

Age Related Changes in Motor Function (II). Decline in Motor Performance Outcomes

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ABSTRACT

Age-related impairments in motor performance are caused by a deterioration in mechanical and neuromuscular functions, which have been investigated from the macro-level of muscle-tendon unit to the micro-level of the single muscle fiber. When compared to the healthy young skeletal muscle, aged skeletal muscle is: (1) weaker, slower and less powerful during the performance of voluntary contractions; (2) less steady during the performance of isometric contractions, particularly at low levels of force; and (3) less susceptible to fatigue during the performance of sustained isometric contractions, but more susceptible to fatigue during the performance of high-velocity dynamic contractions. These impairments have been discussed to be mainly the result of: a) loss of muscle mass and selective atrophy of type II muscle fibers; b) altered tendon mechanical properties (decreased tendon stiffness); c) reduced number and altered function of motor units; d) slower muscle fiber shortening velocity; e) increased oscillation in common synaptic input to motor neurons; and f) altered properties and activity of sarcoplasmic reticulum. In this second part of a two-part review we have detailed the age-related impairments in motor performance with a reference to the most important mechanical and neuromuscular contributing factors.

Introduction

Aging of the musculoskeletal system is of particular interest in our society, as it is a major contributing factor to progressively impaired mobility and loss of functional independence among older individuals. In the first part of this narrative review, we discussed the mechanical and neuromuscular factors responsible for age-related impairments in motor performance [1]. We provided a comprehensive overview of the structural and functional alterations affecting both the muscle-tendon unit and the motor unit (MU).

In this second part of the review we discuss the decline in motor performance associated with age-related changes in mechanical and neuromuscular structure and function. In particular, alterations of muscle strength and power, force control (steadiness) and susceptibility to fatigue, as consequence of aging are discussed. An

understanding of age-related impairments in motor performance is essential to inform the design of appropriate interventions to mitigate the progressive impaired mobility and loss of functional independence among older individuals.

The databases searched for the second part of the review were the US National Library of Medicine (PubMed), Web of Science and Google Scholar. The terms ‘aging/age’, ‘muscle strength/power’, ‘shortening/contraction velocity’, ‘rate of force/torque development’, ‘tendon stiffness’, ‘muscle architecture’, ‘force/torque steadiness/fluctuations/variability’, and ‘muscle fatigue/fatigability’, were used in different combinations to retrieve pertinent articles. Additionally, relevant literature was also sourced from the reference list of articles obtained from database searches.

Maximal Muscle Strength and Power

Maximal muscle strength

A loss of muscle strength is inevitable with aging, even among healthy older individuals. A majority of studies, mostly cross-sectional, report that muscle strength usually peaks between the 2nd and the 3rd decade of life, is maintained or declines slightly between the ages of 40 and 50 years, and then progressively declines thereafter at a rate of ~1.0–1.5 % per year, with more pronounced losses occurring around the age of 65/70 year [2–4]. This is of particular relevance for women, who live ~5–7 years longer than men, but who reach the threshold of dependence at an earlier age and who have lower physical capacities than men at all stages of life [2, 5, 6]. Indeed, previous studies have observed that absolute strength values for women are lower compared to their male counterparts across almost the entire lifespan [5, 7, 8]. Additionally, muscle strength appears to be better preserved in the upper limbs [7–9]. A longitudinal study has shown that age-related losses in the isokinetic muscle strength (at 1.05 rad/s) of elbow flexors and extensors were ~16.4 and 19.4 %, respectively, over a 12-year period, whereas in the same period the strength of the knee extensors (KE) and flexors decreased ~23.7 and 28.5 %, respectively [9]. Therefore, throughout this review, we will focus our discussion on the lower extremities, which are most affected by aging.

The ability to generate force can be assessed statically (i. e. adopting isometric contractions) or dynamically (i. e. adopting isokinetic & isotonic contractions). As outlined in ► **Table 1**, based on the results of cross-sectional studies, healthy individuals in their 70s performing maximal isometric voluntary contractions (MVIC) of the KE appear to have, on average, 30–50 % less maximal muscle strength when compared to their younger counterparts. This decline in isometric strength is even more pronounced in the very old (i. e. individuals > 75 years of age) [5, 10].

Interestingly, age-related decrements in maximal strength during the performance of isokinetic contractions are mode-specific, with many studies reporting greater preservation of strength for eccentric contractions in comparison with either isometric or concentric contractions (► **Table 1**) [5, 11–13]. For instance, Lindle et al. (1997) [5] compared KE maximal strength during isometric and isokinetic eccentric and concentric contractions, in healthy men and women (aged 20–93 years), observing greater decrements both in isometric and concentric strength, at a rate of ~0.8–1.0 % per year from the age of 40. Age-related decrements in maximal isokinetic strength appear to vary depending on the adopted angular velocity. At fast velocities of isokinetic (concentric) contraction, age-related decrements in maximal strength of lower limb muscles, such as KE, are more pronounced compared to those observed for slower contraction velocities (► **Table 1**) [9, 11, 14]. No-

► **Table 1** Difference (%) in maximal muscle strength of the knee extensors between young and older individuals.

