ORIGINAL ARTICLE

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Muscle strength, power and adaptations to resistance training in older people

Accepted: 4 September 2003 / Published online: 25 November 2003 © Springer-Verlag 2003

Abstract Muscle strength and, to a greater extent, power inexorably decline with ageing. Quantitative loss of muscle mass, referred to as "sarcopenia", is the most important factor underlying this phenomenon. However, qualitative changes of muscle fibres and tendons, such as selective atrophy of fast-twitch fibres and reduced tendon stiffness, and neural changes, such as lower activation of the agonist muscles and higher coactivation of the antagonist muscles, also account for the age-related decline in muscle function. The selective atrophy of fast-twitch fibres has been ascribed to the progressive loss of motoneurons in the spinal cord with initial denervation of fast-twitch fibres, which is often accompanied by reinnervation of these fibres by axonal sprouting from adjacent slow-twitch motor units (MUs). In addition, single fibres of older muscles containing myosin heavy chains of both type I and II show lower tension and shortening velocity with respect to the fibres of young muscles. Changes in central activation capacity are still controversial. At the peripheral level, the rate of decline in parameters of the surface-electromyogram power spectrum and in the action-potential conduction velocity has been shown to be lower in older muscle. Therefore, the older muscle seems to be more resistant to isometric fatigue (fatigueparadox), which can be ascribed to the selective atrophy of fast-twitch fibres, slowing in the contractile properties and lower MU firing rates. Finally, specific training programmes can dramatically improve the muscle strength, power and functional abilities of older individuals, which will be examined in the second part of this review.

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Introduction

Human muscle strength, which can be defined as the maximum force generation capacity of an individual, reaches its peak between the second and third decades, shows a slow or imperceptible decrease until about 50 years of age and then begins to decline thereafter at the rate of approximately 12% to 15% per decade, with more rapid losses above the age of 65 years (Asmussen and Heeboll-Nielsen 1962; Larsson et al. 1979; Viitasalo et al. 1985; Vandervoort and McComas 1986; Borges 1989; Narici et al. 1991; Metter et al. 1997; Lindle et al. 1997). Since this trend has been measured in studies with cross-sectional design, it would not be appropriate to use of words such as "decrease", "decline", "drop", etc., which imply that the strength of the older participants in their younger age was the same as that of the younger participants. This is a questionable assumption, because the older people are of a different generation, with a lifetime of physical activity, health and nutrition that is probably unlike the habits of their young counterparts. However, as it is common practice in the literature, words such as "decrease", "decline", "drop", etc., will be used throughout this review even if inappropriate. There are few investigations with a longitudinal design that have determined how strength changes with ageing and, to the best of the authors' knowledge, the same individuals were followed for no longer than 12 years (Aniansson et al. 1986; Kallman et al. 1990; Bassey and Harries 1993; Greig et al. 1993; Winegard et al. 1996; Rantanen et al. 1997; Frontera et al. 2000a). Most of the studies indicate that the decline in strength occurs at a higher rate than reported in cross-sectional investigations (Aniansson et al. 1986; Kallman et al. 1990; Bassey and Harries 1993; Winegard et al. 1996; Frontera et al. 2000a), although no change (Greig at al. 1993) or even a

slight increase in strength (Rantanen et al. 1997) have both been measured. Direct comparisons between groups of young and older individuals have shown that the quadriceps muscles of older people aged around 70 years have approximately 60% of the force-generating ability of young individuals aged 20-30 years (Young et al. 1984, 1985; Klitgaard et al. 1990; Häkkinen and Häkkinen 1991; Overend et al. 1992a; Frontera et al. 2000b), ranging from a minimum of 56% (Klitgaard et al. 1990) to a maximum of 76% (Häkkinen and Häkkinen 1991; Overend et al. 1992a). It is likely that this variability of strength differences reflects different study populations, levels of physical activity, muscle groups investigated and testing methodologies. Moreover, Short and Nair (1999) pointed out that the decline of muscle function in the whole population may be even greater than that reported, because many older individuals are excluded from research studies for the presence of disease. Finally, further evidence of this inevitable process of decay is given by measurements performed on master athletes, whose performance inexorably decline as they age, although 70-year-old athletes can have levels of strength, power and other functional capacities equivalent to those of 20-year-old sedentary individuals (Moore 1975; Meltzer 1994; Pearson et al. 2002).

The loss of strength with ageing is apparently true for both men and women (Danneskiold-Samsoe 1984; Vandervoort and McComas 1986; Borges 1989; Frontera et al. 1991; Lindle et al. 1997). The early study of Asmussen and Heeboll-Nielsen (1962) reported that women began to decline at an earlier age than men, but this observation was not confirmed in further studies. However, it is evident that women are weaker than men in absolute strength of various muscle groups in all stages of life (Danneskiold-Samsoe 1984; Vandervoort and McComas 1986; Borges 1989; Frontera et al. 1991; Lindle et al. 1997). For example, Frontera et al. (1991) reported that women had 60% and 59% the strength of men in the lower extremities when they were tested at slow and fast isokinetic speeds, respectively (the term isokinetic indicates that the movement of the displaced body segment is performed at constant angular speed). Similarly, Borges (1989) found women in different age groups to have 66% and 53% the isokinetic peak torque of men in the knee-extension and knee-flexion, respectively. Although males and females appear to show comparable age-related trends when maximal strength is referred to the unit of muscle cross-sectional area (CSA) (Vandervoort and McComas 1986; Winegard et al. 1996; Lindle et al. 1997), in the latter stages of life absolute values of maximal strength in women can approach the minimal levels necessary to accomplish daily activities, thus suggesting that women should be the first target group in intervention and rehabilitation studies (Skelton et al. 1994).

Regional anatomical differences in the loss of strength have also been reported in the literature (Viitasalo et al. 1985; Frontera et al. 1991; Rantanen

et al. 1997; Lynch et al. 1999). The proximal muscles of the lower extremities are more affected by strength losses than those of the upper extremities, which in older people has been ascribed to a decreasing use of lower compared with upper limb muscles (Viitasalo et al. 1985; Frontera et al. 1991; Lynch et al. 1999). This is supported by the fact that age-related morphological changes are more pronounced in the quadriceps than in the biceps brachii muscle (Aniansson et al. 1986). By contrast, longitudinal data of Rantanen et al. (1997) showed that older men and women slightly increased their knee extensor strength from 75 to 80 years, as opposed to a decrease in upper extremity and trunk strength. The investigators suggested that everyday activities at low intensity might have provided sufficient stimulus to the knee extensor musculature. This is in contrast, however, with the evidence that activities of daily living require little quadriceps strength, as during normal walking the quadriceps is activated only briefly at the beginning and end of the gait cycle (O'Toole 1997). Moreover, individuals with weak quadriceps tend to supplement knee extensor movements with other muscles, such as arm muscles to get up from a chair, or alter their behaviour to avoid activities such as climbing stairs.

Muscle strength can be tested using three different modalities: isometric, dynamic or isokinetic (Frontera and Meredith 1989; Abernethy et al. 1995). Isometric or static strength is the maximum force that can be exerted against an immovable object, which corresponds to the maximum that can be measured in humans. Dynamic strength is the heaviest weight that can be lifted, whilst isokinetic strength is the maximal torque that can be exerted against a pre-set rate-limiting device. Maximum strength is measured during isometric contractions, in which there is no change in muscle length, whilst power is generated in actions that involve movement and is calculated as the product of force and speed at which movement occurs. Fewer studies have been conducted on muscle power as compared to strength, possibly due to methodological difficulties, as will be discussed later in this review.

Lower levels of strength and, to a greater extent, power are associated with functional limitations in daily living activities (Aniansson et al. 1980; Avlund et al. 1994; Skelton et al. 1994; Foldvari et al. 2000). In addition, muscle weakness is associated with an increased risk of falls (Tinetti et al. 1988; Campbell et al. 1989; Wolfson et al. 1995), hip fractures (Aniansson et al. 1984; Langlois et al. 1998) and adverse physiological changes such as loss of bone mineral density (Sinaki et al. 1986), which may predispose to osteoporosis.

This review begins with a systematic examination of the main causes of muscle strength loss in old age. This is then followed by a review of the few studies specifically investigating muscle power, with power being more related to daily functional activities than strength per se. Finally, the focus is on how these age-related changes in muscle function can be improved through appropriate training programmes. Some of the studies on strength training in older people will be critically scrutinized, followed by the more limited number of investigations specifically aimed at improving muscle power and the few works looking at the effects of training on selected functional abilities.

Causes of muscle strength loss in old age

Muscle size and morphology

Muscle size is reduced with ageing and this quantitative loss of muscle, referred to as "sarcopenia" (Evans 1995), affects the generation of force. Sarcopenia has been demonstrated using various techniques, which include measurements of total body potassium (Allen et al. 1960) or creatinine excretion (Tzankoff and Norris 1977), histochemical analysis of muscle fibres, in either biopsy (for example Larsson et al. 1979) or autopsy (Lexell et al. 1983, 1988) specimens, and imaging methods such as ultrasonography (Young et al. 1984, 1985; Häkkinen and Häkkinen 1991), computerized tomography (CT) (Rice et al. 1989; Klitgaard et al. 1990; Overend et al. 1992b) and, more recently, magnetic resonance imaging (MRI) (Jubrias et al. 1997; Kent-Braun and Ng 1999; Kent-Braun et al. 2000).

In the early study of Allen et al. (1960) muscle mass was reduced by 23% in individuals from 20 to 80 years, as estimated from measurements of total body potassium. Similarly, Tzankoff and Norris (1977), at the end of the 1970s, reported that the active muscle mass, as revealed by creatinine excretion, was 35% less in 80-yearold individuals as opposed to those in their twenties. Grimby and Saltin (1983) later pointed out that the loss of muscle mass, which had been reported in the studies of Allen et al. (1960) and Tzankoff and Norris (1977), was in the same order of magnitude as the decline of strength in leg, back and arm muscles, thus relating the weakness of older people entirely to muscle wasting.

Starting in 1977 with Tomonaga, many investigators have carried out a quantitative histochemical analysis of muscle samples, obtained either by biopsy (for example Larsson et al. 1979) or autopsy (for example Lexell et al. 1983, 1988), and have attributed the loss of muscle mass in older people, at the microscopic level, to a reduction in the number and size of muscle fibres. An extensive review of these studies is beyond the purposes of this manuscript and therefore the reader is referred to the work of Lexell (1995). The loss of muscle tissue in older people has been attributed to reduced numbers of both slow-twitch fibres and fast-twitch fibres, plus a reduction in the CSA of single fibres, especially of type II. Fasttwitch fibres are intrinsically stronger than slow-twitch fibres and therefore muscles with the same area, but occupied by a relatively smaller area of fast-twitch fibres, will be able to generate less force (Jones and Round 1990).

With the introduction of modern radiological imaging techniques, it has been possible to estimate muscle mass more directly. Sarcopenia has been documented with ultrasound imaging in the works of Young et al. (1984, 1985), who measured a 25% and 33% smaller quadriceps CSA in older men and women, respectively, (age range 70-81 years) than in young individuals (age range 20-29 years). Also Häkkinen and Häkkinen (1991) have shown a 27% smaller mid-thigh CSA of the quadriceps in older women aged between 66 and 75 years, as compared to the young, aged between 26 and 35 years. In these studies, however, muscle CSA may have been overestimated, particularly in older people, due to the presence of fat and connective tissue within the muscle belly, which cannot be detected and separated in the ultrasound scan. This problem has been overcome by the use of CT and MRI (Rice et al. 1989; Overend et al. 1992b; Kent-Braun et al. 2000), which enabled investigators not only to outline the muscle compartment area on each scan, at different levels of section, but also to estimate the muscle contractile component separately from the intramuscular noncontractile tissues (i.e. connective and fat tissue). The correlation coefficient between cadaver sections of human skeletal muscle and corresponding CT or MRI scans approached unity, with the relative difference between cadaver and imaging measurements being 1.3% for both techniques (Mitsipoulos et al. 1998). The use of both these advanced imaging techniques has provided further evidence of the wasting of contractile muscle occurring in older people with a substantial increase of fat and connective tissue, both within the muscle and in the overall body (Rice et al. 1989; Overend et al. 1992b; Jubrias et al. 1997; Kent-Braun and Ng 1999; Janssen et al. 2000; Kent-Braun et al. 2000; Macaluso et al. 2002). In particular, the recent data of Janssen et al. (2000), which present reference values for whole-body skeletal mass of 468 individuals from 18 to 88 years, show a decline after the end of the fifth decade of 1.9 and 1.1 kg/decade in men and women, respectively, with a preferential decrease in the lower body.

Comparing the time course of the decline in muscle mass with that of the decline in force indicates that the decline in force with ageing is generally greater and starts sooner than that of muscle bulk (Bruce et al. 1997). Similarly, Kallman et al. (1990) have shown that there is no relationship between how quickly subjects lose muscle mass, as indicated by the slope of creatinine excretion versus age, and how fast they lose grip strength, as indicated by the slope of grip strength versus age. This suggests that there may be other causes contributing to the decline in strength, other than muscle wasting, which are specific to the remaining muscle. In further support of this observation, some investigators have shown that muscle strength of the knee extensors is highly correlated with muscle size, but this relationship is higher in young than older populations (Häkkinen and Häkkinen 1991; Overend et al. 1992a). In most of the research studies, however, it is the ratio between muscle strength and CSA, referred to as specific strength, which has been compared between young and older people, or examined across the life span, in order to determine whether strength losses could be attributed entirely to reduced muscle mass or whether other factors had to be taken into account (Young et al. 1984, 1985; Klitgaard et al. 1990; Häkkinen and Häkkinen 1991; Phillips et al. 1993; Jubrias et al. 1997; Kent-Braun and Ng 1999; Frontera et al. 2000b). The results of these studies are still controversial. Young et al. (1985) and Klitgaard et al. (1990) have reported that the isometric specific strength of quadriceps muscle was 19% and 27% smaller, respectively, in young than older sedentary men. Similarly, other studies have observed a drop of isometric (Phillips et al. 1993) and isokinetic (Jubrias et al. 1997) specific strength of adductor pollicis and quadriceps muscles, respectively, in older subjects of both genders. Conversely, Kent-Braun and Ng (1999) and Frontera et al. (2000b) have reported no age-related differences in isometric strength of the ankle dorsiflexors and isokinetic strength of the knee extensors, respectively, after adjusting for CSA. Young et al. (1984) and Häkkinen and Häkkinen (1991) have also indicated that the quadriceps weakness of healthy women in their seventies can be adequately explained by the similarly smaller size of the muscle group. All of these investigators (Young et al. 1984, 1985; Klitgaard et al. 1990; Häkkinen and Häkkinen 1991; Phillips et al. 1993; Jubrias et al. 1997; Kent-Braun and Ng 1999; Frontera et al. 2000b) have used the area of muscle cross-section at right angles to the long axis of the limb, referred to as anatomical CSA, to interpret data on muscle strength relative to muscle size in ageing muscle. However, in pennate muscles, such as the quadriceps, fibres run obliquely to the force-generating axis and insert into the tendon with an angle, referred to as "angle of pennation" (Narici et al. 1992). Therefore, the anatomical CSA cuts a limited number of fibres, whilst it is the sum of the cross-sectional areas of all the muscle fibres within the muscle which should be used. This has been referred to as physiological CSA (PSCA), which can be calculated by measuring, with a combined use of MRI and ultrasonography, three parameters: muscle volume, fibre length and pennation angle. It has been recently found that pennation angle and fibre length in the human gastrocnemius were 13% and 8% less in older than young individuals, respectively (Narici et al. 1999). Therefore, PCSA is expected to decrease with ageing at a different rate than anatomical CSA, which may lead to a misinterpretation of the ratio between force and CSA (Narici 1999). Recently, Miyatani et al. (2001) have suggested that determination of muscle volume is a way of approximating its physiological CSA. Moreover, because the muscle volume can be expressed as a product of physiological CSA and muscle fibre length, torque relative to muscle volume may theoretically be considered as an index with the same dimension as that of muscle force relative to physiological CSA, i.e. specific tension $(kN \cdot m^{-2})$ (Miyatani et al. 2001). In light of

these considerations, Macaluso et al. (2002) have expressed the specific tension of the knee extensors and flexors as the ratio between maximum isometric torque and contractile muscle volume, distinguished from intramuscular non-contractile tissue, and compared it between young and older women. Women in their seventies showed a lower specific tension than women in their twenties, thus suggesting that the lower level of muscle strength in older women is not completely explained by their smaller contractile muscle mass, but also by other factors, which will be presented in the following paragraphs of this review.

