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Merja Hoffrén-Mikkola

Functional Muscle Architecture in Aging

JYVÄSKYLÄN YLIOPISTO

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ABSTRACT

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The present series of studies was designed to examine the effects of aging and training on muscle mechanics and on neural control strategies as well as on the interactions of the two during fast stretch-shortening cycle exercises. The special interest was to examine how the elderly regulate these complicated dynamic actions. The results showed that age-related agonist activity profiles exist during single sledge drop jumps (DJs) and repetitive short contact hopping on the ground. Compared to young subjects, the typical agonist activity pattern of the plantarflexor muscles in the elderly was characterized as high preactivity before contact, with less activity thereafter during the braking phase and increased activity in the push-off phase. Reduced agonist activity during the braking phase influenced the fascicle function in the gastrocnemius medialis muscle in the elderly by making the fascicles shorten considerably less during the braking phase of DJs and hopping. It was also shown that the elderly neuromuscular system has a capacity to change the muscle activity profile but the results suggest that a different kind of muscle activity and fascicle function is optimal for the elderly as compared to the young, possibly due to decreased tendon stiffness and / or age-related motor unit remodeling. Regardless of lower tendon stiffness in the elderly as compared to the young, the present studies suggest that tendon function is maintained in the elderly when movements are performed with the relatively matched exercise intensities for these two age groups. Lower ankle joint stiffness in the elderly as compared to the young during single DJs and high intensity repetitive hopping supports the concept that the elderly neuromuscular system is optimized to match the task demands with their reduced capacities and to shift the load to the stronger muscle groups in situations when the high forces might exceed the tolerable range of weaker muscles. 11 weeks of hopping training increased the hopping performance in the physically active elderly. Therefore hopping training could be recommended for the healthy fit elderly in order to retain and improve the fast force production capacity of ankle joints. This could improve the typically decreased push-off power during walking in the elderly as well as affect the balance control positively.

Keywords: aging, training, stretch-shortening cycle, ultrasonography, muscle mechanics, fascicle, tendon, neural control, joint stiffness regulation

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ORIGINAL PAPERS

This Thesis is based on the following original articles, which are referred to by their Roman numerals.

I Hoffrén M., Ishikawa M. & Komi P.V. (2007). Age-related neuromuscular function during drop jumps. Journal of Applied Physiology 103: 1276–1283.

II Hoffrén M., Ishikawa M., Rantalainen T., Avela J. & Komi P.V. (2011). Age-related muscle activation profiles and joint stiffness regulation in repetitive hopping. Journal of Electromyography and Kinesiology 21: 483–491.

III Hoffrén M., Ishikawa M., Avela J. & Komi P.V. (2012). Age-related fascicle–tendon interaction in repetitive hopping. European Journal of Applied Physiology 112: 4035–4043.

IV Hoffrén-Mikkola M., Ishikawa M., Rantalainen T., Avela J. & Komi P.V. Neuromuscular mechanics and hopping training in elderly. *Submitted for publication.*

ABBREVIATIONS

aEMG	Average electromyogram amplitude
AJS	Ankle joint stiffness
ATF	Achilles tendon force
BEF	Baseline (first) measurement session before training period in study IV
ELDERLY CG	Control group of elderly subjects in study IV
EMG	Electromyography
DJ	Drop jump
Fz	Vertical component of the ground reaction force
GaL	Gastrocnemius lateralis muscle
GaM	Gastrocnemius medialis muscle
GRF	Ground reaction force
KJS	Knee joint stiffness
Maxafter	Maximal hopping trial measured at the end of the measurement session
MHC	Myosin heavy-chain
MTJ	Muscle-tendon junction
MTU	Muscle-tendon unit
MVC	Maximal voluntary contraction
RMS	Root mean square
RSI	Reactive strength index
SJ	Squat jump
SSC	Stretch-shortening cycle
SOL	Soleus muscle
TA	Tibialis anterior muscle
ELDERLY TG	Training group of elderly subjects in study IV
TT	Tendinous tissue
2 WEEKS	Second measurement session after 2 weeks of training in study IV
11 WEEKS	Third and last measurement session after 11 weeks of training in study IV

CONTENTS

1 INTRODUCTION

The number of elderly in the population has increased and will continue to increase rapidly both globally and in Finland. The proportion of over 65 year olds from the Finnish population was 12.1 % in 1980, 17.5 % in 2010 and it is anticipated to increase to 25.6 % in 30 years (Official Statistics of Finland, OSF_A). Because of the increase in longevity the years spent in "very old age" (>75 y) and in "oldest old age" (>85 y) (Shephard 1997) will increase the most. It is estimated that the number of elderly people aged >75 and >85 years will increase 71.7 % and 67.9 %, respectively, between the years 2014 and 2030 in Finland (Official Statistics of Finland, OSF_B). These late life years typically include also years with illnesses and mobility restrictions (Shephard 1997; Portegijs et al. 2014) and that situation brings challenges and costs for the individuals involved as well as for society. Therefore all the knowledge about how elderly people could stay healthy, fit and independent is cost effective and welcome.

Aging is known to be associated with reduction in muscle strength that affects for example the ability to ambulate independently. The loss of muscle mass (sarcopenia) does not fully explain the observed loss in muscle strength but additional factors in the muscle coordination level and inside the muscle-tendon system also play a role (Klein, Rice & Marsh 2001) and these changes may explain at some level the reasons for the increasing number of falls among the elderly population.

Until recent years the aging neuromuscular system, and especially its structure, have mainly been studied in resting conditions or in isometric situations because of the lack of a proper methodology that would have allowed dynamic measurements. It needs to be recognized that it is seldom a static situation that causes problems (loss of balance etc.) among the elderly. Consequently it is necessary to utilize methods that record dynamic types of muscle actions. Normal human locomotion is complex and its behavior cannot be anticipated from isometric measurements. Natural locomotion involves the use of stretch-shortening cycle (SSC) muscle action in which the active muscle is first stretched and subsequently shortened (see Komi 2000 for review). This definition applies to the entire muscle-tendon unit (MTU) but inside the muscle-tendon unit, however, the elastic tendon compartments and force-generating fascicle compartments can behave very differently from this basic mode of SSC (Griffiths 1991; Hoffer et al. 1989; Fukunaga et al. 2001a). The way that these structures interact during human locomotion influences movement efficiency (Fukunaga et al. 2001a) and it has been shown to vary according to movement type (Lichtwark, Bougoulias & Wilson 2007; Ishikawa, Pakaslahti & Komi 2007), intensity (Ishikawa et al. 2006) and the muscle examined (Ishikawa, Finni & Komi 2003; Sousa et al. 2007).

After the introduction of non-invasive imaging techniques, magnetic resonance imaging (MRI) and ultrasonography (US), it has become possible to see inside the muscle-tendon complex and evaluate *in vivo* muscle architecture (fascicles and tendon) both at rest and in locomotion. MRI is considered to be the "golden standard" for muscle size (e.g. cross-sectional area (CSA)) evaluation (e.g. Fukunaga et al. 2001b), which is important when studying the effects of different exercise interventions, disuse or age-related loss of skeletal muscle mass. Ultrasonographic scanning of muscle fascicles on the other hand is a current popular method that allows studying the movement and muscle specific fascicle-tendon interaction *in vivo* even in fast dynamic SSC-type exercises (e.g. walking, running and jumping) (Lichtwark & Wilson 2006; Sousa et al. 2007).

Using US, it has already been shown that with aging humans, the fascicle length and pennation angle decrease (Kubo et al. 2003a; Narici et al. 2003) and, contrary to many animal experiments (see Kjaer 2004 for review), in most of the studies the tendon compliance increases (Kubo 2003b; Karamanidis & Arampatzis 2005; Morse et al. 2005). In addition to that, it has been suggested that there are also age-related differences in fascicle-tendon behavior during human walking (Mian et al. 2007; Panizzolo et al. 2013) and that there are some modifications in neural activation levels in dynamic situations especially in the form of increased antagonist coactivity in the elderly (Häkkinen et al. 1998a; Burnett et al. 2000; Seidler, Alberts & Stelmach 2002). However, at the moment it is not clear to what extent the changes in architecture and neural activation strategies affect the locomotion in the elderly in different movement conditions and what the main factors are which we should concentrate on in rehabilitation in order to develop methods for maintaining functional abilities throughout the aging process. To our knowledge none of the studies have combined simultaneous US assessment of both the fascicle and tendon compartments together with magnitude-based electromyography (EMG) analyses and reaction force measurements at high impact force conditions. This enables examination of the amount of stresses and strains imposed to elderly muscle-tendon compartment during dynamic tasks and neural coordination strategies in the elderly in those situations. Information from that type of studies may be helpful for planning and improving countermeasures for aging effects by building up the more specific training programs for the elderly. For example, if training could demonstrate an increase in Achilles tendon stiffness in the elderly, this could be considered as a proper method to counteract the effects of aging (Kubo 2003b; Karamanidis & Arampatzis 2005; Morse et al. 2005). In practical terms the improvements in the rate of force development, either by improved neural control of muscles and / or changed contractile properties of muscle fibers and / or increased tendon stiffness, and therefore improved balance control, could positively affect the ability of an elderly individual to recover from a perturbation. In order to find out the effects of aging both on structure and function of muscles, architecture should be studied in dynamic natural conditions among young and elderly individuals.

This Thesis concentrated on examining the effects of aging and training on muscle mechanics and neural control strategies as well as their interaction during dynamic exercises. Special focus was placed on the calf muscles function because of its importance in leg stiffness adjustment (Arampatzis et al. 2001; Farley et al. 1998; Kuitunen, Ogiso & Komi 2011) and balance control (Pijnappels, Bobbert & van Dieen 2005a and 2005b; LaRoche et al. 2010) and its role during walking (Beijersbergen et al. 2013; Clark et al. 2013), which is a prerequisite for independent living and the most common form of physical activity among the elderly. Therefore the training of ankle joints could be expected to have functional relevance in the elderly.

2 REVIEW OF THE LITERATURE

2.1 Muscle mechanics during locomotion

2.1.1 Neural control and joint stiffness regulation of SSC exercises

Normal locomotion (walking, running and jumping, for example), involves the use of SSC type muscle actions in which the active muscle is first stretched and subsequently shortened and it has been shown to be beneficial in terms of economy and efficiency, as compared to pure concentric action alone (see Komi 2000 for review). The contact phase of SSC activities include three functional phases with different purposes: preactivity, braking (impact) and push-off phases. Melvill Jones & Watt (1971) showed that muscles become active already before the contact instant in order to prepare the leg for impact. Preactivity is thought to be a centrally mediated motor command (Jones & Watt 1971) and shown to increase with the increase in exercise intensity (Ishikawa & Komi 2004). Avela et al. (1996) suggested that preprogrammed preactivity is influenced by previous experience and modified also by proprioceptive, vestibular and visual inputs. In the braking phase the agonist muscles lengthen and therefore store elastic energy that can be used to enhance the performance in the immediately following push-off phase (Asmussen & Bonde-Petersen 1974; Cavagna 1977). Similarly to preactivity the braking phase activity of agonist muscle increases with increase in exercise intensity (Ishikawa & Komi 2004). Braking phase agonist activity is typically higher than that during the preactivity phase and is influenced by centrally programmed pathways as well as stretch reflexes (Jones & Watt 1971; Dietz, Schmidtbleicher & Noth 1979; Moritani, Oddsson & Thorstensson 1991). Preactivity and braking phase agonist activity have a key role in joint / leg stiffness regulation and therefore strongly affect the performance especially in fast SSC actions (Horita et al. 2002) where high joint stiffness is a prerequisite for good performance (Asmussen & Bonde-Petersen 1974; Cavagna 1977; Gollhofer et al. 1992). In addition to agonist activity also the amount of antagonist coactivity during the braking phase plays a role in joint / leg stiffness adjustment (Hobara, Kanosue & Suzuki 2007; Yoon, Tauchi & Takamatsu 2007). It seems that in SSC exercises the coactivity is high in the preactivity phase in order to stabilize the leg for landing. Thereafter it decreases fast during the early braking phase since increased coactivity in braking phase decreases joint stiffness (Hobara, Kanosue & Suzuki 2007; Yoon, Tauchi & Takamatsu 2007) and therefore is not beneficial in these performances where high joint stiffness is a prerequisite (Asmussen & Bonde-Petersen 1974; Cavagna 1977; Gollhofer et al. 1992). Finally in the push-off phase the agonist muscles shorten. Since elastic energy is recovered from tendons during this phase the high agonist muscle activity is not needed especially in the submaximal level and this increases movement efficiency in SSC actions compared to pure concentric actions alone. The high agonist EMG ratio of the braking phase activity over the push-off phase activity is a characteristic of good efficiency in SSC actions (Asmussen & Bonde-Petersen 1974; Asmussen 1953; Bosco et al. 1982).

2.1.2 Fascicle-tendon interaction in dynamic movements

The stretching followed by the shortening behavior of muscles in SSC actions applies to the entire MTU level. However, inside the MTU, the elastic tendon compartments and force-generating fascicle compartments can behave very differently from this basic mode of SSC (Hoffer et al. 1989; Griffiths 1991) and their behaviors cannot be anticipated from MTU length changes. The way that these structures interact during human locomotion influences movement efficiency (Fukunaga et al. 2001a) and it has been shown to vary according to movement type (Lichtwark, Bougoulias & Wilson 2007; Ishikawa, Pakaslahti & Komi 2007), intensity (Ishikawa et al. 2006) and the muscle examined (Ishikawa, Finni & Komi 2003; Sousa et al. 2007). Recent studies also suggest that there may be age-specific differences in fascicle-tendon interaction during walking (Mian et al. 2007; Panizzolo et al. 2013).

Ultrasonographic scanning of muscle fascicles and muscle-tendon junction (MTJ) is a current popular method to study the movement and muscle specific fascicle-tendon interaction even during fast SSC exercises (see Cronin & Lichtwark 2013 for review). In that method the US probe is tightly fixed on the skin above the muscle belly (figure 1A) or MTJ (figure 1B) that is under scrutiny and the pictures are recorded with frequencies of around 100-200 Hz in order to be able to observe the length changes during various movements. After that the fascicle length and / or MTJ position is digitized frame by frame either manually or, very recently, also automatically (Cronin et al. 2011a). Finally the data is synchronized with kinematics and kinetics in order to be able to come to a conclusion about the roles of fascicles and the tendon during various movements and to calculate the stresses and strains imposed on them when moving.

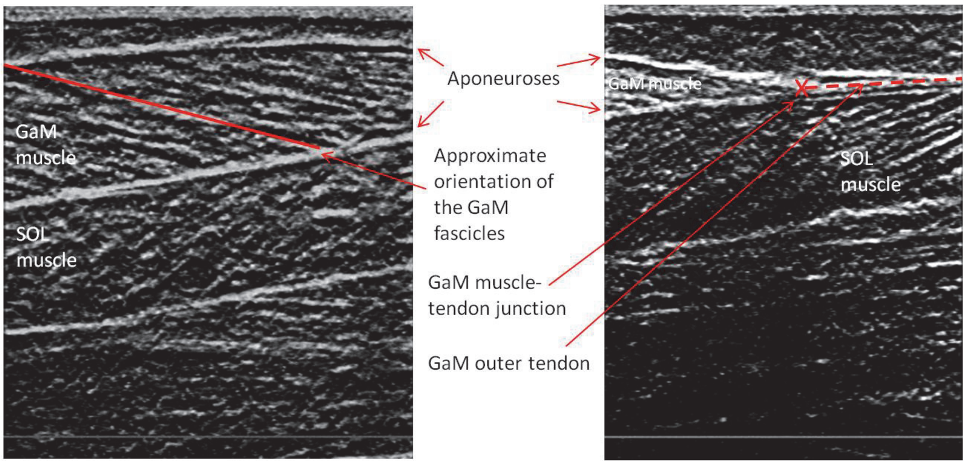

FIGURE 1 Examples of the US pictures from (A) gastrocnemius medialis (GaM) muscle belly and (B) GaM muscle-tendon junction that are used for analyzing the fascicle length and muscle-tendon junction position, respectively. SOL = soleus muscle

2.2 Neuromuscular function in the elderly during dynamic movements

The weakness associated with aging is not only due to a decrease in the size of skeletal muscles (sarcopenia) but is also related to impaired neural control of muscles (for review see e.g. Roos, Rice & Vandervoort 1997 and Enoka 1997) and/or to reduced muscle quality (Barber et al. 2013). Aging decreases the number of both slow (type I) and fast (type II) muscle fibers and selectively the size of type II fibers (see Deschenes 2004 for review). In addition the size of type I motor units increases with aging since slow type I motor neurons reinnervate some of the denervated type II fibers. This phenomenon is called motor unit remodeling with aging and it probably explains to a great extent the decrease in the rate of force development with increasing age (Thompson et al. 2014) as well as less steady force production capacity in the elderly as compared to young individuals (Tracy & Enoka 2002). In addition, aging increases the coexpression of hybrid fibers in skeletal muscles and therefore the terms “slow” and “fast” fibers may not even be relevant when talking about the muscles of elderly individuals (for review see Andersen 2003). In addition to decreases in muscle mass and neural control, the recent technological developments have revealed that the orientation of muscle fascicles (e.g. Kubo et al. 2003a; Narici et al. 2003) as well as the mechanical properties of an *in series* tendon (e.g. Kubo et al. 2003b and Morse et al. 2005) change with aging. This may influence their interaction during dynamic movements (Mian et al. 2007) and affect also the optimal way of the nervous system to control movements in the elderly who have changed neuromuscular properties (Lichtwark & Wilson 2005a). The next two chapters will clarify in more detail the changes with aging in neural control and in muscle architecture and try to explain their potential consequences for performance in SSC exercises. The third chapter deals with the potential of training to retrieve these effects of aging.

2.2.1 Effects of aging on neural control of muscles

There is discrepancy in literature whether the ability to activate muscles during maximal voluntary contractions decreases with aging or not (Piirainen et al. 2010; Barber et al. 2013). Barber et al. (2013) reported a maximum voluntary activation capacity of 90.4 ± 10.7 % in young adults vs. 89.6 ± 14.4 % in older adults in triceps surae muscles with no significant difference between the age groups. In contrast, Piirainen et al. (2010) found that the activation level of the quadriceps muscle group was reduced in the elderly as compared to young subjects (96.2 ± 0.8 % vs. 93.8 ± 2.1 %, $p<0.01$, in the young and the elderly, respectively). Therefore the ability to activate muscles with aging seems to be muscle specific and possible also related to measurement technique and the physical characteristics of the elderly subjects (age, physical activity level) (Scaglioni et al. 2002) .

When the elderly and the young are asked to hold a certain submaximal force level, the force production in the elderly is less steady compared to that of younger subjects (Kallio et al. 2012; Hortobágyi et al. 2001). In addition to that, Kallio et al. (2012) reported lower soleus muscle (SOL) discharge rates during 10 % and 20 % force levels from the maximal voluntary isometric contraction (MVC) in the elderly as compared to the young, suggesting age-related changes in the motor unit control of agonist muscles. Hortobágyi et al. (2001) found that older subjects compared to younger ones made more errors in matching a required quadriceps force level also during isometric force production but especially during dynamic contractions. In all of these cases the elderly produced more force as required. When the rate of torque development was also substantially decreased in the elderly, the authors came to conclusion that the results were primarily because of age-related motor unit remodeling. Hortobágyi et al. (2001) concluded that force control at low force levels was reduced in elderly subjects, which may have important consequences since many daily tasks are executed at only a fraction of maximal strength.

Dynamic setups in the elderly that would have investigated the role of agonist activity strategies under higher force requirements are rare. Hortobágyi & DeVita (2000) showed that the preactivity of agonist muscles was increased in the elderly as compared to young subjects by 136 % and this, together with increased coactivity during ground contact, resulted in higher leg stiffness in the elderly during stepping down from a platform. The authors speculated that the source of heightened muscle preactivity during downward stepping in the elderly was associated with a greater general motor arousal preceding the movement (Hortobágyi & DeVita 2000). Cronin et al. (2013) observed that agonist activity was higher in those elderly subjects who could regain balance from a forward fall with a single step as compared to those who required multiple steps. No significant differences were observed between groups in the onset of muscle activity. The authors concluded that compared to multiple steppers, single steppers recruited a larger proportion of their available motor unit pool during balance recovery, and that the modulation of EMG amplitude played a larger role in balance recovery than EMG timing (Cronin et al. 2013).

It is also suggested that age-specific agonist activity profiles exist in plantarflexor muscles during walking (Panizzolo et al. 2013; Schmitz et al. 2009). Panizzola et al. (2013) showed that elderly individuals had higher SOL activity compared to younger ones during the gait cycle of walking, and that the difference remained similar whether the two age groups walked with the same absolute velocity or whether their preferred walking speeds were compared. This result could mean that the elderly had to use a relatively higher proportion of their maximal available muscle capacity during walking compared to young subjects even when they were allowed to use their preferred walking speed. On the other hand, Smitz et al. (2009) reported that compared to the young adults, the older adults depend less on SOL muscle activity to push-off at walking speeds faster than their preferred speed and the result is likely to contribute to reduced push-off power at fast walking speeds in the elderly. There are several studies that have shown that the neuromuscular system of the elderly is able to redistribute muscular output depending on task demands and in many cases shift the load from the ankle joint to the stronger knee and hip joint muscles during walking (Savelberg et al. 2007; DeVita & Hortobágyi 2000) and ascending stairs (Reeves et al. 2009).

Therefore it seems that the aging process causes inevitable impairments of neuromuscular function but at least the most often used movement patterns in the elderly are optimized to some extent to overcome these limitations. Currently it is not clear how the elderly regulate complicated dynamic actions that require high force production and high rates of force development.

2.2.1.1 Antagonist coactivity

Movement patterns in the elderly are usually slow (Lanza et al. 2003; Norris et al. 2007) and characterized by excessive co-contraction of agonist and antagonist muscle pairs (Tracy & Enoka 2002; Schmitz et al. 2009; Burnett, Laidlaw & Enoka 2000; Häkkinen et al. 1998a; Seidler, Alberts & Stelmach 2002). Increased antagonist coactivity is linked to decreased inter-muscular coordination and it seems to be an age-related phenomenon regardless of movement type (see Hortobágyi & DeVita 2006 for review). The exact mechanisms behind the increased coactivity with aging are not known in detail but may include the decrease in reciprocal inhibition as well as some cortical mechanisms such as a spread of motor command from the agonist’s to the antagonist’s cortical representation areas (Hortobágyi & DeVita 2006). This increased coactivity with aging can partly explain the higher energy cost of walking in the elderly as compared to the young (Malatesta et al. 2003; Hortobágyi et al. 2009; Mian et al. 2006; Peterson & Martin 2010). On the other hand, however, high coactivity during stabilizing actions (down-ward stepping for example) has been shown to increase joint stiffness in the elderly which may improve the stability and safety of locomotion (Hortobágyi & DeVita 2000). Therefore the roles of antagonist coactivity with aging are multifactorial and depend on the movement performed. Very little is known about the effects of aging on coactivity during rapid SSC movements with high force requirements.

2.2.2 Effects of aging on muscle architecture

2.2.2.1 Fascicle compartment

With aging humans, the fascicle length measured at resting state is suggested to decrease on average of 5 mm (10 %) and the pennation angle on average of 3-5 deg (13-20 %) between the ages of 20-70 years (table 1). Some but not all of these age-related differences disappear when age-specific differences in body dimensions (limb length, muscle thickness or CSA) are taken into account (Kubo et al. 2003a; Narici et al. 2003). In addition, the differences between the studies may be due to differences in sample sizes, physical activity levels and age categories of the subject groups. It is suggested that following the changes in muscle mass and strength (Frontera et al. 1991; Hughes et al. 2001), the age-specific differences in muscle architecture would be greater in lower body as compared to upper body muscles. That may be because of differences in the plasticity of these muscles and / or a greater decrease with aging in the use of lower limbs as compared to upper limbs (Kubo et al. 2003a). The data regarding upper limb muscle architecture is limited, however.

TABLE 1 Fascicle length and pennation angle in the young and in the elderly. *) Only non-active subjects were included from Karamanidis & Arampatzis (2005 and 2006) but there were no age-specific differences in runners either. VL = Vastus lateralis –muscle, TB = Triceps brachii –muscle.

