

# Age and contraction type influence motor output variability in rapid discrete tasks

EVANGELOS A. CHRISTOU AND LES G. CARLTON

*University of Illinois at Urbana-Champaign, Champaign, Illinois 61820*

Received 10 April 2001; accepted in final form 10 January 2002

**Christou, Evangelos A., and Les G. Carlton.** Age and contraction type influence motor output variability in rapid discrete tasks. *J Appl Physiol* 93: 489–498, 2002. First published February 15, 2002; 10.1152/jappphysiol.00335.2001.—The purpose of this study was to examine the ability to control knee-extension force during discrete isometric (IC), concentric (CC), and eccentric contractions (EC) in 24 young (mean age  $\pm$  SD = 25.3  $\pm$  2.8 yr) and 24 old (mean age  $\pm$  SD = 73.3  $\pm$  5.5 yr) healthy and active individuals. Subjects were to match a parabola with a time to peak force of 200 ms during IC, CC, and EC at six target levels of force [20, 35, 50, 65, 80, and 90% of the maximum voluntary contraction (MVC)]. ICs were performed at 90° of knee flexion, whereas CCs and ECs ranged from 90 to 80° of knee flexion (0° is full extension) at a slow velocity (25°/s). Results showed that subjects produced similar MVC forces for the three types of contractions. Young subjects produced greater MVC forces than old subjects, and within each age group, men produced greater force than women. The variability (standard deviation) of peak force and impulse in absolute values was greater for young compared with old subjects. When variability was normalized to the force produced [coefficient of variation (CV)], however, old subjects exhibited greater CV than young subjects for peak force and impulse. Both the standard deviation and CV of time to peak force and impulse duration were greater for the old adults. In general, ECs were more variable than ICs and CCs, and old adults exhibited greater CV compared with young adults during rapid, discrete ICs, CCs, and particularly ECs of the quadriceps.

quadriceps; eccentric; concentric; isokinetic

---

THE SUCCESS OF HUMANS to accomplish tasks with precision depends on their capability to control movement. Even the simplest movements in life demand the appropriate application of force, including the magnitude, direction, and timing of force, usually for both the agonist and antagonist muscles. In general, the control of force for the agonist muscle occurs during a concentric contraction, whereas the control of force for the antagonist muscle occurs during an eccentric contraction.

Aggregate of data suggests that the central nervous system (CNS) may regulate gradation of muscle force uniquely during eccentric contractions (20, 21). The strongest evidence comes from neurophysiological

studies indicating a significantly reduced activation level [electromyogram (EMG)], motor evoked potentials, and H reflex during eccentric contractions of a muscle compared with concentric contractions producing the same torque (30, 36). This reduction in EMG amplitude during eccentric contractions appears to be due to a decreased discharge rate of the motor units (33, 34, 46). Although contradictory to the literature (3, 14), some neurophysiological studies suggest that the size principle of motor unit recruitment (27) is not followed during eccentric contractions where specific large motor units are activated first, followed by small motor units (30, 36). Human performance characteristics, furthermore, suggest that, as velocity of movement increases, maximum force production decreases during concentric contractions but is unaffected during eccentric contractions (51).

Although several experiments have examined neural and motor output differences during concentric and eccentric contractions, the ability of young and old individuals to control muscle force during eccentric contractions has been examined only during slow continuous tasks (34, 45). In a continuous task, the participant attempts to match a constant force level represented by a line for a specific time period by usually controlling only force output, and the within-subject variability of force fluctuations is measured (34, 45). A discrete task, however, refers to when a participant attempts to match a force-parabola with a short time over several discrete trials, and the within-subject variability of peak force, impulse, time to peak force, and impulse duration (motor output variability) is measured (9). During both continuous and discrete tasks, it is generally accepted that standard deviation (SD) of force increases and coefficient of variation (CV; equal to SD of force/mean force) decreases as the level of force increases (9, 44). Rapid discrete contractions differ from slow continuous contractions in many respects. The rate of force production is higher, the motor command must be repeated over trials, and the use of kinesthetic feedback is minimized (17). These differences may account for the sixfold increase in the amount of force variability for discrete compared with continuous isometric contractions (12).

---

Address for reprint requests and other correspondence: E. A. Christou, Neural Control of Movement Laboratory, Dept. of Kinesiology and Applied Physiology, Univ. of Colorado at Boulder, Boulder, CO 80309-0354 (E-mail: echristo@colorado.edu).

---

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

Studies suggest that, when old adults perform isometric or slow anisometric continuous contractions, they produce more variable movements compared with young adults (5, 24, 34). Eccentric contractions are significantly more variable than concentric contractions in old adults but not in young adults (15, 34). For rapid discrete tasks, the literature is limited to young adults performing isometric and concentric contractions (9). Differences between young and old adults as a function of contraction type have not been examined during rapid discrete tasks.

It is important to identify whether any differences in the control of muscle force exist between young and old adults during different types of rapid discrete contractions for two reasons. First, rapid discrete contractions are primarily controlled by the descending motor command (17), which must be repeated over several trials. It is possible that variability of the descending command is greater for old adults because corticomotor function declines with increases in age, possibly due to losses of corticomotorneurons (19, 35). Furthermore, the neuromotor system of old adults has been shown to be slower and more variable, possibly due to decreases in transmission from corticospinal and reflex pathways to the motoneurons (26) and particularly to losses of the largest  $\alpha$ -motoneurons (18). Second, studies have shown that old adults exhibit increased kinematic variability compared with young adults, particularly during functional movements that require eccentric contractions (28, 52) and that they prefer to slow down to eliminate errors and loss of balance (28, 42). The interaction between contraction type and age, therefore, may identify whether control of force in old adults is impaired more during eccentric contractions.

The primary purpose of this study was to compare motor output variability for rapid discrete isometric, concentric, and eccentric contractions of the quadriceps femoris muscle group in young and old adults. A secondary purpose was to determine whether motor output variability differs among the three types of muscular contractions. Data that compare the three different types of contractions from the young subjects of this study have been presented previously in abstract form (11).

## METHODS

### Subjects

Twenty-four active young ( $25.3 \pm 2.8$  yr old; 12 men, 12 women) and 24 active old adults ( $73.3 \pm 5.5$  yr old; 12 men, 12 women) volunteered for this experiment (Table 1). All subjects reported that they were right leg dominant. To control for physical activity level differences typically seen between young and old adults, the subjects recruited were healthy and physically active. A medical history questionnaire given to each individual before the study indicated that all subjects were healthy and had no history of knee pathology nor any neurological disorders. On the basis of a physical activity questionnaire (38), which had been previously validated (48), all subjects engaged in moderate to intense regular physical activity ( $>5$  times/wk; greater than moderate intensity;  $>0.5$  h in duration). In addition, none of the subjects had any cognitive deficits, as assessed by the Pfeiffer mental status scale (39). Testing protocols were approved by the institutional review board for research with human subjects, and all subjects gave their informed consent before participating in the study.

### Apparatus and Procedures

**Isokinetic dynamometer.** To assess force production and motor output variability for a knee-extension task during continuous and discrete isometric contractions, a KIN-COM 500H isokinetic dynamometer (Chattanooga Corp., Chattanooga, TN) was used. The device allows for evaluation of force production during isokinetic, isometric, and isotonic actions. Force, velocity, and angle produced by each participant were displayed on the monitor (15 in.) of the isokinetic dynamometer. The KIN-COM 500H has been shown to be a reliable way to assess force (2).

