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ARTICLE *in* SCANDINAVIAN JOURNAL OF MEDICINE AND SCIENCE IN SPORTS · JULY 1995

Impact Factor: 2.9 · DOI: 10.1111/j.1600-0838.1995.tb00026.x · Source: PubMed

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Scand J Med Sci Sports 1995: 5: 129–142
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Scandinavian Journal of
MEDICINE & SCIENCE IN SPORTS
ISSN 0905-7188

Review article

Aging of human muscle: structure, function and adaptability

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Porter MM, Vandervoort AA, Lexell J. Aging of human muscle: structure, function and adaptability.
Scand J Med Sci Sports 1995: 5: 129–142. © Munksgaard, 1995

With increasing age, human skeletal muscles gradually decrease in volume, mainly due to a reduced number of motor units and muscle fibers, and a reduced size of type 2 fibers. As a result, progressive weakening and impaired mobility occur. High-resistance strength training is beneficial, even in the very old, and could possibly reverse some of the detrimental effects of age-related weakness. The importance of exercise for older people affords an excellent opportunity for the medicine community as a major source of information and promotion of physical activity for this rapidly growing segment of the population. In this review, we summarize the current knowledge of the effects of aging on the human neuromuscular system, describe some of the major underlying mechanisms of the aging atrophy and focus on the importance of strength training to improve muscle function in older people.

Key words: aging; muscle; muscular atrophy; physical fitness; physiological adaptation

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Accepted for publication November 18, 1994

With increasing age, skeletal muscle mass is lost, and this aging atrophy is accompanied by a reduction in muscle strength. As a result, many older individuals have impaired mobility, and increased risk of falls and hip fractures, and a considerable number require assistance with everyday activities. In all developed countries throughout the world, the number of older individuals is increasing, and the effects on the health care system may be substantial (1). At the same time, health in general among old people is gradually improving and the rate of disability is beginning to decline (2). Many old men and women are both able and motivated to continue to keep fit and mobile. Physical activity and exercise play a key role, in treatment and rehabilitation, and could possibly be of importance in the prevention of frailty among elderly people. Furthermore, the number of older men and women participating in various sporting activities and competitions has increased during recent years. Whether it is treatment, prevention or competitive sports, knowledge of the neuromuscular system and its response to training in older groups is necessary to enable physicians, physiotherapists and fitness instructors to give the best possible advice and to plan optimal exercise programs for this rapidly growing segment of the population.

During the last decade, attention to the effects of aging on the human locomotor system, the underlying pathophysiological mechanisms of aging atrophy and the importance of physical activity and exercise, in particular strength training, to improve muscle function in older individuals has markedly increased. The number of studies focusing on the aging human muscle, its structure, function and adaptability is steadily growing, particularly in the sports medicine community. Our purposes here are to review these studies, to describe some unsolved problems and to indicate some likely lines of development.

Loss of voluntary muscle strength

One of the most noticeable effects of increasing age is the reduction in muscle strength. A variety of limb muscles have been compared between groups of young, middle-aged and older adults, showing that decreases in voluntary strength do not become apparent until after the age of 60 years (3). When muscles in the upper and lower limb, including proximal and distal locations, have been examined, the size of the age effect revealed only small variations from muscle to muscle. For both men and women the reduction in strength across the adult age range tends to be curvilinear, with some suggestion that the relative effect of aging on isokinetic strength is more pronounced in women.

Particular attention has been paid to the strength of the quadriceps femoris muscle group, which has been measured extensively in test conditions involving all 3 actions of muscles: isometric, concentric and eccentric (Table 1). Healthy people in the seventh and eighth decades score on average 20 to 40% less during isometric and concentric strength tests than young adults, and the very old show even greater (50% or more) reduction.

Only longitudinal studies of the knee muscles are available, and it is of interest to compare these results with data from cross-sectional studies. Aniansson et al. (14) and Grieg et al. (15) found less decline than expected in their 7-year and 8-year follow-up studies of subjects living into the ninth decade. This result may reflect the biological superiority of those who live longer than average or may reflect their adaptive lifestyle. Kallman et al. (16), on the other hand, reported that age versus grip strength was quite comparable between two types of analysis: a cross-sectional survey of subjects of different ages and a semi-longitudinal follow-up of subjects in the Baltimore Longitudinal Study of Aging.

It was recently found that the differences between young and older groups of men and women were consistently less for the eccentric type of muscle action (lengthening) than during either isometric or concentric contractions (9, 11, 13, 17), but the mechanism for this relative advantage of aged muscle to lengthen against resistance remains undetermined. It has been suggested that hormonal factors may affect cross-bridges during shortening or isometric actions but not during lengthening actions (17, 18). In fact, these authors found that postmenopausal women who had been receiving estrogen replacement therapy had greater specific muscle force than non-replaced postmenopausal women, and the decline in specific force in men seemed to follow the more gradual decline in testosterone with age (18). What is important from a functional perspective is that, for a given absolute load, the intensity of muscular effort would be less for an eccentric condition than concentric, thereby suggesting that the aged might find some relative advantage in using muscles under lengthening situations.

Muscle groups at the ankle show comparable declines in strength to the knee extensors when young adults are compared with older adults. Davies et al. (19) examined the triceps surae muscle in elderly men and women (mean age 70 years) and reported 38% and 28% differences, respectively, in ankle plantar flexion strength from young male and female adults. Vandervoort & McComas (20) observed that healthy young and middle-aged men and women had similar isometric strength of ankle plantarflexors and dorsiflexors; values then decreased approximately 15% per decade. Testing of concentric strength of ankle plantar flexors in men also demonstrated a significant age-related decrement (21).

