

Review Article

The Consequences of Resistance Training for Movement Control in Older Adults

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Older adults who undertake resistance training are typically seeking to maintain or increase their muscular strength with the goal of preserving or improving their functional capabilities. The extent to which resistance training adaptations lead to improved performance on tasks of everyday living is not particularly well understood. Indeed, studies examining changes in functional task performance experienced by older adults following periods of resistance training have produced equivocal findings. A clear understanding of the principles governing the transfer of resistance training adaptations is therefore critical in seeking to optimize the prescription of training regimes that have as their aim the maintenance and improvement of functional movement capacities in older adults. The degenerative processes that occur in the aging motor system are likely to influence heavily any adaptations to resistance training and the subsequent transfer to functional task performance. The resulting characteristics of motor behavior, such as the substantial decline in the rate of force development and the decreased steadiness of force production, may entail that specialized resistance training strategies are necessary to maximize the benefits for older adults. In this review, we summarize the alterations in the neuromuscular system that are responsible for the declines in strength, power, and force control, and the subsequent deterioration in the everyday movement capabilities of older adults. We examine the literature concerning the neural adaptations that older adults experience in response to resistance training, and consider the readiness with which these adaptations will improve the functional movement capabilities of older adults.

DEGENERATION of the neuromuscular system with increasing age impedes the ability to generate maximal force, to develop force rapidly, and to control force production (1–6). These deficits are expressed as a reduced ability of older adults to perform the tasks of everyday living (7). Importantly, however, the aging neuromuscular system retains the capacity to adapt in response to a training stimulus (8). It is well established that older adults may enhance muscle strength (maximal force) and power (rapid force development) through the completion of a resistance training regime (9,10). It has been advocated, therefore, that older adults undertake resistance training programs to combat the substantial declines in muscular strength and power with the view to improving or maintaining functional capabilities (11,12). Frailty has been recognized as a major syndrome in older persons to which the loss of muscle strength is recognized as a key contributor (13–15). It is critical, therefore, to determine the efficacy of resistance training as a treatment to restore function.

A vast body of literature has assessed the responsiveness of older adults to resistance training interventions, in terms of changes in muscle strength and power, and in some instances the performance of functional tasks (9,10,16,17). Several investigators have also elucidated the mechanisms of adaptation to resistance training experienced by older adults (9,17–24). In addition, some investigations have examined the expression of such adaptations on transfer tasks beyond the specific training exercise (25,26). Improvements in controlled force production and the performance of

functional movement tasks have also been observed following periods of resistance exercise (25–27). Yet, the specific enhancements of movement control that are directly attributable to the use of progressively increasing resistance loads in a training program remain unclear (28). Indeed improvements in movement control have also been observed following periods of training against minimal loads (26,29,30). Moreover, resistance training adaptations frequently do not transfer effectively beyond the training exercise (31–36). As yet, a sufficient understanding of the principles governing the transfer of resistance training adaptations in older adults has not been achieved. It remains to be determined how resistance training routines may be best structured to maximize the transfer to functional tasks, or if indeed resistance training programs, in their conventional format, are the most appropriate therapeutic intervention.

RESISTANCE TRAINING TRANSFER

It is well established that resistance training can enhance the force production capabilities of an older adult by increasing muscle mass or improving muscle quality (i.e., the force-generating capacity of individual muscle fibers) (10,22,37). Ultimately, however, it is the impact of resistance training on intermuscular and intramuscular coordination that dictates the effectiveness with which training adaptations transfer to improvement on a functional task (38). Training-induced alterations in muscle activation

patterns have the potential to improve or hinder the performance of a related movement task. Positive transfer is to be anticipated in circumstances in which the specific muscle activation patterns reinforced through training are also those required in the alternative task context. In contrast, negative transfer may occur when the muscle activation patterns consolidated by training are maladaptive with respect to performance of a functional movement task (38).

Resistance training can alter the manner in which trained muscles are recruited by the central nervous system (39). This is associated with a change in the input-output properties of the corticospinal pathway, such that a greater degree of muscle activation is generated by the same amount of cortical input (39,40). A reduction in the cortical input necessary to elicit a given level of force may serve to benefit the production of coordinated movements by reducing the level of central drive and thus minimizing the potential for functional interference within the motor cortex (41,42). In contrast, increased levels of muscular strength have also been associated with a decrease in the ability to independently activate the fingers (43). It has been proposed that this is due to increased levels of neural overflow between the muscles controlling the digits (44). The apparent discrepancy in these findings is indicative of the complex nature of the neural adaptations to resistance training. It is also illustrative of the varying effects of increased levels of muscular strength across different task contexts. For example, in a training study that involved strengthening the legs with concurrent hip and knee extension, the resulting increase in quadriceps and hamstring coactivation was beneficial to performance of the training task (45). However, when an isolated knee extension was subsequently required, increased hamstring coactivation persisted despite the fact that this reduced the net knee joint torque.

The outcomes of resistance training for movement control may therefore vary depending on the particular transfer task that is assessed. There also exists the possibility that young and older adults may be distinguished in the expression of resistance training adaptations beyond the training exercise. For example, resistance training has also been associated with increased synchronization in the firing of motor units (46,47), which is likely to decrease the ability to steadily produce force (48). Paradoxically, older adults improved the steadiness of force production following a period of resistance training (25). This is likely explained by differences in the neuromuscular adaptations that young and older adults experience in response to resistance training as a result of the neuromuscular degeneration that accompanies older age.

Deficiencies in the aged neuromuscular system can be expected to impact considerably on the nature and extent of the neural adaptations older adults experience in response to resistance training (20). With increasing age, there occur substantial changes in the organization and control properties of the motor unit (49,50) and degeneration in the higher nervous centers (51–56). It has recently been shown that the neural adaptations that young adults experience in response to resistance training are mediated in large part by changes

in spinal cord circuitry (40,57,58). Death of the alpha motoneurons in the spinal cord is a crucial feature of degeneration in the aging neuromuscular system (51). Perhaps, as a consequence, supraspinal influences may play a relatively greater role in mediating the neuromuscular adaptations that older adults experience in response to training (28). To evaluate the implications of resistance training for movement control in older adults, it is necessary, therefore, to consider both the various dimensions of neuromuscular decline and the scope of the associated responses to training. In addition, in order to determine the functional consequences of resistance training, it is imperative that these training responses be evaluated as they influence the performance of movements beyond the context of the training exercises (7).

NEUROMUSCULAR DETERIORATION AND CONSEQUENT FUNCTIONAL DEFICIENCIES

By the seventh and eighth decades of life, muscle strength has declined to levels approximately 20%–40% lower than that characteristic of young adults, and will continue to decline such that strength in the very old may be reduced to only 50% of levels typical in the young (8). Occurring at a somewhat faster rate than the strength decline is the progressive decrease in the ability of adults aged 60 years and older to produce force rapidly (6,59,60). There is a large volume of literature describing the changes in the aging motor system that are responsible for the deterioration in force production capabilities experienced by older adults (5,8,61). The diminution of muscle strength and power, and the ability to produce force steadily, arise from diffuse degenerative processes affecting muscles, motoneurons, and regions of the central nervous system (61).

In addition to the decrease in muscle mass that accompanies aging (62–64), the dwindling maximal force-generating capacity also arises from reductions in the specific tension of single muscle fibers (65,66), and alterations in the neural activation of individual muscles (67) and groups of muscles (68,69). Disproportionate atrophy of fast-twitch muscle fibers also reduces the ability to generate maximal force and to rapidly produce force (70). Further decrements in the rate of force development emanate from slowing of the contractile velocity of single muscle fibers (66,71,72) (Figure 1).

Muscle Atrophy and Motor Unit Remodeling

The reduction of muscle strength with progressing age is, to a large extent, attributable to the marked muscle atrophy older adults exhibit after the fifth decade of life (11,62–65,73,74). The loss of muscle tissue occurs subsequent to the death of α -motoneurons in the spinal cord (4,51,75). Following α -motoneuron apoptosis, some of the abandoned muscle fibers are reinnervated by collateral sprouting from surviving motoneurons, and thus become incorporated into other motor units (4,76). The denervated fibers that are not reinnervated by collateral sprouting do not survive. The result of these changes is that the muscles of older adults are smaller and contain fewer motor units than the muscles of young adults, but the individual muscle units of older adults are actually larger than those of young adults (76–78).

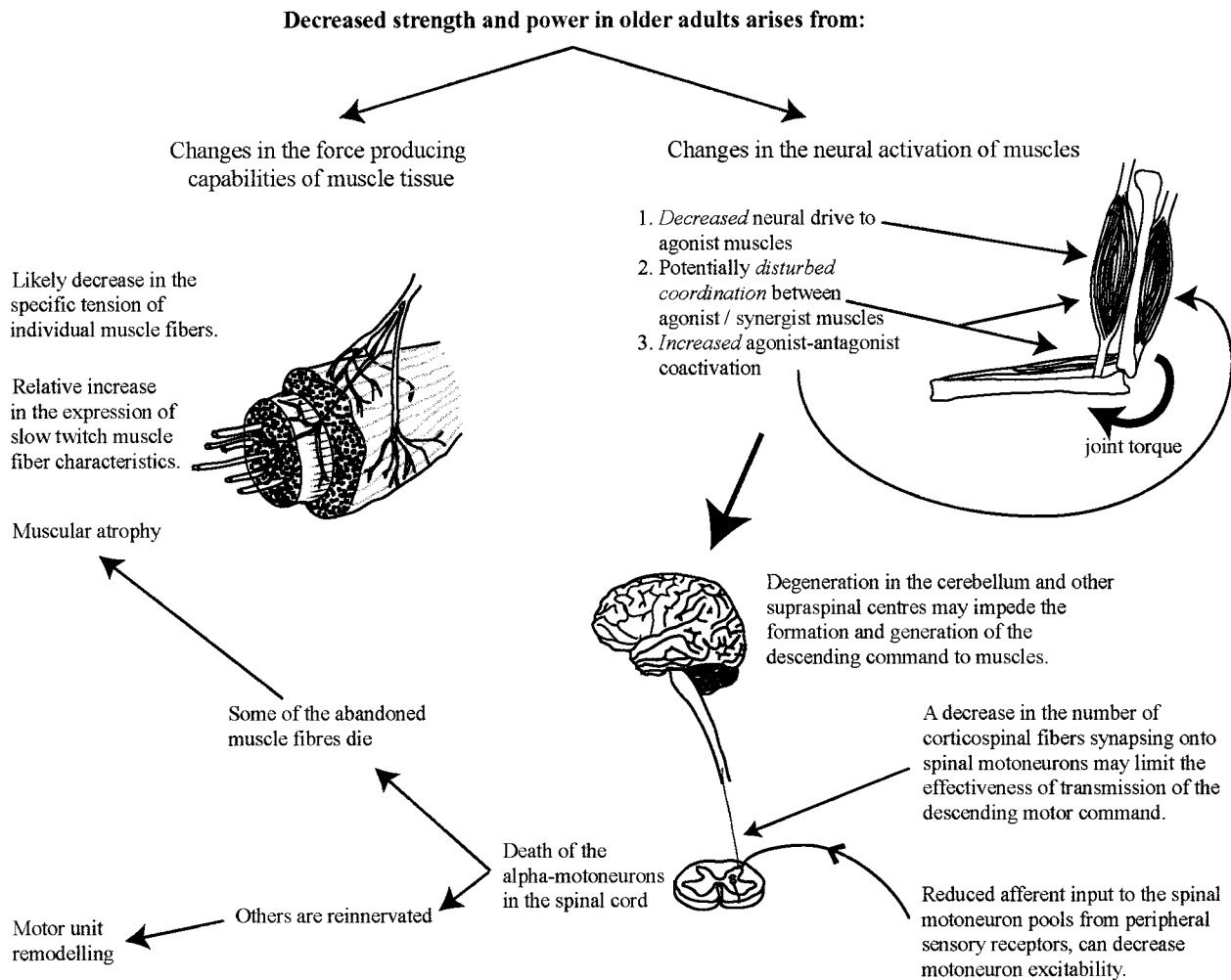


Figure 1. Schematic diagram of the sites of neuromuscular degeneration in older adults contributing to the reduction in muscle strength and power.

In addition to a reduction in the number of muscle fibers, there is also a decrease in individual muscle fiber size (70,79). A disproportionate decline in the size of type II muscle fibers reduces further the maximal force-producing ability of older adults and slows muscle contractility (1,2,70,79–83). It remains unclear whether there is also a change in the relative number of fast-twitch and slow-twitch muscle fibers with increasing age (79,84). It was once believed that a decline in the proportion of fast-twitch muscle fibers arose from a disproportionate loss of large α -motoneurons in the spinal cord, and the subsequent reinnervation of denervated fast muscle fibers by axonal sprouting from slow fibers (61,85–89). More recent evidence suggests that the shift of aging muscle toward predominantly slow-twitch properties arises from dedifferentiation between slow- and fast-twitch muscle, potentially through hormonal changes (61,75). In this regard, senile muscle fibers exhibit an unusually large proportion of muscle fibers in which multiple myosin heavy chain isoforms are expressed, and hence a blurring of the distinction between type I and type II fibers (79,90,91). The extent of muscle atrophy and changes in fiber-type

representation in the skeletal muscles of older adults has been shown to vary between muscle groups (64,65,92) and, in some instances, to differ between older males and females (6,93). Generally, however, for adults aged 60 years and older, a loss of muscle mass at a rate slightly exceeding 1% per year (63,64), in conjunction with a shift towards slow-twitch muscle fiber characteristics, makes a substantial contribution to the age-related reduction in muscle strength and power.

Specific Tension Deficit

While an issue of debate for some time (75), there is now strong evidence that molecular and cellular changes in aged muscle fibers lead to a decrease in the specific tension and maximum shortening velocity of senile muscle (66,71,94–96). Limitations of in vivo measurements of specific tension had prevented a clear consensus on age-related changes in muscle quality (66,97). In calculating the force per unit cross-sectional area of muscle, an increased connective tissue component (98,99) and lipid content (100) of aged muscle and the presence of denervated muscle fibers (101,102) can artificially alter this ratio. Further complicating factors

for the *in vivo* assessment of specific tension include the pennation angle of muscle fibers, coactivation of antagonists, and the variable expression of different muscle fiber types throughout whole muscles (66,97). Recent single-muscle cell experiments have confirmed a specific tension deficit in type I and IIa muscle fibers of older adults, while the specific tension of type IIx (IIb) fast-twitch fibers appears to be preserved (66,72,93). At the molecular level, structural changes in myosin of old rats have been shown to reduce the specific tension of individual muscle fibers by 27% (94). The contractile velocity, and accordingly the power, of individual muscle fibers in older adults decreases as a result of an 18%–25% reduction in the speed of actin sliding on myosin (71,95). Impaired excitation–contraction coupling and changes in the sarcoplasmic reticulum may also contribute to the slowing of muscle fiber contractile speed with older age (72,75,103). However, an increase in the rate of sarcoplasmic reticulum calcium uptake following resistance training did not enhance the contractile speed of the quadriceps muscle in older women (23). This demonstrates that the speed of sarcoplasmic reticulum calcium uptake is not a rate-limiting factor in the slowing of muscle contractile speed with increasing age (23). It is worth noting, however, that some alterations in sarcoplasmic reticulum calcium release have been implicated in a slowing of contractile speed in old rats (72). In summary, it is well supported that a deficit in the force-generating capacity of individual muscle fibers in older adults also makes a substantial contribution to the age-related loss of muscle strength and power. This view is contested, however, by a recent article (104) that suggests there are no age-related differences in the specific tension of individual muscle fibers when force and power are properly normalized to cell size and sedentary young and older adults are compared. The findings of this particular investigation do not, however, account for reported changes at the molecular level in animals and humans that indicate otherwise (71,94).

Alterations in Neural Activation

In addition to the loss of muscle mass and the reduction in the specific tension of muscle fibers, older adults exhibit notable deficits in their force production capabilities that are attributable to alterations in the neural activation of muscles (64,73). The ability to develop maximal force or to produce force rapidly is dependent upon the capacity of the nervous system to maximally activate individual muscles, and to coordinate appropriately the activation of groups of muscles. A multitude of neuromuscular changes contribute to the various deficits displayed by older adults in the activation of individual muscles (intramuscular coordination) and the coordination of groups of muscles (intermuscular coordination).

Activation of individual muscles.—Reduced levels of muscle activation have typically been considered to make a negligible contribution (2%–4% young/old difference) to the reductions in strength observed with increasing age (19,99,105–108). Failure to fully activate a muscle will

occur when there is either inadequate neural drive to a muscle or when excitation–contraction coupling is insufficient to ensure that all motor units in the muscle are active and being fired at the appropriate maximum rate. Studies that have assessed the ability of older adults to maximally activate their muscles have done so by determining whether any additional force is elicited when electrical stimulation is superimposed during an attempted maximal contraction (109). In using only a single-pulse or double-pulse twitch to evoke additional torque, rather than a train of electrical stimuli (110), it is likely that some of these studies overestimated the extent of muscle activation (19,106,107,111). More recent evidence suggests, however, that single-pulse stimuli may be adequate to assess activation maximality (112). Rather, other sources of measurement insensitivities with twitch interpolation have given rise to frequent overestimation of the extent of voluntary activation (113). There is a more general tendency for the extent of muscle activation to be overestimated when using this technique, due to the widely held but erroneous assumption that, as voluntary effort increases, there is a linear decline in the force evoked by a superimposed electrical stimulus (114,115). A recent reexamination of the relationship between the calculated level of muscle activation and the percentage of maximal voluntary contraction force (116) has established that the difference in the activation deficit between young and older adults may be more in the order of 11% (67). Therefore, the inability of older adults to maximally activate muscle is likely to make a significant contribution to the decrement in strength that is observed with increasing age (17,92,115). The extent of this deficit appears to progress with increasing age among older adults, being more prominently expressed by those adults in their seventies, eighties, and older (24).