Authors	Sex	Young		Older		Testing Condition	%Strength
		n	Age (yr)	n	Age (yr)		
Macaluso et al., (2002) [71]	F	10	22.8 ± 5.7	10	69.5 ± 2.4	Isometric	-43%***
Kubo et al., (2007) [148]	M	19	26.4 ± 3.7	17	70.4 ± 4.8	Isometric	-48.3%***
Tracy and Enoka (2002) [99]	M	10	22.4 ± 2.0	10	70.8 ± 3.7	Isometric	-35%*
	F	10	21.7 ± 2.4	10	72.2 ± 4.9	Isometric	-33%*
Dalton et al., (2012) [14]	M	8	25.1 ± 2.6	8	73.6 ± 3.5	Isometric	-26.6%**
Ditroilo et al., (2012) [149]	M	14	22.1 ± 3.0	12	65.4 ± 5.7	Isometric	-32.7%*
Thompson et al., (2013) [57]	M	25	24.9 ± 3.0	18	66.8 ± 4.5	Isometric	-29.2%***
Wu et al., (2016) [32]	M	11	23.7 ± 4.2	11	66.8 ± 3.4	Isometric	-47.4%***
	F	13	23.5 ± 3.4	9	66.1 ± 4.4	Isometric	-32.9%*
						Isokinetic	
Lynch et al., (1999) [150]	M	23	26.8 ± 2.3	58	74.8 ± 3.2	Concentric (30°/s)	-35.1%*
						Eccentric (30°/s)	-32.6%**
	F	31	27.3 ± 2.3	24	74.7 ± 3.0	Concentric (30°/s)	-31%*
						Eccentric (30°/s)	-26.7%*
Vandervoort et al., (1990) [11]	F	26	25 ± 3	26	73 ± 6	Concentric (45°/s)	-47.5%***
						Eccentric (45°/s)	-37.8%***
						Concentric (90°/s)	-53.4%***
						Eccentric (90°/s)	-34.2%***
Porter et al., (1995) [13]	M	28	26 ± 3	25	71 ± 7	Concentric (90°/s)	-41.7%**
						Eccentric (90°/s)	-24.9%**
	F	27	27 ± 3	26	73 ± 6	Concentric (90°/s)	-53.4%**
						Eccentric (90°/s)	-38.3%**
Dalton et al., (2012) [14]	M	8	25.1 ± 2.6	8	73.6 ± 3.5	Concentric (60°/s)	-25.4%**
						Concentric (180°/s)	-35.2%***
Overend et al., (1992) [151]	M	13	24.5 ± 1.5	12	70.7 ± 1.3	Concentric (120°/s)	-31.5%***

Age is mean ± SD; n = number of participants; M = Males; F = Females; * p < 0.05, ** p < 0.01, *** p < 0.001 for the difference between young and older participants.

tably, some older individuals are even unable to achieve velocities greater than 4.71 rad/s during KE constant velocity contractions [15]. The age-related slowing of contraction speed may cause older individuals to have less time to reach peak torque, thus making them particularly weaker at high velocities. It can be explained by a number of alterations in neuromuscular function with aging, including a preferential atrophy of type II muscle fibers [16], a consequent increased proportion of type I fibers due to fiber-type grouping [17, 18], a slowing of cross-bridge cycling [19, 20], as well as the impaired ability to generate high MU firing rate [21]. In addition, a number of longitudinal studies have indicated that, with increasing age, the annual loss in isokinetic (concentric) KE maximal muscle strength ranges between 1.4% and 3.2% (depending on angular velocity) [9, 22–24], which is greater than the loss typically observed in cross-sectional studies (e. g. ↓ ~0.8–1.0% per year by Lindle et al. 1997 [5]; ↓ ~0.9–1.5% per year, by Frontera et al. 1991 [8]).

The decline in maximal muscle strength with advancing age can be attributed not only to loss of muscle mass and changes in the properties of muscle fibers (especially type II fibers) [20, 25, 26], but also to a reduction in voluntary activation [27, 28]. Type II muscle fibers are intrinsically stronger and faster than type I fibers, hence even muscles with the same volume, but with a relatively larger proportion of type I fibers, will generate less force [6]. As detailed in ► **Table 2**, it has been observed that, during the normal aging process, declines in muscle strength occurs at a higher rate than declines in muscle size [i. e. anatomic cross-sectional area (CSA)] in various upper and lower limb muscles, suggesting an overall decline in muscle quality (i. e. specific tension). Indeed, when the maximal strength of a muscle is normalized to its CSA, a significant difference is still observed between healthy younger and older individuals for different muscle groups: elbow flexors [29], KE [16], ankle plantar-flexors [30] and ankle dorsiflexors [31].