To what extent do these age differences reflect a failure of descending drive from the motor cortex? Vandervoort & McComas (20) assessed descending motor drive using the twitch interpolation technique. A brief percutaneous electrical shock was applied to the motor nerve during a maximal voluntary contraction (22). Most of the healthy older subjects, ranging in age from 60 to 100 years, were able to activate their ankle muscles maximally, because a superimposed twitch stimulus added little to their volitional force. Thus, the age-related declines in strength in these healthy older people must have been due predominantly to a decreased excitable muscle mass. It should be remembered that this was an isometric, single joint task, and central nervous system coordination could still be an important factor in dynamic strength maneuvers involving many muscle groups (23).

Table 1. Voluntary knee extension strength in older individuals

Reference	Authors	Year	Sex	Age (years)	Test condition	Proportion of young adult value
4	Larsson et al.	1979	M	60–69	Isometric	75%
5	Murray et al.	1980	M	70–86	Isometric	55%
6	Young et al.	1984	F	71–81	Isometric	65%
7	Murray et al.	1985	F	70–86	Isometric	63%
8	Young et al.	1985	M	70–79	Isometric	61%
9	Vandervoort et al.	1990	F	66–89	Concentric 90°/s	47%
					Eccentric	66%
10	Overend et al.	1992	M	65–77	Isometric	76%
					Concentric 120°/s	68%
11	Poulin et al.	1992	M	60–75	Concentric 180°/s	69%
					Eccentric 180°/s	98%
12	Stanley & Taylor	1993	F	60–70	Concentric 180°/s	51%
					Concentric 300°/s	43%
13	Porter et al.	1994	M	62–88	Concentric 90°/s	58%
					Eccentric 90°/s	75%

Reduction in muscle volume and cross-sectional area

As older men and women are able to activate their muscles maximally, or near maximum, the main reason for the age-related decline in strength must be a reduction in muscle volume and mass. Muscle cross-sectional area and muscle volume have been estimated indirectly using various radiological imaging techniques. Young et al. (24, 25) used ultrasonography and found 25–35% reductions in the cross-sectional area of the quadriceps muscle in older men and women compared with the young. More recently, computed tomography scanning has been applied and has shown similar age-related reductions in cross-sectional area of the psoas major and sacrospinalis muscles (26), the quadriceps muscle (27, 28), the brachial biceps and triceps muscles (29), and the plantarflexors (29).

Two of these studies have also documented increases in non-muscle tissue, i.e., fat and connective tissue, within the older muscle. Rice et al. (29) found 27%, 45% and 81%, respectively, more non-muscle tissue in the arm flexors, arm extensors and plantarflexors of older people. Overend et al. (28) found increases in non-muscle tissue of 59% (quadriceps) and 127% (hamstrings). As a result of this age-related infiltration of fat and connective tissue, the reduction in muscle contractile tissue may be greater than the actual reduction in muscle volume and muscle cross-sectional area.

Direct measurements of the muscle cross-sectional area are, on the other hand, very limited, due to the technical and ethical constraints involved in more direct detailed studies of whole human muscles. Only very small parts of muscles have been analyzed, with consequent difficulties in the interpretation of the results. Large cryomicrotomes and modified morphometric procedures now make it possible to prepare and to analyze cross-sections of whole human (autopsied) muscles (30). Lexell et al. analyzed the vastus lateralis of previously healthy men (31) between 15 and 83 years of age and found that the average reduction in muscle area between 20 and 80 years was 40% (Fig. 1); for this muscle, the reduction in area begins as early as 25 years of age, approximately 10% of the muscle area is lost by the age of 50, and thereafter the reduction accelerates. These findings are, of course, limited to one limb muscle. We can, however, conjecture that other human muscles could be affected in a similar way, although the actual values may be different.

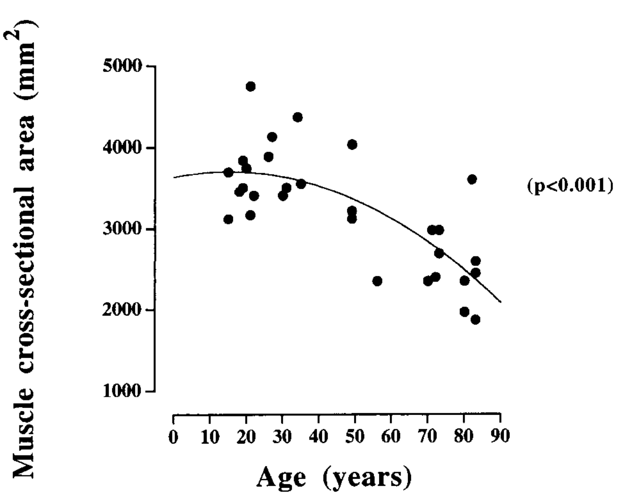

Fig. 1. Relationship between age and muscle cross-sectional area. Data reproduced with permission from Lexell et al. (31).

Changes in sizes, numbers and proportions of muscle fiber types

To understand the causes of the aging atrophy, numerous attempts have been made to assess the muscle morphology of aging muscles. In a majority of these studies, the vastus lateralis of the quadriceps muscle has been examined, and the overall conclusion is very consistent: type 2 (fast-twitch) fiber size is reduced with increasing age, while the size of type 1 (slow-twitch) fibers remains much less affected (31–44). Several studies present only qualitative data and make comparisons only with data from other studies, with apparent limitations in the inferences of the results. Table 2 summarizes studies based on quantitative data.