The possible mechanisms that may reduce the ability of older adults to maximally activate their muscles include inadequate cortical drive (117), altered modulation of cortical drive by the propriospinal premotoneurons (118), reductions in α -motoneuron excitability (24,119,120), inefficient signal transmission at the neuromuscular junction (121), or deficiencies in excitation–contraction coupling (72). There is notable degradation of the neuromuscular junction with increasing age (121). Equivalence in the peak torque of contractions evoked by electrical stimulation of muscle either directly or via the nerve indicates, however, that changes in the neuromuscular junction are not primarily responsible for reductions in contractile tension (122). It has been shown that excitation–contraction coupling in fast-twitch fibers is essentially preserved with age, and while there are changes that might contribute to the reduced speed of contraction, these do not limit the force of contraction (72). Therefore, inadequate central drive at either spinal or supraspinal levels is the more likely source of any age-related difference in the extent of muscle activation.

There is evidence that older age is accompanied by a progressive loss of corticospinal motoneurons and a decrease in synaptic density on spinal motoneurons (52). Pitcher and colleagues (123) used magnetic cortical stimulation to assess changes in the motor cortex input–output properties with increasing age and observed that, in

older adults, higher stimulus intensities were required to elicit maximal motor-evoked potentials. Elderly persons also exhibited a reduced consistency of cortically evoked motor output. These findings are indicative of decay in the transmission of cortical activity to the spinal motoneuron pool. This would be expected to hinder the descending control of α -motoneuron excitability, and thus the modulation of voluntary muscular activity. Similar age-related changes in the size of cortically stimulated motor-evoked potentials and peripherally evoked F-waves have been taken to indicate a parallel reduction in the excitability of the upper motoneuronal pools of the motor cortex and the spinal motoneurons (56). Any reduction in the excitability of the spinal motoneuron pool, for a given level of supraspinal input, will result in the recruitment of fewer motor units or lower motor unit firing rates and hence lower muscle activation.

Excitability of the spinal motoneuronal pools is regulated by several sources of peripheral and central inputs (118,124). Afferent input to the motoneuron pool is a critical regulator of motoneuron excitability; in its absence, motor unit firing rates, and therefore muscle force, are reduced (125). An age-related decline in peripheral sensory feedback is indicated by impairments in stretch reflex sensitivity (126), larger thresholds for the detection of a change in joint angle (127), and alterations in the control of grasping movements that are consistent with reduced cutaneous sensation (128). It is not yet known, however, if any age-related declines in the contribution of afferent input to motoneuron excitability are sufficient to lower maximal voluntary muscle activation levels (115). Presynaptic inputs to the Ia afferents are also strongly implicated in the regulation of spinal motoneuron excitability (118,129). In this regard, it has been shown that older adults rely less on the modulation of presynaptic inhibition during submaximal contractions and more on direct activation to regulate motoneuron pool output (130). In summary, changes in the integrity of corticospinal tracts, in conjunction with possible alterations in the excitability of the spinal motoneuron pool, are likely to culminate in less-dependable transmission of cortical drive to the muscles of older adults. This is also a possible explanation for the observation that older adults are notably less consistent than young adults in the extent of muscle activation achieved during repeated attempts at maximal voluntary contractions (108,131).

While, with increasing age the level of neural drive that is provided to skeletal muscles may be reduced, there are also changes in the force–frequency response of the muscles themselves (3). In producing maximal effort contractions, older adults exhibit lower maximal motor unit discharge rates than young adults (132). However, the decrease in maximal motor unit firing rate does not necessarily limit the capacity of older adults to produce maximal force (132). With increasing age, there is a leftward shift in the force–frequency curve of skeletal muscle, such that tetanus may be achieved at lower frequencies of electrical stimulation (3,106). The slowing of muscle contractile properties reduces the frequency of electrical stimulation necessary to develop a given level of torque, and therefore enhances the efficiency of muscle activation (107). The degree of

slowing varies between different muscles depending upon the magnitude of change in myosin heavy chain expression and possibly some features of sarcoplasmic reticulum function (50,106). The slowing of muscle contractile properties limits the intrinsic capacity of older adults to develop force rapidly, as is indicated by the reduced rate of force development of electrically stimulated contractions (107,120). It is presently unclear whether the additional temporal constraint imposed by rapid contractions exacerbates any deficit in the ability of older adults to maximally activate their muscles. White and Harridge (133) reported that young and older adults were distinguished specifically at very high contraction velocities, in terms of the level of muscle activation achieved during isokinetic plantar flexion. No age-related differences were apparent, however, in the rate of muscular activation or the amount of agonist muscle activity, as indicated by the absolute and normalized electromyograms attained during rapid isometric and isokinetic plantar flexion and dorsiflexion (134). In fact, Clarkson and colleagues (135) demonstrated that older adults could develop greater knee extension torques when maximal voluntary contractions were produced more rapidly. By normalizing voluntary rates of force production to the peak rate of force development of electrically elicited contractions, it was deemed that older adults did not exhibit a deficit in rapid muscle activation (99). Developing force quickly relies on rapid motor unit firing in the early stages of contraction (136), and the rate of force development continues to increase even after motor unit discharge rates exceed the stimulation frequency required to elicit a maximal force contraction (137). While there are decreases in nerve conduction velocity with increasing age that may limit the maximum frequency of stimulation (89), the slowing of muscle contractile properties will reduce the motor unit discharge rates necessary to achieve a given rate of muscle activation (3,107,111). Any deficits in the capacity of older adults to maximally activate individual muscles may not, therefore, be exacerbated under circumstances in which rapid muscle activation is required. Rather, the age-related reduction in muscle power that exceeds the loss of muscle strength may be attributed to the dramatic slowing of muscle contractile properties and perhaps also from difficulties in the coordination of groups of muscles during rapid actions.

Coordinating groups of muscles.—Older adults also exhibit differences in muscle activation patterns when coordinating groups of muscles. The maximum net joint torque that older adults produce is limited by a tendency towards increased coactivation of agonists and antagonists in comparison to young adults (68,69,138,139). Izquierdo and colleagues (59) observed elevated levels of antagonist activation of older men compared with middle-aged men during rapid maximal force dynamic actions but no difference during isometric contractions. Heightened levels of agonist–antagonist coactivation are believed to arise to enhance joint stability (139) by increasing joint stiffness and thus reducing any disturbances to joint position from destabilizing forces (140). Increased levels of agonist–antagonist coactivation have also been considered as a strategy to compensate for the decreased steadiness of

movement that occurs with increasing age (138,141,142). This pattern of muscle activation also reduces the reliance on afferent feedback for effective motor control and may therefore compensate for the reduced peripheral sensation that occurs in older age (128). Although not exhibited in all movement situations (134,143), elevated levels of agonist–antagonist coactivation are displayed by older adults across a broad range of motor tasks and act to limit the maximum force and rate of force development that can be generated (68,69,141). Although it has been proposed that chronic changes in the spinal segmental pathways are responsible for the increased levels of coactivation, a role of supraspinal mechanisms cannot be excluded (61).

In addition to amplified agonist–antagonist coactivation, in some movement contexts older adults exhibit further differences in the coordination of groups of muscles. When producing maximal voluntary contractions with the fingers, older adults displayed a greater reduction than young adults in the total force produced when all four fingers were contracted, compared to the sum of the forces produced when each finger was contracted individually (43). The reduced ability to exert maximal force when activating all fingers together was associated with an enhanced ability of older adults to selectively exert force with individual fingers. It has been suggested that this represents an adaptive strategy that benefits independent finger control, but this apparently occurs at the expense of the ability to coordinate the recruitment of all fingers in a maximal force-producing task. The change in control strategy has been attributed to alterations in motor unit properties and changes in the supraspinal commands to motoneuronal pools (43). It has also been shown that disproportionate degeneration of the force-producing capabilities of subsets of muscles within a synergistic group disrupts the formation of effective patterns of muscle activation by older adults (144). Furthermore, under certain movement conditions, age-related differences have been identified in the distribution of activation between mono-functional and bifunctional elbow flexor muscles (145). This finding raises the possibility that the standard manner by which the nervous system distinguishes these classes of muscles may be disrupted in older age (145,146). However, the activation patterns of groups of muscles during the rapid or maximal exertion of force are not always observed to differ between young and older adults (147).

There is some evidence that older adults experience particular difficulties in coordination during rapid actions (148). When repeatedly performing a rapid discrete force trajectory-matching task, older adults exhibited considerably greater intertrial variability than young adults (148). Darling and colleagues (149) also reported that older adults were more variable in the production of aiming trajectories, particularly when required to move rapidly, and that this was accompanied by less-effective muscle activation patterns. In performing more complex stepping tasks to regain balance or control a stair descent, older adults exhibit notable differences compared with young adults in the timing and magnitude of activation of groups of muscles (139,150). These findings support the view that movement control in older adults deteriorates with increases in speed and complexity of movement (148,151–153). Alterations in

sensory capacities (61,154), greater distraction as a result of the attention demands of concurrent cognitive tasks (155), heightened levels of anxiety (156), and weaker muscles are some of the factors that may contribute to the altered movement strategies exhibited by older adults. To a large extent, however, the age-related changes are likely to be attributable to difficulties experienced by older adults in muscle coordination (157). Degenerative changes in the neuromuscular system with increasing age, such as a decline in the number of corticospinal fibers (52), a decrease in intracortical inhibition (158), neuronal degradation in other higher nervous centers (55), and the reduced number of motoneurons in the spinal cord (51), would be expected to limit the flexibility in the neural circuitry by which muscle coordination patterns are formed. This may potentially impede the ability of older adults to optimally coordinate muscles when attempting to exert maximal force or to develop force rapidly. Furthermore, the extent of this interference may vary depending on the coordination demands of the particular movement task and the specific muscle groups involved.

Decreased steadiness of force production.—Degenerative changes in the aging neuromuscular system also retard the ability of older adults to produce force steadily, accurately, and temporally matched to the demands of particular movement tasks (5,28). The reduced ability of older adults to steadily produce target forces varies depending on the muscle group, the contraction type, and the contraction intensity (5). A series of investigations (25,26,145,159–163) have examined the contribution of various changes in the aging neuromuscular system to the decreased steadiness of force production. [For a detailed review of the expression and etiology of the increased fluctuations in force with progressing age, see Enoka and colleagues (5).] The primary mechanism responsible for the decreased steadiness was considered to be an age-related increase in the variability of motor unit discharge rates (159), possibly arising from an increased prevalence of 10 Hz or lower central oscillations in the electromyogram and a decrease in the 20 Hz and 40 Hz oscillations (5,164,165). Recent evidence has shown, however, that the decreased steadiness of force production across the entire force-generating range of a muscle cannot be explained by a single mechanism that influences motoneuron pool output (166). While it does not appear that the decrease in steadiness is due to the weaker muscles of older adults (5), it has been shown that the steadiness of force production can be improved by undertaking resistance training (25,167).

Deficiencies in Strength, Power, and Functional Task Performance

Beyond the age of 60 years, muscle strength declines at a rate of approximately 1.4% to 2.5% per year (63), while muscle power is frequently reported to decay at an even faster rate (~3.5% per year) than the loss in strength (6,59,60,167–171). The greater loss of muscular power is attributable to the relatively greater atrophy of fast-twitch fibers, as well as the other previously described changes that slow contractile velocity (6,59,168). The rate of decline of

muscle strength and power has in some instances been shown to vary quite markedly between different muscle groups (63,92), and men and women (6,64,73,93,172). Some of these discrepancies are likely to have arisen from differences in the physical activity levels and population demographics of the participants in various studies, as well as variations in the testing methodologies (63). There does appear, however, a general trend for the loss of lower limb strength to exceed the loss of upper limb strength (63,65). This can be explained by a relatively larger decline in lower body skeletal muscle mass with advancing age (62). Similarly, muscle-specific variation in the relative change in muscle fiber type and the slowing of contractile properties should account for differences in the rate of power decline between muscle groups (65). Muscle group or gender-specific differences in the degeneration of either strength or power may potentially lead to task and gender variation in the loss of function.

Deficits in muscle strength and power hinder the ability of older adults to complete certain functional movement tasks, such as rising from a chair, stair-climbing, and locomotion (169,173–177). The relative importance of maximum muscle strength and power vary depending on the force demands of particular activities (178). Indeed, threshold levels of strength and power are required for the completion of many daily tasks (179–183). A maximal force-producing capacity that exceeds threshold levels may still be useful, as it is necessarily accompanied by a larger reserve capacity (178). Alexander and colleagues (181) report that, in rising from a chair, older adults have to use a greater percentage of their maximum knee strength (35%–87%) than do young adults (19%–49%). While older adults may retain sufficient levels of strength and power to complete various functional tasks, the greater fatigue experienced from working at maximal or near-maximal capacity is still debilitating (97,184–186). As the strength levels of older adults decline, movements begin to deteriorate until, eventually, older adults perceive that they are slow or cannot perform the task as frequently as they once did, and a modified strategy is then adopted (187,188) (Figure 2). The speed with which older adults can perform functional movement tasks is influenced by their capacity to accelerate either their body weight or their limbs (179,189). Accelerating a limb or one's body weight is dependent on the impulse (force per unit time) that is developed, thus emphasizing the importance of declines in muscle power in older adults to functional task performance (189–191).

In addition to proceeding at a faster rate than declines in strength, deficiencies in muscle power are more closely associated with functional task performance (189,192). Leg muscle power has been identified as a strong predictor of self-reported functional status for community-dwelling older women with a history of falling (190). It has also been shown that lower leg muscle power is an important predictor of stair-climbing and chair-rising performance in older adults (191). The decreased ability to develop force rapidly seems also to be associated with a lower capacity for the neuromuscular response necessary to control postural sway (193). The literature implicating muscular strength and power in the etiology of falls is extensive (7,182,193–198).

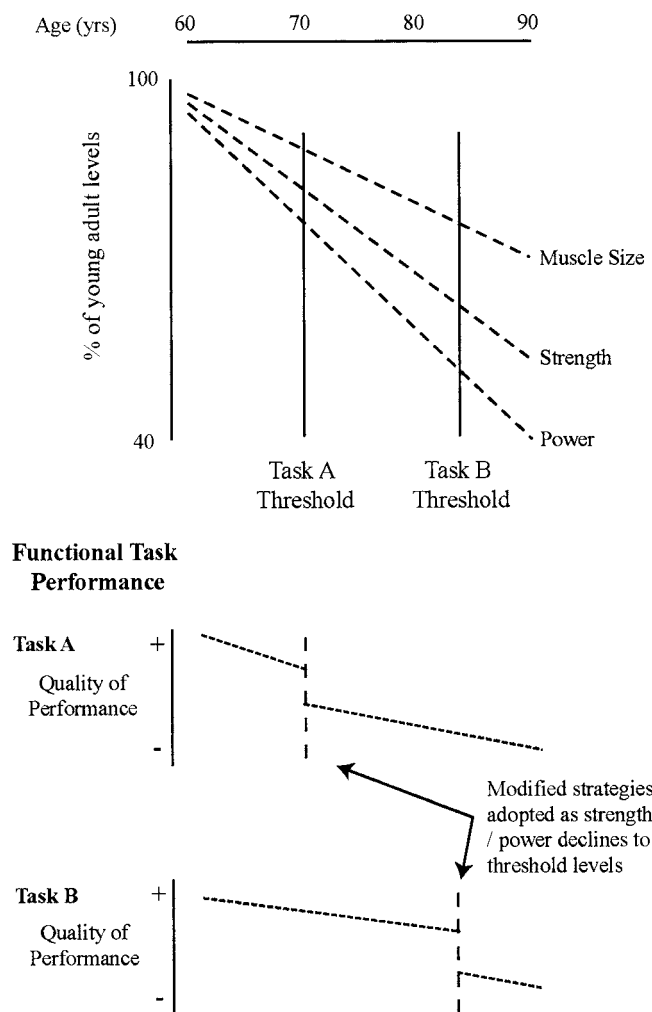


Figure 2. Schematic outline of the relationship between the reduced strength and power of older adults to the deterioration of functional task performance.

The temporal demands of loss of balance situations are heightened further by the slower response initiation that is displayed by older adults (199–202). This acts to reduce the window of time within which a corrective action may be produced, and consequently a more rapid movement may be necessary to successfully maintain balance (198,203,204). The maximal rate of force development or maximum strength, however, do not necessarily determine the ability of older adults to effectively control limbs during balance maintenance tasks (205,206). Although near-maximal levels of strength and power may be utilized in some instances of balance maintenance (206), the coordination of muscles can be more important in producing the rapid actions required in these movement situations (150,157,203).