### Procedures

Strength and motor output variability were assessed during discrete isometric, concentric, and eccentric contractions of the right knee extensors (dominant leg as identified by the subjects) in three different sessions performed within the same week. For each type of contraction, the level of maximum voluntary contraction (MVC) was determined. MVC force produced with rapid contractions was on average 80–85% of a typical isometric MVC. On the basis of the MVC produced, target forces, expressed as a percentage of MVC (%MVC), were determined.

Subjects were seated for testing in the isokinetic dynamometer's chair with the backrest angle at  $90^\circ$ . The axis of rotation of the right knee (lateral epicondyle of the femur)

Table 1. Age, characteristics, and MVC of subjects for isometric, concentric, and eccentric rapid contractions

|                    | Age, yr        | Height, cm      | Weight, kg      | Isometric, N      | Concentric, N     | Eccentric, N      |
|--------------------|----------------|-----------------|-----------------|-------------------|-------------------|-------------------|
| <i>Young</i>       |                |                 |                 |                   |                   |                   |
| All ( $n = 24$ )   | $25.3 \pm 2.8$ | $173.8 \pm 8.9$ | $69.6 \pm 15.3$ | $724.3 \pm 218.7$ | $691.8 \pm 235.9$ | $695.9 \pm 220.8$ |
| Men ( $n = 12$ )   | $26.0 \pm 2.9$ | $179.8 \pm 7.0$ | $79.3 \pm 13.3$ | $913.5 \pm 107.2$ | $850.3 \pm 147.3$ | $837.3 \pm 195.2$ |
| Women ( $n = 12$ ) | $24.7 \pm 2.6$ | $167.8 \pm 6.1$ | $60.1 \pm 10.6$ | $535.1 \pm 102.1$ | $533.5 \pm 108.2$ | $554.6 \pm 142.2$ |
| <i>Old</i>         |                |                 |                 |                   |                   |                   |
| All ( $n = 24$ )   | $73.3 \pm 5.5$ | $169.8 \pm 9.6$ | $69.5 \pm 8.6$  | $393.8 \pm 148.1$ | $406.7 \pm 126.3$ | $451.7 \pm 147.6$ |
| Men ( $n = 12$ )   | $72.6 \pm 4.8$ | $176.2 \pm 8.3$ | $73.3 \pm 9.1$  | $450.4 \pm 153.4$ | $453.8 \pm 138.1$ | $423.6 \pm 93.1$  |
| Women ( $n = 12$ ) | $74.0 \pm 6.3$ | $163.5 \pm 6.1$ | $65.8 \pm 6.6$  | $337.2 \pm 123.8$ | $359.6 \pm 97.1$  | $479.8 \pm 187.5$ |

Values are group means  $\pm$  SD for age and each type of contraction. MVC, maximum voluntary contraction.

was aligned with the axis of rotation of the dynamometer's armature, and the ankle cuff (load cell assembly) was attached 2.5 cm above the dorsal surface of the foot. Each participant removed the right shoe to eliminate any potential load differences due to the weight of the shoe, and the weight of the leg was accounted for by the isokinetic dynamometer. Stabilization straps were placed over the pelvis and chest, and participants positioned their arms across their chests during each trial. For all trials, a rigid soccer shin guard was placed over the right shin to protect subjects from any potential pain and injury due to the large number of knee extensions during each session.

The order of contraction types was counterbalanced. MVC trials and trials at the various %MVC were blocked. The order of %MVC within a contraction type was randomly determined. Before each contraction session, subjects warmed up by walking for 5 min and stretching their quadriceps femoris, hip flexors, and gastrocnemius muscles. MVC of each participant for each type of contraction was measured before each contraction session. Specific warm-up (3 sub-maximal trials) was given to the subjects before MVC testing.

#### Maximum Voluntary Discrete Contractions for 200 ms

For discrete isometric contractions, subjects were asked to produce maximal effort force pulses with brief durations. The criterion time to peak force for each trial was 200 ms. Because longer times to peak force can increase maximum force (7, 37), the 200-ms time to peak force was used to identify the MVC. Furthermore, a rapid time to peak force (200 ms) was used because it minimizes the role of sensory feedback for controlling force (17). Subjects monitored the gradation of force on the monitor of the isokinetic dynamometer. Trials were repeated until three trials with a time to peak force of 200 ms ( $\pm 10\%$ ) were produced. The highest of the three force values produced from the three accepted trials was considered the MVC. After each contraction session, subjects performed another MVC to identify whether fatigue had taken place.

#### Rapid Discrete Contraction Task

The seating position and setup of the participant were the same as that used for the MVCs. Six target force levels were determined on the basis of the maximum force produced by each participant for each type of contraction. These forces were 20, 35, 50, 65, 80, and 90% of MVC, and the time to peak force was 200 ms. The order of target forces was determined randomly for each participant. Isometric contractions were produced at 90°, whereas concentric contractions started with a knee angle of 90° and moved to 80° (0° is full extension). For eccentric contractions, the movement of the dynamometer armature was in the opposite direction of that of concentric contractions; thus knee joint angle ranged from 80 to 90°. A diagrammatic depiction of the methodology used for the three contraction types is provided in Fig. 1.

**Isometric task.** For the discrete isometric task, each participant attempted to match a force-time parabola. The force-time parabola was drawn on a transparency sheet and attached on the monitor of the isokinetic dynamometer. Each participant was instructed to match the target parabola by controlling the knee-extension force. Between trials, subjects had ~5 s to relax and position the knee-extension force back to 0 N.

**Concentric and eccentric contraction tasks.** The procedures were identical to those described for isometric contractions. A 10° range of motion was used with a velocity of 25°/s to match the isometric conditions and obtain a time to peak force of

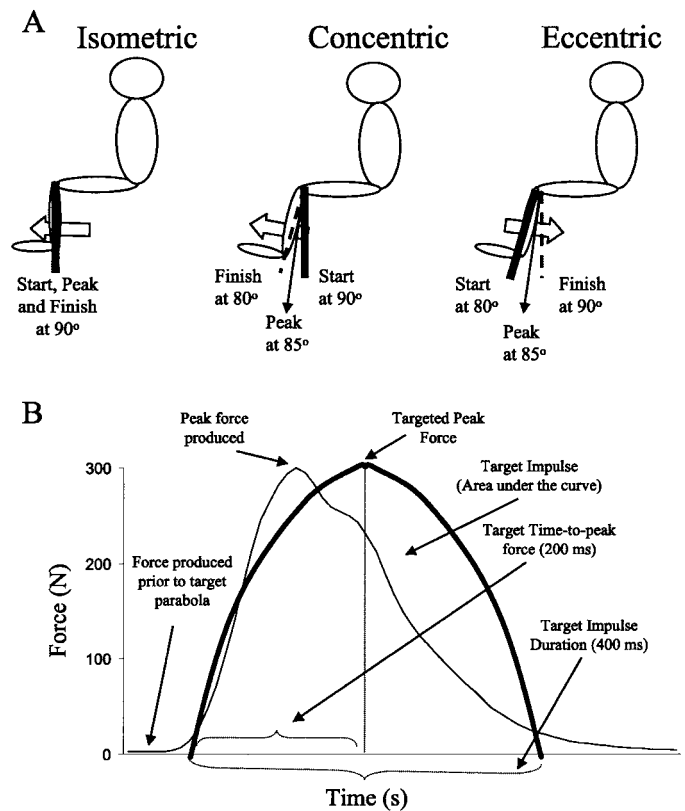


Fig. 1. A: diagrams of the three different contraction types. B: data example from a single trial. The thin line is the actual force produced for a trial, whereas the thick line is the targeted force parabola.

