Effects of age and gender on finger coordination in MVC and submaximal force-matching tasks

MINORU SHINOHARA, SHENG LI, NING KANG, VLADIMIR M. ZATSIORSKY, AND MARK L. LATASH
Department of Kinesiology, The Pennsylvania State University, University Park, Pennsylvania 16802

Submitted 15 July 2002; accepted in final form 11 September 2002

Shinohara, Minoru, Sheng Li, Ning Kang, Vladimir M. Zatsiorsky, and Mark L. Latash. Effects of age and gender on finger coordination in MVC and submaximal force-matching tasks. J Appl Physiol 94: 259–270, 2003. First published September 13, 2002; 10.1152/japplphysiol.00643.2002.—The objective of the study is to examine the effects of age and gender on finger coordination. Twelve young (24 ± 8 yr; 6 men and 6 women) and 12 elderly (75 ± 5 yr; 6 men and 6 women) subjects performed single-finger maximal contraction [maximal voluntary contraction (MVC)], four-finger MVC, and four-finger ramp force production tasks by pressing on individual force transducers. A drop in the force of individual fingers during four-finger MVC tasks compared with single-finger MVC tasks (force deficit) was larger, whereas unintended force production by other fingers during single-finger MVC tasks (enslavling) was smaller, in elderly than in young subjects and in women than in men. Force deficit was smaller and enslaving was larger in subjects with higher peak force. During the ramp task, the difference between the variance of total force and the sum of variances of individual forces showed a logarithmic relation to the level of total force, across all subject groups. These findings suggest that indexes of finger coordination scale with force-generating capabilities across gender and age groups.

AGING LEADS TO A LOSS IN MANUAL dexterity and associated deficiency in the activities of daily living (20, 23, 28, 54). Obviously, hand function relies on the coordinated action of the digits. It is, therefore, possible that finger coordination may change with age, and that may consequently affect the hand function in elderly. Many clinical scales of motor abilities rely heavily on hand function (e.g., Jebsen Hand Function Test [25]). Changes in finger coordination with age, however, have been studied in only a few studies (7, 8, 10).

Our group has been accumulating a significant amount of information related to finger coordination in young healthy subjects (35, 44, 45, 63). In multifinger pressing tasks, total force is shared among the fingers in a certain pattern over a wide range of force magnitudes (sharing). Sharing patterns have been viewed as reflecting a principle of minimization of secondary moments (45), i.e., pronation and supination moments about the functional longitudinal axis of the hand and forearm generated by all four fingers. In four-finger pressing tasks, for instance, the forces shared by the index (I) and middle (M) fingers are approximately equal (~30% of the total force for each finger), whereas the ring (R) and little (L) fingers share the remaining 40% of the total force (35, 45). Finger interaction leads to involuntary force generation by fingers that are not explicitly required to produce force (enslaving). During single-finger maximal voluntary contraction (MVC) tasks, explicitly noninvolved (slave) fingers produced forces ranging from 10 to 50% of their MVC (62, 63). Smaller enslaving has been reported for the dominant hand compared with the nondominant hand and is discussed as a correlate of higher dexterity of the dominant hand related to its better independent finger control (42). In multifinger MVC tasks, total peak force is smaller than the sum of peak forces in single-finger tasks by the involved fingers (force deficit). In four-finger tasks, the average magnitude of the force deficit per finger is ~35–40% of the corresponding MVC forces (43, 46). Both force deficit and enslaving are modified under muscle fatigue (13, 14), suggesting that finger coordination can be modified by alterations in the neuromuscular system.

Recent studies have also shown that individual fingers are controlled as a synergy, in a sense that they compensate for each other’s errors with respect to a functionally important performance variable (38, 39, 56). It is known from the theory of probability that, for the mutually independent and integrable variables, the sum of the variances is equal to the variance of the sum (Bienaymé equality theorem, see Ref. 47). For that reason, if several independent elements contribute, in an additive way, to a common output, the variance of the common output is expected to be equal to the sum of the variances of the outputs of individual elements. Contrary to this expectation, in a multifinger force production task, variance of total force (VarFtot) was shown, at high forces, to be lower than the sum of
variances of individual finger forces ($\Sigma$VarFi) (40, 45). This relation suggests that, if one finger in a particular trial produced a larger force than its expected (average) contribution, other fingers were more likely to produce smaller forces such that the effect on the total force was decreased. This phenomenon has been addressed as error compensation. Comparing the VarFtot and the $\Sigma$VarFi allows one to quantify error compensation among fingers in a pressing task.

The interactions among fingers during force production have been discussed as being due to both peripheral factors (extrinsic multidigit muscles and tendinous connections) and a particular central organization of descending commands (31, 38, 45, 59, 63). Aging leads to changes in the muscular function, in particular in distal arm muscles. Thumb abduction strength decreases after the age of 60 yr, and this correlates with both pinch and grip strength (5). In the thenar muscles of the elderly, larger twitch tension, slower contraction time, and slower half-relaxation time of motor units have been reported with an increased size of action potential of single motor units (17). In the index finger, abduction strength is reduced, and fluctuation of force is increased (22). In the studies of first dorsal interosseus muscle, the discharge rate of motor units has been found to be more variable (33) and the maximal discharge rate to be smaller (29). Moreover, it is likely that the force-frequency curve of a muscle is modified with age (9, 50, 51, 58). Additionally, monosynaptic reflexes in a hand muscle have been shown to be smaller, whereas longer latency responses are unchanged (12).

