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# Mechanisms that contribute to differences in motor performance between young and old adults

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**Abstract**

This paper examines the physiological mechanisms responsible for differences in the amplitude of force fluctuations between young and old adults. Because muscle force is a consequence of motor unit activity, the potential mechanisms include both motor unit properties and the behavior of motor unit populations. The force fluctuations, however, depend not only on the age of the individual but also on the muscle group performing the task, the type and intensity of the muscle contraction, and the physical activity status of the individual. Computer simulations and experimental findings performed on tasks that involved single agonist and antagonist muscles suggest that differences in force fluctuations are not attributable to motor unit twitch force, motor unit number, or nonuniform activation of the agonist muscle, but that they are influenced by the variability and common modulation of motor unit discharge in both the agonist and antagonist muscles. Because the amplitude of the force fluctuations does not vary linearly with muscle activation, these results suggest that multiple mechanisms contribute to the differences in force fluctuations between young and old adults, although the boundary conditions for each mechanism remain to be determined.


*Keywords:* Force fluctuations; Motor unit; Discharge rate; Coactivation; Motor unit synchronization

## 1. Introduction

When an individual performs a steady contraction with hand, arm, or leg muscles, the force exerted by the limb is not constant but rather it fluctuates about an average value [15,54,62,69,73,85]. The variability of the force about the mean, which can be quantified in absolute terms as the standard deviation or in relative terms as the coefficient of variation, often varies with the average force exerted by the involved muscles. Based on protocols that have largely involved low-to-moderate forces during isometric and anisometric (concentric and eccentric) contractions, a number of studies have found that there can be differences between young and old adults in the amplitude of the force fluctuations. This paper describes some of the differences in force fluctuations that have been observed between young and old adults and examines the physiological mechanisms responsible for these differences.

The presence of force fluctuations during a voluntary contraction influences the capacity of an individual to achieve a desired force and to produce an intended limb trajectory. For example, the minimum force exerted by the thumb and index finger when performing the pinch grip must be greater than the friction force required to prevent slipping [17,43]. Furthermore, the rapid performance of a simple aiming movement requires a large activation signal, which increases the variability of the trajectory and reduces the accuracy of the final position [28,34,42,87]. These effects are compounded in repeat performances of a task in that the fluctuations in muscle force during a voluntary contraction cause the exerted force and the movement kinematics to vary from trial to trial [9,11,12,15,19,35]. The activation signals sent from the nervous system to muscles, therefore, must accommodate the force fluctuations for the successful completion of goal-directed movements.

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## 2. Force fluctuations during submaximal contractions

The fluctuations in muscle force during a voluntary contraction have been quantified as the standard deviation of force during isometric contractions and as the standard deviation of acceleration during anisometric contractions in hand, arm, and leg muscles. Although the amplitude of the fluctuations has been found to differ between young and old adults, this is not a consistent finding. The factors that influence this relation include the muscle group performing the task, the type of muscle contraction, the intensity of the muscle contraction, and the physical activity status of the individual.

### *2.1. Muscle group*

The actions produced by muscular contractions are profoundly influenced by the architecture of the muscles that produce the requisite acceleration [53]. These effects include differences in performance capabilities between muscle groups, such as muscle strength and contraction speed, but also the force fluctuations that occur during submaximal contractions. For example, the standard deviation of acceleration during a slow concentric contraction while lifting a light load (5% of the one-repetition maximum; 1-RM load) was 0.22 ± 0.07 $m/s^2$ when the action was produced by an intrinsic hand muscle (first dorsal interosseus) compared with 0.05 ± 0.02 $m/s^2$ for the knee extensor muscles [85]. Both young and old adults exhibit this difference in the force fluctuations between muscle groups.

Within each muscle group, however, there is often a difference in the amplitude of the force fluctuations between young and old adults. For example, the coefficient of variation for force was greater for sedentary old adults compared with young adults when performing low-force isometric contractions with the first dorsal interosseus and knee extensor muscles, but not for the elbow flexor muscles [7,30,32,36,49,83,85]. When there is a difference in the amplitude of the force fluctuations between young and old adults, it is greatest at low forces (Fig. 1). When exerting an abduction force at 2.5% of the maximum voluntary contraction (MVC) force with the index finger, for example, Galganski et al. [30] found that the coefficient of variation for force was 11.0 ± 1.8% for old adults (mean, range: 67, 60–75 years) and 6.6 ± 0.5% for young adults (28, 20–37 years) compared with values of 3.9 ± 0.2 and 2.9 ± 0.2%, respectively, at a target force of 50% MVC force (Fig. 1a).

Although a similar relation has been observed for the knee extensor muscles [83], most studies on large muscle groups have found no difference in the coefficient of variation for force between young and old adults [11,32,85]. For example, the coefficient of variation for the force exerted by the elbow flexor muscles ranged from 2 to 3% and did not differ between young (mean ± SD: 23 ± 4 years) and old (71 ± 8 years) adults across target forces that ranged from 5 to 65% MVC force [32,85]. Presumably the difference between the hand

