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Selva Raj, Isaac; Bird, Stephen; Shield, A

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Aging and the Force-Velocity Relationship of Muscles

Isaac Selva Raj* and Stephen R. Bird

Royal Melbourne Institute of Technology

Anthony J. Shield

Queensland University of Technology

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Address for correspondence:

Isaac Selva Raj
Discipline of Exercise Sciences
School of Medical Sciences
RMIT University
Bundoora West Campus
PO Box 71
Bundoora
Victoria 3083
Australia
Phone: 61 3 9925 7037
Fax: 61 3 9467 8181
E-mail: isaacselva.raj@rmit.edu.au

Abstract

Aging in humans is associated with a loss in neuromuscular function and performance. This is related, in part, to the reduction in muscular strength and power caused by a loss of skeletal muscle mass (sarcopenia) and changes in muscle architecture. Due to these changes, the force-velocity (f-v) relationship of human muscles alters with age. This change has functional implications such as slower walking speeds. Different methods to reverse these changes have been investigated, including traditional resistance training, power training and eccentric (or eccentrically-biased) resistance training. This review will summarise the changes of the f-v relationship with age, the functional implications of these changes and the various methods to reverse or at least partly ameliorate these changes.

Aging and the Force-Velocity Relationship of Muscles

Aging in humans is associated with a loss in neuromuscular function and performance (Carville, Perry, Rutherford, Smith, & Newham, 2007; Doherty, 2003; Hunter, McCarthy, & Bamman, 2004). This is, in part, related to the reduction in strength and power (Macaluso & De Vito, 2004) caused by a loss of skeletal muscle mass (sarcopenia) (Hunter et al., 2004; Narici, Maganaris, Reeves, & Capodaglio, 2003) and changes in muscle architecture. Sarcopenia is attributed to a number of factors, which include: preferential type II myofibre atrophy as a result of motor neuron death (Hunter et al., 2004), decreased physical activity (Doherty, 2003; Macaluso & De Vito, 2004), altered hormonal status, decreased caloric and protein intake, inflammatory mediators, and altered protein synthesis (Doherty, 2003). Along with reduced muscle mass there are concomitant changes in muscle architecture which include alterations in fascicle length and pennation angle, both of which are reduced with age (Narici et al., 2003).

As a consequence of these physiological and structural changes, the force-velocity relationship of human muscles alters with aging, and muscular strength and power are reduced across all contraction speeds (Gajdosik, Vander Linden, & Williams, 1999; Harries & Bassey, 1990; Lanza, Towse, Caldwell, Wigmore, & Kent-Braun, 2003; Lindle et al., 1997; Ochala, Lambertz, Pousson, Goubel, & Hoecke, 2004; Petrella, Kim, Tuggle, Hall, & Bamman, 2005; Thom, Morse, Birch, & Narici, 2005, 2007; Toji & Kaneko, 2007; Trappe et al., 2003; Valour, Ochala, Ballay, & Pousson, 2003). This decline in muscular strength and power, along with other factors such as the aging of the somatosensory and motor nervous systems (Edstrom et al., 2007; Ishiyama, 2009; Shaffer & Harrison, 2007), has functional implications such as slower walking speeds (Bottaro, Machado, Nogueira, Scales, &

Veloso, 2007; Doherty, 2003), an increased risk of falling (Orr et al., 2006; Skelton, Kennedy, & Rutherford, 2002), and a reduced capacity to undertake activities of daily living (ADLs), all of which contribute to a loss of independence and reduction in the quality of life (Doherty, 2003). This is of major concern at both the individual and societal level, as increasing demands on the healthcare system may compromise its capacity to cope in the future. Consequently, interventions that can prevent or ameliorate these declines in function are likely to have significant benefit, and it is therefore important to understand their underlying impact and identify those that are the most efficacious.

This review will focus on the force-velocity (f-v) relationship of human muscles from the context of changes with age, the functional significance of these changes and interventions designed to slow down, stop or reverse these changes.

Changes in the Force-Velocity Relationship of Muscles with Age

Cross-Sectional Studies

Aging typically results in reductions of force generating capacity right across the f-v spectrum but the decline appears greatest for concentric actions (Hortobagyi et al., 1995; Pousson, Lepers, & Van Hoecke, 2001). Table 1 summarises the findings of selected cross-sectional studies that have investigated the effect of aging in healthy adults on the f-v relationship using isokinetic strength tests.

The relative preservation of eccentric strength has been noted by a number of authors (Hortobagyi et al., 1995; Klass, Baudry, & Duchateau, 2007; Lindle et al., 1997; Lynch et al., 1999; Ochala, Dorer, Frontera, & Krivickas, 2006; Porter, Vandervoort, & Kramer, 1997; Poulin, Vandervoort, Paterson, Kramer, & Cunningham, 1992; Pousson et al., 2001; Vandervoort, Kramer, & Wharram, 1990).

With the discovery of the relative preservation of eccentric strength with age first in women (Vandervoort et al., 1990) and then in men (Poulin et al., 1992), Hortobagyi et al. (1995) made the initial effort to explain its cause. They tested sedentary but healthy men (age range 18 to 80 years, *n* = 60) and women (age range 20 to 74 years, *n* = 30) for eccentric, isometric and concentric knee extensor strength on an isokinetic dynamometer, and related the results to fat-free mass and muscle fibre characteristics. This study also found that eccentric strength was relatively preserved in older men, with older women actually being about 5% stronger in eccentric contractions than young women. However, the preservation of eccentric strength with age was found to be independent of muscle mass, muscle fibre type, or size.