Study	Muscle	**Subjects**	**Fascicle length (cm)**	*Difference*	**Pennation angle (deg)**	*Difference*
Narici et al. (2003)	GaM	YOUNG MEN (n=14)	4.8 ± 0.6	*0.49 cm* *10.2 %* *p<0.01*	27.2 ± 4.3	*3.6 deg* *13.2 %* *p<0.01*
		ELDERLY MEN (n=16)	4.3 ± 0.7		23.6 ± 3.0	
Kubo et al. (2003c)	GaM	YOUNG MEN (n=67)	5.8 ± 0.9	*0.55 cm* *9.6 %* *p<0.001*	23.6 ± 2.3	*ns*
		ELDERLY MEN (n=54)	5.2 ± 0.7		21.9 ± 2.1	
		YOUNG WOMEN (n=46)	5.4 ± 0.7	*0.54 cm* *9.9 %* *p<0.001*	21.9 ± 2.2	*ns*
		ELDERLY WOMEN (n=144)	4.9 ± 0.6		21.3 ± 2.4	
	VL	YOUNG MEN	6.9 ± 0.8	*0.46 cm* *6.6 %* *p<0.01*	21.3 ± 2.2	*4.8 deg* *22.5 %* *p<0.001*
		ELDERLY MEN	6.5 ± 1.1		16.5 ± 2.8	
		YOUNG WOMEN	6.5 ± 1.1	*ns*	18.9 ± 2.4	*3.3 deg* *17.5 %* *p<0.001*
		ELDERLY WOMEN	6.4 ± 1.0		15.6 ± 2.7	
	TB	YOUNG MEN	5.9 ± 0.9	*ns*	19.7 ± 2.9	*ns*
		ELDERLY MEN	58 ± 0.9		18.7 ± 2.1	
		YOUNG WOMEN	5.2 ± 0.7	*ns*	15.9 ± 2.1	*ns*
		ELDERLY WOMEN	5.2 ± 1.0		15.2 ± 2.0	
Morse et al. (2005)	GaM	YOUNG MEN (n=15)	6.3 ± 1.2	*1.0 cm* *15.9 %* *p<0.05*	21.6 ± 2.6	*2.9 deg* *13.4 %* *p<0.05*
		ELDERLY MEN (n=12)	5.3 ± 0.6		18.7 ± 3.5	
	GaL	YOUNG	7.0 ± 1.4	*ns*	14.3 ± 2.2	*2.6 deg* *18.2 %* *p<0.01*
		ELDERLY	6.4 ± 0.6		11.7 ± 2.6	
	SOL	YOUNG	4.3 ± 0.8	*ns*	25.3 ± 3.2	*3.8 deg* *15.0 %* *p<0.05*
		ELDERLY	3.6 ± 0.8		21.5 ± 4.2	
Karamanidis & Arampatzis (2005) and (2006) *)	GaM	YOUNG MEN (n=10)	6.3 ± 0.8	*ns*	18.9 ± 2.4	*ns*
		ELDERLY MEN (n=10)	6.5 ± 0.6		18.4 ± 2.6	
	VL	YOUNG	11.2 ± 2.1	*ns*	10.0 ± 2.2	*ns*
		ELDERLY	10.6 ± 1.5		9.8 ± 1.7	
Stenroth et al. (2012)	GaM	YOUNG (n=33) 18 MEN, 15 WOMEN	4.8 ± 0.7	*0.36 cm* *7.5 %* *p<0.05*	24.90 ± 3.95	*ns*
		ELDERLY (n=67) 33 MEN, 34 WOMEN	4.4 ± 0.7		23.78 ± 3.96	
	SOL	YOUNG	4.1 ± 1.0	*ns*	20.24 ± 5.47	*ns*
		ELDERLY	4.0 ± 0.8		18.77 ± 4.36	

2.2.2.2 Tendon compartment

Since fascicle length, even relative to muscle length, decreases with aging, it would be logical that the relative tendon length (to muscle length) would increase with aging. Literature in this regard is scarce but the study by Stenroth et al. (2013) does not support this concept. There are two studies that have reported the increased Achilles tendon CSA with aging in humans (Magnusson et al. 2003a, Stenroth et al. 2013). In addition to the possible changes in tendon dimensions in aging, the US based assessments in humans suggest that tendon compliance increases with aging (Kubo et al. 2003b; Morse et al. 2005; Karamanidis & Arampatzis 2005; Stenroth et al. 2012), although the latest studies have not always supported the finding (Carroll et al. 2008; Couppe et al. 2009) and the majority of animal studies have shown stiffening of tendons with aging (see Kjaer 2004 for review). The adaptation of the tendon to increasing age is thought to be the sum of various mechanisms. Generally the increase in non-reducible collagen cross-linking is observed in aging, which alone would make tendons stiffer. However, at the same time the decrease in the collagen fibril crimp angle, extracellular water and mucopolysacharide content, as well as an increase in elastic content, take place and therefore the combined effect of all these changes is responsible for the age-related decrease in tendon stiffness (see Narici & Maganaris 2006 for review).

Some of the difference in tendon stiffness between the young and the elderly may disappear when maximal force production capacity is taken into account (Stenroth et al. 2012) suggesting that tendon stiffness is closely related to maximal force and may therefore rather be an adaptational strategy for requirements of daily living than a detrimental effect. On the other hand, the increase in tendon compliance would decrease the rate of force development in the elderly (Reeves, Maganaris & Narici 2003) and therefore, together with changes in myosin heavy-chain (MHC) compositions, complicate further the ability to produce force rapidly for example when the balance needs to be corrected quickly after the perturbation. In addition the age-related architectural changes at the fascicle and tendon level may have implications on muscle function in old age by affecting the length-tension as well as force-velocity and power-velocity relations of muscles (Narici et al. 2003). These depend on combined effects of changes in fascicle and tendon levels as well as on muscle activity strategies.

So far, however, only a few studies have investigated the effects of aging on muscle mechanics in real movement situations and their study designs are not comprehensive enough to draw the picture about the mechanisms behind observed age-related differences in muscle mechanics.

2.2.2.3 Muscle mechanical behavior

Mian et al. (2007) observed increased tendinous tissue lengthening and decreased fascicle lengthening of the gastrocnemius lateralis -muscle (GaL) in the elderly as compared to the young during the stance phase of walking with matched speeds for both age groups (figure 2). The authors suggested that higher tendon compliance in the elderly may be the reason for these age-specific differences. A recent paper of Panizzola et al. (2013) confirmed these results for SOL muscle but further showed that age-specific differences in fascicle mechanical behavior disappeared when preferred walking speeds were compared. Therefore the paper suggested that the decrease in preferred walking speed with aging is a strategy to retain the fascicle and tendon function of elderly individuals during walking in a similar manner to that in the young.

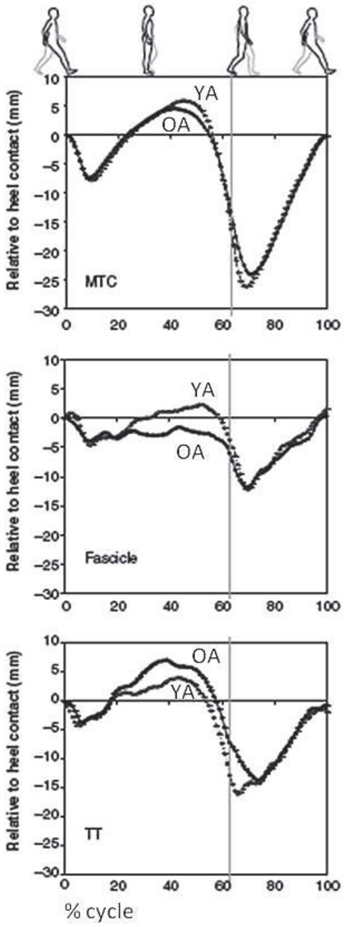

FIGURE 2 The length-times curves of gastrocnemius lateralis (GaL) –muscle muscle-tendon complex (MTC), fascicle and tendinous tissue (TT) in young adults (YA) and in older adults (OA) during walking with the walking speed of 1.11 m/s (4 km/h) in the paper by Mian et al. (2007).

These two studies nicely demonstrate the effect of measured exercise intensity on results and interpretations when two age groups with obviously different neuromuscular capacities are compared during dynamic actions. In addition to walking (Cavagna & Kaneko 1977), the neural activation and therefore also fascicle-tendon interaction during hopping (Finni, Komi & Lepola 2001) is intensity specific in a non-linear fashion. This means that efficient hopping or walking is achieved at moderate intensities. In lower and higher performance intensities the efficiency may be compromised (Cavagna & Kaneko 1977; Finni, Komi & Lepola 2001). When the same absolute exercise intensities are used for the young and the elderly, the chosen intensity is always closer to the maximum for elderly subjects. Consequently, demonstration of the possible existence of age-specific muscle activity profiles and fascicle-tendon interaction would require use of the same relative exercise intensities (stretch levels) for young and elderly subjects.

However, in walking the impact forces are relatively low and the muscles demonstrate low activity during the braking phase of contact. Since walking is the most common form of physical activity among the elderly, it would be logical that the elderly neuromuscular system would be optimized to function efficiently during that activity, at least at reduced speeds. However, also the elderly are momentarily forced into situations with high force requirements and rapid force production. These activities include for example situations when balance needs to corrected quickly after perturbation in order to avoid falling. Therefore it would be important to examine how the fascicle-tendon interaction and consequently the tendon loading takes place among the elderly at higher impact force conditions.

2.3 Training-induced changes on neuromuscular function in the elderly

It is well established that strength training improves maximal force and power in elderly individuals in a similar manner as it does in younger individuals (Reeves, Maganaris & Narici 2003; Newton et al. 2002) and that at the early phase of training the improvement in performance is due to neural adaptation (Häkkinen & Komi 1983). Traditional strength training protocols in the elderly have been shown to decrease antagonist coactivity (Häkkinen et al. 1998b) and in some cases to increase the voluntary drive to agonist muscles (Scaglioni et al. 2002). From a muscle architectural point of view, strength training has increased fascicle length and the pennation angle (Reeves, Narici & Maganaris 2004) as well as tendon stiffness and Young's modulus and has decreased tendon hysteresis in the elderly (Reeves, Maganaris & Narici 2003), therefore partly counteracting the effects of aging.

Despite the positive results of traditional strength training on muscle strength and neuromuscular function in the elderly, alternative training methods are needed. Bone fractures are common in elderly individuals and bring pain for the individuals involved as well as costs for society (Stevens & Olson 2000). Falling is the most common reason for bone fractures, and decreased bone mineral density (osteoporosis) in the elderly further hastens the formation of fractures (Stevens & Olson 2000). High-impact exercise training could be effective in fracture prevention by not only improving bone mineral density but also improving muscle power and dynamic balance (Heinonen et al. 1996). It is suggested that a decrease in movement velocity with aging is the predominant factor in the loss of power between the young and old (McNeil, Vandervoort & Rice 2007) and therefore to target the training for high contraction speeds could be important.

However, today it remains unclear whether high-impact exercise training could be safely applied for the elderly, whether it would improve performance capacity and, if it does, what the mechanisms behind it would be. If training for example increased the agonist activity and / or decreased antagonist coactivity during the early part of contact (braking phase) in SSC exercise in the elderly, that would increase the hopping efficiency (Bosco et al. 1982; Finni, Komi & Lepola 2001; Kuitunen et al. 2007; Kyröläinen, Takala & Komi 1998) and improve joint stiffness (Yoon, Tauchi & Takamatsu 2007; Kuitunen et al. 2007). In addition, in the longer term, cyclic training that includes high strains has been shown to increase tendon stiffness in the young (Arampatzis, Karamanidis & Albracht 2007), but that has not been investigated in elderly individuals.

Ankle joint functional capacity (high rate of development of muscle activity and high plantarflexor moment) is important in balance regain from a trip (Pijnappels, Bobbert & van Dieen 2005a and 2005b) and has been reported to be decreased in elderly fallers compared to non-fallers (LaRoche et al. 2010). In addition, ankle joint functional capacity is the weakest link in the elderly during walking (Beijersbergen et al. 2013; Clark et al. 2013), which is a prerequisite for independent living and the most common form of physical activity among elderly. Therefore the training of ankle joints could be expected to have functional relevance in the elderly.

3 PURPOSE OF THE STUDY

Neural control of muscles as well as fascicle-tendon interaction are specific to the movement type performed (Lichtwark, Bougoulias & Wilson 2007; Ishikawa, Pakaslahti & Komi 2007), to exercise intensity (Finni et al. 2001; Ishikawa et al. 2006) and to the muscle examined (Ishikawa, Finni & Komi 2003; Sousa et al. 2007). Recent developments in US technologies have made the continuous examination of muscle fascicles and tendon possible during specific dynamic movements in different subject populations. This is necessary in order to know the roles of these structures on performance output and therefore to better understand the complex nature of human neuromuscular system during the control of locomotion.

Using US, Mian et al. (2007) and Panizzolo et al. (2013) showed that there are age-specific differences in fascicle-tendon interaction during human walking. It seems that the aging neuromuscular system is optimized to function efficiently with its reduced capacity during the activities mostly performed in daily lives. This is especially true when the elderly can perform the activities at freely chosen speeds that are typically slower than those preferred by younger individuals. However, the elderly are also momentarily forced into situations with higher force requirements and rapid force production. These activities include for example situations in which balance needs to be corrected quickly after perturbation in order to avoid falling. It seems that ankle joint functional capacity is important in regaining balance from a trip (Pijnappels et al. 2005a and 2005b) and has been reported to have decreased in elderly fallers compared to non-fallers (LaRoche et al. 2010). However, currently it is not clear how elderly individuals regulate complicated dynamic actions that require high force production and high rates of force development in plantarflexor muscles. This information on how the fascicle-tendon interaction and consequently the tendon loading takes place among the elderly in higher impact force conditions may be helpful for planning and improving countermeasures for aging effects by building up more specific training programs for the elderly.

In addition, currently it is not clear what causes the observed age-specific differences in fascicle-tendon interaction. If a tendon becomes more compliant with aging (Kubo et al. 2003b; Morse et al. 2005; Karamanidis & Arampatzis 2005; Stenroth et al. 2012), it naturally could affect the fascicle-tendon interaction since it is the difference in stiffness between these two structures that determines the amount of lengthening in them when force is applied (Zajac 1989). However, since fascicle stiffness is controlled by neural activation, it is clear that possible age-specific differences in neural control of muscles (Panizzolo et al. 2013; Schmitz et al. 2009) may also influence fascicle-tendon interaction and therefore when measuring fascicle and tendon behavior, the magnitude of neural activation during different functional phases of SSC should be taken into account. To our knowledge none of the studies has combined simultaneous US assessments of both the fascicles and the tendon together with kinematics, magnitude-based EMG analyses and reaction force measurements at high impact force conditions in the elderly. By doing that it is possible to examine the amount of stresses and strains imposed on different compartments of the elderly muscle-tendon unit during dynamic tasks and neural coordination strategies elderly have in those situations.

This PhD Thesis is intended to fill the gaps in the existing knowledge and has the following objectives and hypotheses:

Obj I: Age-related neuromuscular function in active dynamic SSC-exercises (Original papers I, II and III)

Hyp: High forces need to be produced in a limited time in situations when for example balance has to be corrected after perturbation. It is not known in detail how the elderly regulate these complicated dynamic actions and which parameters in neuromuscular system are most affected by increasing age. Considering that muscle activity profiles for agonist and antagonist muscles may show age-specific differences during dynamic movements, the fascicle-tendon interaction is also expected to demonstrate less tendon utilization among the elderly as compared to the young.

Obj II: Effects of training on neuromuscular function in the elderly in SSC-exercises (Original paper IV)

Hyp: It is well established that strength training improves the maximal force and power also in elderly individuals (Newton et al. 2002). Instead of traditional strength training, the protocol will include more coordination required hopping training that is hypothesised to affect both the neural part as well as muscle and tendon function during dynamic actions in the elderly.

4 METHODS

4.1 Subjects

In total 78 subjects participated in the four series of studies as subjects. 21 of those were young (20-32 years) (YOUNG) and 57 were elderly (65-80 years) (ELDERLY). The background information of the subject groups are presented in table 2. In Experiment 3 the subjects were the same elderly men as in Experiment 2. The subjects in Experiment 3 (n = 24) were randomly assigned to a training group (ELDERLY TG) and to a control group (ELDERLY CG). Two trained subjects did not finish the end measurements due to injury. One of them injured his leg outside the training sessions and other one felt pain in Achilles tendon region possibly due to training. One control subject did not participate in the end measurements because of illness and one did not do maximal hopping in the end measurements because of a leg injury which was not related to the measurements. Therefore 10 trained and 10 control subjects participated in all the measurements and were included for analyses.

All the subjects were physically active. YOUNG were sports science students and ELDERLY were recruited from local senior gym and some other senior clubs. Before measurements the subjects were given an informed consent of the procedures and risks associated with the study and they gave their written consent to participate. Medical screening was performed for ELDERLY before the measurements. Exclusion criteria included coronary artery disease, neurological diseases and current lower extremity and low back pain as well as previous injuries in leg joints. The recommendations contained in the Declaration of Helsinki were followed and the studies were approved by the local ethics committee.

TABLE 2 Background information (mean ± SD) of the subject groups. *) In self reported fitness the categories (1-5) were as follows: 1 = in clearly worse, 2 = slightly worse, 3 = on average the same, 4 = slightly better and 5 = clearly better physical condition than people in my age group on average.

	Experiment 1 (Original paper I)			Experiment 2 (Original papers II and III)			Experiment 3 (Original paper IV)		
	YOUNG N=12 (5 M, 7 W)	ELDERLY N=13 (5 M, 8 W)	*P value*	YOUNG N=9 Men	ELDERLY N=24 Men	*P value*	ELDERLY TG N=10 Men	ELDERLY CG N=10 Men	*P value*
Age (y)	25.2 ± 2.5	69.0 ± 3.8	***<0.001***	25.4 ± 4.1	71.7 ± 4.3	***<0.001***	73.1 ± 4.4	70.9 ± 4.4	*0.28*
Height (cm)	171.4 ± 7.4	168.0 ± 6.7	*0.24*	176.6 ± 5.9	171.5 ± 5.5	***0.033***	170.5 ± 7.4	171.9 ± 3.9	*0.61*
Weight (kg)	66.8 ± 10.7	67.8 ± 9.8	*0.82*	74.3 ± 6.7	75.4 ± 8.6	*0.66*	76.8 ± 9.2	73.4 ± 8.7	*0.40*
BMI (kg/m2)	22.6 ± 2.2	24.0 ± 3.4	*0.24*	23.8 ± 1.3	25.6 ± 2.5	***0.034***	26.4 ± 2.5	24.8 ± 2.4	*0.16*
Self reported fitness compared to age matched counterparts (1-5) *)	4.2 ± 0.7	3.7 ± 0.6	*0.09*	4.2 ± 1.0	3.7 ± 0.7	*0.09*	3.7 ± 0.8	3.7 ± 0.8	*0.93*
Exercise (times/week)	4.0 ± 2.0	4.0 ± 1.3	*0.99*	5.4 ± 2.5	4.2 ± 1.9	*0.55*	4.5 ± 1.8	3.6 ± 1.2	*0.21*
Exercise (h/week)	6.3 ± 3.2	5.1 ± 1.8	*0.25*	10.1 ± 4.4	6.0 ± 3.8	*0.052*	7.4 ± 5.4	4.8 ± 2.2	*0.24*
Participation in guided training	3/12	11/13	***0.002***	3/9	19/24	***0.012***	6/10	9/10	*0.13*
Exercise types	Running, skiing, gym training, bicycling, ball games	Walking, skiing, gym training, gymnastic exercises, swimming		Ball games, gym training, bicycling, running	Gymnastic exercises, Walking, skiing, cycling, swimming		Walking, skiing, gymnastic exercises	Gymnastic exercises, walking, cycling	

4.2 Experimental designs

The Thesis consists of three separate experiments. The first one (Original paper I) was designed to clarify the possible age-specific differences in muscle activity profiles and fascicle-tendon interaction with a simple sledge drop jump (DJ) protocol with maximal DJs performed from low dropping heights. Even if the jumps were performed with maximal effort, the idea was that the exercise intensities were similar in absolute scale for the two age groups. That is because the dropping heights were the same in absolute scale. It is known that rebound heights in DJs are greatly affected by dropping heights (Komi & Bosco 1978) and that optimal dropping heights vary from one individual to another and naturally between the two age groups with obviously different neuromuscular capacities. Therefore the exercise intensities in Experiment 1 were relatively more strenuous for elderly subjects compared to young ones and thus the study followed the principles of previous papers on aging (e.g. Mian et al. 2007) but brought additional aspects to the discussion with magnitude-based EMG analyses measured simultaneously with fascicle and tendinous tissue function. The advantage of the sledge was that it enabled a safe measurement environment also for elderly individuals without concerns about balance. Thereafter with the second experiment (Original papers II and III) the findings of first measurements needed to be confirmed with the same relative exercise intensities for both age groups. That was necessary in order to know that the observed age-related differences in Experiment I were not due to the more strenuous relative exercise intensity for the elderly compared to the young. Therefore both maximal as well as many submaximal hopping intensities were measured during repetitive bilateral hopping on the ground. This protocol brought additional challenges in terms of balance control in the elderly as well as with higher reaction forces and shorter contact times as compared to sledge DJs. It was also in our interest to examine how muscle activity profiles and fascicle-tendon interaction are regulated when hopping intensity is changed from low to maximal levels both in young and in elderly subjects. Finally, the third study (Original paper IV) was a training intervention for the elderly in order to observe if training could modify the muscle activity profiles as well as fascicle and tendon behavior of the elderly to closer to that of young individuals. Instead of traditional strength training, the protocol included more coordination required hopping training that loads mainly the ankle joints.

4.2.1 Experiment 1 (Original paper I)

In Experiment 1 the subjects performed the maximal squat jump (SJ) and maximal DJs bilaterally on a special sledge apparatus (Kaneko, Komi & Aura 1984) with inclination angle of 18° from the horizontal position. In the DJs the dropping heights were 10 cm, 15 cm and 20 cm above standing height. The jumps were performed in randomized order. Five accepted trials were required for averaging. Before the measurements, the subjects performed a 10-min warm-up on a bicycle ergometer and several DJs to determine the lowest position of the sledge seat for each subject. In DJs the subjects were instructed to jump with as little knee bending as possible and this predetermined position was monitored and checked in each trial. In SJs the starting position was this lowest predetermined position and the instruction was to jump as high as possible without countermovement. Figure 3 shows the schematic presentation of the measurement setup and measured parameters.

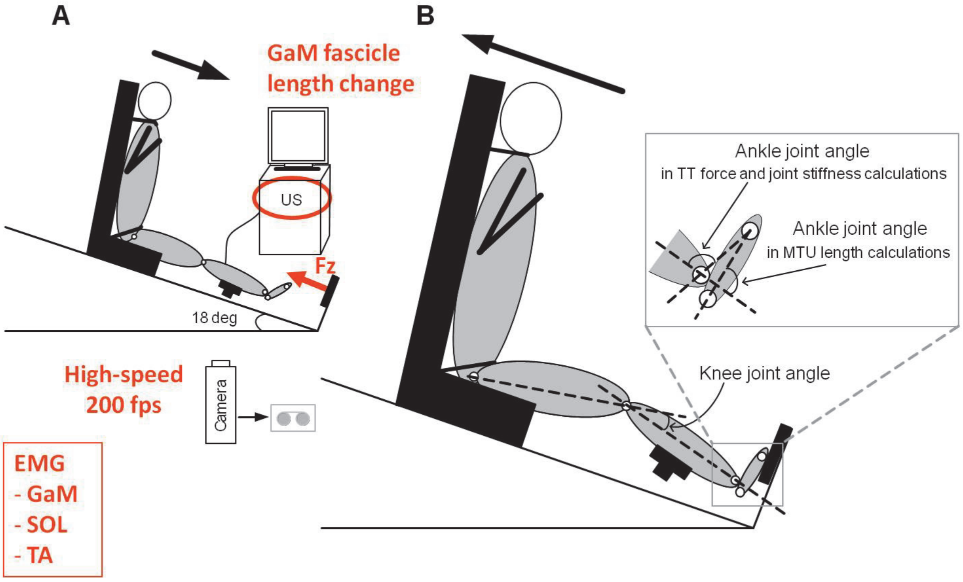

FIGURE 3 Schematic representation of the measurement setup and measured parameters in Experiment 1. The subject was seated in a sledge seat that slides on a rail. The correct dropping height was determined by a person standing behind the sledge and holding a sledge seat up.

4.2.2 Experiment 2 (Original papers II and III)

In Experiment 2 the subjects performed repetitive bilateral hopping on a force plate first with maximal effort and then with several submaximal hopping intensities. Different submaximal hopping intensities were determined from the peak vertical ground reaction force (Fz) (50 %, 65 %, 75 %, 90 % Fz, respectively). The hopping duration at each intensity level was 10 seconds. This gave usually 15 to 20 repeatable hops. In submaximal hopping the subjects received visual feedback about their Fz levels from the monitor in front of them. In order to examine the learning effect within the measurement session the maximal hopping was measured also at the end of the protocol. In each hopping trial the subjects were asked to achieve the required hopping intensity with approximately five hops and then to maintain the required level for at least another five hops. The instruction was to jump with a short contact time and with as little knee flexion as possible. Before the actual measurements, the subjects performed a 10-min warm-up on a bicycle ergometer followed by balance board exercises for three times 20 seconds and 10 heel raises on the edge of a stair. In addition, the subjects were allowed to familiarize themselves for jumping by performing a few submaximal hopping trials on the force plate. Figure 4 shows the measurement setup of Experiment 2. Kinetics (Fz) and kinematics (200 fps) were recorded during hopping together with EMG from gastrocnemius medialis (GaM), GaL, SOL and tibialis anterior (TA) muscles as well as ultrasound. Now we used two ultrasound probes in order to investigate the GaM fascicle and tendon length changes simultaneously. The data from this experiment is divided for Original papers II and III so that paper II includes the muscle activity data and paper III the ultrasound data.