Muscle excitability and contractility

Narici (1999), in his comprehensive review of studies on the changes of muscle contractile properties with ageing, has attributed the loss of strength in older people not only to reduced muscle mass but, more exhaustively, to reduced excitable muscle mass. Therefore, it is suggested to take into account only the amount of muscle that is functionally active, as indicated by the term "excitable". This is strictly dependent, in turn, on the integrity of both the muscle fibres and the nerve cells that control them, namely the motoneurons. Neural and muscular systems cannot therefore be separated and it is appropriate to consider muscle fibres and motoneurons as a whole. A single motoneuron and its family of innervated muscle fibres have been defined by Sherrington (1929) as the motor unit (MU). Fast-twitch MUs are composed by relatively large motoneurons with fast conduction velocities, which generally innervate between 300 and 500 muscle fibres (McArdle et al. 1996). On the contrary, slow-twitch MUs are composed of smaller motoneurons with slow conduction velocities, which innervate a smaller number of fibres. There are at least nine electrophysiological techniques of MU estimation in humans, most of which involve applying electric shocks of varying intensity to a peripheral nerve and measuring the evoked responses in the muscle (for review see McComas 1998). The number of MUs is obtained by comparing an average parameter of the single MU, usually its action potentials, with the corresponding parameter of the whole muscle. The relative size of MUs is determined by comparing their mechanical responses to single or maximal repetitive stimulation, which are referred to as twitch or tetanic contractions, respectively. MUs have been shown to be reduced with ageing in both number and size, thus affecting the capacity of skeletal muscles to produce force (Brown et al. 1988; Doherty and Brown 1993; Doherty et al. 1993). This is in agreement with previous evidence of a reduced number of limb motoneurons, in the human lumbosacral cord, by approximately 25% from the second to the tenth decade (Tomlinson and Irving 1977). Consistent with this observation is the reduction in the number and diameter of motor axons in the ventral roots (Kawamura et al. 1977a, 1977b), which is accompanied by slower axonal

conduction velocity (Metter et al. 1998; Wang et al. 1999). In animal studies, the selective atrophy of fasttwitch fibres, which has been reported earlier in this review, has been ascribed to the progressive loss of motoneurons in the spinal cord with initial denervation of fast-twitch fibres and reinnervation of these fibres by axonal sprouting from adjacent slow-twitch MUs (Brooks and Faulkner 1994). This phenomenon of remodelling is supported, at the microscopic level of muscle analysis in humans, by morphological changes similar to those occurring in motoneuron diseases and chronic neuropathies, which include the presence of larger groups of muscle fibres of the same histochemical type, referred to as fibre type grouping, small and dark fibres with a peculiar geometrical shape, referred to as angulated fibres, and group atrophy (Jennekens et al. 1971; Lexell and Downham 1991). Recent results of increased coexpression of myosin heavy chain (MHC) isoforms in the same fibre as measured with electrophoretic techniques, which will be presented later in this review, are further evidence of this process of ongoing denervation and reinnervation (Andersen et al. 1999).

Results of Galea (1996) suggest that the reduction of excitable muscle mass in the upper limbs is of neuropathic origin, i.e. denervation of MUs due to loss of peripheral motoneurons, for distal muscles, but of myopathic origin, i.e. atrophy of muscle fibres, in proximal muscles. The neuromuscular excitability has been evaluated by measuring the muscle's electrical response evoked by the electrical stimulation of the motor nerve. An M-wave is the result of the direct depolarisation of motoneurons that directly innervate muscle fibres, with its area and amplitude being a measure of their excitability. The number of MUs has been estimated by comparing the average area of a sample of MU action potentials, which are obtained by incremental stimulation of the peripheral nerve, and the area of the maximum M-wave, which is the compound action potential of a muscle. The authors studied the number of MUs and the maximum M-wave of both the thenar muscle, a distal muscle, and the biceps brachii, a proximal muscle, in individuals in their eighties as compared to those in their twenties. In the thenar muscle, older individuals had maximum M-wave area and amplitude values that were 22% and 33% lower, respectively, than the young subjects' values, with a 50% lower number of MUs, thus revealing a loss of MUs with the presence of collateral reinnervation. In contrast, in the biceps brachii, the area and amplitude of maximum M-waves were 50% and 30% less in the older than in the young subjects, respectively, with no significant differences in the number of MUs, thus indicating the presence of less excitable muscle mass entirely due to fibre atrophy.

The older muscle is not only atrophied, but is also slower (Vandervoort and McComas 1986; Narici et al. 1991; Roos et al. 1999), tetanizes at lower fusion frequencies (Narici et al. 1991; Kamen et al. 1995; Connelly et al. 1999; Roos et al. 1999), and is more resistant to isometric fatigue than the young muscle (Narici et al.

1991; Bilodeau et al. 2001a). Slowing in the contractile properties has been demonstrated in various muscles of the lower limbs (Vandervoort and McComas 1986; Roos et al. 1999), and in the adductor pollicis muscle (Narici et al. 1991), by measuring the duration of twitch contraction. Tibialis anterior, tibialis posterior (Vandervoort and McComas 1986) and vastus medialis (Roos et al. 1999) are slower in individuals over 73 than in young people in their twenties, as demonstrated by the longer time taken not only to reach the peak of tension but also to relax after the twitch. Similarly, the maximum relaxation rate has been shown to decline from 20 to 91 years of age in the adductor pollicis muscle (Narici et al. 1991). The reason for this slower relaxation rate (or longer twitch contraction duration) is probably related to the selective atrophy of type II fibres. The muscle relaxes at a lower rate as a result of the predominance of type I fibres, which are slower. At the microscopic level of muscle analysis, the slower relaxation rate can be ascribed to a reduction in sarcoplasmic reticulum activity (Klitgaard et al. 1989; Delbono et al. 1997; Hunter et al. 1999) and actin sliding speed on myosin (Höök et al. 2001). As a result of slowing of relaxation and probably of type II fibre atrophy, it has been shown that muscles of older individuals demonstrate tetanic fusion, i.e. a maximum maintained contraction in response to repetitive stimulation, at lower frequencies of stimulation than is required for young adults, thus enabling the individual MUs to use lower firing frequencies to achieve a full contraction (Narici et al. 1991; Kamen et al. 1995; Connelly et al. 1999; Roos et al. 1999). Slowing of relaxation and type II atrophy may also explain why older people demonstrated more resistance to isometric fatigue that young individuals (Narici et al. 1991), a process which is referred to as the "fatigue-paradox" (Narici 1999).

Recently, Scaglioni et al. (2002) have shown that the excitability in the spinal reflex pathway, expressed as the ratio between the maximum H-reflex and the maximum M-wave, is functionally impaired in older male individuals. Scaglioni et al. (2002) concluded that the impaired functionality of the reflex pathway with ageing, in addition to the lack of changes following resistance training as will be mentioned later in this review, suggests that the $H_{\rm max}/M_{\rm max}$ ratio may be related to degenerative phenomena rather than physical deconditioning. At higher levels of the central nervous system, there are still conflicting results on the possibility of a reduction in the descending drive from supraspinal centres to the motoneurons during maximum voluntary contractions in older individuals, which would be a further explanation for the loss of muscle strength with ageing (Phillips et al. 1992; De Serres and Enoka 1998; Connelly et al. 1999; Harridge et al. 1999b; Kent-Braun and Ng 1999; Roos et al. 1999; Yue et al. 1999; Bilodeau et al. 2001a; Jakobi and Rice 2002; Scaglioni et al. 2002). Some experimenters showed by a twitch interpolation technique, a method based on delivering one or a brief series of electrical stimuli to the motor axons of muscles

during maximum voluntary contraction, that older adults were not able to maximally activate a muscle or muscle group (Harridge et al. 1999b; Yue et al. 1999; Bilodeau et al. 2001a). Other investigators, however, demonstrated that a superimposed stimulus, in the form of a single twitch or a short tetanus, added little or nothing to the volitional force of older people (Phillips et al. 1992; De Serres and Enoka 1998; Connelly et al. 1999; Kent-Braun and Ng 1999; Roos et al. 1999; Jakobi and Rice 2002; Scaglioni et al. 2002). It must be noted that central failure in activation was measured in very old individuals by Harridge et al. (1999b) and that not enough practice may have been given to the subjects in measuring maximum voluntary contraction by Yue et al. (1999) and Bilodeau et al. (2001a). The possibility of underestimating the "real" maximum should therefore be discounted if at least one session of familiarization is practised (Jakobi and Rice 2002) and if the subjects are not too old. Narici (2001) pointed out that activation capacity could be muscle specific, as it appears to be preserved in distal muscles of both upper and lower extremities (Vandervoort and McComas 1986; Phillips et al. 1992), but this issue deserves further investigation as conclusive results on the activation capacity of a muscle may largely depend on the stimulation technique that is adopted. In fact, Behm et al. (2001) have recently indicated that tetanic stimulation superimposed upon single maximal or multiple contractions seems to provide the most valid measure of muscle inactivation. Finally, the authors of this review suggest that voluntary strength testing should be preferred, since electrical stimulation determines a full synchronization of MUs (Solomonow et al. 1994), which is unlikely to occur in real life.

Surface electromyography is a non-invasive method that has been used often to monitor changes due to ageing in the overall neural activation of both agonist and antagonist muscles which, in turn, affects the generation of force (Merletti et al. 1992; Esposito et al. 1996; Häkkinen et al. 1998a; Izquierdo et al. 1999; Merletti et al. 2002). Inter-subject comparisons of sEMG parameters as indicators of muscle function are limited by the presence of skin, subcutaneous and fat layers between the muscle and the recording electrodes, which have a filtering effect on the signal (De Luca 1997). Therefore, although it is evident from the data reported in various studies (Moritani and de Vries 1980; Häkkinen and Häkkinen 1995; Häkkinen et al. 1998c) that the absolute values of sEMG amplitude were lower in groups of older individuals as compared to young or middle-aged subjects, most of the investigators did not remark on the physiological meaning of this difference, with the exception of Esposito et al. (1996) and Merletti et al. (2002). The authors speculated that the lower RMS in the biceps brachii of individuals in their seventies, as compared to those in their twenties, may be due not only to the different thickness or conductivity of the layers between the muscle and the recording electrodes, but also to the different MU firing rates between the two

groups. This is supported by the observation of a decrease in the maximal MU firing rate with ageing in studies where the intramuscular EMG signal was recorded (Kamen et al. 1995; Connelly et al. 1999; Erim et al. 1999). The lower sEMG amplitude in older people has also been ascribed to the reduced number of MUs (Esposito et al. 1996), in agreement with the observation made by others with electrophysiological techniques of MU estimation (Brown et al. 1988; Doherty and Brown 1993; Doherty et al. 1993), which are reported at the beginning of this paragraph. In agreement with Esposito et al. (1996) and Merletti et al. (2002), Macaluso et al. (2002) have attributed the smaller RMS in older individual to either a smaller number of recruited MUs or a decreased firing rate of the individual MUs. As an additional factor to explain the smaller RMS, the authors have suggested the possibility of a decreased MU synchronization. However, the relative roles played by MU recruitment, MU firing rate and synchronization of the individual MUs cannot be distinguished with surface EMG. Some authors (Häkkinen et al. 1998a; Izquierdo et al. 1999), alternatively, used the sEMG to measure the coactivation of antagonist muscles, which is referred to the maximum EMG activity of the same muscle group during the agonist action. In this measure the influence of subcutaneous and skin layers can be discounted, although it may increase the danger of cross-talk from nearby muscles (Solomonow et al. 1994), thus contaminating the signal and misleading its interpretation. Coactivation, also referred to as cocontraction, may serve to protect and stabilize the joint during forceful contractions (Baratta et al. 1988). The higher levels of antagonist coactivation, which have been observed in 70-year-old men and women as opposed to 40- and 20year-old individuals (Häkkinen et al. 1998a; Izquierdo et al. 1999; Macaluso et al. 2002), could be an additional explanation for the age-related decline in force production. In other words, the net force exerted about a joint during a given action, e.g. knee extension, would be reduced in older people due to the greater simultaneous activation of the muscles exerting a torque in the direction which is opposite to that of the movement (i.e. hamstrings).

Comparisons between young and older individuals in the frequency-domain parameters of sEMG have been performed during sustained isometric contractions of the biceps brachii (Bilodeau et al. 2001b; Merletti et al. 2002) and tibialis anterior muscles (Merletti et al. 1992). A decline in median frequency (MDF), mean frequency (MNF) or other parameters of the power spectrum, which can be attributed to muscle fatigue, has been observed in both young and older individuals, with the rate of decrease of spectral parameters being lower in the older subjects. This observation further supports the "fatigue-paradox" reported in the previous pages (Narici et al. 1999), which can be ascribed to selective atrophy of type II fibres, slowing in the contractile properties, and lower MU firing rates of the older muscle. By contrast, Hara et al. (1998) and Bilodeau et al. (2001a) did not find significant differences between young and older subjects in the decline of spectral parameters of the abductor digiti minimum and elbow flexors, respectively, during sustained contractions. The interpretation of these results is unclear. Hara et al. (1998) have explained the occurrence of a similar decline in spectral parameters of young and older individuals with ischemia, which is due to a stronger muscle contraction in the young and to a smaller capillary bed in the older subjects. This would result in a similar decrease in the two groups of the pH of interstitial fluids, as blood flow determines the rate of metabolites' removal, thus affecting the decline in spectral parameters. Merletti et al. (2002) attributed the results of Bilodeau et al. (2001a) to the lack of specific criteria in selecting the best electrode location.