Other limb muscles have been assessed much less. A comparison of young and old tibialis anterior (45) revealed a selective hypotrophy of type 2 fibers of the same magnitude as in the vastus lateralis. When the muscle morphology of the vastus lateralis and the biceps brachii of 78- to 81-year-old men and women was analyzed (38), the mean area of type 2 fibers was significantly smaller in the leg than in the arm, particularly in women. This could indicate differences in the aging process and/or a difference in the activity pattern between arms and leg. Further studies of muscles in the upper and lower extremity in the same individual and comparisons with data from young and old are needed to explain this finding.

In many studies, the reduction in fiber size is moderate in comparison with the reported muscle volume reduction, and in particular, the expected reduction in muscle contractile tissue. It has therefore been questioned whether decreased fiber areas alone can explain the muscle hypotrophy or if a loss of fibers also occurs (46). A reduction in the number of fibers was reported in vocal muscles (47) and in the minor pectoral muscles (48). It was not until techniques allowed analysis of whole large muscles that it became evident that the total number of fibers was sig-

Table 2. Reductions in size of different types of muscle fibers in the vastus lateralis muscle of older individuals

Reference	Authors	Year	Sex	Age (years)	Muscle fiber size reduction	
					type 1 fibers	type 2 fibers
34	Tomonaga	1977	M/F	60–90+	7%	52%
35	Larsson et al.	1978	M	22–65	1%	25%
36	Scelsi et al.	1980	M/F	65–89	7%	24%
42	Essén-Gustavsson & Borges	1986	M	20–70	15%	19%
			F	20–70	25%	45%
31	Lexell et al.	1988	M	15–83	1%	29%
44	Lexell & Taylor	1991	M	19–86	6%	35%

nificantly reduced with increasing age (49). When this initial study was extended (31), it was found that the aging atrophy of the vastus lateralis muscle was caused by both a loss of fibers and a reduction in the size of fibers (Fig. 2A–B). It was also concluded that the loss of fibers begins at 25 years of age and thereafter accelerates, and that the fiber size reduction can be explained mainly by an effect on type 2 fibers.

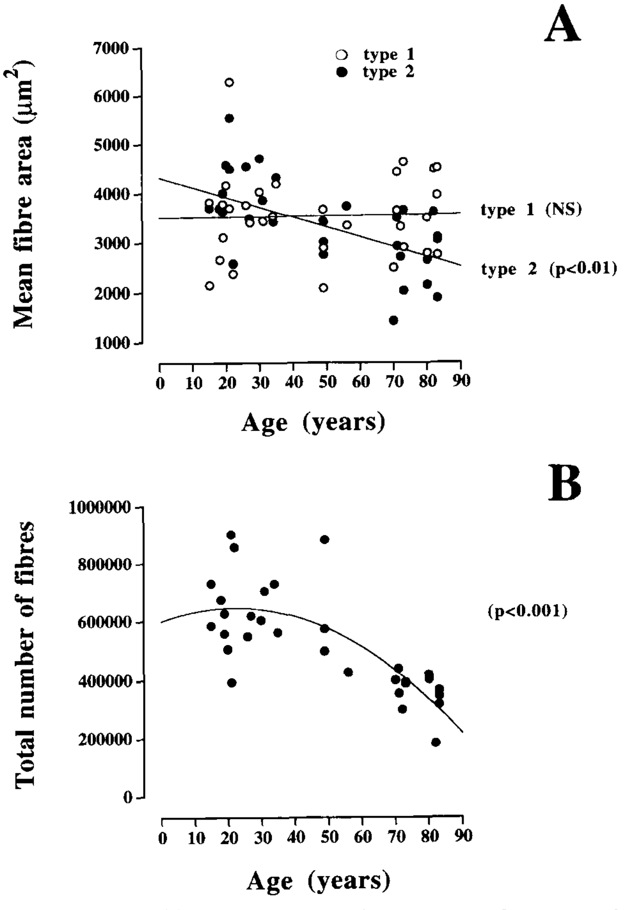

Fig. 2. Relationship between age and mean area of type 1 and type 2 fibers (**A**) and between age and total numbers of fibers (**B**). Data reproduced with permission from Lexell et al. (31).

In an attempt to identify the determinants of the size of human muscles at different ages, the original data have been reanalyzed (50). The cross-sectional area of the vastus lateralis muscle is mainly determined by the total number of fibers, and to a lesser extent by the size and/or the number of type 2 fibers. Thus, the loss of fibers seems to be the main explanation for the reduced area of this muscle with increasing age. However, we should be aware that no other limb muscle has been analyzed with respect to the total number of fibers. It remains therefore to be established whether the same mechanism is responsible for the atrophy of muscles in the arm and other muscles in the leg.

A reduction in the total number of fibers with advancing age could involve a loss of a specific type of fiber. This could alter the fiber type proportion, provided that fibers retain their original histochemical characteristics throughout life. Several studies have attempted to determine the effects of age on the proportion of type 2 fibers using data from single biopsies – again only the vastus lateralis muscle – but the findings are conflicting (36, 40, 41, 51, 52). Data from studies of whole muscle cross-sections (31) show that the average proportion of type 2 fibers in the vastus lateralis is unaffected with increasing age; the mean proportion of type 1 fibers at 20 years of age is 51% and at 80 years of age 55%. All other studies have found similar mean type 1 fiber proportions in old muscles, while the mean proportion for young muscles have varied and in some studies have been reported to be as low as 40% (51). An extensive survey of the literature (53) has persuasively shown that the mean proportion of type 1 fibers is close to 50% in the young human vastus lateralis muscle. In addition, the proportion of fiber types can vary considerably as a function of depth within the vastus lateralis (30, 31). Thus, sampling variability is a likely reason for some of the discrepancies in the literature, and the conclusion is that the overall reduction in fiber numnber with increasing age – for a whole population – seems to affect type 1 and type 2 fibers to the same extent.