200 ms. During concentric contractions, each participant moved the dynamometer's armature by producing a knee-extension force, whereas during eccentric contractions, subjects resisted the movement of the dynamometer's armature by producing a knee-extension force. For both contraction types, peak force occurred at 85° of knee flexion, and movement of the armature was initiated when the participant exerted force approximately equal to his or her leg weight. Similar to the isometric contractions, subjects had ~5 s between trials to relax and position the knee-extension force back to 0 N. During this time, the dynamometer's actuator was repositioned by the experimenter.

**Practice.** For all three types of contractions, each participant received 30 practice trials followed by 40 experimental trials at each force level. Custom-made software identified experimental trials as acceptable only if they were within  $\pm 3$  SD of the mean. If not (<20 trials in all 48 subjects), the trials were substituted from the latest practice trials (*trials 28–30*). Both the force-time parabola and the force produced by the participant were displayed on the monitor during the task for the first 10 practice trials. During the last 20 practice trials and all experimental trials, the force-time parabola was hidden during the knee-extension force production. Immediately after the trial, visual feedback of the force-time curve produced and the force-time target parabola were provided. In addition, subjects received verbal feedback regarding the amount of force and temporal characteristics they produced to enhance learning and accuracy for matching the referenced parabola. A brief rest period of 120 s was given to each participant between levels of target force.

### Statistical Analysis

An initial examination of variability of force (SD of force) indicated that men were more variable than women. This was expected because men had greater MVCs (Table 1), and the criterion force level at any %MVC was greater compared with that of the female subjects. CV was used to normalize the variability of performance around the target force level, and this normalization resulted in a nonsignificant gender effect for peak force, impulse, time to peak force, and impulse duration for all types of contractions. The two gender groups, therefore, were combined for all analyses except maximum force production.

A three-factor complete-factorial ANOVA (2 age groups  $\times$  3 contraction types  $\times$  6% MVC), with repeated measures on contraction type and %MVC, was used to examine the mean, SD, and CV of peak force, impulse, time to peak force, and impulse duration. MVC was examined by using a three-factor complete-factorial ANOVA (2 age groups  $\times$  2 genders  $\times$  3 contraction types), with repeated measures on contraction type. When significant effects were found, Tukey-Kramer post hoc tests were performed to determine the location of the effect. The probability level for all statistical tests was 0.05.

## RESULTS

### Strength

Young subjects produced greater discrete knee-extension force (MVC) than old subjects, and men pro-

duced greater force than women ( $P < 0.01$ ). Nonetheless, MVC produced during concentric and eccentric contractions was similar ( $P > 0.05$ ) (Table 1). Although strength was significantly different between age groups ( $P < 0.01$ ), old men produced similar MVC force with young women ( $P = 0.213$ ). For young subjects, the MVC was similar among the three types of contractions, whereas for the old subjects, MVC was higher during eccentric contractions (not significant after post hoc analysis). For all subjects, MVCs before and after each contraction session were not significantly different ( $P > 0.05$ ), indicating that quadriceps fatigue did not occur.

### Variability of Peak Force

**Mean peak force.** A comparison between the mean peak force produced and the target force level indicates that, on average, young and old subjects produced higher peak forces at low %MVC and lower peak forces at high %MVC.

**SD of peak force.** Young subjects exhibited greater absolute variability than old subjects (Table 2), and eccentric contractions were more variable than isometric but not concentric contractions (all  $P < 0.01$ ; Table 3). As expected, the SD of peak force increased as the level of force increased ( $P < 0.01$ ). Paired contrasts

Table 2. Group mean and within-subject SD of peak force, impulse, time to peak force, and impulse duration for isometric, concentric, and eccentric rapid contractions at each level of force