Despite being unable to find a reason for eccentric force preservation with age, Hortobagyi and colleagues (1995) suggested possible explanations for this. Firstly, they suggested that the greater amount of intramuscular connective tissue observed in older adults may provide increased passive resistance during muscle lengthening while not affecting concentric or isometric force production. They also suggested that older adults might have less sarcomere instability due to the elimination of weak sarcomeres, adding that the increase in force production with increasing eccentric contraction velocity observed in the elderly but not in the young may support this idea. The third possible explanation they provided is that cross-bridge cycling during eccentric contractions may be somehow modified with age, thus allowing more force to be generated during muscle lengthening.

In a later experiment, Porter et al. (1997) made an attempt to test two of the explanations proposed by Hortobagyi et al. (1995). They tested the eccentric and concentric strength of the plantar flexors and dorsiflexors in 16 older women (mean age 67 ± 4 years) and 16 young women (mean age 27 ± 4 years). Passive resistive torque of the plantar flexors and average rate of torque development of the plantar flexors and dorsiflexors were also measured. In agreement with previous studies, they found that eccentric strength was relatively preserved in the plantar and dorsiflexors with ageing when compared with concentric strength. Although passive resistive torque of the plantar flexors was significantly higher in the older women, it was determined that this factor did not have a role to play in the preservation of eccentric torque. With regards to rate of torque development, it was found that older women had significantly lower values than young women in both plantar and dorsiflexors. The investigators attributed this finding to the greater loss of type II muscle fibres, as well as a slowing of cross-bridge cycling with age. They argue that while slower cross-bridge cycling may be detrimental to concentric contractions at high velocities, they may be advantageous in eccentric contractions. Thus, Porter et al. (1997) put forward the finding of a slower rate of torque development with age as an indirect explanation of the relative preservation of eccentric force with age.

Most recently, Ochala et al. (2006) attempted to explain this phenomenon by studying the behaviour of single vastus lateralis muscle fibres from 6 young men (mean age 31.6 years) and 6 older men (mean age 66.1 years). They applied a quick stretch to the fibres while they were maximally activated. This caused an immediate rise in tension (phase 1) followed by a reduction (phase 2) and then a secondary delayed and transient rise in tension in the fibres (phase 3). Finally the tension in the fibres reached a constant value (phase 4), which was lower than phase 3 but higher than the initial tension in the maximally activated fibre. Ochala et al. (2006) discovered that despite fibres from older men having a lower absolute maximal isometric force, the increases in tension in phases 3 and 4 were preserved in the older men. The investigators thus suggest that this discovery could be another possible explanation for the relative preservation of eccentric strength in the elderly.

Despite the important findings of the studies mentioned above, the mechanism for the smaller decrease in eccentric strength compared to concentric and isometric strength in the elderly is still not fully understood. The large decline in concentric force suggests that significant efforts should be made to improve this capacity although, for reasons discussed later in this review, the potential of eccentric training for older adults should be explored further in future research.

Longitudinal Studies

Longitudinal studies investigating the loss of strength with age generally agree with cross-sectional studies, finding losses in strength in the ankle plantar flexors, dorsiflexors, knee extensors and flexors, and elbow extensors and flexors at all contraction velocities tested (Aniansson, Hedberg, Henning, & Grimby, 1986; Frontera et al., 2000; Grimby, 1995; Winegard, Hicks, Sale, & Vandervoort, 1996). Aniansson and colleagues (1986) re-measured the knee extensor strength of 23 healthy males, 73 to 83 years old, between 30º/s and 300º/s 7 years after an initial strength measurement. They found losses of strength between 10 and 22% ($P < 0.05$) at all contraction velocities between the two examinations, and a decrease in the mean vastus lateralis fibre area of 11% ($P < 0.05$). Eleven years after the initial measurement, Grimby (1995) reported losses of 25 to 35% in knee extensor strength in a sub-group of 9 men from the original Aniansson et al. (1986) study. However, only strength at 30º/s declined to a significant ($P < 0.05$) extent between the second and third measurements. A possible reason for this is that these 9 men were reported to participate in moderate level physical activity for at least 4 hours per week, and all except two of the subjects reported unchanged levels of physical activity between the second and third measurements. This observation provides a good illustration of the importance of maintaining physical activity in old age for muscular strength.

Similarly, Frontera et al. (2000) carried out a longitudinal study of knee and elbow extensors and flexors in 9 healthy men (mean initial age 65.4 ± 4.2 years) and found losses in strength of between 20 and 30% ($P < 0.05$) after 12 years. The velocities at which the muscles were tested were 60 and 240º/s for the knee extensors and flexors and 60 and 180º/s for the elbow extensors and flexors. Computerised tomography scans of the thighs of 7 of the 9 men showed a reduction of 14.7% ($P < 0.05$) in the cross-sectional area of the thigh muscles over the 12 years. A more detailed look at these results reveals that knee extensor and flexor strength dropped by between 23.7 and 29.8% at both angular velocities tested (Frontera et al., 2000). However, elbow extensors and flexors showed losses of 19.4 and 16.4% respectively at 60º/s, while at 180º/s, only elbow flexors showed a significant loss in strength of 26.5% (Frontera et al., 2000).