Many studies have shown that reduced muscle strength measured in elderly individuals is associated with substantial alterations

in muscle architecture [32, 33]. As mentioned in the first part of our review [1], age-related reductions in muscle thickness and pennation angle result in less contractile tissues being attached to a given tendon or aponeurosis area; resulting in a smaller muscle CSA, which suggests a reduction in the number of sarcomeres placed in parallel and a resultant lower relative force output [34, 35]. In turn, shortened fascicle lengths imply a reduction in the number of sarcomeres placed in series (i. e. contractile tissues), but not of the sarcomere's length [36], which reduces the relative shortening velocities and the length range of force development, as well as the power generating capacity [37, 38]. Indeed, age-related declines in muscle strength and shortening velocity likely lead to changes in the force-velocity relationship, shifting the curve downwards (decrease in muscle strength) and to the left (slowing of contractile velocity) [19]. Therefore, when a loss of strength and contractile velocity are combined, power capacity becomes the most critical factor affected in the elderly.

Maximal muscle power

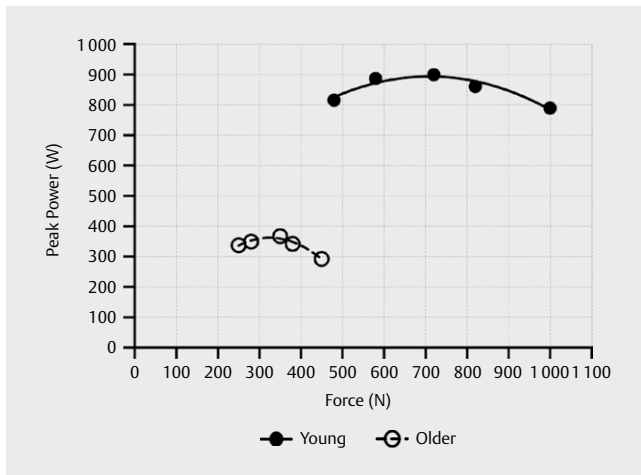
A large number of studies investigating age-related deterioration in motor performance have focused on the assessment of maximal muscle strength. Most habitual daily activities, however, are actually associated with muscle power (i. e. the product of muscle force and shortening velocity). Several studies have reported that loss of muscle power is more pronounced than loss of muscle strength in older individuals [39, 40]. For instance, it has been shown that, during unilateral leg press exercise, older women generate 61% less peak power and 50% less MVIC when compared to their younger counterparts [39].

Reductions in ankle dorsiflexor [41] and leg [42] peak power have been associated with impaired functional performance during daily activities in mobility-limited older individuals. Bean et al. (2002) [42] reported that performance of some typical activities of daily living is more strongly correlated with (i. e. explained by)

► **Table 2** Difference (%) in anatomical cross-sectional area (ACSA) and muscle strength between young and older individuals for different muscle groups.

Authors	Sex	Young		Older		Muscle	%Strength	%ACSA
		n	(age)	n	(age)			
Young et al., (1985) [152]	M	12	21–28	12	70–79	KE	–39%***	–25%***
Coupe et al., (2009) [153]	M	10	27±2	7	67±3	KE	–30.4%*	–26.3%**
Piasecki et al., (2018) [154]	M	48	18–40	53	65–90	KE	–38.6%***	–29.7%***
Quinlan et al., (2018) [60]	M	28	23.9±1.1	22	68.5±0.5	KE	–27.7%***	–25.6%***
Overend et al., (1992) [151]	M	13	19–34	12	65–77	KE	–23.6%**	–22.4%**
						KF	–22.3%*	–14.0%
Morse et al., (2004) [30]	M	14	19–35	21	70–82	PF	–39.1%***	–14.9%***
Morse et al., (2005) [155]	M	12	25.3±4.4	19	73.8±3.5	PF	–47%**	–17%**
Stenroth et al., (2012) [156]	M/F	33	18–30	67	70–80	PF	–38.6%**	–15.2%
Kent-Braun and Ng, (1999) [66]	M/F	21	26–44	24	65–83	DF	–19.2%*	–17.5%*
Piasecki et al., (2018) [154]	M	48	18–40	53	65–90	DF	–22.9%**	–18.7%***
McNeil et al., (2007) [31]	M	13	19–33	13	80–90	DF	–33%*	–9.8%
Akagi et al., (2009) [157]	M/F	52	20–34	51	60–77	EF	–17.4%*	–9.1%*
Klein et al., (2001) [29]	M	20	20–29	13	76–95	EF	–27.2%***	–16.3%***
						EE	–32.5%***	–26.2%***

M = men; F = female; n = number of participants; KE = knee extensors; KF = knee flexors; PF = ankle plantar-flexors; DF = ankle dorsiflexors; EF = elbow flexors; EE = elbow extensors; * p < 0.05, ** p < 0.01, *** p < 0.001 for significant difference between young and older individuals.