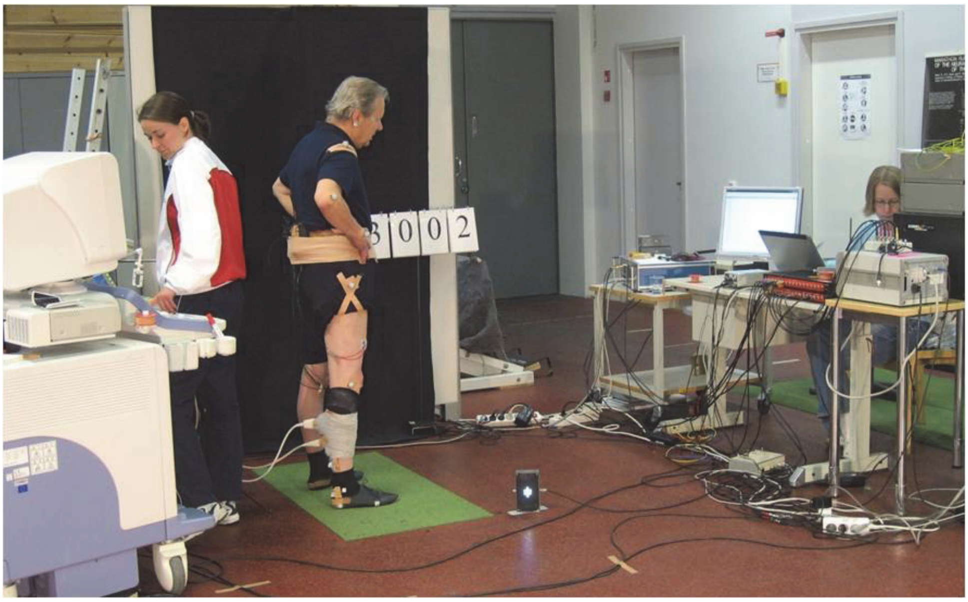

FIGURE 4 Picture of the measurement setup of Experiments 2 and 3. The subject is standing on a floor mounted force platform. The target vertical ground reaction forces during submaximal hopping are visible for subject from the screen in front of him.

4.2.3 Experiment 3 (Original paper IV)

The Experiment 3 was a training intervention for elderly individuals. The subjects were the same elderly men that participated in Experiment 2 and those measurements were used as baseline measurements for exercise intervention. Randomizing for training (ELDERLY TG) and control (ELDERLY CG) groups was performed with concealed envelopes executed by drawing lots blindly. Figure 5 summarizes the study design.

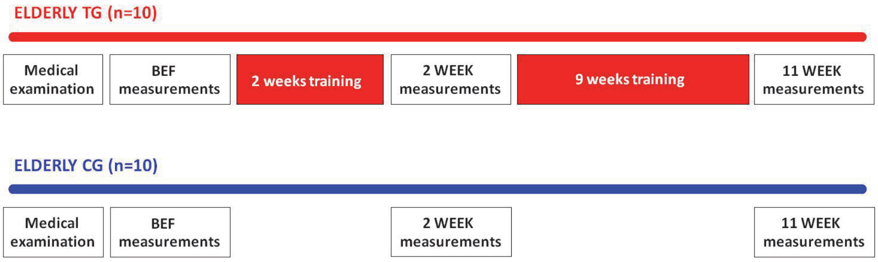

FIGURE 5 Study design of Experiment 3. See also a picture of the measurement setup in figure 4.

ELDERLY TG performed 11 weeks of supervised training three times per week, Monday, Wednesday and Friday, in an exercise laboratory. Training included 10 minutes warm-up on a bicycle ergometer with freely chosen intensity followed by balance board exercises for three times 20 seconds and 10 heel raises on the edge of a stair. That was followed by repetitive submaximal bilateral hopping on top of a force platform. One hopping trial lasted for 10 seconds followed by 1-5 minutes rest between trials. The subjects were instructed to rest until heart beat recovered to resting values. During hopping subjects got continuous visual feedback about their ground reaction force values from the monitor in front of them. Training volume was increased progressively by increasing the number of hopping trials as well as the intensity (table 3). Maximal hopping was measured every 2 weeks for proper adjustment of submaximal intensity levels. ELDERLY CG did not participate in training sessions and were asked to continue their normal daily routines. Both groups participated in measurements three times: before training as well as after 2 weeks and 11 weeks. These measurement time points are referred to as BEF, 2 WEEKS and 11 WEEKS, respectively, in Results and Discussion. The measurements were the same as in Experiment 2.

TABLE 3 Progression of the exercise intervention (adopted from Rantalainen et al. 2011).

Week	1	2	3	4	5	6	7	8	9	10	11
Sets * Intensity	4*75	2*75	1*75	1*75	1*75	2*75	2*75	2*75	2*75	2*75	2*75
(% of maximal GRF)		3*90	4*90	4*90	4*90	5*90	5*90	5*90	5*90	5*90	5*90

4.3 Data recording procedures

During DJs and hopping the reaction forces and EMG activity of selected muscles of the right leg were stored simultaneously to a personal computer through an AD converter (Power 1401, Cambridge Electronics Design Ltd, England). The sampling rate was 2 kHz in Experiment 1 and 1 kHz in

Experiments 2 and 3. In Experiment 1 also the sledge displacement and velocity of the sledge displacement were recorded. An electronic pulse was used to synchronize the kinetic, kinematic, EMG and ultrasonographic data.

4.3.1 Kinetics

In Experiment 1 the custom made force platform with strain gauges (University of Jyvaskyla, Finland, natural frequency 140 Hz, custom made amplifier: University of Jyvaskyla, Finland) was placed perpendicularly to the sliding surface of the sledge apparatus. In Experiments 2 and 3 the floor mounted piezoelectric force platform (Kistler® model 9281B, Kistler Instrumente AG, Winterthur, Switzerland, natural frequency ~600 Hz, Kistler amplifier model 9861A) was used. In Experiment 1 only the reaction force perpendicular to the movement plane of the sledge seat (Fz) was stored and in Experiments 2 and 3 all the 3D ground reaction force components (Fz, Fy, Fx) were recorded.

4.3.2 EMG

Bipolar miniature size surface electrodes (Blue Sensor N-00-S/25, diameter 6 mm; interelectrode distance 21 mm, Medicotest A/S, Olstykke, Denmark) were used for EMG recordings. The recording system was EISA in Experiment 1 (EISA 16-2, bandwidth 10 Hz to 1 kHz per 3 dB, Freiburg, Germany) and Glonner in Experiments 2 and 3 (Glonner electronic, Munich, Germany; bandwidth 20–640 Hz / -3 dB, input impedance >25 MΩ, common mode rejection ratio >90 dB). Before electrode placement the skin was shaved, abraded and cleaned with alcohol in order to secure an inter-electrode resistance value below 5 kΩ. The electrode placement followed the SENIAM guidelines (Hermens et al. 1999) as accurately as possible. Examined muscles were SOL, GaM and TA of the right leg. In addition to these the right leg GaL muscle was examined in Experiments 2 and 3.

4.3.3 Kinematics

All jumps were video-recorded with a high speed video camera at 200 fps (Peak Performance Inc, USA) from the right side perpendicular to the line of motion. Reflective markers were placed on trochanter major, on the approximate centre of rotation of the knee, on the lateral malleolus, on the lateral side of the heel and on the fifth metatarsal head. In addition to these points, in Experiments 2 and 3, the markers were placed also behind the foot on top of the calcaneus and on the calf under the ultrasound probes in order to be able to calculate GaM outer tendon length changes later on. The positions of markers in the lower leg are visible in figure 6. These points were then digitized automatically and filtered with the Butterworth fourth-order filter (cut-off frequency 8Hz in Experiment 1 and 10 Hz in Experiments 2 and 3) using Motus software (Peak Performance Inc, USA) in order to calculate knee and ankle joint angles and GaM MTU length changes.

4.3.4 Ultrasonography

In Experiment 1 the longitudinal images of GaM muscle fascicles of the right leg were recorded during all movements using a B-mode ultrasonography (SSD-5500, Aloka, Japan) with a 6 cm linear array probe (scanning frequency of 7.5 MHz). The images were obtained at 50 images s^{-1}. In Experiments 2 and 3 the same device and probe was used for right leg GaM MTJ examination. However, the recordings were now obtained at 96 images s^{-1}. In addition, in Experiments 2 and 3 the longitudinal images of GaM muscle fascicles of the right leg were recorded using another B-mode ultrasonography (α10; Aloka, Japan) with 4 cm linear array probe (scanning frequency of 13 MHz). These images were obtained at 204 images s^{-1}. The probes were fixed securely with a special support device made of polystyrene and strapped with elastic bandages. The superficial and deep aponeuroses and GaM fascicle as well as GaM MTJ were digitized and tracked manually from each image.

4.4 Analyses

In general, four to five DJs (I) or hops (II, III and IV) were averaged for each subject per intensity level in all other parameters except for the fascicle and tendon length in Experiments 2 and 3. The criteria for choosing the hops were as follows: 1) the force level matched the required intensity (Experiments 2 and 3), 2) balance during DJs or hopping was maintained and 3) the signals were free from noise. Due to the time-consuming and challenging analyzing process of the manual digitizing of fascicle and MTJ length, only one contact was analyzed per subject per intensity in Experiments 2 and 3.

4.4.1 EMG

In order to examine the EMG profiles, the EMG-signals in Experiment 1 were first full-wave rectified and then low-pass filtered at 50 Hz. In Experiments 2 and 3 the EMG-signals were first band-pass filtered (10–500 Hz), full-wave rectified and then low-pass filtered at 75 Hz (Butterworth type 4th-order digital filter). The filtered EMG signals were then integrated and averaged (aEMG) (Experiment 1) for the three functional phases of hopping: preactivity, braking and the subsequent push-off phases. In Experiments 2 and 3 the root-mean-square values (RMS) were calculated instead of aEMGs. The preactivity phase was defined as the 100 ms period preceding the ground contact (Komi et al. 1987). The transition from the braking to the push-off phase was determined in Experiment 1 while the sledge was at its lowest position and in Experiments 2 and 3 when the ankle joint angle was at its minimum (dorsiflexion).

In order to compare the EMG profiles over age groups (I and II), training groups (IV) or intensities (I and II), the EMG ratio of braking phase aEMG or RMS over push-off phase aEMG or RMS was calculated. High braking to push-off phase activity ratio resembles efficient jumping performance (Aura & Komi 1986; Kyröläinen, Takala & Komi 1998). In addition, when comparing the EMG values between the age groups in different functional phases of hopping, the aEMG values were normalized to maximal SJ push-off phase activity in Experiment 1 and RMS values relative to preactivity (100 ms) of maximal hopping in Experiment 2. In Experiment 3 the normalization was done relative to RMS values during isometric MVC in order to compare the measurement time points.

TA muscle serves as an antagonist to plantarflexors during the braking phase of DJs and hopping. Coactivity of the TA muscle during the braking phase was calculated by dividing TA aEMG or RMS in the braking phase by SOL, GaM or GaL aEMG or RMS in the braking phase (TA/SOL, TA/GaM and TA/GaL, respectively). In addition, in order to obtain the TA activity during the braking phase of DJs more accurately in Experiment 1, the braking phase was divided into two halves and TA aEMGs were calculated separately for those two halves. After that the activity relative to TA preactivity was defined (change in activity in relation to preactivity value). These calculations were done only for the two highest dropping conditions since the 10cm dropping height was so low that it was initiated with greater dorsiflexion by some subjects and therefore higher TA preactivity.

4.4.2 Muscle-tendon unit (MTU) length

The model of Grieve et al. (1978) was used to calculate GaM MTU length changes in Experiment 1 and the model of Hawkins & Hull (1990) in Experiments 2 and 3. In both of these models the GaM MTU lengths are estimated from the knee and ankle joint angles during jumping or hopping combined with the shank segment lengths during standing.

4.4.3 Tendinous tissue (TT) length (Experiment 1)

MTU data was re-sampled at 50 Hz to match the time scale of the ultrasound data. The length of the GaM tendinous tissue (TT) in Experiment 1 was calculated by subtracting the horizontal length part of the fascicle from the MTU length (Fukunaga et al. 2001a; Kurokawa, Fukunaga & Fukashiro 2001). It is important to note that in this model the TT length represents the summed length of the proximal and distal free tendons as well as aponeuroses.

$L_{TT} = L_{MTU} - L_{fa} * \cos\alpha$, where

L_{TT} = TT length,
L_{MTU} = MTU length,
L_{fa} = fascicle length
α = pennation angle between fascicle line and the deep aponeurosis

4.4.4 Outer tendon length (Experiments 2 and 3)

Digitized GaM MTJ data was interpolated to 200 Hz with Matlab to match the time scale of the kinematic data. The following equation was used to determine the GaM outer tendon length (L_{tendon}) changes during hopping in Experiments 2 and 3 (see also figure 6):

$$L_{tendon} = (X_{hopping} - X_{standing}) + (Y_{hopping} - Y_{standing}) + Z_{standing}, \text{ where}$$

X = Achilles tendon (AT) segment length marked with reflective markers on the calcaneus and under the ultrasound probes and analyzed from the kinematic data

Y = GaM muscle-tendon junction (MTJ) length analyzed from ultrasound data

Z = GaM tendon length from the calcaneus to MTJ measured with measuring tape during standing before any measurement devices were attached to the skin. The position of MTJ was determined with ultrasonography.

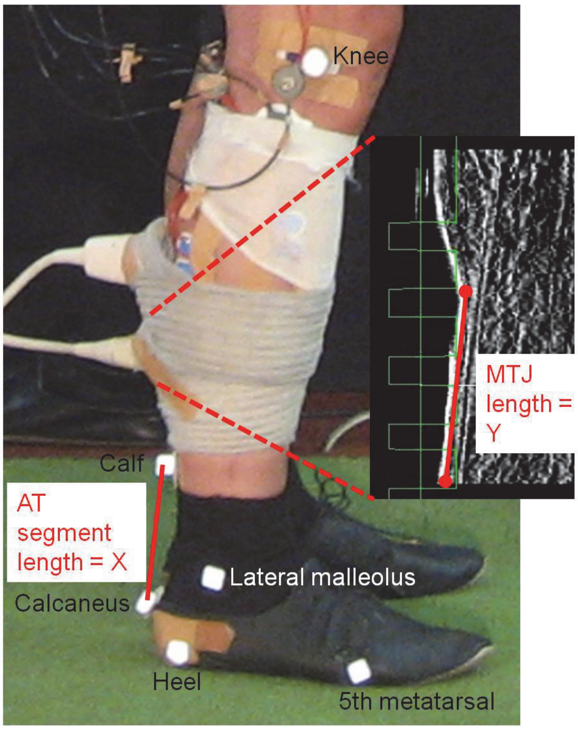

FIGURE 6 Reflective markers of lower leg and parameters needed in gasctrocnemius medialis (GaM) outer tendon length determination. X = Achilles tendon (AT) segment length marked with reflective markers on calcaneus and under the ultrasound probes and analyzed from the kinematic data. Y = GaM muscle-tendon junction (MTJ) length analyzed from ultrasound data.

It must be noted that the straight tendon model used in these studies does not take into account the tendon curvature and therefore the results concerning tendon length may be slightly underestimated and tendon elongation and strain overestimated compared to the curved tendon model (Stosic and Finni 2011).

4.4.5 Fascicle length

GaM fascicle length was defined as the length of the fascicle line between the superficial and deep aponeuroses and the pennation angle as the angle of the fascicle line and the deep aponeurosis. In Experiments 2 and 3 the fascicle length was analyzed with three points: insertion to deep and superficial aponeuroses and one point in between them in order to take into account the fascicle curvature visible in some subjects. When the fascicle length exceeded the analyzing window, the linear extrapolation of superficial aponeurosis and the fascicle line was performed in order to determine the fascicle insertion to superficial aponeurosis and therefore the fascicle length.

The reliability of the ultrasound method to estimate fascicle length, a coefficient of variation of about 3-5 %, has been reported in previous studies (Cronin et al. 2011b; Ishikawa, Pakaslahti & Komi 2007; Kurokawa, Fukunaga & Fukashiro 2001). In Experiment 3 the intra-class correlation coefficients (ICC) and 95 % confidence intervals (CI) were calculated for fascicle lengths measured at resting condition as well as at various points of maximal repetitive hopping for ELDERLY CG between BEF and 2 WEEKS. The values were the following: fascicle length measured at resting condition ICC of 0.831 (95 % CI of 0.457-0.955), at contact instant of 100% hopping ICC of 0.735 (95 % CI of 0.239-0.937), at transition point from braking to push-off phase ICC of 0.820 (95 % CI of 0.431-0.952) and at the take-off instant ICC of 0.876 (95 % CI of 0.579-0.968).

4.4.6 Joint moment, tendon force and tendon stiffness

In Experiment 1 the ankle joint moment (TQ) (Nm) of the right leg was estimated from the Fz and kinematics with the following equation (Kawakami et al. 2002):

$$TQ = Fz / 2 * L_1 * \cos (A_j\text{-}90), \text{ where}$$

Fz = vertical component of the ground reaction force (N)
L_1 = the length from the estimated center of ankle joint to the ball of the foot (measured for each subject) (m)
A_j = ankle joint angle (deg)

In Experiments 2 and 3 the ankle and knee joint moments (Nm) were calculated with inverse dynamics (Winter 1990). Masses of the foot and shank segments as well as the locations of center of masses and the radius of gyrations of the segments were determined from anthropometric data according to Dempster

(Winter 1990). It must be noted that these two methods, Kawakami et al. (2002) and inverse dynamics (Winter 1990) do not give similar ankle joint moment values and are not therefore comparable. Based on our observations during the analyzing process of the 2nd manuscript, the method of Kawakami et al. (2002) gives about twofold values to that of inverse dynamics.

Achilles tendon forces (ATF) (N) of the right leg were estimated by dividing the ankle joint moment over the Achilles tendon moment arm. Moment arm values were based on literature (Rugg et al. 1990) and the calculation took into account the change in moment arm length due to change in the ankle joint angle.

Average tendon stiffness (N/mm) during the braking phase of hopping was calculated by dividing the peak ATF (N) over the GaM tendon stretch from contact to peak length (mm) (Lichtwark & Wilson 2005b).

4.4.7 Joint stiffness

The quotient of change in ankle or knee joint moment generated by a the right leg (from contact to peak) divided by change in ankle or knee joint angle (from contact to min) (Kuitunen, Komi & Kyröläinen 2002) was used as a value of ankle joint stiffness (AJS) and knee joint stiffness (KJS), respectively, during the braking phase. It must be noted that the peak ankle joint moment and the min ankle joint angle do not necessarily occur at the same time. Originally, in Experiment 1, we calculated the AJS in two ways, with the min ankle joint angle and the peak ankle joint moment and also with the min ankle joint angle and corresponding moment. As the results were similar, it was decided to use the peak ankle joint moment for AJS calculations.

4.4.8 Reactive strength index (RSI)

RSI can be used to characterize the explosiveness of jumping and hopping, in other words, the ability to create high forces in minimal time (Flanagan, Ebben & Jensen 2008). RSI was first introduced by Young (1995) and is calculated as flight time divided by contact time. In the present studies RSI was calculated in Experiments 2 and 3 during repetitive hopping in order to compare YOUNG and ELDERLY as well as the effects of training on the explosiveness of hopping.

4.5 Statistics

All statistical analyses were performed with the SPSS^{TM} program (SPSS Inc, USA). The results are presented as means and standard deviations (SD). Differences in background information between age or training groups were tested using a t-test for independent samples. Normality of the parameters was tested using the Shapiro-Wilk test and the equality of variances with Levene's test. If either of these tests failed, the non-parametric Mann-Whitney U test was used. The ANOVA for repeated measurements on two factors was used to test the main effects of exercise intensity and age group or training period and training group as well as the interactions on different parameters. When applicable, the ANOVA for repeated measurements on one factor and post hoc bonferroni were used to determine the significant differences between exercise intensities or training time points separately in the young and the elderly or in the training and control groups. In addition, differences between in the young and elderly or training and control groups at different exercise intensity levels were tested using a t-test for independent samples. The same procedures with normality and homogenity of variance were followed as with background information parameters. Relationships between variables were investigated using Pearson's product-moment correlation coefficient. The level of statistical significance was set at $p < 0.05$.

5 RESULTS

This chapter gives the overview of the results from the three experiments. For more details the Original papers I-IV should be consulted.

5.1 Rebound height, contact time and peak Fz

As expected, the rebound heights in ELDERLY were considerably lower and contact times longer as compared to YOUNG. ELDERLY jumped 28.2 %, 22.7 ± 1.3 % and 76.6 ± 11.5 lower than YOUNG in maximal SJs on a sledge, in sledge DJs with absolutely similar exercise intensities and in repetitive hopping with relatively similar intensities, respectively (figure 7). Contact times in ELDERLY, as compared to YOUNG, were 26.3 %, 22.8 ± 2.3 and 19.6 ± 6.4 % longer during SJ, DJs and repetitive hopping, respectively (figure 7).

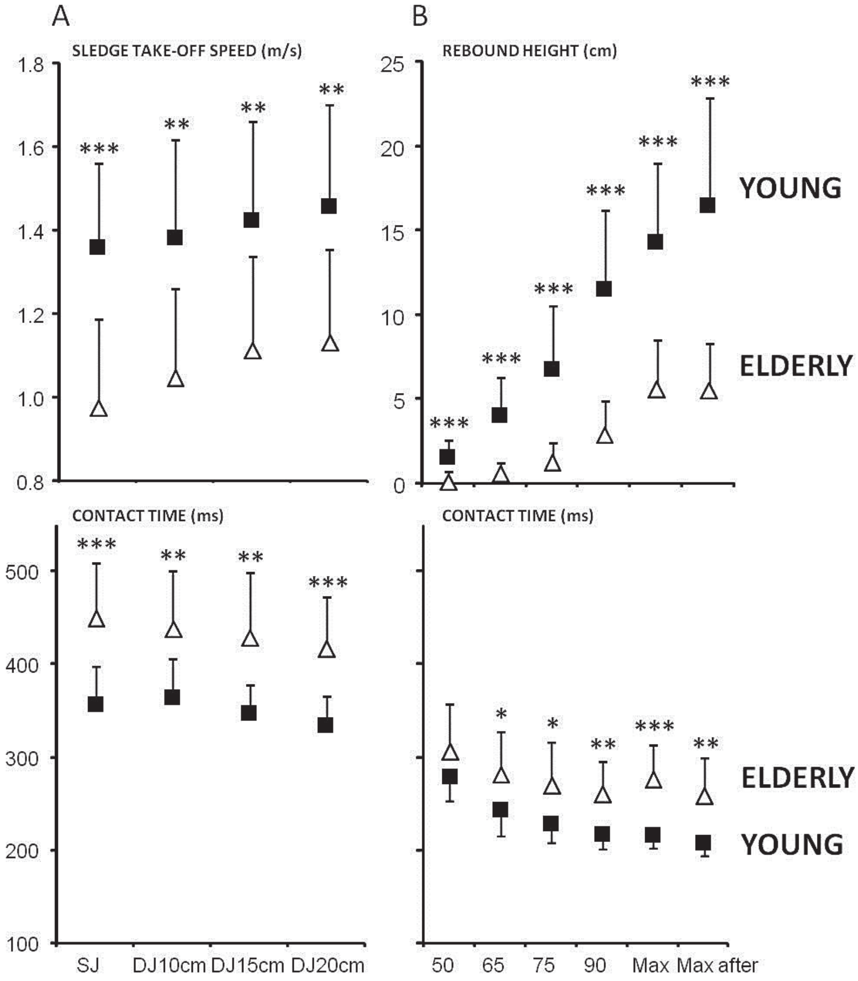

FIGURE 7 Rebound heights and contact times in (A) maximal sledge jumps: squat jump (SJ) and drop jumps (DJ) from different dropping heights as well as in (B) repetitive hopping with different intensities in YOUNG and in ELDERLY. *, ** and ***: significant difference between YOUNG and ELDERLY ($p<0.05$, $p<0.01$ and $p<0.001$, respectively).

In DJs only the push-off phase time was longer in ELDERLY ($p<0.001$) but in repetitive hopping both the braking phase time as well as the push-off phase time were longer (both $p<0.01$). Rebound height increased and contact time decreased with an increase in exercise intensity in both age groups (figure 7).

Hopping training was effective in increasing the rebound height in ELDERLY TG from 2 WEEKS to 11 WEEKS ($p<0.01$) and decreasing the contact time already in 2 WEEKS ($p<0.05$) (figure 8).