Force deficit may be viewed as a consequence of both incomplete recruitment of motor units and their reduced discharge rate. Because of the increased innervation ratio of motor units with aging (e.g., Ref. 34 for review), a lack of recruitment of a certain number of motor units may be expected to result in a relatively larger drop in force in elderly subjects. In addition, possible effects of reduced discharge rate of motor units on force deficit may be related to changes in the force-frequency dependence. During natural voluntary contractions, only the steep part of the force-frequency relation (S shaped) is used (11, 59). It is known that this steep portion has a higher slope in slow muscles and motor units (6, 30). Hence, one could expect the force-frequency curve of the elderly to have a steeper slope. If the force-frequency curve of hand muscles in the elderly is steeper, then a standard drop in the force-frequency curve to the left (steeper portion) during single-finger MVC; consequently, the relative amount of force reduction during multifinger MVC, i.e., force deficit, would be larger.

Connective tissue replaces contractile proteins with aging (64), and this could be expected to lead to an increase in enslaving due to increased force transmis-

A recent pilot study of the effects of aging on finger coordination in a small subject group (6 elderly and 6 young subjects) has only partly supported the predicted changes in indexes of finger interaction (15). It has suggested that aging is associated with decreased or unchanged enslaving, increased force deficit, and selective weakening of intrinsic hand muscles. The apparent discrepancy of these observations with the predicted changes in enslaving suggests a possibility that neural control of fingers adjusts to the changes in the periphery, using the phenomena of neural plasticity, to optimize hand performance in every day motor tasks.

The increased size and more variable discharge rate of motor units may be expected to lead to less efficient error compensation across fingers in elderly subjects. In addition, alterations in the distribution of activity among synergistic muscles, observed in elderly subjects (24), may lead to changes in the ability of controlling force. Thus it is also hypothesized that aging will lead to less efficient error compensation across fingers in the ramp force production task, reflected in decreased difference between VarFtot and the $\Sigma$VarFi ($\Delta$Var). Correspondingly, there are two major goals within the present study: 1) to investigate age-related changes in indexes of finger coordination in MVC tasks using a larger number of subjects, with equal representations of men and women; and 2) to study age-related changes in the relations between VarFtot and the $\Sigma$VarFi in tasks that require accurate control of the total force.

There are also reports suggesting that muscles in women differ from those in men. Other than showing lower muscle strength, women have been reported to have smaller twitch force of a whole muscle (49), higher proportion of type I fibers (57), and longer half-relaxation time (27) in some muscles. These features are similar to those seen in muscles of elderly persons. Hence, we hypothesize that indexes of finger interaction in women may show features similar to those in the elderly. Most previous studies on finger coordination have not found significant differences between men and women (except for the lower forces in women), and the data were typically pooled for analysis (37, 45). Those studies, however, used relatively small numbers of subjects per group, and all of the subjects were
young adults. Hence, another purpose of the present study was to investigate possible gender-related differences in finger coordination by using subject groups that cover a wider range of age and ability to produce force.

METHODS

Subjects

Twelve (6 men and 6 women) young and twelve (6 men and 6 women) elderly subjects took part in the experiment. All the subjects were healthy and right-handed, according to their preferential use of the hand during writing and eating. The average age of the young and elderly subjects was 24 ± 8 (means ± SD) and 75 ± 5 yr, respectively. The average height and body mass were 1.67 ± 0.08 m and 63.0 ± 9.7 kg for the young subjects; 1.64 ± 0.14 m and 62.7 ± 9.6 kg for the elderly subjects; 1.76 ± 0.07 m and 70.6 ± 7.9 kg for the men; and 1.58 ± 0.05 m and 56.5 ± 4.7 kg for the women, respectively. All of the subjects gave informed consent according to the procedures approved by the Office for Regulatory Compliance of The Pennsylvania State University.

Apparatus

The subject was seated in a chair facing the testing table and a monitor with his or her right upper arm at ~45° of abduction in the frontal plane and ~45° of flexion in the sagittal plane and the elbow at ~135° of flexion. A wooden board supported the wrist and the forearm; two pairs of Velcro straps were used to prevent forearm or hand motion during the tests. A wooden piece shaped to fit comfortably under the subject’s palm was placed underneath the palm to help maintain a constant configuration of the hand and fingers. The metacarpophalangeal joints and all of the interphalangeal joints were flexed by ~20° such that the hand formed a dome. The subject viewed the monitor, which displayed the total force produced by fingers. The experimental setup is basically similar to the ones utilized repeatedly in our laboratory (36, 38, 39, 45, 62). (See Fig. 1 of Ref. 45 for a schematic illustration.)