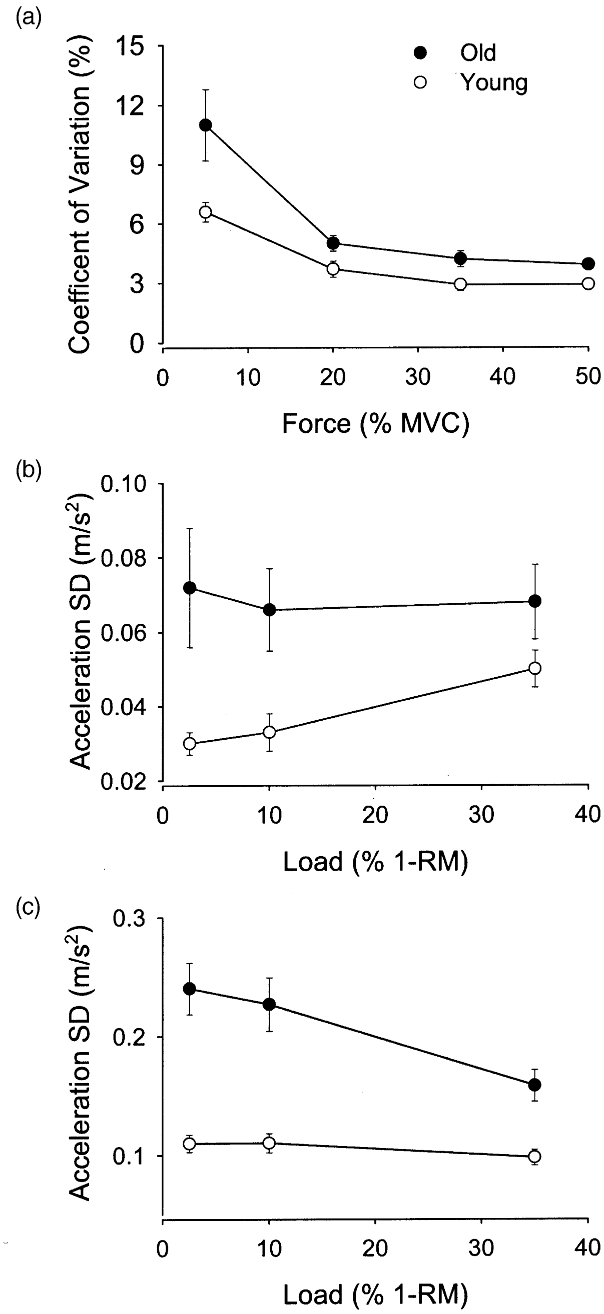


Fig. 1. Fluctuations in the abduction force (mean ± SE) exerted by the index finger of young and old adults during submaximal contractions with the first dorsal interosseus muscle. (a) Normalized fluctuations in force (coefficient of variation) as the index finger pushed against a force transducer by performing an isometric contraction [30]. (b) The standard deviation (SD) of acceleration of the index finger as it supported an inertial load while maintaining a constant position [50]. (c) The standard deviation (SD) of acceleration of the index finger as it slowly lifted and lowered an inertial load [50]. The data for the concentric and eccentric contractions are combined for each age group.

muscle and the limb muscles is due to the greater absolute forces exerted by the limb muscles at the relative target forces (% MVC force), as suggested by the absence of a difference in the normalized force fluctuations between young and old adults when the first dorsal interosseus exerts large forces.

Despite the similarities of the findings for the elbow flexor and knee extensor muscles, the amplitude of the force fluctuations during submaximal isometric contractions (2.5 to 50% MVC) were only moderately correlated ($r^2$ = 0.25 to 0.50) within the same individuals for the elbow flexor and knee extensor muscles. Furthermore, there was no significant association between the amplitude of the force fluctuations for first dorsal interosseus and the other two muscle groups [85]. Although the amplitude of the force fluctuations differs among the three muscle groups, the fluctuations are modulated similarly as a function of target force [15,85]. Thus, the force capacity of the involved muscles during an isometric contraction appears to influence the magnitude of the difference in force fluctuations between young and old adults.

### 2.2. Contraction type

Although the recruitment order of motor units is usually similar for isometric and slow anisometric contractions [49,70,81], the recruitment threshold and modulation of discharge rate often differs with contraction type [46,74,75,76]. These differences in motor unit activity likely underlie the greater force fluctuations exhibited during slow anisometric contractions compared with isometric contractions. For example, the standard deviation of acceleration for the index finger was much greater when young and old adults used the first dorsal interosseus muscle to lift a light load compared with supporting the load (Fig. 1b,c) [49,50,85]. Furthermore, the force fluctuations can differ during the shortening and lengthening contractions that occur during a movement. Although the standard deviation of acceleration was often similar for slow concentric and eccentric contractions [15], for example, the fluctuations were greater for eccentric contractions at moderate-to-fast speeds [14] and the trial-to-trial variability was also greater for rapid eccentric contractions [11,15]. As with the isometric contractions, the amplitude of the fluctuations in acceleration during slow anisometric contractions was less for the elbow flexor and knee extensor muscles compared with first dorsal interosseus [85].

