.034 | 0.436 |
| SPI duration, s | 0.303 | 0.519 | 0.504 | 0.517 |
| SPI peak to FDI peak, s | -0.516 | -0.842 | 0.635 | 0.813 |
| SPI onset to FDI onset, s | -0.427 | -0.802 | 0.126 | 0.575 |
| Concurrent activity, % | 0.263 | 0.443 | -0.045 | 0.443 |
| SD peak FDI, % | 0.156 | 0.325 | 0.069 | 0.102 |
| SD peak FDI to peak force, % | -0.253 | -0.700 | 0.280 | 0.044 |
| SD FDI duration, s | -0.017 | -0.131 | 0.665 | 0.485 |
| SD peak SPI, % | 0.642 | 0.035 | 0.387 | 0.202 |
| SD peak SPI to peak force, s | -0.045 | -0.529 | -0.170 | 0.331 |
| SD SPI duration, s | 0.474 | 0.095 | -0.144 | -0.020 |
| SD SPI peak to FDI peak, s | -0.198 | -0.650 | 0.344 | 0.229 |
| SD SPI onset to FDI onset, s | 0.278 | -0.016 | -0.330 | 0.130 |

Bold numbers indicate significant Pearson correlation ($P < 0.05$).

thews 2005) and movement-time processing (Lewis et al. 2004).

Initial practice trials and age-associated differences in endpoint accuracy

The largest impairments in force and time endpoint accuracy for the old adults occurred during the initial five to ten trials. The force endpoint error in the first block of trials was strongly ($R^2 = 0.96$) associated with the trajectory variability in force, whereas the time endpoint error was associated ($R^2 = 0.67$) with the trajectory variability in force and the variability in time-to-peak force. These strong associations demonstrate that the impairment of force and time accuracy of old adults in the initial block of trials was associated with greater motor-output variability (variability of the force trajectory and time-to-peak force) compared with the young adults. The force endpoint error during the first five trials was predicted ($R^2 = 0.82$) from the agonist EMG amplitude and the variability of the agonist EMG duration, indicating that the old adults exhibited greater agonist EMG amplitude and greater variability in the agonist EMG duration. The time endpoint error during the first five trials was predicted ($R^2 = 0.78$) from the agonist EMG amplitude and the variability in the timing of the FDI peak EMG relative to the peak force. Therefore the less accurate and more variable performance of the old adults during the first five trials likely arose from differences in the amplitude and timing of the agonist EMG.

The large age differences in endpoint error during the first five to ten trials may be explained by differences in attentional demands and processing as a result of the greater variability in the force trajectory and in the time-to-peak force exhibited by old adults. In addition, there is evidence that mental processing is slower for older adults (Simon and Pouraghabagher 1978), which can explain the number of trials required to match the performance of the young adults. The greater motor-output variability displayed by the old adults, which potentially influenced force and time endpoint accuracy, may be associated with greater variability in the descending command as the

result of a significant decrease in the number of cortical motor neurons (Eisen et al. 1996; Henderson et al. 1980) or as a result of the loss of alpha motor neurons (Doherty 2003).

Adjustments with practice for young and old adults

Thirty-five practice trials improved force and time endpoint accuracy in both young and old adults. The rate of improvement, however, was greater for older adults, most likely arising from the large differences in the first five to ten trials. A major finding of the current study was that the adjustments with practice differed for the two age groups.

Although the improvements in force endpoint accuracy for both the young and old adults were strongly associated with reductions of force-trajectory variability, the improvements in force accuracy were associated with different adjustments in muscle activation. Young adults adjusted both the agonist and antagonist EMG to improve force endpoint accuracy, whereas old adults adjusted only the agonist muscle EMG to improve force endpoint accuracy. The results for the young adults are consistent with previous work on goal-directed isometric contractions with the elbow flexor muscles (Ghez and Gordon 1987). The results for old adults are similar to those reported for tetraplegic patients who lacked control of the antagonist muscle (Wierzbicka and Wiegner 1996).

Improvements in time endpoint accuracy for old adults were associated with reductions of force-trajectory variability and time-to-peak force variability. In contrast, the young adults increased the time-to-peak force variability and the change in force-trajectory variability was not significant. Those young subjects who had the greatest improvements in time endpoint accuracy had the smallest decreases in time-to-peak force variability. This result is contrary to the minimum-variance theory (Harris and Wolpert 1998; discussed in the following text), at least for the time domain, and suggests that young subjects who had the greatest improvement in endpoint accuracy retained a higher level of endpoint variance to aid them in achieving the target. The EMG burst parameter that was associated with the reduction in time endpoint error was similar

for the young and old adults and involved the delay between the peak EMG of the agonist and antagonist muscles. However, the adjustment occurred in opposite directions: young adults shortened the delay and old adults lengthened it.