Four piezoelectric sensors (model 208C02, PCB Piezotronics, Depew, NY) were used to measure the force production of individual fingers. Analog output signals from the sensors were connected to separate signal conditioners (model 484B11, PCB Piezotronics). The signal conditioners operated in a direct-current-coupled mode, utilizing the sensor’s discharge time constant, as established by the built-in microelectronic circuits within the sensors. As such, the time constant of the sensor was ~500 s. The system involved ~1% error over the typical epoch of recording of a constant signal. Cotton covers were attached to the upper surface of the sensors to increase friction and prevent the influence of skin temperature on the measurements. The sensors were placed under each finger of the right hand.

The sensors were mounted inside a steel frame (140 × 90 mm). The sensors were mediolaterally distributed 30 mm apart within the frame. The position of the sensors could be adjusted in the forward-backward direction within a range of 60 mm to fit the individual subject’s anatomy. The steel frame was placed inside a groove in the wooden board and positioned so that the subject could place his or her fingers comfortably on the sensors while preserving the described arm configuration. Once adjusted, the position of all of the sensors remained unchanged throughout the experiment. A Gateway 450-MHz microcomputer with a 16-bit analog-to-digital converter (PCI-MIO-16XE-50, National Instruments, Austin, TX) was used for data acquisition and processing. The force measured by each sensor was sampled at 1,000 Hz. Possible force range of the sensor was ±444.8 N, and the resolution of the system was 2.715 mN/bit. The high resolution was made possible by allotting only the force range of ±88.96 N to the 16-bit analog-to-digital converter.

Procedure

The subjects performed two tasks, maximal force production (MVC) and accurate production of force, following a template shown on the monitor. MVC tasks involved five experimental conditions. In the first four, the subjects were asked to produce maximal force with one finger only: I, M, R, or L. The fifth condition was a four-finger task (IMRL). The order of the conditions was pseudorandomized among subjects. During each trial, all of the fingers were on the sensors, and subjects were explicitly instructed not to lift other “uninvolved” fingers off the sensors. They were asked not to pay attention to possible force generation by those fingers as long as the force by the instructed fingers was maximal.

At the beginning of each MVC trial, the computer generated two tones (“get ready”) and then a trace showing the total force produced by the explicitly involved fingers started to move across the screen. The subjects were asked to produce peak force within a 2-s time interval, shown on the screen by two vertical lines, and then to relax. Each subject performed three trials using each finger combination. The trial with the highest force in the four-finger task was used as a reference to adjust the target force in the ramp tests.

During accurate force production trials, the subjects were always instructed to press with all four fingers (IMRL). An oblique yellow line was shown on the screen corresponding to the force increase from 0 to 30% of the MVC over 3 s, and the task was to trace this line in time with the cursor representing total finger force. These particular task parameters were selected based on our previous experience with studies on young control subjects and on persons with Down syndrome (36, 40, 45). In particular, they lead to measurable finger force variations across trials and do not induce fatigue. The force displayed on the screen was the sum of the I, M, R, and L finger forces. The forces for individual fingers were not shown on the screen, but they were recorded. The ramp task was repeated 12 times. The interval between successive trials was ~15 s. Subjects never reported fatigue.

Data Processing

For each MVC trial, the instantaneous force produced by each finger was measured at the moment when the maximal force value was reached by the explicitly involved fingers (MVC force). These data were used to compute enslaving force during single-finger trials, force deficit during IMRL trials, and force sharing during IMRL trials.

Enslaving forces were produced by slave fingers, i.e., by those fingers that were not explicitly involved in a task. They were measured at a time when the explicitly instructed finger reached its peak force. For each slave finger, the enslaving force was expressed in absolute units (N) and in percent with respect to this finger’s MVC force in its single-finger task. These indexes of enslaving were averaged across all slave fingers for further comparisons.

Force deficit for a finger was defined as the difference between this finger’s MVC in its single-finger task and its force when peak force was reached during the four-finger task. Force deficit was expressed in absolute units (N) and in
percent of the finger's peak force in its MVC single-finger task. Thereafter, indexes of force deficit were averaged across all fingers for further comparisons. Furthermore, we mostly focus on normalized indexes of finger interaction to make comparisons across subjects with different abilities to generate large forces. However, we also present data in absolute units, which may be more relevant for everyday tasks of object manipulation, in which certain absolute magnitudes of force need to be produced independently of the MVC of a particular person.

Force sharing was calculated by dividing the instantaneous force of each finger by the four-finger MVC force (MVC-4).

In ramp tests, for each subject, 12 trials of a series were aligned by the moment of ramp initiation, and average profiles of individual finger forces and of the combined force across the 12 trials were computed. Time profiles of the variances of the individual finger forces and VarF_{tot} across the 12 trials were computed [VarF_{i}(t) and VarF_{i,\text{tot}}(t), respectively]. The time profile of the \( \Sigma \text{Var}F_{i}(t) \) across the 12 trials was also computed. Furthermore, variance values across the 12 trials were computed. Time profiles of the variances of the individual forces were used. Factors were chosen being divided by the corresponding average MVC force squared. The ramp task was split into three segments because, in our laboratory's earlier studies, we saw differences in finger interaction during the first 1-s segment of force production and the remaining time over the ramp (36, 40).