| %MVC                            | Young Adults      |                   |                   | Old Adults        |                   |                   |
|---------------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
|                                 | Isometric         | Concentric        | Eccentric         | Isometric         | Concentric        | Eccentric         |
| <i>SD peak force, N</i>         |                   |                   |                   |                   |                   |                   |
| 20                              | 23.3 $\pm$ 6.8    | 23.8 $\pm$ 8.2    | 27.1 $\pm$ 12.2   | 18.4 $\pm$ 7.0    | 22.6 $\pm$ 7.9    | 25.0 $\pm$ 9.2    |
| 35                              | 31.4 $\pm$ 11.7   | 33.9 $\pm$ 12.2   | 30.8 $\pm$ 13.6   | 23.5 $\pm$ 9.5    | 29.1 $\pm$ 11.6   | 26.9 $\pm$ 7.4    |
| 50                              | 37.4 $\pm$ 15.3   | 34.4 $\pm$ 9.9    | 36.3 $\pm$ 14.4   | 26.7 $\pm$ 13.0   | 31.4 $\pm$ 12.0   | 30.3 $\pm$ 11.9   |
| 65                              | 39.2 $\pm$ 14.0   | 36.9 $\pm$ 12.8   | 38.8 $\pm$ 13.2   | 24.7 $\pm$ 8.6    | 32.5 $\pm$ 13.1   | 29.5 $\pm$ 11.9   |
| 80                              | 39.7 $\pm$ 15.1   | 38.8 $\pm$ 14.1   | 41.0 $\pm$ 11.3   | 28.9 $\pm$ 13.8   | 27.7 $\pm$ 7.1    | 30.7 $\pm$ 9.4    |
| 90                              | 38.3 $\pm$ 14.3   | 39.1 $\pm$ 18.9   | 43.7 $\pm$ 13.2   | 24.4 $\pm$ 9.6    | 25.5 $\pm$ 8.4    | 33.8 $\pm$ 14.8   |
| <i>SD impulse, N·s</i>          |                   |                   |                   |                   |                   |                   |
| 20                              | 6.6 $\pm$ 2.7     | 6.5 $\pm$ 4.2     | 10.0 $\pm$ 7.8    | 5.4 $\pm$ 2.4     | 5.5 $\pm$ 2.8     | 8.6 $\pm$ 4.2     |
| 35                              | 9.7 $\pm$ 4.4     | 10.9 $\pm$ 6.0    | 11.2 $\pm$ 5.2    | 7.7 $\pm$ 3.9     | 8.1 $\pm$ 5.1     | 11.6 $\pm$ 5.5    |
| 50                              | 13.0 $\pm$ 5.3    | 12.9 $\pm$ 7.6    | 16.0 $\pm$ 8.6    | 9.6 $\pm$ 4.1     | 11.1 $\pm$ 5.9    | 13.7 $\pm$ 6.8    |
| 65                              | 17.3 $\pm$ 7.8    | 15.2 $\pm$ 5.7    | 18.8 $\pm$ 9.3    | 9.7 $\pm$ 3.7     | 13.5 $\pm$ 7.1    | 16.0 $\pm$ 10.0   |
| 80                              | 19.8 $\pm$ 7.8    | 20.6 $\pm$ 9.5    | 23.8 $\pm$ 10.1   | 14.1 $\pm$ 6.8    | 16.6 $\pm$ 9.3    | 20.1 $\pm$ 9.7    |
| 90                              | 23.6 $\pm$ 11.6   | 21.6 $\pm$ 9.0    | 26.4 $\pm$ 11.7   | 13.2 $\pm$ 5.3    | 17.5 $\pm$ 9.6    | 22.0 $\pm$ 10.2   |
| <i>SD time to peak force, s</i> |                   |                   |                   |                   |                   |                   |
| 20                              | 0.023 $\pm$ 0.012 | 0.024 $\pm$ 0.014 | 0.023 $\pm$ 0.018 | 0.042 $\pm$ 0.020 | 0.030 $\pm$ 0.017 | 0.037 $\pm$ 0.020 |
| 35                              | 0.028 $\pm$ 0.013 | 0.027 $\pm$ 0.012 | 0.028 $\pm$ 0.015 | 0.040 $\pm$ 0.022 | 0.033 $\pm$ 0.020 | 0.035 $\pm$ 0.020 |
| 50                              | 0.025 $\pm$ 0.011 | 0.030 $\pm$ 0.012 | 0.033 $\pm$ 0.016 | 0.031 $\pm$ 0.017 | 0.040 $\pm$ 0.023 | 0.039 $\pm$ 0.026 |
| 65                              | 0.029 $\pm$ 0.010 | 0.029 $\pm$ 0.010 | 0.028 $\pm$ 0.012 | 0.031 $\pm$ 0.019 | 0.034 $\pm$ 0.016 | 0.034 $\pm$ 0.019 |
| 80                              | 0.031 $\pm$ 0.008 | 0.028 $\pm$ 0.011 | 0.030 $\pm$ 0.012 | 0.033 $\pm$ 0.020 | 0.032 $\pm$ 0.015 | 0.037 $\pm$ 0.015 |
| 90                              | 0.028 $\pm$ 0.009 | 0.026 $\pm$ 0.012 | 0.028 $\pm$ 0.011 | 0.032 $\pm$ 0.017 | 0.030 $\pm$ 0.013 | 0.037 $\pm$ 0.016 |
| <i>SD impulse duration, s</i>   |                   |                   |                   |                   |                   |                   |
| 20                              | 0.048 $\pm$ 0.037 | 0.050 $\pm$ 0.042 | 0.097 $\pm$ 0.068 | 0.070 $\pm$ 0.038 | 0.059 $\pm$ 0.024 | 0.147 $\pm$ 0.101 |
| 35                              | 0.051 $\pm$ 0.020 | 0.057 $\pm$ 0.047 | 0.103 $\pm$ 0.055 | 0.086 $\pm$ 0.104 | 0.055 $\pm$ 0.023 | 0.127 $\pm$ 0.082 |
| 50                              | 0.062 $\pm$ 0.030 | 0.061 $\pm$ 0.038 | 0.117 $\pm$ 0.066 | 0.072 $\pm$ 0.056 | 0.065 $\pm$ 0.029 | 0.130 $\pm$ 0.081 |
| 65                              | 0.074 $\pm$ 0.037 | 0.068 $\pm$ 0.033 | 0.127 $\pm$ 0.071 | 0.080 $\pm$ 0.069 | 0.064 $\pm$ 0.028 | 0.140 $\pm$ 0.091 |
| 80                              | 0.093 $\pm$ 0.061 | 0.085 $\pm$ 0.054 | 0.155 $\pm$ 0.055 | 0.096 $\pm$ 0.055 | 0.074 $\pm$ 0.040 | 0.171 $\pm$ 0.102 |
| 90                              | 0.092 $\pm$ 0.034 | 0.083 $\pm$ 0.041 | 0.165 $\pm$ 0.072 | 0.086 $\pm$ 0.050 | 0.081 $\pm$ 0.043 | 0.153 $\pm$ 0.096 |

Values are group means  $\pm$  SD for age and each type of contraction. SD, standard deviation.

Table 3. SD and CV exhibited by all subjects for peak force, impulse, time to peak force, and impulse duration during isometric, concentric, and eccentric rapid contractions

| Motor Output Characteristic | Isometric     | Concentric    | Eccentric     |
|-----------------------------|---------------|---------------|---------------|
| SD of peak force, N         | 29.7 ± 8.6    | 31.3 ± 7.3    | 32.8 ± 8.3    |
| CV of peak force, %         | 11.4 ± 1.7    | 12.8 ± 1.8    | 12.6 ± 1.4    |
| SD of impulse, N            | 12.5 ± 3.6    | 13.3 ± 3.6    | 16.5 ± 5.3    |
| CV of impulse, %            | 17.5 ± 2.7    | 20.2 ± 3.7    | 22.9 ± 4.7    |
| SD of time to peak force, s | 0.032 ± 0.009 | 0.070 ± 0.015 | 0.031 ± 0.008 |
| CV of time to peak force, % | 21.1 ± 5.0    | 32.3 ± 6.8    | 19.3 ± 3.9    |
| SD of impulse duration, s   | 0.076 ± 0.026 | 0.066 ± 0.021 | 0.136 ± 0.039 |
| CV of impulse duration, %   | 15.7 ± 4.9    | 15.4 ± 4.3    | 25.5 ± 6.9    |

Values are group means ± SD for each type of contraction. CV, coefficient of variation.

between the two age groups at the six levels of force indicated that young subjects produced significantly greater SD of peak force at all six levels of force ( $P < 0.05$ ), except at 20% MVC ( $P > 0.05$ ). In young subjects, eccentric contractions were more variable than concentric and isometric contractions ( $P < 0.05$ ), whereas, in old subjects, eccentric and concentric contractions were more variable than isometric contractions ( $P < 0.05$ ). Nevertheless, Tukey's multiple-comparison post hoc test did not detect any significant difference among contraction types for young or old subjects. A comparison of the three contraction types across different levels of force indicated that eccentric contractions were significantly different from isometric contractions at 20 and 90% MVC ( $P < 0.01$ ) (Table 2).

**CV of peak force.** Old subjects exhibited greater relative variability (CV) than young subjects, and eccentric and concentric contractions exhibited greater CV than isometric contractions (all  $P < 0.01$ ; Table 3). As expected, the CV decreased as the level of force increased ( $P < 0.01$ ). Paired contrasts between the two age groups at the six levels of force indicated that old subjects exhibited significantly greater CV at all six levels of force ( $P < 0.01$ ); however, these differences were greater up to 50% MVC (Fig. 2A). Comparisons of the contractions across the six levels of force detected significant differences between isometric and concentric contractions at 20% MVC and eccentric contractions compared with isometric and concentric contractions at 90% MVC (all  $P < 0.05$ ). For the rest of the levels of force, the three types of contractions did not produce significantly different CV for peak force ( $P > 0.05$ ).

#### Variability of Impulse

**Mean impulse.** Mean impulse increased systematically with increases in level of force. The mean impulse error indicated that, on average, young and old subjects produced greater impulses at all percentages of MVC compared with the goal impulse.

**SD of impulse.** Young subjects exhibited greater variability than old subjects (Table 2), and eccentric contractions were more variable than isometric and concentric contractions (all  $P < 0.01$ ; Table 3). As expected, SD of impulse increased as the level of force increased. Paired contrasts between the two age groups for different levels of force indicated that the

two groups were not significantly different up to 50% MVC ( $P > 0.05$ ); however, from 65% MVC and beyond, young subjects produced significantly greater SD of impulse ( $P < 0.05$ ).