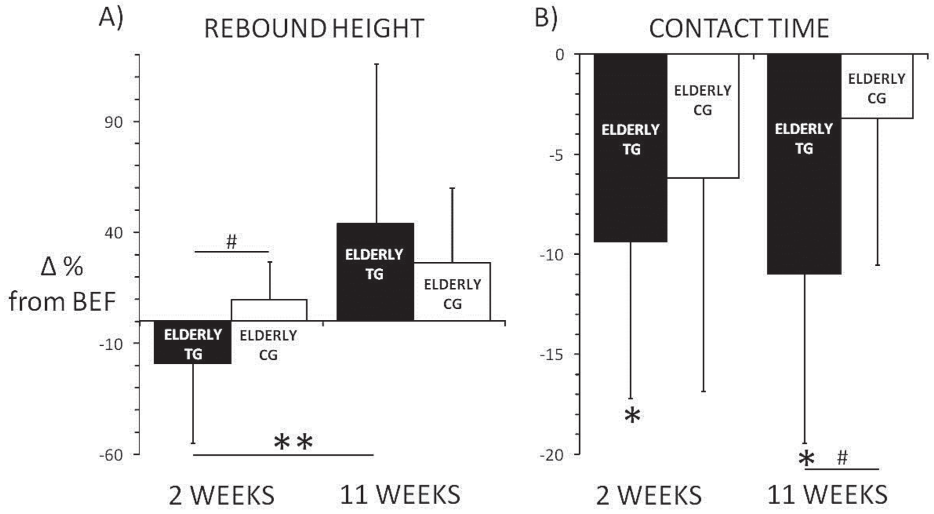

FIGURE 8 Changes (%) from BEF values in (A) rebound height and (B) contact time of maximal repetitive hopping. *; significant training effect (p<0.05). #; significant group effect (p<0.05).

In repetitive hopping the RSI was 60.3 ± 9.8 % lower in ELDERLY as compared to YOUNG (p<0.001) and increased in ELDERLY TG on average 30.2 ± 10.4 % with 11 weeks of hopping training (figure 9).

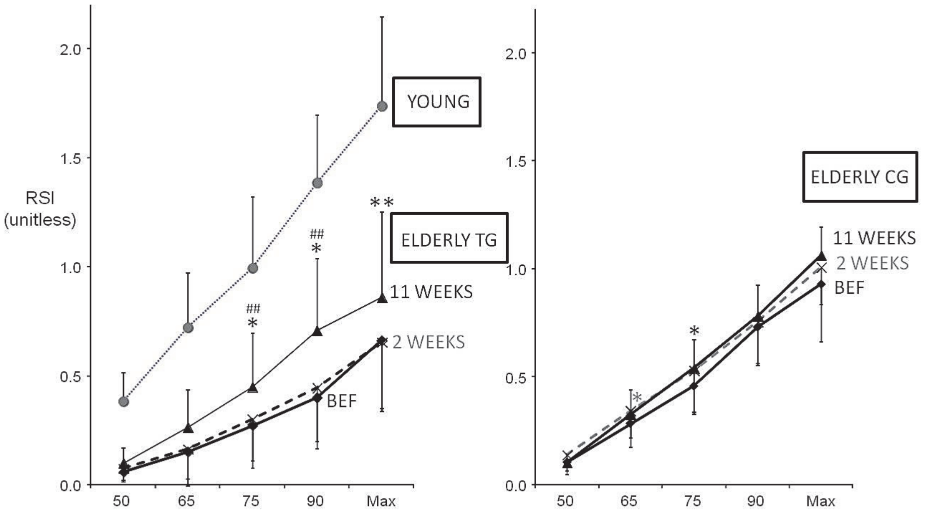

FIGURE 9 Reactive strength index (RSI) (flight time divided by contact time) at different intensity levels in YOUNG as well as in ELDERLY TG and ELDERLY CG at BEF, 2 WEEKS and 11 WEEKS. * and **; significantly different from BEF (p<0.05 and p<0.01, respectively). ##; significantly different from 2 WEEKS (p<0.01).

Although the absolute dropping heights in Experiment I were the same in both age groups, the relative peak Fz (per body weight) during DJs were on average 25.0 ± 1.8 % lower in ELDERLY as compared to YOUNG (figure 10). The same was true also in repetitive hopping (32 %) (figure 10). Peak forces were 2-3 times higher during maximal repetitive hopping on the ground as compared to sledge DJs. Peak Fz increased from SJ to DJs ($p<0.001$ in both groups) and with increasing dropping height (YOUNG $p<0.01$, ELDERLY $p<0.05$) and hopping intensity (both age groups $p<0.001$). After hopping training peak Fz increased in ELDERLY TG from BEF to 11 WEEKS ($p<0.05$) and from 2 WEEKS to 11 WEEKS ($p<0.01$) but did not change in ELDERLY CG (figure 11).

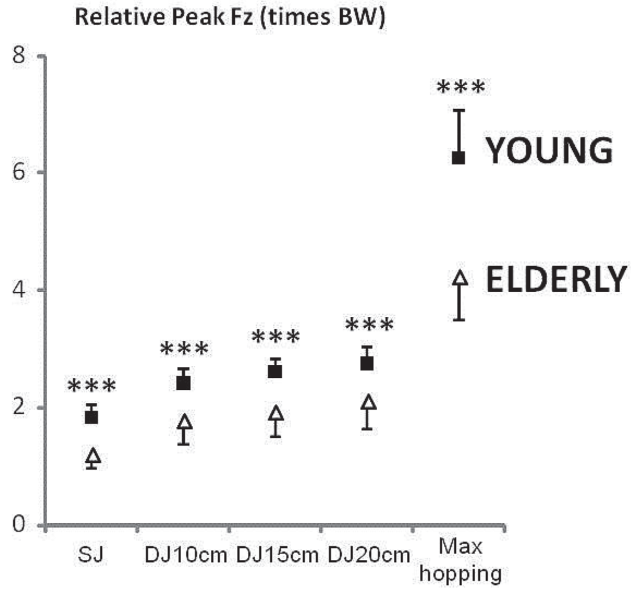

FIGURE 10 Peak vertical ground reaction force (Fz) relative to body weight (BW) in SJ, DJs from different dropping heights and in maximal repetitive hopping in YOUNG and in ELDERLY. ***: significant difference between YOUNG and ELDERLY ($p<0.001$).

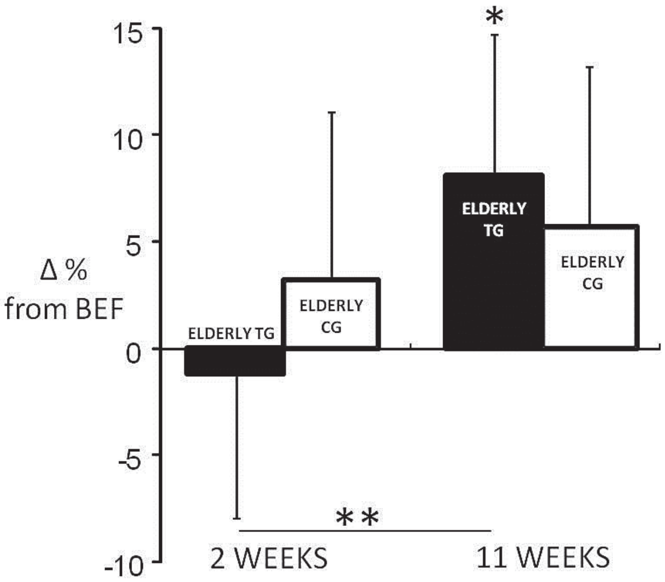

FIGURE 11 Change (%) from BEF values in peak vertical ground reaction force (Fz) of maximal hopping in ELDERLY TG and ELDERLY CG. *; significant training effect ($p<0.05$).

5.2 Kinematics

There were some age-related kinematic modifications during hopping. The angle-time curves of knee and ankle joint angles during the highest DJ condition (DJ20cm) and maximal repetitive hopping are presented in figure 12 separately for YOUNG and ELDERLY. It must be noted that the minimum ankle and knee joint angles at the end of the braking phase were always the same for both age groups.

First of all, ELDERLY had more flexed knees at the instant of ground contact during repetitive hopping as compared to YOUNG ($p<0.01$) (figure 13A). Also the ankles were more flexed (dorsiflexion) in ELDERLY from low to moderate hopping intensities (50 %-75 %) but not during maximal hopping. Thereafter, at take-off ELDERLY had more flexed knees ($p<0.01$) and ankles ($p<0.01$) at all hopping intensities.

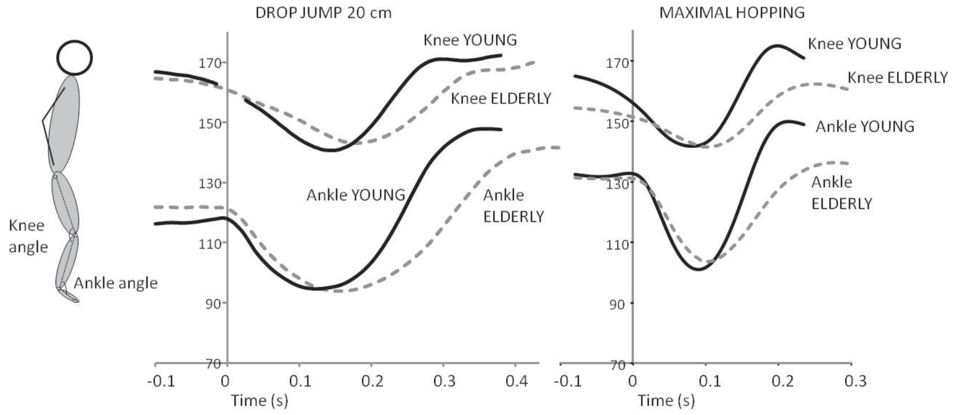

FIGURE 12 Ankle and knee joint angles in DJ20cm and in maximal hopping in YOUNG and in ELDERLY.

Knee joint angle at the instant of ground contact decreased both in YOUNG ($p<0.05$) and in ELDERLY ($p<0.001$) with increasing hopping intensity (figure 13A). Ankle joint angle at the contact instant increased (plantarflexion) with intensity in ELDERLY ($p<0.01$) but not in YOUNG. Knee and ankle joint angles at the lowest position (at the end of the braking phase) decreased and the angles at take-off increased with increasing intensity both in YOUNG and ELDERLY. Take-off knee and ankle angles were larger in maximal hopping as compared to submaximal hopping in both age groups.

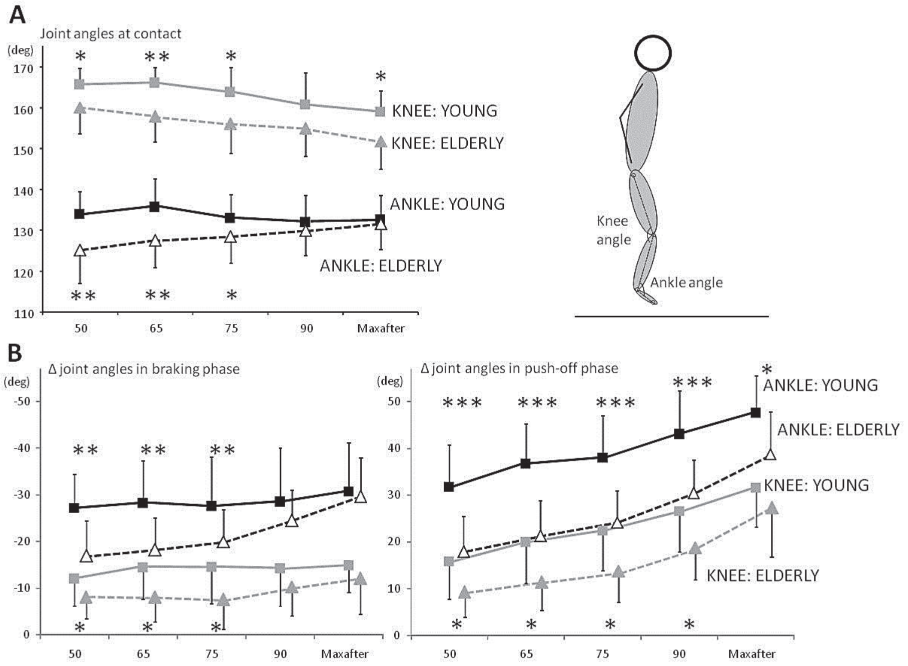

FIGURE 13 Knee and ankle joint angles (A) at the contact instant of repetitive hopping with different intensities and (B) joint displacement amplitudes in the braking and push-off phases. *, ** and ***: significant difference between YOUNG and ELDERLY ($p<0.05$, $p<0.01$ and $p<0.001$, respectively). Joint displacement amplitudes in the braking phase were calculated from the angle at the instant of ground contact to the minimum angle and in the push-off phase from the minimum angle to the angle at take-off. 180 deg indicates full knee extension and ankle plantarflexion. An increase in ankle angle indicates plantarflexion and a decrease in ankle angle indicates dorsiflexion. In knee angle an increase in value indicates knee extension and a decrease in value indicates knee flexion.

Joint displacement amplitudes during the braking and push-off phases of repetitive hopping are summarized in figure 13B. Knee joint displacement in the braking phase did not change in either group with hopping intensity. In the ankle joint, however, it increased clearly in the braking phase in ELDERLY ($p<0.001$) as a function of increase in exercise intensity. This was not observed in YOUNG. In the push-off phase both the ankle and knee joint displacements increased with increasing intensity in YOUNG ($p<0.01$) and ELDERLY ($p<0.001$).

Hopping training in the elderly caused only minor modifications to kinematics (figure 14). Ankle and knee joint angles at take-off instant increased in ELDERLY TG from 2 WEEKS to 11 WEEKS (both $p<0.05$) (figure 14). In addition knee and ankle angle amplitudes during the braking phase (both $p<0.05$) as well as ankle angle amplitude during the push-off phase ($p<0.01$) decreased in ELDERLY TG from BEF to 2 WEEKS.

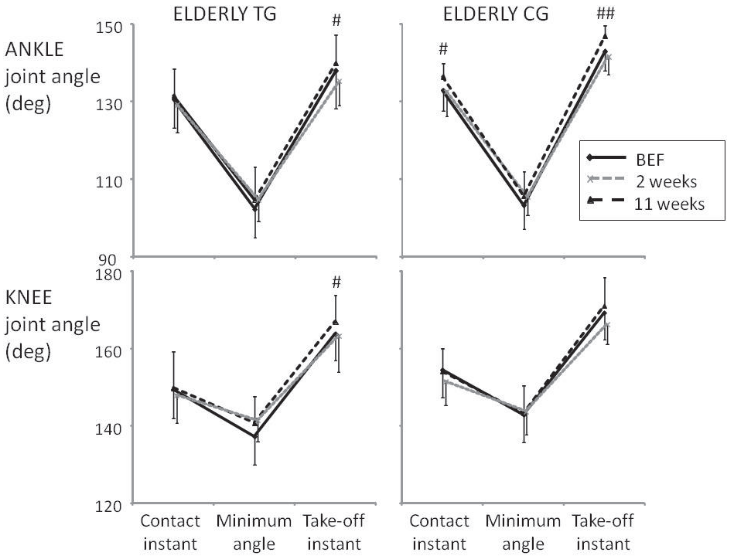

FIGURE 14 Ankle and knee joint angles in ELDERLY TG and ELDERLY CG at the instant of ground contact, minimum angle and angle at take-off instant at baseline (BEF) as well as at 2 WEEKS and 11 WEEKS measurement points at maximal hopping intensity. # and ##; 11 WEEKS significantly different from 2 WEEKS ($p<0.05$ and $p<0.01$, respectively).

5.3 Joint stiffness

ELDERLY had lower AJS during the braking phase of DJs ($p<0.05$) and high intensity (90 % and maximal) repetitive hopping as compared to YOUNG (figure 15). In YOUNG, AJS increased from 50 % intensity to higher hopping intensities ($p<0.05$). In ELDERLY, AJS did not change with increasing intensity. Already short term hopping training increased AJS in maximal hopping intensity in ELDERLY TG (figure 16). There were no training effects in AJS in submaximal level.

Knee joint stiffness increased with increasing hopping intensity both in YOUNG ($p<0.01$) and in ELDERLY ($p<0.05$) (figure 15). However, there were no differences in knee joint stiffness values between the age groups at any studied hopping intensity. In addition, hopping training did not have any effect on knee joint stiffness values.

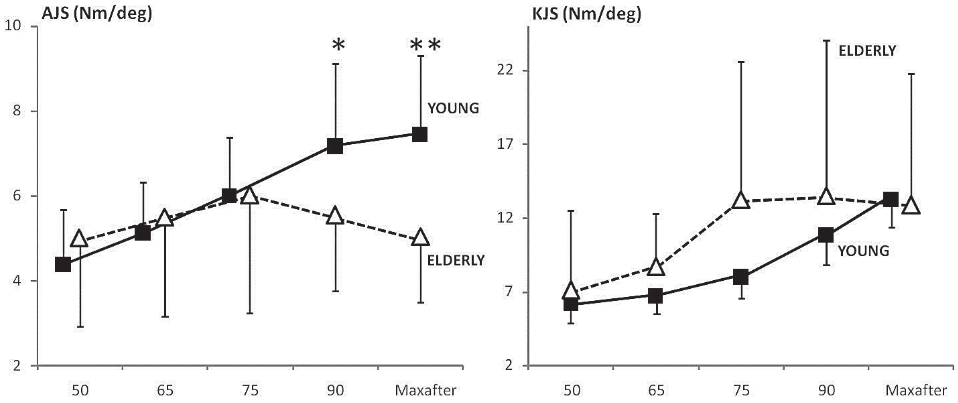

FIGURE 15 Ankle joint stiffness (AJS) and knee joint stiffness (KJS) in repetitive hopping with different intensities in YOUNG and in ELDERLY. *, **: significant difference between YOUNG and ELDERLY (p<0.05, p<0.01, respectively).

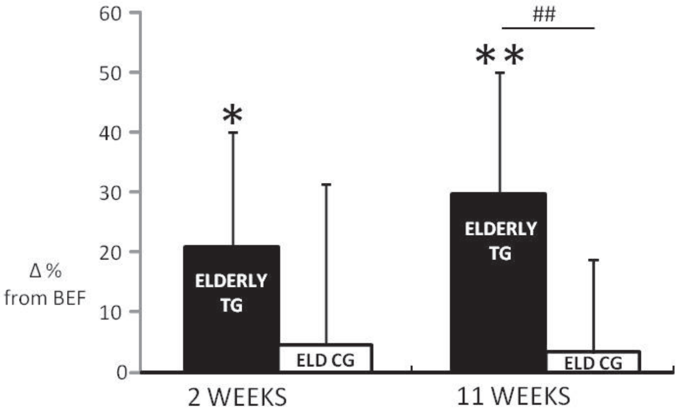

FIGURE 16 Change (%) from BEF values in ankle joint stiffness (AJS) during the braking phase of maximal repetitive hopping. AJS was calculated as the change in ankle joint moment (from contact to peak) generated by the right leg divided by change in ankle joint angle (from contact to min). * and **; significant training effect (p<0.05 and p<0.01, respectively). ##; significant group effect (p<0.01).

5.4 EMG

The EMG-time curves of SOL, GaM and TA muscles during DJs in YOUNG and in ELDERLY are shown in figure 17. Clear preactivity of agonist muscles was followed by increasing activity in the braking phase and by decreasing activity towards the late push-off in both age groups. The activity curves during repetitive hopping were very similar to those during DJs.

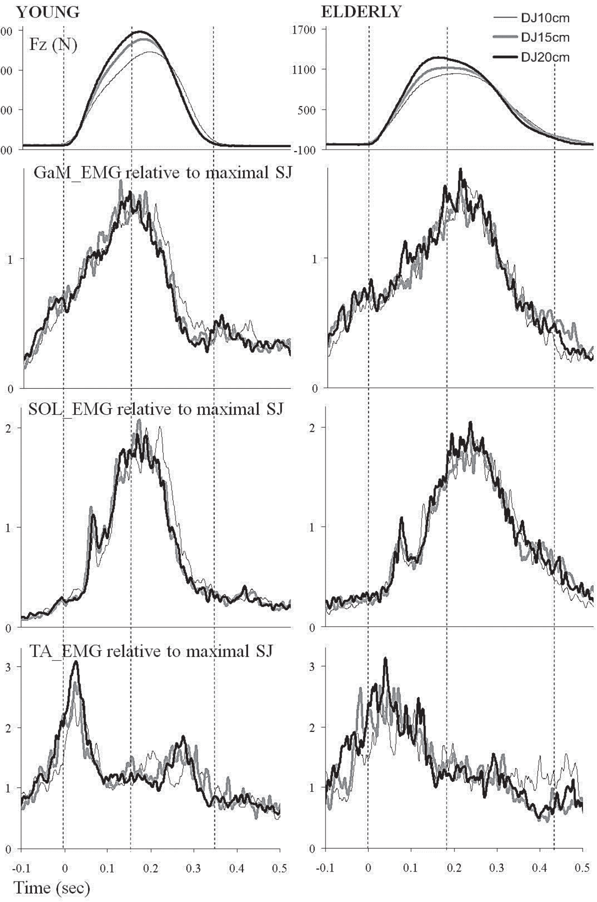

FIGURE 17 Averaged force-time and EMG-time curves for YOUNG and ELDERLY in different DJ conditions. Vertical lines denote the contact instant, the transition point from the braking to push-off phase and the take-off instant. Fz is vertical ground reaction force. EMG is normalized to maximal squat jump (SJ) push-off phase average EMG (aEMG).

There were some differences in relative EMG amplitudes between the age groups in different functional phases of hopping. YOUNG activated their GaM muscles more in the braking phase than ELDERLY during DJs ($p<0.05$) as well as during hopping ($p<0.05$). Thereafter, ELDERLY had higher activity in the push-off phase in GaM and SOL muscles in DJs as compared to YOUNG (both $p<0.05$). The relative EMG amplitudes in YOUNG and in ELDRLY in different functional phases of repetitive hopping with different intensities are presented in figure 18.

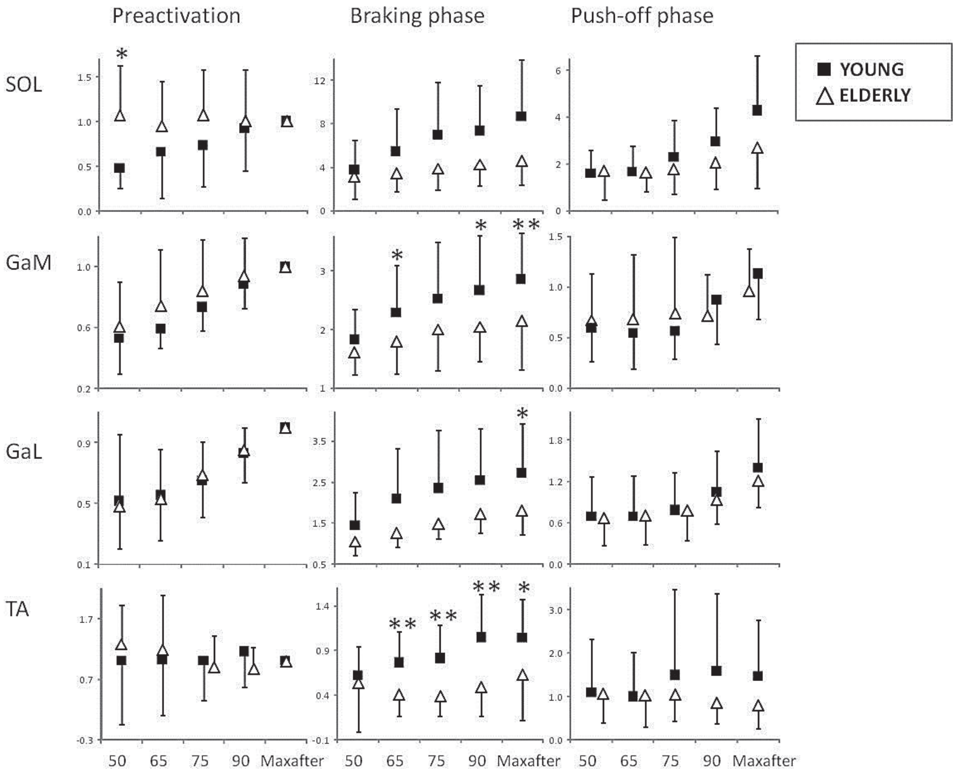

FIGURE 18 Relative EMG activity (to preactivity of maximal hopping = 1) of plantarflexors and antagonist TA muscle in different functional phases of hopping. Different hopping intensities are on the X-axis. Preactivity was defined as 100 ms preceding the ground contact. SOL, soleus; GaM, gastrocnemius medialis; GaL, gastrolateralis; TA, tibialis anterior. 1 = preactivity (100 ms) in maximal hopping. Please note that for better visual inspection the vertical axes are not scaled the same way in all cases. *, **: significant difference between YOUNG and ELDERLY ($p<0.05$, $p<0.01$, respectively).