While it is clear that many factors in addition to muscle strength and power affect the movement capabilities of older adults, threshold levels of strength and power are necessary to complete everyday movement tasks (179,181,207). Strength and power levels in excess of these thresholds are still valuable to physical function, as this reserve capacity can act to reduce the physiological demands of task

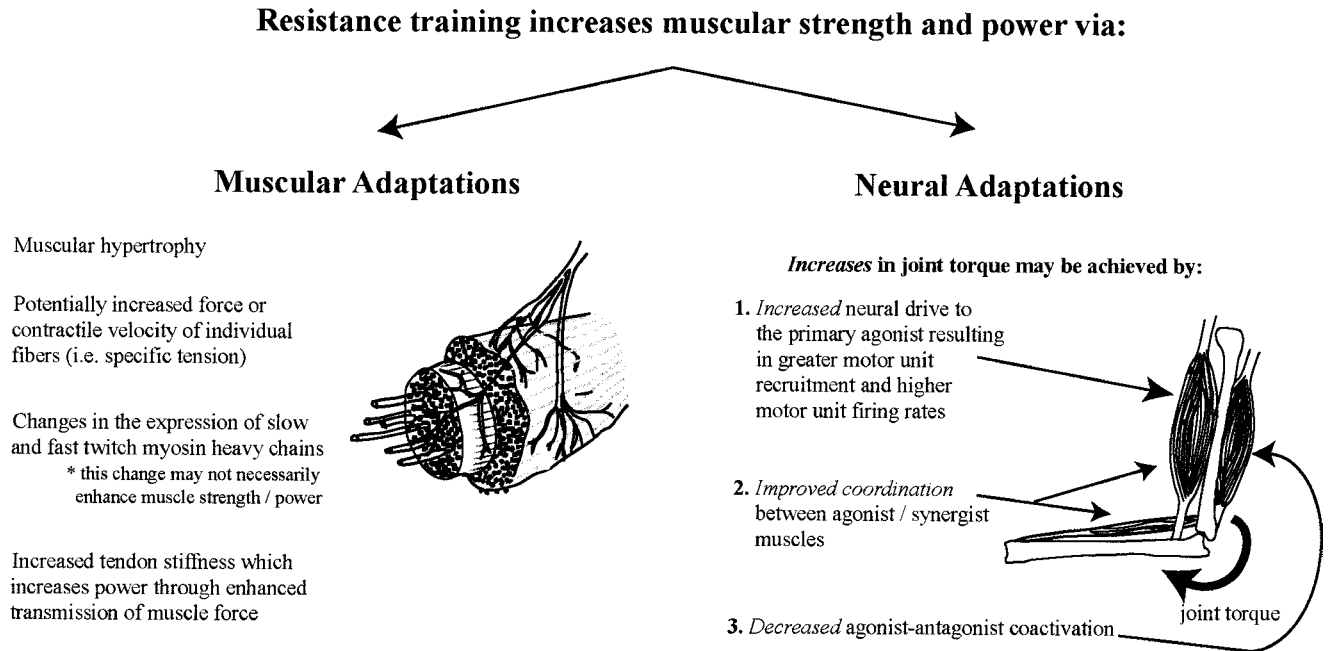


Figure 3. Basic outline of the musculotendinous and neural adaptations to resistance training.

completion (97,181). This should also act to reduce the perceived difficulty of performing a task, and thus the task may be completed without the adoption of a modified strategy (188). It is well established that deficiencies in the maximal rate of force development bear particular significance to functional movement tasks (189,190). Perhaps of greater consequence to functional task performance are the changes in muscle coordination that limit the rapid production of force in particular movement contexts (150,157). In this regard, some age-related differences in the control of muscles during functional tasks seemingly arise to compensate for limitations in muscle strength and power (181,197). In other instances, these differences may be directly attributable to neuromuscular degeneration, which alters the control of muscles (139,145,208,209), or different muscle coordination strategies may be adopted as a result of elevated levels of anxiety that emerge under conditions such as an increased threat of losing balance (156,197).

TRAINING TO ENHANCE FORCE PRODUCTION AND THE MECHANISMS OF ADAPTATION

Resistance training has been recommended to older adults seeking to increase muscle strength and power with the view to improving their functional capabilities. In addition to increasing muscle mass and improving the specific force that can be generated by muscle fibers, resistance training induces neural adaptations that augment the ability of older adults to generate force. While these adaptations result in increased levels of strength and power, a training intervention intended to enhance the movement capabilities of older adults must also improve the ability to control muscle force, and this adaptation must persist during the performance of motor tasks other than the specific training

exercise (28). Much research has focused on the ability of older adults to control submaximal forces and the manner in which this capacity is influenced by resistance training exercise (25,26,35,167,210). Indeed, many of the tasks encountered by older adults in the course of everyday living have force requirements that are submaximal, and notable motor control deficiencies are evident in the performance of such tasks (211). Deficits in coordination are also apparent during the production of maximal force levels (131) or rapid contractions (148). Degeneration of motor performance with older age is expressed as impaired performance across a broad spectrum of functional tasks that are encountered in everyday living. However, it is not practical for every one of these impaired movement tasks to be specifically trained. It is therefore necessary to understand the manner in which resistance training alters the behavior of trained muscles during a variety of movement tasks.

As noted previously, the influence of resistance training on intermuscular and intramuscular coordination dictates the effectiveness with which training adaptations transfer to improvement on a functional task (38). Moreover, training-induced alterations in muscle activation patterns have the potential to improve or hinder the performance of a related movement task. Degenerative changes in the aging motor system would be expected to influence the adaptive strategies available to the neuromuscular system (7,8). Therefore, the changes in intramuscular and intermuscular coordination arising through resistance training are likely to display adaptive features unique to older adults (142). This will not only influence the nature of adaptations that may be experienced in response to resistance training, but will also affect the subsequent transfer of training adaptations beyond the training exercise (Figure 3 provides an outline of resistance training adaptations).

Muscle Hypertrophy and Muscle Fiber Adaptations

Older adults retain the capacity for muscles to hypertrophy in response to resistance exercise (37,212,213), even into the 10th decade of life (10). There remains some contention, however, as to whether this capacity is limited in comparison with young adults (9,214–217). Hasten and colleagues (212) showed that, while a group aged 78–84 years exhibited lower resting myosin heavy chain and protein synthesis rates than a group aged 23–32 years, both groups displayed a similar increase in protein synthesis rates following resistance training. Roth and colleagues (216) argue that the traditional practice of assessing muscle hypertrophy by changes in muscle cross-sectional area has lead incorrectly to the conclusion that muscle hypertrophy is limited in older adults. Instead, when muscle volume was used as an index of hypertrophy, young and old adults exhibited a similar gain in muscle mass in response to resistance training.

Ultimately, however, there are ongoing physiological changes with increasing age that act to reduce muscle mass and, although the progression of such changes may be slowed by resistance training, these processes cannot be halted. Increased loading of the muscles of older rats was shown to have no influence on the rate of motoneuronal loss (218), thus demonstrating that resistance training cannot prevent the muscle atrophy that results when muscle fibers become denervated. Endocrine changes in older adults are characterized by reduced basal levels of anabolic hormones and dampened hormonal responses to resistance training (16,219–222). Measurements of gene-activating signals (223) and gene expression (224) indicate that, at rest, the skeletal muscles of older adults exhibit increased levels of cellular activity, and, consequently, changes in skeletal muscle gene expression and signaling following a bout of resistance exercise were reduced in older adults (223–225). While older adults may achieve a similar degree of muscle hypertrophy to young adults in response to particular resistance training routines, in the long term, the benefit of resistance training in this regard may be confined to the maintenance of muscle mass or the slowing of age-related sarcopenia. In comparing well-trained older adults with untrained age-matched controls and young adults, it was observed that the well-trained older adults were able to maintain muscle mass through resistance exercise up until the age of 70 years (81). Furthermore, in a study assessing maintenance of training-induced increases in muscle mass, older men were shown to maintain gains in muscle mass by training only 1 day per week over 6 months, subsequent to an initial 12-week period training 3 days per week (226). It has also been shown that the gains in muscle mass achieved by older adults through resistance training may be augmented by nutritional supplementation (227). The increases in muscle mass that may be achieved with resistance training will ultimately be limited by progression of the aging process. However, over the short term (months), older adults may exhibit notable increases in muscle mass, and the maintenance of muscle mass is itself an extremely important benefit of resistance training, which may be achieved with relatively low training frequencies.

Resistance training has been shown to induce hypertrophy in both the type I (slow-twitch) and type II (fast-twitch) muscle fibers of older adults (37,213). Single muscle fiber studies have revealed that resistance training increases muscle cell size, strength, contractile velocity, and power of slow-twitch and fast-twitch fibers, but these changes are more pronounced in type I muscle fibers (22). Older adults retain plasticity in the expression of muscle fiber types (myosin heavy chain isoforms) as a response to resistance training, and, similar to young adults, a decrease in the expression of type IIb (IIx) fibers and an increased expression of type IIa fibers has been reported (228–230). The increased expression of type IIa fibers was not statistically significant (229,230), however, or differed between the male and female groups (228,230). The significant decrease in the expression of type IIb fibers was consistently observed for both men and women. Discriminating the relative alteration in different fiber types is complicated in older adults by the increased prevalence of hybrid fibers in which multiple myosin heavy chain isoforms are expressed (90,91,228). It has been shown that after older adults perform 12 weeks of progressive resistance training, the coexpression of myosin heavy chains in single muscle fibers decreases and there is an increase in type I myosin heavy chains (231). In contrast, young adults exhibit a shift towards type IIa myosin heavy chains as the coexpression of myosin heavy chains decreases (232). Therefore, while older adults may be able to achieve the same proportional increase in muscle mass as young adults by undertaking resistance training, they do so with greater adaptation in the slow-twitch component of muscle (22,223,232). An increased expression of type I myosin heavy chains would account for the overall slowing of muscle contractile properties that has been reported to occur following the performance of resistance training by older adults (21,33).

Neural Adaptations

As with young people, elderly people also exhibit strength gains following resistance training that do not parallel muscular hypertrophy, especially in the early phase of training (233). These adaptations comprise changes in the neural activation of muscles, with modifications occurring in both intramuscular and intermuscular coordination (7). Such adaptations may include decreased antagonist coactivation (234), improved coordination of synergist muscles (235), and increased neural drive to agonist muscles resulting in the recruitment of additional motor units (236,237) and increased motor unit firing rates (20,136). As muscle hypertrophy plays a lesser role as an adaptive response to resistance training in older adults (25), it is possible that the primary means by which benefits to functional tasks will be derived is via the neuromuscular adaptations to resistance training (8,233). The specific neural adaptations experienced by older adults and the mechanisms by which these changes occur will determine to what extent such changes benefit the performance of movements other than the training exercises (38).

It is well supported that the expression of resistance training adaptations is limited across different movement contexts (238). This specificity of adaptations has been

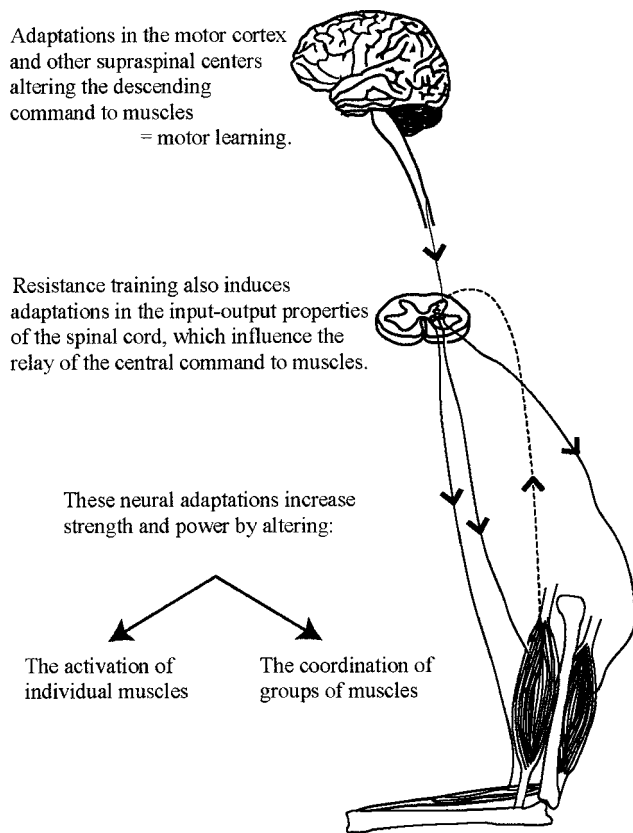


Figure 4. The sites of the neural adaptations to resistance training as demonstrated in young adult humans (40,252) and rats (57,58). The extent to which training adaptations are expressed in movements other than the particular training exercise will vary depending on the level of the neuraxis at which adaptations take place.

attributed to adaptations in the patterns of muscle coordination that are specific to the particular training exercise (235,239). These so-called motor-learning adaptations are mediated by supraspinal mechanisms, which are known to include changes in the organization of the motor cortex (57,240,241). Importantly, these changes are observed to occur whether or not a training movement is performed against progressively increasing loads (57), but are limited in the range of movements across which they are expressed. For young adults, recent evidence has shown that resistance training also leads to adaptations distinct from those of normal motor learning, inducing changes in the behavior of spinal cord circuitry (40,57,58). It has been demonstrated that resistance training adaptations mediated at the spinal cord may benefit the manner in which muscles are coordinated during related movement tasks (39,40), and the particular nature of this adaptation is such that it is likely to be expressed whenever the motoneuron pool of the trained muscle is activated. Thus the changes that occur at the spinal cord can enhance the activation of muscles, and this adaptation is likely to be more generally expressed than changes mediated at a supraspinal level (Figure 4).

This is not to say that all motor learning mediated at a supraspinal level is expressed minimally in movements that are different from the particular exercise performed

throughout training. Indeed, it has been shown that, when a movement is practiced in a novel force field, the learning that occurs is subsequently expressed in a consistent and predictable fashion across all combinations of muscle activation (242,243). In contrast, the motor learning that occurs during resistance training results in a consolidation of the patterns of intermuscular and intramuscular coordination that are specific to the particular movements performed repetitively throughout training. As outlined earlier in the review, the effectiveness with which these adaptations transfer to related movements depends on the similarity between those muscle activation patterns consolidated through the regular performance of the training exercise and those required during different movement tasks. Positive transfer is to be anticipated in circumstances in which the specific muscle activation patterns reinforced through training are also those required in the alternative task context. For situations in which the activation patterns consolidated by training are maladaptive with respect to performance of a functional movement task, these patterns may disrupt performance of the functional task and hence result in negative transfer. Alternatively, any undesirable features of muscle activation that are reinforced through training may be inhibited by specific control strategies implemented by the central nervous system and, as such, neither benefit nor impede the performance of the related task (38).

It has been established that some of the neural adaptations that young adults experience in response to resistance training are also displayed by older adults, such as a decrease in agonist-antagonist coactivation (9,234). That which is less clear is whether the mechanisms mediating these changes are the same for young and older adults. In consideration of the degeneration experienced in the aging spinal cord and differences in the neuromuscular adaptations displayed by young and older adults in response to certain training schemes, it has been suggested that supraspinal mechanisms may mediate, to a greater degree, the adaptations experienced by older adults (28,61). If, indeed, degeneration of the spinal cord circuitry with increasing age does impede the plasticity of these pathways to respond to resistance training in the manner demonstrated in young adults (40), then in older adults, motor-learning adaptations, mediated by supraspinal mechanisms, would become the dominant means of neural adaptation (28). As a consequence, it may be expected that the strength gain that older adults achieve through resistance training may be less generally expressed across different movements.

Adaptations in the activation of individual muscles.—

While it appears that older adults may exhibit a greater deficit than young adults in the ability to maximally activate muscles (67,115), it remains unclear whether this capability is amenable to the influence of training (17,19). Young individuals have been shown to increase maximal motor unit firing rates (20) and to activate more muscle tissue following resistance training (236). Accordingly, increased levels of voluntary muscle activation have been shown in young adults following the completion of a strength-training routine (244). While older adults exhibit reduced maximal motor

Table 1. Summary of Experimental Investigations of Changes in Muscle Activation Following Resistance Training in Older Adults

Source	Age of Groups (N)	Training	Adaptation	Comment
Moriani and deVries, 1980 (233)	67–72 y (5 males?) 18–26 y (5 males)	8 weeks, 3 times per week, moderate–high-intensity elbow flexion	Increase in agonist EMG	
Hakkinen et al., 1998 (247)	60.8 ± 4.0 y (10 males) 29.2 ± 5.0 y (8 males)	10 weeks, 3 times per week, mixture of heavy resistance training and explosive exercises for lower and upper body	Increase in agonist EMG (knee extensors)	These 3 studies, and several other similar investigations, provide indirect evidence of an increase in muscle activation following resistance training
Connelly and Vandervoort, 2000 (246)	70–85 yrs (13 males, 15 females)	2 weeks, 3 times per week, plantar/dorsiflexion explosively at heavy loads	Increase in agonist EMG	
Harridge et al., 1999 (17)	85–97 y (3 males, 8 females)	12 weeks, 3 times per week, high-intensity knee extension	Twitch interpolation revealed no significant increase in muscle activation (pre: 81% ± 7%, post: 85% ± 10%)	This technique can reveal directly if muscle activation is increased after resistance training; but, specific application of the technique may not have been sufficiently sensitive to detect training changes
Knight and Kamen, 2001 (19)	67–81 y (6 males, 1 female) 18–29 y (4 males, 4 females)	6 weeks, 3 times per week, moderate–high-intensity knee extension	Twitch interpolation revealed a small (1.7%) but significant increase in muscle activation for pooled data of young and older adults	Single-pulse superimposed twitch demonstrated a small increase in muscle activation but only for pooled data, and the change in means was greater for the young group; perhaps insufficient sample size or sensitivity of twitch interpolation
Scaglioni et al., 2003 (24)	65–80 y (14 males) 24–35 y (10 males) Young group did not train	16 weeks, 3 times per week, moderate–high-intensity leg press and calf raise	H-reflex/maxM—no change, twitch interpolation revealed a small muscle activation increase (3.7%), but no change in voluntary MVC/predicted MVC using extrapolation of interpolated twitches at various forces	H-reflex used to assess changes in spinal reflex pathway excitability but inadequately examined to be conclusive; deemed no increase in muscle activation on basis of small change in interpolated twitch data and no change with extrapolation technique
Leong et al., 1999 (245)	67–79 y (7 older weightlifters) 67–80 y (5 untrained controls)	Cross-sectional study only	Motor unit discharge rate during maximal contraction: weightlifters: 23.8 ± 7.7 Hz, untrained: 19.1 ± 6.3 Hz	Older weightlifters exhibited increased motor unit firing rates, difference could be by virtue of more active lifestyle rather than resistance training specifically
Patten et al., 2001 (20)	75.8 ± 7.4 y (3 males, 3 females) 23.2 ± 3.5 y (3 males, 3 females)	6 weeks, 5 days per week, 2 sets of 10 reps maximal isometric index finger abduction (adductor digiti minimi tested)	MVC force: +25% young, +33% old, after 2 days max motor unit discharge rate +11% young, +23% old group, who thereafter returned to initial levels	Increase in motor unit firing rates after 2 days, but subsequent decrease after 6 weeks for older group; by contrast, firing rates increased for the young group and remained elevated
Kamen et al., 1998 (250)	77.0 y (7) 21.4 y (8)	6 weeks of isometric and dynamic resistance training for the leg extensors (vastus lateralis)	Increase in max motor unit discharge rate across 2 test day baseline, further increase after resistance training: 11.4% young, 47.0% old	Increased motor unit firing rates in the leg extensors of young and older adults, with the greatest increase in older adults (abstract only)

Note: EMG = electromyography; MVC = maximal voluntary contraction.