**CV of impulse.** There was a significant effect for age, contraction type, and level of force. Old subjects exhibited greater CV than young subjects, and eccentric

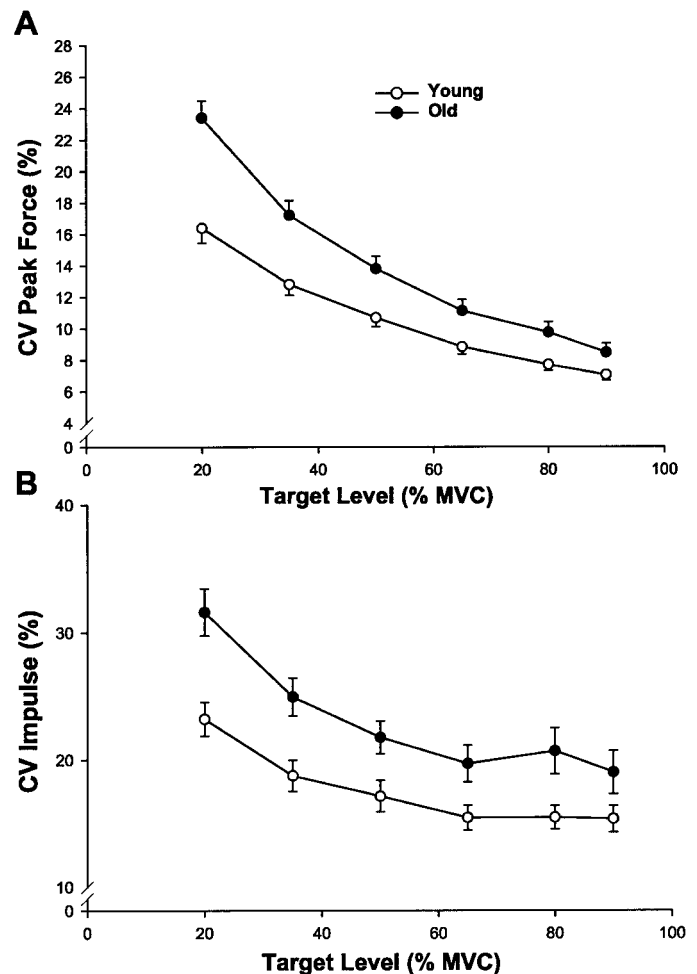


Fig. 2. A: interaction between young (○) and old (●) age groups and levels of force on the coefficient of variation (CV) of peak force. B: same interaction as A on the CV of impulse. In both variables, old adults are more variable compared with young adults, particularly at low levels of muscle activation. Values are means ± SE. MVC, maximum voluntary contraction.

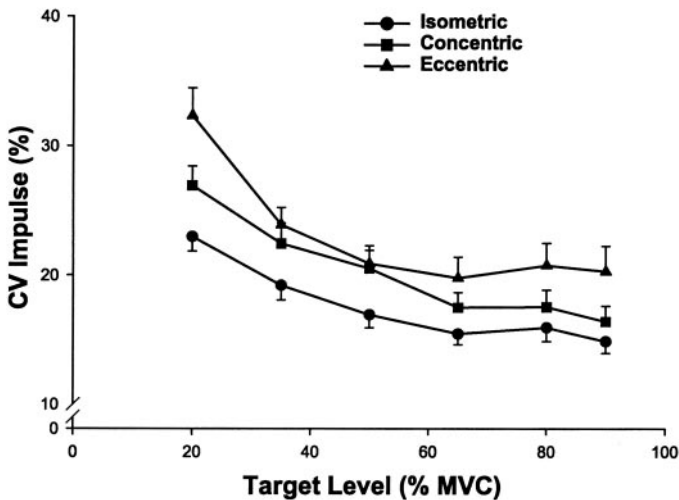


Fig. 3. Interaction between contraction type and level of force on the CV of impulse. In general, eccentric contractions (▲) are more variable than isometric (●) and concentric (■) contractions, particularly at low and high levels of muscle activation (see text for details). Values are means ± SE.

contractions resulted in significantly greater CV compared with isometric and concentric contractions (all  $P < 0.01$ ; Table 3). As expected, the CV of impulse decreased as the level of force increased ( $P < 0.01$ ). Paired contrasts between the two age groups for the six levels of force indicated that old subjects exhibited significantly greater CVs at all six levels of force ( $P < 0.01$ ); however, these differences were greater below 50% MVC (Fig. 2B). Comparison of the three contraction types with level of force indicated that eccentric contractions were more variable than isometric contractions at all levels of force and more variable than concentric contractions only at 20 and 90% MVC, and the difference between isometric and concentric contractions was only at 50% MVC ( $P < 0.05$ ; Fig. 3).

Variability of Temporal Characteristics

*Mean time to peak force.* Eccentric contractions produced shorter mean time to peak force than isometric and concentric contractions, and the mean time to peak force increased as the level of force increased (all  $P < 0.01$ ). Old subjects produced progressively shorter times to peak force than young subjects as levels of force increased. Paired contrasts between the two age groups for the six levels of force, however, indicated significant differences between the two age groups only at 80% MVC ( $P < 0.05$ ). Time to peak force during isometric contractions was significantly longer than concentric and eccentric contractions only at 20% MVC ( $P < 0.05$ ). Beyond 65% MVC, eccentric contractions had a shorter time to peak force than concentric and isometric contractions.

*SD of time to peak force.* Old subjects exhibited greater variability than young subjects ( $P < 0.01$ ; Table 2). Paired contrasts between the two age groups for the six levels of force indicated that old subjects produced significantly greater variability than young sub-

jects at force levels of 20 and 35% MVC ( $P < 0.05$ ). At levels of force from 50% and beyond, there were no significant differences between age groups. There was also a significant interaction between contraction type and level of force ( $P < 0.05$ ). Tukey's post hoc multiple-comparison test failed to detect any significant differences between the three types of contractions at any of the levels of force (Table 3). The interaction between age group and contraction type ( $P > 0.05$ ), and the three-way interaction between age group, contraction type, and level of force ( $P > 0.05$ ), were not significant.

*CV of time to peak force.* Old subjects exhibited greater relative variability (CV) than young subjects, and eccentric and isometric contractions produced significantly lower CV than concentric contractions (all  $P < 0.01$ ; Table 3). The CV of time to peak force decreased as the level of force increased ( $P < 0.05$ ). The three-way interaction between age group, contraction type, and level of force was also significant ( $P < 0.05$ ). Old subjects had greater CV for time to peak force than young subjects. CV in old adults was higher during eccentric contractions at levels of force >50% MVC. In the young group, variability was similar for the three different types of contractions. For the old group, Tukey's post hoc multiple-comparison test detected significant differences between eccentric and concentric contractions at 80 and 90% MVC, whereas, for the young group, isometric contractions had lower CVs than both eccentric and concentric contractions at 50% MVC ( $P < 0.05$ ; Fig. 4).

*Mean impulse duration.* Eccentric contractions produced greater mean impulse duration than isometric and concentric contractions, and the mean impulse duration increased as the level of force increased ( $P < 0.01$ ; Table 3).