With regards to isometric strength, Winegard et al. (1996) examined isometric dorsiflexor and plantar flexor strength in 11 men (mean initial age 73.5 ± 7.5 years) and 11 women (mean initial age 69.5 ± 6.4 years) and re-examined them 12 years later. All participants were generally in good health, and none were taking medication that would affect muscle contractile properties. They found losses of 25.2 and 30% ($P < 0.01$) in plantar flexor strength in females and males respectively (Winegard et al. 1996). Highlighting the different effects of reduced physical activity levels on postural and non-postural muscles were the observations that dorsiflexor strength declined significantly less (3.6 and 9.6% ($P < 0.05$) in males and females respectively) than plantar-flexor strength. In contrast to the longitudinal studies mentioned above, the study by Greig, Botella and Young (1993) found no significant loss of isometric quadriceps strength in 4 elderly men (age range 79 to 84 years) and 10 elderly women (age range 79 to 89 years) after 8 years. The authors report that all except one of the participants maintained or increased their physical activity levels over the 8 years and this could account for the preservation of isometric strength among the participants. This finding again underscores the importance of physical activity in preserving strength in the elderly, and indicates that interventions may assist with the maintenance of strength.

Maximum Shortening Velocity of Muscles

In-vivo studies have consistently found that the estimated maximum contraction velocity (V_{max}) of muscles is lower in healthy older adults compared to their younger counterparts (Labarque, 'T Eijnde, & Van Leemputte, 2002; Narici, Maganaris, & Reeves, 2005; Thom et al., 2005, 2007; Valour et al., 2003) (see Table 2). Ochala and colleagues (2004) did not estimate or directly measure V_{max}, but reported an index of maximal shortening velocity (VI_{max}). This index was taken as the speed of contraction of the plantar flexors under a load of 10% of each subject's maximal voluntary isometric torque. The group of 11 older men (mean age 67.9 ± 3.6 years) had a mean VI_{max} that was 83% ($P < 0.05$) of the mean VI_{max} of the young group ($n = 12$, mean age 21.7 ± 1.5 years).

The majority of in-vitro experiments comparing single muscle fibres of young versus older adults have found that the maximum unloaded shortening velocity (V_0) of single fibres is lower in older adults (Korhonen et al., 2006; Krivickas et al., 2001; Larsson, Li, & Frontera, 1997; Ochala, Frontera, Dorer, Van Hoecke, & Krivickas, 2007; Yu, Hedstrom, Cristea, Dalen, & Larsson, 2007). For example, Larsson, Li, and Frontera (1997) compared single fibres from the vastus lateralis muscles of 4 young (age range 25 to 31 years) and 4 older men (age range 73 to 81 years). They found that the V_0 values of type I and IIa muscle fibres from the older men were significantly (*P* < 0.001) lower than those from the young men (about 57% of young men for type I fibres and about 72% of young men for type IIa fibres). In contrast, despite examining fibres from the same muscle (vastus lateralis), Trappe et al. (2003) found no differences in the V_0 of muscle fibres of 6 young men (mean age 25 ± 1 years) and 6 young women (mean age 25 ± 1 years) as compared to 6 older men (mean age 80 ± 4 years) and 6 older women (mean age 78 ± 2 years). It should be noted, however, that differences in the methods used to analyse the muscle fibres compared to the other studies could explain this discrepancy, as the V_0's reported by Trappe and colleagues in their study were two to four times higher than the V_0's reported by others.

Power-Velocity Relationship

The power-velocity (p-v) relationship of human muscles shows age-related reductions in maximum power (P_{max}), force at maximum power (F_{opt}) and contraction velocity at maximum power (V_{opt}) (see Table 2). The decline in P_{max} is markedly greater than the decline in isometric and dynamic strength and has been shown in a number of recent aging studies that have used derivatives of Hill's (1938) equation to calculate power from the f-v relationship (Narici et al., 2005; Thom et al., 2005, 2007; Toji & Kaneko, 2007; Valour et al., 2003). This reduction in the P_{max} (and thus F_{opt}) with age is much more marked in the study by Thom et al. (2007), where it is only 20% of that of young adults. This discrepancy is hard to explain, but a comparison of the absolute plantar flexor torques produced by the older men in the studies by Narici et al. (2005), Thom et al. (2005) and Thom et al. (2007) reveals that the older men in the Thom et al. (2007) study produced less torque than the older men in the other two studies. Thus, there is a possibility that the older men in the Thom et al. (2007) study were more frail than the older men in the other two studies.

Physiological Basis of Changes to the Force-Velocity Relationship

The reasons for the reductions in muscular strength with age have been extensively reviewed elsewhere (Doherty, 2001, 2003; Macaluso & De Vito, 2004; Vandervoort, 2002). Briefly, the main cause of the age-related loss of isometric and concentric muscle strength is the loss of muscle mass. However, although skeletal muscle mass declines significantly with age, there is evidence that declines in the force-producing capacity of muscles occurs earlier and at a faster rate than the reduction in muscle mass (e.g. Macaluso & De Vito, 2004). Also, studies that have investigated changes in the f-v relationship of muscles with age and looked at the contribution of changes in muscle cross-sectional area or volume to these changes have found that normalisation of torque to cross-sectional area or volume significantly reduced, but did not eliminate age-related differences in torque (Thom et al., 2005, 2007; Toji & Kaneko, 2007). This implies that the loss of muscle mass alone cannot account for the reduction in the isometric and concentric strength of muscles. Other factors include lower single fibre specific force (or force per unit cross-sectional area), changes in muscle architecture and the infiltration of skeletal muscle by fat and connective tissue (Klein, Rice, & Marsh, 2001).