However, the relationship between fiber number, fiber size and fiber type proportion is much more complex, and the effects of increasing age on type 1 and type 2 fibers may be somewhat counterbalanced. This would indicate that fiber type properties are not static and that muscle fibers can alter their histochemical profile throughout life. Electrophoretic analysis of single muscle fibers (54) have revealed that elderly subjects have a higher proportion of fibers showing coexpression of myosin heavy chain types 1 and 2A as well as 2A and 2B. These authors suggested that it could reflext an ongoing transition process or a "dynamic equilibrium" between the fiber populations, due to denervation and/or disuse.

In the study of the fiber type composition of whole vastus lateralis (31), it was noted that the mean proportion of type 2 fibres varied much more between individuals in the old age-group than in the young. Some old individuals had a high proportion of type 1 fibers, while others had a clear predominance of type 2 fibers; this could be due to a selective loss of one fiber type or an equal loss of type 1 and type 2 fibers with a transformation of fiber types. When the proportion of type 2 fibers and the mean area of type 2 fibers were combined to form the relative type 2 fiber area and regressed against age, the relationship was found to be stronger than the two individual relationships (Fig. 3) (55). This indicates that the proportion of the fiber area in the muscle cross-section occupied by type 2 fibers is significantly reduced with increasing age, and that this reduction is accounted for by a concurrent effect on the fiber number and fiber size. In those muscles where type 2 fibers are lost to a great extent, the size of type 2 fibers seems to be retained. If there is an equal loss of type 1 and type 2 fibers, or even a greater reduction of type 1 fibers, there is selective type 2 hypotrophy. Thus, for the vastus lateralis muscle, increasing age is accompanied by a greater loss of contractile material of fast-twitch type than of slow-twitch type. This loss is mediated through a reduction in number and/or size of type 2 fibers. Such a process is likely to be a major contributor to the aging atrophy in the vastus lateralis muscle, and the concomitant reduction in muscle strength.

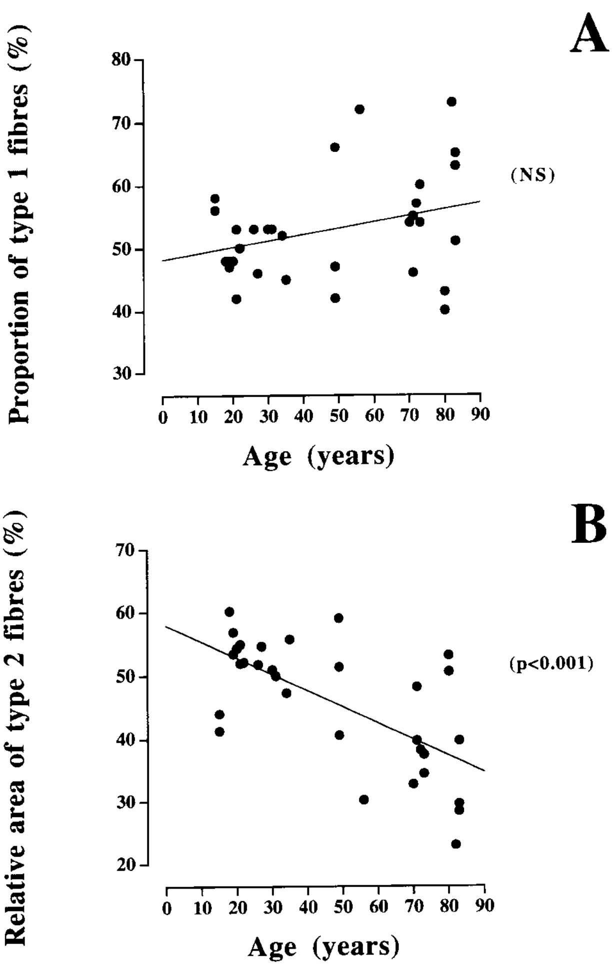

Fig. 3. Relationship between age and proportion of type 1 fibers (**A**) and between age and relative area of type 2 fibers (**B**). Data reproduced with permission from Lexell & Downham (55).

Changes in the nervous system and motor unit properties

There exists clear indirect and direct evidence for quantitative as well as qualitative changes in motor units with increasing age. Studies of the number of motor neurons in the spinal cord (56) and of the numbers and sizes of motor axons in ventral roots (57–59) have shown that with increasing age there is a loss of alpha motor neurons from the spinal cord with a subsequent degeneration of their axons. The number of motor neurons in the lumbosacral cord (56) was reduced above the age of 60 years, with some cases exhibiting counts of only 50% of those in young. This was supported by studies of Kawamura et al. (57, 58) in which a loss of motor neurons in the lumbar spinal cord was accompanied by a reduction in the numbers of large and intermediate ventral root fibers.

Quantitative electromyography (EMG) has shown changes in both duration and amplitude of motor unit action potentials (MUAP) (60, 61). Subsequent analysis of the motor unit size, using macro EMG (62–64), has clearly revealed an increase in motor unit size in several limb muscles above the age of 60 years, i.e., an increased number of muscle fibers per motor unit. Estimates of the number of motor units (65–69) are all in agreement with other neurophysiological studies, and indicate a reduced number of motor units in older individuals.