Table 2. Summary of Resistance Training Studies in Older Adults, Assessing the Use of Heavy or Light Training Loads and the Subsequent Transfer of Adaptations to the Performance of Functional Tasks

Source	Age (N)	Training	Strength/Performance Gain	Functional Outcome/Comments
Earles et al., 2000 (31)	77 \pm 5 y (6 males, 12 females) 78 \pm 5 y (7 males, 15 females)	12 weeks, 3 times per week, high velocity leg exercises, moderate-heavy loads, also a walking group moderate intensity 30 min daily 6 days per week	Power group: 23% increase in peak leg power; walking group 7% decrease; 22% and 12% respective increases in strength	Minimal improvement in functional performance for healthy older adults; improved walking performance in both groups; no change in chair-rise or single-leg stance for either group
Fielding et al., 2002 (255)	73 \pm 1 y (30 females)	16 weeks, 3 times per week, leg press and knee extension, 70% Max; high velocity group and a low velocity group, i.e., performed same training with either fast or slow contractions	Similar strength increases for high 35%, low 33%; power at all loads increased more in high velocity group; peak increase 84% greater than low for leg press, 34% greater for knee extension	No assessment of functional task performance and same training load used by both groups, but demonstrates a potential value of emphasizing rapid contractions in resistance training interventions
Miszko et al., 2003 (275)	72.5 \pm 6.3 y (39 males/females)	16 weeks, 3 times per week, first 8 weeks both training groups moderate-high intensity upper and lower body strength training performed slowly; 9–16 weeks, one group continued while another trained light (40% Max) and fast	Similar increase in maximal strength for power (13%) and strength training (23%) groups and max power, 12% and 7%, respectively	Power training more effective at improving whole-body physical function, but primarily through measures of balance and endurance, and not of lower and upper body strength
Vincent et al., 2002 (284)	60–83 y (62 males/females)	24 weeks, 3 times per week, dynamic upper and lower body resistance training: low intensity group at 50% Max, high intensity group at 80% Max	Total strength increase 17.2% for low and 17.8% for high, leg muscle endurance increase 79% low, 105% high, stair ascent 62.6% improvement low, 39.5% improvement high	Strength and functional performance may improve similarly by training with only light-moderate loads
Hortobagyi et al., 2001 (167)	66–83 y (30 males/females) 20–24 y (10 males/females)	10 weeks, 3 times per week, of leg press at either heavy: 80% Max (4–6 reps) or light: 40% Max (8–12 reps) loads	Strength increase: 35% heavy group, 33% light group; power: 20% heavy, 8% light; similar overall improvement in steadiness/accuracy of quadriceps force production	Training with heavy or light loads improved strength and the control of submaximal force similarly
Stavrinou et al., 2000 (294)	60–85 y (15 males/females)	8 weeks, 3 times per week, training upright row, shoulder press and chest press at either heavy 80% max or light 20% max loads	51% strength increase for heavy group, 9% increase for light group; shoulder joint range of motion only improved significantly for heavy group	Demonstrates that training with only very light loads may be insufficient for older adults to achieve certain functional improvements
Hunter et al., 2001 (286)	61–77 y (15 males, 15 females)	25 weeks, 3 times per week, resistance training for upper and lower body, heavy group each day at 80% Max, variable group 1 day 50%, 1 day 65%, 1 day 80% Max	Similar increase in strength for the heavy and variable training groups in knee extension, 24% and 28%, respectively	Variable resistance group experienced the greatest decrease in muscle activity while carrying a box; perhaps greater enhancement of submaximal performance by training that includes loads similar to functional tasks

unit discharge rates during maximum voluntary contractions (132), older weightlifters have been shown to retain higher maximal discharge rates than untrained elderly adults (245). In conjunction with the likelihood that there is incomplete activation of muscles by older adults (67), it seems probable that increases in strength following resistance training might be accompanied by additional motor unit recruitment or increased maximal motor unit discharge rates. In support of this contention, increased electromyographic activity has been observed in the agonist muscles of older adults following periods of resistance training (233,246,247). Yet, there are also indications that older adults do not necessarily exhibit higher maximal motor unit discharge rates following 6 weeks of resistance training (20) nor do they always achieve greater levels of muscular activation as a result of such training (17,19,24,248). Potentially, the failure of these latter studies to demonstrate notably increased levels of muscle activation subsequent to resistance training may be due to methodological considerations. These studies assessed the degree of muscle activation using only a single- or double-pulse twitch interpolation technique, whereas using more intense electrical stimulation may have revealed that training can increase activation levels, as has been shown in young adults (249). Furthermore, other measurement insensitivities with the twitch interpolation technique can mask any training-induced changes (113).

To reiterate, increased levels of muscle activation are achieved by increases in the firing rate of each motor unit and the recruitment of more motor units. Only two investigations with older adults have directly examined resistance training-induced changes in motor unit behavior during maximal effort contractions, and these have produced equivocal findings (20,250). Kamen and colleagues (250) reported in abstract form that maximal motor unit firing rate in the quadriceps muscle of older adults increased following an initial experimental session and continued to increase throughout 6 weeks of resistance training, with the extent of this increase exceeding that observed in young adults (47% in older adults compared with 11.4% in young adults). In contrast, in the Patten and colleagues (20) investigation, maximal motor unit discharge rate of the adductor digiti minimi increased for young adults but was not observed to increase for older adults following 6 weeks of strength training. However, for older adults, an increase in firing rate was observed after only 2 days of training, which returned to baseline levels by the end of the training period (20). The observation of an initial increase in maximal motor unit discharge rate in both studies suggests that older adults retain the capacity to increase firing rates and that this is not necessarily a limiting factor in the production of maximal force. The possibility is raised, therefore, that different neural strategies are adopted by older adults in adapting to resistance training. To explain the observed increase in strength in the absence of an increase in maximal motor unit discharge rate, it was suggested by Patten and colleagues (20) that training may have resulted in the recruitment of more motor units. In support of this possibility, a greater number of active motor units in the adductor digiti minimi of older adults were observed after 2 weeks of strength training (20). Investigations using muscle-

imaging techniques have revealed that a greater proportion of a muscle may be activated after strength training (236). Carroll and colleagues (40) produced evidence in a study of young adults that the entire population of motor units in a muscle were recruited at a lower torque level following resistance training. Patten and colleagues (20) suggested that an enhanced recruitment of motor units would permit an increase in maximal force without the need to drive motor units at excessively high discharge rates.

The findings of another experiment by Patten and Kamen (142), however, provide evidence that training induced alterations in motor unit discharge rates may be, to some extent, under the influence of strategy and may not be so readily equated to increased strength. When older adults were trained to modulate submaximal forces to match a template, there occurred an increase in maximal motor unit discharge rate. Yet, this was not accompanied by an increase in strength. Young adults, who were exposed to the same task, did not experience an increase in maximal motor unit discharge rates, but did display greater maximal force following 2 weeks of force control training. Expanding on the contrasting changes displayed by young and older adults, Patten (28) noted that the young adults were able to generalize the performance benefits across the modalities, as indicated by an increase in strength following training that involved only the control of submaximal forces (142), but exhibited neural adaptations that were specific to either the resistance training (20) or force control training routines (142). It was suggested that the adaptations to the two types of training may have been mediated by a process occurring at different levels of the neuraxis (Figure 4). Indeed, there exists experimental evidence that supports this contention (40,57). In contrast, the older adults displayed similar neural adaptations to the two types of training, but were less able to generalize the performance benefits. Strength training improved maximal force production, while force control training only enhanced force control and not strength. The disparity in the changes exhibited by young and older adults in these two experiments was taken to suggest that increased supraspinal influences mediate adaptations to either resistance or force control training in older adults (28). This suggestion by Patten (28) is consistent with the possibility that resistance training adaptations experienced by older adults may be considered akin to motor learning and, consequently, are likely to be less transferable across different movement contexts.

In an attempt to elucidate the neural origin of any change in the level of muscle activation that may be achieved by older adults, Scaglioni and colleagues (24) assessed the excitability of spinal reflex pathways prior to and following 16 weeks of resistance training. There was no modulation of the excitability of the Ia reflex arc, as indicated by the absence of a training-induced change in the ratio of the peak of the Hoffman reflex (H_{max}) to the maximum compound muscle action potential (M_{max}). Although possibly limited by the sensitivity of experimental techniques, the level of muscle activation also was not observed to increase as a consequence of resistance training. The absence of a training-induced increase in muscle activation or modulation of the reflex arc was considered to indicate that the total

inhibitory and excitatory effects that influence the α -motoneuron pool are seemingly not influenced by resistance training (24). In consideration also of the aforementioned possibility that increased supraspinal influences mediate resistance training adaptations in older adults, it is perhaps tempting to conclude that there is an attenuated plasticity of α -motoneuron pool excitability in older adults to change in response to resistance training. This may seem a quite plausible interpretation in light of recent findings that neural adaptations to resistance training in young adults appear to be attributable primarily to processes occurring within the spinal cord (40). Whereas, older adults display marked neural degeneration of this region (51,85) and potentially a reduced capacity to modulate spinal cord excitability (130). In the absence of training data from a group of young adults, the failure to assess the Hoffman reflex while the trained muscles were contracting, and, moreover, the inherent limitations of the use of the Hoffman reflex to assess training-induced alterations in α -motoneuron excitability (251), it is, however, premature to draw definitive conclusions. In a similar resistance training study conducted with young adults, a change in the Hmax to Mmax ratio was apparent, but only while the trained muscles were activated, and no change in excitability was observed at rest (252). It is apparent that older adults are able to achieve greater motor unit firing rates (20,250) and modulate motor unit recruitment thresholds (142) as an adaptation to training. There is still, however, only indirect evidence provided by increases in the surface electromyogram (246,247) that older adults experience an increase in the total neural drive to a muscle following resistance training. While there is reason to suppose that any such adaptations may be mediated predominantly by supraspinal centers (28), this has not yet been substantiated.

Adaptations in coordinating groups of muscles.—As with young adults, older adults also exhibit changes in the coordination of groups of muscles as a response to resistance training. These changes represent a significant aspect of the adaptations (235) to resistance training and are particularly important to the transfer of adaptation to functional movement tasks (38). It has been shown that the increased level of agonist–antagonist coactivation typically exhibited by older adults decreases following resistance training (9). Coactivation of antagonists during an isometric leg extension was unchanged in middle-aged men and women but decreased by 3% in older men and by 7% in older women following 6 months of resistance training. While this adaptation is known to occur in both young (234) and older adults (9), it is likely that the reduction in coactivation observed in older adults arises for different reasons than for younger people. For older adults, the decrease in coactivation probably occurs because of improvements in the steadiness of the force output of motor units (28) derived from resistance training (25,26,210). Thus, there is a reduced requirement for coactivation to stabilize the joint during contraction so as to enhance the steadiness of force production (141). A decrease in the level of agonist–antagonist coactivation, however, does not always accompany resistance training in older adults (246,253).

Training to Enhance the Rate of Force Development in Older Adults

In consideration of the notable power losses experienced by older adults, and the close association with functional task deficiencies, it has been advocated that resistance training routines for older adults should be tailored to emphasize the rate of force development (189). As it has been demonstrated that resistance training shifts the contractile properties of senile muscles towards slow-twitch characteristics, it is perhaps somewhat incongruous that improvements in the rate of force development have been achieved following such training. Although resistance training further increases the prevalence of slow-twitch fibers in the muscles of older adults, at the single-fiber level, the power and the contractile velocity of all fiber types have been found to increase after resistance training (22). Despite this, the increase in the proportion of slow-twitch fibers can be of such an extent that the rate at which force is produced by an electrically stimulated muscle may actually decrease after 12 to 24 weeks of resistance training (21,33). Nonetheless, substantial improvements in the rate of force development or muscle power are typically demonstrated by older adults following resistance training (9,31,254–257). To some extent, these gains are attributable to increases in muscle mass (257) and also to increases in tendon stiffness, which enhance the transmission of rapidly developed muscle force (258). It is frequently reported, however, that the magnitude of the increase in the rate of force development is greater than that which can be accounted for by muscle hypertrophy or connective tissue changes (9). Furthermore, such changes would also be expected to have influenced the rate of force development during electrically stimulated contractions. There must occur, therefore, adaptations in the neural activation of muscles, which negate any slowing of muscle contractile characteristics (246). Candidate mechanisms include more-rapid excitement of individual motor units, earlier recruitment of larger motor units, decreased co-contraction of antagonists, and improved coordination of synergists.

Young adults, in adapting to training that enhanced the rate of force development, demonstrated increased motor unit firing rates in the initial phase of muscle activation (<100 ms) and an increased occurrence of very high frequency (200 Hz) doublet discharges (136). There is indirect evidence that a similar adaptation occurs in elderly people, for whom it has been observed that an enhanced rate of force development following resistance training was accompanied by increases in the surface electromyogram in the initial 500 ms of muscle activation (9). Experiments with single motor unit recordings have demonstrated, however, that after 6 weeks of resistance training, older adults may not necessarily display an increase in peak motor unit firing rates (20). This experiment involved a *conventional resistance training* regime that did not emphasize the rate of force development. Potentially, an increase in motor unit firing rate is more likely to occur in response to training that is specifically designed to enhance the *rate of force development*. A study by Patten and colleagues (20) also showed that, after 2 days of the *conventional strength*

training, older adults exhibited a rise in the maximal motor unit discharge rate to approach that of young adults, and a similar increase was observed after a period of *force control exercises* (142). In addition, despite the slower nerve conduction velocity beyond the age of 60 years (89,259), high-frequency double discharges (>50 Hz) have still been recorded from older adults (159). These observations indicate that older adults retain the capacity to increase the rate of motor unit discharge in response to training and may still be capable of producing high firing rates. At the same time, a shift to the left in the force–frequency curve of senile muscle, as a result of resistance training (21), may permit a muscle to be activated at the same given rate at a lower frequency of motor unit discharge (3). Indeed, given the extent of slowing of muscle contractile characteristics in response to resistance training, an increase in the motor unit firing rate might, at first glance, appear to be redundant. It has been shown, however, that the *rate of force development* of a motor unit continues to increase with firing rates in excess of that which is required to achieve maximum tetanic tension (137,260). The production of supramaximal firing rates can therefore serve to increase the rate of force development, even when it does not elevate the maximal voluntary contraction force (261).

Hakkinen and colleagues (9) demonstrated substantial improvements in knee extension rapid force production by elderly men (21%) and women (22%) following 6 months of strength training, according to a protocol that incorporated explosive exercises tailored to improve the rapid production of force. The increase in the rate of force development was accompanied by an increase in the surface electromyogram recorded from agonists during the initial 500 ms of activation. This could indicate that there is more rapid motor unit firing or greater motor unit recruitment in the early stages of contraction. In young adults, improvements in the rate of force development have been attributed to increases in neural drive in the first 100 ms of muscle activation (136,261). It remains to be determined if older adults demonstrate an increase in neural drive in the initial phase of muscle activation as an adaptation to rate of force-development training.

In an earlier study that followed a conventional progressively increasing resistance training schedule without explosive exercises, no increase in the rate of force development was achieved by older men, while it did improve in young men (247). It was suggested that, to induce increases in muscle power in older adults, it is necessary to train specifically short duration rapid movements against moderate loads in the order of 50%–60% of maximum (9). Other investigators have, however, recorded increases in muscular power following traditional resistance training routines with loads of 80% of maximum and no emphasis on the speed of contraction (257). Increases in muscle mass were considered to be the primary contributor to the power gain in these circumstances, as no changes were observed in agonist electromyographic activity (257). In this instance, an increase in maximal force-producing ability may have been sufficient to result in a given level of force being achieved more rapidly after training (34).

Training strategies that emphasize the rate of force development typically incorporate rapid force-generating exercises performed against moderate loads, with the explicit intention of maximizing the power developed during training (9,189). Performing exercises against resistance loads in the region of 30%–70% of maximum ensures that contraction profiles are in the vicinity of the peak of the force–velocity curve (262). Attempting to contract as rapidly as possible appears to be of particular importance for training strategies designed to enhance the rate of force development, as this is necessary to invoke rapid motor unit activation (263,264). Emphasizing to older adults that they attempt to contract as rapidly as possible during training exercises has indeed been shown to maximize the improvement in the rate of force development (255). Training regimes that combine exercises performed rapidly at moderate loads with conventional heavy-load strength training have proven an effective means of delivering benefits to both maximal strength and the rate of force development (9,265). The adoption of this approach to training ensures that adaptations are achieved in both muscle hypertrophy and increases in tendon stiffness, in addition to improvements in muscle activation. While the strategies outlined in this paragraph may be implemented in tailoring resistance training routines to maximize the rate of force development in older adults, it is uncertain to what extent any enhancement of the rate of force development will transfer to improved performance of functional tasks.

Transfer to the Performance of Functional Tasks

The effectiveness with which resistance training adaptations are translated into improved performance of functional tasks by older adults remains to be clarified (266). While it has been demonstrated that improvements in balance, gait, and the performance of tasks such as rising from a chair may result from resistance training programs (10,27,32,176,267–269), it is also frequently the case that the training-induced adaptations do not transfer effectively beyond the training context (31,33–36,270–272). Two recent reviews have compiled detailed summaries of a multitude of resistance training studies conducted with older adults, all of which assessed the accompanying change in the performance of functional tasks (273,274). The considerable range of outcomes evident in these studies is likely to have arisen from differences in the training interventions, variations in the age, gender, and health of the participants, and the specific transfer tasks that were examined. Fundamentally, however, the extent to which resistance training will benefit the performance of everyday functional tasks is restricted by the specificity of resistance training adaptations, whereby an increase in strength is greatest for tasks that are most similar to the training exercise (235).