The difference between the two variance indexes \( \Delta \text{Var}(t) = \Sigma \text{Var}F_{i}(t) - \text{Var}F_{i,\text{tot}}(t) \) was computed to assess the predominance of positive or negative covariations among individual finger forces. Note that if \( \Delta \text{Var}(t) > 0 \), negative covariations among finger forces dominate, revealing partial compensation of errors introduced by individual fingers in separate trials. If \( \Delta \text{Var}(t) < 0 \), positive covariations dominate, revealing amplification of errors introduced by individual fingers. The \( \Delta \text{Var}(t) \) was averaged over each 1-s segment of the ramp and analyzed both in newtons squared and after being divided by corresponding average \( \Sigma \text{Var}F_{i}(t) \).

Statistics

Standard descriptive statistics and ANOVAs, with or without repeated measures, were used. Factors were chosen based on particular comparisons. Factors included age (elderly and young), gender (men and women), task (I, M, and L), finger (I, M, R, and L), and time (3 levels: first, second, and third segments of the ramp). For comparisons that included finger or time, repeated-measures ANOVAs were used. For comparison of sharing patterns, multivariate ANOVA was used, including age and gender factors, and Bonferroni's correction. Linear regression analysis was used to analyze relations between indexes of finger interaction ( enslaving and force deficit) and MVC-4. Level of significance was set at \( P = 0.05 \). The data are presented as means and SDs in the text and Table 1. The data in Figs. 1, 2, 4, and 5 are presented as means and SEs.

RESULTS

Effects of Age and Gender on Finger Interaction During MVC Tests

MVC force and sharing patterns. During trials that required maximal force production by individual fingers, the peak forces were the largest for the I finger, followed by the M finger. Peak forces produced by the R and L fingers were not different from each other; they were both smaller than those produced by I and M fingers. Women produced lower peak forces than men (on average, by 48%), whereas elderly subjects produced lower peak forces than young subjects (on average, by 21%). These results are presented in Table 1 as averages and SDs of peak forces for the single-finger tasks. The mentioned differences have been analyzed by a three-way ANOVA with two between factors (age and gender) and one within factor (finger). The ANOVA showed main effects of all three factors: finger \( [F_{(6,60)} = 89.2, P < 0.01], \) age \( [F_{(1,20)} = 5.12, P < 0.05] \), and gender \( [F_{(1,20)} = 37.15, P < 0.01] \). The differences between individual finger forces were significant at

| Table 1. Indexes of finger performance and interaction in single-finger MVC tests |
|-----------------|-----------------|-----------------|-----------------|
|                 | Index           | Middle          | Ring            | Little          |
| MVC force, N    | Men             | Young           | Elderly         | Women           |
|                 |                 | 47.5 ± 12.2     | 35.5 ± 11.5     | 26.1 ± 9.7      | 25.4 ± 6.3      |
|                 | Women           | 36.5 ± 9.9      | 33.6 ± 9.2      | 24.0 ± 7.9      | 22.0 ± 3.4      |
| Sharing, %      | Men             | 29.3 ± 4.5      | 21.1 ± 2.6      | 13.7 ± 2.1      | 13.9 ± 2.3      |
|                 | Women           | 18.6 ± 5.0      | 14.8 ± 3.5      | 8.6 ± 2.2       | 9.4 ± 4.1       |
| Enslaving, %    | Men             | 34.0 ± 10.2     | 30.9 ± 6.5      | 22.0 ± 1.8      | 13.0 ± 5.0      |
|                 | Women           | 27.8 ± 13.5     | 29.6 ± 10.9     | 21.5 ± 7.7      | 21.1 ± 7.6      |
| Force deficit, %| Men             | Young           | Elderly         | Women           |
|                 | 33.9 ± 13.4     | 31.7 ± 14.1     | 17.4 ± 6.4      | 16.9 ± 17.6     |
|                 | Elderly         | 5.5 ± 4.1       | 12.3 ± 3.9      | 17.1 ± 9.4      | 15.8 ± 12.0     |
|                  |                 | 6.4 ± 4.0       | 16.0 ± 5.2      | 24.7 ± 16.0     | 10.1 ± 7.7      |
|                  | Elderly         | 5.2 ± 7.4       | 9.8 ± 10.9      | 11.9 ± 10.8     | 4.7 ± 5.4       |

Average values across subjects are shown as means ± SD for each finger and each subject subgroup separately. Enslaving and force deficit for each finger were normalized by the corresponding single-finger maximal voluntary contraction (MVC) for each subject and then averaged across subjects within each group.
finger (22%) interaction was also significant \(F_{(3,60)} = 5.05, P < 0.01\), reflecting the larger loss of MVC of the I finger in elderly subjects compared with young subjects \((P < 0.05)\).

During the four-finger MVC test, similar age- and gender-related differences were found in the total force produced by the four fingers (Fig. 1A). Elderly subjects had lower MVC force than young subjects (on average, by 29%), whereas women had lower MVC force than men (on average, by 54%). These results have been confirmed by main effects of age \(F_{(1,20)} = 9.77, P < 0.01\) and gender \(F_{(1,20)} = 46.84, P < 0.01\) in a two-way ANOVA.