Tendinous factors

Human tendons are responsible for the transmission of force from muscles to bones and in vitro studies have shown that ageing is associated with a decrease in their stiffness (Vogel 1991). Only in recent times have tendon mechanical properties been studied in vivo using ultrasonography (Maganaris 2001; Kubo et al. 2003; Reeves et al. 2003a, 2003b). A lower gastrocnemius tendon stiffness, reported as the ratio between force and tendon elongation, was measured in a group of six older individuals in their seventies with respect to a control group of six healthy young adults in their twenties (Maganaris 2001). The older tendons were more compliant in the higher regions of the maximal tendon force, thus suggesting that older individuals may operate closer to muscle optimal length as a compensatory mechanism for the reduction in force (Maganaris 2001; Reeves et al. 2003b). A functional consequence of the reduced tendon stiffness in older people is likely to be a decrease in the rate of force development, affecting for example the time necessary to decelerate body mass, a factor related to the prevention of falls (Kubo et al. 2003; Reeves et al. 2003b). Increased tendon compliance would also increase the likelihood of strain injury (Reeves et al. 2003a). The mechanisms contributing to reduced tendon stiffness are unclear, with decreased diameter and packing density of collagen fibrils and changes in collagen crimp structure being likely factors (Reeves et al. 2003b).

Hormonal factors

A decline in the levels of many hormones has been measured in older people, particularly growth hormone (GH) (Rudman et al. 1990; Welle et al. 1996a), insulinlike grow factor 1 (IGF-1) (Butterfield et al. 1997), testosterone (Tenover 1992; Urban et al. 1995; Baumgartner et al. 1999) and oestrogen (Phillips et al. 1993; Taaffe et al. 1995; Bassey et al. 1996; Skelton et al. 1999; Onambele et al. 2001), but how these changes are related to strength and power is still largely unclear (Short and Nair 1999).

The action of GH, which is known to promote growth, protein synthesis and fat mobilization, is mediated by IGF-1 (Rooyackers and Nair 1997). The hormone deficiency, which has been measured in older individuals (Rudman et al. 1990), determines a reduction in muscle mass and an increase in fat mass. The administration of recombinant human GF to healthy older adults for 1 month increased circulating IGF-1 and led to a 50% increase in mixed muscle protein synthesis, as measured using biopsy samples (Butterfield et al. 1997). However, 3 months of treatment with slightly higher doses did not produce any significant change in protein synthesis of another group of older subjects, although muscle mass and strength increased (Welle et al. 1996a). Yarasheski at al. (1992, 1995) have suggested that, as adding GH to a 12- or 16-week resistance training programme led to an increase in fatfree mass and whole body protein synthesis but not in mixed muscle protein synthesis, the hormone enhanced protein synthesis in non-muscle tissues. Taaffe et al. (1994, 1996) gave evidence that administering GH during the final 10 weeks of a 24-week resistance training programme did not produce any further gains in muscle size and strength. Harridge and Young (1998), in their notable review on skeletal muscle in older people, pointed out that a treatment for life with GH may lead to gains that may be equally achieved with exercise training, with the latter having no undesirable sideeffects of drug administration, such as fluid retention, with consequent joint swelling and arthralgias, or hypertension, atrial fibrillation, gynecomastia, and hyperglycemia. Undesirable side-effects were also observed after administration of IGF-I (Butterfield et al. 1997), which was associated with an increase in protein synthesis, but muscle strength and size were not monitored, thus requiring further investigation.

It is known that testosterone has a trophic action on skeletal muscle, which is mediated by androgen receptors in the myofibrils (Celotti and Negri Cesi 1992). Iannuzzi-Sucich et al. (2002) recently reported that bioavailable testosterone is a strong predictor of muscle mass in men, together with body mass index, strength and power. As many changes associated with testosterone deficiency in young men, such as muscle atrophy and weakness, are similar to the changes associated with the declined testosterone levels in older men, it has been suggested that testosterone supplementation may prevent or reverse the effects of ageing (Gruenewald and Matsumoto 2003). Serum testosterone increased following hormone replacement to a level comparable to that of young men, with a significant gain in muscle mass after 3 months (Tenover 1992). In the study of Urban et al. (1995), administering testosterone to hormone-deficient men for 4 weeks was accompanied by an increase in both strength and mixed protein synthesis. Kraemer et al. (1999) have shown that older men

showed a significant increase in testosterone levels in response to resistance training. Häkkinen and Pakarinen (1994) suggested that the balance between anabolic and catabolic hormones in ageing men is associated with muscle atrophy and decreased voluntary force production, as the ratio between circulating levels of serum testosterone and serum cortisol correlated with muscle CSA and strength. Izquierdo et al. (2001) have shown that serum total testosterone and free testosterone correlated with the magnitude of the training-related increase in strength and power output in both groups of middle-aged and older men. Androgens also appear to be responsible for the reduced release of neurotransmitters and other neurotrophic agents that, in turn, effect the partial denervation of muscle fibres and the consequent sarcopenia (Gutmann and Hanzlikovà 1970, cited in Narici 1999), as reported earlier in this review. In a recent cross-sectional study, which involved 121 male and 170 female volunteers aged 65-97 years (Baumgartner et al. 1999), a significant correlation between muscle mass and serum free-testosterone was found in men, whilst there was no association between oestrogen levels and strength in women. However, oestrogen levels in women, which fall at menopause, may play a role in the loss of force, but conflicting results have been found in postmenopausal women who were receiving hormone replacement therapy (HRT) (Phillips et al. 1993; Taaffe et al. 1995; Bassey et al. 1996; Skelton et al. 1999; Onambele et al. 2001). In the study of Phillips et al. (1993), 25 postmenopausal women, who had been on HRT for between 1 and 25 years, showed a 26% higher specific strength in the adductor pollicis muscle than those not receiving HRT. Similarly, another group of postmenopausal women treated with HRT for 6-12 months increased their strength by 12%, as opposed to a slight decline in the control group, with both groups being accompanied by no significant change in muscle CSA (Skelton et al. 1999). A follow-up study after 2–4 years on the same population showed that the benefit of HRT on the isometric muscle strength of adductor pollicis was maintained in those women who continued treatment beyond 1 year, although no further increase in muscle strength was found (Onambele et al. 2001). However, other studies suggest that oestrogen status does not have any effect on the maximal muscle strength of older women (Taaffe et al. 1995; Bassey et al. 1996).

Levels of physical activity

It has been shown that the amount of physical activity decreases with ageing but it is unclear whether this is a cause or an effect of the age-related loss of muscle function (Harridge and Young 1998). It seems that the decrease in strength with ageing cannot be explained only on the basis of a decreased level of physical activity, since also highly competitive veteran sportsmen inexorably decline (Meltzer 1994; Pearson et al. 2002). In addition, muscle disuse results in a reduction in muscle fibre size (Ferretti et al. 1997) and not, like ageing, in muscle fibre number (Larsson et al. 1979; Lexell et al. 1988). As a limitation of current studies, habitual physical activity levels have often been reported in descriptive rather than quantitative terms, making them difficult to interpret (O'Toole 1997). For example, individuals were classified as inactive if they participated in normal activities of daily living or sedentary leisure-time activities and active if they participated in moderated physical activity more than once a week or had physically demanding jobs (Borges 1989). In another study (Rantanen et al. 1997), the active category was made by individuals reporting at least 1 or 2 h a week of moderate activity, but include also individuals involved in strenuous activities several times a week. Interestingly, O'Toole (1997) pointed out in her editorial that it is intuitive to think that higher activity levels should preserve strength better, but further studies are required to see whether habitual low to moderate intensity activity for just a few hours a week can provide an adequate stimulus to maintain muscle strength and function. The author reported the results of Rantanen et al. (1997), who observed similar rates of changes in strength over a period of 5 years in individuals classified as active, who maintained their level of physical activity, and those classified as sedentary and remained sedentary. However, individuals who were sedentary initially and became more active were able to slow down their decline in strength, even though their level of strength remained lower than that of active individuals. Those who were active initially but for some reason became sedentary, without changes in their health status, incurred in the highest rate of strength decline.

Muscle power in older people

Muscle power, i.e. the rate of performing mechanical work, is also significantly reduced with advancing age (see for example Bassey et al. 1992; Ferretti et al. 1994; De Vito et al. 1998). In this review, muscle power will be considered as that generated in a single explosive movement, lasting a fraction of a second, where muscle metabolism does not limit the performance. This is different from "sustained power", which describes the ability to maintain a submaximal level of power output in activities of longer duration such as cycling or running (Sargeant 1994). Skelton et al. (1994) have reported that, between the ages of 65 and 89 years, its decline occurs at an even higher rate than isometric strength (3–4% per annum as compared to 1-2% of the value for a 77-yearold), thus revealing that power is more vulnerable than strength to the ageing process. This loss of power has been demonstrated to have severe functional consequences (Bassey et al. 1992; Krebs et al. 1998; Suzuki et al. 2001). Bassey et al. (1992) indicated that very old adults who require the use of aids to perform functional tasks, such as stair climbing, raising from a chair and walking, had 42-54% less leg extensor power than those who could complete these tasks without assistance. Suzuki et al. (2001) have recently demonstrated a positive association between muscle power of the ankle flexors and functional limitations in community-dwelling older women. Among a group of sedentary, communitydwelling older women, aged between 70 and 95 years, leg power was the strongest predictor of functional status, as compared to other physiological parameters (Foldvari et al. 2000). Rantanen and Avela (1997) have suggested that diminished leg extensor power may be a key predictor for mobility problems. Improved knowledge on the mechanisms of power decline is therefore crucial with regard to the development of effective prevention and treatment programmes for restoring mobility and independence in older people.

As reported earlier in this review, power is the product of force and speed at which movement occurs. The amount of force produced during a muscle contraction varies with the velocity of shortening, as first demonstrated by Fenn and Marsh in 1935 and then further investigated by Hill in 1938, who described a "characteristic equation" for the speed of shortening under a load in isolated animal muscle. The nature of the force/velocity relationship dictates that power will have its own distinct relationships with force and velocity of movement. Thus, there is an optimum force and an optimum velocity at which maximum power is developed. In isolated animal muscle, these correspond to about 30% of P_0 and 25–30% of V_{max} , respectively (Åstrand and Rodahl 1986). However, measurements of force/velocity and power/velocity relationships in humans in vivo represent the resultant of relatively complex situations, as human muscles are attached to bones via tendons that cross over one or two articular joints in order to produce a moment. Not only must the contractile elements of muscle cells be considered, but also factors such as neural influences, muscle architecture and intercellular connective tissue. The optimal values of force and speed for maximum power production in vivo may therefore be different from those recorded in isolated muscles or skinned single fibre preparations.

In the literature, investigations looking at muscle power in older people are not as numerous as those carried out on muscle strength. According to Earles et al. (2000), this is because muscle power in single explosive movements is much more difficult to measure than muscle strength. Isokinetic dynamometers allow power to be assessed in single muscle groups from the torque measured whilst the limb rotates at constant angular velocity, but do not reflect everyday activity where older subjects have to work against resistance and overcome speed (Harridge et al. 1999a). Moreover, the maximum speed of isokinetic devices (about 300°/s) is too low with respect to the maximum that can be achieved during "unloaded" movements of human limbs (estimated at 832°/s, as reported by Perrine 1986), which limits the measure of power above these values of speed. Explosive power has been traditionally measured in older people using a simple whole body movement, that

is a vertical jump on a force platform (Grassi et al. 1991; Ferretti et al. 1994; De Vito et al. 1998). Force platforms essentially operate like a scale for measuring weight. Velocity of movement of the individual's centre of gravity is calculated by integration of the acceleration, which in turn is calculated by the vertical component of the ground reaction force (VGRF) according to the Netwon's Second Law of Motion, and power is the product of force (obtained by subtracting body weight from VGRF) and velocity of movement (Davies and Rennie 1968). This method presents two limitations: (1) it may not be safe in very-old frail individuals; (2) older people have to lift their body weight, which represents a high percentage of their maximum strength, and therefore may be forced to work in a less favourable portion of the force/velocity curve, thus performing the movement at slower speed that is away from the optimal speed for maximum power production. The first problem has been overcome by Bassey and Short (1990), who developed a piece of apparatus that measures the average power generated by the lower limb muscles during a single leg extensor thrust against a pedal which, in turn, accelerates a heavy flywheel of a known inertia. This, however, does not solve the second issue, in that both young and older individuals have to overcome the same fixed inertia, with weak-old individuals being forced to use a relatively greater proportion of their maximum force-generating ability. Pearson et al. (2001) have recently introduced a variable inertial testing system mounted in the apparatus designed by Bassey and Short (1990), which has the potential to overcome the limitations due to the use of a single inertia. A safe device for testing older individuals could also be the sledgeergometer designed by Antonutto et al. (1999), on which individuals sitting on a carriage-seat push with both feet on two force platforms. In this device different inertial loads can be obtained by positioning the sledge at different angles with respect to the horizontal (Zamparo et al. 2000). Power can also be tested at different inertial loads by using instrumented weight-stack machines, where force is measured by a transducer or derived by the mass of the stack, and velocity by an electrogoniometer at the individual's joint (Harman 1995). However, the masses of plates in weight-stack machines have been found both to be variable and to differ from labelled values, thus complicating the measurement technique. All things considered, dynamic force testing, which is performed by measuring the maximum weight that can be lifted, is also a test of power, as the individual is exerting a given force at a given speed that, however, is not measured, thus not enabling the calculation of power. Thomas et al. (1996) have developed a pneumatic system mounted on a double leg-press machine that also allows one to use the optimal resistance for maximum power, expressed as a percentage of maximum dynamic strength. To the authors' knowledge, there is only one study in which explosive power has been compared between middle-aged and older men after optimizing the load (Izquierdo et al. 1999), and

another investigation (Macaluso and De Vito 2003), which has considered this issue in women. In both studies, the maximum power of the lower limbs, which was lower in the older individuals, was measured by pushing a load corresponding to about 60% of maximum force. Only Macaluso and De Vito (2003), however, have focused their attention on the two determinants of power output, i.e. optimal force and optimal speed, and reported that the inferior ability to generate power was due to a lesser ability to develop both force and speed. Moreover, as optimal speed was measured when optimal force was the same percentage of maximum voluntary contraction in the two groups (60%), thus standardizing for differences in optimal force, the authors concluded that the older women generated less power because they were slower than the young even when using the same percentage of their maximum strength. This finding is in contrast with the recent results of the same authors, carried out in collaboration with some other investigators (Pearson et al. 2002), who compared a population of weightlifter athletes with untrained healthy individuals by using a variable inertial testing system (Pearson et al. 2001) mounted in apparatus designed for measuring explosive power in older people (Bassey and Short 1990). In their study, weaker individuals achieved maximum power output at lower inertial loads than stronger individuals. but the speed component was found to be not significantly different between the two groups. The discrepancy between the results of these two studies could be ascribed to the different study population and testing methodology and deserves further investigation.