Accordant with the specificity of strength-training adaptations, it has been shown that when older adults train with heavy loads to increase maximal strength, the relative improvement in force production capabilities across a range of different velocities is greatest at slower velocities of contraction (37). By comparison, training with slightly lighter loads at faster speeds most effectively enhanced muscle power and resulted in relatively smaller gains in

maximal strength (31). Consequently, it has been suggested that it is important to determine if one mode is superior to another in improving the functional capabilities of older adults (31). Given the strong associations that exist between the ability of older adults to produce force rapidly and functional task performance, training to improve rapid force production would appear to be of critical importance to elderly people (189). One might anticipate, therefore, that a training routine that develops muscular power will deliver greater benefits to the performance of functional tasks than a traditional resistance training routine. Perhaps surprisingly, in one of only a few studies that has focused specifically on the development of muscular power, minimal improvements in the functional performance of older adults were observed (31). Improvements in walking and jumping performance have, however, been displayed by older adults following 24 weeks of training designed to increase muscle power that combined heavy resistance exercises and explosive strength training (18). Furthermore, in a recent study that compared conventional strength training and power-oriented training, greater improvements in several indices of balance and coordination were exhibited by the power-training group (275). In the same study, however, neither group exhibited any notable improvements for several other functional measures, including those measures for which there was an emphasis on the contribution of muscle strength. It appears that, even though the rate of force development is considered critical to movement control in older adults, improvement of muscle power with resistance training does not necessarily enhance functional capabilities. In order to evaluate the likelihood with which resistance training will benefit the performance of everyday tasks, we shall review exactly how the specific adaptations that are accrued through training may be expected to influence the performance of everyday tasks.

The benefits to the performance of everyday functional tasks that older adults may experience as a result of resistance training are contingent on: a) the strength and power demands of a particular functional task (178,179), b) the extent of improvements in strength derived via muscle hypertrophy and an increase in the specific tension of individual fibers, and c) the transfer of adaptations in both intramuscular and intermuscular coordination to the performance of functional movement tasks (38). As outlined earlier in the review, there are threshold levels of strength or power that are necessary to enable an older adult to efficiently complete a given functional task (179,183). Accordingly, the performance of more-intense physical tasks such as stair-climbing are more closely related to knee strength than less-intense tasks such as a short walk or a reaching movement (178). It follows that tasks that require supramaximal, maximal, or near-maximal efforts prior to training would be likely to benefit most from an increase in strength or power (183,274). A common observation in training studies with older adults is that the greatest improvements in functional task performance are experienced by participants who, at the outset, have the lowest levels of muscle strength (273,276,277). Nevertheless, the reduction in the physiological demands of performing a given task that is afforded by the development of strength

and power that exceeds threshold levels can serve to benefit the performance of a given task (33,181). Additionally, older adults exhibit notable deficits in functional abilities across a broad range of force levels (138,163,211,278,279), and even the performance of tasks at very low force levels has been shown to improve with resistance training (25,26). Although it was noted earlier that the respective increase in maximal strength or power may be quite specific to the particular load and velocity at which training is performed, resistance training adaptations are observed to transfer effectively to functional task performance at a range of force levels. However, in noting the high degree of specificity in many other aspects of resistance training outcomes, Brown and colleagues (33) recommended that training exercises prescribed for older adults should simulate as closely as possible the most common tasks of daily living. Task-specific resistance training techniques have been demonstrated to lead to improved performance by healthy older adults in a chair-rise task (267).

To the extent that improvements in strength and power are derived from increases in muscle mass and enhancement of the specific tension of individual fibers, it is likely that functional capabilities will be restored in a less-restricted manner than those increases in strength derived via certain neural mechanisms, in particular those neural adaptations that may be conceived of as motor learning. Still, while restoration of the quantity and quality of muscle mass is valuable to older adults, the manner in which muscles are activated during a particular movement dictates the effectiveness of transfer to a functional task. The degree to which resistance training adaptations transfer between a training movement and a particular functional task is influenced by the relative similarity in the posture (238), the contraction type (280,281), and the velocity (282) of the different movements. The limited transfer of resistance training adaptations is attributable to the neural adaptations that accompany such training (38,235). Specifically, the transfer of resistance training-induced adaptations to the performance of related movement tasks is contingent on the degree to which the muscle activation patterns consolidated by the particular training movements are similar to those engaged during the performance of related tasks (38). As discussed at the beginning of the review, the expression of resistance training adaptations in the coordination of individual muscles and groups of muscles can act to benefit or disturb the performance of a functional task. While, as described later in the review, the expression of training-induced changes in muscle activation patterns is determined by the location within the central nervous system of the specific sites that mediate the adaptations (38) (Figure 4).

To better understand the capacity of resistance training to restore movement control deficiencies in older adults, it is necessary to investigate further the mechanisms of neural adaptations that older adults experience with such training and to assess the expression of these adaptations during related movement tasks. Several investigations have focused on the decreased steadiness of force production exhibited with older age, which is associated with an increase in the variability of motor unit discharge rates (159). Keen and colleagues (25) demonstrated that the steadiness of

submaximal force production with the index finger was enhanced after 12 weeks of strengthening the first dorsal interosseus. In a follow-up to this experiment, Laidlaw and colleagues (26) observed improvements in the steadiness of a load-bearing movement task following a 4-week training period that were equivalent for a group that completed their training with heavy loads (80% maximum) and a group that completed training with light loads (10%). Kornatz and colleagues (210) recently reported in abstract form that the decrease in the variability of force produced by the index finger subsequent to training was indeed associated with a reduction in motor unit discharge variability. However, the reduction in discharge variability and the accompanying improvement in steadiness were achieved after an initial 2 weeks of training with minimal loads (10%); a subsequent 4-week period of resistance training at 70% of maximum did not result in any further improvement. For the knee extensor muscles, it also seems that it is unnecessary to train against progressively increasing loads to reduce the fluctuations in force production (5,35,167,283). These results suggest that the enhanced steadiness and the accompanying reduction in motor unit discharge variability may arise from improvements in coordination that arose from the regular execution of the training movement, rather than the strength increases incurred as a result of regular training against progressively increasing loads. If indeed most of the benefits that older adults derive from resistance training are essentially arising from motor learning that occurs through the regular performance of a training exercise, it is important to consider what benefits are actually gained by training with progressively increasing loads.

Training with progressively increasing loads versus training with minimal loads: resistance training or skill training.—Several studies have identified that older adults may achieve similar improvements in either functional task performance (26,284) or strength and power (167,284,285) by training with heavy loads or somewhat lighter loads. While a group of older adults achieved a 45% increase in strength following 12 months of resistance training at 80% of maximum, a 42% improvement was displayed by a group that trained with only 40% of maximum (285). After 10 weeks of leg-strengthening exercises performed at either 80% or 40% of maximum, a group of older men and women exhibited similar improvements in muscle strength and power, as well as the control of submaximal force (167). Six months of resistance training at either 80% or 50% of maximum also led to similar gains in strength (17.2% vs 17.8%), while only the light-load group significantly improved stair-climbing performance (284). The low-load resistance training groups in each of these studies did, however, perform additional repetitions of the training exercises. Still, if it is possible to achieve equivalent benefits to movement control by training with only light loads, there are several advantages in doing so. Training with only light loads is likely to be better tolerated by older adults (167,286), and it should reduce the occurrence of injuries during training or minimize the aggravation of preexisting ailments that are so prevalent in this population (287,288).

Training with minimal loads has been shown to benefit other functional activities performed by older adults. For example, 8 weeks of Tai Chi exercise improved the accuracy and steadiness of arm movements (30). Balance-training interventions have been shown to enhance the movement control of older adults in various tasks (289), as has walking (269) and a skillful object-manipulation task (29). There are certainly merits to these various training regimes, and, when included as an adjunct to resistance training interventions, they have proved to be very effective means of restoring or maintaining function (270,290,291). There are, however, some important benefits for older adults that may only be achieved by progressive resistance exercise performed at high intensities (11). The use of progressively increasing loads are critical to achieve increases in muscle mass (70) and to derive other important benefits such as improved bone mineral density (292) and a reduced susceptibility to eccentric exercise-induced muscle damage (293). Furthermore, while there are instances in which quite similar gains in strength have been reported after training with either heavy or light loads, typically the strength gain from training with light or moderate loads is less than that achieved by training at high intensities (80% of maximum) (11,12,274). Training at high intensities is also likely to be important when seeking to improve the performance of many functional tasks. For instance, a group of adults aged 60 years and older experienced improved shoulder joint function after 8 weeks of resistance training at 80% of maximum, while a group that trained only at 20% of maximum did not derive this benefit (294).

The degree of similarity in the improvements that can be exhibited by older adults, when training with light or heavy loads, suggests that, in this group, there may be relatively minor distinctions in the mechanisms of adaptation to simple skill training or to training with progressively increasing loads. In young adults, it has been demonstrated that the neural adaptations that transpire when a movement is performed regularly against progressively increasing loads are distinct from the adaptations that would arise if the movement were performed against minimal loads (40,57). Progressive resistance training results in neural adaptations mediated at the spinal cord level (40,58), while improvements in skilled movement production are predominantly associated with supraspinal changes (57). Thus far, no evidence has been produced that older adults exhibit specific neural adaptations when they perform progressive resistance training that could not similarly be achieved by training against comparatively minimal loads. A decrease in motor unit discharge variability may arise from resistance training, but this can be achieved equally well by training with only light loads (26,210). Increases in maximal motor unit firing rates, alterations in motor unit recruitment thresholds, and reductions in agonist-antagonist coactivation have also been observed to arise from force control training at loads reaching only 60% of maximum (142).

The studies by Patten and colleagues discussed in a previous section of this review provide some evidence to suggest that older adults may be distinguished from young adults in the sites of resistance training adaptations. While this possibility was inferred from a remarkable

similarity in adaptations to progressive resistance or force-control training in older adults, it was also important to note that the older adults were less able than young adults to transfer the training benefits across different tasks (61). Therefore, not only does the possibility exist that young and older adults may be distinguished in the mechanisms of neural adaptations experienced in response to resistance training, but this may confer a lesser ability for older adults to transfer these adaptations across different task contexts. The resistance training adaptations experienced by older adults may be practically indistinguishable from those adaptations derived from the motor learning that occurs through the regular rehearsal of a particular movement pattern, regardless of the training load (57). Apart from the adaptations in the recruitment properties of spinal motoneurons, which may be expected to enhance muscle activation across a broad range of movements, the neural adaptations that older adults derive from training with progressively increasing loads may be quite limited in their capacity to enhance the execution of movements that are different from the particular training exercise. Resistance training, by nature, involves the repetitive performance of only a small subset of movements, which, considered in the context of motor learning, are unlikely to promote effective transfer of adaptations. It is therefore necessary to develop an understanding of the adaptations older adults experience in response to resistance training in terms of the patterns of muscle coordination that arise through training against progressively increasing loads, and the manner by which these adaptations influence movements different to the training exercise.

A recent investigation of eccentric resistance training adaptations in older adults has produced promising findings, with demonstrated improvements in both strength and muscle mass, as well as enhanced performance of functional tasks (295,296). This particular mode of exercise has the advantage of permitting greater levels of muscle overload to be achieved than when performing concentric actions, potentially resulting in enhanced gains in strength and muscle hypertrophy (296). Eccentric training also enables higher levels of muscle force to be generated with reduced energetic demands (296). Furthermore, older adults have been observed to exhibit particular difficulties in producing eccentric force (159,297), which may itself warrant training in this mode. It is important to note, however, that the central nervous system employs unique activation strategies when generating eccentric force (298,299). It is to be anticipated, therefore, that the neural adaptations experienced through training in this modality may be limited in the transfer to functional tasks completed concentrically or isometrically. This is an important avenue of investigation to evaluate eccentric resistance training interventions for older adults. In this regard, it is interesting that in an investigation by LaStayo and colleagues (295), the eccentric training group exhibited greater improvements than the traditional training group in not only a stair-descent task but also in a "timed up-and-go" test. Substantial differences, however, in the training intervention for these groups beyond simply the mode of contraction somewhat limits the comparisons that may be made in terms of the transfer of training adaptations.

CONCLUSION

Progressive degeneration of strength and power is an intrinsic part of the aging process, attributable in varying proportions to natural decline, decreased activity levels, and pathological conditions (300). At a physiological level, muscular atrophy, a relative decrease in fast-twitch muscle fibers, a decrement in the specific tension of muscle fibers, and neural degeneration are responsible for the decline in muscular strength and power. The observed behavioral outcomes are decreases in maximal force production and, to an even larger extent, decreases in the rapid development of force. In addition, there is impairment of the ability to produce force steadily, and also to produce force that is accurately matched to the requirements of a given movement task. Degeneration of these capacities gives rise to notable deficiencies in many of the motor acts that older adults perform in the course of everyday living. These declines in the neuromuscular system have motivated the prescription of resistance training routines for older adults with the intent of restoring muscular strength and consequently improving the performance of functional tasks. The exaggerated declines in muscle power seen in elderly people and the close association of this capacity with functional task capabilities have highlighted the importance of developing training strategies that are tailored to enhance the rate of force development.

Resistance training is highly effective in improving both strength and power in older adults, and these gains are accompanied by increases in muscle mass and the specific tension of individual muscle fibers. As with young adults, older adults experience significant neural adaptations to resistance training that influence the activation of individual muscles and the coordination of groups of muscles. The loss of muscle mass with progressing age ultimately limits the benefits from resistance training that may be achieved by muscle hypertrophy. Consequently, neural adaptations are the primary means by which strength and power are enhanced. While improvements in functional task performance have been observed in older adults following periods of resistance training, it is frequently the case that training-induced adaptations do not transfer effectively beyond the training exercises. Clearly, the transfer of adaptations in intermuscular and intramuscular coordination are crucial in mediating the desired improvements in the performance of functional tasks.

Progressive degradation of the neuromuscular system, in particular degeneration of spinal motoneurons, the loss of corticospinal fibers, and cerebellar degeneration, will alter the nature of the neural adaptations that older adults exhibit in response to resistance training. These factors will, in turn, influence the readiness with which training adaptations lead to improved performance in everyday movement tasks. An understanding of the principles that govern the transfer of adaptations beyond the training context is therefore critical in seeking to optimize the prescription of training regimes for the maintenance and improvement of functional movement capacities in older adults. The similarity of adaptations that is, on occasion, displayed by older adults when training with progressively increasing loads or only with minimal loads does suggest that there may be a limitation in elderly

individuals on some aspects of neural plasticity that are known to be exploited by young adults who partake in resistance training. If it is indeed the case that the neural adaptations exhibited by older adults in response to resistance training are more akin to motor learning, in so much as they are mediated to a greater degree by supraspinal changes, it might be expected that a more restricted transfer to functional movement tasks will be conferred in elderly people.

