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Functional relevance of eccentric strength maintenance with age during walking

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Chapter 1

General introduction

1.1 Muscle mechanics in aging

1.1.1 The age-associated loss of muscle strength is less during active muscle lengthening

Natural, healthy aging has profound effects on the ability to generate maximal muscle strength (i.e., torque) voluntarily[1]. The age-related muscle weakness, or dynapenia[2], starts at about the age of 50 and is the result of structural changes in the neuromuscular system. Marked age-specific changes include reductions in muscle mass (i.e., sarcopenia)[3], fiber specific tension[4], and peripheral motor nerve conduction velocity[5], motor unit reorganization[6] and a reduction in tendon stiffness[7] which, as the elastic component lying in-series to the muscle fascicles, shifts the fascicle operating length down the ascending limb of the length-tension curve, lowering the fascicle force generation capacity[8]. Active human skeletal muscles (i.e., the muscle-tendon units) generate torque under three mechanical conditions: When the internal muscle torque is exceeded by, matches or exceeds the external torque, muscles perform an eccentric (lengthening), isometric (remains at constant length) or concentric (shortening) contraction, respectively. Older age differently affects the generation of the three types of torque. By age 70, maximal voluntary concentric and isometric muscle torques decline by up to 40%[9]. However, also by age 70, the age-typical decline in maximal voluntary eccentric muscle torque is only ~20%. This muscle action-dependent rate of torque loss suggests a relative maintenance of maximal voluntary eccentric muscle strength in older adults.

The age-related maintenance of eccentric strength appears to be a robust phenomenon. It was first reported in the knee extensor muscles of healthy older females three decades ago[10], and later confirmed in healthy older males[11,12], aging mice[13], and upper-[14] and other lower-extremity muscle groups[15,16]. Eccentric strength maintenance is also observed in middle-aged and older people with chronic conditions such as stroke[17] and COPD[18] and children with cerebral palsy[19] when compared to age-matched controls, suggesting that chronic conditions may induce an inflated aging-effect on maximal voluntary muscle strength.

Although the maintenance of eccentric strength is a robust finding, several of its aspects are still unclear. First, the potential underlying mechanisms of eccentric strength maintenance may originate from changes residing in active and passive muscular elements that affect muscle stiffness[9]. Specifically, the age-related slowing of cross-bridge cycling[20] and increased muscle fiber stiffness[21] might increase active muscle stiffness, whereas an age-related accumulation of connective tissue[22] could increase passive muscle stiffness. Second, eccentric strength maintenance may be accentuated in older females versus males[9], perhaps due to a greater age-related slowing of cross-bridge cycles in females[16]. Third, whereas a large body of evidence exists on the maintenance of eccentric strength for the knee extensors and ankle dorsiflexors, such evidence have remained inconclusive for the ankle plantarflexors[15], a key locomotor muscle group affected by age[23]. Knowing the underlying mechanisms of eccentric strength maintenance and whether the maintenance magnitude differs by sex and muscle group would assist in designing interventions that could more specifically counteract such functional impairments. However, those studies would become more relevant if it became clear in the first place that eccentric strength maintenance has functional benefits for the execution of daily mobility tasks.

1.2 Muscle mechanics during walking

Walking is the most common form of human locomotion. Also, 60% of all falls occur during this type of gait[24] and preferred walking speed independently predicts many adverse events, such as falls, hospitalization, and even mortality[25]. Moreover, walking is characterized by cycles of lengthening, isometric, and shortening muscle contractions, and during non-level walking (e.g., negotiating stairs or ramps) humans predominantly rely on lengthening or shortening (e.g., incline or decline walking, respectively) muscle function[26,27]. Thus, walking is an appropriate task to study the functional relevance of eccentric strength maintenance in healthy older adults.

Walking is also a complex task that includes lower limb muscles performing up to ~90%[28] of the body's negative and positive joint work (i.e., eccentric and concentric contractions, respectively) during each stride, whereas upper body muscles behave more isometric in general. When performing negative or positive work (i.e., mechanical energy absorption or generation, respectively), the muscle decelerates or accelerates movement of the segment it is inserted on[29]. Hence, muscles act like dampers when actively absorbing energy and subsequently dissipating this energy as heat, whereas muscles act like motors when actively generating energy[30]. In addition, muscles act as springs when absorbed energy is partly re-used during an immediate following phase of energy generation, also known as the stretch-shortening cycle[31,32]. Mechanical energy absorption (i.e., eccentric function) is not only important in controlling joint angular movement and potentially enhancing energy generation[32], it also decelerates and redirects the body's center of mass (COM) trajectory during early stance to prevent limb collapse[33].

Through lower limb work, the body's COM shows a cyclical exchange between kinetic and gravitational potential energy during each stride[34]. Such exchange includes the redirection of the COM during double support, in which the leading limb performs negative work to decelerate the COM's downward and forward motion and the trailing limb performs positive work to accelerate the COM upwards and forwards[34]. Compared to level walking, leg muscles perform ~50% more work during non-level walking, biased towards positive (incline) or negative (decline) work to raise or lower the COM at each step, respectively[35]. Across the three major leg joints, the knee extensor muscles perform most of the negative work (i.e., ~50% of the total) during level and decline walking, followed by the ankle plantarflexor muscles (level and ramp: 25%, stair: 45%)[35]. In addition, the ankle plantarflexors perform most of the positive work (i.e., ~55% of the total) during level and incline walking, followed by the hip flexors and extensors (level: 25%, ramp: 35%, stair: 15%), and knee extensors (level and ramp: 15%, stair: 50%).