► **Fig. 1** The peak power output in young and older women during unilateral leg press exercise (isotonic mode) plotted as a function of force at 40, 50, 60, 70 and 80% maximal voluntary isometric contraction (MVIC). Notably, the force at peak power obtained by the younger group exceeds the MVIC (not reported in the figure) of the older participants.

leg power than muscle strength. In another study, which included 1032 older subjects (aged 65–95 years), Bean et al. (2003) [43] demonstrated, the individuals with lower leg power (composite power for leg power, right and left KE power) had a two- to three-fold higher likelihood of mobility impairments when compared to those individuals with lower KE strength. Compared with maximal muscle strength, therefore, these findings suggest that maximal lower extremity muscle power might be a more relevant determinant of functional performance in older individuals, particularly for those with established functional limitations [44].

Ideally, muscle power should be measured across a range of different external resistances, in order to identify the optimal load for maximal power generation. Typically, this load is between 60% and 85% of the one-repetition maximum (1-RM) during a leg press exercise [42, 45, 46]. For instance, Macaluso and De Vito (2003) [39] and Bean et al. (2002) [42] measured peak power at a load of 40–80% MVIC and 40–90% of 1-RM during a leg press exercise, showing that peak power output occurred at ~60% MVIC (► **Fig. 1**) and 70% 1-RM, respectively. Furthermore, the relative age-related reduction in peak power was greater when compared with the corresponding reduction in either MVIC or 1-RM [39, 45]. It is suggested that older individuals also generate slower optimal contraction velocities when compared to young (\downarrow ~21%) [39] and middle-aged (\downarrow ~20%) [45] individuals. Indeed, the independent influence of the shortening velocity on muscle power has been discussed previously [44], with the difference between younger and older individuals in KE power becoming larger as the velocity demand increases [15]. The greater loss of muscle power in the old muscle at high velocities of contraction can be partly explained by altered muscle architecture of pennate muscles. In these muscles the contraction velocity of the single muscle fibers may differ from the velocity of the whole muscle-tendon unit. This depends mainly on the increase in pennation angle and muscle thickness during the actual contraction, which increases force and reduces velocity of

individual muscle fibers. As a result, a difference between muscle tendon unit velocity and single muscle fiber velocity is observed, which may be further affected by the level of tendon stiffness. The ratio ‘muscle-tendon unit velocity/muscle fiber velocity’ is the gearing [47]. A functional advantage of a greater gearing ratio is a larger force output at high velocity movements, with benefits to power production. The gearing ratio is reduced in the old muscle, which can help explain the age-related reduction in muscle power, especially at high velocities during isotonic movements [48].

Shortening velocity and Rate of torque development

The general slowing down of contractile properties associated with aging can be assessed by examining the time course of an elicited muscle twitch in a specific muscle or muscle group. Previous studies, in fact, have shown that the muscle twitches elicited in older individuals are characterized by prolonged time-to-peak and half-relaxation time (HRT) in various lower limb muscles: ankle dorsiflexors [31], ankle plantar-flexors [49] and KE [14, 50]. A selective shift toward the slow-twitch MUs and the altered myocyte contractile machinery could be responsible for most of the slowing of the isometric twitch in advanced age [17]. Another potential factor, discussed in the first part of our review [1], could be linked to the reduction in the rate of Ca^{2+} release and reuptake by the sarcoplasmic reticulum (SR), as well as to alterations in function and expression of contractile protein [51–53]. Indeed, a relationship between the duration of the isometric twitch and SR Ca^{2+} uptake activity has been demonstrated previously [54].

Not surprisingly, the muscle-tendon unit of older individuals also exhibits a lower rate of force or torque development (RFD or RTD), which can be considered, in functional terms, as an essential mechanical parameter for performance in power-demanding (dynamic) activities. Rapid movements typically involve muscle contractions lasting 50–250 ms, a range which is significantly less than the time needed to reach maximal force during a voluntary isometric contraction (i. e. 300–500 ms) [55, 56]. The age-related reduction in RFD/RTD may be functionally important in that this could affect activities of daily living, such as rising from a chair, stair walking, as well as the capacity to counteract unexpected mechanical perturbations (i. e. loss of balance). Several previous studies have identified that the rapid force generation capacity (i. e. RFD or RTD) of different lower limb muscle groups was ~25–67% smaller in older compared to younger individuals, for the KE [7, 32], the knee flexors [57], the ankle dorsiflexors [58] and the ankle plantar flexors [59]. Furthermore, when considering the same muscle group, the age-related decrease in RFD/RTD has been found to be greater than the decrease in maximal isometric muscle strength [7, 32, 57].