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REFERENCES

- Larsson L, Grimby G, Karlsson J. Muscle strength and speed of movement in relation to age and muscle morphology. *J Appl Physiol*. 1979;46:451–456.
- Lexell J, Taylor CC, Sjostrom M. What is the cause of the ageing atrophy? Total number, size and proportion of different fiber types studied in whole vastus lateralis muscle from 15- to 83-year-old men. *J Neurol Sci*. 1988;84:275–294.
- Narici MV, Bordini M, Cerretelli P. Effect of aging on human adductor pollicis muscle function. *J Appl Physiol*. 1991;71:1277–1281.
- Doherty TJ, Vandervoort AA, Taylor AW, Brown WF. Effects of motor unit losses on strength in older men and women. *J Appl Physiol*. 1993;74:868–874.
- Enoka RM, Christou EA, Hunter SK, et al. Mechanisms that contribute to differences in motor performance between young and old adults. *J Electromyogr Kinesiol*. 2003;13:1–12.
- Metter EJ, Conwit R, Tobin J, Fozard JL. Age-associated loss of power and strength in the upper extremities in women and men. *J Gerontol Biol Sci*. 1997;52A:B267–B276.
- Grabiner MD, Enoka RM. Changes in movement capabilities with aging. *Exerc Sport Sci Rev*. 1995;23:65–104.
- Vandervoort AA. Aging of the human neuromuscular system. *Muscle Nerve*. 2002;25:17–25.
- Hakkinen K, Kallinen M, Izquierdo M, et al. Changes in agonist-antagonist EMG, muscle CSA, and force during strength training in middle-aged and older people. *J Appl Physiol*. 1998;84:1341–1349.
- Fiatarone MA, Marks EC, Ryan ND, Meredith CN, Lipsitz LA, Evans WJ. High-intensity strength training in nonagenarians. Effects on skeletal muscle. *JAMA*. 1990;263:3029–3034.
- Fiatarone-Singh MA. Exercise comes of age: Rationale and recommendations for a geriatric exercise prescription. *J Gerontol Med Sci*. 2002;57A:M262–M282.
- Fiatarone MA, Evans WJ. The etiology and reversibility of muscle dysfunction in the aged. *J Gerontol*. 1993;48(Spec Iss):77–83.
- Bortz WM II. A conceptual framework of frailty: a review. *J Gerontol Med Sci*. 2002;57A:M283–M288.
- Lipsitz LA. Dynamics of stability: the physiologic basis of functional health and frailty. *J Gerontol Biol Sci*. 2002;57A:B115–B125.
- Morley JE, Perry HM, Miller DK. Something about frailty. *J Gerontol Med Sci*. 2002;57A:M698–M704.
- Hakkinen K, Pakarinen A, Newton RU, Kraemer WJ. Acute hormone responses to heavy resistance lower and upper extremity exercise in young versus old men. *Eur J Appl Physiol Occup Physiol*. 1998;77:312–319.
- Harridge SD, Kryger A, Stensgaard A. Knee extensor strength, activation, and size in very elderly people following strength training. *Muscle Nerve*. 1999;22:831–839.
- Hakkinen K, Alen M, Kallinen M, Newton RU, Kraemer WJ. Neuromuscular adaptation during prolonged strength training, detraining and re-strength-training in middle-aged and elderly people. *Eur J Appl Physiol*. 2000;83:51–62.
- Knight CA, Kamen G. Adaptations in muscular activation of the knee extensor muscles with strength training in young and older adults. *J Electromyogr Kinesiol*. 2001;11:405–412.
- Patten CT, Kamen G, Rowland DM. Adaptations in maximal motor unit discharge rate to strength training in young and older adults. *Muscle Nerve*. 2001;24:542–550.
- Rice CL, Cunningham DA, Paterson DH, Dickinson JR. Strength training alters contractile properties of the triceps brachii in men aged 65–78 years. *Eur J Appl Physiol Occup Physiol*. 1993;66:275–280.
- Trappe S, Williamson D, Godard M, Porter D, Rowden G, Costill D. Effect of resistance training on single muscle fiber contractile function in older men. *J Appl Physiol*. 2000;89:143–152.
- Hunter SK, Thompson MW, Ruell PA, et al. Human skeletal sarcoplasmic reticulum Ca²⁺ uptake and muscle function with aging and strength training. *J Appl Physiol*. 1999;86:1858–1865.
- Scaglioni G, Ferri A, Minetti AE, et al. Plantar flexor activation capacity and H reflex in older adults: adaptations to strength training. *J Appl Physiol*. 2002;92:2292–2302.
- Keen DA, Yue GH, Enoka RM. Training-related enhancement in the control of motor output in elderly humans. *J Appl Physiol*. 1994;77:2648–2658.
- Laidlaw DH, Kornatz KW, Keen DA, Suzuki S, Enoka RM. Strength training improves the steadiness of slow lengthening contractions performed by old adults. *J Appl Physiol*. 1999;87:1786–1795.
- Taaffe DR, Duret C, Wheeler S, Marcus R. Once-weekly resistance exercise improves muscle strength and neuromuscular performance in older adults. *J Am Geriatr Soc*. 1999;47:1208–1214.
- Patten CT. Reeducating muscle force control in older persons through strength training. *Top Geriatric Rehabil*. 2000;15:47–59.
- Ranganathan VK, Siemionow V, Sahgal V, Liu JZ, Yue GH. Skilled finger movement exercise improves hand function. *J Gerontol Med Sci*. 2001;56A:M518–M522.
- Yan JH. Tai chi practice reduces movement force variability for seniors. *J Gerontol Med Sci*. 1999;54A:M629–M634.
- Earles DR, Judge JO, Gunnarsson OT. Velocity training induces power-specific adaptations in highly functioning older adults. *Arch Phys Med Rehabil*. 2001;82:872–878.
- Judge JO, Lindsey C, Underwood M, Winsemius D. Balance improvements in older women: effects of exercise training. *Physical Ther*. 1993;73:254–262.
- Brown AB, McCartney N, Sale DG. Positive adaptations to weight-lifting training in the elderly. *J Appl Physiol*. 1990;69:1725–1733.
- Porter MM, Vandervoort AA. Standing strength training of the ankle plantar and dorsiflexors in older women, using concentric and eccentric contractions. *Eur J Appl Physiol Occup Physiol*. 1997;76:62–68.
- Bellew JW. The effect of strength training on control of force in older men and women. *Aging Clin Exp Res*. 2002;14:35–41.
- Schlicht J, Camaione DN, Owen SV. Effect of intense strength training on standing balance, walking speed, and sit-to-stand performance in older adults. *J Gerontol Med Sci*. 2001;56A:M281–M286.
- Frontera WR, Meredith CN, O'Reilly KP, Knuttgen HG, Evans WJ. Strength conditioning in older men: skeletal muscle hypertrophy and improved function. *J Appl Physiol*. 1988;64:1038–1044.
- Carroll TJ, Riek S, Carson RG. Neural adaptations to resistance training: implications for movement control. *Sports Med*. 2001;31:829–840.
- Carroll TJ, Barry B, Riek S, Carson RG. Resistance training enhances the stability of sensorimotor coordination. *Proc R Soc Lond B Biol Sci*. 2001;268:221–227.
- Carroll TJ, Riek S, Carson RG. The sites of neural adaptation induced by resistance training in humans. *J Physiol*. 2002;544:641–652.
- Carson RG, Riek S. The influence of joint position on the dynamics of perception-action coupling. *Exp Brain Res*. 1998;121:103–114.
- Carson RG. Neuromuscular-skeletal constraints upon the dynamics of perception-action coupling. *Exp Brain Res*. 1996;110:99–110.
- Shinohara M, Li S, Kang N, Zatsiorsky VM, Latash ML. Effects of age and gender on finger coordination during force production tasks. *J Appl Physiol*. 2002;94:259–270.

44. Zatsiorsky VM, Li ZM, Latash ML. Enslaving effects in multi-finger force production. *Exp Brain Res*. 2000;131:187–195.
45. Baratta R, Solomonow M, Zhou BH, Letson D, Chuinard R, D'Ambrosia R. Muscular coactivation. The role of the antagonist musculature in maintaining knee stability. *Am J Sports Med*. 1988;16:113–122.
46. Milner-Brown HS, Stein RB, Lee RG. Synchronization of human motor units: possible roles of exercise and supraspinal reflexes. *Electroencephalogr Clin Neurophysiol*. 1975;38:245–254.
47. Semmler JG, Nordstrom MA. Motor unit discharge and force tremor in skill- and strength-trained individuals. *Exp Brain Res*. 1998;119:27–38.
48. Yao W, Fuglevand RJ, Enoka RM. Motor-unit synchronization increases emg amplitude and decreases force steadiness of simulated contractions. *J Neurophysiol*. 2000;83:441–452.
49. Erim Z, Beg MF, Burke DT, de Luca CJ. Effects of aging on motor-unit control properties. *J Neurophysiol*. 1999;82:2081–2091.
50. Roos MR, Rice CL, Vandervoort AA. Age-related changes in motor unit function. *Muscle Nerve*. 1997;20:679–690.
51. Tomlinson BE, Irving D. The numbers of limb motor neurons in the human lumbosacral cord throughout life. *J Neurol Sci*. 1977;34:213–219.
52. Eisen A, Entezari-Taher M, Stewart H. Cortical projections to spinal motoneurons: changes with aging and amyotrophic lateral sclerosis. *Neurology*. 1996;46:1396–1404.
53. Earles DR, Kocaja DM, Shively CW. Environmental changes in soleus h-reflex excitability in young and elderly subjects. *Int J Neurosci*. 2000;105:1–13.
54. Kamen G, Kocaja DM. Contralateral influences on patellar tendon reflexes in young and old adults. *Neurobiol Aging*. 1989;10:311–315.
55. Sjöbeck M, Dahlen S, Englund E. Neuronal loss in the brainstem and cerebellum—part of the normal aging process? A morphometric study of the vermis cerebelli and inferior olivary nucleus. *J Gerontol Biol Sci*. 1999;54A:B363–B368.
56. Rossini PM, Desiato MT, Caramia MD. Age-related changes of motor evoked potentials in healthy humans: non-invasive evaluation of central and peripheral motor tracts excitability and conductivity. *Brain Res*. 1992;593:14–19.
57. Remple MS, Bruneau RM, VandenBerg PM, Goertzen C, Kleim JA. Sensitivity of cortical movement representations to motor experience: evidence that skill learning but not strength training induces cortical reorganization. *Behav Brain Res*. 2001;123:133–141.
58. VandenBerg P, Bruneau R, Remple M, Soroka N, Cooper N, Kleim JA. Strength vs skill: differential patterns of plasticity within the rat motor system. *Soc Neurosci Abstr*. 2001;27:931.3.
59. Izquierdo M, Ibanez J, Gorostiaga E, et al. Maximal strength and power characteristics in isometric and dynamic actions of the upper and lower extremities in middle-aged and older men. *Acta Physiol Scand*. 1999;167:57–68.
60. Hakkinen K, Hakkinen A. Muscle cross-sectional area, force production and relaxation characteristics in women at different ages. *Eur J Appl Physiol Occup Physiol*. 1991;62:410–414.
61. Patten CT, Craik RL. Sensorimotor changes and adaptation in the older adult. In: AA Guccione, ed. *Geriatric Physical Therapy*. 2nd Ed. St. Louis: Mosby; 2000:78–109.
62. Janssen I, Heymsfield SB, Wang ZM, Ross R. Skeletal muscle mass and distribution in 468 men and women aged 18–88 yr. *J Appl Physiol*. 2000;89:81–88.
63. Frontera WR, Hughes VA, Fielding RA, Fiatarone MA, Evans WJ, Roubenoff R. Aging of skeletal muscle: a 12-yr longitudinal study. *J Appl Physiol*. 2000;88:1321–1326.
64. Hughes VA, Frontera WR, Wood M, et al. Longitudinal muscle strength changes in older adults: influence of muscle mass, physical activity, and health. *J Gerontol Biol Sci*. 2001;56A:B209–B217.
65. Lynch NA, Metter EJ, Lindle RS, et al. Muscle quality. I. Age-associated differences between arm and leg muscle groups. *J Appl Physiol*. 1999;86:188–194.
66. Larsson L, Li X, Frontera WR. Effects of aging on shortening velocity and myosin isoform composition in single human skeletal muscle cells. *Am J Physiol*. 1997;272:C638–C649.
67. Stevens JE, Stackhouse SK, Binder-Macleod SA, Snyder-Mackler L. Are voluntary muscle activation deficits in older adults meaningful? *Muscle Nerve*. 2003;27:99–101.
68. Klein CS, Rice CL, Marsh GD. Normalized force, activation, and coactivation in the arm muscles of young and old men. *J Appl Physiol*. 2001;91:1341–1349.
69. Macaluso A, Nimmo MA, Foster JE, Cockburn M, McMillan NC, De Vito G. Contractile muscle volume and agonist-antagonist coactivation account for differences in torque between young and older women. *Muscle Nerve*. 2002;25:858–863.
70. Lexell J. Human aging, muscle mass, and fiber type composition. *J Gerontol A Biol Sci Med Sci*. 1995;50(Spec Iss):11–16.
71. Hook P, Sriramoju V, Larsson L. Effects of aging on actin sliding speed on myosin from single skeletal muscle cells of mice, rats, and humans. *Am J Physiol Cell Physiol*. 2001;280:C782–C788.
72. Plant DR, Lynch GS. Excitation-contraction coupling and sarcoplasmic reticulum function in mechanically skinned fibres from fast skeletal muscles of aged mice. *J Physiol*. 2002;543:169–176.
73. Akima H, Kano Y, Enomoto Y, et al. Muscle function in 164 men and women aged 20–84 yr. *Med Sci Sports Exerc*. 2001;33:220–226.
74. Kallman DA, Plato CC, Tobin JD. The role of muscle loss in the age-related decline of grip strength: cross-sectional and longitudinal perspectives. *J Gerontol*. 1990;45:M82–M88.
75. Larsson L, Ansved T. Effects of ageing on the motor unit. *Prog Neurobiol*. 1995;45:397–458.
76. McComas AJ. Motor unit estimation: Anxieties and achievements. *Muscle Nerve*. 1995;18:369–379.
77. Brown WF, Strong MJ, Snow R. Methods for estimating numbers of motor units in biceps-brachialis muscles and losses of motor units with aging. *Muscle Nerve*. 1988;11:423–432.
78. Doherty TJ, Brown WF. The estimated numbers and relative sizes of thenar motor units as selected by multiple point stimulation in young and older adults. *Muscle Nerve*. 1993;16:355–366.
79. Andersen JL. Muscle fibre type adaptation in the elderly human muscle. *Scand J Med Sci Sports*. 2003;13:40–47.
80. Larsson L, Sjödin B, Karlsson J. Histochemical and biochemical changes in human skeletal muscle with age in sedentary males, age 22–65 years. *Acta Physiol Scand*. 1978;103:31–39.
81. Klitgaard H, Mantoni M, Schiaffino S, et al. Function, morphology and protein expression of ageing skeletal muscle: a cross-sectional study of elderly men with different training backgrounds. *Acta Physiol Scand*. 1990;140:41–54.
82. Aagaard P, Andersen JL. Correlation between contractile strength and myosin heavy chain isoform composition in human skeletal muscle. *Med Sci Sports Exerc*. 1998;30:1217–1222.
83. Gur H, Gransberg L, VanDyke D, Knutsson E, Larsson L. Relationship between in vivo muscle force at different speeds of isokinetic movements and myosin isoform expression in men and women. *Eur J Appl Physiol*. 2003;88:487–496.
84. Grimby G, Aniansson A, Zetterberg C, Saltin, B. Is there a change in relative muscle fibre composition with age? *Clin Physiol*. 1984;4:189–194.
85. Kawamura Y, O'Brien P, Okazaki H, Dyck PJ. Lumbar motoneurons of man ii: the number and diameter distribution of large- and intermediate-diameter cytons in “motoneuron columns” of spinal cord of man. *J Neuropathol Exp Neurol*. 1977;36:861–870.
86. Kawamura Y, Okazaki H, O'Brien PC, Dyck PJ. Lumbar motoneurons of man: I) number and diameter histogram of alpha and gamma axons of ventral root. *J Neuropathol Exp Neurol*. 1977;36:853–860.
87. Mittal KR, Logmani FH. Age-related reduction in 8th cervical ventral nerve root myelinated fiber diameters and numbers in man. *J Gerontol*. 1987;42:8–10.
88. Kadhiresan VA, Hassett CA, Faulkner JA. Properties of single motor units in medial gastrocnemius muscles of adult and old rats. *J Physiol*. 1996;493(Pt 2):543–552.
89. Wang FC, de Pasqua V, Delwaide PJ. Age-related changes in fastest and slowest conducting axons of thenar motor units. *Muscle Nerve*. 1999;22:1022–1029.
90. Klitgaard H, Zhou M, Schiaffino S, Betto R, Salvati G, Saltin B. Ageing alters the myosin heavy chain composition of single fibres from human skeletal muscle. *Acta Physiol Scand*. 1990;140:55–62.
91. Andersen JL, Terzis G, Kryger A. Increase in the degree of co-expression of myosin heavy chain isoforms in skeletal muscle fibers of the very old. *Muscle Nerve*. 1999;22:449–454.