With regards to reductions in V_{max} with age, Thom and colleagues (2007) found that the V_{max} of gastrocnemius medialis (GM) muscles in 9 older men (mean age 74.7 ± 4.0 years was 38.2% ($P < 0.001$) lower than the GM V_{max} of 15 young men (mean age 25.3 ± 4.5 years). When velocity was normalised to muscle fascicle length (L_f), the difference in V_{max} between older men and young men was reduced to 15.9%. Thus, L_f is a significant determinant of V_{max}. Even so, normalisation of velocity to L_f did not eliminate the difference in V_{max} between older and young men, which means that there are other factors that contribute to the lower V_{max} observed in older adults.

One of these factors could be the selective atrophy of type II muscle fibres with age (Andersen, Terzis, & Kryger, 1999; Lexell, Taylor, & Sjostrom, 1988). However, according to D'Antona et al. (2007), this is caused by the decrease in physical activity that occurs with ageing, rather than ageing per se. Nevertheless, this could partly explain the lower V_{max} of the muscles of older adults. Importantly, D'Antona et al. (2007) also found that the V_{max} of type IIa fibres of the vastus lateralis muscles is lower in older adults than in young individuals, regardless of their physical activity levels. In addition to the above findings, Höök, Sriramoju, and Larsson (2001) have observed that the actin sliding speed on myosin in type I fibres from the vastus lateralis muscle is lower with age. Thus, there seems to be a decline in the intrinsic speed of the myosin molecule with age.

The Role of Muscle Architecture

Muscle fascicle length and pennation angle are routinely reported to be lower in elderly subjects than young adults (Morse, Thom, Birch, & Narici, 2005; Narici et al., 2003; Thom et al., 2007). The decline in pennation angle is secondary to muscle fibre atrophy which, of course, is not advantageous even though a higher percentage of muscle fascicle forces is transferred to tendons (Blazevich, 2006). With regards to L_f, the shorter fascicles (now with fewer sarcomeres arranged in series) will generate force over a smaller range of motion and exhibit reduced maximum shortening speeds (Blazevich & Sharp, 2005). Shorter fascicles will also generate less force at any given rate of shortening than longer fascicles because their sarcomere shortening rates are higher (Blazevich & Sharp, 2005).

A number of relatively recent studies have investigated the changes in L_f and θ with age (Morse et al., 2005; Narici et al., 2003; Thom et al., 2007). Narici et al. (2003) used ultrasonography to evaluate the muscle architecture of the gastrocnemius medialis (GM) muscles in 14 young (age range 27 to 42 years) and 16 older (age range 70 to 81 years) males. All participants were healthy and were matched for physical activity, height and body mass. L_f and θ were found to be smaller in older males by 10.2% ($P < 0.01$) and 13.2% ($P < 0.01$) respectively.

Similarly, Thom et al. (2007) found that GM L_f was 19.3% ($P < 0.05$) smaller in a group of 9 healthy older men (age range 69 to 82 years) when compared to 15 young men (age range 19 to 35 years). Morse et al. (2005) also found GM L_f to be 16% ($P < 0.01$) smaller in 12 healthy elderly men (age range 70 to 82 years) than in 15 young men (age range 19 to 35 years). In addition, they found that values of θ for all triceps surae muscles were 15 to 18% ($P < 0.05$) smaller in the elderly group.

As can be seen from the studies above, there is clear evidence that L_f and θ are reduced with age. Although a smaller θ is an advantage in terms of fibre force transmission to tendons, the combined effect of these changes to muscle architecture is a reduction in the force-producing capacity of older muscles. As stated earlier, shorter muscle fascicles also mean that the shortening speed of muscles is reduced, partly explaining the lower values of estimated V_{max} and power at high shortening velocities seen in older individuals. Thom et al. (2007) showed that about 22% of the age-related decline in V_{max} was due to shorter fascicle lengths.

Exercise interventions that aim to reverse or at least reduce the effects of aging should address not only muscle atrophy but also the reductions in fascicle length that also occur, as muscle architecture may be as important, if not more important, to muscle function than other factors such as fibre type (Blazevich, 2006; Burkholder, Fingado, Baron, & Lieber, 1994).

Summary

In summary, aging is associated with a downward and leftward shift of the f-v curve (as indicated by arrow 1 in Figure 1) due the lower force-producing capacity of muscles across all contraction speeds. This loss of strength is in the order of about 20 to 40% by the 7^{th} and 8^{th} decades. There is, however, a relative preservation of eccentric strength compared to concentric strength, with losses in eccentric strength 10 to 30% less than losses in concentric strength. In addition, there is a reduction in V_{max} of about 20 to 40% in adults in their 7^{th} and 8^{th} decades compared to young adults. With regards to the p-v relationship, a downward and leftward shift of the curve (as indicated by arrow 2 in Figure 1) is observed with aging. Thus, P_{max}, F_{opt}, and V_{opt} are lower, with losses in P_{max} of around 30 to 80% by the 7^{th} and 8^{th} decades.

Functional Implications

Logically, the changes in the f-v relationship (and therefore p-v relationship) that have been discussed will affect the daily function of the elderly in terms of the amount of force applied in movements and the speed of movement. This section will discuss selected studies that have made the link between these changes and the impairments in daily function that are observed in the elderly.