As power is the product of force and velocity, anything that will affect force production or speed of shortening of a muscle will also affect its power output. Therefore, all of the factors that have been reviewed in the previous paragraph to explain the loss of muscle strength in older age can be transferred to power. In addition, all of the factors that may affect speed of shortening must be taken into account. The selective atrophy of type II fibres with advancing age may partly explain power losses, because the power output of type II muscle fibres is four times that of type I fibres, as reported in animal studies (Faulkner et al. 1986). The speed at which a muscle fibre shortens is determined by the expression of the different isoforms of the MHC, as measured with a technique based on identification of MHC as molecular marker with gel electrophoresis (Harridge et al. 1996). Type I, IIa and IIb fibres of the traditional classification, based on ATPase sensitivity to pH, express mainly MHC-I, MHC-IIA and MHC-IIX isoforms, respectively. Fast fibres have the potential to generate higher power output, with greater forces and higher speed of shortening than slow fibres. The significant reduction in the size of type II fibres, as described earlier in this review (Lexell et al. 1988), would result in a decrease in the proportion of the muscle that is occupied by fast contracting MHC isoforms (Harridge and Young 1998). Moreover, it has been shown, by

using electrophoretic techniques, that fibres in older muscle co-express more than one MHC isoform (hybrid fibres) to a greater extent than fibres in young muscle (Klitgaard et al. 1990; Andersen et al. 1999). This increased presence of hybrid fibres, which had not been clearly identified by the earlier technique based on the ATPase reaction, may indicate a shift towards a slower older muscle (Harridge and Young 1998) and, as reported earlier in this review, is further evidence of the process of ongoing denervation and reinnervation of the ageing muscle (Vandervoort 2002). The shift towards a slower muscle with ageing has been confirmed by studies on the contractile mechanics of single fibres, in which it was shown that both MHC-I and MHC-IIA single fibres have lower specific tension and maximum shortening velocity if they originate from the muscles of an older person as opposed to a young person (Larsson et al. 1997; Frontera et al. 2000b). Moreover, Höök et al. (2001) recently reported an age-related slowing in the actin sliding speed on myosin by studying an in vitro motility assay, in which myosin is extracted and immobilized from a 2- to 4-mm single muscle fibre segment, in order to focus on actomyosin interactions without interference from cytoskeletal or regulatory proteins. As previously pointed out, measurements taken from skinned single fibre preparations or in vitro motility assays have the advantage that they allow the researcher to study directly the contractile elements of muscle cells, thus ruling out the confounding effects of factors such as neural influences, muscle architecture, and intercellular connective tissue (Frontera et al. 2000b). However, these factors should be taken into account when examining the speed of shortening of the whole body segments in vivo and the exact interpretation of these phenomena is still unknown. Metter et al. (1997) speculated that normal ageing changes in the basal ganglia, consisting of a continuing loss of dopaminergic neurons in the substantia nigra (Morgan et al. 1994), could contribute to the observed slowing in speed, coordination and power, together with peripheral changes such as slowing in nerve conduction velocities (Norris et al. 1953). Another potential cause of lower power production could be an age-related decrease in tendon stiffness, which has been briefly reviewed in a previous paragraph.

The effect of resistance training on muscle strength, power and selected functional abilities in older individuals

Strength

At the end of the 1980s, Frontera et al. (1988) reported that a heavy-resistance training programme led to an increase in strength of the quadriceps muscles of older men aged between 60 and 72 years, which was accompanied by an increase in muscle fibre size. Since then, a growing number of studies each year continue to document the benefits of resistance training in older people, even in individuals over 90 years of age. Resistancetraining programmes are based on the application of the overload principle, which states that muscles worked close to their force-generating capacity will increase in strength (McArdle et al. 1996). The term exercise session refers to the block of time devoted to the training. The number of training sessions completed per week is termed frequency. The basic unit of a resistance training session is the repetition which, for a given training movement, is the completion of a whole cycle from the starting position, through the end of the movement and back to the start. When a series of repetitions is completed this is termed a set. Volume is typically calculated as the product of repetitions and sets (Fry and Newton 2002). Intensity refers to the relative load or resistance that the muscle is exercising against, usually expressed as a percentage of the maximum weight that could be lifted once, i.e. 1 repetition maximum (1-RM). In the older population, these programmes have a similar structure to those undertaken by younger people, for example they can have a duration of 12 weeks, with a frequency of 3 times per week, where subjects perform 3–4 sets of 8 repetitions at an intensity equal to 80% of 1-RM. To elicit gains in muscle strength, the loads must be progressively increased so that the relative intensity remains high enough to provide an adequate overload throughout the whole duration of the training programme. The results of some of the studies that have examined the effects of heavy-resistance training on muscle strength and size on the most frequently studied muscle, the quadriceps group, are summarized in Table 1.

One of the main problems of between-study comparisons is the variation in the population of subjects. Studies have been performed on males, females and mixed populations. The mean age of the participants has also varied greatly, with older people ranging from those in their sixties (Häkkinen et al. 1998b) to those in their nineties (Fiatarone et al. 1990; Harridge et al. 1999b). The presence of medical conditions and the baseline fitness of participants are among other variables that have to be taken into account (Greig et al. 1994). Additional factors that make the comparison between studies problematic are the duration and frequency of the training programme, the number of sets and repetitions of each session, and finally the intensity at which these repetitions are performed. Resistance training programmes in older people varied considerably in length from just 4 weeks (Sherrington and Lord 1997) to 84 weeks (McCartney et al. 1996). On average, however, most resistance training studies lasted 8-12 weeks (Frontera et al. 1988; Fiatarone et al. 1990; Charette et al. 1991; Grimby et al. 1992; Lexell et al. 1995; Häkkinen et al. 1998b; Harridge et al. 1999b; Hunter et al. 1999; Tracy et al. 1999; Hortobágyi et al. 2001). Most studies involved subjects performing three training sessions per week, but the number could be as great as seven per week (Sherrington and Lord 1997). Recently, Taaffe et al. (1999) have demonstrated that strength gains can be obtained even with a training frequency of

once per week. The number of sets was three in most of the studies, but could vary up to six (Charette et al. 1991; Häkkinen et al. 1998b; Häkkinen et al. 2001). The number of repetitions also changed from study to study, with the most common number of repetitions being eight, although it ranged between 3 (Häkkinen et al. 1998b, 1998c) and 18 (Häkkinen et al. 2001). The intensity of heavy-resistance training was around 80% in most studies and there have also been few studies comparing low- versus high-intensity resistance training (Pruitt et al. 1995; Hortobágyi et al. 2001; Fielding et al. 2002). Strength changes have been quite variable across studies, which is likely a reflection of the key design factors that have just been reviewed. Moreover, variability in the results depends on the modalities used to test strength (isometric vs. 1-RM), which are defined at the beginning of this review. It is important to remark that even very old people can benefit from progressive resistance training (Fiatarone et al. 1990; Harridge et al. 1999b). Lexell (2000) pointed out that the lower the initial levels of strength, such as those in individuals in their nineties, the higher the magnitude of the percentage increase with respect to the baseline.

Various factors can contribute to strength gains following heavy-resistance training in both young and older subjects. These include, in the first phase of training (about 1–2 weeks), a rapid improvement in the ability to perform a training exercise, such as lifting weights, which is mainly the result of a learning effect. The learning effect, which is mediated by changes in motor skill coordination and level of motivation, can be substantial especially when the test adopted to evaluate muscle strength requires high levels of skill (Jones and Round 1990). In the second phase, which lasts 3-4 weeks, muscle strength gains are obtained without a matching increase in size of the trained muscles. The improvement in this phase has been mainly attributed to neural adaptations (Moritani and de Vries 1980; Sale 1988; Häkkinen et al. 2001). The term neural adaptations includes many elements such as an increased activation of prime mover muscles (number of recruited MUs or firing rate and synchronization of the individual MUs), a better coordination of synergistic and antagonist muscles, and an increased neural drive from the highest levels of the central nervous system (Sale 1988). There are, however, few studies investigating changes in neural properties following strength training in aged humans (Rice 2000). Some investigations have shown significant improvements in agonist sEMG with concurrent reductions in the activity of antagonist muscles (Häkkinen et al. 1998b, 1998c). An increase in M-wave potentials following strength training has been measured in older individuals by Hicks et al. (1992), thus suggesting a training-induced increase of muscle membrane excitability. However, Scaglioni et al. (2002) have recently shown that the modulation of neuromuscular excitability, expressed as the ratio between the maximum Hoffman reflex and the maximum M-wave, did not change in older male adults following 16 weeks of

ne quadriceps muscle in older individuals. (CSA Cross-sectional area, CT computerized tomography, F female,	asion, LP leg press, M male, MRI magnetic resonance imaging, MVC maximal voluntary contraction, NS non-	ed, 5RM five repetitions of maximum weight that could be lifted, Ultr ultrasonography, vol volume)
(CS	RI magnetic resonanc	kimum weight that co
ps muscle in older in	eg press, M male, M.	ve repetitions of max
size of the quadrice	knee extension, LP lo	uld be lifted, 5RM fiv
ig on muscle strength and	, Isok isokinetic, KE	mum weight that co
f resistance training on	tht bearing exercises, I	one repetition of maxi
Table 1 Effect of re	<i>GWBE</i> general weig	significant, IRM on

Authors Subjects Training programme % Change	Subjects	s	þ	Training programme	ogramme	-		с 		% Change	lge) 1		
	Age	Gender N	Ν	Exercise	Duration	Sessions	Sets	Sets Repetitions	% of 1RM	Strength		CSA	Fibre size increase	increase
				movement	(weeks)	per week				IRM	MVC		Type I	Type II
Frontera et al. 1988	60-72	М	12	KE	12	3	3	8	80	107	17	CT: 9	34	28
Fiatarone et al. 1990	86 - 96	M/F	10	KE	8	n	ς	8	80	174	Í	CT: 11	I	
Charette et al. 1991	64 - 86		13	LP, KE	12	e	9	9	75	28–93		I	7 NS	20
Grimby et al. 1992	78–84	М	6	KE	8-12	ω	ŝ	8	Isok	10 at 30°s ⁻¹	°s^-1	CT: 3	8 NS	5 NS
Pyka et al. 1994	61 - 78	M/F	25	LP, KE	52	ŝ	ŝ	8	75	53-95		I	59*	67*
Lexell et al. 1995	70–77	M/F	23	KE	11	n	m	9	85	163	Ι		4 NS	-8 NS
McCartney et al. 1996	60 - 80	M/F	113	LP	84	2	m	12	80	32	Ι	CT: 9	I	1
Sherrington and Lord 1997	64–94	M/F	21	GWBE	4	7	Ι	I	I	I	22	I	I	Ι
Häkkinen et al. 1998b	61	Ž	10	KE	10	n	3–6	3-15RM	I	Ι	17	MRI: 9	23	27
Häkkinen et al. 1998c	70	M/F	20	KE	26	2	3^{-6}	3-15	50 - 80	26	Ι	Ultr: 6 (F)	I	Ι
Harridge et al. 1999b	85–97	M/F	11	KE	12	m	ę	8	80	134	37	MRI: 10	Ι	Ι
Taaffe et al. 1999	65-79	M/F	46	LP, KE	24	1	ε	8	80	23-71	Ι	I	Ι	I
Tracy et al. 1999	65–75	M//F	23	KE	6	c,	б	5-10RM	Ι	28	Ι	MRI(vol): 12	5	Ι
Hunter et al. 1999	64-79	M/F	11	KE	12	ŝ	ŝ	8RM	I	39	I	I	-4 NS	-2 NS
Hortobágyi et al. 2001	66–83	M/F	27	LP	10	n	5	4-12	40 - 80	35	26	I		1
Häkkinen et al. 2001	71	M/F	21	LP	26	2	3–6	10 - 18	70–80	26	26	I	32 (F)	32 (F)
•														

*After 30 weeks

resistance training of plantar flexor muscles. A 30% increase in maximal MU firing rate has been measured in the tibialis anterior muscle of six older individuals in their seventies following 2 weeks of training (Patten and Kamen 2000). However, the same authors (Patten et al. 2001) reported a bimodal response of maximal MU discharge rate of the adductor digiti minimi to 6 weeks of isometric training – an initial increase followed by a return towards baseline – which is surprising and difficult to explain. The third phase of adaptation to strength training (>6 weeks) is characterized by an increase in both the size and strength of the exercised muscles. Muscle size has been measured before and after training using various non-invasive techniques, such as ultrasonography (Häkkinen et al. 1998c), CT (Frontera et al. 1988; Fiatarone et al. 1990; Grimby et al. 1992; Mc-Cartney et al. 1996) or MRI (Häkkinen et al. 1998b; Harridge et al. 1999b). Notable is the recent study of Tracy et al. (1999), who measured a 12% increase in quadriceps muscle volume, by MRI, following 9 weeks of resistance training in both groups of 65- to 75-yearold men and women. Both type I and type II fibres retain their capacity for hypertrophy in response to resistance training (Frontera et al. 1988; Brown et al. 1990; Charette et al. 1991; Pyka et al. 1994; Häkkinen et al. 1998b, 2001), although some studies demonstrated little or no change (Grimby et al. 1992; Lexell et al. 1995; Hunter et al. 1999). Häkkinen et al. (1998b) have reported a type MHC II subtype transformation going from type MHC IIb to IIab to IIa in older men, similar to previous training studies in young individuals (Adams et al. 1993; Harridge et al. 1998). In a further study (Sharman et al. 2001), the same result was also found in a group of 65year-old women following 24 weeks of heavy resistance training. Williamson et al. (2000) have measured a significant increase in the expression of MHC I as a result of 12 weeks of low-intensity resistance training, thus indicating that higher-threshold MUs may not have been recruited during the programme. Recent investigations on single fibres indicated that 12 weeks of progressive resistance training increased muscle cell size, strength and peak power in both older men (Trappe et al. 2000) and women (Trappe et al. 2001). Interestingly, in contrast with the older men, no change in fibre unloaded shortening velocity or peak power normalized to cell size was observed in older women, thus suggesting that men and women respond differently, at the cell level, to the same resistance-training stimulus. The mechanisms of this phenomenon are still unknown. Some studies (Yarasheski et al. 1995; Welle et al. 1999) have also given evidence that resistance training leads to an increase in protein synthesis, accompanied by significant improvements in muscle strength. Less is known about the long-term effects of resistance training in older people, as most of the available studies did not continue after 12-24 weeks. Following a 1-year exercise trial involving 25 individuals aged between 61 and 78, Pyka et al. (1994) measured increases in strength ranging from 30 to 97% over the first 3 months, which then

maintained a plateau in the remaining months of the experiment. Similarly, Morganti et al. (1995) showed that a 1-year training programme with a frequency of twice a week resulted in strength gains of various muscle groups, ranging from 4% to 74% in a population of 39 healthy postmenopausal women, with the greatest gains seen in the first 3 months of training. McCartney et al. (1996) reported instead progressive strength gains and moderate muscle hypertrophy in an older group that continued to participate in a resistance-training programme for 2 years. Rapid detraining will result if programmes are interrupted, but the initial gains can be maintained with a reduced exercise frequency of even once per week (Lexell et al. 1995; Taaffe et al. 1999; Trappe et al. 2002).