92. Winegard KJ, Hicks AL, Sale DG, Vandervoort AA. A 12-year follow-up study of ankle muscle function in older adults. *J Gerontol Biol Sci.* 1996;51A:B202–B207.
93. Frontera WR, Suh D, Krivickas LS, Hughes VA, Goldstein R, Roubenoff R. Skeletal muscle fiber quality in older men and women. *Am J Physiol Cell Physiol.* 2000;279:C611–C618.
94. Lowe DA, Surek JT, Thomas DD, Thompson LV. Electron paramagnetic resonance reveals age-related myosin structural changes in rat skeletal muscle fibers. *Am J Physiol Cell Physiol.* 2001;280:C540–C547.
95. Larsson L, Li X, Yu F, Degens H. Age-related changes in contractile properties and expression of myosin isoforms in single skeletal muscle cells. *Muscle Nerve Suppl.* 1997;5:S74–S78.
96. Bruce SA, Newton D, Woledge RC. Effect of age on voluntary force and cross-sectional area of human adductor pollicis muscle. *Q J Exp Physiol.* 1989;74:359–362.
97. Brooks SV, Faulkner JA. Skeletal muscle weakness in old age: underlying mechanisms. *Med Sci Sports Exerc.* 1994;26:432–439.
98. Kent-Braun JA, Ng AV, Young K. Skeletal muscle contractile and noncontractile components in young and older women and men. *J Appl Physiol.* 2000;88:662–668.
99. Kent-Braun JA, Ng AV. Specific strength and voluntary muscle activation in young and elderly women and men. *J Appl Physiol.* 1999;87:22–29.
100. Goodpaster BH, Carlson CL, Visser M, et al. Attenuation of skeletal muscle and strength in the elderly: the health ABC study. *J Appl Physiol.* 2001;90:2157–2165.
101. Urbanchek MG, Picken EB, Kalliainen LK, Kuzon WM Jr. Specific force deficit in skeletal muscles of old rats is partially explained by the existence of denervated muscle fibers. *J Gerontol Biol Sci.* 2001;56A:B191–B197.
102. Kalliainen LK, Jejuriar SS, Liang LW, Urbanchek MG, Kuzon WM Jr. A specific force deficit exists in skeletal muscle after partial denervation. *Muscle Nerve.* 2002;25:31–38.
103. Klitgaard H, Ausoni S, Damiani E. Sarcoplasmic reticulum of human skeletal muscle: age-related changes and effect of training. *Acta Physiol Scand.* 1989;137:23–31.
104. Trappe SW, Gallagher P, Harber M, Carrithers J, Fluckey J, Trappe T. Single muscle fibre contractile properties in young and old men and women. *J Physiol (Lond).* 2003;552:47–58.
105. De Serres SJ, Enoka RM. Older adults can maximally activate the biceps brachii muscle by voluntary command. *J Appl Physiol.* 1998;84:284–291.
106. Roos MR, Rice CL, Connelly DM, Vandervoort AA. Quadriceps muscle strength, contractile properties, and motor unit firing rates in young and old men. *Muscle Nerve.* 1999;22:1094–1103.
107. Vandervoort AA, McComas AJ. Contractile changes in opposing muscles of the human ankle joint with aging. *J Appl Physiol.* 1986;61:361–367.
108. Phillips SK, Bruce SA, Newton D, Woledge RC. The weakness of old age is not due to failure of muscle activation. *J Gerontol.* 1992;47:M45–M49.
109. Merton PA. Voluntary strength and fatigue. *J Physiol.* 1954;123:553–564.
110. Kent-Braun JA, Le Blanc R. Quantitation of central activation failure during maximal voluntary contractions in humans. *Muscle Nerve.* 1996;19:861–869.
111. Connelly DM, Rice CL, Roos MR, Vandervoort AA. Motor unit firing rates and contractile properties in tibialis anterior of young and old men. *J Appl Physiol.* 1999;87:843–852.
112. Allen GM, McKenzie DK, Gandevia SC. Twitch interpolation of the elbow flexor muscles at high forces. *Muscle Nerve.* 1998;21:318–328.
113. Gandevia SC. Spinal and supraspinal factors in human muscle fatigue. *Physiol Rev.* 2001;81:1725–1789.
114. Dowling JJ, Konert E, Ljucovic P, Andrews DM. Are humans able to voluntarily elicit maximum muscle force? *Neurosci Lett.* 1994;179:25–28.
115. Yue GH, Ranganathan VK, Siemionow V, Liu JZ, Sahgal V. Older adults exhibit a reduced ability to fully activate their biceps brachii muscle. *J Gerontol Med Sci.* 1999;54A:M249–M253.
116. Stackhouse SK, Stevens JE, Johnson CD, Snyder-Mackler L, Binder-Macleod SA. Predictability of maximum voluntary isometric knee extension force from submaximal contractions in older adults. *Muscle Nerve.* 2003;27:40–45.
117. Gandevia SC, Allen GM, Butler JE, Taylor JL. Supraspinal factors in human muscle fatigue: evidence for suboptimal output from the motor cortex. *J Physiol.* 1996;490(Pt 2):529–536.
118. Pierrot-Deseilligny E. Propriospinal transmission of part of the corticospinal excitation in humans. *Muscle Nerve.* 2002;26:155–172.
119. deVries HA, Wiswell RA, Romero GT, Heckathorne E. Changes with age in monosynaptic reflexes elicited by mechanical and electrical stimulation. *Am J Phys Med.* 1985;64:71–81.
120. Vandervoort AA, Hayes KC. Plantarflexor muscle function in young and elderly women. *Eur J Appl Physiol Occup Physiol.* 1989;58:389–394.
121. Balice-Gordon RJ. Age-related changes in neuromuscular innervation. *Muscle Nerve Suppl.* 1997;5:S83–S87.
122. Brown M, Hasser EM. Complexity of age-related change in skeletal muscle. *J Gerontol Biol Sci.* 1996;51A:B117–B123.
123. Pitcher JB, Ogston KM, Miles TS. Age and sex differences in human motor cortex input-output characteristics. *J Physiol (Lond).* 2003;546:605–613.
124. Wolpaw JR, Tennissen AM. Activity-dependent spinal cord plasticity in health and disease. *Annu Rev Neurosci.* 2001;24:807–843.
125. Macefield VG, Gandevia SC, Bigland-Ritchie B, Gorman RB, Burke D. The firing rates of human motoneurons voluntarily activated in the absence of muscle afferent feedback. *J Physiol.* 1993;471:429–443.
126. Corden DM, Lippold OC. Age-related impaired reflex sensitivity in a human hand muscle. *J Neurophysiol.* 1996;76:2701–2706.
127. Thelen DG, Brockmiller C, Ashton-Miller JA, Schultz AB, Alexander NB. Thresholds for sensing foot dorsi- and plantarflexion during upright stance: effects of age and velocity. *J Gerontol Med Sci.* 1998;53A:M33–M38.
128. Cole KJ, Rotella DL, Harper JG. Mechanisms for age-related changes of fingertip forces during precision gripping and lifting in adults. *J Neurosci.* 1999;19:3238–3247.
129. Angulo-Kinzler RM, Mynark RG, Kocaja DM. Soleus h-reflex gain in elderly and young adults: modulation due to body position. *J Gerontol Med Sci.* 1998;53A:M120–M125.
130. Earles DR, Vardaxis V, Kocaja D. Regulation of motor output between young and elderly subjects. *Clin Neurophysiol.* 2001;112:1273–1279.
131. Jakobi JM, Rice CL. Voluntary muscle activation varies with age and muscle group. *J Appl Physiol.* 2002;93:457–462.
132. Kamen G, Sison SV, Du CC, Patten C. Motor unit discharge behavior in older adults during maximal-effort contractions. *J Appl Physiol.* 1995;79:1908–1913.
133. White MJ, Harridge SDR. At high angular velocities voluntary activation limits maximal isokinetic torque generation in elderly and young human triceps surae. *J Physiol.* 1990;429:52P.
134. Thelen DG, Ashton-Miller JA, Schultz AB, Alexander NB. Do neural factors underlie age differences in rapid ankle torque development? *J Am Geriatr Soc.* 1996;44:804–808.
135. Clarkson PM, Kroll W, Melchionda AM. Age, isometric strength, rate of tension development and fiber type composition. *J Gerontol.* 1981;36:648–653.
136. Van Cutsem M, Duchateau J, Hainaut K. Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. *J Physiol.* 1998;513(Pt 1):295–305.
137. Nelson AG. Supramaximal activation increases motor unit velocity of unloaded shortening. *J Appl Biomech.* 1996;12:285–291.
138. Spiegel KM, Stratton J, Burke JR, Glendinning DS, Enoka RM. The influence of age on the assessment of motor unit activation in a human hand muscle. *Exp Physiol.* 1996;81:805–819.
139. Hortobagyi T, DeVita P. Muscle pre- and coactivity during downward stepping are associated with leg stiffness in aging. *J Electromyogr Kinesiol.* 2000;10:117–126.
140. Milner TE. Adaptation to destabilizing dynamics by means of muscle cocontraction. *Exp Brain Res.* 2002;143:406–416.
141. Seidler-Dobrin RD, He J, Stelmach GE. Coactivation to reduce variability in the elderly. *Motor Control.* 1998;2:314–330.
142. Patten CT, Kamen G. Adaptations in motor unit discharge activity with force control training in young and older human adults. *Eur J Appl Physiol.* 2000;83:128–143.

143. Pousson M, Lepers R, Van Hoecke J. Changes in isokinetic torque and muscular activity of elbow flexors muscles with age. *Exp Gerontol*. 2001;36:1687–1698.
144. Shinohara M, Latash ML, Zatsiorsky VM. Age effects on force production by the intrinsic and extrinsic hand muscles and finger interaction during maximal contraction tasks. *J Appl Physiol*. 2003;95:1361–1369.
145. Graves AE, Kornatz KW, Enoka RM. Older adults use a unique strategy to lift inertial loads with the elbow flexor muscles. *J Neurophysiol*. 2000;83:2030–2039.
146. van Bolhuis BM, Gielen CC, van Ingen Schenau GJ. Activation patterns of mono- and bi-articular arm muscles as a function of force and movement direction of the wrist in humans. *J Physiol*. 1998;508(Pt 1):313–324.
147. Valour D, Ochala J, Ballay M, Pousson M. The influence of ageing on the force-velocity-power characteristics of human elbow flexor muscles. *Exp Gerontol*. 2003;38:387–395.
148. Christou EA, Carlton LG. Old adults exhibit greater motor output variability than young adults only during rapid discrete isometric contractions. *J Gerontol Biol Sci*. 2001;56A:B524–B532.
149. Darling WG, Cooke JD, Brown SH. Control of simple arm movements in elderly humans. *Neurobiol Aging*. 1989;10:149–157.
150. Thelen DG, Muriuki M, James J, Schultz AB, Ashton-Miller JA, Alexander NB. Muscle activities used by young and old adults when stepping to regain balance during a forward fall. *J Electromyogr Kinesiol*. 2000;10:93–101.
151. Yan JH, Thomas JR, Stelmach GE. Aging and rapid aiming arm movement control. *Exp Aging Res*. 1998;24:155–168.
152. Yan JH. Effects of aging on linear and curvilinear aiming arm movements. *Exp Aging Res*. 2000;26:393–407.
153. Light KE, Spirduso WW. Effects of adult aging on the movement complexity factor of response programming. *J Gerontol*. 1990;45B:P107–P109.
154. Whipple R, Wolfson L, Derby C, Singh D, Tobin J. Altered sensory function and balance in older persons. *J Gerontol*. 1993;48(Spec Iss):71–76.
155. Brauer SG, Woollacott M, Shumway-Cook A. The influence of a concurrent cognitive task on the compensatory stepping response to a perturbation in balance-impaired and healthy elders. *Gait Posture*. 2002;15:83–93.
156. Brown LA, Gage WH, Polych MA, Sleik RJ, Winder TR. Central set influences on gait age-dependent effects of postural threat. *Exp Brain Res*. 2002;145:286–296.
157. Morgan M, Phillips JG, Bradshaw JL, Mattingley JB, Iansek R, Bradshaw JA. Age-related motor slowness: simply strategic? *J Gerontol Med Sci*. 1994;49A:M133–M139.
158. Peinemann A, Lehner C, Conrad B, Siebner HR. Age-related decrease in paired-pulse intracortical inhibition in the human primary motor cortex. *Neurosci Lett*. 2001;313:33–36.
159. Laidlaw DH, Bilodeau M, Enoka RM. Steadiness is reduced and motor unit discharge is more variable in old adults. *Muscle Nerve*. 2000;23:600–612.
160. Laidlaw DH, Hunter SK, Enoka RM. Nonuniform activation of the agonist muscle does not covary with index finger acceleration in old adults. *J Appl Physiol*. 2002;93:1400–1410.
161. Burnett RA, Laidlaw DH, Enoka RM. Coactivation of the antagonist muscle does not covary with steadiness in old adults. *J Appl Physiol*. 2000;89:61–71.
162. Semmler JG, Steege JW, Kornatz KW, Enoka RM. Motor-unit synchronization is not responsible for larger motor-unit forces in old adults. *J Neurophysiol*. 2000;84:358–366.
163. Tracy BL, Enoka RM. Older adults are less steady during submaximal isometric contractions with the knee extensor muscles. *J Appl Physiol*. 2002;92:1004–1012.
164. Vaillancourt DE, Larsson L, Newell KM. Effects of aging on force variability, single motor unit discharge patterns, and the structure of 10, 20, and 40 Hz EMG activity. *Neurobiol Aging*. 2003;24:25–35.
165. Vaillancourt DE, Newell KM. Aging and the time and frequency structure of force output variability. *J Appl Physiol*. 2003;94:903–912.
166. Taylor AM, Christou EA, Enoka RM. Multiple features of motor-unit activity influence force fluctuations during isometric contractions. *J Neurophysiol*. 2003;90:1350–1361.
167. Hortobagyi T, Tunnel D, Moody J, Beam S, DeVita P. Low- or high-intensity strength training partially restores impaired quadriceps force accuracy and steadiness in aged adults. *J Gerontol Biol Sci*. 2001;56A:B38–B47.
168. Hakkinen K, Kraemer WJ, Kallinen M, Linnamo V, Pastinen UM, Newton RU. Bilateral and unilateral neuromuscular function and muscle cross-sectional area in middle-aged and elderly men and women. *J Gerontol Biol Sci*. 1996;51A:B21–B29.
169. Skelton DA, Greig CA, Davies JM, Young A. Strength, power and related functional ability of healthy people aged 65–89 years. *Age Ageing*. 1994;23:371–377.
170. Davies CT, White MJ, Young K. Electrically evoked and voluntary maximal isometric tension in relation to dynamic muscle performance in elderly male subjects, aged 69 years. *Eur J Appl Physiol Occup Physiol*. 1983;51:37–43.
171. Bosco C, Komi PV. Influence of aging on the mechanical behavior of leg extensor muscles. *Eur J Appl Physiol Occup Physiol*. 1980;45:209–219.
172. Danneskiold-Samsøe B, Kofod V, Munter J, Grimby G, Schnohr P, Jensen G. Muscle strength and functional capacity in 78–81-year-old men and women. *Eur J Appl Physiol Occup Physiol*. 1984;52:310–314.
173. Dayhoff NE, Suhrheinrich J, Wigglesworth J, Topp R, Moore S. Balance and muscle strength as predictors of frailty among older adults. *J Gerontol Nurs*. 1998;24:18–27;quiz 54–15.
174. Gross MM, Stevenson PJ, Charette SL, Pyka G, Marcus R. Effect of muscle strength and movement speed on the biomechanics of rising from a chair in healthy elderly and young women. *Gait Posture*. 1998;8:175–185.
175. Krebs DE, Jette AM, Assmann SF. Moderate exercise improves gait stability in disabled elders. *Arch Phys Med Rehabil*. 1998;79:1489–1495.
176. Judge JO, Underwood M, Gennosa T. Exercise to improve gait velocity in older persons. *Arch Phys Med Rehabil*. 1993;74:400–406.
177. McGibbon CA, Krebs DE. Age-related changes in lower trunk coordination and energy transfer during gait. *J Neurophysiol*. 2001;85:1923–1931.
178. Salem GJ, Wang MY, Young JT, Marion M, Greendale GA. Knee strength and lower- and higher-intensity functional performance in older adults. *Med Sci Sports Exerc*. 2000;32:1679–1684.
179. Ploutz-Snyder LL, Manini T, Ploutz-Snyder RJ, Wolf DA. Functionally relevant thresholds of quadriceps femoris strength. *J Gerontol Biol Sci*. 2002;57A:B144–B152.
180. Chandler JM, Duncan PW, Studenski S. Choosing the best strength measure in frail older persons: importance of task specificity. *Muscle Nerve Suppl*. 1997;5:S47–S51.
181. Alexander NB, Schultz AB, Ashton-Miller JA, Gross MM, Giordani B. Muscle strength and rising from a chair in older adults. *Muscle Nerve Suppl*. 1997;5:S56–S59.
182. Wolfson L, Judge J, Whipple R, King M. Strength is a major factor in balance, gait, and the occurrence of falls. *J Gerontol A Biol Sci Med Sci*. 1995;50(Spec Iss):64–67.
183. Young A. Exercise physiology in geriatric practice. *Acta Med Scand Suppl*. 1986;711:227–232.
184. Brooks SV, Faulkner JA. Maximum and sustained power of extensor digitorum longus muscles from young, adult, and old mice. *J Gerontol*. 1991;46:B28–B33.
185. Schwendner KI, Mikesky AE, Holt WS Jr, Peacock M, Burr DB. Differences in muscle endurance and recovery between fallers and nonfallers, and between young and older women. *J Gerontol Med Sci*. 1997;52A:M155–M160.
186. Hortobagyi T, Mizelle C, Beam S, DeVita P. Old adults perform activities of daily living near their maximal capabilities. *J Gerontol Med Sci*. 2003;58A:M453–M460.
187. Fried LP, Bandeen-Roche K, Chaves PH, Johnson BA. Preclinical mobility disability predicts incident mobility disability in older women. *J Gerontol Med Sci*. 2000;55A:M43–M52.
188. Gregory PC, Fried LP. Why do older adults decide they are having difficulty with a task? *Am J Phys Med Rehabil*. 2003;82:9–16.
189. Evans WJ. Exercise strategies should be designed to increase muscle power. *J Gerontol Med Sci*. 2000;55A:M309–M310.
190. Foldvari M, Clark M, Laviolette LC, et al. Association of muscle power with functional status in community-dwelling elderly women. *J Gerontol Med Sci*. 2000;55A:M192–M199.