Extensive neuropathic changes are also common in muscles of old/very old individuals (32–34). When the fiber type arrangement in the vastus lateralis muscle at various ages was examined, an increase in fiber type grouping – an indirect evidence of a neuropathological process – was seen in old muscles (70, 71). All these results point in the same direction: increasing age is accompanied by a reduction in the number of functioning motor units with an increase in the size of remaining/surviving motor units. This implies that the fiber population with increasing age undergoes several cycles of denervation followed by reinnervation, resulting from death of motor neuron in the spinal cord or from irreparable damage to peripheral nerve axons.

Changes in muscle contractile properties: effects on neuromuscular performance

There is also indirect and direct evidence for age-related changes in intrinsic properties of muscle fibers. With regard to contractile characteristics, the distal muscle groups are more feasible for investigation in humans. Most frequently studied are the components of the triceps surae group at the ankle, as a whole or separate studies of the gastrocnemius and soleus. Davies et al. (19) reported a significant increase in both the time to peak tension and the time to relaxation following evoked twitches of the triceps surae in elderly subjects. Vandervoort & McComas (20) reported the same finding in both the plantar flexor and dorsiflexor muscle groups of the ankle. While similar results have been shown for individual muscles of the lower leg and foot (72, 73), only minor age-related differences have been presented for the elbow flexors (69, 74).

The observed slowing of contraction may stem in part from the reduced proportional contribution of type 2 fibers to the twitch contraction. Vandervoort & McComas (20) found a pronounced effect of age on the gastrocnemius muscle twitch but less on the soleus, the latter having fewer fast-twitch motor units than the gastrocnemius muscle of young adults (75, 76). The effects of age on the proportion of type 2 fibers in the quadriceps muscles (31, 55) can also be observed in the reduced rate of force development and ability to accelerate the limb (4, 12). An interesting observation from the sample of Vandervoort & McComas (20), which covered an age range from 20 to 100 years, was that the twitch times increased in a linear fashion with age, but changes in muscle strength did not become evident until the seventh decade (Fig. 4A–B).

Twitch prolongation with aging could reflect greater efficiency for the contraction of elderly muscles, as lower frequencies of nerve impulses are required to attain a given muscle tension or reach tetanic fusion (19, 77). Further to this effect, does the aged muscle show greater resistance to fatigue? The research in this area has been inconclusive, partly due to the variety of methods used to induce fatigue. For example, Narici et al. (78) used a 30 Hz stimulation protocol and observed a decrease in fatiguability across ages in a study of the adductor pollicus in men, but Lennmarken et al. (79) observed increased fatiguability in a similar study done at 20 Hz. Klein et al. (80) reported no differences between samples of young and older men in fatigability of the triceps surae muscle, but Davies et al. (19) found increased susceptibility to fatigue in their aged sample. The latter investigators felt that blood flow may have been more occluded in the older subjects, thereby diminishing

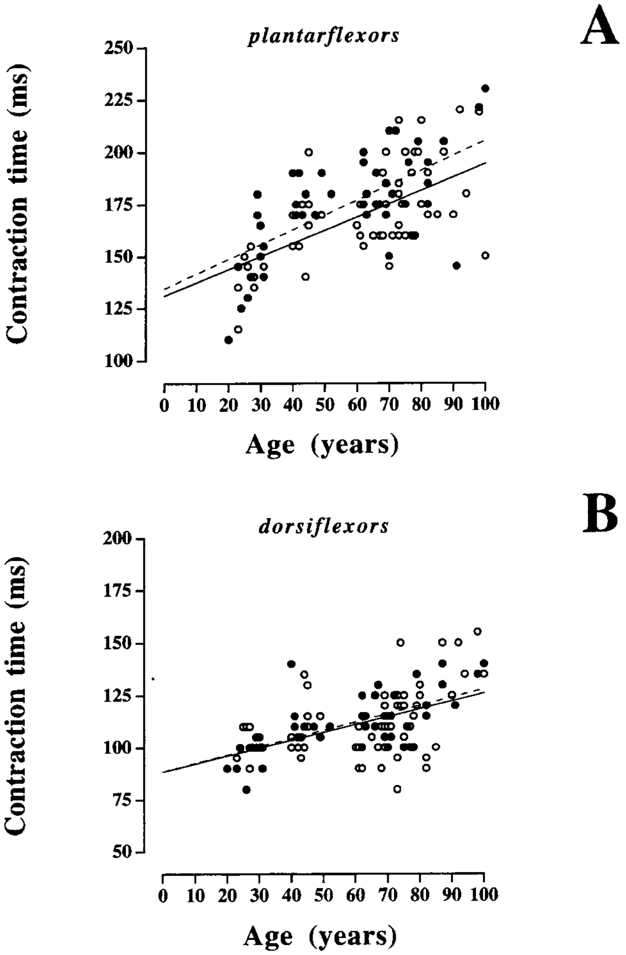

Fig. 4. Relationship between age and contraction time of the ankle plantar flexor muscle groups (**A**) and between age and contraction time of the ankle dorsiflexor muscle groups (**B**). Evoked twitches were obtained from men (open circles, continuous lines) and women (filled circles, interrupted lines). In both sexes the two muscle groups showed significant ($P<0.001$) correlation with age. Data reproduced with permission from Vandervoort & McComas (20).

the capacity of the predominately aerobic muscle to sustain contraction.

When sustained voluntary contractions have been studied, the results have been more consistent in demonstrating that there is no effect of aging on muscle fatigability (81–83). These investigations all examined leg muscles, but varied in the use of submaximal versus maximal contractions, and sustained versus intermittent efforts. Despite the relatively greater proportion of type 1 fibers available for force generation, fatigue-resistance of aged muscle is not enhanced. The reason for this is not known, but the capacity of aged muscle may not be optimized due to a lack of training (84, 85). Otherwise, healthy, fit older individuals could potentially experience less metabolic stress during a submaximal exercise bout than sedentary young adults (86).