These differences in the fluctuations between contraction types are accompanied by differences due to the age of the individual. For the first dorsal interosseus muscle, for example, the force fluctuations were greater for old adults (69 ± 3 years) compared with young adults (23 ± 3 years) when supporting and lifting light-to-moderate loads (Fig. 1b,c). Furthermore, the standard deviation of acceleration was greater during eccentric contractions (0.24 ± 0.11 $m/s^2$ at 2.5% 1-RM load) compared with concentric contractions (0.13 ± 0.08 $m/s^2$ at 2.5% 1-RM load) for old adults, but not young adults (0.11 ± 0.05 and 0.10 ± 0.04 $m/s^2$ at 2.5% 1-RM load, respectively), when they lifted light loads with the index finger [7,49]. In contrast, there was no difference in the standard deviation of acceleration between the two groups of subjects when they performed concentric and eccentric contractions with the elbow flexor muscles (Fig. 2a) [85]. However, the maximum standard deviation of acceleration during the concentric contractions (0.24 ± 0.13 $m/s^2$ at the 50% 1-RM load) was greater than that for the eccentric contractions (0.16 ± 0.05 $m/s^2$ at the 5% 1-RM load) for the two groups of subjects. For the knee extensor muscles (Fig. 2b,c), the maximum standard deviation of acceleration during the concentric contractions (0.35 ± 0.24 $m/s^2$ at the 50% 1-RM load) was greater than that during the eccentric contractions (0.22 ± 0.11 $m/s^2$ at the 50% 1-RM load) for the young adults, but not for the old adults (0.13 ± 0.04 $m/s^2$ and 0.13 ± 0.04 $m/s^2$, respectively, both at the 50% 1-RM load).

In contrast to the isometric contractions, Tracy et al. [85] found no significant correlations between pairs of muscles in the standard deviation of acceleration when subjects performed slow anisometric contractions with the first dorsal interosseus, elbow flexor, and knee extensor muscles. For a given individual, therefore, the amplitudes of the fluctuations in acceleration for these three muscle groups were unrelated to one another during slow anisometric contractions. These results indicate that the amplitude of the force fluctuations during a muscle contraction depends on the age of the individual, the muscle group performing the task, and the type of contraction being performed.

### 2.3. Contraction intensity

The amount of motor unit activity during a muscle contraction varies with the magnitude of the force that is exerted, the speed of the movement, and the type of contraction. The standard deviation of force during an isometric contraction increases with target force for all muscles examined in both young and old adults [7,13,30,39,49,69,83,85]. The coefficient of variation for force, however, exhibits a non-monotonic relation with the greatest value at 2.5% MVC force, minimum values at intermediate forces, and moderate values at target forces greater than 50% MVC force [7,32,83]. The coefficients of variation for force during isometric contractions are usually similar for young and old adults at moderate-to-high forces, but are dissimilar at low forces ($\leq$20% MVC force) for the first dorsal interosseus and knee extensor muscles.

The standard deviation of acceleration during slow anisometric contractions with different loads has exhib-

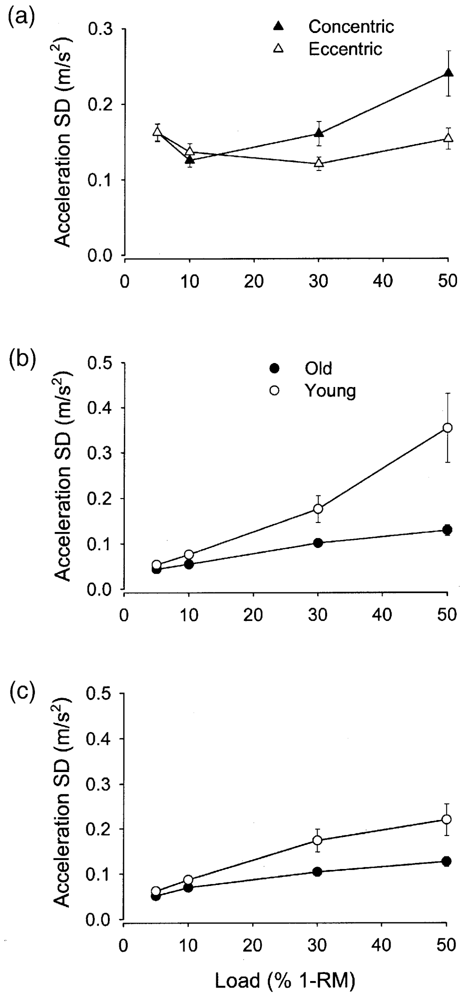


Fig. 2. Standard deviation (SD) of acceleration (mean ± SE) during slow concentric and eccentric contractions performed by young and old adults [85]. (a) The standard deviation of acceleration for concentric and eccentric contractions with the elbow flexor muscles. Each line indicates the average values for the young and old subjects combined. (b) The standard deviation of acceleration for concentric contractions performed with the knee extensor muscles. (c) The standard deviation of acceleration for eccentric contractions performed with the knee extensor muscles.

ited a range of relations for the three muscle groups. The standard deviation of acceleration did not change with load (2.5–75% 1-RM load) when the first dorsal interosseus muscle performed slow anisometric contractions (0.11 ± 0.07 $m/s^2$), except for old adults who experienced the greatest fluctuations (0.24 ± 0.11 $m/s^2$) when lowering light loads with eccentric contractions [7,15]. In contrast, the standard deviation of acceleration for the elbow flexor muscles varied non-monotonically as a function of load (Fig. 2a) for both groups of subjects, with no difference between the two contraction types for either group of subjects [85]. The maximum standard deviation of acceleration occurred with the 50% load during the concentric contractions (0.24 ± 0.13 $m/s^2$) but with the 5 and 50% 1-RM loads (0.16 ± 0.05 and 0.15 ± 0.06 $m/s^2$, respectively) during the eccentric contractions. For the knee extensor muscles, however, the standard deviation of acceleration increased monotonically with load from a minimum at the 5% 1-RM load to the maximum at the 50% 1-RM load for both groups of subjects during the concentric and eccentric contractions (Fig. 2b,c). In addition, the standard deviation of acceleration was greater for the young subjects compared with the old subjects at the higher loads (30 and 50% 1 RM) during both the concentric and eccentric contractions.