Mechanical factors also contribute to the observed reduced RFD/RTD with aging, such as a decrease in tendon stiffness. It has been noticed that in the normal aging process decreased patellar tendon stiffness is associated with a decrease in muscle strength and RTD [60], but these alterations can be counteracted and even improved by an appropriate resistance training intervention [61]. It has been suggested that increased tendon compliance with aging may have a direct impact on muscle mechanical behavior by increasing the degree and rate of muscle fiber shortening [62], and in turn shifting the optimal angle for force generation [62, 63]. In addition to mechanical factors, age-related alterations in MU re-

cruitment and firing characteristics also contribute to the slower force development in older individuals (discussed below) [58].

Voluntary activation and Reflex responses

The loss of muscle strength and power observed in older individuals might also be attributed to an inadequate (i. e. incomplete MU recruitment) voluntary activation of the remaining MUs. During the performance of a maximal voluntary contraction, voluntary activation capacity can be assessed using neuromuscular electrical stimulation, which involves delivering supramaximal electrical impulses to the motor nerve (femoral nerve in the case of the quadriceps muscle group) or directly to the muscle surface (percutaneously). This procedure can generate an extra increment (interpolated twitch) in force whose amplitude is used to assess the degree of voluntary activation. No additional twitch elicited by the stimulation means that the voluntary activation is complete, while the presence of an additional twitch is used to quantify the deficit in voluntary activation. Using this technique, some studies have shown that older individuals exhibit a deficit in voluntary activation of both upper [28, 64] and lower [65] limb muscles, when compared to their younger counterparts, whereas other studies have reported no differences between younger and older individuals [66, 67], and even young vs. very old (>80 years) individuals [68]. Furthermore, it has been observed that older individuals can exhibit similar levels of voluntary activation as young individuals, when appropriate practice/familiarization and feedback are provided [69, 70]. Interestingly, it has been shown that activation levels can be improved in older individuals even after only one practice session, but this has not been observed in young individuals [69].

A loss of muscle strength and power in healthy older individuals has been observed to be accompanied by reduced absolute surface EMG (sEMG) amplitude when compared to either young [32, 71] or middle-aged [45, 72] individuals, and even older master weightlifters [73]. Moreover, older individuals with limited mobility have been reported to exhibit a lower level of muscle strength, power and sEMG amplitude compared to older but otherwise healthy individuals [74]. The observed age-related decrement in sEMG amplitude can be ascribed to the decreased number and firing rate of recruited MUs [71, 75, 76]. However, recent studies have indicated that the amplitude of sEMG signals is rather variable among subjects and only provides global features, and hence does not necessarily reflect MU recruitment and individual MU properties [77, 78]. In fact, there are various confounding factors that may challenge the ability of traditional sEMG to compare activation parameters across different participants and/or tasks, such as cross-talk contamination [79] and the EMG amplitude cancellation phenomenon [80].

On the other hand, several aging studies using intramuscular EMG alone or combined with multichannel sEMG have observed altered MU recruitment strategies and reduced firing rates across different muscles, such as the tibialis anterior [21, 58] and the vastus lateralis [81]. As detailed by Kamen et al. (1995), the reduced MU firing rate and recruitment are likely to be among the factors explaining the reduction in muscular strength with aging [82]. In addition, Klass et al. (2008) [58] using intramuscular EMG during rapid voluntary contractions, demonstrated that in older individuals, the lower RTD was accompanied by a lower MU firing rate. More

recently, Del Vecchio and colleagues (2019) [83] using high-density sEMG (HDsEMG) in conjunction with a signal decomposition algorithm [84, 85], have shown that, for example, maximal RFD is related to the speed of identified MUs recruitment during rapid isometric contractions of tibialis anterior in recreationally active young men. Such a relationship has yet to be studied in older individuals, therefore, further exploration is warranted. It is important to specify that the intramuscular needle EMG can provide only a limited representation of the cumulative MU activity that occurs within the muscle [86, 87], therefore, methods evaluating MU firing rate should be sampled from spatially distinct areas and depths [88]. On the other hand, HDsEMG can be also biased towards recording peripherally located MUs. In particular, it could be influenced by the distance between the muscle and the electrodes and the physical characteristics of the tissue (e. g. subcutaneous adipose tissue thickness) due to the filtering effect of the volume conductor [84, 89].