191. Suzuki T, Bean JF, Fielding RA. Muscle power of the ankle flexors predicts functional performance in community-dwelling older women. *J Am Geriatr Soc.* 2001;49:1161–1167.
192. Bean JF, Kiely DK, Herman S, et al. The relationship between leg power and physical performance in mobility-limited older people. *J Am Geriatr Soc.* 2002;50:461–467.
193. Izquierdo M, Aguado X, Gonzalez R, Lopez JL, Hakkinen K. Maximal and explosive force production capacity and balance performance in men of different ages. *Eur J Appl Physiol Occup Physiol.* 1999;79:260–267.
194. Gehlsen GM, Whaley MH. Falls in the elderly: Part ii, balance, strength, and flexibility. *Arch Phys Med Rehabil.* 1990;71:739–741.
195. Graafmans WC, Ooms ME, Hofstee HM, Bezemer PD, Bouter LM, Lips P. Falls in the elderly: A prospective study of risk factors and risk profiles. *Am J Epidemiol.* 1996;143:1129–1136.
196. Thelen DG, Schultz AB, Alexander NB, Ashton-Miller JA. Effects of age on rapid ankle torque development. *J Gerontol Med Sci.* 1996;51A:M226–M232.
197. Thelen DG, Wojcik LA, Schultz AB, Ashton-Miller JA, Alexander NB. Age differences in using a rapid step to regain balance during a forward fall. *J Gerontol Med Sci.* 1997;52A:M8–M13.
198. Schultz AB, Ashton-Miller JA, Alexander NB. What leads to age and gender differences in balance maintenance and recovery? *Muscle Nerve Suppl.* 1997;5:S60–S64.
199. Clarkson PM. The effect of age and activity level on simple and choice fractionated response time. *Eur J Appl Physiol Occup Physiol.* 1978;40:17–25.
200. Lord SR, Fitzpatrick RC. Choice stepping reaction time: a composite measure of falls risk in older people. *J Gerontol Med Sci.* 2001;56A:M627–M632.
201. Luchies CW, Schiffman J, Richards LG, Thompson MR, Bazuin D, DeYoung AJ. Effects of age, step direction, and reaction condition on the ability to step quickly. *J Gerontol Med Sci.* 2002;57A:M246–M249.
202. Medell JL, Alexander NB. A clinical measure of maximal and rapid stepping in older women. *J Gerontol Med Sci.* 2000;55A:M429–M433.
203. van den Bogert AJ, Pavol MJ, Grabiner MD. Response time is more important than walking speed for the ability of older adults to avoid a fall after a trip. *J Biomech.* 2002;35:199–205.
204. Owings TM, Pavol MJ, Grabiner MD. Mechanisms of failed recovery following postural perturbations on a motorized treadmill mimic those associated with an actual forward trip. *Clin Biomech (Bristol, Avon).* 2001;16:813–819.
205. Hall CD, Woollacott MH, Jensen JL. Age-related changes in rate and magnitude of ankle torque development: implications for balance control. *J Gerontol Med Sci.* 1999;54A:M507–M513.
206. Wojcik LA, Thelen DG, Schultz AB, Ashton Miller JA, Alexander NB. Age and gender differences in peak lower extremity joint torques and ranges of motion used during single-step balance recovery from a forward fall. *J Biomech.* 2001;34:67–73.
207. Landers KA, Hunter GR, Wetzstein CJ, Bamman MM, Weinsier RL. The interrelationship among muscle mass, strength, and the ability to perform physical tasks of daily living in younger and older women. *J Gerontol Biol Sci.* 2001;56A:B443–B448.
208. DeVita P, Hortobagyi T. Age causes a redistribution of joint torques and powers during gait. *J Appl Physiol.* 2000;88:1804–1811.
209. Seidler RD, Alberts JL, Stelmach GE. Changes in multi-joint performance with age. *Motor Control.* 2002;6:19–31.
210. Kornatz KW, Christou EA, Enoka RM. Steadiness training reduces the variability of motor unit discharge rate in isometric and anisometric contractions performed by older adults. *Soc Neurosci Abstr.* 2002;28:665.1.
211. Ranganathan VK, Siemionow V, Sahgal V, Yue GH. Effects of aging on hand function. *J Am Geriatr Soc.* 2001;49:1478–1484.
212. Hasten DL, Pak-Loduca J, Obert KA, Yarasheski KE. Resistance exercise acutely increases MHC and mixed muscle protein synthesis rates in 78–84 and 23–32 yr olds. *Am J Physiol Endocrinol Metab.* 2000;278:E620–E626.
213. Pyka G, Lindenberger E, Charette S, Marcus R. Muscle strength and fiber adaptations to a year-long resistance training program in elderly men and women. *J Gerontol.* 1994;49A:M22–M27.
214. Welle S, Totterman S, Thornton C. Effect of age on muscle hypertrophy induced by resistance training. *J Gerontol Med Sci.* 1996;51A:M270–M275.
215. Roth SM, Martel GF, Ivey FM, et al. Skeletal muscle satellite cell characteristics in young and older men and women after heavy resistance strength training. *J Gerontol Biol Sci.* 2001;56A:B240–B247.
216. Roth SM, Ivey FM, Martel GF, et al. Muscle size responses to strength training in young and older men and women. *J Am Geriatr Soc.* 2001;49:1428–1433.
217. Ivey FM, Roth SM, Ferrell RE, et al. Effects of age, gender, and myostatin genotype on the hypertrophic response to heavy resistance strength training. *J Gerontol Med Sci.* 2000;55A:M641–M648.
218. Kanda K, Hashizume K, Miwa T, Miwa Y. Overloading a muscle does not alter the rate of motoneuronal loss in aged rats. *Neurobiol Aging.* 1996;17:613–617.
219. Kraemer WJ, Hakkinen K, Newton RU, et al. Acute hormonal responses to heavy resistance exercise in younger and older men. *Eur J Appl Physiol Occup Physiol.* 1998;77:206–211.
220. Kraemer WJ, Hakkinen K, Newton RU, et al. Effects of heavy-resistance training on hormonal response patterns in younger vs older men. *J Appl Physiol.* 1999;87:982–992.
221. Hakkinen K, Pakarinen A, Kraemer WJ, Hakkinen A, Valkeinen H, Alen M. Selective muscle hypertrophy, changes in EMG and force, and serum hormones during strength training in older women. *J Appl Physiol.* 2001;91:569–580.
222. Pyka G, Taaffe DR, Marcus R. Effect of a sustained program of resistance training on the acute growth hormone response to resistance exercise in older adults. *Horm Metab Res.* 1994;26:330–333.
223. Williamson DL, Gallagher P, Harber M, Hollon C, Trappe SW. Mitogen-activated protein kinase (MAPK) pathway activation: Effects of age and acute exercise on human skeletal muscle. *J Physiol (Lond).* 2003;547:977–987.
224. Jozsi AC, Dupont-Versteegden EE, Taylor-Jones JM, et al. Aged human muscle demonstrates an altered gene expression profile consistent with an impaired response to exercise. *Mech Ageing Dev.* 2000;120:45–56.
225. Jozsi AC, Dupont-Versteegden EE, Taylor-Jones JM, et al. Molecular characteristics of aged muscle reflect an altered ability to respond to exercise. *Int J Sport Nutr Exerc Metab.* 2001;11(Suppl):S9–S15.
226. Trappe S, Williamson D, Godard M. Maintenance of whole muscle strength and size following resistance training in older men. *J Gerontol Biol Sci.* 2002;57A:B138–B143.
227. Brose A, Parise G, Tamopolsky MA. Creatine supplementation enhances isometric strength and body composition improvements following strength exercise training in older adults. *J Gerontol Biol Sci.* 2003;58A:B11–B19.
228. Sharman MJ, Newton RU, Triplett-McBride T, et al. Changes in myosin heavy chain composition with heavy resistance training in 60- to 75-year-old men and women. *Eur J Appl Physiol.* 2001;84:127–132.
229. McGuigan MRM, Bronks R, Newton RU, et al. Resistance training in patients with peripheral arterial disease: effects on myosin isoforms, fiber type distribution, and capillary supply to skeletal muscle. *J Gerontol Biol Sci.* 2001;56A:B302–B310.
230. Bamman MM, Hill VJ, Adams GR, et al. Gender differences in resistance-training-induced myofiber hypertrophy among older adults. *J Gerontol Biol Sci.* 2003;58A:B108–B116.
231. Williamson DL, Godard MP, Porter DA, Costill DL, Trappe SW. Progressive resistance training reduces myosin heavy chain coexpression in single muscle fibers from older men. *J Appl Physiol.* 2000;88:627–633.
232. Williamson DL, Gallagher PM, Carroll CC, Raue U, Trappe SW. Reduction in hybrid single muscle fiber proportions with resistance training in humans. *J Appl Physiol.* 2001;91:1955–1961.
233. Moritani T, deVries HA. Potential for gross muscle hypertrophy in older men. *J Gerontol.* 1980;35:672–682.
234. Carolan B, Cafarelli E. Adaptations in coactivation after isometric resistance training. *J Appl Physiol.* 1992;73:911–917.
235. Rutherford OM, Jones DA. The role of learning and coordination in strength training. *Eur J Appl Physiol Occup Physiol.* 1986;55:100–105.
236. Akima H, Takahashi H, Kuno SY, et al. Early phase adaptations of muscle use and strength to isokinetic training. *Med Sci Sports Exerc.* 1999;31:588–594.
237. Adams GR, Harris RT, Woodard D, Dudley GA. Mapping of electrical muscle stimulation using MRI. *J Appl Physiol.* 1993;74:532–537.

238. Wilson GJ, Murphy AJ, Walshe A. The specificity of strength training: the effect of posture. *Eur J Appl Physiol Occup Physiol*. 1996;73:346–352.
239. Rutherford OM. Muscular coordination and strength training. Implications for injury rehabilitation. *Sports Med*. 1988;5:196–202.
240. Kleim JA, Barbay S, Nudo RJ. Functional reorganization of the rat motor cortex following motor skill learning. *J Neurophysiol*. 1998;80:3321–3325.
241. Sanes JN, Donoghue JP. Plasticity and primary motor cortex. *Ann Rev Neurosci*. 2000;23:393–415.
242. Shadmehr R, Moussavi ZMK. Spatial generalization from learning dynamics of reaching movements. *J Neurosci*. 2000;20:7807–7815.
243. Malfait N, Shiller DM, Ostry DJ. Transfer of motor learning across arm configurations. *J Neurosci*. 2002;22:9656–9660.
244. Maffiuletti NA, Pensini M, Martin A. Activation of human plantar flexor muscles increases after electromyostimulation training. *J Appl Physiol*. 2002;92:1383–1392.
245. Leong B, Kamen G, Patten C, Burke JR. Maximal motor unit discharge rates in the quadriceps muscles of older weight lifters. *Med Sci Sports Exerc*. 1999;31:1638–1644.
246. Connelly DM, Vandervoort AA. Effects of isokinetic strength training on concentric and eccentric torque development in the ankle dorsiflexors of older adults. *J Gerontol Biol Sci*. 2000;55:B465–B472.
247. Hakkinen K, Newton RU, Gordon SE, et al. Changes in muscle morphology, electromyographic activity, and force production characteristics during progressive strength training in young and older men. *J Gerontol Biol Sci*. 1998;53A:B415–B423.
248. Chan KM, Amirjani N, Sumrain M, Clarke A, Strohschein FJ. Randomized controlled trial of strength training in post-polio patients. *Muscle Nerve*. 2003;27:332–338.
249. Duchateau J, Enoka RM. Neural adaptations with chronic activity patterns in able-bodied humans. *Am J Phys Med Rehabil*. 2002;81:S17–S27.
250. Kamen G, Knight CA, Laroche DP, Asermely DG. Resistance training increases vastus lateralis motor unit firing rates in young and old adults. *Med Sci Sports Exerc*. 1998;30:S337.
251. Zehr PE. Considerations for use of the Hoffmann reflex in exercise studies. *Eur J Appl Physiol*. 2002;86:455–468.
252. Aagaard P, Simonsen EB, Andersen JL, Magnusson P, Dyhre-Poulsen P. Neural adaptation to resistance training: changes in evoked V-wave and H-reflex responses. *J Appl Physiol*. 2002;92:2309–2318.
253. Connelly DM, Carnahan H, Vandervoort AA. Motor skill learning of concentric and eccentric isokinetic movements in older adults. *Exp Aging Res*. 2000;26:209–228.
254. Jozsi AC, Campbell WW, Joseph L, Davey SL, Evans WJ. Changes in power with resistance training in older and younger men and women. *J Gerontol Med Sci*. 1999;54A:M591–M596.
255. Fielding RA, LeBrasseur NK, Cuoco A, Bean J, Mizer K, Fiatarone Singh MA. High-velocity resistance training increases skeletal muscle peak power in older women. *J Am Geriatr Soc*. 2002;50:655–662.
256. Labarque V, Eijnde BO, Van Leemputte M. Resistance training alters torque-velocity relation of elbow flexors in elderly men. *Med Sci Sports Exerc*. 2002;34:851–856.
257. Ferri A, Scaglioni G, Pousson M, Capodaglio P, Van Hoecke J, Narici MV. Strength and power changes of the human plantar flexors and knee extensors in response to resistance training in old age. *Acta Physiol Scand*. 2003;177:69–78.
258. Reeves ND, Maganaris CN, Narici MV. Effect of strength training on human patella tendon mechanical properties of older individuals. *J Physiol*. 2003;548:971–981.
259. Dorfman LJ, Bosley TM. Age-related changes in peripheral and central nerve conduction in man. *Neurology*. 1979;29:38–44.
260. Grimby L, Hannerz J, Hedman B. The fatigue and voluntary discharge properties of single motor units in man. *J Physiol*. 1981;316:545–554.
261. Aagaard P, Simonsen EB, Andersen JL, Magnusson P, Dyhre-Poulsen P. Increased rate of force development and neural drive of human skeletal muscle following resistance training. *J Appl Physiol*. 2002;93:1318–1326.
262. Kaneko M, Fuchimoto T, Toji H, Sui K. Training effect of different loads on the force-velocity relationship and mechanical power output in human muscle. *Scand J Sports Sci*. 1983;5:50–55.
263. Sahaly R, Vandewalle H, Driss T, Monod H. Surface electromyograms of agonist and antagonist muscles during force development of maximal isometric exercises-effects of instruction. *Eur J Appl Physiol*. 2003;89:79–84.
264. Behm DG, Sale DG. Intended rather than actual movement velocity determines velocity-specific training response. *J Appl Physiol*. 1993;74:359–368.
265. Newton RU, Hakkinen K, Hakkinen A, McCormick M, Volek J, Kraemer WJ. Mixed-methods resistance training increases power and strength of young and older men. *Med Sci Sports Exerc*. 2002;34:1367–1375.
266. Rantanen T. Muscle strength, disability and mortality. *Scand J Med Sci Sports*. 2003;13:3–8.
267. Alexander NB, Galecki AT, Grenier ML, et al. Task-specific resistance training to improve the ability of activities of daily living-impaired older adults to rise from a bed and from a chair. *J Am Geriatr Soc*. 2001;49:1418–1427.
268. Alexander NB, Gross MM, Medell JL, Hofmeyer MR. Effects of functional ability and training on chair-rise biomechanics in older adults. *J Gerontol Med Sci*. 2001;56A:M538–M547.
269. Rooks DS, Kiel DP, Parsons C, Hayes WC. Self-paced resistance training and walking exercise in community-dwelling older adults: Effects on neuromotor performance. *J Gerontol Med Sci*. 1997;52A:M161–M168.
270. Judge JO, Whipple RH, Wolfson LI. Effects of resistive and balance exercises on isokinetic strength in older persons. *J Am Geriatr Soc*. 1994;42:937–946.
271. Bellow JW, Yates JW, Gater DR. The initial effects of low-volume strength training on balance in untrained older men and women. *J Strength Cond Res*. 2003;17:121–128.
272. Skelton DA, Young A, Greig CA, Malbut KE. Effects of resistance training on strength, power, and selected functional abilities of women aged 75 and older. *J Am Geriatr Soc*. 1995;43:1081–1087.
273. Keysor JJ, Jette AM. Have we oversold the benefit of late-life exercise? *J Gerontol Med Sci*. 2001;56A:M412–M423.
274. Connelly DM. Resisted exercise training of institutionalized older adults for improved strength and functional mobility: a review. *Top Geriatric Rehabil*. 2000;15:6–28.
275. Miszko TA, Cress ME, Slade JM, Covey CJ, Agrawal SK, Doerr CE. Effect of strength and power training on physical function in community-dwelling older adults. *J Gerontol Med Sci*. 2003;58A:M171–M175.
276. Chandler JM, Hadley EC. Exercise to improve physiologic and functional performance in old age. *Clin Geriatr Med*. 1996;12:761–784.
277. Chandler JM, Duncan PW, Kochersberger G, Studenski S. Is lower extremity strength gain associated with improvement in physical performance and disability in frail, community-dwelling elders? *Arch Phys Med Rehabil*. 1998;79:24–30.
278. Galganski ME, Fuglestad AJ, Enoka RM. Reduced control of motor output in a human hand muscle of elderly subjects during submaximal contractions. *J Neurophysiol*. 1993;69:2108–2115.
279. Cole KJ, Beck CL. The stability of precision grip force in older adults. *J Mot Behav*. 1994;26:171–177.
280. Higbie EJ, Cureton KJ, Warren GL III, Prior BM. Effects of concentric and eccentric training on muscle strength, cross-sectional area, and neural activation. *J Appl Physiol*. 1996;81:2173–2181.
281. Hortobagyi T, Barrier J, Beard D, et al. Greater initial adaptations to submaximal muscle lengthening than maximal shortening. *J Appl Physiol*. 1996;81:1677–1682.
282. Behm DG, Sale DG. Velocity specificity of resistance training. *Sports Med*. 1993;15:374–388.
283. Tracy BL, Kern DS, Mehoudar S, Sehnert RM, Enoka RM. Strength training does not improve the steadiness of muscle contractions in the knee extensors of older adults. *Med Sci Sports Exerc*. 2001;33:S254.
284. Vincent KR, Braith RW, Feldman RA, et al. Resistance exercise and physical performance in adults aged 60 to 83. *J Am Geriatr Soc*. 2002;50:1100–1107.
285. Pruitt LA, Taaffe DR, Marcus R. Effects of a one-year high-intensity versus low-intensity resistance training program on bone mineral density in older women. *J Bone Miner Res*. 1995;10:1788–1795.
286. Hunter GR, Wetzstein CJ, McLafferty CL Jr, Zuckerman PA, Landers KA, Bamman MM. High-resistance versus variable-resistance training in older adults. *Med Sci Sports Exerc*. 2001;33:1759–1764.

287. Skelton DA, Beyer N. Exercise and injury prevention in older people. *Scand J Med Sci Sports*. 2003;13:77–85.
288. Ettinger WH Jr, Burns R, Messier SP, et al. A randomized trial comparing aerobic exercise and resistance exercise with a health education program in older adults with knee osteoarthritis. The fitness arthritis and seniors trial (fast). *JAMA*. 1997;277:25–31.
289. Wolf SL, Barnhart HX, Ellison GL, Coogler CE. The effect of tai chi quan and computerized balance training on postural stability in older subjects. Atlanta FICSIT group. Frailty and injuries: co-operative studies on intervention techniques. *Phys Ther*. 1997;77:371–381.
290. Lord SR, Lloyd DG, Nirui M, Raymond J, Williams P, Stewart RA. The effect of exercise on gait patterns in older women: a randomized controlled trial. *J Gerontol Med Sci*. 1996;51A:M64–M70.
291. Wolfson L, Whipple R, Derby C, et al. Balance and strength training in older adults: intervention gains and tai chi maintenance. *J Am Geriatr Soc*. 1996;44:498–506.
292. Taaffe DR, Pruitt L, Pyka G, Guido D, Marcus R. Comparative effects of high- and low-intensity resistance training on thigh muscle strength, fiber area, and tissue composition in elderly women. *Clin Physiol*. 1996;16:381–392.
293. Ploutz-Snyder LL, Giamis EL, Formikell M, Rosenbaum AE. Resistance training reduces susceptibility to eccentric exercise-induced muscle dysfunction in older women. *J Gerontol Biol Sci*. 2001;56A:B384–B390.
294. Stavrinou TM, Scarbek Y, Galambos G, Fiatarone-Singh MA, Singh NA. The effects of low intensity versus high intensity progressive resistance weight training on shoulder function in the elderly: a randomised controlled trial. *Aust N Z J Med*. 2000;30:305.
295. LaStayo PC, Ewy GA, Pierotti DD, Johns RK, Lindstedt S. The positive effects of negative work: increased muscle strength and decreased fall risk in a frail elderly population. *J Gerontol Med Sci*. 2003;58A:M419–M424.
296. Hortobagyi T. The positives of negatives: clinical implications of eccentric resistance exercise in old adults. *J Gerontol Med Sci*. 2003;58A:M417–M418.
297. Christou EA, Carlton LG. Age and contraction type influence motor output variability in rapid discrete tasks. *J Appl Physiol*. 2002;93:489–498.
298. Enoka RM. Eccentric contractions require unique activation strategies by the nervous system. *J Appl Physiol*. 1996;81:2339–2346.
299. Semmler JG, Komatz KW, Dinno DV, Zhou S, Enoka RM. Motor unit synchronisation is enhanced during slow lengthening contractions of a hand muscle. *J Physiol*. 2002;545:681–695.
300. Hunter SK, White M, Thompson, M. Techniques to evaluate elderly human muscle function: a physiological basis. *J Gerontol Biol Sci*. 1998;53A:B204–B216.

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