In contrast to the different relations between the standard deviation of acceleration and load for slow anisometric contractions with first dorsal interosseus, modulation of contraction intensity by varying movement speed had a consistent effect on the fluctuations in acceleration. For example, the standard deviation of acceleration increased monotonically when the same load (15% of maximum) was lifted at different speeds (0.03–1.16 rad/s) with concentric and eccentric contractions of the first dorsal interosseus muscle (Fig. 3a) [14]. Although the young adults had a greater average standard deviation of acceleration than old adults at a given movement speed (e.g., young = 0.61 ± 0.17 and old = 0.31 ± 0.11 $m/s^2$ for an eccentric contraction at 0.12 rad/s), there was no difference between the two groups of subjects in the ability to achieve the desired movement speed. However, the old adults were less accurate across multiple trials in producing the target movement speed (Fig. 3b), exhibited more variability in the standard deviation of acceleration across trials, and the eccentric contractions were more variable than the concentric contractions for the old adults. Thus, the effect of contraction intensity (load and speed) on the force fluctuations depends on the age of the individual, the muscle group performing the task, and the type of muscle contraction.

### 2.4. Physical activity status

Although healthy older adults frequently present with greater force fluctuations during submaximal contractions, this does not appear to be due to weaker muscles. For example, Burnett et al. [7] found that the force fluctuations for first dorsal interosseus were greater for old adults (74 ± 6 yrs) compared with young adults (23 ± 3 yrs) when performing low-force isometric contractions and lowering light loads with eccentric contractions, despite comparable levels of muscle strength for the young and old adults (MVC force = 32 ± 12 N and 35 ± 8 N, respectively; 1-RM load = 1.7 ± 0.6 kg and 1.3 ± 0.5 kg, respectively). Conversely, Tracy et al. [85] found no difference in the force fluctuations exhibited by young (22 ± 3 yrs) and old (72 ± 4 yrs) men when performing isometric and anisometric contractions with first dorsal interosseus in association with no difference in the MVC force (37 ± 10 N) between the two groups of men, but a greater 1-RM load for the young men (2.55

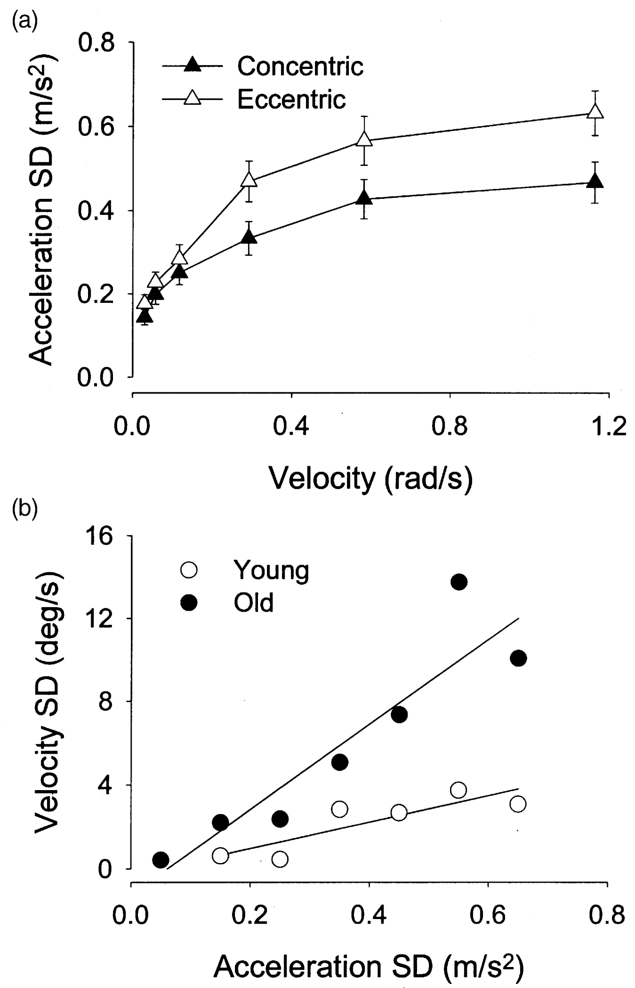


Fig. 3. Fluctuations in acceleration and movement accuracy as young and old adults performed concentric and eccentric contractions at increasing speeds [14]. (a) The standard deviation (SD) of acceleration (mean ± SE) increased for both concentric and eccentric contractions performed with first dorsal interosseus when a 15% 1-RM load was lifted at faster speeds. The data for young and old adults are combined for each type of contraction. The standard deviation of acceleration for the index finger was greater at the fastest speeds for the eccentric contractions compared with the concentric contractions. (b) Movement accuracy declined as the fluctuations in acceleration increased. Movement accuracy is denoted as the standard deviation of the average angular velocity for the three trials at each movement speed. For a given level of fluctuations in acceleration, the old subjects were less accurate compared with the young subjects.

± 0.51 kg) compared with the old men (1.76 ± 0.46 kg). A similar mixture of results has been reported for the elbow flexor muscles [32,85] and the knee extensor muscles [11,36,62,83]. These divergent results indicate that not all older adults exhibit greater force fluctuations compared with young adults during submaximal contractions, and that the existence of a difference in the amplitude of the force fluctuations is not related to a deficit in muscle strength.