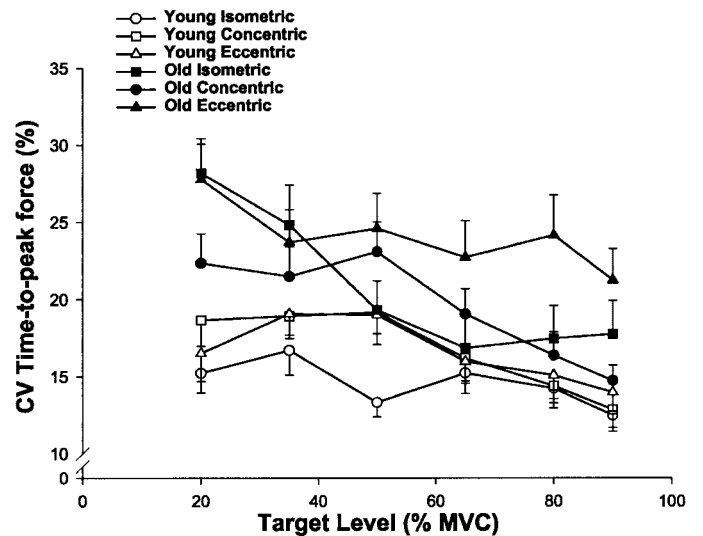


Fig. 4. Three-way interaction among age group, contraction type, and level of force on the CV of time to peak force. Old subjects (solid symbols) were more variable than young subjects (open symbols), and the time to peak force variability was amplified during eccentric contractions of >50% MVC. In the young, however, variability was similar for the three different types of contractions. Values are means ± SE.

*SD of impulse duration.* Eccentric contractions were more variable compared with isometric and concentric contractions (Table 3), and the SD of impulse duration increased as the level of force increased (all  $P < 0.01$ ; Table 2). Old subjects exhibited greater SD of impulse duration than young subjects only at levels of force  $< 50\%$  MVC ( $P = 0.06$ ).

*CV of impulse duration.* Subjects produced significantly greater CV during eccentric contractions compared with isometric and concentric contractions (Table 3), and the CV of impulse duration decreased as the level of force increased (all  $P < 0.01$ ). There was a significant interaction between age group and level of force ( $P < 0.05$ ). Paired contrasts between the two age groups at the six levels of force indicated that old subjects had significantly greater CV than young subjects only at 20% MVC ( $P < 0.05$ ; Fig. 5).

## DISCUSSION

The present study examined strength and the ability of active young and old individuals to control force during a wide range of submaximal rapid contractions. The study produced two novel findings. 1) Old adults were more variable in force (CV) and temporal characteristics of muscular contractions (SD and CV) compared with young adults and 2) eccentric contractions were more variable (SD and CV) compared with isometric and concentric contractions.

### Rapid Strength

Results from the present experiment show that strength for rapid discrete contractions of the quadriceps in old adults was lower by  $\sim 45\%$  for isometric, 41% for concentric, and 35% for eccentric contractions compared with young adults. These results provide partial support to previous research reporting that old men and women maintain eccentric strength, whereas concentric and isometric strength significantly decline

compared with young adults (29, 40). The differences in findings for eccentric contractions may be due to methodological differences in measuring strength. The primary aim of this study was to identify age-related differences in motor output variability. Therefore, maximum strength during rapid discrete contractions was measured with similar temporal characteristics to the target-force parabolas (200-ms time to peak force). In previous studies (29, 40), velocity characteristics and range of movement were different, whereas time to peak force was free to vary. Although active and healthy old individuals were recruited, the results suggest that when time to peak force is short and fixed, maximum force in the old adults is significantly lower than that in young adults in all contractions; nevertheless, this reduction in strength is smaller during eccentric contractions. The lower strength compared with young adults and the relatively better maintenance of eccentric strength may potentially be caused by two factors. 1) There is an increase in collagen tissue (connective tissue) in the belly of the muscle with age, which can increase the stiffness of the muscle and passively contribute to eccentric force production (29). 2) If indeed eccentric contractions selectively recruit fewer and larger motor units (36), then the ability of old adults to produce eccentric force may be better maintained because some of the small motoneurons that are reorganized to innervate more muscle fibers (41) may be recruited.

### Age and Motor Output Variability

The present experiment demonstrated that old adults exhibited higher relative variability (CV) than young adults during rapid discrete isometric, concentric, and especially eccentric contractions of the quadriceps when the level of force was expressed as %MVC. This finding was robust for peak force, impulse, time to peak force, and impulse duration. Thus not only were the old adults more variable in producing force, but they also were more variable in the timing of their contractions.

Accuracy in movement is influenced by both variability of force and temporal variability associated with the force produced (8, 32). Although the variability of peak force appears to be similar between young and old adults as a function of absolute force (in N), the variability of impulse (the aggregate of force and time) is greater in old adults, particularly for eccentric contractions. This was also true for the temporal characteristics examined, such as time to peak force and impulse duration. During activities of daily living that require precision in both absolute force and timing (impulse), such as ascending or descending stairs, it is probable that old adults will perform significantly poorer compared with young adults. These differences appear to be magnified during eccentric contractions. This study provides support to previous findings indicating that performance decreases during eccentric contractions. Such findings include the inability of the old adults to decelerate during aiming movements (16), braking

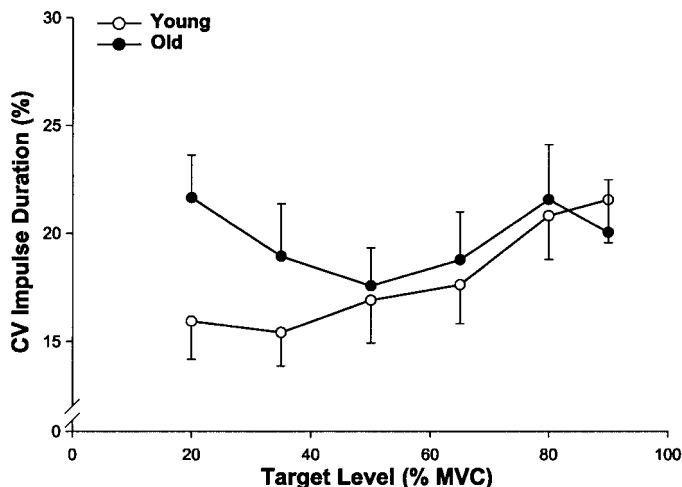


Fig. 5. Interaction between age group and level of force on the CV of impulse duration. Old subjects (●) were more variable than young subjects (○) only at 20% MVC (see text for details). Values are means  $\pm$  SE.

movements with an eccentric activation of the antagonist muscle (47), and control force during slow continuous eccentric muscular contractions (15, 34).

Several factors can produce the increased motor output variability observed in old compared with young individuals in this study. Nonetheless, there is evidence that some potential factors do not correlate with the increased variability exhibited by old individuals. Such factors that do not explain the increased variability found in old adults include the increased average force produced by motor units (31), the pattern of coactivation by the agonist and antagonist muscles (5), and synchronization of motor units (44). This study also suggests that differences in variability between young and old adults are not due to differences in the use of sensory feedback, given the nature of the task used in this study. The performance of rapid contractions is largely determined by the descending command and eventually the excitation of the motoneuronal pool because the use of sensory feedback is eliminated when the voluntary movement is completed in <210 ms (17). Therefore, the impairment in old adults may be part of an open-loop control system that controls discharge rate of the motor units. The following paragraph discusses potential mechanisms.