The sharing pattern during the four-finger MVC test was not affected by age or gender \((Rao’s R_{(3,18)} < 1.2, P > 0.3)\). Both I and M fingers produced ~30% of the total force each, and that amount was larger than the shared force of the R finger (post hoc, \(P < 0.01\)).

Enslaving. During single-finger MVC tests, all four fingers produced force. When the instructed (master) finger reached its peak force, other (enslaved) fingers showed forces ranging from 5 to 35% of their MVC values in their respective single-finger tasks. The average enslaving force per finger was 7.9, 2.5, 3.3, and 0.9 N in young men, young women, elderly men, and elderly women, respectively. After being expressed as a percentage of the corresponding MVC in single-finger tasks (see METHODS), enslaving forces were smaller in elderly subjects compared with young subjects, on average, by 46%. They were also smaller in women compared with men, on average, by 39%. The average values are shown in Table 1, and the main effects are illustrated in Fig. 1B. These results have been confirmed by a three-way ANOVA with repeated measures \((age \times gender \times finger)\), which showed main effects of age \(F_{(1,20)} = 5.49, P < 0.05\), gender \(F_{(1,20)} = 6.03, P < 0.05\), and finger \(F_{(3,60)} = 3.63, P < 0.05\). Post hoc analyses have confirmed the smallest force deficit observed in the R finger (post hoc, \(P < 0.05\)). There was no interaction among the three factors.

Relations between MVC and indexes of finger interaction. Age- and gender-related differences in indexes of finger interaction described in the previous sections suggest that they may be defined by a single factor related to different force-generating capabilities of the subjects in the four minigroups. To analyze this possibility, the data were pooled over all 24 subjects. Figure 2, A and B, shows the enslaving and force deficit as functions of MVC-4. There was a significant positive relation between enslaving and MVC-4 \((P < 0.01)\) and a significant negative relation between force deficit and MVC-4 \((P < 0.01)\). Qualitatively similar results have been obtained when the magnitudes of each index of finger interaction were averaged across subjects of each minigroup separately (Fig. 2C). When the same indexes were expressed in the absolute units, both indexes increased with MVC-4 (Fig. 2D).

Fig. 1. Total maximal voluntary contraction (MVC) force in 4-finger tests (A), enslaving in single-finger tests (B), and force deficit in 4-finger tests (C). Enslaving and force deficit for each finger were measured in absolute units (N) and then expressed in percentage of the finger’s MVC in its single-finger test. Furthermore, the values were averaged across fingers for each subject and then averaged across subjects. Open bars, young subjects; solid bars, elderly subjects. Values are means ± SE. Total MVC force was larger in elderly than young subjects and in men than women. Enslaving was smaller and force deficit was larger in elderly subjects. Significant differences for men vs. women, \(* P < 0.05\) or \(** P < 0.01\); and for elderly vs. young, \(+ P < 0.05\) or \( + + P < 0.01\).
Effects of Age on Profiles of Force Variance During Accurate Force Production

During tests with accurate force production matching the ramp template, we analyzed two indexes of variability of finger forces. The VarF\textsubscript{tot} reflects the overall quality of performance in the task. It showed a nearly flat profile over the ramp duration; i.e., its magnitude did not depend on the absolute level of the total force. The \( \Sigma\text{VarF}_i \) reflects the total variance in the force space, which is expected to be equal to VarF\textsubscript{tot} if all fingers act as independent force generators. However, it showed a different behavior, namely an increase over the duration of the ramp. These findings are illustrated in Fig. 3 for a representative subject.

To quantify these time profiles, average values of VarF\textsubscript{tot} and \( \Sigma\text{VarF}_i \) were computed over every 1-s segment of the ramp for each subject. Average values of these indexes are shown in Fig. 4 for the four subject groups. When expressed in percentage of MVC-4, there is a positive relation for enslaving (A, C) and a negative one for force deficit (B, C). Note the positive relations between MVC-4 and each of indexes when they are expressed in absolute values (D).

and young subjects became more pronounced, which was particularly apparent for elderly women \( [F_{(1,20)} = 7.58, P < 0.01] \). There was no main effect of time on VarF\textsubscript{tot} in either absolute or relative units, although there was an interaction of gender \( \times \) time when VarF\textsubscript{tot} was expressed in absolute units \( [F_{(2,40)} = 4.19, P < \)
It reflected the fact that men had larger $\text{VarF}_{\text{tot}}$ than women in absolute units for the first two segments of the ramp ($t$-tests with the Bonferroni correction, $P < 0.05$), and the difference dropped below the level of significance for the third segment.

The other index of variance, $\Sigma \text{VarFi}$, is shown by squares in Fig. 4. When expressed in newtons squared, $\Sigma \text{VarFi}$ tended to be higher in elderly subjects compared with young subjects [main effect of age, $F_{(1,20)} = 3.98$, $P = 0.060$]. This difference became significant when normalized values of $\Sigma \text{VarFi}$ were compared [$F_{(1,20)} = 9.83$, $P < 0.01$]. Men showed higher absolute values of $\Sigma \text{VarFi}$ compared with women [main effect of gender, $F_{(1,20)} = 14.6$, $P < 0.01$], but the difference disappeared after the normalization by squared MVC force [$F_{(1,20)} = 0.11$, $P > 0.7$]. $\Sigma \text{VarFi}$ increased over the ramp duration in both absolute and normalized units [main effects of time; $F_{(2,40)} > 29$, $P < 0.01$].