5.4.1 EMG ratio

YOUNG and ELDERLY showed different agonist activity profiles during DJs and hopping. EMG ratio of braking phase activity over push-off phase activity can be used to describe the efficiency of hopping with higher values indicating high efficiency (Bosco et al. 1982; Finni, Komi & Lepola 2001; Kuitunen et al. 2007; Kyröläinen, Takala & Komi 1998). First of all, when sledge DJs and repetitive short contact hopping on the ground were compared, significantly higher values were found during repetitive hopping. In addition, the EMG ratio was significantly lower in ELDERLY as compared to YOUNG especially in gastrocnemius muscles and especially in DJs (figure 19). In both age groups the EMG ratio showed an inverse parabolic shape with hopping intensity, first increasing from 50 % intensity until 65 % or 75 % intensity and then decreasing towards maximal hopping, indicating that the highest efficiencies are achieved at intermediate hopping intensities.

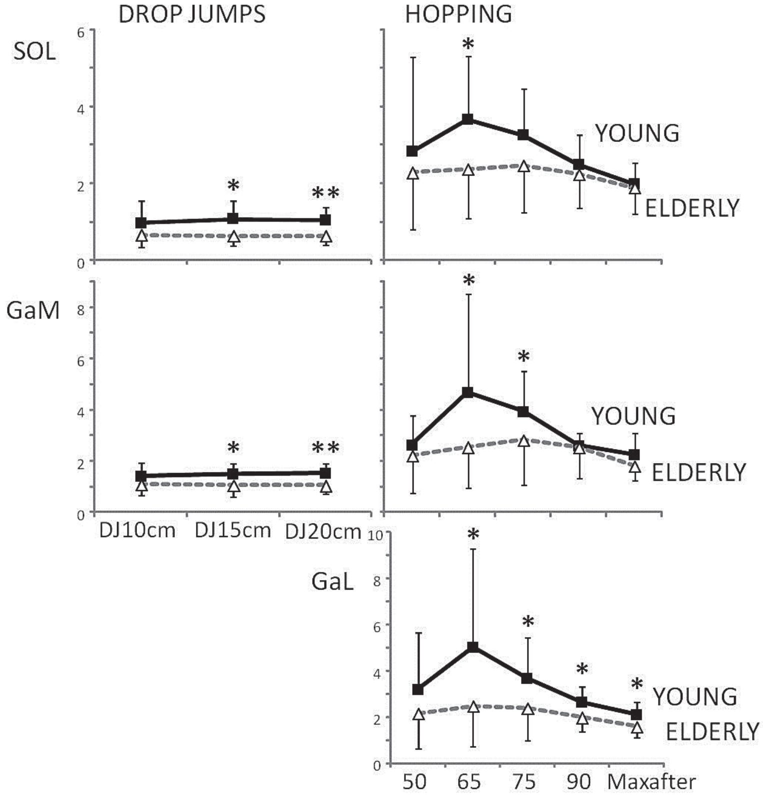

FIGURE 19 EMG ratio of braking phase aEMG (DJs) or RMS (hopping) over push off – phase aEMG or RMS in DJs and repetitive hopping with different intensities in YOUNG and in ELDERLY. *, **: significant difference between YOUNG and ELDERLY ($p<0.05$, $p<0.01$, respectively).

With hopping training in the elderly the EMG ratio of all agonist muscles increased in ELDERLY TG from BEF to 2 WEEKS at maximal hopping intensity indicating increasing hopping efficiency. For simplicity, these changes are presented in figure 20 only for the GaM muscle. However, the EMG ratio decreased again in ELDERLY TG from 2 WEEKS to 11 WEEKS in GaM ($p<0.05$) and in SOL and GaL the trends were similar although not statistically significant (SOL $p = 0.084$ and GaL $p = 0.111$, ns).

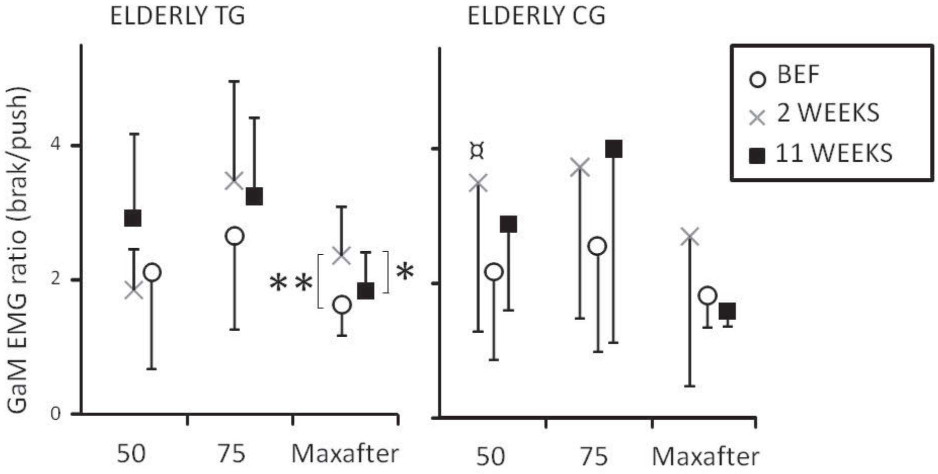

FIGURE 20 GaM muscle EMG ratio of braking phase RMS over push off –phase RMS in repetitive hopping with different intensities at BEF, 2 WEEKS and 11 WEEKS in ELDERLY TG and ELDERLY CG. * and **: significant training effect ($p<0.05$ and $p<0.01$, respectively). ¤: significant difference between training and control groups ($p<0.05$).

5.4.2 Coactivity

TA muscle serves as an antagonist to plantarflexors during the contact phase of DJs and hopping. In DJs the TA activity decreased in YOUNG rapidly after the contact instant but in ELDERLY the activity remained higher during the braking phase (figure 17). Therefore ELDERLY had higher TA activity than YOUNG during the first half of the braking phase in DJs with the same absolute exercise intensities ($p<0.05$). Also, when coactivity during the whole braking phase of DJs was calculated for both age groups, ELDERLY showed higher values in TA/SOL activity ($p<0.05$) and in TA/GaM coactivity the trend was similar ($p = 0.13$). During repetitive hopping, however, with the same relative intensities the TA activity during the braking phase was very minimal also in ELDERLY and there were no differences between the age groups in coactivity values of any examined muscle pairs. In addition, coactivity did not change with hopping intensity or with hopping training.

5.5 Muscle architecture at rest

The architectural characteristics of the GaM muscle at rest during relaxed upright standing position are summarized in table 4. In the whole study population (n = 21 YOUNG, n = 37 ELDERLY) ELDERLY had 5.6 % (0.33 cm) shorter GaM fascicle length and 5.1 % (1.0 deg) lower pennation angle as compared to YOUNG but the differences were not statistically significant ($p = 0.20$ and $p = 0.22$, respectively).

TABLE 4 Muscle architectural characteristics in YOUNG and in ELDERLY as well as in ELDERLY TG and ELDERLY CG. Fascicle length and pennation angle are measured at rest during a relaxed upright standing position. #) GaM tendinous tissue (TT) stiffness is the combined stiffness of GaM tendons and aponeuroses and is measured during the braking phase of DJ20cm as peak ATF divided by GaM TT stretch from contact to peak length. *) GaM outer tendon stiffness is calculated during the braking phase of maximal repetitive hopping as peak ATF divided by GaM tendon stretch from contact to peak length.

	Experiment 1 (Original paper I)			Experiment 2 (Original paper III)				Experiment 3 (Original paper IV)			
	YOUNG (n=12)	ELDERLY (n=13)	*P value*	YOUNG (n=9)	ELDERLY (n=24)	*P value*		Baseline	2 WEEKS	*11 WEEKS*	*P value (Base - 11 W)*
GaM fascicle length (cm)	5.6 ± 1.0	5.3 ± 1.0	*0.43*	5.9 ± 0.8	5.5 ± 0.9	*0.22*	ELDERLY TG	5.1 ± 1.1	5.1 ± 0.9	5.2 ± 0.9	*0.55*
							ELDERLY CG	5.8 ± 0.7	5.7 ± 1.0	5.8 ± 1.0	*0.96*
GaM pennation angle (deg)	19.5 ± 2.9	18.7 ± 3.2	*0.52*	20.7 ± 2.0	19.1 ± 3.2	*0.20*	ELDERLY TG	19.6 ± 4.5	20.2 ± 3.7	20.7 ± 2.0	*0.27*
							ELDERLY CG	19.5 ± 2.0	19.6 ± 1.6	19.0 ± 1.8	*0.81*
GaM outer tendon length (cm)	Not measured			19.4 ± 2.0	19.6 ± 2.5	*0.82*	ELDERLY TG	20.2 ± 3.0	20.3 ± 3.2	21.2 ± 2.3	*0.12*
							ELDERLY CG	19.2 ± 2.1	19.6 ± 2.1	20.4 ± 1.8	*0.12*
GaM outer tendon length / shank length (%)	Not measured			44.4 ± 3.1	46.9 ± 4.8	*0.24*	ELDERLY TG	48.8 ± 5.2	49.1 ± 5.3	51.3 ± 2.8	*0.14*
							ELDERLY CG	45.6 ± 4.8	46.5 ± 4.4	48.4 ± 3.4	*0.10*
GaM TT stiffness (N/mm) #)	313 ± 113	218 ± 79	***0.03***	Not measured			Not measured				
GaM outer tendon stiffness (N/mm) *)	Not measured			298 ± 57	200 ± 81	***0.005***	ELDERLY TG	210 ± 81	217 ± 111	219 ± 65	*0.58*
							ELDERLY CG	190 ± 89	224 ± 81	199 ± 56	*0.71*

5.6 Mechanical behavior of GaM

The length-time curves of GaM MTU, TT /outer tendon and fascicle during DJ15cm and repetitive hopping with different intensities are presented in figure 21 separately for YOUNG and ELDERLY. In general, the braking phase of DJs and hopping were characterized by stretching of MTU and tendon whereas the fascicles were shortening or did not change length. Then in the push-off phase MTU as well as tendon and fascicles shortened, although fascicle shortening was minimal compared to that of MTU and tendon. The age comparison showed some differences in this behavior especially at fascicle level in the braking phase. The next paragraphs will highlight the major age specific differences in different levels during DJs and hopping as well as training induced changes in muscle mechanics.

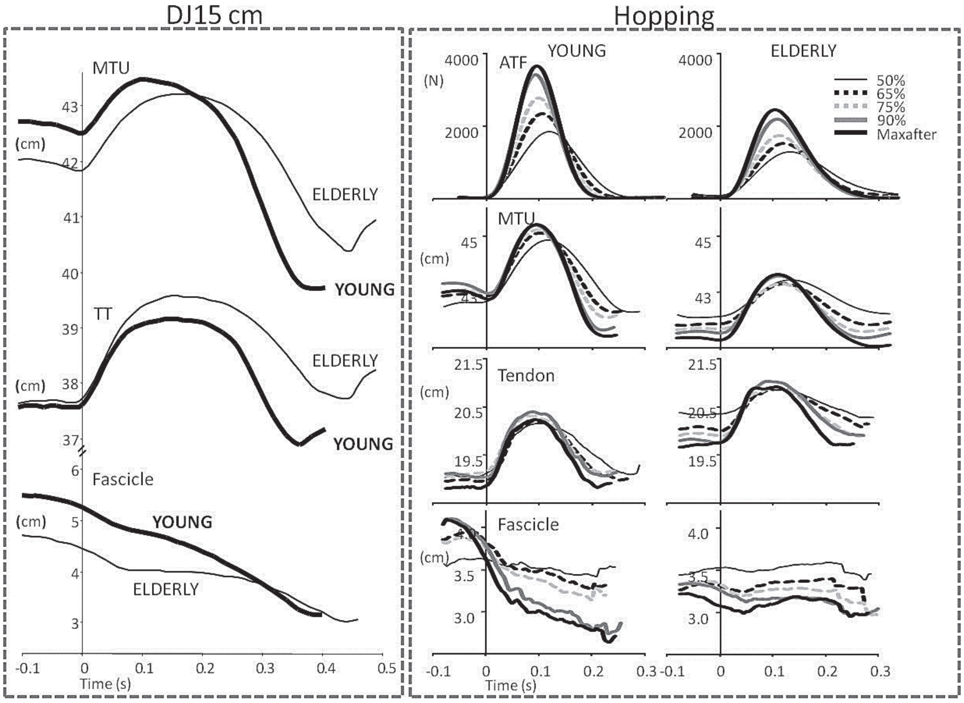

FIGURE 21 The length-time curves of GaM muscle-tendon unit (MTU), tendinous tissue (TT) (DJ15cm) or outer tendon (hopping) as well as fascicle in YOUNG and in ELDERLY during DJ15cm and different intensity hopping. In addition, the Achilles tendon force-time curves are presented during repetitive hopping with different intensities. Time 0 is the contact instant.

5.6.1 MTU and Tendon

GaM MTU length at the instant of ground contact was shorter in ELDERLY as compared to YOUNG only in maximal repetitive hopping ($p<0.05$) although the similar trends were observed in submaximal level and in DJs (figure 21). The absolute stretching amplitudes of MTU and TT did not show significant differences between the age groups in DJs or during high intensity hopping (90 % and max). Only during low intensity hopping the MTU stretch was lower in ELDERLY ($p<0.01$ at 50 % and 65 % intensity, $p<0.05$ at 75 % intensity). Similarly, the GaM outer tendon stretch was lower in ELDERLY at 50 % intensity repetitive hopping ($p<0.05$) but there were no differences between the age groups at higher intensities or in TT stretch during DJs (figure 22A).

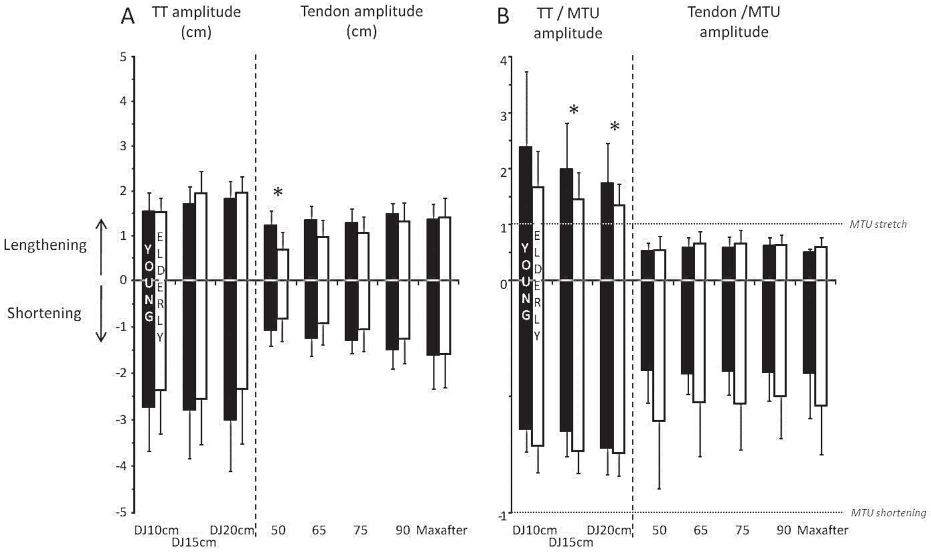

FIGURE 22 (A) GaM tendinos tissue (TT) or outer tendon stretching and shortening amplitudes during DJs and hopping with different intensities in YOUNG and in ELDERLY. (B) GaM tendinos tissue (TT) or outer tendon stretch relative to muscle-tendon unit (MTU) stretch during DJs and hopping with different intensities in YOUNG and in ELDERLY. Stretching amplitude was calculated from contact to the peak length and in the shortening amplitude from peak length to take-off. *: significant difference between YOUNG and ELDERLY ($p<0.05$).

During DJs the lengthening of MTU and TT in the braking phase increased with increasing dropping height both in YOUNG (MTU $p<0.01$, TT $p<0.05$) and in ELDERLY (MTU $p<0.001$, TT $p<0.01$). However, during hopping the MTU and tendon stretch in the braking phase increased with hopping intensity only in ELDERLY (MTU $p<0.001$, tendon $p<0.01$). Tendon strain during maximal repetitive hopping was 7.6 ± 2.0 % in YOUNG and 7.1 ± 2.3 % in ELDERLY with no significant differences between the age groups.

In the push-off phase there were no significant differences in shortening amplitudes of either MTU or TT between the age groups in DJs, but in repetitive hopping the MTU shortening was clearly less in ELDERLY at all hopping intensities ($p<0.001$). However, GaM outer tendon shortening amplitudes did not differ between the age groups in hopping either (figure 22A). In DJs the recoil amplitude of TT increased with increasing dropping height in YOUNG ($p<0.05$) but not in ELDERLY. In contrast, in repetitive hopping the tendon shortening amplitude increased in ELDERLY with increasing intensity ($p<0.01$) but did not change in YOUNG.

When GaM TT or outer tendon stretch was calculated in relation to MTU stretch (TT/MTU and tendon/MTU, respectively), ELDERLY showed lower values in DJs ($p<0.05$) but not during repetitive hopping (figure 22B). It must be remembered here that in DJs the whole GaM combined TT length changes were estimated whereas in repetitive hopping the outer tendon was examined. TT/MTU and outer tendon/MTU shortening ratios were also similar in two age group although there was a tendency for higher values in ELDERLY ($p = 0.07$-0.19). In the whole study population GaM outer tendon stretching accounted on average for 60.0 ± 20.5 % of the total MTU stretching amplitude. Tendon shortening accounted for 50.1 ± 16.6 % from the MTU shortening.

Training induced changes on muscle mechanics in different muscle levels in ELDERLY are presented in figures 23, 24 and 25. First of all, the peak ATF increased 24.3 ± 19.0 % in ELDERLY TG from 2 WEEKS to 11 WEEKS ($p<0.01$). In addition, the general trend was that, due to training, the MTU and tendon stretching and shortening amplitudes first decreased in ELDERLY TG from BEF to 2 WEEKS and then increased again from 2 WEEKS to 11 WEEKS (figure 24). Training did not have any effect on tendon / MTU stretching or shortening ratios.

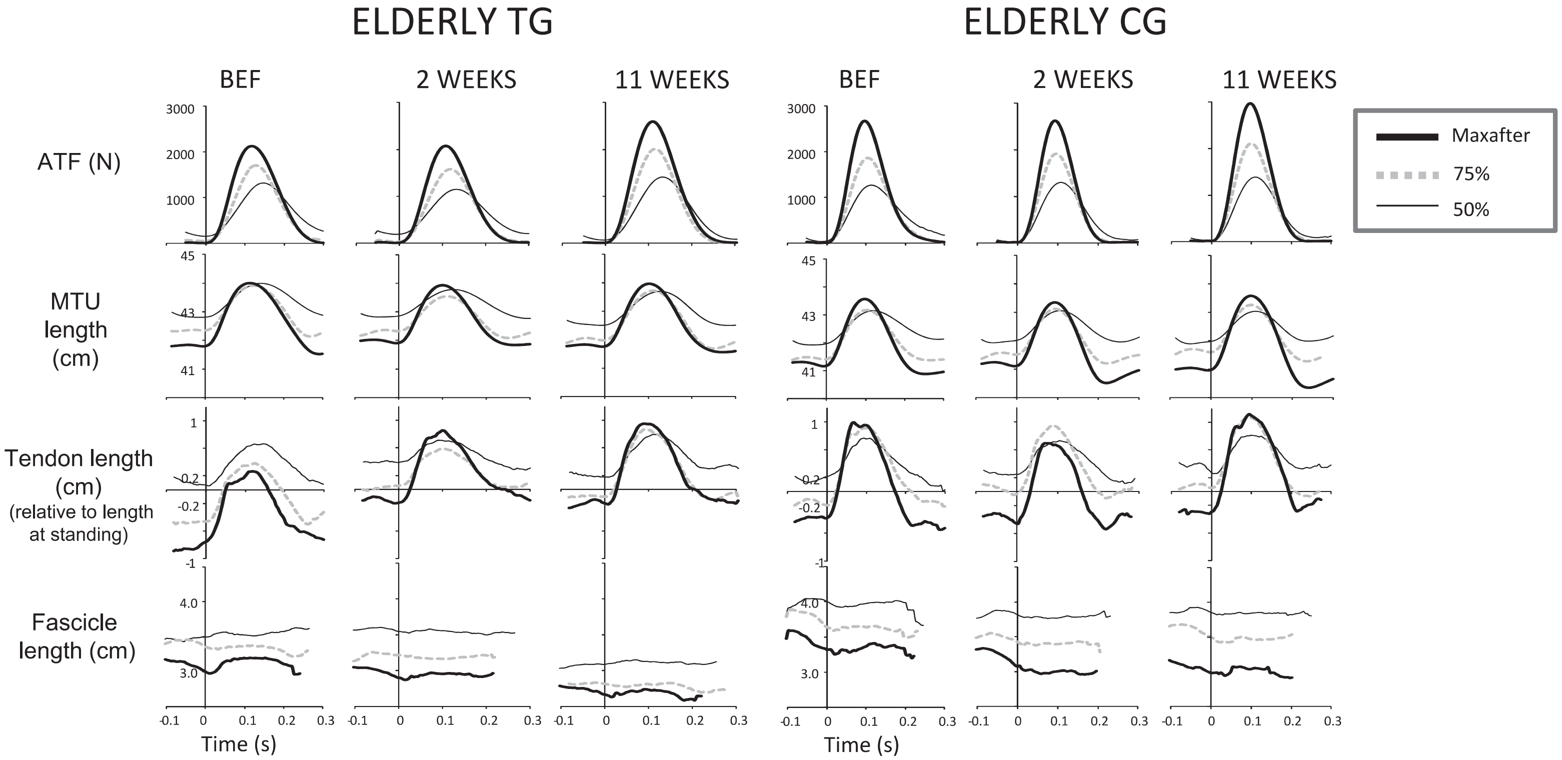

FIGURE 23 The mechanical behavior of GaM at the level of muscle-tendon unit (MTU), outer tendon and fascicle as well the Achilles tendon force (ATF) separately in ELDERLY TG and ELDERLY CG at baseline measurements (BEF) as well as at 2 WEEKS and 11 WEEKS measurement points at 50 %, 75 % and maximal hopping intensities.

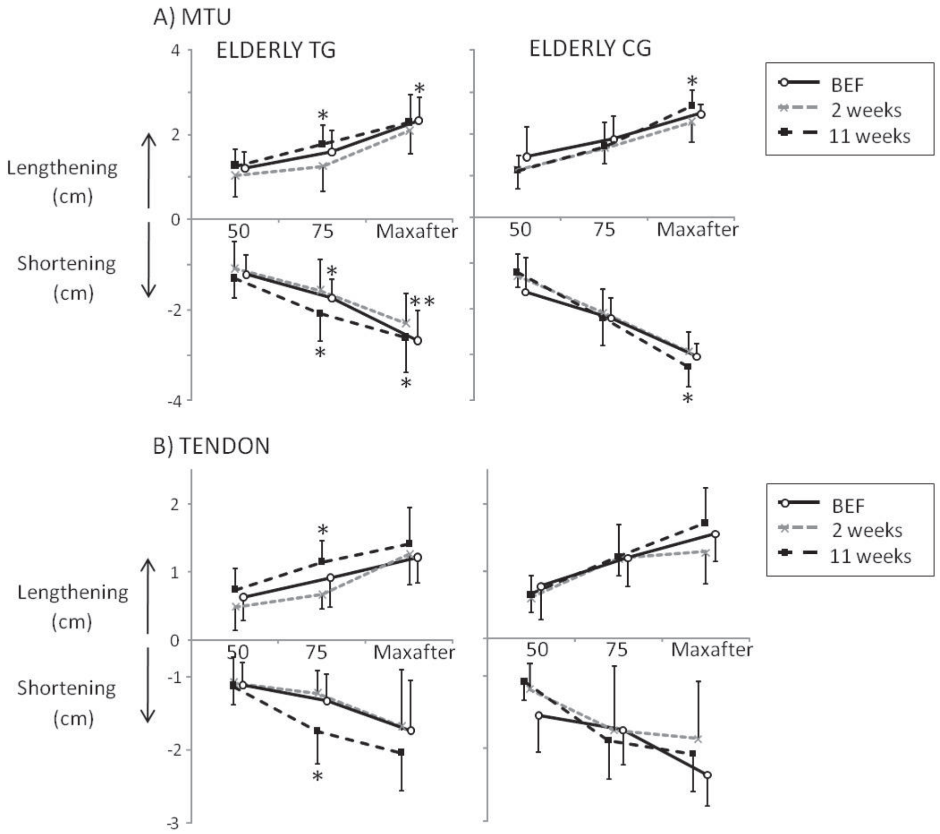

FIGURE 24 GaM (A) muscle-tendon unit (MTU) and (B) outer tendon lengthening and shortening amplitudes (cm) in ELDERLY TG and ELDERLY CG during jumping with different intensities. Stretching amplitudes are calculated from length during contact instant to peak length and shortening amplitudes from peak length to length at take-off instant.* and **: significantly different from 2 WEEKS ($p<0.05$ and $p<0.01$, respectively).