Motor-output variability and endpoint accuracy

Based on the minimum-variance theory (Hamilton et al. 2004; Harris and Wolpert 1998; van Beers et al. 2002), improvements in endpoint accuracy with practice should be directly associated with reductions in signal-dependent noise, which has been proposed to originate in cortical and spinal centers (Stein et al. 2005; van Beers et al. 2004). The functional significance of signal-dependent noise is that it increases trajectory variability (Hamilton et al. 2004) and consequently endpoint variance (Harris and Wolpert 1998), which impairs endpoint accuracy (Hamilton et al. 2004; Harris and Wolpert 1998; van Beers et al. 2002). Therefore reductions in force-trajectory variability should lower endpoint variance and improve endpoint accuracy.

The findings of the current study support the predictions of the minimum-variance hypothesis for the force domain, but not the time domain. Consistent with the minimum-variance hypothesis, force-trajectory variability was strongly associated with peak-force variability ($r = 0.75$, $P < 0.001$) and force endpoint accuracy ($r = 0.98$, $P < 0.001$) in the first block of five trials. Furthermore, the decrease in force endpoint error with initial practice was strongly associated with a decrease in force-trajectory variability ($r = 0.9$, $P < 0.001$) for both young and old adults. These results support previous findings that increases in trajectory fluctuations increase endpoint variance and decrease endpoint accuracy (Christou and Carlton 2002; Christou et al. 2003; Enoka et al. 2003; Hamilton et al. 2004; Jones et al. 2002; Selen et al. 2005).

The time domain findings, however, appear to contradict the propositions of the minimum-variance hypothesis. For example, the variability in the force trajectory and time-to-peak force (time endpoint variability) was not associated during the first five trials, despite the large variance observed in both variables from the age-associated differences in motor-output variability. Furthermore, there was no association between the decrease in both force-trajectory variability and time-to-peak force variability with initial practice for both age groups. Also, the improvements of the time endpoint error for young adults were not associated with any measurement of motor-output variability.

These findings therefore suggest that force-trajectory variability and time endpoint variability are the consequence of different physiological mechanisms. It appears that force-trajectory variability is associated with force development, which may relate primarily to the activation of the motor units in the agonist muscle (Enoka et al. 2003; Taylor et al. 2003). Consistent with this possibility, the trajectory fluctuations were strongly associated with the rate of force development ($r = 0.8$), peak-force variability, and force endpoint error ($r = 0.77$) but not time endpoint error. In contrast, time-to-peak force variability and time endpoint error, for both young and old adults, appear to be related more to the timing and the variability in timing between the agonist and antagonist EMGs.

The current study was largely designed to address the predictions of the minimum-variance theory (Hamilton et al.

2004; Harris and Wolpert 1998; van Beers et al. 2002) for force and time accuracy as young and old adults learned a novel task. The finding that old adults primarily adjusted the activity of the agonist muscle, whereas young adults adjusted the activity of both the agonist and antagonist muscle to improve force accuracy seems to be consistent with other theories of how the control of motor output might be compromised in old adults. For example, Newell and colleagues demonstrated that old adults do not use all available degrees of freedom to adapt their motor output to task demands (Sosnoff and Newell 2006; Vaillancourt and Newell 2002). Similarly, Latash and colleagues showed that multieffector synergies are impaired in old adults (Olafsdottir et al. 2007; Shim et al. 2004). Thus despite the differences that could exist between abduction of the index finger and tasks that involve multiple muscles and body segments, which could be influenced by joint interaction torques (Zhang et al. 2006), the underlying mechanism may be similar. Further research is needed, however, to determine whether the current results can be generalized across joints and contraction types in young and old adults.

In summary, the findings of the study indicate that although old adults were less accurate than young adults during the initial trials of rapid, isometric contractions, 35 practice trials significantly improved endpoint accuracy to similar levels for young adults. Nonetheless, the adaptations differed for young and old adults. Force endpoint accuracy was improved by changing the EMG activity, both the agonist and antagonist muscles for the young adults, but only the agonist muscle for the old adults. The young adults improved time endpoint accuracy without changing motor-output variability, whereas old adults significantly reduced the variability in both force trajectory and time-to-peak force.