Impact of Loss of Strength and Power

The majority of studies investigating this area have assessed the relationship between lower limb muscle strength or power (or both) and function in tasks such as stair-climbing, rising from a chair, or walking (Bassey et al., 1992; Bean et al., 2002; Bendall, Bassey, & Pearson, 1989; Bonnefoy, Jauffret, & Jusot, 2007; Brown, Sinacore, & Host, 1995; Cuoco et al., 2004; Ostchega, Dillon, Lindle, Carroll, & Hurley, 2004; Petrella, Miller, & Cress, 2004; Puthoff & Nielsen, 2007; Rantanen & Avela, 1997; Runge, Rittweger, Russo, Schiessl, & Felsenberg, 2004; Suzuki, Bean, & Fielding, 2001; Visser, Deeg, Lips, Harris, & Bouter, 2000). Two studies have also looked at upper limb strength and power in relation to functional capacity (Herman et al., 2005; Skelton, Greig, Davies, & Young, 1994), while only one study investigated the relationship between V_{opt} and physical functional performance in elderly women (Clémençon, Hautier, Rahmani, Cornu, & Bonnefoy, 2008). There is a general consensus that there is a correlation between muscular strength (Bendall et al., 1989; Ostchega et al., 2004) and power (Bassey et al., 1992; Rantanen & Avela, 1997) and performance in functional tasks, with the relationship between power and function stronger than the relationship between strength and function (Bean et al., 2002; Cuoco et al., 2004; Puthoff & Nielsen, 2007; Suzuki et al., 2001). At this point, it is important to bear in mind that correlations, no matter how strong, have their limitations, as they do not prove causation.

For example, in an early study, Bendall et al. (1989) ascertained that walking speed was positively associated with isometric calf strength in a group of 67 women (mean age 72 ± 4 years; $r = 0.36$; $P \leq 0.01$) and 58 men (mean age 71 ± 4 years; $r = 0.41$; $P \leq 0.01$). In a more recent large study, Ostchega et al. (2004) (758 men and 741 women aged 50 years and older) supported these earlier findings when they found that isokinetic knee extensor strength was associated with walking speed after adjusting for age, ethnicity, weight, and height ($P < 0.01$).

Impact of Loss of Power on Function

With regards to the link between power and function, Bassey et al. (1992) found that the leg extensor power of 13 frail elderly men (mean age 88.5 ± 6 years) and 13 frail elderly women (mean age 86.5 ± 6 years) was significantly correlated with the time taken to rise from a chair, climb a flight of stairs, and walk 6.1 meters. Similar results were obtained by Rantanen and Avela (1997), who measured leg extension power in healthy elderly adults using a sledge ergometer in a sitting position. Participants were asked to "jump" while attached to an inclined sliding chair that was on rails. Power was measured using a force plate, which was positioned at the feet. Maximal walking speed was also measured over a distance of 10 meters. The investigators discovered that walking speed was correlated with leg extension power in 80-year-old men ($n = 41$; $r = 0.412$; $P = 0.007$), 80-year-old women ($n = 56$; $r = 0.619$; $P < 0.001$), 85-year-old men ($n = 8$; $r = 0.939$; $P = 0.001$), and 85-year-old women ($n = 23$; $r = 0.685$; $P = 0.001$).

Bean et al. (2002) found that leg power, as measured during bilateral leg press and unilateral knee extension in 45 mobility-limited older adults (age range 65 to 83 years), was more closely related to functional performance than leg strength. The functional performance tests employed in their study were stair-climb time, tandem gait, habitual gait, maximal gait, and the short physical performance battery (SPPB). The SPPB involved the testing of standing balance, a timed 2.4-meter walk, and a timed test of rising from a chair and sitting down five times. The study by

Cuoco et al. (2004), which used similar measures in 48 elderly men and women (age range 65 to 91 years), had comparable findings.

Suzuki et al. (2001) also confirmed the assertion that peak muscle power is a more important factor in functional performance in older adults than muscle strength. They used an isokinetic dynamometer to measure dorsiflexor and plantar flexor isokinetic peak torque, peak power and isometric peak torque in 34 older women (mean age 75.4 ± 5.1 years) with self-reported functional limitations. They assessed functional capacity with stair climb time, repeated chair rise time, and maximal and habitual gait velocity. Dorsiflexor peak power was found to be correlated to chair rise time ($r = 0.50$; $P < 0.002$) and stair climb time ($r = 0.49$; $P < 0.003$), and plantar flexor isometric strength was correlated with habitual ($r = 0.53$; $P < 0.001$) and maximal gait velocity ($r = 0.47$; $P < 0.005$).

More recently, the study by Puthoff and Nielsen (2007) added to the growing body of evidence that power has greater influence over functional capacity than strength. In their study they assessed lower-extremity strength and power in 25 older women and 5 older men (mean age 77.3 ± 7.0 years) with mild to moderate functional limitations by means of a bilateral leg press machine. Functional capacity was assessed using the SPPB and a six-minute walk test, where participants were asked to cover as much distance as possible within six minutes. Although both strength and power were significantly correlated to the measures of functional capacity, power consistently explained more of the variance in functional ability than strength (Puthoff & Nielsen, 2007).

With regards to the relationship between function and upper limb strength and power, experiments by Herman et al. (2005) showed that triceps strength and power in 37 mobility-limited older adults (age range 65 to 93 years) were significantly correlated with performance in the SPPB, a timed stair climb test and 4-metre walk time. And yet again the correlation was found to be greater for power (r = 0.88-0.89; $P < 0.001$) than strength ($r = 0.69$; $P < 0.001$).

The Role of Contraction Speed

Recognising the large amount of evidence suggesting that muscular power rather than strength is the key determinant of physical functioning in daily life, Clémençon et al. (2008) investigated the relationships between the determinants of maximal leg power (optimal velocity and optimal torque) and functional performance in 39 healthy elderly women (age range 72 to 96 years). They found that optimal velocity significantly correlated with 6-metre walking speed, chair-stand time ($r = -0.596$; $P < 0.01$) and stair-climb time ($r = -0.522$; $P < 0.001$), however, optimal torque did not correlate with any of the functional performance measures (Clémençon et al., 2008).