It has been suggested that at least part of the observed age-related loss of muscle strength could be dependent on alterations in the co-activation of antagonist muscles [90]. During a joint movement, the net moment generated around the joint is the algebraic sum of the opposing moments produced by the agonist and antagonist muscles. Therefore, a higher level of co-activation of antagonist muscles could decrease agonist muscle performance via the opposing antagonist-generated torque [91]. Previous studies adopting bipolar sEMG technique have suggested that older individuals attempt to generate maximum torque output by adopting a strategy characterized by a heightened level of antagonist co-activation compared to young individuals – this has been observed for both the upper [29] and lower [71, 92] limbs. The higher level of antagonist co-activation observed in older individuals has been often attributed to an altered balance between excitation and inhibition of spinal circuits [90]. The observation of Kido and colleagues (2004), who examined the reciprocal inhibition (short-latency) in participants aged 22–82 years from the soleus and tibialis anterior muscle by stimulating the common peroneal and tibial nerve, may support this assumption [93]. They observed that there was a negative relationship between the magnitude of inhibition and age, hence concluding that reciprocal inhibition through the α inhibitory interneurons decreases with age [93]. Thus, aging may involve a remodeling of spinal circuitry affecting, at least the MUs innervating the muscles of the lower limbs. In old age, indeed, afferent feedback may become less effective due to an impairment in the excitability of spinal reflex pathways [93]. Previous studies have examined the spinal circuitry function through the recording of the Hoffmann reflex (H-reflex), a surrogate of the spinal reflex excitability. H-reflex responses have been shown to be lower in older compared to young individuals both at rest [94, 95], during quiet standing [93, 96] and walking [93], suggesting that aging may be accompanied by a depression in the efficacy of α afferents to activate spinal motor neurons and possibly due to an increase in the level of presynaptic inhibition. Moreover, it is important to note that the age-associated reflex response in the elderly is not only reduced in amplitude but also slower than that normally observed in young individuals, and this can have significant implications in terms of their capacity to respond and correct mechanical perturbations (e. g. loss of balance due to tripping, etc.) [93, 95].

In summary, in this section we have described reductions in muscle strength and power in older individuals. The evidence suggests that with advanced age both mechanical and neuromuscular alterations ultimately contribute to the decline of muscle strength and power.

Force Control (Force Steadiness)

When an individual performs a steady voluntary muscle contraction, the force exerted is not constant but fluctuates around a mean value [97]. During dynamic (anisometric) concentric and eccentric contractions, this variability of force output is usually quantified as the standard deviation (SD) of acceleration; whereas during isometric contractions, it is quantified as the SD of the force at an imposed target force [98–100]. For instance, Tracy and Enoka (2002) [99] have shown that, in both younger and older individuals, the steadiness of force output was similar between 10% and 50% of 1-RM for both concentric and eccentric contractions (i. e. SD of acceleration), but the steadiness of isometric contraction (i. e. SD of the force output) increased as a function of contraction intensity (i. e. 2%, 5%, 10% and 50% MVIC). Obviously, during an isometric contraction, the SD of the force is closely associated to the contraction intensity, thus being greater in higher than lower intensity contractions, a pattern normally referred to as signal-dependent noise [101, 102]. Therefore, during isometric contractions, to allow comparisons among groups of individuals with different absolute strength (e. g. young vs. older), the SD is usually normalized to the mean force and expressed as the coefficient of variation (CV) [97]. The studies reviewed below will cover force control analyzed using the CV of the force measured during isometric contractions and defined as force steadiness.

Previous studies have investigated the steadiness during isometric contractions of both upper and lower limb muscles in younger and older individuals at target contraction intensities ranging from 2% to 80% MVIC: elbow flexors [103–105], KE [99, 103, 106], ankle dorsiflexors and plantar-flexors [107, 108]. In general, most of these studies have shown that older individuals are less steady (greater CV) than young individuals at target force levels generally lower than 35% MVIC, but the results become less consistent at relatively higher levels of contraction (e. g. > 40% MVIC) [100].

One of the factors that may influence force steadiness during an isometric contraction is muscle length, which can be tested by simply varying the joint angle [106, 109]. This phenomenon is presumably the result of the variation in the level of afferent feedback originating from the proprioceptors due to the alterations in muscle length [110, 111]. Force steadiness has been also used to predict functional performance in older individuals [112]. For instance, Carville and colleagues (2007) [113] have shown that individuals aged over 70 years with a history of falls presented lower levels of force steadiness compared to those individuals who did not have a history of falls – this observation was independent of an individual's maximal muscle strength. Moreover, following a light-load training program, increased steadiness and MVIC of the KE has been associated with improved functional performance (e. g. chair rise, balance, stair ascent and descent) in healthy older individuals, suggesting that increasing steadiness may facilitate a reduction in functional limitations in older individuals [114].