Another functional implication of the slowing of contraction is that it gives older muscle a reduced capacity for power (87) or rapid production of force in protective reflexes (88), thereby amplifying the impact of muscle weakness on mobility (89, 90). Earlier research has already shown that the peripheral segmental reflex loop has a significant delay in older subjects (91, 92), and Vandervoort & Hayes (88) demonstrated a 45% difference between young and very old women in the rate of torque development of an H-reflex contraction of the ankle plantarflexors. Furthermore, the capacity of a twitch to potentiate due to prior activation is reduced with increased age (20, 72, 93). Hicks et al. (83, 93) have noted that both muscle excitability and twitch potentiation appear to be enhanced following strength training, but it remains to be determined if actual reflex function can be influenced by an exercise program. Contractile changes with aging are also coupled with an increased passive resistance of the connective tissue structures of the antagonistic muscles, a factor that acts against rapid elongation and therefore rotation of aged joints, particularly in older women (94).

Strength training in older adults

Can appropriate exercise programming reduce or prevent the age-related changes in muscle structure and function? The adaptability of aging muscles, in particular the possibility of improving muscle strength and increasing muscle mass in older adults, is receiving more and more interest from researchers, health care workers and older adults themselves who want to maximize the quality of their retirement. Many studies have related low muscular strength with other conditions such as increased susceptibility to falls and fractures and increasing dependence in older adults (95, 96). Also, as much as half of the loss in aerobic fitness (relative to body weight) seen with aging has been attributed to a loss of muscle mass (97). Thus, many of the physical function problems seen in elderly individuals could be alleviated by improving muscle mass and strength. In this review we focus on the effects of aging on muscle strength and how strength may be improved by training. Thus, high-intensity strength training, involving near maximal lifting, is the type of resistance exercise of primary interest; for general information on the effects of exercise on older individuals, other reviews can be consulted (98–100).

Strength training can be defined as progressively overloading the neuromuscular system using near maximal muscle contractions against high resistance. Its purpose is to increase the ability to perform maximal contractions or increase muscle size. Performing sets of 10 RM loads or less are typically used for strength training, with 1 RM (one repetition maximum) being the maximum weight an individual can lift one time, and 10 RM being the weight an individual can lift exactly 10 times. These values represent 100% and approximately 70% of maximum capability for 1 RM and 10 RM, respectively.

The different methods of training and types of muscle actions used put different physiological demands on the neuromuscular system, so the adaptations would also be expected to be different (101). The different types of muscle actions include concentric (shortening), isometric (static), eccentric (lengthening), isotonic (constant load), and isokinetic (constant velocity). The 1 RM is usually reported as the maximum concentric isotonic capability for a certain movement.

In recent years, interest in the effects of strength training in older men and women has increased dramatically and the number of studies has grown exponentially. Table 3 summarizes controlled and dynamic high-intensity strength training studies in older individuals. Experimental controls for these studies included nonexercising limbs (102, 103), contralateral limbs (84, 93), sedentary self-selected subjects (107, 109) sedentary randomly selected subjects (84, 86, 105, 106, 108, 111), endurance training subjects (86) and placebo exercise subjects (112). Although the studies in Table 3 have attempted to use controls for learning or placebo effects, it should be noted that strength training studies can seldom be done as rigorously controlled randomized trials, for the following reasons: i) the inability to totally blind the subjects to the treatment; ii) subjects are volunteers from a particular community and may not be representative; and iii) the lack of blinding of the experimenters. Also, there is often a lack of reliability analysis of the testing procedures. With these limitations in mind, the research findings from these studies will be presented.

Table 3. Improvements in muscle strength following high intensity dynamic training in older individuals

Reference	Authors	Year	Sex	Age (years)	*n*	Muscle action	Duration; sets/reps	Strength gain
102	Frontera et al.	1988	M	60–72	12	Knee flex	12 weeks	1 RM: 227%
						Knee ext	3/8	1 RM: 107%
								MVC: 16/7%
86	Hagberg et al.	1989	M/F	70–79	23	Chest press	26 weeks	1 RM: 18%
						Leg ext	1/8–12	1 RM: 9%
103	Brown et al.	1990	M	60–70	14	Elbow flex	12 weeks	
							4/10	1 RM: 48%
104	Fiatarone et al.	1990	M/F	86–96	10	Knee ext	8 weeks	
							3/8	1 RM: 174%
105	Charette et al.	1991	F	64–86	13	Knee flex	12 weeks	1 RM: 115%
						Leg press	6/6	1 RM: 28%
						Hip ext		1 RM: 28%
93	Hicks et al.	1991	M/F	66.3*	11	Dorsiflex	12 weeks	1 RM: 48%
							4/10–15	MVC: 15%
84	Grimby et al.	1992	M	78–84	9	Knee ext	25 sessions	Con: 10%
						Con/ecc	Complex	Ecc: 19%
106	Judge et al.	1993	M/F	71–97	18	Knee flex	12 weeks	
							3/8–10	1 RM: 32%
107	Menkes et al.	1993	M	50–70	11	Upper/lower	16 weeks	3 RM: 45%
						body	1–2/15	PT: 32–55%
108	Nichols et al.	1993	F	67.8%	18	Upper/lower	24 weeks	
						body	3/8–10	1 RM: 18–71%
109	Rice et al.	1993	M	65–78	10	Elbow ext	26 weeks	1 RM: 30%
							4/6–8	MVC: 20%
110	Roman et al.	1993	M	67.7*	5	Elbow flex	12 weeks	
							13**/8	PT: 23–50%
111	Pyka et al.	1994	M/F	61–78	25	Upper/low	30 weeks	1 RM: 23–62%
						body	3/8	
							50 weeks	1 RM: 30–95%
112	Fiatarone et al.	1994	M/F	72–98	100	Hip/knee ext	10 weeks	
							3/8	1 RM: 113%

flex=flexion; ext=extension; 1 RM=one repetition maximum; MVC=maximal voluntary contraction; PT=isokinetic peak torque; con=concentric; ecc=eccentric; * only mean age available; ** 4 sets of isokinetic training and 3 sets of 3 free weight exercises. (All strength gains are statistically significant.)