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REFERENCES

- Burnett RA, Laidlaw DH, Enoka RM.** Coactivation of the antagonist muscle does not covary with steadiness in old adults. *J Appl Physiol* 89: 61–71, 2000.
- Chao EYS, An KN, Cooney WP, Linschied RL.** *Biomechanics of the Hand. A Basic Research Study.* Teaneck, NJ: World Scientific, 1989.
- Christou EA, Carlton LG.** Age and contraction type influence motor output variability in rapid discrete tasks. *J Appl Physiol* 93: 489–498, 2002.
- Christou EA, Poston B, Enoka JA, Enoka RM.** Coactivation lowers variability in time to peak force and enhances end-point accuracy. *Progress In Motor Control V: A Multidisciplinary Perspective.* State College, PA: The Pennsylvania State Univ., 2005.
- Christou EA, Shinohara M, Enoka RM.** Fluctuations in acceleration during voluntary contractions lead to greater impairment of movement accuracy in old adults. *J Appl Physiol* 95: 373–384, 2003.
- Corcos DM, Agarwal GC, Flaherty BP, Gottlieb GL.** Organizing principles for single-joint movements. IV. Implications for isometric contractions. *J Neurophysiol* 64: 1033–1042, 1990.
- Corcos DM, Gottlieb GL, Agarwal GC.** Organizing principles for single-joint movements. II. A speed-sensitive strategy. *J Neurophysiol* 62: 358–368, 1989.
- Corcos DM, Jaric S, Agarwal GC, Gottlieb GL.** Principles for learning single-joint movements. I. Enhanced performance by practice. *Exp Brain Res* 94: 499–513, 1993.