Although several investigations have shown that the capacity to improve muscle strength is not impaired with increasing age (see the studies of Table 1), few investigations have made a direct comparison of the magnitude of the responses in older and young individuals to the same training programme. Jozsi et al. (1999) have shown that 60-year-old individuals can improve strength and power in response to 12 weeks of resistance training, with the same magnitude as that of individuals in their twenties. Welle et al. (1996b) found that the increase in specific tension following 3 months of resistance training in young (22-31 years) and older (62-72 years) individuals was similar for elbow flexion (about 20%) and knee extension (about 35%), but was more than double in the older subjects for the knee flexors. Larsson (1982), on the contrary, had previously shown that the average increase in isokinetic strength of the knee extensors following 15 weeks of training at low resistance and high repetition tended to be higher in a group of 56- to 65year-old males (7.5%) as compared to the 20- 39-yearold group (2.9%). In contrast, in the study of Macaluso et al. (2000), after 6 weeks of isometric training the force gain of the biceps brachii muscle followed the same temporal pattern in the two groups of young and older women, in that after 4 weeks the maximum voluntary contraction reached a plateau, but the absolute force increments were different, 22.4% in the young and 13.4% in the older women.

Power

In recent times, greater attention has been focused on the need to design exercise strategies in order to increase muscle power (Earles et al. 2000; Evans 2000; Fielding et al. 2002). "The preservation of muscle power into late life can greatly decrease the risk of disability and enhance functional independence" (Evans 2000). As pointed out by Earles et al. (2000), it is important to determine whether high-velocity training is comparable or superior to low-velocity high-resistance programmes in order to improve function and quality of life in older individuals. Table 2 summarizes the results of the training studies in which, to the authors' knowledge, explosive power has been measured. The subjects' age

Table 2 Effect of resistance training on muscle power of various muscle groups in older individuals. (*AP* arm pull, *BP* bench press, *F* female, *HE* hip extension, *HI* high velocity, *HS* half-squat, *KE* knee

extension, LO low velocity, LP leg press, M male, NS non-significant, PRM pneumatic resistance machine, IRM one repetition of maximum weight that could be lifted, SC stair climbing, VJ vertical jump)

Authors	Subjec	ts		Training progr	amme					Testing	Power gain	Measurement
	Age	Gender	Ν	Exercise movement	Duration (weeks)	Sessions per week	Sets	Repe- titions	% of 1RM	movement		apparatus
Frontera et al. 1988	60–72	М	12	KE	12	3	3	8	80	KE	None	Isokinetic dynamometer
Fiatarone et al. 1994	72–98	M/F	100	KE, HE	10	3	3	8	80	SC	28%	Stair-climbing
Skelton et al. 1995	76–93	M/F	20	Elastic tubing or rice bags	12	3	3	4–8	_	LP	18% (NS)	Nottingham Rig
De Vito et al. 1999	60–70	F	11	Low-intensity general conditioning	12	3	-	_	_	VJ	24%	Force platform
Jozsi et al. 1999	56–66	M/F	17	KE, AP	12	2	3	8–12	80	KE, AP	10–26%	PRM
Izquierdo et al. 2001	64 (2)	М	11	KE, HS, BP	16	2	3–4	8–15	50-80	KE, HS, BP	21-37%	Instrumented weight-stack machines
Earles et al. 2000	77 (5)	M/F	18	LP	12	3	3	10	50-70	LP	22%	PRM
Fielding et al. 2002	73 (1)	F	30	LP	16	3	3	8–10	70	LP	HI: 97% LO: 45%	PRM

and gender, training mode and testing methodology are included.

To date there is only one published study, to the authors' knowledge, which was specifically designed to increase power in older people (Fielding et al. 2002). Older women in their seventies with mild functional limitations were randomized into one of two groups: high-velocity (HI) and low-velocity (LO), in which absolute training force and total work performed were similar between groups, but power output was significantly higher in HI, since individuals were asked to perform each repetition as fast as possible. HI and LO have improved leg-press power output by 97% and 45%, respectively, over 16 weeks of training. This training programme was designed starting from the assumption that muscle-strengthening exercises may not always produce an optimum increase in power. The authors pointed out that traditional low-velocity resistance training resulted in a small but significant increase in muscle power ranging from 18% to 25% (Fiatarone et al. 1994; Skelton et al. 1995; Jozsi et al. 1999) despite much larger increases in muscle strength. Fiatarone et al. (1994) showed that in frail very old nursing-home residents progressive resistance exercise over a 10-week period produced 113% and 28% increases in muscle strength (knee-extension 1-RM) and power output, respectively, with power being assessed during a stairclimbing test (Bassey et al. 1992). Similarly, in 20 healthy, independent, very old women, Skelton et al. (1995) observed a 27% increase in knee-extension isometric strength and an 18% increase in leg-extension power standardized for body weight, which was measured using the Nottingham Power Rig (Bassey and Short 1990). Jozsi et al. (1999) found that 12 weeks of progressive resistance-training in men and women in their sixties resulted in an increase in the strength of knee extension and arm pull movements of 30% and 18%, respectively, versus an increase of 26% and 10% in power, with power being measured with a pneumatic resistance machine (Thomas et al. 1996). Also Frontera et al. (1988), in their notable study that has been cited in the previous paragraph on the effects of resistance training on strength, examined the effect of resistance training on quadriceps power, with power being measured with an isokinetic dynamometer, but did not see any significant change. It can be speculated that the effect of training on muscle power may have been seen if power had been measured with the same dynamometer used to carry out the training programme. Even a lowintensity general conditioning programme has been successful in obtaining a 24% increase in peak power during a vertical jump on a force platform in 20 healthy older women in their sixties (De Vito et al. 1999), but higher improvements may have been observed if the programme had been more specific. Earles et al. (2000) have therefore pointed out the importance of performing movements at high velocity during resistance training in order to increase power output. Forty-three volunteers over the age of 70 years were randomized into one of two groups: the power group, in which individuals participated in high-velocity resistance exercise 3 times a week, and the walking group, in which individuals performed moderate intensity exercise 30 min daily, 6 days per week. Leg-press power and maximal knee extensor strength substantially increased in the first group, but not in the second. Similarly, Izquierdo et al. (2001) reported that in middle-aged and older men a prolonged total strength training programme, which included high

velocity movements, led to gains in maximal strength and power of the upper and lower extremity muscles, with the improvements being limited in magnitude possibly due to neuromuscular or age-related endocrine impairments.

As reported in the paragraph entitled "muscle power in older people", there is an optimum value of force and velocity at which maximum power is generated. De Vito et al. (1999) showed that the training-induced increase in peak power output, which was measured by performing a vertical jump on a force platform, was due to an increase in both optimal force (18%) and optimal velocity (13%) at which maximum power was measured. However, as argued earlier in this review, explosive power output on a force platform was assessed using a fixed inertia, which is the subjects' body weight and corresponds to a high percentage of their maximum, thus not representing the optimal value of force for maximum power production. Other authors have overcome this problem by measuring power output using different loads before and after training (Jozsi et al. 1999; Earles et al. 2000; Izquierdo et al. 2001; Fielding et al. 2002), but do not seem to have focused much of their attention on whether the training-induced changes in maximum power were due to an increase of optimal force, optimal velocity or both. Most of the investigators (Jozsi et al. 1999; Izquierdo et al. 2001; Fielding et al. 2002) showed how power output varied as a function of different loads, expressed as a percentage of 1-RM, thereby identifying the load at which maximum power was measured, but they did not discuss the role of velocity of movement in maximum power generation. In the work of Earles et al. (2000), both power output and velocity of movement were plotted in two different graphs against the resistance used, expressed as a percentage of body mass. However, also these authors did not discuss the relative role of both optimal force and velocity, but simply commented that minimal improvements in power were measured at low resistance, whilst large improvements occurred at higher resistance, in agreement with the principle of specificity of training (McCafferty and Horvath 1977). From a closer analysis of the graphical results of Earles et al. (2000), it is clear that maximum power was measured before and after training at 30% and 50% of body mass, respectively, with the optimal speed at maximum power being decreased after training, although this was not remarked upon by the authors. Improvements in power can therefore be interpreted with the fact that individuals were able to push higher loads despite a decrease in optimal speed of movement.

Possible mechanisms underlying the improvement in peak power may include specific increases in the CSA of type II muscle fibres and increases in specific force and shortening velocity of single muscle fibres, as speculated by Fielding et al. (2002). Notably, Van Cutsem et al. (1998) have shown that changes in single MU behaviour contribute to the increase in contraction speed after dynamic training in humans, which could justify training-induced changes in power. These changes in MU behaviour include earlier MU activation, extra doublets, i.e. brief (2-5 ms) MU interspike intervals, and enhanced maximal firing rate. Also Izquierdo et al. (2001) have speculated that power increases could be due to training-induced changes in the neural component, which they vaguely refer to as "voluntary or reflex/induced rapid neural activation of MUs". Indeed, the various factors included under the term "neural adaptations" that have been presented in the previous paragraph to explain gains in strength following heavyresistance training, i.e. increased activation of the prime mover muscles, better coordination of synergistic and antagonist muscles and increased neural drive from the highest levels of the central nervous system, can also explain improvements in power. However, studying these mechanisms during dynamic contractions by sEMG or other electrophysiological techniques could be problematic, as various mechanical, physiological, anatomical and electrical modifications occur throughout the contraction that affect, in substantial ways, the relationship between signal amplitude and muscle force (De Luca 1997). Also the slowing in nerve conduction velocities due to ageing (Norris et al. 1953) may be a mechanism to be recovered following power training. However, Scaglioni et al. (2002) have recently shown that the conduction velocity of the posterior tibial nerve did not change in older male adults following 16 weeks of resistance training of plantar flexor muscles, thus suggesting that decreased nerve conduction velocity may be due to degenerative phenomena rather than disuse. Moreover, if decreased tendon stiffness, as recently shown in vivo on human individuals by Maganaris (2001), is another potential cause for decreased power with ageing, an appropriate training intervention may also affect this mechanism. Recent results of Reeves et al. (2003a, 2003b) showed that the patella-tendon stiffness increased by 65% in 74-year-old men following 14 weeks of resistance training, which was accompanied by a 14–23% increase in dynamic strength during leg extension and leg press. In contrast, in a population of older women, it has been shown that 6 months of lowload resistance training produced no significant changes in stiffness of the tendon-aponeurosis structures of the vastus lateralis muscle, but an increase in elasticity (Kubo et al. 2003).

Selected functional abilities

Functional ability can been described as an individual's competence in performing everyday physical tasks, like rising from a chair, climbing stairs or lifting shopping bags (Harridge et al. 1999a). Although, as reported in the previous paragraph on muscle power, it has been shown that muscle strength and power correlate with the ability to perform functional tasks (Bassey et al. 1992; Skelton et al. 1994; Rantanen and Avela 1997; Foldvari et al. 2000; Suzuki et al. 2001), this is an area of research that remains unclear. Some authors (Skelton et al. 1994;

Buchner et al. 1996; and Levy et al. 1994, cited in Harridge et al. 1999a) have attempted to identify functional "threshold" values of muscle performance below which older people lose their ability to perform basic daily tasks. Skelton et al. (1994), who measured the greatest height of step that could be mounted without using the hands in healthy men and women aged from 65 to 89 years, found a significant correlation between step height and lower limb extensor power, but failed to identify a universally applicable threshold value, even after adjusting for limb length. In contrast, Levy et al. (1994, cited in Harridge et al. 1999a) reported that unilateral power/weight ratios of 1.5 and 2.5 W/kg could be considered as threshold values for mounting a 30- and 50-cm step, respectively. Buchner et al. (1996), who used a slightly different model based on an inverse transformation of strength, found a significant correlation between lower limb strength and self-chosen walking speed. However, they also concluded that a "universal threshold" might not exist due to a compensation for deficiencies in strength by using reserve capacity in other determinants of walking speed. Regardless of the difficulties in identifying a precise value, this "threshold" concept makes it easy to recognize that small changes in physiological capability can have large effects on the functional ability of a frail person, but little or no effect in a more robust person.

There are few studies that have investigated the effects of training protocols on selected functional abilities in older people (Table 3). It should be noted that in most of these studies (Judge et al. 1993; Fiatarone et al. 1994; Hunter et al. 1995; Skelton et al. 1995; Skelton and McLaughlin 1996; Rooks et al. 1997; Sherrington and Lord 1997) the age range of participants is widespread, with individuals in their nineties and in their sixties or seventies being included in the same group. As these investigations, with the exception of Fiatarone et al. (1994), were carried out on a relatively small number of individuals, the interpretation of results might have been limited by pulling together subjects within a wide age range, since in the very old individuals small changes in physiological capability are likely to have larger effects on functional ability than in relatively younger subjects. Health and functional status also vary considerably between studies, with the participants ranging from frailinstitutionalized (Fiatarone et al. 1990, 1994) to relatively independent (Judge et al. 1993; Skelton and McLaughlin 1996) or healthy active (Earles et al. 2000; Häkkinen et al. 2000), thus limiting inter-study comparisons. Regardless of these limitations, the relationship between resistance training and the ability to perform functional tasks remains unclear. As reported in Table 3, the effects of resistance training on selected functional abilities vary from no change (Earles et al. 2000) to a 48% gain (Fiatarone et al. 1990), with most of the studies reporting improvements in only some of the functional abilities investigated (Skelton et al. 1995; Rooks et al. 1997; Sherrington and Lord 1997; Taaffe et al. 1999). Skelton and McLaughlin (1996) have concluded that improvements in functional abilities may be a carried-over effect of strength and power training, but are more likely to occur if the functional task is also practised. More recently, Earles et al. (2000) have also pointed out that power training per se may not necessarily improve functional task performance. Following a 12-week high-velocity training programme, 34 individuals of both genders in their late seventies increased their muscle strength and peak power of lower limb muscles by 22%, but did not improve functional task performance. Rooks et al. (1997), on the contrary, noted a 20% improvement in stair climb time after 10 months of moderate-resistance high-velocity training, but similar changes were also observed in a group of individuals performing a walking programme.

Three selected functional abilities appear to be the most frequently used in assessing the effects of intervention programmes: chair raising, stair climbing and maximum or self-selected walking speed. Chair raising is usually assessed as the time taken by older individuals to rise from a standard chair (seat height 43 cm) with their arms folded (Fiatarone et al. 1990; Skelton et al. 1995; Skelton and McLaughlin 1996; Taaffe et al. 1999; Earles et al. 2000). Stair climbing normally consists of ascending and often descending a staircase without stopping at a comfortable pace, with or without using the handrail (Fiatarone et al. 1994; Skelton et al. 1995; Skelton and McLaughlin 1996; Rooks et al. 1997). The time to complete the task is timed. Maximum walking speed is measured by asking the subjects to walk as fast as possible over a distance, which is usually around 6 m, and recording the time taken to cover that distance (Hunter et al. 1995; Skelton and McLaughlin 1996). Other authors have measured the so-called usual or habitual velocity, by instructing the subjects to walk as they normally do (Fiatarone et al. 1990, 1994; Judge et al. 1993; Skelton et al. 1995; Sherrington and Lord 1997). In some cases, subjects were asked to walk placing the heel of one foot directly in front of the toe of the other with the shoe touching, which is referred to as tandem walk (Fiatarone et al. 1990), or walking backward using the same pattern (Taaffe et al. 1999). It is reasonable to expect that the choice of discriminatory tests of functional abilities in a population of older individuals who are healthy and active could be more problematic than in a group of frail individuals.