5.6.1.1 Tendon stiffness

When average GaM outer tendon stiffness was calculated during the braking phase of maximal repetitive hopping, ELDERLY showed 30.5 % lower values as compared to YOUNG (table 4). Average tendon stiffness increased in YOUNG from low hopping intensities (50 % and 65 %) to maximal hopping ($p<0.05$) but did not change in ELDERLY. Hopping training did not have any effect on average GaM tendon stiffness (table 4).

5.6.2 Fascicle

The most obvious age-related differences in muscle mechanics were observed at fascicle level. First of all, ELDERLY had shorter GaM fascicle length than

YOUNG at the contact instant of DJs (5.4 ± 0.9 cm in YOUNG vs. 4.5 ± 0.7 cm in ELDERLY, $p<0.01$) (figure 21). The same tendency was observed during repetitive hopping but the difference was not statistically significant (3.6 ± 0.9 cm in YOUNG vs 3.1 ± 0.5 cm in ELDERLY in maximal hopping, ns) (figure 21). Fascicle length at contact instant decreased in ELDERLY with increasing hopping intensity ($p<0.01$).

The fascicle behavior during the braking phase of hopping clearly differed between the age groups. As compared to YOUNG. the fascicles in ELDERLY shortened less during the braking phase of DJs ($p<0.05$) and hopping ($p<0.001$) (figures 21 and 25). In fact, during submaximal repetitive hopping in ELDERLY, fascicles maintained the same length in the braking phase when comparison was made between two points only: the contact point and the transition point from the braking to the push-off phase. The early part of the braking phase showed shortening followed by stretching of the fascicles in ELDERLY. This was most prominent in maximal hopping condition but visible also at submaximal intensities. In maximal hopping, the fascicles in the majority of elderly subjects were stretched also when values between the contact point and the transition point were compared. In YOUNG, fascicles constantly shortened (except for the rapid short-latency stretch shortly after the contact) in the braking phase at all intensities except at 50 % where the length did not change between the contact and transition points. Fascicle shortening in the braking phase increased with increasing hopping intensity in YOUNG ($p<0.05$).

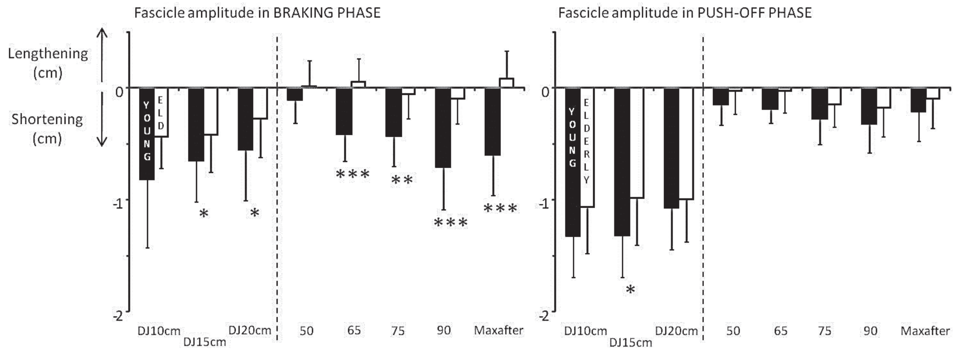

FIGURE 25 GaM fascicle amplitudes in braking and push-off phases of DJs and hopping. Amplitude in the braking phase was calculated from contact to the transition point from the braking to the push-off phase. Fascicle amplitude in the push-off phase was calculated from transition point to take-off.*, ** and ***: significant difference between YOUNG and ELDERLY ($p<0.05$, $p<0.01$ and $p<0.001$, respectively).

In the push-off phase there were no statistically significant differences in fascicle lengths between the transition point and the take-off instant at most of the intensities. In some cases the fascicles shortened slightly between these two points: significant shortening in YOUNG at 65 % intensity ($p<0.05$) and in ELDERLY at 75 % ($p<0.05$) and 90 % intensities ($p<0.05$). In general there were no differences in fascicle shortening amplitudes between the age groups in the push-off phase in DJs or in repetitive hopping although the trend was that fascicle shortened more in YOUNG as compared to ELDERLY (figure 25). During hopping the fascicle behavior in the push-off phase did not change with change in hopping intensity in either age group. During DJs the fascicle shortening in the push-off phase decreased with increased dropping height in YOUNG ($p<0.01$) but not in ELDERLY.

Training had only a minor effect on fascicle behavior except for the shift of the fascicle to lower lengths at the 11 WEEK condition in ELDERLY TG (figure 23). Except for this obvious shift of fascicles to lower lengths at the 11 WEEK measurement point, there were no differences in the fascicle length change pattern between ELDERLY TG and ELDERLY CG at any intensity level or measurement point.

5.7 Relationship between performance and neuromuscular function in elderly

In sledge DJs the AJS correlated positively with rebound height both in YOUNG ($p<0.01$) and in ELDERLY ($p<0.001$). In repetitive hopping on the ground the relationship was not that straightforward but the high AJS in ELDERLY in maximal hopping intensity was associated with a short contact time ($r = -0.61$, $p<0.01$, $n = 24$). Thereafter the negative correlation was observed between contact time and performance (flight time) ($r = -0.44$, $p<0.05$, $n = 24$). These results highlight the importance of high AJS during low amplitude hopping, since it reduces the contact time and therefore enables better performance.

High AJS in ELDERLY in sledge DJs was achieved with high agonist EMG and low antagonist coactivity during the braking phase (table 5). These results were confirmed in repetitive hopping since the EMG ratio of braking phase RMS over push-off phase RMS of the agonist muscles (SOL, GaM and GaL) was positively associated with AJS in ELDERLY ($n = 24$) in maximal hopping (figure 26). In addition, the EMG ratio of the antagonist TA muscle in maximal hopping was negatively correlated with AJS in ELDERLY. The correlations did not reach statistical significance in YOUNG possibly due to the smaller sample size ($n = 8$).

TABLE 5 Correlation coefficients between the selected parameters and ankle joint stiffness (AJS) (Nm/deg) during the braking phase of DJs. n = 36 YOUNG, n = 19 ELDERLY. *, ** and ***; $p<0.05$, $p<0.01$ and $p<0.001$, respectively.

	Take-off speed (ms^{-1})	GM aEMG (mV)	SOL aEMG (mV)	TA aEMG (mV)	TA /GM activation (unitless)	TA /SOL activation (unitless)	TT /MTU stretch (unitless)
YOUNG	0.54 **	0.06	0.60 ***	-0.19	-0.30	-0.52 **	0.48 **
ELDERLY	0.63 ***	0.55 **	0.63 ***	0.009	-0.40 *	-0.62 ***	0.77 ***

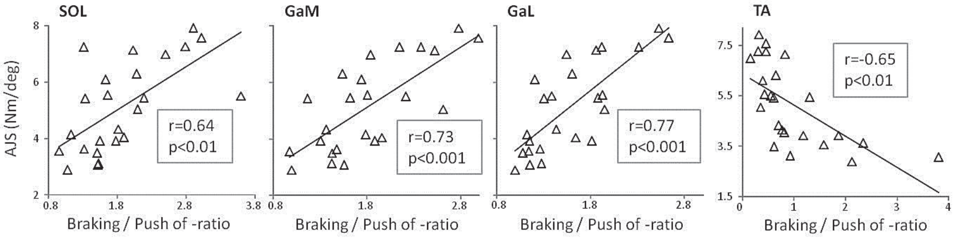

FIGURE 26 Correlations of ankle joint stiffness (AJS) to EMG ratios of braking phase RMS over push-off phase RMS in SOL, GaM, GaL and TA muscles in ELDERLY (n = 24).

From the muscle mechanics point of view, the fascicle shortening amplitude in the braking phase of maximal hopping was positively associated with AJS in ELDERLY (figure 27). Those ELDERLY who could shorten their fascicles in the braking phase (fascicle behavior similar to that of YOUNG), had higher AJS.

Those trained elderly subjects that jumped the best at the 11 WEEK condition after hopping training had high ATF and MTU and tendon stretching and shortening amplitudes during maximal hopping. In addition, their GaM fascicles did not shorten much in the push-off phase (table 6). Finally, those trained elderly subjects that increased their rebound height the most from 2 WEEKS to 11 WEEKS had the highest increase in GaM MTU stretch ($r = 0.67$, $p<0.05$, $n = 10$) and tendon strain ($r = 0.79$, $p<0.01$, $n = 10$).

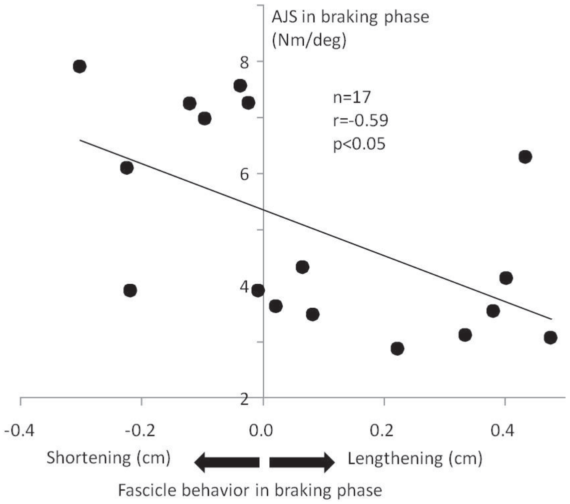

FIGURE 27 Correlation between the fascicle behavior in the braking and AJS in the braking phase in ELDERLY in maximal hopping.

TABLE 6 Correlation coefficients between the selected parameters and maximal rebound height (cm) at 11 WEEK measurements in ELDERLY TG and ELDERLY CG. n = 10 trained, n = 10 controls. * and **: $p<0.05$ and $p<0.01$, respectively.

	Peak ATF (N)	GaM fascicle shortening in push-off phase (cm)	GaM MTU stretch (cm)	GaM MTU shortening (cm)	GaM tendon strain (% relative to length at standing)	GaM tendon shortening (cm)
ELDERLY TG	0.86 **	-0.66 *	0.74 *	0.76 *	0.64 *	0.66 *
ELDERLY CG	-0.35	-0.22	-0.50	-0.31	-0.33	-0.10

6 DISCUSSION

The main findings of the present project were as follows:

1) ELDERLY, as compared to YOUNG, had lower AJS during the braking phase of DJs and high intensity hopping. That may partly explain the lower rebound heights in ELDERLY.

2) Age-related agonist activity profiles exist during DJs and hopping. ELDERLY had high agonist preactivity but thereafter less activity during the braking phase as compared to YOUNG and increased activity in the push-off phase. Therefore, from the muscle activity point of view the hopping performance in ELDERLY was less efficient as compared to YOUNG although it may not be so simple to compare efficiencies in two age groups with different neuromuscular properties, as is discussed in chapters that follow. These age-related activity profiles were visible both with absolutely as well as with relatively similar exercise intensities for two age groups.

3) Less agonist activity during the braking phase affects the fascicle function in ELDERLY and therefore GaM fascicles shorten considerably less during the braking phase of DJs or hopping in ELDERLY as compared to YOUNG.

4) Decreased agonist activity and fascicle shortening during the braking phase in ELDERLY as compared to YOUNG are also linked to lower AJS in ELDERLY during the braking phase of DJs and high intensity hopping.

5) ELDERLY had higher antagonist coactivity only during DJs with absolutely similar exercise intensities for two age groups. During repetitive hopping on the ground the ELDERLY could also keep their TA activity at a low level, which is a positive sign since negative

correlations were found between coactivity during the braking phase and AJS.

6) Tendon forces were considerably lower during hopping in ELDERLY as compared to YOUNG. In spite of that, no age-related differences in tendon stretching and shortening amplitudes were observed. Therefore the present series of studies support the previous literature that tendon stiffness decreases with aging. However, TT/MTU stretch ratio was lower in ELDERLY only during DJs with the same absolute exercise intensities. It seems therefore that tendon function may be impaired in ELDERLY during dynamic movements when YOUNG and ELDERLY are forced to the same performance requirements, but it is maintained when comparisons are made with matched intensities on a relative scale.

7) 11 weeks of hopping training increased the rebound height and RSI in physically active elderly men without changing muscle activity profiles or GaM tendon stiffness.

8) The improvement in performance after training was achieved with shorter GaM operating lengths and therefore increased fascicle stiffness and improved tendon utilization.

The following discussion makes effort to clarify these points and discuss their potential mechanisms.

6.1 Ankle joint stiffness during short-contact hopping

High leg / joint stiffness during the braking phase has been shown to be beneficial for good performance in SSC exercises (see Butler, Crowell & Davis 2003 for review). The present studies support this by reporting a positive correlation between AJS and rebound height both in young subjects as well as in the elderly during DJs (I). In repetitive hopping on a ground the relationship was not that straightforward, but the high AJS in the elderly in maximal hopping intensity was associated with a short contact time, and short contact time correlated positively with flight time. Therefore the results of the present series of studies highlight the importance of high AJS during low amplitude hopping since it reduces the contact time and thereafter increases the rebound height.

However, AJS was lower in the elderly as compared to the young during DJs (I) as well as during high intensity (90 % and maximal) hopping on a ground (II) therefore supporting the findings of Liu et al. (2006) that reported lower leg stiffness in the elderly during counter movement jumps. It has been shown that in hopping with a short contact time the leg stiffness modulation is mainly sensitive to changes in AJS (Arampatzis et al. 2001; Farley et al. 1998; Kuitunen, Ogiso & Komi 2011). Lower AJS in the elderly as compared to young subjects in the present studies is explained by age-specific differences in neural control strategies, as discussed in detail in chapters that follow, as well as by modifications in ankle joint position at the instant of ground contact in the elderly. Increased plantarflexion at contact instant in the elderly results in an increase of the joint displacement amplitude in the braking phase of high exercise intensities (II). The most probable explanation for differences in kinematics between age groups is that it is a safety strategy for the elderly to adjust plantarflexor muscles to a shorter length in order to absorb the impact forces and leave room for stretching in high impact force conditions. Several studies have shown that the neuromuscular system of the elderly is able to match the task demands with their reduced neuromuscular capacities. (e.g. Savelberg et al. 2007; DeVita & Hortobágyi 2000; Reeves et al. 2009). The present results regarding AJS support these studies since KJS was still high in the elderly even during high intensity hopping (II) and therefore it is suggested that the elderly redistribute muscular output depending on task demands (Savelberg et al. 2007; DeVita & Hortobágyi 2000; Reeves et al. 2009), and in this case shift the load to the knee and most probably also to hip joint muscles.

On the other hand it can be argued that reduced AJS during hopping is not actually an age-related phenomenon since with two weeks of hopping training the elderly increased their AJS 21.0 ± 19.3 % resulting in a nonsignificant difference as compared to values of young individuals (p = 0.14, ns) (IV). Therefore it seems that lower AJS in the elderly before training is a safety strategy to reduce the impact loads or inability to load ankle joints due to unfamiliar exercise. Thereafter with a relatively short training period the elderly learn the similar loading technique to the young.

6.1.1 Stiffness regulation strategies

High leg / joint stiffness during the braking phase can be achieved by high activity of agonist muscles in the preactivity and early braking phases (Asmussen & Bonde-Petersen 1974; Cavagna 1977; Yoon, Tauchi & Takamatsu 2007; Kuitunen et al. 2007). In the present studies positive correlation was found between agonist activity during the braking phase and AJS both in young subjects and in the elderly during DJs (I) as well as between agonist EMG ratios (braking phase RMS and push-off phase RMS) and AJS in the elderly during repetitive hopping on a ground (II). Therefore the present studies are well in line with previous observations (Asmussen & Bonde-Petersen 1974; Cavagna 1977; Yoon, Tauchi & Takamatsu 2007; Kuitunen et al. 2007) by highlighting the role of neural activation in AJS regulation.

The role of antagonist coactivity in leg / joint stiffness adjustment during the SSC exercises has been much less clear. Hobara, Kanosue & Suzuki (2007) concluded that coactivity may not play a role in leg stiffness regulation during repetitive hopping, by showing that coactivity decreased even though leg stiffness increased from preferred contact time hopping to short contact time hopping. Similarly Yoon, Tauchi & Takamatsu (2007) showed that TA activity during the braking phase decreased but AJS increased when DJs were compared to 5-repetition rebound jumps. In the present series of studies coactivity during the braking phase showed an inverse relationship with AJS among elderly both during sledge DJs (I) as well as during repetitive hopping on the ground (II). Therefore it can be concluded that joint stiffness is downregulated with an increase in TA coactivity during the braking phase in short-contact hopping.

6.2 Age-related muscle activity profiles during SSC actions

First of all, during repetitive ground contact hopping the activity of plantarflexor muscles (SOL, GaM and GaL) increased with increasing hopping intensity in all functional phases of hopping (preactivity, braking and push-off phase) in both age groups (II). This increase in agonist muscle activity with increasing intensity supports earlier findings (Ishikawa & Komi 2004; Finni, Komi & Lepola 2001; Komi et al. 1987). However, one exception to this behavior was SOL preactivity that was very prominent at low intensities in the elderly and remained at the same level in all exercise intensities. This muscle specificity may imply an already well documented difference between SOL and the gastrocnemius muscles regarding balance control, where SOL plays a greater role (e.g. Smith et al. 1977). Since low intensity hopping in the elderly does not include a long flight phase it poses a challenge regarding balance control. Moritani, Oddsson & Thorstensson (1991) have showed similar high SOL preactivity in very fast short-contact hopping with low force and a mean rebound height of <1 cm.

In DJs on a sledge the preactivity of GaM and SOL increased as well with increasing dropping height in both age groups (I). However, the braking phase activity did not change significantly, probably because of too low an increase (5 cm) in dropping height. Significant age x dropping height interaction in the push-off phase activities (with increasing dropping height the agonist activity increased in the elderly, but decreased in the young) highlights the fact that two age groups were at different positions on their dropping height to rebound height curve (Komi & Bosco 1978) because of the same absolute exercise intensities used for both age groups.

6.2.1 Agonist activity

Although there were no age-specificity in a way the two age groups modulated the muscle activity in terms of exercise intensity, age-related differences were observed in muscle activity profiles during the contact phase of hopping. In general, as compared to young subjects, the elderly activated their agonist muscles less in the braking phase during both DJs (I) and repetitive hopping (I) and thereafter had more activity in the following push-off phase during DJs (I).

As expected, the age-specific differences were greater in DJs with absolutely similar exercise intensities and smaller during hopping with intensities matched on the relative scale for the two age groups. This is because muscle activity profiles in hopping are intensity specific in a non-linear fashion (Finni, Komi & Lepola 2001). When two age groups with obviously different neuromuscular capacities are compared with the same absolute exercise intensity, the chosen intensity is always closer to maximum for elderly subjects. The present series of studies confirm the findings of Finni, Komi & Lepola (2001) that there is a certain submaximal intensity (65 %-75 %) in which the efficiency of hopping is highest. Both the young and the elderly followed the same “inverse parabolic” shape in the braking phase to push-off phase activity ratio. This means that the economy of hopping is compromised at maximal hopping intensity. Nonetheless, the lower braking phase to push-off activity ratios in the elderly suggest that their hopping performance from the point of view of muscle activity is less efficient as compared to that of the young (Asmussen & Bonde-Petersen 1974; Asmussen 1953; Bosco et al. 1982). On the other hand it may be unrealistic to suppose that the same kind of muscle activity would be optimal for two age groups with obviously different neuromuscular properties both in muscle contractile apparatus (see Andersen 2003 for review) as well as in tendons (Karamanidis & Arampatzis 2005; Kubo et al. 2003b; Morse et al. 2005). This issue will be discussed below in more detail.

It is well established that strength training improves maximal force and power in elderly individuals in a similar manner as it does in younger individuals (Newton et al. 2002; Reeves, Maganaris & Narici 2003). Since it is also known that at early phase of training the improvement in performance is due to neural adaptation (Häkkinen & Komi 1983), it was hypothesized that short term explosive type of training in the elderly would lead to modulation of their muscle activity profiles (increased EMG ratio of braking phase activity to push-off phase activity) so that they would more closely resemble those of young individuals (IV). The results indeed supported our hypotheses, since EMG ratios of SOL, GaM and GaL increased with 2 weeks of training at maximal hopping intensity but simultaneously the rebound height decreased rather than increased. Thereafter, although we found an increase in rebound height from 2 weeks to 11 weeks in ELDERLY TG, the EMG ratios returned to baseline levels between those time points. Therefore it seems that this EMG profile of a lower braking phase to push-off phase activity ratio is more natural / optimal for the elderly during hopping and age-related muscle activity profiles exist even when elderly subjects have trained, at least in the time frame of 11 weeks. It seems that the elderly do have a capacity to change their muscle activity profiles closer to those of young individuals, but that does not lead to improved performance and is therefore not optimal for their neuromuscular system. It is likely that the age-related motor unit remodeling (for review see Andersen 2003) and decreased tendon stiffness (Kubo et al. 2003b; Morse et al. 2005; Karamanidis & Arampatzis 2005) favor a different kind of muscle activity for optimal efficiency and power output in these two age groups (Lichtwark & Wilson 2005a).

6.2.2 Antagonist coactivity

Generally high coactivity especially during dynamic movements (squat jumps, walking, targeting movements) is linked to aging (Häkkinen et al. 1998; Seidler, Alberts & Stelmach 2002; Hortobágyi et al. 2009) and it is considered to increase joint stiffness and therefore improve the stability and safety of locomotion in the elderly (Hortobágyi & DeVita 2000). To support these observations, the elderly showed greater coactivity of TA muscle during the braking phase of DJs than the young. However, a little to our surprise, coactivity during the repetitive hopping was very low also in the elderly.

As discussed already above, in contrast to stabilizing actions (Baratta et al. 1988; van Dieen, Cholewicki & Radebold 2003), the role of coactivity in SSC exercises is likely not to increase joint stiffness but rather to decrease it (Hobara, Kanosue & Suzuki 2007; Yoon, Tauchi & Takamatsu 2007). Therefore the role of increased coactivity during the braking phase of single DJs in the elderly is probably related to the strategy to increase the safety of locomotion by decreasing AJS in situations where the impact forces may otherwise exceed the tolerable range. In contrast, possibly because of the continuous hopping and therefore adaptation to the required stretch levels, the elderly could also keep their TA activity low during repetitive ground contact hopping (II). A similar suggestion has been drawn also before by Yoon, Tauchi & Takamatsu (2007) when comparing DJs and repetitive hopping in young individuals. Due to this adaptation to required stretch levels, there is no need for increased coactivity as a safety strategy to reduce the impact loads. As mentioned already, high AJS in the braking phase is needed for good hopping performance (Asmussen & Bonde-Petersen 1974; Cavagna 1977; Gollhofer et al. 1992) and therefore low TA activity in the elderly is especially beneficial because their agonist activity is low. On the other hand it cannot be totally ruled out that, simply because of similar relative exercise intensities for these two age groups during repetitive hopping, as compared to DJs, the coactivity levels were also similar.

6.3 Age-related muscle mechanics during SSC actions

6.3.1 Fascicle function

Less agonist activity during the braking phase of hopping in the elderly as compared to the young leads to age-specific differences in fascicle function during the braking phase. In the present series of studies the GaM fascicles shortened clearly less during the braking phase in the elderly as compared to the young. This difference was visible both in DJs with the same absolute exercise intensities (I) as well as in hopping with relatively similar intensities

(III) and the fascicle length change pattern during the contact phase of hopping did not change due to training in the elderly (IV). The results of the present series of studies are therefore in accordance with the findings of Mian et al. (2007) and Panizzola et al. (2013) that both reported more isometric fascicle function in the elderly as compared to young subjects during walking with absolutely similar walking velocities for both age groups. However, Panizzola et al. (2013) further showed that age-specificity in fascicle function disappeared when both age groups walked at their preferred walking speeds, suggesting that the elderly neuromuscular system is optimized for the walking velocity regularly used in everyday life. Probably it was the more complicated task and the higher force requirements during hopping, as compared to walking, which kept the age-specificity in the fascicle function similar in the present series of studies, regardless of whether the comparisons were made with absolutely or relatively similar intensities. The lack of change in fascicle length change patterns after hopping training in elderly further suggests that this kind of fascicle behavior is optimal for elderly individuals during hopping.

6.3.1.1 Efficiency vs. power output

Isometric muscle action has been suggested to be more efficient compared to concentric one since it reduces the active work done by the fascicles and therefore the energy cost (Hill 1938). Because of attachment to the compliant tendon the muscle fascicles do not necessarily need to produce work during movement, but instead the elastic tendon can stretch and simultaneously store elastic energy which it can thereafter release in immediately following push-of phase, thereby increasing movement efficiency (Cavagna 1977). Because of more constant fascicle lengths during the braking phase of hopping in the elderly as compared to the young, the fascicle function of elderly subjects could be considered to be more beneficial in terms of efficiency. However, speed plays a major role in efficiency values so that the increase in the speed of the lengthening action (eccentric) increases efficiency, while the increase in the speed of the shortening action (concentric) decreases efficiency (see Kyröläinen & Komi 2011 for review). Since the shortening speed of fascicles even in young subjects in the present study (III) (2.7 ± 0.6 Lo/s in maximal hopping) was still very low compared to maximal contraction speed of muscles (10 Lo/s in Zajac 1989), the energy cost due to concentric action may not be high.