Impact of a Reduction in Eccentric Strength and Steadiness

Although eccentric strength is relatively preserved with old age, it has been observed that older adults find tasks involving eccentric contractions, such as stair descent, especially difficult (Startzell, Owens, Mulfinger, & Cavanagh, 2000). One possible explanation for this is the increased variability, or unsteadiness, of force production in older adults compared to young adults (Enoka et al., 2003). Recently, Carville et al. (2007) measured steadiness during isometric, eccentric and concentric contractions in 44 young adults (mean age 29.3 ± 0.6), 34 older adults with a history of falls (mean age 70.6 ± 4.6), and 44 older adults without any history of falling (mean age 75.9 ± 0.6). Steadiness during dynamic (eccentric and concentric) contractions was measured by the standard deviation of acceleration during the contractions. They showed that healthy older people were significantly less steady during dynamic contractions than young adults ($P < 0.002$) (Carville et al., 2007). In addition, older fallers were significantly less steady during eccentric contractions than older non-fallers ($P < 0.013$) (Carville et al., 2007).

Summary

In summary, the age-related decline in skeletal muscle's force-producing capacity and contraction velocity (and thus, power) is associated with a decline in measures of functional capacity in older adults. The relationship between muscular strength and to a greater extent, power, with functional performance has been demonstrated in numerous studies despite differing methods used to assess strength, power and functional capacity. Therefore, it may be inferred that improving the muscular power of older adults could improve their ability to perform daily tasks such as walking and climbing stairs. Also, recent evidence suggests that the optimal contraction velocity of muscles is correlated with functional capacity, which indicates a need to focus attention on methods for improving contraction velocity under varying loads as a means of improving functional performance. Finally, reduced steadiness during eccentric contractions with age is a possible explanation for the difficulty experienced by older adults when performing tasks involving eccentric contractions.

Methods for Improving the Force-Velocity Relationship in Old Age

The changes to the f-v and p-v relationships that occur with age and the functional implications of these changes have led many researchers to investigate different methods of improving these relationships, and thus the functional capacity of older adults. These include traditional resistance training (TRT), power training (PT), and eccentric (or eccentrically biased) resistance training (ERT). Ideally, interventions to improve the f-v relationship would result in an upward and rightward shift in the f-v curve, as well as an increase in V_{opt}. This would mean that muscles could produce more force at all contraction velocities (eccentric and concentric) and the maximum contraction velocity of muscles would be higher. In terms of muscle architecture, the adaptations expected to be associated with these improvements in strength and contraction velocity would be increases in fascicle pennation angle (secondary to fibre hypertrophy) and fascicle length. The practical functional benefits of this may include improvements in functional capacity, and balance recovery following a stumble (Pijnappels, Reeves, Maganaris, & van Dieen, 2008).

Traditional Resistance Training

Most early intervention studies involved TRT, which consists of lifting and lowering heavy loads (2 to 3 sets of 8 to 10 repetitions at more than 65% of the 1-repetition maximum [1RM] performed 2 to 3 days per week) at a slow speed. This type of training maximally overloads only the concentric portion of each lift (Sayers, 2007). According to the systematic review of strength training studies involving older adults by Latham, Bennett, Stretton, and Anderson (2004), most progressive TRT studies continued for a duration of 8 to 12 weeks, but the duration ranged from 2 to 104 weeks. These interventions showed a significant positive effect on strength, but only modest effects on functional measures such as gait speed and time taken to rise from a chair.

With regards to how TRT affects the f-v and p-v relationship in healthy older adults, the general finding of intervention studies is that isometric strength, strength at slow to medium contraction velocities and P_{max} is increased. In other words, there is an upward displacement of the f-v curve (see Table 3). However, there seems to be little change in the ability of older muscles to produce force eccentrically following TRT (Reeves, Maganaris, Longo, & Narici, 2009; Reeves, Maganaris, & Narici, 2005), which as previously indicated is important in many activities of daily living and falls prevention (Carville et al., 2007; Enoka et al., 2003; Startzell et al., 2000).

Relatively few studies involving older adults have extrapolated the f-v curve to determine if there was any change in estimated V_{max} as a result of TRT (Ferri et al., 2003; Labarque et al., 2002). Ferri and colleagues (2003) found no change in estimated V_{max} while Labarque et al. (2002) observed an increase in the estimated V_{max}. One possible reason for this difference in findings could be because the study by Ferri et al. (2003) employed a high-intensity training protocol (10 repetitions at 80% of 1RM) while Labarque et al. (2002) employed a low- to moderate-intensity training protocol (30 repetitions at 30RM). Also, Labarque et al. (2002) tested isokinetic elbow flexor strength between 100 and 600º/s. However, most isokinetic strength tests involving older adults include velocities only up to about 360 to 400º/s. Lanza et al. (2003) illustrate this point by reporting that some older but none (few) of the younger subjects in their study were unable to reach angular velocities of more than 270º/s during knee extension and 120º/s during ankle dorsiflexion.

With regards to in-vitro experiments, one study by Trappe et al. (2000) looked at changes in single vastus lateralis muscle fibres in 7 older men (mean age 74 ± 2 years) following 12 weeks of TRT performed 3 days per week at 80% of 1RM. They found that the diameter of type I and IIa fibres increased by 20 and 13%

($P < 0.05$) respectively. F_{max}, fibre V_0 and power were 55, 75 and 128% ($P < 0.05$) higher in type I fibres and 25, 45 and 61% ($P < 0.05$) higher in type IIa fibres respectively following TRT. These changes are of a higher magnitude than that observed in in-vivo studies, as single fibre segments are not influenced by neural control or muscle architecture.