Nonetheless, the greater coefficient of variation for force exhibited by old adults at low forces with the first dorsal interosseus muscle disappeared after a few weeks of strength training [4,39]. This effect, however, was found for both isometric and slow anisometric contractions whether the subjects trained with light or heavy loads [51], which underscores the minor role of modest deficits in strength as contributing to the enhancement of force fluctuations. Consistent with this explanation, practice of a skilled hand movement reduced the force fluctuations during a submaximal pinch grip (<20% MVC force) but did not alter strength [60]. Similarly, 8 weeks of Tai Chi practice by old adults, which does not involve load-bearing activities for the arms, reduced the force fluctuations and improved the accuracy of an arm movement [92].

In contrast, increases in muscle strength do seem to be associated with decreases in force fluctuations during isometric and anisometric contractions with the knee extensor muscles. Hortobágyi et al. [36] reported that 10 weeks of strength training the knee extensor muscles increased both MVC force (26 ± 18%) and 1-RM load (35 ± 20%) and reduced the standard deviation of force during submaximal (25 N) concentric (20 ± 16%) and eccentric (40 ± 26%), but not isometric (7 ± 18%), contractions on an isokinetic dynamometer. The submaximal contractions corresponded to target forces of 6% MVC force for the young subjects and 12% for the old subjects. Although Tracy et al. [84] found that 16 weeks of strength training the knee extensor muscles with heavy loads increased both MVC force (24 ± 11%) and 1-RM load (30 ± 20%) but did not reduce either the force fluctuations during submaximal isometric contractions (2-50% MVC force) or the position fluctuations during submaximal anisometric contractions, there was a significant reduction in the force fluctuations (coefficient of variation declined from 3.7 ± 1.0 to 1.7 ± 0.5%) during the training exercise in subjects who were instructed to lift the load (80% 1 RM) as steadily as possible. Furthermore, 20 weeks of Tai Chi training improved MVC force of the knee extensor muscles in some subjects (33 ± 4%), but not others (−1 ± 3%), and only in those subjects who experienced an increase in strength was there a decrease in the average force fluctuations (~30%) during isometric contractions at target forces of 2, 30, 60, and 90% [16]. However, Bellew [3] reported that 12 weeks of strength training the knee extensor muscles increased MVC force (14 ± 12%) in a group of old men and women but did not alter the coefficient of variation during isometric contractions at 30, 60, and 90% MVC force. Thus, strengthening exercises that involve lifting loads with the knee extensor muscles do appear to be associated with reductions in force fluctuations during submaximal anisometric contractions.

These findings indicate that the amplitude of the force fluctuations during submaximal contractions performed by healthy older adults can often be reduced by physical activity, and may specifically reduce the force fluctuations at the mean force exerted during the activity. The mechanisms underlying the adaptations, however, appear to be associated with strength gains for some muscles (knee extensors) but not other muscles (first dorsal interosseus).

## 3. Mechanisms that influence force fluctuations

The unitary functional element of the neuromuscular system is the motor unit. The net force exerted by a muscle when many motor units are activated results in a force of varying amplitude, the fluctuations of which depend on the contractile and discharge characteristics of the most recently recruited motor units [2,10,25] and are, according to the Size Principle, the largest motor units that have been activated for the task. Based on this rationale, it is evident that fluctuations in the force exerted by a single muscle can be influenced by both the properties of the individual motor units and the behavior of the population of motor units [24,29]. When the action involves multiple muscles, however, the fluctuations are less influenced by individual motor unit properties [29] and depend more on the distribution of activity among these muscles [32]. The subsequent discussion of the potential mechanisms focuses on those features of motor unit properties and population characteristics that could influence the force fluctuations observed when a single muscle produces the action.

### *3.1. Motor unit properties*

The two motor unit properties that could influence the amplitude of the force fluctuations are motor unit force and discharge rate variability. Apoptosis of spinal motor neurons results in a decline in the number of motor units in the muscles of older adults but an increase in the innervation number of surviving motor units [8,22,31,56,82]. Accordingly, the spike-triggered average forces of motor units in the first dorsal interosseus muscle are larger in older adults [30,39,68]. Thus, the fluctuations in motor unit force when the unit is first recruited and discharging action potentials at low rates (3-8 Hz) [48,71,90] are greater in older adults, which could contribute to the difference in the force fluctuations at low forces between young and old adults.

Despite this rationale, computer simulations indicated that increases in the amplitude of motor unit twitch forces have a negligible effect on force fluctuations during an isometric contraction [78,79]. The computer model comprised 120 motor neurons with systematic variations in recruitment threshold, range of discharge rates, innervation ratio, conduction velocity of sarcolemmal action potentials, motor unit territory, amplitude and duration of the twitch force, and the specific shape of the force-frequency relation [29,93]. In the default condition, the model comprised 120 motor units with an exponential distribution of twitch forces, ranging from 1 arbitrary unit (au) for motor unit 1 to 100 au for motor unit 120. To assess the influence of twitch force on the force fluctuations, the coefficient of variation for force at 11 different levels of motor unit activity for this condition (120/100) was compared with those for a population of 90 motor units (90/30) in which the twitch force of the low-threshold motor units was increased to maintain the same force capacity of the model muscle (Fig. 4a). The force capability of the muscle remained the same in the two conditions, but the second condition (90/30) comprised 90 motor units with twitch force rang-