Comparison of the two indexes of variance, $\text{VarF}_{\text{tot}}$ and $\Sigma \text{VarFi}$, allows assessment of predominance of positive or negative covariations of individual finger forces across trials (see METHODS). Hence, the $\Delta \text{Var}$ was analyzed in both absolute units ($N^2$) and after being divided by the corresponding MVC force squared ($\text{VarFi}$, dimensionless). The values of these indexes averaged across subjects are shown in Fig. 5. Over the first segment of the ramp, $\Delta \text{Var}$ was $<0$ in each subject group. It increased progressively over the ramp duration and reached positive values for the second and third segments for all groups except elderly women. Men showed higher values of $\Delta \text{Var}$ compared with women. These findings were confirmed by main effects of time [$F_{(2,40)} = 42.9$, $P < 0.01$] and gender.
\[ F(1,20) = 11.3, P < 0.01 \] in a three-way ANOVA with repeated measures (age \times gender \times time). There was no main effect of age. Elderly men showed higher \( \Delta \text{Var} \) than any other subject group, which was confirmed by an age \times gender interaction \([F(1,20) = 5.0, P < 0.05]\) with post hocs (Neuman-Keuls test, \( P < 0.05 \)).

Normalized values of \( \Delta \text{Var} \) for the four subject groups are shown in Fig. 5B. For three subject groups out of four, this figure shows a clear change in \( \Delta \text{Var} \) from negative to positive values over the ramp duration. The exception was the elderly women who showed negative values of \( \Delta \text{Var} \) over the first two segments of the ramp test and barely above zero in the third segment; these values were smaller compared with those of any other subject group. Main effects of time and gender were significant [for time, \( F(2,40) = 135, P < 0.01 \); for gender, \( F(1,20) = 6.33, P < 0.05 \)]. There was a significant age \times gender interaction \([F(1,20) = 9.42, P < 0.01]\) and a gender \times time interaction \([F(2,40) = 4.13, P < 0.05]\). The latter reflected the fact that, except for the first segment of the ramp, women had smaller \( \Delta \text{Var} \) than men (\( t \)-tests with Bonferroni correction, \( P < 0.05 \)).

Elderly women had the lowest peak forces in MVC tests (see Fig. 1A). To test whether their apparent differences from other groups in \( \Delta \text{Var} \) were related to the lower MVC values, \( \Delta \text{Var} \) (dimensionless) for the four subject groups is plotted against the mean actual force in each ramp segment in Fig. 6. It shows that \( \Delta \text{Var} \) increases with the actual force across all four subject groups as confirmed by the strong logarithmic relation between actual force and \( \Delta \text{Var} \) (\( R^2 = 0.827 \)). The fitted curve crosses zero at \( \sim 6 \text{ N} \), indicating that \( \Delta \text{Var} \) was negative when the actual total force was \(< 6 \text{ N} \). Data points for the elderly women (solid circles) are within the distribution of the data from other subjects group; their only difference is that they all lie within the force range from 0 to 6 N.

This indicates that the smaller \( \Delta \text{Var} \) in elderly women was not an exceptional finding for this subjects group, but it was only apparent due to the lower forces of these subjects.

**DISCUSSION**

Results of our study provide evidence that allows us to test the main hypotheses formulated in the introduction. In particular, it has been hypothesized that aging is associated with higher force deficit in MVC tasks. The present results provide good evidence to support this hypothesis, but only if force deficit is expressed in percentage of the corresponding MVC values, as it has commonly been done in earlier studies (43, 44, 62). The differences disappeared when force deficit was expressed in absolute values (N).

For submaximal ramp tasks, it has been hypothesized that aging leads to changes in the relation between VarFtot and \( \Sigma \text{Var}_i \). The results disprove this hypothesis: apparent age-related differences in the \( \Delta \text{Var} \) disappeared when the data were related to actual force produced by the subjects during the tests rather than to percentages of their MVC force.

One of the more striking findings in the study is the apparent similarity of the differences between the young and elderly subjects and between men and women. Most statistically significant effects were qualitatively similar with respect to the age and gender factors, and the differences even showed quantitative similarities (e.g., 46 vs. 39% differences in enslaving, and 19 vs. 20% differences in force deficit). This observation becomes particularly striking compared with data on changes in finger interaction with fatigue in young healthy subjects, which also leads to a qualitatively similar set of changes, including smaller MVC forces, smaller enslaving, and larger force deficit (13, 14). Taken together, these findings lead to a question: Is there a single factor, possibly peak force, that defines differences in indexes of finger coordination across men vs. women, young vs. elderly, and fatigued vs. nonfatigued comparisons?

**Finger Coordination and Neuromuscular Changes With Aging**

Interactions among fingers during force production may be due to peripheral factors and a particular central organization of descending commands (31, 38, 45, 63). The replacement of contractile proteins with connective tissue, together with the reported enlargement of motor units associated with aging (34, 64), could have lead to increased enslaving. Hence, the present finding of decreased enslaving, whether expressed in absolute units of force or in percent with respect to MVC (see Fig. 1), strongly suggests changes at the level of neural commands to motoneuronal pools in the elderly.