As indicated earlier, muscle architecture plays an important biomechanical role in the ability of a muscle to produce force. The effect of TRT on muscle architecture in older adults has been examined in a number of studies (Morse, Thom, Mian, Birch, & Narici, 2007; Reeves et al., 2005; Reeves, Narici, & Maganaris, 2004a, 2004b, 2006; Suetta et al., 2008). The recurrent finding is that there is an increase in muscle fascicle pennation angle following TRT, which means that more sarcomeres are added in parallel, allowing muscles to produce more force across all concentric contraction speeds. However, there is contradictory evidence with regards to whether muscle fascicle length of older adults changes following TRT, with one study showing no change (Morse et al., 2007) and others finding an increase in fascicle length (Reeves et al., 2005; Reeves et al., 2004a, 2004b, 2006). A factor to consider is the role of increased muscle excursion on L_f. Older adults who become more active as a result of participating in resistance training would be expected to respond to the increased muscle excursion by increasing fascicle length. Therefore, resistance training studies that compare the effects of different resistance training modes on L_f are needed to determine the most efficacious mode.

Power Training

Recognition that power declines faster than strength with advancing age and that power is the more important determinant of functional capacity has led researchers to focus on methods for improving muscular power in older adults (Bottaro et al., 2007; Caserotti, Aagaard, Larsen, & Puggaard, 2008; de Vos et al., 2008; Fielding et al., 2002; Henwood, Riek, & Taaffe, 2008; Henwood & Taaffe, 2005; Orr et al., 2006; Sayers, 2007).

The power training (PT) interventions in the available studies typically last between 8 and 16 weeks, and generally require participants to lift loads corresponding to 20 to 80% of their 1RM as quickly as possible during the concentric phase of each exercise. Training frequency is usually 2 to 3 times per week, with each session consisting of 3 to 4 sets of 8 to 14 repetitions for each exercise. All of the above studies reported significant improvements in isometric and concentric strength and power as a result of PT, with some reporting improved functional performance (Bottaro et al., 2007; Henwood et al., 2008; Henwood & Taaffe, 2005), rate of force development, impulse during isometric contractions (Caserotti et al., 2008), and balance (Orr et al., 2006). However, to date, no power training studies involving older adults have investigated changes in muscle architecture with training.

Although most PT studies involving older adults have not directly investigated the effect of training on the f-v relationship, some conclusions can be drawn from the results of these studies. For example, de Vos et al. (2008) randomised 112 healthy older adults into groups to perform explosive resistance training at 20% (n = 28, mean age 69.4 ± 5.8 years), 50% (n = 28, mean age 68.1 ± 4.5 years), or 80% (n = 28, mean age 69.0 ± 6.4 years) of 1RM and a non-training control group (n = 28, mean age 67.6 ± 6.0 years). The training was performed over 8 to 12 weeks twice weekly, with each training session consisting of 5 exercises performed for 3 sets of 8 explosive concentric and slow eccentric contractions. The exercises (bilateral horizontal leg press, seated chest press, bilateral knee extension, seated row, and seated bilateral knee flexion) were performed on digital pneumatic resistance machines. The velocity of concentric contractions at peak power did not improve significantly and was similar between all groups, but force at peak power increased significantly (12 to 16%; $P < 0.001$) in all training groups. Thus, it was concluded that older adults are able to produce higher peak power outputs with greater loads without losing movement velocity after 8 to 12 weeks of PT.

In another study involving 20 old (mean age 62.7 ± 2.2 years) and 12 very old (mean age 81.8 ± 2.7 years) adults, 12 weeks of explosive heavy (75 to 80% 1RM) resistance training was performed twice a week (Caserotti et al., 2008). Each session consisted of 4 sets of 8 to 10 repetitions of the following exercises: bilateral knee extension; horizontal leg press; hamstring curls; calf raise and inclined leg press performed on isoinertial resistance training equipment. Contractile rate of force development (RFD) was before and after training during maximal isometric voluntary contractions performed on a leg press device. RFD increased ($P = 0.005$) in the old and very old groups as a result of the training protocol.

Some studies that compared TRT and PT have found that they are equally effective at improving muscular strength (Bottaro et al., 2007; Fielding et al., 2002), but that PT is more effective at improving muscular power and functional capacity in older adults than TRT (Bottaro et al., 2007; Fielding et al., 2002). However, a recent study by Henwood et al. (2008) observed similar improvements in maximal isometric strength, peak and average muscle power, and functional performance after TRT and PT. Although more research comparing TRT and PT in older adults is needed, it seems at this stage that PT is at least as effective as, if not more effective than TRT in improving functional capacity in older adults.

Eccentric Resistance Training

Numerous studies involving young adults have found greater hypertrophy and strength gains after eccentric training when compared to concentric training (Hortobagyi, Barrier et al., 1996; Hortobagyi, Hill et al., 1996; Norrbrand, Fluckey, Pozzo, & Tesch, 2008). And this was also found in the study by (Farthing & Chilibeck, 2003) who compared isokinetic eccentric and concentric strength training in young males, and found that eccentric training resulted in greater hypertrophy and strength gains (both eccentric and concentric strength) than concentric training. Although there are other studies that have shown almost identical muscle hypertrophy in response to eccentric-only and concentric-only resistance training (Jones & Rutherford, 1987; Reeves et al., 2009; Smith & Rutherford, 1995), the balance of evidence does seem to support the superiority of eccentric training over concentric training with regards to muscle hypertrophy. Even if the benefits of eccentric and concentric training with regards to hypertrophy are similar, there may be other advantages to eccentric training, as discussed below.