There is accumulating evidence that discharge rate variability of the motor units is greater in old compared with young adults (15, 22, 34). More variable discharge rates of the motor units occur with faster muscle contractions (50), and numerous findings suggest that the ability of old adults to control force and movement appears to decline with increases in speed and complexity of movement (13, 53). Potential mechanisms that can explain the increased variability of the discharge rate of motor units in old adults and the decline in force control, especially during eccentric contractions (34), include the increase in loss of corticomotorneurons after the age of 50 yr (19), the decrease in transmission velocity from corticospinal and reflex pathways to the motoneurons (23), the 25% reduction in the total number of lumbosacral spinal cord motoneurons (23, 26), and particularly the loss of the largest  $\alpha$ -motoneurons and their myelinated axons (18). The above mechanisms can individually or in combination affect the increased motor output variability exhibited in old adults.

The motor output of young and old subjects in this study was primarily determined by an open-loop task that was repeated several times. The ability of old adults to repeatedly produce the same motor output (within-subject, between-trial variability) was severely compromised. This was especially notable for the temporal characteristics of the movement and during eccentric contractions. Collectively, the results of this study provide support to the notion that the descending command and the excitation of the motoneuronal pool (motor program) of old adults are impaired compared with those of young adults.

### *Contractions and Motor Output Variability*

It has been hypothesized that eccentric contractions are distinctly controlled by the CNS (20). Several differences in motor output performance between concentric and eccentric contractions have been described in the literature (20); however, few attempts have been made to examine their motor output variability (10, 34). The present experiment demonstrated that rapid discrete eccentric contractions are more variable compared with discrete isometric and concentric contractions. This finding is consistent for peak force, impulse, time to peak force, and impulse duration for both young and old groups. These results support and extend previous findings that reported greater variability during discrete eccentric contractions (10). Differences between types of contractions, however, cannot be attributed to velocity characteristics, length of muscle, or moment arm, because the findings were based on isometric, slow (25°/s), and short-range (10°) knee-extension movements. Maximum force output was not significantly different among discrete isometric, concentric, and eccentric contractions. Therefore, force-velocity characteristics in this experiment did not significantly influence production of force. The findings about variability in this study were largely influenced by the task requirements, which required the repetition of the motor program and, therefore, provide further support to the hypothesis that the CNS has a unique scheme to control eccentric contractions compared with concentric and isometric contractions.

Support for the hypothesis that descending commands modify and/or influence the excitability or selection of motoneurons during eccentric contractions comes from at least three lines of evidence. First, the original finding by Nardone et al. (36) suggests that there is an alternative recruitment order of motor units during eccentric contractions (30); nonetheless, this finding is controversial (3, 14, 34), and the exact mechanism that the CNS utilizes to selectively recruit high-threshold motoneurons is unknown (4). Second, the synchronization of motor units is greater during eccentric than during concentric contractions, suggesting that the descending command may be different (43). Muscle-excitation studies provide the third and most robust evidence for alternative descending commands. For example, EMG at various levels of muscle excitation is significantly reduced during eccentric contractions compared with concentric contractions, and this reduction in EMG appears to be due to a reduction in the mean discharge rate of the motor units (33, 46). Further evidence comes from studies where superimposition of electrical stimulation onto maximal voluntary contractions produces an increase in eccentric but not concentric force. These findings indicate the existence of a potential neural inhibitory mechanism that limits the recruitment or discharge of the motor units (1, 49). The participant's intention to perform an eccentric contraction, moreover, was associated with decreased muscle activation (lower EMG) of the quadriceps muscle (25). Current findings, additionally, suggest

that differences in EMG between concentric and eccentric contractions appear to be magnified with increases in movement speed (13). This occurs because muscle activation increases with increases in speed of movement during concentric contractions, whereas muscle activation is unaffected by the speed of eccentric contractions.

In summary, this study resulted in two major findings. First, old adults who are healthy and physically active are more variable compared with healthy and active young individuals during rapid discrete isometric, concentric, and particularly eccentric contractions of the quadriceps. This suggests that repetition of the descending command and eventual excitability of the motoneuronal pool is impaired in old adults. Second, the ability of humans to repeatedly perform a task requiring a muscular contraction with appropriate force and timing (impulse) is more variable during eccentric than concentric and isometric contractions. This finding provides further evidence to the hypothesis that eccentric contractions may be uniquely controlled by the CNS (20).

The authors are grateful to Dr. Sandra Hunter and Kurt Kornatz for comments on a draft of the manuscript. In addition, we thank the reviewers for helpful and constructive comments on the submitted manuscript.