Mechanisms affecting force steadiness

Although, the force exerted by a muscle results from the activation of various MUs, each generating a force of varying amplitude, the last recruited MU has the largest influence on force variability [97, 115]. In older individuals, due to the age-associated MU remodeling described in the first part of our review [1], fewer but larger activated MUs with greater firing variability are preferentially recruited, thus resulting in a more variable force output [116, 117]. This effect is particularly noticeable at lower intensities of contraction, where each recruited MU provides a large contribution to the net force [115, 118]. Nevertheless, a previous simulation study indicated that increased MU twitch force has a negligible contribution to the force steadiness during isometric contractions [119]. In line with the computer simulation, an experimental study has demonstrated a lower level of steadiness in older compared with young individuals at all measured intensities (i. e. 2.5%, 5%, 7.5% & 10% MVIC), but their twitch forces were similar [117].

Contrary to the previous assertion of a negligible influence of MU twitch force on force steadiness, it has been suggested that the variability of single MU firing rate might substantially contribute to force steadiness [97]. Several studies have observed a lower level of steadiness accompanied by a more variable MU firing rate (i. e. greater CV for firing rate) in older individuals when compared to their younger counterparts during low intensity (i. e. $\leq 5\%$ MVIC) isometric contractions of the first dorsal interosseous muscle [117, 120]. On the other hand, more recently, Farina and Negro (2015) [87] indicated that individual motor neuron input may provide only a limited contribution to the force control due to the non-linear nature of its output. They suggested that the common input received by the pool of motor neurons might be primarily responsible for the force control, which linearly reproduces the sources of common input and cancels the sources of independent input [87]. In 20 participants aged 24–75 years, Castronovo and colleagues (2018) [121] reported that, during isometric contractions (20% MVIC), the age-related decrease in force steadiness was related to an increased variability in common synaptic input to motor neurons innervating the tibialis anterior muscle at low frequencies, but not related with an independent synaptic input. Similar results were also documented by Feeney et al. (2018), who reported a significant correlation between force steadiness and estimated variability of common input, but not the variability of single MU firing rate, in both younger and older individuals during isometric contractions of the wrist extensors performed at 10 and 20% MVIC [122]. These results taken together may suggest that, with advanced age, the impairment in force steadiness, particularly at low contraction intensities, is predominantly determined by the increased oscillations in common input to motor neurons at low frequencies, which is likely arising from the possible age-related neuro-degenerative process impacting cortical control [115, 123].

Fatigability

A traditionally accepted definition of muscle fatigue is described as the exercise-induced decrease in maximal voluntary muscle force or power [124, 125]. For an older individual, muscle fatigue can, in some circumstances, become a critical factor for the performance of activities of daily living activities [126, 127]. It is commonly ac-

cepted that age-associated alterations in the function and morphology of MUs, as described in previous sections, account for the different levels of fatigability observed between younger and older individuals [125, 128].

Task dependency

Fatigability is highly dependent upon the different experimental conditions and the criterion measure adopted, such as the intensity and the type of the contraction (i. e. isometrically vs. dynamically either slow or fast) [e. g. 14, 127, 129, 130 among the others]. Therefore, not surprisingly, reports on aging and fatigability are equivocal, showing that older individuals could be either less [131, 132], similarly [14, 130, 132], or more [14, 49, 50] susceptible to fatigue compared to their younger counterparts. For instance, during intermittent maximal [131] and prolonged submaximal [133] isometric contraction tasks, healthy older individuals are usually less fatigable than healthy young individuals. In this regard, it is important to stress that this refers to a contraction intensity corresponding to relative MVIC (i. e. %MVIC). On the other hand, when muscle fatigue is induced using dynamic (concentric) contraction tasks, the age-related difference in fatigability (assessed as difference between pre- and post-fatigue MVIC) between younger and older individuals seems to progressively increase as contraction velocity of the task increases [14, 49, 50]. For instance, when concentric contractions were executed at slow to moderate velocities (e. g. 0.87–3.15 rad/s), younger and older individuals often exhibited a similar relative reduction in post-fatigue MVIC of both upper and lower limb muscles [14, 132, 134, 135]. In contrast, using high-velocity fatiguing contractions, in particular those involving unconstrained (isotonic) fast velocity shortening contractions, older individuals often exhibited a greater reduction in power than young individuals [14, 50, 127].