Macaluso et al. (2003) have been the first authors to adopt cycling as a novel approach to perform three different regimes of resistance training (one performed at a light intensity with a high speed of movement, another performed at a heavy intensity with a slower speed of movement, a third based on a combination of both) in a population of healthy older women aged 65 to 74 years. All of the participants improved their maximum walking speed and other functional abilities (box-stepping and vertical jumping), with a parallel increase in muscle strength and power, regardless of the training regime adopted (Macaluso et al. 2003). These are the novel findings which deserve to be remarked upon: (1) even fit

Authors	Subjects	sts			Training programme	gramme						Functional ability	Gain %
	Age	Gender	N	Health and functional status	Practice of functional task	Exercise movement	Duration (weeks)	Sessions Per wk	Sets	Reps	% of 1RM	investigated	
Fiatarone	86–96	86–96 M/F	10	Frail institutionalized	NO	KE	8	3	3	8	80	CR, MWV, tandem	48^{+}
et al. 1990 Judge	71–97	71–97 M/F	31	Relatively healthy	ON	KE, HA, AD, HE, VE DCE	12	3	ŝ	8-12	75-80	gant speed MWV, usual gait	°8
Fiatarone	72–98	M/F	100	100 Frail institutionalized	ON	NF, FCE KE, HE	10	3	З	8	80	velocity Habitual gait	12
et al. 1994 Hunter	60–77	ц	14	Healthy independent	ON	LP, BP, EF, EE, VE HA	16	3	7	12RM	Ι	Velocity MWV, iEMG during	18 §
Skelton	76–93	ц	20	Healthy independent	NO	Elastic tubing,	12	3	З	4-8	I	FR, SC, WR, SR, HR, BI CD FDS VD DS	Only KR,
et al. 1995 Skelton and McLaughlin	7489	ц	18	Relatively independent	YES	rice bags Elastic tubing, tin cans, sponge	8	1S-2U	1–3	4-8	I	ER, CR, TUG, MWV, SR, FRS, SC, BT	11–22 in only five
1996 Sherrington		64–94 M/F	21	Indep. after hip fracture	NO	balls GWBE	4	7	I	I	I	FR, habitual walking	n.r.#
and Lord 199/ Rooks		65–95 M/F	37	Independent community	YES*	HE, KE, AD, PF, FF	43	3	ŝ	8-15	ds	Velocity SC time; pen pick-up	20; -24
et al. 1997 Taaffe	65-79	65-79 M/F	46	uwening Healthy	NO	LP, KE	24	1	З	8	80	cR, backward tandem	24 ^X
et al. 1999 Häkkinen	62–77	62–77 M/F	10	Healthy active	NO	LP, KE, BP, KF, EE SUI	24	2	3-5	8-12	50-80	waik MWV	13
et al. 2000 Earles et al. 2000	77 ± 5	\mathbf{M}/\mathbf{F}	18	Highly functioning	YES ^x	LP, HF, SU, CR, PF	12	ю	б	10	50-70	CR; 8-foot walk;	None

⁺Tandem gait speed only; ^ousual only; ^{sdecreased} iEMG in CR and CB by36% and 40%, respectively; ^sSC only; ^xCR only; n.r.# habitual walking velocity only; percentage increase not reported

older women still have a margin for improvement in functional abilities; (2) the training-induced increase in power output was due to a combined increase in both of the two determinants of power, optimal force and optimal velocity; (3) the lack of difference between the three training regimes seems to suggest that it is not the intensity nor the speed of movement, but the level of mechanical work, with this being similar in the three groups, which represents the training stimulus.

References

- Abernethy P, Wilson G, Logan P (1995) Strength and power assessment. Issues, controversies and challenges. Sports Med 19:401–417
- Adams GR, Hather BM, Baldwin KM, Dudley GA (1993) Skeletal muscle myosin heavy chain composition and resistance training. J Appl Physiol 74:911–915
- Allen TH, Anderson EC, Langham WH (1960) Total body potassium and gross body composition in relation to age. J Gerontol 15A:348–357
- Andersen JL, Terzis G, Kryger A (1999) Increase in the degree of coexpression of myosin heavy chain isoforms in skeletal muscle fibers of the very old. Muscle Nerve 22:449–454
- Aniansson A, Rundgren A, Sperling L (1980) Evaluation of functional capacity in activities of daily living in 70-year-old men and women. Scand J Rehabil Med 12:145–154
- Aniansson A, Zetterberg C, Hedberg M (1984) Impaired muscle function with ageing: a background factor in the incidence of fractures of the proximal end of the femur. Clin Orthop 191:192–210
- Aniansson A, Hedberg M, Henning GB, Grimby G (1986) Muscle morphology, enzymatic activity, and muscle strength in elderly men: a follow-up study. Muscle Nerve 9:585–591
- Antonutto G, Capelli C, Girardis M, Zamparo P, di Prampero PE (1999) Effects of microgravity on maximal power of lower limbs during very short efforts in humans. J Appl Physiol 86:85–92
- Asmussen E, Heeboll-Nielsen K (1962) Isometric muscle strength in relation to age in men and women. Ergonomics 5:167
- Astrand P, Rodhal K (1986) Textbook of work physiology. Mc Graw Hill, Singapore, pp 43–44
- Avlund K, Schroll M, Davidsen M, Lovborg B, Rantanen T (1994) Maximal isometric muscle strength and functional ability in daily activities among 75-year-old men and women. Scand J Med Sci Sports 4:32–40
- Baratta R, Solomonow M, Zhou M, Letson D, D'Ambrosia R (1988) Muscular coactivation. The role of antagonist musculature in maintaining knee joint stability. Am J Sports Med 16:113–122
- Bassey EJ, Harries UJ (1993) Normal values for handgrip strength in 920 men and women aged over 65 years and longitudinal changes over 4 years in 630 survivors. Clin Sci 84:331–337
- Bassey EJ, Short AH (1990) A new method for measuring power output in a single leg extension: feasibility, reliability and validity. Eur J Appl Physiol 60:385–390
- Bassey EJ, Fiatarone MA, O'Neill EF, Kelly M, Evans WJ, Lipsitz LA (1992) Leg extensor power and functional performance in very old men and women. Clin Sci 82:321–327
- Bassey EJ, Mockett SP, Fentem PH (1996) Lack of variation in muscle strength with menstrual status in healthy women aged 45–54 years: data from a national survey. Eur J Appl Physiol 73:382–386
- Baumgartner RN, Waters DL, Gallagher D, Morley JE, Garry PJ (1999) Predictors of skeletal muscle mass in elderly men and women. Mech Ageing Dev 107:123–136
- Behm D, Power K, Drinkwater E (2001) Comparison of interpolation and central activation ratios as measures of muscle inactivation. Muscle Nerve 24:925–934

- Bilodeau M, Erb MD, Nichols JM, Joiner KL, Weeks JB (2001a) Fatigue of elbow flexor muscles in younger and older adults. Muscle Nerve 24:98–106
- Bilodeau M, Henderson TK, Nolta BE, Pursley PJ, Sandfort GL (2001b) Effect of aging on fatigue characteristics of elbow flexor muscles during sustained submaximal contraction. J Appl Physiol 91:2654–2664
- Borges O (1989) Isometric and isokinetic knee extension and flexion torque in men and women aged 20–70. Scand J Rehabil Med 21:45–53
- Brooks SV, Faulkner JA (1994) Skeletal muscle weakness in old age: underlying mechanisms. Med Sci Sports Exerc 26:432–439
- Brown AB, McCartney N, Sale DG (1990) Positive adaptation to weight-lifting training in the elderly. J Appl Physiol 69:1725– 1733
- Brown WF, Strong MJ, Snow R (1988) Methods for estimating numbers of motor units in biceps-brachialis muscle and losses of motor units with aging. Muscle Nerve 11:423–432
- Bruce SA, Phillips SK, Woledge RC (1997) Interpreting the relation between force and cross-sectional area in human muscle. Med Sci Sports Exerc 29:677–683
- Buchner DM, Larson EB, Wagner EH, Koepsell TD, DeLateur BJ (1996) Evidence for a non-linear relationship between leg strength and gait speed. Age Ageing 25:386–391
- Butterfield GE, Thompson J, Rennie MJ, Marcus R, Hintz RL, Hoffman AR (1997) Effect of rhGH and rhIGF-I treatment on protein utilization in elderly men. Am J Physiol 272:E94–E99
- Campbell AJ, Borrie MJ, Spears GF (1989) Risk factors for falls in a community-based prospective study of people 70 years and older. J Gerontol 44A:M112–M117
- Celotti F, Negri Cesi P (1992) Anabolic steroids: a review of their effects on the muscles, of their possible mechanisms of action and of their use in athletics. J Steroid Biochem Mol Biol 43:469–477
- Charette SL, McEvoy L, Pyka G, Snow-Harter C, Guido D, Wiswell RA, Markus R (1991) Muscle hypertrophy response to resistance training in older women. J Appl Physiol 70:1912– 1916
- Connelly DM, Rice CL, Roos MR, Vandervoort AA (1999) Motor unit firing rates and contractile properties in tibialis anterior of young and old men. J Appl Physiol 87:843–852
- Danneskiold-Samsoe B (1984) Muscle strength and functional capacity in 78 to 81 years old men and women. Eur J Appl Physiol 52:310–314
- Davies CTM, Rennie R (1968) Human power output. Nature 217:770–771
- De Luca CJ (1997) The use of surface electromyography in biomechanics. J Appl Biomech 13:135–163
- De Serres SJ, Enoka RM (1998) Older adults can maximally activate the biceps brachii muscle by voluntary command. J Appl Physiol 84:284–291
- De Vito G, Bernardi M, Forte R, Pulejo C, Macaluso A, Figura F (1998) Determinants of maximal instantaneous muscle power in women aged 50–75 years. Eur J Appl Physiol 78:59–64
- De Vito G, Bernardi M, Forte R, Pulejo C, Figura F (1999) Effects of a low-intensity conditioning programme on VO2max and maximal instantaneous peak power in elderly women. Eur J Appl Physiol 80:227–232
- Delbono O, Renganathan M, Messi ML (1997) Excitation-Ca²⁺ release-contraction coupling in single aged human skeletal muscle fibre. Muscle Nerve 20:S88–S92
- Doherty TJ, Brown WF (1993) The estimated number and relative sizes of thenar motor units as selected by multiple point stimulation in young and older adults. Muscle Nerve 16:355–366
- Doherty TJ, Vandervoort AA, Taylor AW, Brown WF (1993) Effects of motor unit losses on strength in older men and women. J Appl Physiol 74:868–874
- Earles DR, Judge JO, Gunnarsson OT (2000) Velocity training induces power-specific adaptations in highly functioning older adults. Arch Phys Med Rehabil 82:872–878
- Erim Z, Beg MF, Burke DT, De Luca CJ (1999) Effects of aging on motor unit control properties. J Neurophysiol 82:2081–2091

- Esposito F, Malgrati D, Veicsteinas A, Orizio C (1996) Time and frequency domain analysis of electromyogram and sound myogram in the elderly. Eur J Appl Physiol 73:503–510
- Evans WJ (1995) What is sarcopenia? J Gerontol 50A (Spec No):5– 8
- Evans WJ (2000) Exercise strategies should be designed to increase muscle power. J Gerontol 55A:M309–M310
- Faulkner JA, Claffin DR, McCully KK (1986) Power output of fast and slow fibres from skeletal muscles. In: Jones NL, McCartney N, McComas AJ (eds) Human muscle power. Human Kinetics, Champaign, Ill., pp 81–94
- Fenn WO, Marsh BS (1935) Muscular force at different speed of shortening. J Physiol (Lond) 85:277–297
- Ferretti G, Narici MV, Binzoni T, Gariod L, Le Bas JF, Reutenauer H, Cerretelli P (1994) Determinants of peak muscle power: effects of age and physical conditioning. Eur J Appl Physiol 68:111–115
- Ferretti G, Antonutto G, Denis C, Hoppeler H, Minetti AE, Narici MV, Desplanches D (1997) The interplay of central and peripheral factors in limiting maximal oxygen consumption in man after prolonged bed rest. J Physiol (Lond) 501:677–686
- Fiatarone MA, Marks EC, Ryan ND, Meredith CN, Lipsitz LA, Evans WJ (1990) High-intensity strength training in nonagenarians. J Am Med Assoc 263:3029–3034
- Fiatarone MA, O'Neill EF, Ryan ND, Clements KM, Solares GR, Nelson ME, Roberts SB, Kehayias JJ, Lipsitz LA, Evans WJ (1994) Exercise training and nutritional supplementation for physical frailty in very elderly people. N Engl J Med 330:1769– 1775
- Fielding RA, LeBrasseur NK, Cuoco A, Bean J, Mizer K, Fiatarone Singh MA (2002) High-velocity resistance training increases skeletal muscle peak power in older women. J Am Geriatr Soc 50:655–662
- Foldvari M, Clark M, Laviolette LC, Bernstein MA, Kaliton D, Castaneda C, Pu CT, Hausdorff JM, Fielding RA, Fiatarone Singh MA (2000) Association of muscle power with functional status in community-dwelling elderly women. J Gerontol 55A:M192–M199
- Frontera WR, Meredith CN (1989) Strength training in the elderly. In: Harris R, Harris S (eds) Physical activity, aging and sports. Center for the Study of Aging, Albany, New York, pp 319–333
- Frontera WR, Meredith CN, O'Reilly KP, Knuttgen HG, Evans WJ (1988) Strength conditioning in older men: skeletal muscle hypertrophy and improved function. J Appl Physiol 64:1038– 1044
- Frontera WR, Hughes VA, Lutz KJ, Evans WJ (1991) A crosssectional study of muscle strength and mass in 45- to 78-yr-old men and women. J Appl Physiol 71:644–650
- Frontera WR, Hughes VA, Fielding RA, Fiatarone MA, Evans WJ, Roubenoff R (2000a) Aging of skeletal muscle: a 12-yr longitudinal study. J Appl Physiol 88:1321–1326
- Frontera WR, Suh D, Krivickas LS, Hughes VA, Goldstein R, Roubenoff R (2000b) Skeletal muscle fiber quality in older men and women. Am J Physiol 279:C611–C618
- Fry AC, Newton RU (2002) A brief history of strength training and basic principles and concepts. In: Kraemer WJ, Häkkinen K (eds) Strength training for sport. Blackwell Science, Oxford, pp 1–19
- Galea V (1996) Changes in motor unit estimates with ageing. J Clin Neurophysiol 13:253–260
- Grassi B, Cerretelli P, Narici MV, Marconi C (1991) Peak anaerobic power in master athletes. Eur J Appl Physiol 62:394–399
- Greig CA, Botella J, Young A (1993) The quadriceps strength of healthy elderly people remeasured after eight years. Muscle Nerve 16:6–10
- Greig CA, Young A, Skelton DA, Pippet E, Butler FMM, Mahmud SM (1994) Exercise studies with elderly volunteers. Age Ageing 23:185–189
- Grimby G, Saltin B (1983) The ageing muscle: a mini-review. Clin Physiol 3:209–218