- Cordo P, Carlton L, Bevan L, Carlton M, Kerr GK.** Proprioceptive coordination of movement sequences: role of velocity and position information. *J Neurophysiol* 71: 1848–1861, 1994.
- Darling WG, Cooke JD.** Changes in the variability of movement trajectories with practice. *J Mot Behav* 19: 291–309, 1987a.
- Darling WG, Cooke JD, Brown SH.** Control of simple arm movements in elderly humans. *Neurobiol Aging* 10: 149–157, 1989.
- Darling WG, Cooke WG.** Movement related EMGs become more variable during learning of fast accurate movements. *J Mot Behav* 19: 311–331, 1987b.
- Doherty TJ.** Invited review: aging and sarcopenia. *J Appl Physiol* 95: 1717–1727, 2003.
- Eisen A, Entezari-Taher M, Stewart H.** Cortical projections to spinal motoneurons: changes with aging and amyotrophic lateral sclerosis. *Neurology* 46: 1396–1404, 1996.
- Enoka RM, Christou EA, Hunter SK, Kornatz KW, Semmler JG, Taylor AM, Tracy BL.** Mechanisms that contribute to differences in motor performance between young and old adults. *J Electromyogr Kinesiol* 13: 1–12, 2003.
- Floyer-Lea A, Matthews PM.** Distinguishable brain activation networks for short- and long-term motor skill learning. *J Neurophysiol* 94: 512–518, 2005.
- Ghez C, Gordon J.** Trajectory control in targeted force impulses. I. Role of opposing muscles. *Exp Brain Res* 67: 225–240, 1987.
- Gordon J, Ghez C.** EMG patterns in antagonist muscles during isometric contraction in man: relations to response dynamics. *Exp Brain Res* 55: 167–171, 1984.
- Gordon J, Ghez C.** Trajectory control in targeted force impulses. II. Pulse height control. *Exp Brain Res* 67: 241–252, 1987a.
- Gordon J, Ghez C.** Trajectory control in targeted force impulses. III. Compensatory adjustments for initial errors. *Exp Brain Res* 67: 253–269, 1987b.
- Gottlieb GL, Corcos DM, Jaric S, Agarwal GC.** Practice improves even the simplest movements. *Exp Brain Res* 73: 436–440, 1988.
- Gottlieb GL, Latash ML, Corcos DM, Liubinskas TJ, Agarwal GC.** Organizing principles for single joint movements. V. Agonist–antagonist interactions. *J Neurophysiol* 67: 1417–1427, 1992.
- Green SB, Salkind NJ.** *Using SPSS for the Windows and Macintosh: Analyzing and Understanding Data*. Upper Saddle River, NJ: Prentice Hall, 2002.
- Hamilton AF, Jones KE, Wolpert DM.** The scaling of motor noise with muscle strength and motor unit number in humans. *Exp Brain Res* 157: 417–430, 2004.
- Harris CM, Wolpert DM.** Signal-dependent noise determines motor planning. *Nature* 394: 780–784, 1998.
- Henderson G, Tomlinson BE, Gibson PH.** Cell counts in human cerebral cortex in normal adults throughout life using an image analysing computer. *J Neurol Sci* 46: 113–136, 1980.
- Hikosaka O, Nakamura K, Sakai K, Nakahara H.** Central mechanisms of motor skill learning. *Curr Opin Neurobiol* 12: 217–222, 2002.
- Jones KE, Hamilton AF, Wolpert DM.** Sources of signal-dependent noise during isometric force production. *J Neurophysiol* 88: 1533–1544, 2002.
- Kornatz KW, Christou EA, Enoka RM.** Practice reduces motor unit discharge variability in a hand muscle and improves manual dexterity in old adults. *J Appl Physiol* 98: 2072–2080, 2005.
- Laidlaw DH, Hunter SK, Enoka RM.** Nonuniform activation of the agonist muscle does not covary with index finger acceleration in old adults. *J Appl Physiol* 93: 1400–1410, 2002.
- Lewis PA, Wing AM, Pope PA, Praamstra P, Miall RC.** Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. *Neuropsychologia* 42: 1301–1312, 2004.
- Li ZM, Pfaeffle HJ, Sotereanos DG, Goitz RJ, Woo SL.** Multi-directional strength and force envelope of the index finger. *Clin Biomech (Bristol, Avon)* 18: 908–915, 2003.
- Muller H, Sternad D.** Decomposition of variability in the execution of goal-oriented tasks: three components of skill improvement. *J Exp Psychol Hum Percept Perform* 30: 212–233, 2004.
- Newell KM.** Knowledge of results and motor learning. *Exerc Sport Sci Rev* 4: 195–228, 1976.
- Olafsdottir H, Zhang W, Zatsiorsky VM, Latash ML.** Age-related changes in multi-finger synergies in accurate moment of force production tasks. *J Appl Physiol* (January 4, 2007). doi:10.1152/jappphysiol.00966.2006.
- Oldfield RC.** The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9: 97–113, 1971.
- Osu R, Kamimura N, Iwasaki H, Nakano E, Harris CM, Wada Y, Kawato M.** Optimal impedance control for task achievement in the presence of signal-dependent noise. *J Neurophysiol* 92: 1199–1215, 2004.
- Sainburg RL.** Evidence for a dynamic-dominance hypothesis of handedness. *Exp Brain Res* 142: 241–258, 2002.
- Seidler-Dobrin RD, He J, Stelmach GE.** Coactivation to reduce variability in the elderly. *Motor Control* 2: 314–330, 1998.
- Selen LP, Beek PJ, Dieen JH.** Can co-activation reduce kinematic variability? A simulation study. *Biol Cybern* 93: 373–381, 2005.
- Shim JK, Lay BS, Zatsiorsky VM, Latash ML.** Age-related changes in finger coordination in static prehension tasks. *J Appl Physiol* 97: 213–224, 2004.
- Simon JR, Pouraghabagher AR.** The effect of aging on the stages of processing in a choice reaction time task. *J Gerontol* 33: 553–561, 1978.
- Sosnoff JJ, Newell KM.** The generalization of perceptual-motor intra-individual variability in young and old adults. *J Gerontol B Psychol Sci Soc Sci* 61: 304–310, 2006.
- Sosnoff JJ, Vaillancourt DE, Newell KM.** Aging and rhythmical force output: loss of adaptive control of multiple neural oscillators. *J Neurophysiol* 91: 172–181, 2004.
- Spiegel KM, Stratton J, Burke JR, Glendinning DS, Enoka RM.** The influence of age on the assessment of motor unit activation in a human hand muscle. *Exp Physiol* 81: 805–819, 1996.
- Stein RB, Gossen ER, Jones KE.** Neuronal variability: noise or part of the signal? *Nat Rev Neurosci* 6: 389–397, 2005.
- Taylor AM, Christou EA, Enoka RM.** Multiple features of motor-unit activity influence force fluctuations during isometric contractions. *J Neurophysiol* 90: 1350–1361, 2003.
- Ungerleider LG, Doyon J, Karni A.** Imaging brain plasticity during motor skill learning. *Neurobiol Learn Mem* 78: 553–564, 2002.
- Vaillancourt DE, Newell KM.** Changing complexity in human behavior and physiology through aging and disease. *Neurobiol Aging* 23: 1–11, 2002.
- Vaillancourt DE, Sosnoff JJ, Newell KM.** Age-related changes in complexity depend on task dynamics. *J Appl Physiol* 97: 454–455, 2004.
- Valero-Cuevas FJ.** Predictive modulation of muscle coordination pattern magnitude scales fingertip force magnitude over the voluntary range. *J Neurophysiol* 83: 1469–1479, 2000.
- van Beers RJ, Baraduc P, Wolpert DM.** Role of uncertainty in sensorimotor control. *Philos Trans R Soc Lond B Biol Sci* 357: 1137–1145, 2002.
- van Beers RJ, Haggard P, Wolpert DM.** The role of execution noise in movement variability. *J Neurophysiol* 91: 1050–1063, 2004.
- Wierzbicka MM, Wiegner AW.** Accuracy of motor responses in subjects with and without control of antagonist muscle. *J Neurophysiol* 75: 2533–2541, 1996.
- Woodworth RS.** The accuracy of voluntary movement. In: *The Psychological Review*, edited by Baldwin JM, Cattell JM. New York: Macmillan, 1899, p. 1–114.
- Zhang W, Zatsiorsky VM, Latash ML.** Accurate production of time-varying patterns of the moment of force in multi-finger tasks. *Exp Brain Res* 175: 68–82, 2006.