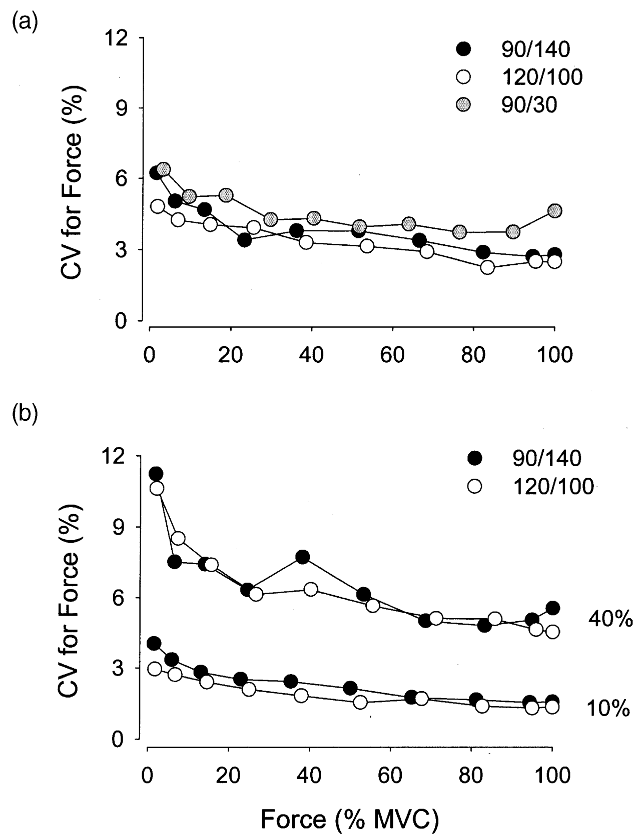


Fig. 4. The coefficient of variation for force as a function of the contraction force (% maximum voluntary contraction; MVC) achieved by pools of motor neurons during simulated contractions. (a) A comparison of the effects of motor unit number and twitch force on the coefficient of variation. The populations of motor units comprised either 90 or 120 motor neurons with twitch forces that ranged from 3.5 to 100 au (30-fold range), 1 to 100 (100-fold range), or 1 to 140 (140-fold range). The 30-fold range corresponded to the condition in which the twitch forces of low-threshold motor units was increased relative to the 100-fold range, whereas the 140-fold range represented the condition where the twitch force of the high-threshold motor units was increased. (b) The influence of discharge rate variability on the coefficient of variation for force. The simulations involved either 90 (filled circles) or 120 (open circles) motor units with the average coefficient of variation for discharge rate set at either low (10%) or high (40%) values as observed experimentally [49,59]. Data from Taylor et al. [78].

ing from 3.5 au to 100 au (30-fold range). The coefficients of variation were similar for the two populations of motor units. To distinguish between the effects of twitch force and motor unit number on the force fluctuations, the twitch forces of high-threshold motor units was increased (1 au for motor unit 1 and 140 au for motor unit 90) in a population of 90 motor units (90/140). The results indicate that both the number of motor units and variation in twitch force had a minimal effect on the coefficient of variation for force (Fig. 4a).

Consistent with the prediction of the computer simulations, several weeks of strengthening exercises performed with the first dorsal interosseus muscle reduced the coefficient of variation for force (≤20% MVC force) in old adults (59–74 years) but did not change either the mean motor unit force (13 ± 3 mN before and after training) or the distribution of spike-triggered average forces of the motor units [39]. Although the young adults experienced a comparable increase in MVC force (young = 37 ± 12%; old = 41 ± 8%), their coefficients of variation for force did not change with training (2–5% at target forces of 2.5–50% MVC force). Furthermore, most of the decrease in the coefficient of variation for the old adults occurred within the first four weeks of training [39,51], prior to the time required for muscle fibers to hypertrophy [1,72] and thereby increase motor unit twitch force. Similarly, there was no change in the time course of the spike-triggered average forces (contraction time and one-half relaxation time), which could have altered the degree of fusion and hence the fluctuations in the force exerted by each motor unit [79]. Taken together, the results of the computer simulations and the experimental findings suggest that the larger motor units in the first dorsal interosseus muscle of older adults do not appear to contribute to the difference in the force fluctuations between young and old adults.

In contrast to the negligible effect of twitch force on the force fluctuations, the regularity with which motor neurons discharge action potentials can influence the coefficient of variation for force. Computer simulations indicate that varying the coefficient of variation for discharge rate within physiological limits (10 vs 40%) has a more marked effect on the amplitude of the force fluctuations than does reducing in the number of motor units by an amount (25%) suggested by experimental findings (Fig. 4b). Experimental measurements indicate that the average discharge rate of motor units in the first dorsal interosseus muscle when subjects exert low forces and lift light loads is not different between young and old adults [49,68], yet the discharge rate during these tasks can be more variable and be associated with increased fluctuations in force and acceleration for older adults [45,49]. For example, the coefficient of variation for discharge rate was 18% for young adults when exerting a force at 2.5% MVC force compared with 34% for old adults, which were associated with coefficients of variation for force of 4.1 ± 0.5% and 9.6 ± 1.3%, respectively [49]. A similar relation existed when the target force was 5% MVC force and when light inertial loads were lifted. Furthermore, discharge rate was more variable and the force fluctuations were greater for eccentric contractions compared with concentric contractions for old adults. The lower discharge rate and more variable motor unit activity during an eccentric contraction [46,49] undoubtedly contribute to the reduced interference EMG and greater force fluctuations during eccentric contractions [14].

Nonetheless, experimental measurements also indicate that the coefficient of variation for force can differ between young and old adults without a difference in the coefficient of variation for discharge rate. For example, Semmler et al. [68] found that a lower coefficient of variation for discharge rate (old = 18 ± 4, young = 19 ± 4%) by low-threshold motor units in the first dorsal interosseus muscle of old adults was accompanied by greater force fluctuations (old = 6.6 ± 3.3%, young = 3.4 ± 1.3%) at low forces (2.5 and 5% MVC force). Taken together, the computer simulations and experimental results suggest that the amplitude of the force fluctuations can be influenced by discharge rate variability, but the mixed experimental findings indicate that other mechanisms also contribute to this phenomenon.