## REFERENCES

1. Aagaard P, Simonsen EB, Andersen JL, Magnusson SP, Halkjaer-Kristensen J, and Dyhre-Poulsen P. Neural inhibition during maximal eccentric and concentric quadriceps contraction: effects of resistance training. *J Appl Physiol* 89: 2249–2257, 2000.
2. Arnold B and Perrin D. The reliability of four different methods of calculating quadriceps peak torque and angle specific torques at 30°, 60°, and 75°. *J Sport Rehab* 2: 243–250, 1993.
3. Bawa P and Jones KE. Do lengthening contractions represent a case of reversal in recruitment order? *Prog Brain Res* 123: 215–220, 1999.
4. Burke RE. Selective recruitment of motor units. In: *Motor Control: Concepts and Issues*, edited by Humphrey DR and Freund HJ. Chichester, UK: Wiley, 1991.
5. Burnett RA, Laidlaw DH, and Enoka RM. Coactivation of the antagonist muscle does not covary with steadiness in old adults. *J Appl Physiol* 89: 61–71, 2000.
7. Carlton LG and Newell KM. Force variability in isometric tasks. In: *Biomechanics IX*, edited by Winter DA, Norman RW, Hayes KC, Wells RP, and Patla A. Champaign, IL: Human Kinetics, 1985, p. 128–132.
8. Carlton LG and Newell KM. Force variability and movement accuracy in space-time. *J Exp Psychol Hum Percept Perform* 14: 24–36, 1988.
9. Carlton LG and Newell KM. Force variability and characteristics of force production. In: *Force Variability*, edited by Newell KM and Cordo P. Champaign, IL: Human Kinetics, 1993, p. 128–132.
10. Christou EA and Carlton LG. Motor output variability during concentric and eccentric contractions of the quadriceps femoris muscle group. In: *Proceedings of the 23rd Annual Meeting of the American Society of Biomechanics, Pittsburgh, PA*, 1999, p. 129–130.
11. Christou EA and Carlton LG. Eccentric contractions of the quadriceps femoris muscle have greater motor output variability than isometric and concentric contractions. In: *Proceedings of the 24th Annual Meeting of the American Society of Biomechanics, Chicago, IL*, 2000, p. 137–138.
12. Christou EA and Carlton LG. Old adults exhibit greater motor output variability than young adults only during rapid discrete isometric contractions. *J Gerontol A Biol Sci Med Sci* 56: B524–B532, 2001.
13. Christou EA, Shinohara M, and Enoka RM. The changes in EMG and steadiness with variation in movement speed differ for concentric and eccentric contractions. In: *Proceedings of the 25th Annual Meeting of the American Society of Biomechanics, San Diego, CA*, 2001, p. 333–334.
14. Christova P and Kossev A. Human motor unit activity during concentric and eccentric movements. *Electromyogr Clin Neurophysiol* 40: 331–338, 2000.
15. Connelly DM, Rice CL, Roos MR, and Vandervoort AA. Motor unit firing rates and contractile properties in tibialis anterior of young and old men. *J Appl Physiol* 87: 843–852, 1999.
16. Cooke JD, Brown SH, and Cunningham DA. Kinematics of arm movements in elderly humans. *Neurobiol Aging* 10: 159–165, 1989.
17. Cordo P, Carlton L, Bevan L, Carlton M, and Kerr GK. Proprioceptive coordination of movement sequences: role of velocity and position information. *J Neurophysiol* 71: 1848–1861, 1994.
18. Doherty TJ, Vandervoort AA, Taylor AW, and Brown WF. Effects of motor unit losses on strength in older men and women. *J Appl Physiol* 74: 868–874, 1993.
19. Eisen A, Entezari-TaHER M, and Stewart H. Cortical projections to spinal motoneurons: changes with aging and amyotrophic lateral sclerosis. *Neurology* 46: 1396–1404, 1996.
20. Enoka RM. Eccentric contractions require unique activation strategies by the nervous system. *J Appl Physiol* 81: 2339–2346, 1996.
21. Enoka RM and Fuglevand AJ. Motor unit physiology: some unresolved issues. *Muscle Nerve* 24: 4–17, 2001.
22. Erim Z, Beg MF, Burke DT, and de Luca CJ. Effects of aging on motor-unit control properties. *J Neurophysiol* 82: 2081–2091, 1999.
23. Evans WJ and Starr A. Electroencephalography and evoked potentials in the elderly. In: *Clinical Neurology of Aging*, edited by Albert ML and Knoefel JE. New York: Oxford Univ. Press, 1994, p. 235–265.
24. Galganski ME, Fuglevand AJ, and Enoka RM. Reduced control of motor output in a human hand muscle of elderly subjects during submaximal contractions. *J Neurophysiol* 69: 2108–2115, 1993.
25. Grabiner MD, Owings TM, George MR, and Enoka RM. Eccentric contractions are specified a priori by the CNS. In: *Proceedings of the VXth Congress of the International Society of Biomechanics, Jyväskylä, Finland*, 1995, p. 338–339.
26. Henderson G, Tomlinson BE, and 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.
27. Henneman E. Relation between size of neurons and their susceptibility to discharge. *Science* 126: 1345–1347, 1957.
28. Hortobagyi T and DeVita P. Altered movement strategy increases lower extremity stiffness during stepping down in the aged. *J Gerontol A Biol Sci Med Sci* 54: B63–B70, 1999.
29. Hortobagyi T, Zheng D, Weidner M, Lambert NJ, Westbrook S, and Houmard JA. The influence of aging on muscle strength and muscle fiber characteristics with special reference to eccentric strength. *J Gerontol A Biol Sci Med Sci* 50: B399–B406, 1995.
30. Howell JN, Fuglevand AJ, Walsh ML, and Bigland-Ritchie B. Motor unit activity during isometric and concentric-eccentric contractions of the human first dorsal interosseus muscle. *J Neurophysiol* 74: 901–904, 1995.
31. Keen DA, Yue GH, and Enoka RM. Training-related enhancement in the control of motor output in elderly humans. *J Appl Physiol* 77: 2648–2658, 1994.
32. Kim S, Carlton LG, and Newell KM. Preload and isometric force variability. *J Mot Behav* 22: 177–190, 1990.
33. Kossev A and Christova P. Discharge pattern of human motor units during dynamic concentric and eccentric contractions. *Electroencephalogr Clin Neurophysiol* 109: 245–255, 1998.
34. Laidlaw DH, Bilodeau M, and Enoka RM. Steadiness is reduced and motor unit discharge is more variable in old adults. *Muscle Nerve* 23: 600–612, 2000.

35. **Matsunaga K, Uozumi T, Tsuji S, and Murai Y.** Age-dependent changes in physiological threshold asymmetries for the motor evoked potential and silent period following transcranial magnetic stimulation. *Electroencephalogr Clin Neurophysiol* 109: 502–507, 1998.
36. **Nardone A, Romano C, and Schieppati M.** Selective recruitment of high-threshold human motor units during voluntary isotonic lengthening of active muscles. *J Physiol* 409: 451–471, 1989.
37. **Newell KM and Carlton LG.** On the relationship between peak force and peak force variability in isometric tasks. *J Mot Behav* 17: 230–241, 1985.
38. **Paffenbarger RS Jr, Wing AL, and Hyde RT.** Physical activity as an index of heart attack risk in college alumni. *Am J Epidemiol* 108: 161–175, 1978.
39. **Pfeiffer E.** A short portable mental status questionnaire for the assessment of organic brain deficits in elderly patients. *J Am Geriatr Soc* 23: 261–299, 1975.
40. **Porter MM, Myint A, Kramer JF, and Vandervoort AA.** Concentric and eccentric knee extension strength in older and younger men and women. *Can J Appl Physiol* 20: 429–439, 1995.
41. **Roos MR, Rice CL, and Vandervoort AA.** Age-related changes in motor unit function. *Muscle Nerve* 20: 679–690, 1997.
42. **Schultz AB, Alexander NB, and Ashton-Miller JA.** Biomechanical analyses of rising from a chair. *J Biomech* 25: 1383–1391, 1992.
43. **Semmler JG, Kutzscher DV, Zhou S, and Enoka RM.** *Motor Unit Synchronization is Enhanced During Slow Shortening and Lengthening Contractions of the First Dorsal Interosseus Muscle.* New Orleans, LA: Society of Neuroscience Abstracts, 2000.
44. **Semmler JG, Steege JW, Kornatz KW, and Enoka RM.** Motor-unit synchronization is not responsible for larger motor-unit forces in old adults. *J Neurophysiol* 84: 358–366, 2000.
45. **Slifkin AB and Newell KM.** Noise, information transmission, and force variability. *J Exp Psychol Hum Percept Perform* 25: 837–851, 1999.
46. **Sogaard K, Christensen H, Jensen BR, Finsen L, and Sjogaard G.** Motor control and kinetics during low level concentric and eccentric contractions in man. *Electroencephalogr Clin Neurophysiol* 101: 453–460, 1996.
47. **Vrtunski PB, Alphas LD, and Meltzer HY.** Isometric force control in schizophrenic patients with tardive dyskinesia. *Psychiatry Res* 37: 57–72, 1991.
48. **Washburn RA, Goldfield SR, Smith KW, and McKinlay JB.** The validity of self-reported exercise-induced sweating as a measure of physical activity. *Am J Epidemiol* 132: 107–113, 1990.
49. **Webber S and Kriellaars D.** Neuromuscular factors contributing to in vivo eccentric moment generation. *J Appl Physiol* 83: 40–45, 1997.
50. **Wessberg J and Kakuda N.** Single motor unit activity in relation to pulsatile motor output in human finger movements. *J Physiol* 517: 273–285, 1999.
51. **Westing SH, Seger JY, Karlson E, and Ekblom B.** Eccentric and concentric torque-velocity characteristics of the quadriceps femoris in man. *Eur J Appl Physiol* 58: 100–104, 1988.
52. **Williams K.** Intralimb coordination of older adults during locomotion: stair descent. *J Hum Mov Stud* 34: 95–117, 1998.
53. **Yan JH, Thomas JR, Stelmach GE, and Thomas KT.** Developmental features of rapid aiming arm movements across the lifespan. *J Mot Behav* 32: 121–140, 2000.