Increased force deficit in elderly subjects may be explained by alterations in motor unit properties and in the strategy of supraspinal control. These may include increased innervation ratio and modification of
force-frequency curve in combination with decreased discharge rate of motor units. It is not clear whether the force-frequency curve shifts to the left with age [adductor pollicis (50), quadriceps (58), tibialis anterior (9)] or not [tibialis anterior (51)]. But steeper slope in the force-frequency curve of the elderly has been reported for tibialis anterior muscle (9, 51).

Hand muscles may use a special strategy for recruitment and rate coding of motor units. It has been suggested that recruitment of motor units may be completed by ~40–50% of MVC in first dorsal interosseous (16) and adductor pollicis muscle (32). If this is true for most of the hand muscles, rate coding of motor units becomes responsible for high-force production. The maximal discharge rate of motor units is significantly lower in elderly subjects during MVC in hand muscles, such as first dorsal interosseous muscle (29) and abductor digitii minimi muscle (52). A reduction in the maximal discharge rate of motor units has also been observed in hand muscles after immobilization (18). Taken together, these observations suggest that a drop in maximal force with age is likely due to the drop in the maximal discharge rate of motor units. This could result from the elongated postspike motoneuron after hyperpolarization, as seen in aged animals (19), or from adaptive changes in central commands to match the slowed contractile properties of muscles, as seen during fatigue in human subjects (2, 3).

Taken together, changes in enslaving and force deficit with age strongly suggest changes at both segmental and suprasegmental levels of the generation of neural commands to hand muscles.

Changes in Multifinger Synergies With Aging

The ΔVar may be viewed as a measure of “compensated variance” (compare Refs. 39, 56), i.e., magnitude of the variance of individual finger forces not reflected in the variance of the total output of the four fingers. If this difference is positive, variations in the outputs of individual fingers are mostly negatively covaried (error compensation), whereas, if ΔVar is negative, the forces of individual fingers are mostly positively covaried (which may be interpreted as error amplification).

In our study, elderly subjects showed significantly higher indexes of VarFtot (Fig. 4), i.e., lower accuracy. When the ΔVar was analyzed, elderly women showed persisting negative values of ΔVar over the ramp, whereas the subjects in the other three minigroups showed negative ΔVar only at the beginning of the ramp, and then it turned positive (Fig. 5B). These observations suggest that, at low forces, positive covariations among finger forces dominate, and then, at high forces, they are substituted with negative covariations in all subjects except the elderly women. One should take into account, however, that elderly women in our study showed the lowest peak forces, and the ramp task was normalized to the MVC. Hence these subjects worked in a force range that was shifted into lower values compared with other subjects. In fact, when the data for all four groups were pooled together and compared with the actual forces along the ramp, the data for elderly women fitted the same regression curve as the rest of the data (Fig. 6). Hence, one may conclude that there is a general dependence between the total force and an ability of fingers to show error compensation during such tasks. This dependence is the same in men and women, and it does not change with age.

An Adaptation Hypothesis

Changes in maximal finger force, enslaving, and force deficit in elderly subjects strongly resemble findings in young subjects under fatigue induced by a 1-min exercise at maximal force production by all four fingers (13). These similarities, taken together with the conclusions of the previous subsection, suggest that a drop in finger force, whether associated with normal aging or with fatigue, leads to similar adaptive changes in the central neural commands to changed muscle properties (an adaptation hypothesis).

There are certain similarities in changes in the muscle properties with fatigue and with age. In particular, both aged muscle (9) and fatigued muscle (3) show slowing of the contractile properties, which could lead to an increase in the slope of the force-frequency relation (6, 30). The steep portion of the force-frequency curve is steeper after fatigue in hand muscle (flexor pollicis longus) (21) and quadriceps muscle (4). Besides, a reduction in the maximal discharge rate of motor units has been observed under muscle fatigue (2, 3), resembling changes that occur with age (29, 52). These partly similar changes in the muscle properties may be associated with similar adaptive changes in the neural control signals leading to the described similarities in changed indexes of finger interaction.

These adaptive changes may be viewed as rather successful. In particular, a drop in enslaving with age may be viewed as a positive factor for independent finger control. Note, however, that a drop in enslaving may be detrimental for synergetic control of fingers in multifinger prehension tasks (60, 61). Force deficit increased in the elderly, but only when expressed in relative units (with respect to the actual MVC), whereas it showed a decrease when expressed in absolute force units (N). Patterns of sharing of the total force among the fingers in the four-finger MVC tests are preserved with age. Although actual pronation and supination moments were not examined in the present study, sharing patterns in elderly subjects were not different from those in young subjects, and the values were comparable to those previously reported (13, 14, 44), indicating that the principle of minimization of secondary moment in MVC task seems to persist in elderly subjects.