### 3.2. Population characteristics

As with the possible contribution of motor unit properties to the force fluctuations, it appears that some features of population activity can also influence the fluctuations in motor output. Some of the potential population factors include nonuniform activation of the agonist muscle, alternating activity of the agonist and antagonist muscles, and common input to the motor neuron pool.

A muscle is an anatomical entity that can comprise several functionally distinct compartments; for example, a muscle that has broad attachments or multiple heads [23,40,91]. The direction of the force exerted by such a muscle on the skeleton depends on the relative activation of the different compartments [58]. Nonuniform activation has been observed in several muscles [37,57,80,88], including first dorsal interosseus [94,95]. The first dorsal interosseus is a bipennate muscle with two proximal heads: a superficial head that arises from the dorsal surface of the ulnar border of the first metacarpal and a deep head that attaches to the proximal three-quarters of the radial border of the second metacarpal [52]. Although different amounts of EMG can be recorded from the two heads in both young and old adults during a position-tracking task with the index finger, Laidlaw et al. [50] found no association between this nonuniform activation of first dorsal interosseus and differences in the standard deviation of acceleration.

Thus, the greater force fluctuations observed in older adults during both position-holding and position-tracking tasks with the index finger were not associated with the nonuniform activation of first dorsal interosseus.

Another possibility is that fluctuations in the motor output could be caused by coactivation of the antagonist muscle, involving either differences in the average level of coactivation or alternating activation of the agonist and antagonist muscles [64,86]. Because the net force exerted by a limb depends on the difference in the forces contributed by the agonist and antagonist muscles, alternating activation of the agonist and antagonist muscles can cause fluctuations in force and acceleration. Vallbo and Wessberg [86], for example, found that young adults used reciprocal activation of agonist and antagonist muscles when performing slow finger movements that resulted in acceleration fluctuations at 8-10 Hz. Nonetheless, although older adults coactivate the antagonist muscle (second palmar interosseus) more often and at a greater intensity than young adults when exerting an abduction force with the index finger, there was no consistent pattern of alternating coactivation between first dorsal interosseus and second palmar interosseus during isometric and slow anisometric contractions [7,50,71]. Furthermore, there was no association between the standard deviation of acceleration and average levels of EMG in the antagonist muscle during slow anisometric contractions of the first dorsal interosseus (Fig. 5).

One of the limitations of these studies on coactivation, however, has been the use of the rectified EMG to infer details about the control strategy. Although the EMG signal represents the sum of the motor unit potentials, it does not indicate the total motor output from the spinal cord. For example, the cancellation of overlapping positive and negative phases of motor unit potentials can cause the rectified EMG to underestimate the total motor unit activity by up to 80% during an intense contraction [20]. Similarly, synchronization of motor unit discharge can markedly enhance the amplitude of the interference EMG without any change in the number of action potentials [93]. Furthermore, the convergence of motor unit discharge rates to similar, but asynchronous, values will cause the EMG to comprise bursts of activity [29,47,77]. Because of these effects, the observation that the discharge rates of motor units in an antagonist muscle are modulated at 8-10 Hz during a slow movement [89] suggests that the potential contribution of alternating coactivation to the force fluctuations remains unresolved.

The mechanisms responsible for the force fluctuations are likely to differ for postural contractions and movements. For example, the amplitude of the force fluctuations is greater during slow movements, such as a position-tracking task, compared with a contraction that is used to maintain a position (Fig. 1b,c) [38,50]. Furthermore, fluctuations in acceleration consistently peak in the 1-12 Hz band of the power density spectrum during movement [38,50,86,89], whereas the peaks are distributed in the 1-12 and 16-32 Hz bands during position-holding contractions [33,50]. The location of these peaks is similar for young and old adults for these two tasks [50].