- Grimby G, Aniansson A, Hedberg M, Henning GB, Grangard U, Kvist H (1992) Training can improve muscle strength and endurance in 78- to 84-yr-old men. J Appl Physiol 73:2517–2523
- Gruenewald DA, Matsumoto AM (2003) Testosterone supplementation therapy for older men: potential benefits and risks. J Am Geriatr Soc 51:101–115
- Gutmann E, Hanzlicovà V (1970) Effect of androgens no histochemical fibre type. Differentiation in the temporal muscle of the guinea-pig. Histochemistry 24:287–291
- Häkkinen K, Häkkinen A (1991) Muscle cross-sectional area, force production and relaxation characteristics in women at different ages. Eur J Appl Physiol 62:410–414
- Häkkinen K, Häkkinen A (1995) Neuromuscular adaptations during intensive strength training in middle-aged and elderly males and females. Electromyogr Clin Neurophysiol 35:137– 147
- Häkkinen K, Pakarinen A (1994) Serum hormones and strength development during strength training in middle-aged and elderly males and females. Acta Physiol Scand 150:211–219
- Häkkinen K, Alen M, Kallinen M, Izquierdo M, Jokelainen K, Lassila H, Malkia E, Kraemer WJ, Newton RU (1998a) Muscle CSA, force production, and activation of leg extensors during isometric and dynamic actions in middle-aged and elderly men and women. J Aging Phys Activ 6:232–247
- Häkkinen K, Newton RU, Gordon SE, McCormick M, Volek JS, Nindl BC, Gotshalk LA, Campbell WW, Evans WJ, Häkkinen A, Humphries BJ, Kraemer WJ (1998b) Changes in muscle morphology, electromyographic activity, and force production characteristics during progressive strength training in young and older men. J Gerontol 53:B415–B423
- Häkkinen K, Kallinen M, Izquierdo M, Jokelainen K, Lassila H, Malkia E, Kraemer WJ, Newton RU, Alen M (1998c) Changes in agonist-antagonist EMG, muscle CSA, and force during strength training in middle-aged and older people. J Appl Physiol 84:1341–1349
- Häkkinen K, Alen M, Kallinen M, Newton RU, Kraemer WJ (2000) Neuromuscular adaptation during prolonged strength training, detraining and re-strength-training in middle-aged and elderly people. Eur J Appl Physiol 83:51–62
- Häkkinen K, Kraemer WJ, Newton RU, Alen M (2001) Changes in electromyographic activity, muscle fibre and force production characteristics during heavy resistance/power strength training in middle-aged and older men and women. Acta Physiol Scand 171:51–62
- Hara Y, Findley TW, Sugimoto A, Hanayama K (1998) Muscle fiber conduction velocity (MFCV) after fatigue in elderly subjects. Electromyogr Clin Neurophysiol 38:427–435
- Harman EA (1995) The measurement of human mechanical power. In: Maud PJ, Foster C (eds) Physiological assessment of human fitness. Human Kinetics, Champaign, Ill., pp 87–113
- Harridge SDR, Young A (1998) Skeletal muscle. In: Pathy MJS (ed) Principles and practice of geriatric medicine. Wiley, London, pp 898–905
- Harridge SDR, Bottinelli R, Canepari M, Pellegrino MA, Reggiani C, Esbjornsson M, Saltin B (1996) Whole muscle and single fibre contractile characteristics and myosin heavy chain isoforms in man. Pflugers Arch 432:913–920
- Harridge SDR, Bottinelli R, Canepari M, Pellegrino MA, Reggiani C, Esbjornsson M, Balsom PD, Saltin B (1998) Sprint training, in vitro and in vivo muscle function, and myosin heavy chain expression. J Appl Physiol 84:442–449
- Harridge SDR, Pearson SJ, Young A (1999a) Muscle power loss in old age: functional relevance and effects of training. In: Capodaglio P, Narici MV (eds) Physical activity in the elderly. Maugeri Foundation Books and PI-ME Press, Pavia, pp 123– 137
- Harridge SDR, Kryger A, Stensgaard A (1999b) Knee extensor strength, activation, and size in very elderly people following strength training. Muscle Nerve 22:831–839
- Hicks AL, Cupido CM, Martin J, Dent J (1992) Muscle excitation in elderly adults: the effects of training. Muscle Nerve 15:87–93

- Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc R Soc Biol 126:136–195
- Höök P, Vidyasagar S, Larsson L (2001) Effects of aging on actin sliding speed on myosin from single skeletal muscle cells of mice, rats, and humans. Am J Physiol 280:C782–C788
- Hortobágyi T, Tunnel D, Moody J, Beam S, De Vita P (2001) Lowor high-intensity strength training partially restores impaired quadriceps force accuracy and steadiness in aged adults. J Gerontol 56A:B38–B47
- Hunter GR, Treuth MS, Weinsier RL, Kekes-Szabo T, Kell SH, Roth DL, Nicholson C (1995) The effects of strength conditioning on older women's ability to perform daily tasks. J Am Geriatr Soc 43:756–760
- Hunter SK, Thompson MW, Ruell PA, Harmer AR, Thom JM, Gwinn TH, Adams RD (1999) Human skeletal sarcoplasmic reticulum Ca²⁺ uptake and muscle function with aging and strength training. J Appl Physiol 86:1858–1865
- Iannuzzi-Sucich M, Prestwood KM, Kenny AM (2002) Prevalence of sarcopenia and predictors of skeletal muscle mass in healthy, older men and women. J Gerontol 57A:M772–M777
- Izquierdo M, Ibanez J, Gorostiaga E, Garrues M, Zuniga A, Anton A, Larrion JL, Häkkinen K (1999) 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 167:57–68
- Izquierdo M, Häkkinen K, Ibanez J, Garrues M, Anton A, Zuniga A, Larrion JL, Gorostiaga E (2001) Effects of strength training on muscle power and serum hormones in middle-aged and older men. J Appl Physiol 90:1497–1507
- Jakobi JM, Rice CL (2002) Voluntary muscle activation varies with age and muscle group. J Appl Physiol 93:457–462
- Janssen I, Heymsfield SB, Wang Z, Ross R (2000) Skeletal muscle mass and distribution in 468 men and women aged 18–88 years. J Appl Physiol 89:81–88
- Jennekens FGI, Tomlinson BE, Walton J (1971) Histochemical aspects of five limb muscles in old age: an autopsy study. J Neurol Sci 14:259–276
- Jones DA, Round JM (1990) Skeletal muscle in health and disease.
 A textbook of muscle physiology. Manchester University Press, Manchester, pp 23–25, 105–107
 Jozsi AC, Campbell WW, Joseph L, Davey SL, Evans WJ (1999)
- Jozsi AC, Campbell WW, Joseph L, Davey SL, Evans WJ (1999) Changes in power with resistance training in older and younger men and women. J Gerontol 54A:M591–M596
- Jubrias SA, Odderson IR, Esselman PC, Conley KE (1997) Decline in isokinetic force with age: muscle cross-sectional area and specific force. Pflugers Arch 434:246–253
- Judge JO, Underwood M, Gennosa T (1993) Exercise to improve gait velocity in older persons. Arch Phys Med Rehabil 74:400–406
- Kallman DA, Plato CC, Tobin JD (1990) The role of muscle loss in the age-related decline of grip strength: cross-sectional and longitudinal perspectives. J Gerontol 45:M82–M88
- Kamen G, Sison SV, DukeDu CC, Patten C (1995) Motor unit discharge behavior in older adults during maximal-effort contractions. J Appl Physiol 79:1908–1913
- Kawamura Y, Okazaki H, O'Brien PC, Dyck PJ (1977a) Lumbar motoneurons of man. I. Numbers and diameter histograms of alpha and gamma axons and ventral roots. J Neuropathol Exp Neurol 36:853–860
- Kawamura Y, O'Brien PC, Okazaki H, Dyck PJ (1977b) Lumbar motoneurons of man. II: numbers and diameter distributions of large- and intermediate-diameter cytons in motoneuron columns of spinal cord of man. J Neuropathol Exp Neurol 36:861– 870
- Kent-Braun JA, Ng AV (1999) Specific strength and voluntary muscle activation in young and elderly women and men. J Appl Physiol 87:22–29
- Kent-Braun JA, Ng AV, Young K (2000) Skeletal muscle contractile and noncontractile components in young and older women and men. J Appl Physiol 88:662–668
- Klitgaard H, Ausoni S, Damiani E (1989) Sarcoplasmic reticulum of human skeletal muscle: age-related changes and effect of training. Acta Physiol Scand 137:23–31

- Klitgaard H, Mantoni M, Schiaffino S, Ausoni S, Gorza L, Laurent-Winter C, Schnohr P, Saltin B (1990) Function, morphology and protein expression of ageing skeletal muscle: a cross-sectional study of elderly men with different training backgrounds. Acta Physiol Scand 140:41–54
- Kraemer WJ, Häkkinen K, Newton RU, Nindl BC, Volek JS, McCormick M, Gotshalk LA, Gordon SE, Fleck SJ, Campbell WW, Putukian M, Evans WJ (1999) Effects of heavy-resistance training on hormonal response patterns in younger vs. older men. J Appl Physiol 87:982–992
- Krebs DE, Robbins CE, Lavine L, Mann RW (1998) Hip biomechanics during gait. J Orthop Sports Phys Ther 28:51–59
- Kubo K, Kanehisa H, Miyatani M, Tachi M, Fukunaga T (2003) Effect of low-load resistance training on the tendon properties in middle-aged and elderly women Acta Physiol Scand 178:25– 32
- Langlois JA, Visser M, Davidovic LS, Maggi S, Li G, Harris TB (1998) Hip fracture risk in older White men is associated with change in body weight from age 50 years to old age. Arch Intern Med 158:990–996
- Larsson L (1982) Physical training effects on muscle morphology in sedentary males at different ages. Med Sci Sports Exerc 14:203– 206
- Larsson L, Grimby G, Karlsson J (1979) Muscle strength and speed of movement in relation to age and muscle morphology. J Appl Physiol 46:451–456
- Larsson L, Xiaopeng L, Frontera WR (1997) Effects of aging on shortening velocity and myosin isoform composition in single human skeletal muscle cells. Am J Physiol 272:C638–C649
- Levy DI, Young A, Skelton DA, Yeo AL (1994) Strength, power and functional ability. In: Passeri M (eds) Geriatrics '94. CIC Edizioni Internazionali, Rome, pp 85–93
- Lexell J (1995) Human aging, muscle mass, and fiber type composition. J Gerontol 50A (Spec No):11–16
- Lexell J (2000) Strength training and muscle hypertrophy in older men and women. Top Geriatr Rehabil 15:41–46
- Lexell J, Downham DJ (1991) The occurrence of fibre type grouping in healthy human muscle: a quantitative study of cross-sections of whole vastus lateralis from men between 15 and 83 years. Acta Neuropathol 81:377–381
- Lexell J, Henriksson-Larsén K, Winblad B, Sjostrom M (1983)
 Distribution of different fiber types in human skeletal muscles.
 3. Effects of aging studied in whole muscle cross sections. Muscle Nerve 6:588–595
- Lexell J, Taylor AW, Sjostrom M (1988) What is the cause of the aging 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 84:275–283
- Lexell J, Downham DJ, Larsson Y, Bruhn E, Morsing B (1995) Heavy-resistance training in older Scandinavian men and women: short- and long-term effects on arm and leg muscles. Scand J Med Sci Sports 5:329–341
- Lindle RS, Metter EJ, Lynch NA, Fleg JL, Fozard JL, Tobin J, Roy TA, Hurley BF (1997) Age and gender comparisons of muscle strength in 654 women and men aged 20–93 yr. J Appl Physiol 83:1581–1587
- Lynch NA, Metter EJ, Lindle RS, Fozard JL, Tobin JD, Roy TA, Fleg JL, Hurley BF (1999) Muscle quality. I. Age-associated differences between arm and leg muscle groups. J Appl Physiol 86:188–194
- Macaluso A, De Vito G (2003) Comparison between young and older women in explosive power output and its determinants during a single leg-press action after optimisation of load. Eur J Appl Physiol DOI 10.1007/s00421-003-0866-7
- Macaluso A, De Vito G, Felici F, Nimmo MA (2000) Electromyogram changes during sustained contraction after resistance training in women in their 3rd and 8th decades. Eur J Appl Physiol 82:418–424
- Macaluso A, Nimmo MA, Foster JE, Cockburn M, McMillan NC, De Vito G (2002) Contractile muscle volume and agonistantagonist coactivation account for differences in torque between young and older women. Muscle Nerve 25:858–863