In addition, it seems that especially under high force requirements the fascicles either need to shorten in the braking phase or possibly to shift to shorter operating lengths to keep fascicle stiffness high enough under increased force requirements, even if this may compromise movement efficiency. It can be suggested that the use of these two mechanisms is age-related, as is discussed in the paragraph that follows.

6.3.1.2 Regulation of fascicle length during the preactivity vs. braking phase

In repetitive hopping it was clear that fascicle shortening during the braking phase increased in young subjects with increasing hopping intensity. This behavior of increased fascicle shortening during the braking phase with increase in tendon forces in young subjects is visible when fascicle behavior in walking is compared to that in running (Ishikawa, Pakaslahti & Komi 2007; Lichtwark, Bougoulias & Wilson 2007). In all of these conditions with young subjects (Original paper III; Ishikawa, Pakaslahti & Komi 2007; Lichtwark, Bougoulias & Wilson 2007) the fascicle length at the contact instant is fairly unchanged with increasing exercise intensity, but the intensity-specific regulation in fascicle length occurs during the braking phase of the contact cycle.

It seems, however, that the elderly have obtained a different strategy for increasing fascicle stiffness when force requirements increase. Although there were no dramatic changes in fascicle length change patterns during the contact phase of hopping in the elderly, clear modifications seem to exist already before the contact instant when the hopping intensity was changed from low to maximum (III) (figure 21). Fascicle length at the contact instant moved to shorter operating lengths in the elderly with increasing hopping intensity. These results are in accordance with the findings of Panizzola et al. (2013) which showed that SOL fascicles in elderly subjects shifted to shorter lengths without any significant changes in length change patterns during the contact phase of walking when walking velocity was increased from their preferred velocity to that matched with the preferred velocity of young subjects. Actually these results as well as the EMG results of the present study (II) are also well in line with Hortobágyi & DeVita (2000) who reported 136 % higher preactivity in the elderly as compared to young subjects during stepping down from a platform. Thereafter the magnitude of EMG activity during the impact phase increased 70 % in the young but only 26 % in old subjects. Therefore the authors concluded that such data would suggest that the elderly modify the control of a voluntary stepping movement as early as in the phase of preparation for the critical component of movement (Hortobágyi & DeVita 2000). Although data is still limited regarding this issue, it seems that the elderly adapt to increased force requirements by decreasing the operating length of muscle fascicles already before the contact instant, whereas the regulation occurs during the braking phase in young individuals. This idea is further supported by our hopping training study in the elderly (IV) that showed the shift of GaM fascicles to shorter operating lengths, but unchanged length change patterns during the contact phase of hopping, with a simultaneous increase in tendon forces at the 11 weeks measurement point.

It would be interesting to examine whether these age-specific movement regulation strategies have implications for muscle spindle function and therefore for stretch reflexes. It could be speculated that decreased fascicle length at the instant of ground contact with increasing hopping intensity in the elderly could induce spindle slack if alpha-gamma coactivation does not work effectively.

6.3.1.3 Possible candidates to explain age-specific differences in fascicle function

Regarding the noticed age-specific differences in fascicle function, it is not an easy task to identify the actual origins of this behavior. As discussed already above, the age-specific differences in muscle activity levels provide one explanation since the elderly activate their agonist muscles less during the braking phase of DJs and hopping as compared to the young. At maximal hopping intensity in repetitive hopping (III), it is suggested that fascicles in the majority of the elderly cannot tolerate the impact forces and are therefore stretched after the initial shortening in the early braking phase (figure 21). Most probably this stretch is due to cross-bridge detachment because of high impact forces (Rack & Westbury 1974) and not due to eccentric action with attached cross-bridges. However, the cross-bridge detachment and therefore fascicle stretching in the elderly seem to happen only at maximal hopping intensity and therefore they do not explain the different behavior between the age groups also at lower exercise intensities. As discussed already in terms of neural activation, the most probable candidate for explaining the more isometric fascicle function in the elderly is the age-specific decrease in tendon stiffness (Karamanidis & Arampatzis 2005; Kubo et al. 2003b; Morse et al. 2005). This is because with decreased tendon stiffness the fascicles do not need to be that stiff any more to allow the tendon to be stretched, since it is the difference in stiffness between these two structures that determines the amount of lengthening on them when force is applied (Zajac 1989). It must also be highlighted that among elderly subjects, the great variability was observed in the braking phase fascicle behavior at maximal hopping intensity. In some subjects, the fascicles shortened but in some cases lengthened. Fascicle shortening amplitude in the braking phase of maximal hopping was positively associated with AJS in the elderly (figure 27). Those elderly who could shorten their GaM fascicles in the braking phase (fascicle behavior similar to that of young subjects), had higher AJS and therefore shorter contact time and better performance. Therefore it seems that some elderly, probably the most fit and strong, had similar fascicle function as compared to that in the young but that was not the typical pattern among the elderly.

The regulation of fascicle length during the preactivity phase with increasing hopping intensity in the elderly compared to the braking phase in the young is not easily explained at the moment. The regulation already before the contact instant in the elderly is probably linked to the high preactivity of agonist muscles and consequently to kinematic modifications in knee and ankle joint angles (II) and therefore to decreased MTU length at contact instant with increasing hopping intensity (figure 21). The purpose of these modifications is likely to adjust plantarflexor muscles of elderly subjects to a shorter length in order to be able to absorb the impact forces and leave room for stretching in high impact force conditions. It still remains open, however, whether this happens purposely or unconsciously. Training induced decrease in GaM muscle operating length to a shorter position could be achieved with shifted MHC isoform composition of muscle fibers from slow (I) to fast (IIa), as shown by Liu et al. (2003) with combined strength plus ballistic SSC type-of training. Unfortunately passive twitch was not measured or muscle biopsies taken in the present study (IV) in order to demonstrate that. Malisoux et al. (2006) found some evidence that SSC training could also increase the cross-bridge mechanics of fast twitch muscle fibers by reporting increased normalized peak power of type IIa muscle fibers after 8 weeks of SSC training. It is suggested that increase in fascicle stiffness after training enables tendon to utilize more elastic energy since, as mentioned already, it is the difference in stiffness between these two structures that determines the amount of lengthening on them when force is applied (Zajac 1989). In addition, the shift of fascicles to a shorter position after training may have another functional relevance in tendon function by removing the tendon slack already before the ground contact and therefore enabling the faster tendon stretch.

6.3.2 Tendon function

Mian et al. (2007) showed that the relative contribution of TT to MTU stretch is increased in the elderly during walking with the same absolute walking velocity for both age groups. To contradict these results it was found that during DJs with the same absolute dropping heights for young and elderly subjects the TT/MTU stretch ratio was decreased in the elderly (I). This result suggests that during DJs with the same absolute dropping heights the elderly utilize tendon elasticity less efficiently than their younger counterparts. The possible explanation for these contradicting results is that in Mian et al. (2007) there were no age-specific differences in MTU stretching amplitudes whereas in DJs the MTU stretch was higher in the elderly as compared to young subjects (I). This is likely to be due to less agonist muscle activity and increased coactivity during the braking phase of DJs in the elderly and consequently their reduced ability to stiffen the fascicles and ankle joints resulting in increased MTU stretch and finally a lower TT/MTU stretch ratio. In line with this suggestion, the TT/MTU stretch ratio and jumping performance intercorrelated positively in both age groups, but especially in the elderly (table 5). That means that those elderly subjects who could shorten their fascicles more in the braking phase, and thus had higher TT/MTU stretch ratio, jumped better. A more compliant tendon could also increase the TT/MTU stretch ratio under high agonist activity, leading to adequate joint stiffness, but that was not the case in the elderly.

However, during repetitive hopping with the same relative exercise intensities there were no differences in TT/MTU stretch ratio between the young and the elderly. That suggests that tendon function is not impaired in elderly individuals when exercises are performed with the same relative intensities. Also the absolute tendon stretching amplitudes were the same in both age groups, despite significantly lower tendon forces in the elderly, suggesting decreased tendon stiffness in the elderly as compared to the young. This issue is discussed in paragraphs below.

The results regarding tendon shortening further support the observation that tendon function is not impaired in the elderly especially with the same relative exercise intensities. Tendon shortening amplitudes during repetitive hopping were actually a little bit, although not statistically significantly, higher in the elderly as compared to the young (figure 22).

6.3.2.1 Tendon stiffness

It has been shown by several research groups using ultrasonography that tendon stiffness and Young's modulus decrease with aging (Karamanidis & Arampatzis 2005; Kubo et al. 2003b; Morse et al. 2005). In contrast to the isometric method used in those studies (Karamanidis & Arampatzis 2005; Kubo et al. 2003b; Morse et al. 2005) the tendon stiffness was calculated as average GaM tendon stiffness in the braking phase of hopping in study III. The method was similar to that used by Lichtwark & Wilson (2005b), and values observed (244-311 N/mm in maximal hopping in YOUNG) were also in a similar physiological range considering that the GaM muscle was examined in the present study and GaL by Lichtwark & Wilson (2005b) (145-231 N/mm). The present study (III) partly supports the concept that tendon is more compliant in the elderly as compared to the young (Karamanidis & Arampatzis 2005; Kubo et al. 2003b; Morse et al. 2005) since average stiffness during the braking phase of hopping was lower in elderly subjects as compared to young ones from moderate to high exercise intensities (75 %-max) (figure 28). Tendon forces increased in both age groups with increases in hopping intensity, but tendon stretching amplitudes increased only in the elderly. Therefore it was found that tendon stiffness in the braking phase increased with increasing hopping intensity in the young but did not change in the elderly. In other words the results of the present study (III) suggest that tendon stiffness is loading rate dependent in young subjects but not in the elderly.

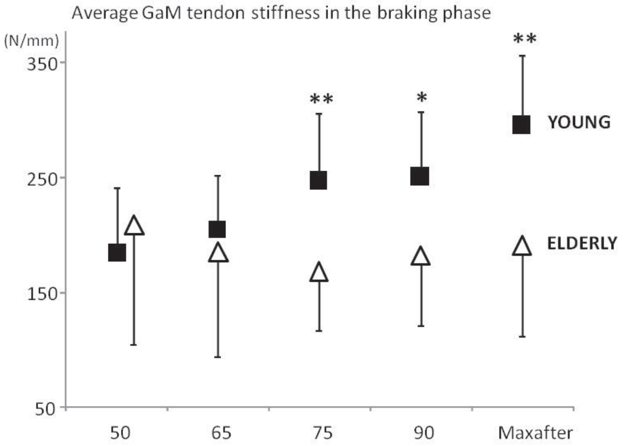

FIGURE 28 Average GaM tendon stiffness during the braking phase of repetitive hopping in YOUNG and in ELDERLY. * and **; Significant difference between YOUNG and ELDERLY ($p<0.05$ and $p<0.01$, respectively). Stiffness is calculated by dividing the peak Achilles tendon force (N) over the tendon stretching amplitude during the whole braking phase (mm).

There are controversies in literature about the viscous properties of human tendons. Pearson, Burgess & Onambele (2007) and Gerus, Rao & Berton (2011) reported loading rate dependent tendon stiffness while Peltonen et al. (2013) have showed that tendon stiffness is independent of loading rate. It has been suggested that stiffness of elastic structures may change with increase in muscle activity (Hof 1998; Hof 2003) which may give a partial explanation for the results of the present study, since the young increased their plantarflexor activity more in the braking phase with increasing intensity as compared to the elderly (II). Increase in stretching velocity may also increase stiffness due to viscoelastic properties of the tendon (Butler et al. 1978). However, no difference was found in the increase of peak tendon stretching velocity between the age groups (increase of 16 ± 12 cm/s in the young vs. 19 ± 10 cm/s in the elderly from 50 % to max intensity). Therefore the mechanism behind these age-specific differences in tendon stiffness with increase in hopping intensity are not clear at the moment. One must notice, however, that in the present study the average tendon stiffness was calculated for the whole braking phase. That includes the toe region as well as the linear region of tendon force-length -curve and no effort was made to distinguish between those two parts. Therefore the possible age-specific differences in tendon slack length and thus in toe region could explain this data.

6.3.2.2 Training induced changes in tendon function

Contrary to our original hypotheses, tendon stiffness did not change with 11 weeks hopping training in the elderly. There are several studies that have found an increase in outer tendon / tendon-aponeurosis stiffness after strength training (Onambele-Pearson & Pearson 2012; Reeves, Maganaris & Narici. 2003) or alpine skiing training (Seynnes et al. 2011) in the elderly as well as after strength training (Kubo et al. 2006; Kubo et al. 2007) or isometric cyclic training in the young (Arampatzis, Karamanidis & Albracht 2007). It has been shown that the tendon requires high strains in order to adapt (Arampatzis, Karamanidis & Albracht 2007). Arampatzis, Karamanidis & Albracht (2007) found an increase in GaM tendon-aponeurosis stiffness after 14 weeks (4 days per week) of isometric cyclic training that caused high tendon strains (4.7 %) but not with low strain (2.97 %) training. Hopping training in the present study was performed with 75 % and 90 % intensities from peak Fz and the average tendon strain during those intensities was 5.1 ± 2.3 % (relative to length during relaxed standing) which is very high in relation to reported maximal physiological tendon strain values (Wren et al. 2001 reported failure strain value of 7.5 ± 1.1 % for human Achilles tendon substance) as well as with high strain rate of 43.0 ± 19.6 % / s. Therefore, the training intensity was most probably as high as it safely could be. The training group performed on average 134 ± 28 jumps per training session and in total 4268 ± 638 jumps over the 11 week training period.

There are several other studies that found unchanged tendon stiffness after plyometric training (Hansen et al. 2003; Houghton, Dawson & Rubenson 2013; Kubo et al. 2007) and Kubo et al. (2007) found that tendon stiffness increased after strength training but not after plyometric training. Lack of tendon adaptation after plyometric training as compared to that after strength training may suggest that in addition to high loading magnitude the high loading duration per contraction is required for tendon adaptation, as suggested also by Arampatzis et al. (2010) and Kubo et al. (2001). On the other hand, according to Kubo et al. (1999) the increase in tendon stiffness would result in decreased elastic energy savings during SSC exercise. Therefore it can be speculated that an increase in tendon stiffness would not be beneficial for hopping performance and therefore this adaptation does not occur after plyometric training. In addition, it can be argued that since tendon stiffness is closely related to strength level (Stenroth et al. 2012) the calf muscle strength may not have changed much with hopping training (Kyröläinen et al. 2005; Piirainen et al. 2014) and therefore the stiffness also remained unchanged.

On the other hand, it must be noted that the GaM outer tendon was measured in the present study whereas most of the studies have measured the combined stiffness of the tendon-aponeurosis structure (e.g. Arampatzis, Karamanidis & Albracht 2007; Kubo et al. 2006). Since it is known that the outer tendon and the aponeurosis have different mechanical properties (Finni et al. 2003; Kubo, Kanehisa & Fukunaga 2005; Magnusson et al. 2003b) it may be that their adaptability also differs and therefore it can be speculated that adaptation might have occurred at the aponeurosis level that was not investigated in the present study. Similar conclusions have been suggested before (Kubo et al. 2006). Another possibility is that it would require a longer training period for the elderly tendon to increase its stiffness due to longer adaptation to the correct loading technique, although the changes have been observed in 2 months after the start of strength training in young subjects (Kubo et al. 2012).

However, although the tendon stiffness remained unchanged with training, some adaptations in tendon function were observed with training. Tendon stretching and shortening amplitudes followed the changes in the MTU level and in tendon force, and increased with training from 2 weeks to 11 weeks (figure 9). In addition, those elderly who increased their rebound height the most from 2 weeks to 11 weeks also increased their tendon strain highlighting the importance of tendon function during this kind of short contact hopping. In addition, the tendon seemed to adapt also beyond the level of MTU, since tendon recoil relative to MTU shortening was higher in the trained as compared to the controls at 11 week measurements. Therefore, although tendon stiffness remained unchanged, the results suggest that utilization of tendon elastic energy was increased after training. That was achieved with increased fascicle stiffness through decreased operating lengths of the fascicles after training. These results nicely demonstrate that fascicle and tendon interact during human locomotion and their behaviors cannot be defined independently.

6.4 Strengths and limitations

Since the present series of studies examined only calf muscles and in terms of muscle mechanics more specifically GaM, the results and interpretations may not be generalized to other muscles or muscle groups. It is generally known that plasticity of muscles due to aging (Frontera et al. 1991; Hughes et al. 2001; Frontera et al. 2008), disuse (de Boer et al. 2008) and training (Cureton 1988; Welle, Totterman & Thornton 1996) differs from one muscle group to another and also possibly inside the muscle group between synergists. Further, the interaction between muscle fascicles and tendon is known to be specific to movement type (Ishikawa, Pakaslahti & Komi 2007; Lichtwark, Bougoulias & Wilson 2007), intensity (Ishikawa et al. 2006) and to the muscle examined (Ishikawa, Finni & Komi 2003; Sousa et al. 2007). Therefore the results of the present series of studies may not be generalized to other movement types, especially to those with considerably longer contact times and thus different neural control strategies. Therefore, much more research with different muscle groups and movement types is needed in order to confirm the age-specificity in muscle activity profiles and fascicle-tendon interactions in other muscle groups than plantarflexors, as well as in other movement conditions.

In addition, another important question is whether the present results can be explained by the aging process itself and / or by the influence of reduced physical activity with increasing aging (Hunter, Thompson & Adams 2000), especially high-intensity exercises that require fast force production (Candow & Chilibeck 2005; Morse et al. 2004). The elderly subjects in the present studies were recruited from the local senior gym and therefore represent the active population of their generation. With regard to physical activity levels, the young and the elderly subjects had similar physical activity levels in hours per week. Consequently the major cause of differences may be the aging process itself. On the other hand, it seems that the young and the elderly select different kinds of exercise types as training methods. The young may favor exercise types that include high-impact loading (running, ball games) and the elderly typically prefer low-impact walking and cycling as training methods (table 2). Thus to separate the roles of changes in physical activity and the aging process itself may not be so simple.

When EMG amplitudes are compared across individuals and time points the proper normalization is needed. The most often used method is to normalize amplitudes during various phases of movements to that during MVC. Since no MVC was measured in study I that could not be done. In study I the normalization was done relative to aEMG during maximal SJ. This process assumes that activation levels during SJs are maximal or at least similar in the young and the elderly. If activation level during maximal SJ was lower in the elderly as compared to the young, the EMGs during preactivity, braking and push-off phases would be overestimated in the elderly. Therefore, at least the lower EMG activity during the braking phase of DJs in the elderly as compared to the young, as reported in study I, is valid even in a case of failed normalization process. In addition, naturally the normalization does not affect the EMG ratio of braking phase activity over push-off phase activity and therefore to compare EMG ratios across individuals and training time points is always appropriate. In study II the MVC was measured but not analyzed in first place and therefore it was decided to normalize EMGs relative to aEMG during the preactivity of maximal hopping. The reason why we chose to normalize EMG to the preactivity of maximal hopping is that preactivity presents the centrally programmed motor command (Jones & Watt 1971). However, since the reviewer questioned this method during the review process of the manuscript, the aEMGs during MVC were analyzed and the EMGs during different functional phases of hopping were calculated also relative to aEMG during MVC. Since age-related differences during hopping stayed similar, it was decided not to change the normalization. Finally in study IV the EMGs during functional phases of hopping were normalized to that during MVC. However, the superimposed twitch was not measured during MVC and therefore it is not known whether the capacity to voluntarily activate calf muscles improved with training. If the activation capacity was insufficient at baseline measurements, that would overestimate the normalized EMG values of the BEF condition and therefore possible hide the improved neural drive due to training. However, since the activation capacity of calf muscles during maximal plantarflexion has been shown to be high in the elderly (Barber et al. 2013), it is not expected to change greatly with training. Finally, if passive twitch had been measured, it would have revealed the possible changes in contractile properties of the muscles and thus allowed to make interpretations on possibly changed MHC isoforms with training.

One more limitation must be highlighted. Although the subjects of the training study (IV) were randomly assigned for training and control groups, the groups were not perfectly similar at baseline. Although the difference in rebound height of maximal hopping was not statistically significant there was a tendency for controls to jump better than the training group at baseline. Controls were also a few years younger and had lower body mass index as compared to the training group (table 2). This difference between the subject groups at baseline is seen in many variables and somewhat complicates the results and interpretations, although we think that it does not affect the overall picture.

The strength of the present series of studies is that many intensity levels were investigated and both the similar intensities in absolute vs. in relative scale for young and elderly subjects were measured. Therefore the results of the present studies are not limited only to one exercise intensity level and the studies considerably broaden the understanding of how the elderly neuromuscular system regulates complicated dynamic actions from very light to maximal exercise intensities. In addition, since the present studies combined kinetics, kinematics, EMG and ultrasound assessments of both the tendon and fascicle compartments of MTU, the mechanisms behind age-associated movement control strategies can be discussed in detail. However, it must be mentioned that since the previous literature regarding the fast dynamic actions in the elderly is limited, discussing the possible mechanisms behind age-specific differences in neural control strategies and fascicle-tendon interaction was not always easy. Finally, the strength of the present measurement setup was that since elderly individuals also performed training, we were able to investigate what parameters were affected already by short term hopping training and therefore to discuss whether the differences were due to aging *per se* or because of an unfamiliar exercise type. This is especially important since elderly individuals do not regularly perform this kind of fast high-impact exercises.

PRIMARY FINDINGS AND CONCLUSIONS

1) Lower AJS in the elderly during single DJs (I) and high intensity repetitive hopping (II) supports the hypothesis that the elderly neuromuscular system can be optimized to match the task demands with their reduced capacities and to shift the load to the stronger knee and most probably also to hip joint muscles in situations when the high forces might otherwise increase above the tolerable range. Since AJS increased 21.0 ± 19.3 % in trained elderly subjects with 2 weeks of hopping training (IV) it seems that lower AJS in the elderly before training is a safety strategy to reduce the impact loads or inability to load ankle joints due to unfamiliar exercise.

2) The present series of studies highlight the importance of high AJS during short contact hopping (I, II). In addition the studies support previous literature that high AJS is achieved with high agonist activity and low antagonist coactivity in the braking phase (I, II).

3) Age-related agonist activity profiles exist during DJs (I) and repetitive hopping (II). Typical agonist activity pattern in the elderly is high preactivity, thereafter less activity during the braking phase as compared to the young, and increased activity in the push-off phase. 2 weeks of hopping training increased the EMG ratio of braking phase RMS over push-off phase RMS in trained elderly (IV), suggesting that the elderly neuromuscular system has a capacity to change the agonist activity profile. It is suggested, however, that a lower EMG ratio is optimal for elderly individuals, possibly due to decreased tendon stiffness, observed also in the present studies (I and III) and /or age-associated motor unit remodeling.

4) Less agonist activity during the braking phase affects the fascicle function in the elderly and therefore GaM fascicles shorten considerably less during the braking phase of DJs (I) and hopping (II)

in elderly subjects as compared to the young ones. Hopping training, in the time frame of 11 weeks, did not have any effect on fascicle length change patterns during the contact phase of hopping (IV) suggesting that this kind of fascicle behavior is optimal for the elderly again possibly due to different tendon properties.

5) Regardless of lower tendon stiffness in the elderly as compared to the young, the present series of studies suggest that tendon function is maintained in the elderly when movements are performed with intensities matched on a relative scale for these two age groups (III). This maintained tendon function is most probably achieved with the observed different muscle activity strategies and therefore age-specific fascicle function.

6) Based on the results of the present studies (III, IV) it seems that the young and the elderly have obtained a different strategy to increase fascicle stiffness when force requirements increase. It seems that the elderly adapt to increased force requirements by decreasing the operating length of muscle fascicles already before the contact instant whereas in young individuals the regulation occurs during the braking phase. The exact reasons for this age-specificity need to be confirmed in future studies.

7) 11 weeks of hopping training increased the rebound height and RSI in the physically active elderly (IV). The improvement in performance after training was not caused by increased neural drive or GaM tendon stiffness, but was achieved with shorter GaM operating lengths and therefore increased fascicle stiffness and improved tendon utilization.

8) Based on results of the present study (IV), hopping training could be recommended at least for healthy fit elderly to retain and improve fast force production capacity. In addition, the short contact hopping performed in the present study that loads mainly ankle joints could also help walking ability in the elderly by increasing push-off power since the ankle joints are reported to be the weakest link during walking in the elderly.