Although few studies have compared the effects of exclusively eccentric resistance training (ERT) with those of TRT or PT in older adults, there are some potential advantages to ERT. For example, ERT allows participants to perform the same amount of work at a lower metabolic cost and perceived rate of exertion than concentric training (Meyer et al., 2003; Okamoto, Masuhara, & Ikuta, 2006a; Overend, Versteegh, Thompson, Birmingham, & Vandervoort, 2000). Also in contrast to concentric training, 8 weeks of ERT has not been found to increase arterial stiffness, which has been reported following concentric training (Okamoto, Masuhara, & Ikuta, 2006b). Furthermore, as mentioned earlier, there is no reason to believe that the absence of concentric contractions from a resistance training program will reduce its positive effects on muscle mass (Mueller et al., 2009; Reeves et al., 2009; Roig et al., 2008).

Exclusively eccentric resistance training has also been reported to increase vastus lateralis fascicle lengths in the elderly to a greater extent than TRT (Reeves et al., 2009). This fascicle elongation, which has previously been observed as a consequence of eccentric training in young adults (Duclay, Martin, Duclay, Cometti, & Pousson, 2009; Potier, Alexander, & Seynnes, 2009) and after decline running in rats (Lynn & Morgan, 1994; Lynn, Talbot, & Morgan, 1998) counters the decline which appears to occur in elderly muscle (Morse et al., 2005; Narici et al., 2003; Thom et al., 2007). As fascicle shortening and the associated loss of sarcomeres in series is thought to account for a significant portion of the decline in muscle power observed in old age (Thom et al., 2007) it might be expected that eccentric resistance training will have positive effects on torque and power generation during high velocity concentric actions. Reeves and colleagues (2009) reported that the effects of their ERT were largest when measured during eccentric isokinetic actions but there was also a significant improvement in the torque generated at the fastest concentric velocity employed (3.49 rads.s^{-1}). Some ERT studies in young people have shown similar effects on high velocity concentric torques (Paddon-Jones, Leveritt, Lonergan, & Abernethy, 2001; Shepstone et al., 2005). Clearly more research is needed to more fully describe the effects of ERT on changes in fascicle length and the effects of those changes on performance in the elderly.

Valour et al. (2004) explored the effect of 7 weeks of elbow flexor ERT performed 3 times a week on elbow flexor characteristics in 8 older female adults (mean age 65 ± 6 years). The training involved 5 sets of 6 unilateral eccentric elbow flexor contractions of the dominant arm at an intensity corresponding to 100% of the

3RM (3 repetition maximum). Free weights were used for the training. The force-velocity and power-velocity relationship of the elbow flexors was determined before and after training. It was found that P_{max}, torque produced at all inertial conditions (2, 10, 20, 30, 40 and 50% of F_{max}) and the index of maximal contraction velocity (VI_{max}) increased significantly ($P < 0.05$). Thus, it can be concluded that the force-velocity relationship was shifted upwards and V_{max} was increased.

With regard to the functional benefits of ERT, LaStayo et al. (2003) investigated the effects of 11 weeks of lower extremity training performed 3 times a week on a recumbent high-force eccentric leg cycle ergometer as compared to TRT in 11 male and 10 female frail elderly subjects (age range 70 to 93 years). Participants were randomised to the eccentric training group ($n = 11$) or the TRT group ($n = 10$). Vastus lateralis muscle fibre cross-sectional area increased significantly after training in both groups ($P < 0.05$), and isometric knee extension strength increased significantly only in the eccentric training group ($P < 0.05$). Balance and stair descent ability improved only in the eccentric training group ($P < 0.05$) while timed up and go task ability improved ($P < 0.05$) in both groups, however, only the eccentric training group improved timed up and go task performance to a sufficient extent to cross the falls-risk threshold of 14 seconds (LaStayo et al., 2003).

Summary

In general, TRT increases isometric and concentric strength, thus shifting the f-v curve upwards in the concentric portion of the relationship. However, there seems to be contradicting evidence as to whether V_{max} increases as a result of TRT in older adults. Muscle fascicle pennation angle increases with TRT, but increases in fascicle length have not been observed in all studies. Power training in older adults has been found to increase both strength and power. Although V_{max} has not been investigated in PT studies involving older adults, increases in RFD and impulse indicate greater contraction velocity of muscles. Older adults have also been found to perform better in functional tests after PT. Eccentric resistance training has not been widely investigated in older adults, but the limited data available shows that functional capacity can be improved with this approach and that potentially favourable increases in muscle fascicle length may occur.

Conclusion

The decrease in muscular strength and contraction velocity with age, as illustrated by changes in the force-velocity and power-velocity relationships, leads to a loss of mobility and independence that is often observed in older adults. This is of mounting concern with an aging population as the potential increased demand on our healthcare system may compromise its capacity to cope in the future.

Due to the high social relevance of this issue, much research has focused on interventions that increase muscular strength and power in older adults. In light of recent evidence that contractile velocity impairments have a significant role to play in mobility loss with age, it is recommended that future research investigate interventions that not only increase strength and power but also increase the concentric contraction speed at which power is maximised. Eccentric training is an intervention that shows potential in this regard while also having possible advantages over other training modes. However, more research is needed to elucidate the effects of this strength training mode on contraction velocity and functional capacity in older adults to determine if this mode is indeed the most efficacious.

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