Important strength training variables

The intensity of training seems to be a critical variable, with higher-intensity training leading to larger increases in strength. Studies involving low-intensity training in older adults report strength increases less than 20% (96). In comparison, high-intensity training (>70% of 1 RM) has resulted in increases of up to 227% in 1 RM (Table 3).

In addition to intensity, variables like the number of sets and repetitions of a given exercise, the frequency and duration of a program, the muscle group(s) exercised, and the type of testing and training, must be considered when strength training programs are analyzed. With all of these variables and different subject groups (i.e., age, gender, initial strength), direct comparison between studies is difficult. Those reported in Table 3 had training frequencies of 2 to 3 times per week, durations of 8 to 52 weeks, with most using 8 weeks or 12 weeks, and 1 to 4 sets per training session. Although Hagberg et al. (86) used one of the longest (26 weeks) programs, the first 13 weeks was a low-intensity adaptation phase, with only 1 set of each exercise done over the whole study, which may explain why the subjects only increased strength by 9 to 18%. As well, the training volume can be an important aspect of optimizing the adaptive response to strength training (113).

The increases in 1 RM strength values are variable, but 12 weeks of high intensity (>70% of 1 RM) resistance training will result in a large improvement in strength, as measured dynamically by 1 RM. However, maximal voluntary isometric contraction (MVC) changes in these same studies ranged from no change (102, 103) to an average increase of 22.6% (114). Studies done with young subjects have also shown increases in 1 RM but not MVC (115). This discrepancy may be attributed to the specificity of neural adaptations (23) or the fact that, unless strict biomechanical restrictions are adhered to, 1 RM testing may not be appropriate for measuring strength

(84). Isokinetic testing, which has more precision, has also failed to show dramatic increases in strength (84, 102, 103).

All studies referred to above have investigated isometric or concentric strength gains following training, even though eccentric muscle actions are part of most isotonic strength training exercises and most daily activities. Also, there are differences in the capabilities of older individuals when performing eccentric muscle actions versus concentric (9, 11, 13). One investigation reported that eccentric strength gains can be elicited with isokinetic eccentric testing and training (84). The subjects followed a complicated training routine with a mixture of isometric and concentric and eccentric isokinetic actions using both Cybex and Kin-Com dynamometers. Increases in eccentric strength were slightly larger than concentric, but both were much lower compared with increases reported by others for 1 RM testing.

While the previously active men in the study by Grimby et al. (84) experienced no muscle or joint problems with this type of training, eccentric actions have been shown to produce muscle damage, from which older subjects seem to recover more slowly (116). Training involving eccentric actions should certainly receive more attention, but this type of training and testing may have to be done more cautiously (117).

Mechanisms of strength gains in older individuals: adaptability of the muscle and role of the nervous system

Several factors are believed to explain strength gains following high-intensity resistance training. These include changes in muscle morphology and muscle biochemistry, muscle and connective tissue biomechanics, central nervous system activation, motor skill coordination and psychological drive (101). Only recently have studies attempted to elucidate to what extent morphological, neurophysiological and intrinsic muscle property adaptations contribute to strength gains in old people.

Moritani & deVries (114) studied how muscle hypertrophy and neural factors affected strength changes of the elbow flexors in young and older men. While both groups increased maximal isometric strength and neural activation, only the young group demonstrated significant increases in muscle cross-sectional area. They concluded that neural factors alone might be responsible for the increases in strength seen in older subjects.

In contrast, Frontera et al. (102) reported that 60- to 72-year-old men had gained 107% and 227% in knee extension and knee flexion 1 RM strength, respectively, along with an 11% increase in total muscle area of the thigh, and an increase in protein turnover. They concluded, in contrast to Moritani & deVries (114), that muscles, even of old individuals, have the potential to hypertrophy in response to high-intensity resistance training.

The different conclusions of Moritani & deVries (114) and Frontera et al. (102) may be explained by variations in training intensity, measurement techniques and/or muscle groups trained. First, the intensity of training used by the former was only 66% of 1 RM, whereas the latter used 80% of 1 RM. The measurement techniques for hypertrophy were also quite different. The earlier study (114) used anthropometry to estimate changes in muscle size, whereas the latter used computed tomography (102). More recent studies using CT scans (103) and MRI (110) have shown that high-intensity resistance training does result in muscle hypertrophy, even in nursing home residents up to 98 years of age (104, 112).

Hypertrophy of both type 1 and type 2 fibers have been demonstrated following short-term high intensity training in older adults (Table 4). There appears to be a tendency for greater hypertrophy of type 2 fibers, although this conclusion remains tentative. When changes were minor and nonsignificant, it was consistent with small strength gains (84).