In tasks that required accurate ramp force production, elderly subjects showed higher VarFtot; i.e., they performed the task less accurately. However, their ability to show error compensation among fingers, as reflected by the difference between the ∑VarFi and the

J Appl Physiol • VOL 94 • JANUARY 2003 • www.jap.org
VarF$_{tot}$ was preserved and showed the same dependence on absolute total force level.

The adaptation hypothesis, however, can hardly be invoked to describe differences in indexes of finger interaction between men and women. This leads to the next step in the discussion.

**A Strength-Dexterity Trade-off Hypothesis**

Previous studies have failed to detect any differences between men and women in indexes of finger interaction, except for the expected higher peak forces in the men (43, 45). In our experiments, however, differences between men and women were as large as those between young and elderly subjects. The differences in the results of these studies could be partly due to the relatively large number of subjects in the present study, as well as to the wider range of motor abilities due to variations of the age factor. The similarities of the outcomes of the men vs. women and young vs. elderly comparisons suggest that the differences in indexes of finger interaction may be related, not to such factors as gender and age but to a factor that covaries with each of them. We assumed that a certain index of finger strength could be such a factor and used, rather arbitrarily, the peak force in the four-finger MVC test (MVC-4). Regression analyses using both data of individual subjects and data averaged over subjects within each minigroup (elderly women, young women, elderly men, and young men) have shown strong relations of indexes of finger interaction to MVC. These analyses suggest that the observed changes in indexes of finger interaction are indeed not age or gender specific but are MVC specific.

Recent studies have provided evidence that indexes of finger interaction reflect functioning of a central neural network responsible for finger coordination in multifinger tasks (13, 14, 37, 45). Multifinger synergies are likely developed in a way that optimizes the overall performance of the hand in functionally important, everyday tasks. It is conceivable that, depending on the actual force-generating capabilities of the hand of a particular person, these synergies differ. If one person is weaker than another due to genotype, anthropometric factors, experience, age, fatigue, and maybe other factors, differences between finger interaction indexes in these two persons seem to be predictable on the basis of a single property, namely peak force.

One finding is of a particular interest, namely the increase in enslaving with an increase in MVC. Note (Figs. 1 and 2) that this relation has been significant when expressed in both absolute force units and in percentage of MVC. Depending on particular motor tasks, enslaving can be viewed as a negative or as a positive factor. On the one hand, control of individual fingers, such as during playing piano or guitar, likely benefits from better individual finger control, i.e., low enslaving. On the other hand, manipulation of objects using all the digits may benefit from enslaving, which may be an important component of multidigit synergies (60, 61). Enslaving can also contribute to moment stabilization (63). Recent studies of the effects of practice on finger coordination in persons with Down syndrome have shown an increase in enslaving in parallel to the overall improvement in the performance in the tests (36).

There is no universally accepted definition of dexterity (compare Ref. 41). For example, Bernstein (1) defined dexterity rather generally as an ability to adequately solve any emerging motor problem correctly, quickly, rationally, and resourcefully. On the other hand, The American Heritage Dictionary defines dexterity as “skill and grace in physical movement, especially in the use of the hands.” Hand dexterity is commonly associated with and assessed as an ability to control digits individually and to manipulate small hand-held objects. In particular, dexterity has been quantified as an ability to produce pinch force (in contrast to grip force), to open containers of different size, to perform manipulations with small objects that require grasping with only two digits as in pegboard tests, etc. (26, 48, 53, 55). Studies of relations between grip strength and dexterity have typically failed to reveal strong correlations between the two. For example, there are only weak correlations between grip and pinch peak forces (55), and a drop in grip force with age is not accompanied by a comparable drop in pinch force (48). In a more recent study, Haward and Griffin (26) observed significantly higher grip forces in men than in women in the absence of gender effects on performance in the pegboard test. The same study did not find any age-related difference in either grip strength or manual dexterity. Weak relations between grip and pinch forces have been reported by Rahman et al. (53) in their study of elderly subjects. There were virtually no relations between the force indexes and the ability to open standard containers (53, 55).

If one accepts a definition that hand dexterity can be associated with better individual control of fingers, higher enslaving may be interpreted as a correlate of worse dexterity (compare Refs. 42, 43). Hence we end up with a strength-dexterity trade-off hypothesis: there exists a trade-off between finger strength and dexterity, valid across variations in such factors as gender, age, and fatigue.

**Concluding Comments**

Our experiments have provided evidence for differences in the ability of elderly persons to perform maximal and submaximal force production tasks. Some of the findings strongly suggest adaptive changes in neural control strategies with age, in particular the decreased enslaving. However, the apparent decrease in the performance in both types of tasks with age, such as low MVC and higher indexes of variability, has been contrasted with similar dependences of indexes of finger interaction on maximal finger force across all subjects. We do not know why force deficit is smaller and enslaving is larger in stronger people. This is a problem to be addressed in future studies. However, the uniformity
of these relations suggests that the central nervous system may use similar control strategies to coordinate digits of a hand in young and elderly, male and female persons. These strategies may be modified with a single factor scaled with respect to the maximal force that the fingers can produce.

The authors acknowledge helpful comments of Kevin G. Keenan (University of Colorado).

This study was supported in part by National Institutes of Health Grants AG-18751, NS-35032, and M01 RR-10732.

REFERENCES