- Macaluso A, Young A, Gibb KS, Rowe DA, De Vito G (2003) Cycling as a novel approach to resistance training increases muscle strength, power and selected functional abilities in healthy older women. J Appl Physiol DOI 10.1152/japplphysiol.00416.2003
- Maganaris CN (2001) In vivo tendon mechanical properties in young adults and healthy elderly [Online]. http://www.mmu.a-c.uk/c-a/exspsci/research/invivo.htm
- McArdle WD, Katch FI, Katch VL (1996) Exercise physiology. Williams and Wilkins, Baltimore, Md., pp 350, 393
- McCafferty WB, Horvath SM (1977) Specificity of exercise and specificity of training: a subcellular review. Res Q 48:358– 371
- McCartney N, Hicks AL, Martin J, Webber CE (1996) A longitudinal trial of weight training in the elderly: continued improvements in year 2. J Geront 51A:B425–B433
- McComas AJ (1998) Motor units: how many, how large, what kind? J Electromyogr Kinesiol 8:391–402
- Meltzer DE (1994) Age dependence of Olympic weightlifting ability. Med Sci Sports Exerc 26:1053–1067
- Merletti R, Lo Conte LR, Cisari C, Actis MV (1992) Age related changes in surface myoelectric signals. Scand J Rehabil Med 24:25–36
- Merletti R, Farina D, Gazzoni M, Schieroni MP (2002) Effect of age on muscle functions investigated with surface electromyography. Muscle Nerve 25:65–76
- Metter EJ, Conwit R, Tobin J, Fozard JL (1997) Age-associated loss of power and strength in the upper extremities in women and men. J Gerontol 52:B267–B276
- Metter EJ, Conwit R, Metter B, Pacheco T, Tobin J (1998) The relationship of peripheral motor nerve conduction velocity to age-associated loss of grip strength. Aging Clin Exp Res 10:471–478
- Mitsipoulos N, Baumgartner RN, Heymsfield SB, Lyons W, Gallagher D, Ross R (1998) Cadaver validation of skeletal muscle measurement by magnetic resonance imaging and computerized tomography. J Appl Physiol 85:115–122
- Miyatani M, Kanehisa H, Masuo Y, Masamitsu I, Fukunaga T (2001) Validity of estimating limb muscle volume by bioelectrical impedance. J Appl Physiol 91:386–394
- Moore DH (1975) A study of age group track and field records to relate age and running speed. Nature 253:264–265
- Morgan M, Phillips JG, Bradshaw JL, Mattingley JB, Iansek R, Bradshaw JA (1994) Age related motor slowness: simply strategic? J Gerontol 49A:M133–M139
- Morganti CM, Nelson ME, Fiatarone MA, Dallal GE, Economos CD, Crawford BM, Evans WJ (1995) Strength improvements with 1 yr of progressive resistance training in older women. Med Sci Sports Exerc 27:906–912
- Moritani T, deVries HA (1980) Potential for gross muscle hypertrophy in older men. J Gerontol 35A:672–682
- Narici MV (1999) Effect of ageing on muscle contractile properties. In: Capodaglio P, Narici MV (eds) Physical Activity in the elderly. Maugeri Foundation Books and PI-ME Press, Pavia, pp 61–67
- Narici MV (2001) Structural and functional adaptations of human skeletal muscle to disuse and ageing [Online]. http:// www.mmu.ac.uk/c-a/exspsci/research/structural.htm
- Narici MV, Bordini M, Cerretelli P (1991) Effect of aging on human adductor pollicis muscle function. J Appl Physiol 71:1277– 1281
- Narici MV, Landoni L, Minetti AE (1992) Assessment of human knee extensor muscles stress from in vivo physiological crosssectional area and strength measurements. Eur J Appl Physiol 65:438–444
- Narici MV, Susta D, Ciuffreda L, Ferri A, Scaglioni G, Capodaglio P (1999) Changes in human gastrocnemius muscle architecture with ageing. J Physiol (Lond) 518P:87
- Norris AĤ, Shock NW, Wagman IH (1953) Age changes in the maximum conduction velocity of motor fibers of human ulnar nerves. J Appl Physiol 5:589–593

- O'Toole ML (1997) Do older individuals need more than usual physical activities to maintain muscle strength and function? J Am Geriatr Soc 45:1534–1535
- Onambele NG, Skelton DA, Bruce SA, Woledge RC (2001) Follow-up study of the benefits of hormone replacement therapy on isometric muscle strength of adductor pollicis in postmenopausal women. Clin Sci 100:421–422
- Overend TJ, Cunningham DA, Kramer JF, Lefcoe MS, Paterson DH (1992a) Knee extensor and knee flexors strength: crosssectional area ratios in young and elderly men. J Gerontol 47A:M204–M210
- Overend TJ, Cunningham DA, Paterson DH, Lefcoe MS (1992b) Thigh composition in young and elderly men determined by computed tomography. Clin Physiol 12:629–640
- Patten C, Kamen G (2000) Adaptations in motor unit discharge activity with force control training in young and older human adults. Eur J Appl Physiol 83:128–143
- Patten C, Kamen G, Rowland DM (2001) Adaptations in maximal motor unit discharge rate to strength training in young and older adults. Muscle Nerve 24:542–550
- Pearson SJ, Harridge SDR, Grieve DW, Young A, Woledge RC (2001) A variable inertial system for measuring the contractile properties of human muscle. Med Sci Sports Exerc 33:2072– 2076
- Pearson SJ, Young A, Macaluso A, De Vito G, Nimmo MA, Cobbold M, Harridge SDR (2002) Muscle function in elite master weightlifters. Med Sci Sports Exerc 34:1199–1206
- Perrine JJ (1986) The biophysics of maximal muscle power outputs: methods and problems of measurement. In: Jones NL, Mc-Cartney N, McComas AJ (eds) Human muscle power. Human Kinetics, Champaign, Ill., pp 15–25
- Phillips SK, Bruce SA, Newton D, Woledge RC (1992) The weakness of old age is not due to failure of muscle activation. J Gerontol 47A:M45–M49
- Phillips SK, Rook KM, Siddle NC, Bruce SA, Woledge RC (1993) Muscle weakness in women occurs at an earlier age than in men, but strength is preserved by hormone replacement therapy. Clin Sci 84:95–98
- Pruitt L, Taaffe DR, Marcus R (1995) Effects of a one year high intensity versus low-intensity resistance training program on bone mineral density in older women. J Bone Miner Res 10:1788–1795
- Pyka G, Lindenberger E, Charette SL, Markus R (1994) Muscle strength and fiber adaptations to a year-long resistance training program in elderly men and women. J Gerontol 49A:M22–M27
- Rantanen T, Avela J (1997b) Leg extension power and walking speed in very old people living independently. J Gerontol 52A:M225–M231
- Rantanen T, Era P, Heikkinen E (1997a) Physical activity and the changes in maximal isometric strength in men and women from the ages of 75 to 80 years. J Am Geriatr Soc 45:1439– 1445
- Reeves ND, Maganaris CN, Narici MV (2003a) Effect of strength training on human patella tendon mechanical properties of older individuals. J Physiol (Lond) 548:971–981
- Reeves ND, Maganaris CN, Narici MV (2003b) Strength training alters the viscoelastic properties of tendons in elderly humans. Muscle Nerve 28:74–81
- Rice CL (2000) Muscle function at the motor unit level: consequences of aging. Top Geriatr Rehabil 15:70–82
- Rice CL, Cunningham DA, Paterson DH, Lefcoe MS (1989) Arm and leg composition determined by computed tomography in young and elderly men. Clin Physiol 9:207–220
- Rooks DS, Kiel DP, Parsons C, Hayes WC (1997) Self-paced resistance training and walking exercise in community-dwelling older adults: effects on neuromotor performance. J Gerontol 52A:M161–M168
- Roos MR, Rice CL, Connelly DM, Vandervoort AA (1999) Quadriceps muscle strength, contractile properties and motor unit firing rates in young and old men. Muscle Nerve 22:1094– 1103

- Rooyackers OE, Nair KS (1997) Hormonal regulation of human muscle protein metabolism. Annu Rev Nutr 17:457–485
- Rudman D, Feller AG, Nagraj HS, Gergans GA, Lalitha PY, Goldberg AF, Schlenker RA, Cohn L (1990) Effects of human growth hormone in men over 60 years old. N Engl J Med 323:1– 6
- Sale DG (1988) Neural adaptation to resistance training. Med Sci Sports Exerc 20:S135–S145
- Sargeant AJ (1994) Human power output and muscle fatigue. Int J Sports Med 15:116–121
- Scaglioni G, Ferri A, Minetti AE, Martin A, Van Hoecke J, Capodaglio P, Sartorio A, Narici MV (2002) Plantar flexors activation capacity and H reflex in older adults: adaptations to strength training. J Appl Physiol 92:2292–2302
- Sharman MJ, Newton RÚ, Triplett-McBride T, McGuigan MRM, McBride JM, Häkkinen A, Häkkinen K, Kraemer WJ (2001) Changes in myosin heavy chain composition with heavy resistance training in 60- to 75-year old men and women. Eur J Appl Physiol 84:127–132
- Sherrington C, Lord SR (1997) Home exercise to improve strength and walking velocity after hip fracture: a randomized controlled trial. Arch Phys Med Rehabil 78:208–212
- Sherrington CS (1929) Some functional problems attaching to convergence. Proc R Soc Lond 105:332–362
- Short KR, Nair KS (1999) Mechanisms of sarcopenia of aging. J Endocrinol Invest 22:95–105
- Sinaki M, McPhee MC, Hodgson SF, Merritt JM, Offord KP (1986) Relationship between bone mineral density of spine and strength of back extensors in healthy postmenopausal women. Mayo Clinic Proc 61:116–122
- Skelton DA, McLaughlin AW (1996) Training functional ability in old age. Physiotherapy 82:159–167
- Skelton DA, Greig CA, Davies JM, Young A (1994) Power and related functional ability of healthy people aged 65–89 years. Age Ageing 23:371–377
- Skelton DA, Young A, Greig CA, Malbut KE (1995) Effects of resistance training on strength, power, and selected functional abilities of women aged 75 and older. J Am Geriatr Soc 43:1081–1087
- Skelton DA, Phillips SK, Bruce SA, Naylor CH, Woledge RC (1999) Hormone replacement therapy increases isometric muscle strength of adductor pollicis in post-menopausal women. Clin Sci 96:357–364
- Solomonow M, Baratta R, Bernardi M, Zhou M, Lu Y, Zhu M, Acierno S (1994) Surface and wire EMG crosstalk in neighbouring muscles. J Electromyogr Kinesiol 4:131–142
- Suzuki T, Bean JF, Fielding RA (2001) Muscle power of the ankle flexors predicts functional performance in community dwelling older women. J Am Geriatr Soc 49:1161–1167
- Taaffe DR, Pruitt L, Reim J, Hintz RL, Butterfield GE, Hoffman AR, Marcus R (1994) Effect of recombinant human growth hormone on the muscle strength response to resistive exercise in elderly men. J Clin Endocrinol Metab 79:1361–1366
- Taaffe DR, Luz Villa M, Delay R, Marcus R (1995) Maximal muscle strength of elderly women is not influenced by oestrogen status. Age Ageing 24:329–333
- Taaffe DR, Jin IH, Vu TH, Hoffman AR, Marcus R (1996) Lack of effect of recombinant human growth hormone (GH) on muscle morphology and GH-insulin-like growth factor expression in resistance trained elderly men. J Clin Endocrinol Metab 81:421– 425
- Taaffe DR, Duret C, Wheeler S, Marcus R (1999) Once-weekly resistance exercise improves muscle strength and neuromuscular performance in older adults. J Am Geriatr Soc 47:1208–1214
- Tenover JS (1992) Effects of testosterone supplementation in the aging male. J Clin Endocrinol Metab 75:1092–1098
- Thomas M, Fiatarone MA, Fielding RA (1996) Leg power in young women: relationship to body composition, strength, and function. Med Sci Sports Exerc 28:1321–1326
- Tinetti ME, Speechley M, Ginter SF (1988) Risk factors for falls among elderly persons living in the community. N Engl J Med 319:1701–1707

- Tomlinson BE, Irving D (1977) The numbers of limb motor neurons in the human lumbosacral cord throughout life. J Neurol Sci 34:213–219
- Tomonaga M (1977) Histochemical and ultrastructural changes in senile human skeletal muscle. J Am Geriatr Soc 25:125–131
- Tracy BL, Ivey FM, Hurlbut D, Martel GF, Lemmer JT, Siegel EL, Metter EJ, Fozard JL, Fleg JL, Hurley BF (1999) Muscle quality. II. Effects of strength training in 65- to 75-yr-old men and women. J Appl Physiol 86:195–201
- Trappe S, Williamson D, Godard M, Porter D, Rowden G, Costill D (2000) Effect of resistance training on single muscle fiber contractile function in older men. J Appl Physiol 89:143–152
- Trappe S, Godard M, Gallagher D, Carroli C, Rowden G, Porter D (2001) Resistance training improves single muscle fiber contractile function in older women. Am J Physiol 281:C398–C406
- Trappe S, Williamson D, Godard M (2002) Maintenance of whole muscle strength and size following resistance training in older men. J Gerontol 57A:B138–B143
- Tzankoff SP, Norris AH (1977) Effect of muscle mass decrease on age related BMR changes. J Appl Physiol 43:1001–1006
- Urban RJ, Bodenburg YH, Gilkison C, Foxworth J, Coggan AR, Wolfe DR, Ferrando A (1995) Testosterone administration to elderly men increases skeletal muscle strength and protein synthesis. Am J Physiol 269:E820–E826
- Van Cutsem M, Duchateau J, Hainaut K (1998) Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. J Physiol (Lond) 513:295–305
- Vandervoort AA (2002) Aging of the human neuromuscular system. Muscle Nerve 25:17–25
- Vandervoort AA, McComas AJ (1986) Contractile changes in opposing muscles of the human ankle joint with aging. J Appl Physiol 61:361–367
- Wang FC, De Pasqua V, Delwaide PJ (1999) Age-related changes in fastest and slowest conducting axons of thenar motor units. Muscle Nerve 22:1022–1029
- Welle S, Thornton C, Statt M, McHenry B (1996a) Growth hormone increases muscle mass and strength but does not rejuvenate myofibrillar protein synthesis in healthy subjects over 60 years old. J Clin Endocrinol Metab 81:3239–3243
- Welle S, Totterman S, Thornton C (1996b) Effect of age on muscle hypertrophy induced by resistance training. J Gerontol 51A:M270–M275
- Welle S, Bhatt K, Thornton CA (1999) Stimulation of myofibrillar synthesis by exercise is mediated by more efficient translation of mRNA. J Appl Physiol 86:1220–1225
- Viitasalo JT, Era P, Leskinen AL, Heikkinen E (1985) Muscular strength profiles and anthropometry in random samples of men aged 31–35, 51–55 and 71–75 years. Ergonomics 28:1563–1574
- Vogel HG (1991) Species differences of elastic and collagenous tissue – influence of maturation and age. Mech Ageing Dev 57:15–24
- Williamson D, Godard M, Porter D, Costill D, Trappe S (2000) Progressive resistance training reduces myosin heavy chain coexpression in single muscle fibres from older men. J Appl Physiol 88:627–633
- Winegard KJ, Hicks AL, Sale DG, Vandervoort AA (1996) A 12year follow-up study of ankle muscle function in older adults. J Gerontol 51A:B202–B207
- Wolfson L, Judge J, Whipple R, King M (1995) Strength is a major factor in balance, gait, and the occurrence of falls. J Gerontol 50A (Spec No):64–67
- Yarasheski KE, Campbell JA, Smith K, Rennie MJ, Holloszy JO, Bier DM (1992) Effect of growth hormone and resistance exercise on muscle growth in young men. Am J Physiol 262:E261–E267
- Yarasheski KE, Zachwieja JJ, Campbell JA, Bier DM (1995) Effect of growth hormone and resistance exercise on muscle growth and strength in older men. Am J Physiol 268:E268–E276
- Young A, Stokes M, Crowe M (1984) Size and strength of the quadriceps muscles of old and young women. Eur J Clin Invest 14:282–287

- Young A, Stokes M, Crowe M (1985) The size and strength of the quadriceps muscles of old and young men. Clin Physiol 5:145–154
- Yue GH, Ranganathan VK, Siemionov V, Liu JZ, Sahgal V (1999) Older adults exhibit a reduced ability to fully activate their biceps brachii muscle. J Gerontol 54A:249–253
- Zamparo P, Antonutto G, Capelli C, di Prampero PE (2000) Effects of different after-loads and knee angles on maximal explosive power of the lower limbs in humans. Eur J Appl Physiol 82:381–390