A recent study reported that the rate of synthesizing proteins is similar in young and older subjects following short-term resistance training (118). This study, and those described above, provide evidence that the aging human muscle is capable of adapting to increased short-term physical demands. However, the hypertrophic changes with long-term (several months/years) training remain to be determined, and, while it is evident that aged muscle can increase in size following strength training, hypertrophy is relatively small compared with the large increase in 1 RM strength reported. Furthermore, the large increases are not fully transferrable to different modes of test-

Table 4. Increases in muscle fiber size following high-intensity, dynamic strength training in older individuals

			Muscle fiber size increase	
Reference	Authors	Year	type 1	type 2
102	Frontera et al.	1988	34%	28%
103	Brown et al.	1990	14%	30%
105	Charette et al.	1991	7%$^{\mathrm{NS}}$	20%
84	Grimby et al.	1992	8%$^{\mathrm{NS}}$	5%$^{\mathrm{NS}}$
110	Roman et al.	1993	24%$^{\mathrm{NS}}$	37%
111	Pyka et al.	1994		
	a) 15 weeks		25%	20%$^{\mathrm{NS}}$
	b) 30 weeks		48%	62%

NS represents not significant; all other changes are statistically significant ($P<0.05$).

ing (i.e., 1 RM *vs* MVC or isokinetic). This suggests that a certain amount of skill or motor coordination is required depending on the movement, and that specific neural adaptations are made to activate the prime movers while inhibiting co-contraction of antagonists following training (23).

In older adults, Brown et al. (103) found that complete (98%) motor unit activation was achieved pre- and post-training in the elbow flexors, using the interpolated twitch technique (22). While these results suggest that nervous system activation of muscle is not important, it is certainly possible that during dynamic movements, as opposed to isometric MVC maneuvers, central nervous system coordination or activation is a contributing factor (96).

Intrinsic characteristics of muscle, such as excitation/contraction coupling, muscle fiber packing density and muscle fiber composition can alter force production (101), which, in turn, may be reflected in the evoked contractile properties. Following strength training in older adults, Brown et al. (103) reported increases in rate of force development, but slowing of relaxation. They speculated that this slowing of muscles following training, in addition to the slowing following aging (20), would allow older adults to utilize lower rates of nervous system activation to achieve maximal force production. Rice et al. (109) reported a longer time to peak force but no change in any other contractile variables. They suggested that this was due to training-induced changes in muscle morphology that made the muscle more elastic or compliant. It is evident that results for contractile property changes with training are not clear and other measurements, such as joint stiffness (94, 119), may be of importance.

The ability to transfer strength gains into improved performance of daily activities would be most important for frail individuals. Fiatarone et al. (112) demonstrated increases in gait velocity (11%), stair-climbing power (28%) and spontaneous physical activity (34%) following resistance training in 72- to 98-year-old nursing home residents. Although these increments were statistically significant, the absolute changes in gait velocity were not very large, and all were small compared with the increases in muscle strength. Other variables such as muscle power may be more important in terms of performing functional tasks (87, 120).

Whither

Several factors may account for the reduction in muscle volume and concomitant loss of strength with increasing age (Fig. 5). Although knowledge of these factors has increased, more research is needed to understand the detailed mechanisms behind the structural and functional changes in the aging muscle. For example, how is concentric versus eccentric strength affected with increasing age? Are the mechanisms known to be responsible for the atrophy of the thigh muscles, also involved in the atrophy of distal leg muscles and of muscles in the arm? What is the significance of the connective tissue increase? What causes the deterioration in the nervous system and can the loss of motor units be prevented? Which age-related subcellular and molecular changes take place in individual muscle fibers and how is the function of the whole aged muscle affected?

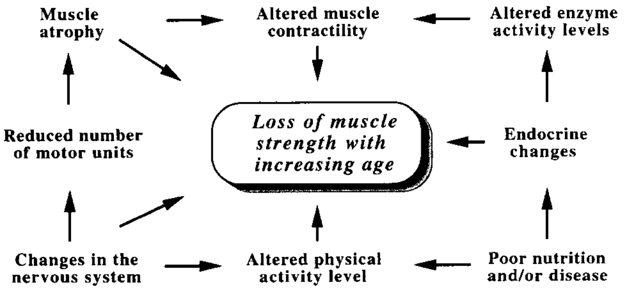

Fig. 5. Proposed mechanisms leading to the loss of muscle strength with increasing age.

The results of high-resistance strength training clearly indicate that we should never accept aging as an unalterable process of decline and loss. To successfully promote active aging, rehabilitation and physical activity for older people, several issues need to be clarified, at least partially. One of the main areas is the relative importance of muscle hypertrophy and neural adaptation for the improvement in strength, and this requires more controlled studies to decrease learning effects, tester bias and placebo effects. Furthermore, the complexity of the neural adaptation needs to be understood to make inferences about the specificity of training and the transferability of strength from the training mode to other tasks. We must also clarify to what extent functional improvements can be achieved with strength training, and how this improvement in strength can be maintained over a longer period.

Human aging and longevity have replaced birth rate as the most important issue in developed countries (121, 122). Over the next decade, we can envisage increased attention to the aging of human muscle, its structure, function and adaptability, and this affords an excellent opportunity for the medicine community as a major source of information and promotion of physical activity for this rapidly growing segment of the population.

Acknowledgements

Our results underlying this review come from studies supported by grants from different funds, in Sweden: the Research Council of the Swedish Sports Federation, the Swedish Society of Medicine, the Hans and Loo Osterman Foundation and the County Council of Norrbotten, and in Canada: Natural Science and Engineering Research Council (NSERC) and the Canadian Fitness and Lifestyle Research Institute (CFLRI).

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