Mechanisms affecting muscle fatigue

As illustrated in ► **Fig. 1** in the first part of the review [1], the mechanism for the age-associated difference in fatigability under different types of muscle contraction could be attributable to a number of factors including: the slowing of muscle contractile properties; the age-related MU remodeling with a selective shift in myosin heavy chain isoforms to a predominately slow type expression; a greater type I:II muscle fiber composition ratio; a higher innervation rate (i. e. each MU innervating a greater number of muscle fibers) and a lower reliance on glycolytic metabolism observed in older compared with young individuals [17, 51, 70, 128, 136, 137]. For instance, during isometric fatiguing contractions, the aged muscle may experience a lower ATP cost due to a reduced reliance on anaerobic glycolysis and therefore a lower level of accumulation of metabolic by-products and a reduced intramuscular acidification [H^+] [128, 138]. Older individuals are weaker and have smaller muscle mass with respect to their younger counterparts and consequently generate lower intramuscular pressure. Therefore, especially during high-intensity isometric fatiguing contraction tasks, they would experience smaller blood flow occlusion and this could be likely an additional factor contributing to reduce the accumulation of metabolic by-products and [H^+] [139, 140]. These factors taken together can potentially interfere with force output and could result in greater fatigue resistance in older individuals.

On the other hand, during unconstrained high-velocity fatiguing contraction tasks, some studies have reported a greater loss of peak power and a longer HRT (during the twitch torque assessment) in older than young individuals [14, 49]. However, when the post-fatigue MVIC was used to evaluate fatigability, these studies showed either a similar [14] or a lower [49] level of fatigability in older compared with young individuals. It appears appropriate then to suggest that, when performing velocity-dependent fatiguing contraction tasks, particularly with lower limb muscles, the measurement of maximal isometric force alone might not be able to provide sufficient information on fatigue-induced differences between younger and older individuals. Indeed, age-related lengthening in HRT has been often observed to be associated with a loss of muscle power [49, 131, 141], as a result of slowing of cross-bridge kinetics [142]. Interestingly, longer HRTs have been observed, in older individuals, only following fast fatiguing contraction tasks [14, 49], but not after slow-velocity and isometric contraction tasks [131, 134, 143]. Overall, these investigations indicate that the selection of the type and velocity of the contraction might be a key factor affecting the age-related responses to fatigue.

Another important aspect of fatigue-induced changes in motor function that is associated with aging is the variability of the performance. During the performance of isometric fatiguing contraction tasks, the variability of force output deteriorates over time and is normally quantified as the rate of change in steadiness (i. e. CV of exerted torque). For instance, a progressive increase in CV (i. e. decrease in steadiness) has often been observed, with the extent of change (\uparrow CV) being similar [103] and lower [144, 145] in older compared to younger individuals during isometric contractions performed at 20% MVIC. However, the results are still inconclusive when considering responses to dynamic fatiguing exercises, due to the different methodologies adapted. For instance, Senefeld et al. (2017) [127] quantified the variability of performance by the CV of peak velocity during unconstrained KE fast contractions, and observed a more variable peak velocity (a greater CV) in older than in young individuals. Moreover, Wu et al. (2019a) [135] and Laverder and Nosaka (2007) [146] compared the force steadiness during submaximal isometric contractions following isokinetic (concentric and/or eccentric) contraction tasks, and observed similar fatigue-induced decreases in steadiness between two age groups. Although the mechanisms have yet to be identified, these results confirm augmented variability in motor output and neural responses with advanced age during the execution of a fatiguing task.

Conclusions and Future Directions

This two-part review paper details the age-related structural and functional changes from the macro-level of the muscle-tendon unit to the micro-level of the single muscle fiber, attempting to examine concurrently mechanisms and motor performance outcomes of the aging process. In this second part, we have described the age-related alterations in maximal muscle strength and power, in force control and fatigability. Both muscle strength and power decline as a result of aging, and at a faster rate in the lower compared to upper limbs. Muscle power, which associates more with tasks of everyday living, is proportionally more affected by aging than muscle strength. Elderly persons are less steady than younger individ-

uals at lower force levels, whereas the results are less consistent at higher levels of force. Aging is usually associated with a lower level of fatigability during the performance of isometric contraction tasks, but with a higher level of fatigability during the performance of dynamic contraction tasks, especially at high contraction velocities. These alterations are the consequence of changes at the level of: a) the muscle-tendon unit, with a loss of muscle mass, remodeling of muscle architecture and reduction in tendon stiffness; and b) the MU, with structural changes such as a reduced number of MUs and a preferential atrophy of fast-twitch muscle fibers; and with functional changes such as the slowing of muscle fiber shortening velocity, a decreased MU firing rate, as well as an increased variability in common input to motor neurons and an altered SR properties and activity.

Future research on age-related impairments in motor performance and interventions to mitigate the progressive impaired mobility and loss of functional independence among older individuals should attempt to:

- undertake longitudinal studies to gain a better understanding of individual variations in susceptibility to structural and functional alterations in the muscle-tendon unit and MU
- study very old populations (i. e. > 80 years) and older individuals with superior neuromuscular function (e. g. master athletes or former athletes) in order to provide novel insights into the aging mechanisms and the impact that long lasting physical activity has on muscle function.

Conflict of Interest

The authors declare that they have no conflict of interest. The manuscript was conceived and written based on the IJSM ethical standards [147].

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