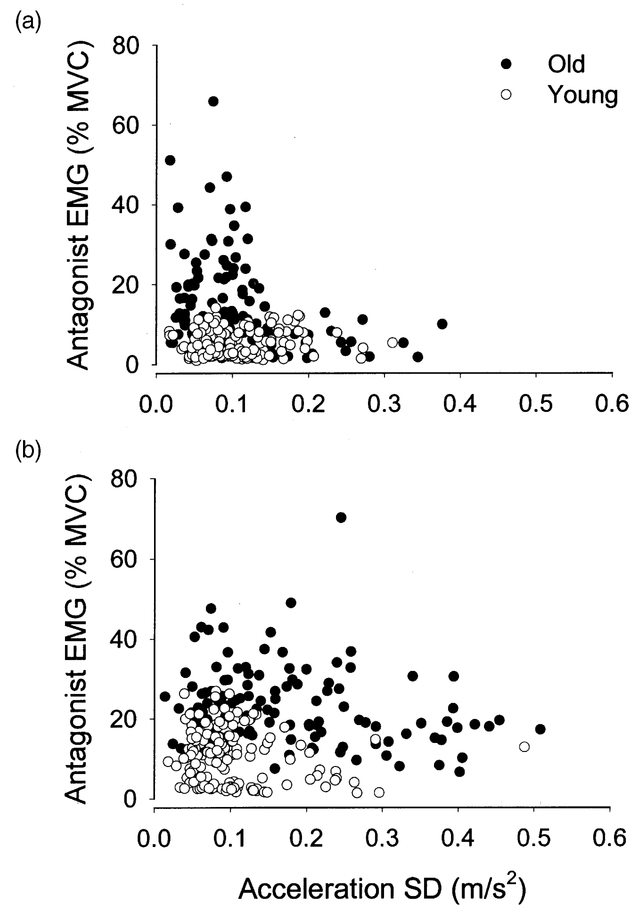


Fig. 5. Scattergrams of the standard deviation of acceleration and the average rectified EMG of the antagonist muscle (second palmar interosseus) during slow anisometric contractions of the first dorsal interosseus by young (open circles) and old (filled circles) adults. Each data point indicates the average values of the two dependent variables during a single trial of one individual while lifting an inertial load of 2.5, 5, 20, 50, or 75% of the 1-RM load. (a) Concentric contractions to raise the load. (b) Eccentric contractions to lower the load. Data from Burnett et al. [7].

The frequency characteristics of the force fluctuations are not attributable to the discharge rates of the activated motor units, but rather appear to involve the common modulation of motor unit discharge [6,18,21,27,33, 38,41,89]. For example, Wessberg and Kakuda [89] found that the median discharge rate of motor units in the extensor digitorum communis muscle during a slow finger movement was 17 Hz (range 11–22 Hz), whereas the fluctuations in acceleration were dominated by an 8–10 Hz component. Similarly, Halliday et al. [33] reported that the fluctuations in finger acceleration during position holding displayed a peak frequency of 20

Hz compared with average discharge rates of 12 Hz for motor units in the muscle (extensor digitorum communis) that supported the finger.

Common modulation of motor unit activity can be assessed either by performing a coherence analysis or by determining the level of synchronization between the discharge times of pairs of motor units [61,65,66]. Coherent fluctuations in motor unit discharge, which occur in the 1–12 and 16–32 Hz bands, can be associated with the level of synchronization between pairs of motor units [5,27,33,41,55]. For example, Semmler et al. [66] found that significant amounts of the variation in synchronization among pairs of motor units in first dorsal interosseus could be explained by coherence in the 2–12 Hz (concentric contraction = 45%, eccentric contraction = 30%) and the 16–32 Hz (concentric contraction = 36%) bands. However, none of the variation in motor unit synchronization during a position-holding task could be explained by coherent fluctuations in either band. These results suggest that common input to motor neurons can occur by branched inputs from a common source or by independent oscillatory inputs [26,44,63].

When motor unit discharge is synchronized, computer simulations indicate that there is an increase in motor unit force and the fluctuations in force during submaximal isometric contractions [79,93]. Although force fluctuations are present in the absence of motor unit synchronization, Halliday et al. [33] determined that motor unit synchronization can account for up to 20% of the fluctuations in acceleration in the 1–12 and 15–30 Hz bands during a position-holding contraction with extensor digitorum communis. Nonetheless, experimental measurements indicate that older adults do not exhibit greater levels of motor unit synchronization between pairs of motor units in first dorsal interosseus during low-force isometric contractions (young = $0.66 \pm 0.4$, old = $0.72 \pm 0.5$ extra action potentials per second), even though the force fluctuations were greater [68]. However, recent analysis of these data revealed that the old adults displayed greater coherence between motor units in the 2–20 Hz range compared with young adults (Semmler, Kornatz, & Enoka, unpublished observations). Although these associations have not yet been examined during anisometric contractions when the level of motor unit synchronization differs from that measured during a position-holding contraction [67], common modulation of motor unit discharge is likely a significant contributor to differences in force fluctuations between young and old adults.

## 4. Summary

Despite the functional significance of fluctuations in the motor output for the accuracy of goal-directed movements and its deterioration with advancing age, there is not yet a physiological explanation of the mechanisms that are responsible for this phenomenon. The task of identifying the mechanisms is complicated by the dependence of the force fluctuations on the muscle group performing the task, the type and intensity of the muscle contraction, and the physical activity status of the individual. Both computer simulations and experimental studies performed on a simple motor system that involves a single agonist (first dorsal interosseus) and antagonist (second palmar interosseus) muscle suggest that the force capacity of the muscle and patterns of motor unit activity can contribute to the differences in force fluctuations between young and old adults. The factors that do not appear to contribute to this difference include motor unit twitch force, the number of motor units that innervate a muscle, and nonuniform activation of the agonist muscle. In contrast, the factors that appear most responsible for the difference in force fluctuations between young and old adults are the variability and common modulation of motor unit discharge rate in both the agonist and antagonist muscles.

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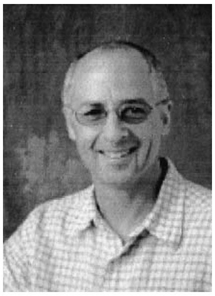

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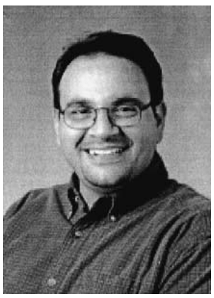

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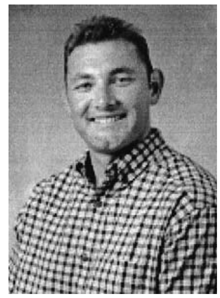

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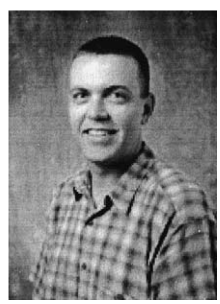

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