1.3 Does lower limb eccentric muscle strength affect walking performance?

Dynapenia lowers the muscle's maximal torque generation capacity, which increases the muscle's relative effort while executing a task such as walking. A higher relative effort would lead to fatigue and perturbed inter-joint coordination more quickly, unless the task demand is lowered by for example adopting a slower walking speed or redistributing the joint torques (discussed in section 1.3.2). This example illustrates the concept of relative effort[36]. Relative effort is the ratio between the peak joint torque generated during the functional task and the subject's maximum available joint torque usually assessed using dynamometry[37,38] or a demanding locomotor task[39,40]. This concept offers a means to better understand why dynapenia associates with slower walking[41,42], why dynapenia is the primary risk factor for mobility disability[43], and how eccentric strength maintenance might have positive functional implications on walking speed and the underlying joint mechanical outputs during walking.

1.3.1 Does knee extensor eccentric strength affect walking speed?

Older adults with low vs. high maximal voluntary knee extensor isometric and concentric strength typically perform walking tasks slower[41,42], less easily[44], and with more effort[23,36]. It is unclear, however, whether maximal voluntary knee extensor eccentric strength also affects walking speed. Determining this relationship could provide insights into whether there is specificity in the relationship between the type of muscle contraction strength and walking task performance (level, ascent, descent). For example, knee extensor eccentric vs. concentric strength may better predict decline walking speed because the task is biased towards eccentric muscle contractions. An understanding of this type of specificity is relevant because it could increase the accuracy of predicting disability for certain tasks when muscle strength is measured specific vs. non-specific to those tasks.

1.3.2 Does knee extensor eccentric strength affect joint mechanics underlying walking?

At preferred walking speeds, older compared with younger adults typically show lower joint mechanical outputs because they generally walk slower[45]. However, age-related differences in joint mechanics can also be observed at matched walking speeds, excluding the confounding effects of walking speed on joint mechanics. One well-documented example is the redistribution of positive work, including lower ankle plantarflexor work and greater hip flexor and/or extensor work in older compared with younger adults[46–48]. The lower plantarflexor output may be because this muscle group operates near (i.e., ~85%[23,38,40]) its maximum torque capacity or underutilizes its maximum torque potential[49]. The underlying mechanism of decreased plantarflexor output is likely multifactorial and may include plantarflexor weakness[50], lower plantarflexor activation[51], increase in trunk lean[52], lower ankle flexibility[53], and altered Achilles tendon deformations with age[49]. It is generally assumed that the hip muscles compensate for the lower plantarflexor output. However, whether there is also an age-related redistribution of negative joint work during walking is unclear. Examining this distribution would not only enrich our current understanding of how healthy aging affects muscle function during walking, but may also help explain the age-related redistribution of positive work. An age-related redistribution of negative joint work, if any, may be attenuated due to eccentric strength maintenance.

An age-related maintenance of knee extensor negative work during walking seems functionally relevant, as it is generally assumed that this muscle group is the main decelerator of knee flexion during weight acceptance in order to prevent limb collapse. This assumption is qualitatively inferred from lower limb joint moments measured by inverse dynamics and muscle activation measured by surface electromyography[54,55]. However, the contribution of each joint moment to knee angular movement can be quantitatively examined using an induced acceleration analysis (IAA). This is because, unlike inverse dynamics, IAA can determine the effects of torque generation at one joint on adjacent joints and help understand the dynamics of inter-joint coupling[56]. Therefore, IAA could provide direct insights into the relative importance of eccentric knee extensor function on stabilizing the knee and whether this effect is affected by age.

1.4 Thesis aim and outline

The aim of this thesis is to determine the functional relevance of the age-related relative maintenance of maximal voluntary knee extensor eccentric strength to walking speed and underlying joint mechanics at prescribed walking speeds. All experiments were cross-sectional in nature and conducted in younger (age 18-35) and older (age 65+) adults.

Chapters 2 and 3 examine the effects of sex and muscle group on the maintenance of eccentric knee extensor and ankle plantarflexor strength. Chapter 2 also examines whether there is specificity between the type of maximal voluntary knee extensor strength (eccentric, concentric) and walking speed during level, ascending, and descending tasks. In the experiments described in chapters 3-5, walking speeds were controlled to eliminate the confounding effects of walking speed on joint mechanics. Chapter 3 determines the effects of age, walking speed, and surface inclination on positive and negative joint work distributions, and whether maximal knee extensor eccentric strength correlates with knee extensor negative work during walking. Chapter 4 aims to discover the functional relevance of knee extensor eccentric function during walking by quantifying joint moments contributions to knee flexion deceleration using a joint-coupling perspective. Chapter 5 examines neural-based mediating effects on the age-related reconfiguration of mechanical joint work observed in chapter 3. Specifically, we determined the relationship between joint work (positive and negative) and muscle activation during ramp ascent and descent. Lastly, chapter 6 presents an integrated discussion of the main findings from the earlier chapters and the broader impacts of our discoveries. The hypotheses behind this work are that i) age-related differences in joint work during walking are attenuated during phases of eccentric force generation relative to phases of concentric force generation, and ii) maximal voluntary knee extensor eccentric torque correlates positively with level and decline walking speed, and with knee extensor negative work during decline walking in healthy older adults.

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