YHTEENVETO

Toiminnallinen lihasarkkitehtuuri ikääntyneillä

Ikääntymisen tiedetään johtavan lihasten voimantuottokyvyn laskuun, millä on vaikutusta esimerkiksi ikääntyneiden ihmisten kykyyn liikkua itsenäisesti. Lihasmassan lasku (sarkopenia) ei täysin selitä voimantuottokyvyn laskua vaan muita vaikuttavia tekijöitä ovat mm. keskushermoston kyky aktivoida lihasta sekä lihaksen supistuvan komponentin (lihassolukimput eli fasikulukset) ja jänteen mekaaniset ominaisuudet ja yhteistoiminta. Erityisesti 2000-luvun alkuun saakka ihmisen hermolihasjärjestelmän ikääntymistä ja erityisesti sen rakennetta käsittelevät tutkimukset keskittyivät lähes yksinomaan isometrisiin tilanteisiin. Luonnollinen liikkumisemme on kuitenkin luonteeltaan dynaamista ja hyvin monimutkaista hermolihasjärjestelmän toiminnan kannalta, joten kun halutaan saada tietoa ikääntymisen vaikutuksista tilanteissa, joissa mm. suurin osa kaatumisista tapahtuu, tulee mittauksia pystyä tekemään myös dynaamisissa kuormitustilanteissa.

Ultraääniteknologian kehittyessä viime vuosina siitä on tullut väline, joka on mahdollistanut lihaksen toiminnan tutkimisen myös liikkeen aikana ja täten luonut mahdollisuuden myös konkreettisesti nähdä, miten ikääntyminen vaikuttaa lihaksen supistuvan komponentin ja jänteen yhteistoimintaan erilaisissa dynaamisissa kuormitustilanteissa. Fasikulusten ja jänteen yhteistoiminta liikkeen aikana vaikuttaa mm. liikkumisen taloudellisuuteen ja sen on aikaisemmissa tutkimuksissa todettu olevan riippuvainen liikkumisen muodosta (esim. kävely, juoksu, hyppely), intensiteetistä ja tutkittavasta lihaksesta.

Aikaisemmat tutkimukset, joita löytyy hyvin vähän, ovat raportoineet, että ikääntyminen vaikuttaa lihaksen supistuvan komponentin ja jänteen yhteistoimintaan kävelyssä. Vaikuttaa siltä, että vaikka hermolihasjärjestelmän toimintakyky vääjäämättä heikkenee ihmisen ikääntyessä, toimii se optimaalisesti sellaisissa tilanteissa, joita kohdataan yleisesti jokapäiväisessä elämässä. Tämä on nähtävissä erityisesti silloin kun ikääntyneet saavat valita itse oman toimintaintensiteettinsä (esim. kävelynopeus), joka on yleensä alhaisempi kuin nuorten vastaava. Kuitenkin ikääntyneet kohtaavat välillä myös tilanteita, joissa tarvitaan tavanomaista korkeampia voimatasoja ja erityisesti nopeaa voimantuottokykyä. Näin on esimerkiksi, kun tasapaino yritetään pitää yllä horjahtaessa tai liukastuessa. Tällä hetkellä on hyvin vähän tietoa siitä, miten ikääntyminen vaikuttaa monimutkaisten dynaamisten liikkeiden säätelyyn ja lihaksen supistuvan komponentin ja jänteen yhteistoimintaan niiden aikana. Lisäksi on epäselvää, ovatko mahdolliset ikämuutokset selitettävissä eroilla keskushermoston kyvyssä aktivoida lihaksia vai muutoksilla lihasjännekompleksin mekaanisissa ominaisuuksissa.

Tämän väitöskirjaprojektin tarkoituksena oli selvittää, mitä vaikutuksia ihmisen ikääntymisellä on hermolihasjärjestelmän toimintaan sekä fasikulusten ja jänteen yhteistoimintaan monimutkaisissa hyvin nopeissa dynaamisissa kuormitustilanteissa. Lisäksi tutkimus pyrki selvittämään, ovatko mahdolliset ikämuutokset palautettavissa harjoittelulla lähemmäs nuorten tasoa ja jos ovat niin millä hermolihasjärjestelmän osa-alueilla muutoksia tapahtuu. Tutkittavaksi lihasryhmäksi valittiin nilkan ojentajalihakset (plantaarifleksorit), sillä niillä on tärkeä rooli tasapainon ylläpidossa sekä kävelyn aikana. Lisäksi tutkimuksissa on todettu, että nilkkanivelen toimintakyky on heikoin lenkki ikääntyneillä kävelyssä, joten siihen vaikuttavien rakenteiden harjoittaminen on toiminnallisesti tärkeää.

Väitöskirja koostuu kolmesta osatutkimuksesta, joista kaksi on poikittaistutkimuksia, joissa verrataan nuoria ja ikääntyneitä toisiinsa. Kolmas tutkimus on pitkittäistutkimus, jossa toteutettiin 11 viikon hyppelyharjoittelu ikääntyneille. Tutkimussarjan koehenkilöinä olivat 21 nuorta 20-32 –vuotiasta ja 57 ikääntynyttä 65-80 –vuotiasta vapaaehtoista, jotka harrastivat liikuntaa keskimäärin neljä kertaa (6 tuntia) viikossa. Tutkimussarjassa mitattiin pudotushyppyjä kelkkaergometrissä (1. osatutkimus) sekä nopeakontaktista päkiähyppelyä tasamaalla (2. osatutkimus). Ikääntyneille toteutettu harjoittelu (3. osatutkimus) oli päkiähyppelyä, jota tehtiin laboratorio-olosuhteissa 11 viikon ajan kolme kertaa viikossa. Hyppyjen aikana rekisteröitiin yhtä aikaisesti reaktiovoimia, kinematiikkaa, lihasaktivaatiota sekä lihaksen supistuvan komponentin ja jänteen pituuden muutoksia ultraäänilaitteella.

Väitöskirjaprojektin tulokset osoittivat, että ikääntyneillä ja nuorilla on erilaiset nilkan ojentajalihasten aktivaatiomallit pudotushyppyjen ja päkiähyppelyn aikana. Nuoriin verrattuna tyypillinen agonistiaktivaatiomalli ikääntyneillä on korkea esiaktivaatio, alhaisempi aktivaatio jarrutusvaiheessa ja korkeampi aktivaatio hypyn työntövaiheessa. Erilainen aktivaatiomalli vaikuttaa myös fasikulusten toimintaan jarrutusvaiheessa, jolloin fasikulukset lyhenevät selvästi vähemmän ikääntyneillä kuin nuorilla. Tutkimuksessa havaittiin myös, että ikääntyneillä on kyky muuttaa lihasaktivaatiomalliaan. Tästä huolimatta näyttäisi siltä, että ikääntyneillä ja nuorilla on erilaiset optimaaliset lihasaktivaatiomallit ja siten fasikulusten toiminta. Tämä johtuu todennäköisesti ikääntymisen seurauksena tapahtuvasta motoristen yksiköiden uudelleenjärjestäytymisestä ja / tai jänteen löystymisestä, joka havaittiin myös tässä väitöskirjaprojektissa. Tutkimuksen tulokset osoittavat kuitenkin, että jänteen toiminta säilyy ikääntymisessä erityisesti silloin kun ikääntyneet ja nuoret liikkuvat suhteellisesti samanlaisilla kuormitusintensiteeteillä. Tutkimuksen tulokset vahvistavat lisäksi teoriaa, jonka mukaan ikääntyneiden hermolihasjärjestelmä pystyy optimoimaan siihen kohdistuvan kuormituksen siten, että suuret voimat ohjataan kohdistumaan suuremmille lihasryhmille silloin kuin ne voisivat ylittää heikompien lihasryhmien sietokyvyn. Väitöskirjaprojektin viimeinen osatutkimus osoitti, että 11 viikon hyppelyharjoittelu oli turvallisesti toteutettavissa fyysisesti aktiivisille iäkkäille miehille. Harjoittelu paransi iäkkäiden suorituskykyä ja sitä voidaan siten suositella terveille hyväkuntoisille ikääntyneille pitämään yllä ja parantamaan nilkan ojentajalihasten nopeaa voimantuottokykyä. Harjoittelun kohdistaminen nimenomaan nilkan ojentajille parantaa todennäköisesti kävelynopeutta kasvattamalla työntövoimaa kontaktin loppuvaiheessa sekä parantaa tasapainokykyä ja siten edesauttaa ikääntyneiden itsenäistä ja turvallista liikkumista.

REFERENCES

Andersen, J. L. 2003. Muscle fibre type adaptation in the elderly human muscle. Scandinavian Journal of Medicine & Science in Sports 13 (1), 40-47.

Arampatzis, A., Peper, A., Bierbaum, S. & Albracht, K. 2010. Plasticity of human Achilles tendon mechanical and morphological properties in response to cyclic strain. Journal of Biomechanics 43 (16), 3073-3079.

Arampatzis, A., Karamanidis, K. & Albracht, K. 2007. Adaptational responses of the human Achilles tendon by modulation of the applied cyclic strain magnitude. The Journal of Experimental Biology 210 (Pt 15), 2743-2753.

Arampatzis, A., Schade, F., Walsh, M. & Bruggemann, G. P. 2001. Influence of leg stiffness and its effect on myodynamic jumping performance. Journal of Electromyography & Kinesiology 11 (5), 355-364.

Asmussen, E. 1953. Positive and negative muscular work. Acta Physiologica Scandinavica 28 (4), 364-382.

Asmussen, E. & Bonde-Petersen, F. 1974. Storage of elastic energy in skeletal muscles in man. Acta Physiologica Scandinavica 91 (3), 385-392.

Aura, O. & Komi, P. V. 1986. Effects of prestretch intensity on mechanical efficiency of positive work and on elastic behavior of skeletal muscle in stretch-shortening cycle exercise. International Journal of Sports Medicine 7 (3), 137-143.

Avela, J., Santos, P. M. & Komi, P. V. 1996. Effects of differently induced stretch loads on neuromuscular control in drop jump exercise. European Journal of Applied Physiology and Occupational Physiology 72 (5-6), 553-562.

Baratta, R., Solomonow, M., Zhou, B. H., Letson, D., Chuinard, R. & D'Ambrosia, R. 1988. Muscular coactivation. The role of the antagonist musculature in maintaining knee stability. American Journal of Sports Medicine 16 (2), 113-122.

Barber, L. A., Barrett, R. S., Gillett, J. G., Cresswell, A. G. & Lichtwark, G. A. 2013. Neuromechanical properties of the triceps surae in young and older adults. Experimental Gerontology 48 (11), 1147-1155.

Beijersbergen, C. M., Granacher, U., Vandervoort, A. A., DeVita, P. & Hortobágyi, T. 2013. The biomechanical mechanism of how strength and power training improves walking speed in old adults remains unknown. Ageing Research Reviews 12 (2), 618-627.

Bosco, C., Ito, A., Komi, P. V., Luhtanen, P., Rahkila, P., Rusko, H. & Viitasalo, J. T. 1982. Neuromuscular function and mechanical efficiency of human leg extensor muscles during jumping exercises. Acta Physiologica Scandinavica 114 (4), 543-550.

Burnett, R. A., Laidlaw, D. H. & Enoka, R. M. 2000. Coactivation of the antagonist muscle does not covary with steadiness in old adults. Journal of Applied Physiology 89 (1), 61-71.

Butler, R. J., Crowell, H. P.,3rd & Davis, I. M. 2003. Lower extremity stiffness: implications for performance and injury. Clinical Biomechanics 18 (6), 511-517.

Butler, D. L., Grood, E. S., Noyes, F. R. & Zernicke, R. F. 1978. Biomechanics of ligaments and tendons. Exercise and Sport Sciences Reviews 6, 125-181.

Candow, D. G. & Chilibeck, P. D. 2005. Differences in size, strength, and power of upper and lower body muscle groups in young and older men. Journals of Gerontology Series A-Biological Sciences & Medical Sciences 60 (2), 148-156.

Carroll, C. C., Dickinson, J. M., Haus, J. M., Lee, G. A., Hollon, C. J., Aagaard, P., Magnusson, S. P. & Trappe, T. A. 2008. Influence of aging on the in vivo properties of human patellar tendon. Journal of Applied Physiology 105 (6), 1907-1915.

Cavagna, G. A. 1977. Storage and utilization of elastic energy in skeletal muscle. Exercise & Sport Sciences Reviews 5, 89-129.

Cavagna, G. A. & Kaneko, M. 1977. Mechanical work and efficiency in level walking and running. The Journal of Physiology 268 (2), 467-81.

Clark, D. J., Manini, T. M., Fielding, R. A. & Patten, C. 2013. Neuromuscular determinants of maximum walking speed in well-functioning older adults. Experimental Gerontology 48 (3), 358-363.

Couppe, C., Hansen, P., Kongsgaard, M., Kovanen, V., Suetta, C., Aagaard, P., Kjaer, M. & Magnusson, S. P. 2009. Mechanical properties and collagen cross-linking of the patellar tendon in old and young men. Journal of Applied Physiology 107 (3), 880-886.

Cronin, N. J. & Lichtwark, G. 2013. The use of ultrasound to study muscle-tendon function in human posture and locomotion. Gait & Posture 37 (3), 305-312.

Cronin, N. J., Barrett, R. S., Lichtwark, G., Mills, P. M. & Carty, C. P. 2013. Decreased lower limb muscle recruitment contributes to the inability of older adults to recover with a single step following a forward loss of balance. Journal of Electromyography and Kinesiology 23 (5), 1139-1144.

Cronin, N. J., Carty, C. P., Barrett, R. S. & Lichtwark, G. 2011a. Automatic tracking of medial gastrocnemius fascicle length during human locomotion. Journal of Applied Physiology 111 (5), 1491-1496.

Cronin, N. J., Peltonen, J., Sinkjaer, T. & Avela, J. 2011b. Neural compensation within the human triceps surae during prolonged walking. Journal of Neurophysiology 105 (2), 548-553.

Cureton, K. J., Collins, M. A., Hill, D. W. & McElhannon, F. M.,Jr 1988. Muscle hypertrophy in men and women. Medicine and Science in Sports and Exercise 20 (4), 338-344.

de Boer, M. D., Seynnes, O. R., di Prampero, P. E., Pisot, R., Mekjavic, I. B., Biolo, G. & Narici, M. V. 2008. Effect of 5 weeks horizontal bed rest on human muscle thickness and architecture of weight bearing and non-weight bearing muscles. European Journal of Applied Physiology 104 (2), 401-407.

Deschenes, M. R. 2004. Effects of aging on muscle fibre type and size. Sports Medicine 34 (12), 809-824.

DeVita, P. & Hortobágyi, T. 2000. Age causes a redistribution of joint torques and powers during gait. Journal of Applied Physiology 88 (5), 1804-1811.

Dietz, V., Schmidtbleicher, D. & Noth, J. 1979. Neuronal mechanisms of human locomotion. Journal of Neurophysiology 42 (5), 1212-1222.

Enoka, R. M. 1997. Neural adaptations with chronic physical activity. Journal of Biomechanics 30 (5), 447-455.

Farley, C. T., Houdijk, H. H., Van Strien, C. & Louie, M. 1998. Mechanism of leg stiffness adjustment for hopping on surfaces of different stiffnesses. Journal of Applied Physiology 85 (3), 1044-1055.

Finni, T., Hodgson, J. A., Lai, A. M., Edgerton, V. R. & Sinha, S. 2003. Nonuniform strain of human soleus aponeurosis-tendon complex during submaximal voluntary contractions in vivo. Journal of Applied Physiology 95 (2), 829-837.

Finni, T., Komi, P. V. & Lepola, V. 2001. In vivo muscle mechanics during locomotion depend on movement amplitude and contraction intensity. European Journal of Applied Physiology 85 (1-2), 170-176.

Flanagan, E. P., Ebben, W. P. & Jensen, R. L. 2008. Reliability of the reactive strength index and time to stabilization during depth jumps. Journal of Strength and Conditioning Research 22 (5), 1677-1682.

Frontera, W. R., Reid, K. F., Phillips, E. M., Krivickas, L. S., Hughes, V. A., Roubenoff, R. & Fielding, R. A. 2008. Muscle fiber size and function in elderly humans: a longitudinal study. Journal of Applied Physiology 105 (2), 637-642.

Frontera, W. R., Hughes, V. A., Lutz, K. J. & Evans, W. J. 1991. A cross-sectional study of muscle strength and mass in 45- to 78-yr-old men and women. Journal of Applied Physiology 71 (2), 644-650.

Fukunaga, T., Kubo, K., Kawakami, Y., Fukashiro, S., Kanehisa, H. & Maganaris, C. N. 2001a. In vivo behaviour of human muscle tendon during walking. Proceedings.Biological Sciences/The Royal Society 268 (1464), 229-233.

Fukunaga, T., Miyatani, M., Tachi, M., Kouzaki, M., Kawakami, Y. & Kanehisa, H. 2001b. Muscle volume is a major determinant of joint torque in humans. Acta Physiologica Scandinavica 172 (4), 249-255.

Gerus, P., Rao, G. & Berton, E. 2011. A method to characterize in vivo tendon force-strain relationship by combining ultrasonography, motion capture and loading rates. Journal of Biomechanics 44 (12), 2333-2336.

Gollhofer, A., Strojnik, V., Rapp, W. & Schweizer, L. 1992. Behaviour of triceps surae muscle-tendon complex in different jump conditions. European Journal of Applied Physiology & Occupational Physiology 64 (4), 283-291.

Grieve, D., Pheasant, S. & Cavanagh, P. R. 1978. Prediction of gastrocnemius length from knee and ankle joint posture. In E. Asmussen & K. Jorgensen (Eds.) International Series on biomechanics, vol. 2A. Baltimore: University Park Press, 405-405–412.

Griffiths, R. I. 1991. Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. Journal of Physiology 436, 219-236.

Häkkinen, K., Alen, M., Kallinen, M., Izquerdo, M., Jokelainen, K., Lassila, H., Mälkiä, E., Kraemer, W. J. & Newton, R. U. 1998a. Muscle CSA, force production, and activation of leg extensors during isometric and dynamic actions in middle-aged and elderly men and women. Journal of Aging and Physical Activity (6), 232-232-247.

Häkkinen, K., Kallinen, M., Izquierdo, M., Jokelainen, K., Lassila, H., Malkia, E., Kraemer, W. J., Newton, R. U. & Alen, M. 1998b. Changes in agonist-antagonist EMG, muscle CSA, and force during strength training in middle-aged and older people. Journal of Applied Physiology 84 (4), 1341-1349.

Häkkinen, K. & Komi, P. V. 1983. Electromyographic changes during strength training and detraining. Medicine and Science in Sports and Exercise 15 (6), 455-460.

Hansen, P., Aagaard, P., Kjaer, M., Larsson, B. & Magnusson, S. P. 2003. Effect of habitual running on human Achilles tendon load-deformation properties and cross-sectional area. Journal of Applied Physiology 95 (6), 2375-2380.

Hawkins, D. & Hull, M. 1990. A method for determining lower extremity muscle-tendon lengths during flexion / extension movements. Journal of Biomechanics 23 (5), 487-494.

Heinonen, A., Kannus, P., Sievanen, H., Oja, P., Pasanen, M., Rinne, M., Uusi-Rasi, K. & Vuori, I. 1996. Randomised controlled trial of effect of high-impact exercise on selected risk factors for osteoporotic fractures. Lancet 348 (9038), 1343-1347.

Hermens, H. J., Freriks, B., Merletti, R., Hägg, G., Stegeman, D. & Blok, J. e. a. 1999. SENIAM 8: European recommendations for surface electromyography. Roessingh Research and Development bv.

Hill, A. V. 1938. The heat of shortening and the dynamic constants of muscle. Proceedings of the Royal Society B: Biological Sciences 126, 136-136-195.

Hobara, H., Kanosue, K. & Suzuki, S. 2007. Changes in muscle activity with increase in leg stiffness during hopping. Neuroscience Letters 418 (1), 55-59.

Hof, A. L. 2003. Muscle mechanics and neuromuscular control. Journal of Biomechanics 36 (7), 1031-1038.

Hof, A. L. 1998. In vivo measurement of the series elasticity release curve of human triceps surae muscle. Journal of Biomechanics 31 (9), 793-800.

Hoffer, J. A., Caputi, A. A., Pose, I. E. & Griffiths, R. I. 1989. Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat. Progress in Brain Research 80, 75-85.

Horita, T., Komi, P. V., Nicol, C. & Kyrolainen, H. 2002. Interaction between pre-landing activities and stiffness regulation of the knee joint musculoskeletal system in the drop jump: implications to performance. European Journal of Applied Physiology 88 (1-2), 76-84.

Hortobágyi, T., Solnik, S., Gruber, A., Rider, P., Steinweg, K., Helseth, J. & DeVita, P. 2009. Interaction between age and gait velocity in the amplitude and timing of antagonist muscle coactivation. Gait & Posture 29 (4), 558-564.

Hortobágyi, T. & DeVita, P. 2006. Mechanisms responsible for the age-associated increase in coactivation of antagonist muscles. Exercise and Sport Sciences Reviews 34 (1), 29-35.

Hortobágyi, T., Tunnel, D., Moody, J., Beam, S. & DeVita, P. 2001. Low- or high-intensity strength training partially restores impaired quadriceps force accuracy and steadiness in aged adults. The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences 56 (1), B38-47.

Hortobágyi, T. & DeVita, P. 2000. Muscle pre- and coactivity during downward stepping are associated with leg stiffness in aging. Journal of Electromyography & Kinesiology 10 (2), 117-126.

Houghton, L. A., Dawson, B. T. & Rubenson, J. 2013. Effects of plyometric training on achilles tendon properties and shuttle running during a simulated cricket batting innings. Journal of Strength and Conditioning Research 27 (4), 1036-1046.

Hughes, V. A., Frontera, W. R., Wood, M., Evans, W. J., Dallal, G. E., Roubenoff, R. & Fiatarone Singh, M. A. 2001. Longitudinal muscle strength changes in older adults: influence of muscle mass, physical activity, and health. The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences 56 (5), B209-17.

Hunter, S. K., Thompson, M. W. & Adams, R. D. 2000. Relationships among age-associated strength changes and physical activity level, limb dominance, and muscle group in women. The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences 55 (6), B264-73.

Ishikawa, M., Pakaslahti, J. & Komi, P. V. 2007. Medial gastrocnemius muscle behavior during human running and walking. Gait & Posture 25 (3), 380-384.

Ishikawa, M., Komi, P. V., Finni, T. & Kuitunen, S. 2006. Contribution of the tendinous tissue to force enhancement during stretch-shortening cycle exercise depends on the prestretch and concentric phase intensities. Journal of Electromyography & Kinesiology 16 (5), 423-431.

Ishikawa, M. & Komi, P. V. 2004. Effects of different dropping intensities on fascicle and tendinous tissue behavior during stretch-shortening cycle exercise. Journal of Applied Physiology 96 (3), 848-852.

Ishikawa, M., Finni, T. & Komi, P. V. 2003. Behaviour of vastus lateralis muscle-tendon during high intensity SSC exercises in vivo. Acta Physiologica Scandinavica 178 (3), 205-213.

Jones, G. M. & Watt, D. G. 1971. Observations on the control of stepping and hopping movements in man. The Journal of Physiology 219 (3), 709-727.

Kallio, J., Sogaard, K., Avela, J., Komi, P., Selanne, H. & Linnamo, V. 2012. Age-related decreases in motor unit discharge rate and force control during isometric plantar flexion. Journal of Electromyography and Kinesiology 22 (6), 983-989.

Kaneko, M., Komi, P. V. & Aura, O. 1984. Mechanical efficiency of concentricand eccentric exercises performed with medium to fast contractionrates. Scandinavian Journal Sports Science (6), 15-20.

Karamanidis, K. & Arampatzis, A. 2006. Mechanical and morphological properties of human quadriceps femoris and triceps surae muscle-tendon unit in relation to aging and running. Journal of Biomechanics 39 (3), 406-417.

Karamanidis, K. & Arampatzis, A. 2005. Mechanical and morphological properties of different muscle-tendon units in the lower extremity and running mechanics: effect of aging and physical activity. Journal of Experimental Biology 208 (Pt 20), 3907-3923.

Kawakami, Y., Muraoka, T., Ito, S., Kanehisa, H. & Fukunaga, T. 2002. In vivo muscle fibre behaviour during counter-movement exercise in humans reveals a significant role for tendon elasticity. Journal of Physiology 540 (Pt 2), 635-646.

Kjaer, M. 2004. Role of extracellular matrix in adaptation of tendon and skeletal muscle to mechanical loading. Physiological Reviews 84 (2), 649-698.

Klein, C. S., Rice, C. L. & Marsh, G. D. 2001. Normalized force, activation, and coactivation in the arm muscles of young and old men. Journal of Applied Physiology 91 (3), 1341-1349.

Komi, P. V. 2000. Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. Journal of Biomechanics 33 (10), 1197-1206.

Komi, P. V. & Bosco, C. 1978. Utilization of stored elastic energy in leg extensor muscles by men and women. Medicine & Science in Sports 10 (4), 261-265.

Komi, P. V., Gollhofer, A., Schmidtbleicher, D. & Frick, U. 1987. Interaction between man and shoe in running: considerations for a more comprehensive measurement approach. International Journal of Sports Medicine 8 (3), 196-202.

Kubo, K., Ikebukuro, T., Maki, A., Yata, H. & Tsunoda, N. 2012. Time course of changes in the human Achilles tendon properties and metabolism during training and detraining in vivo. European Journal of Applied Physiology 112 (7), 2679-2691.

Kubo, K., Morimoto, M., Komuro, T., Yata, H., Tsunoda, N., Kanehisa, H. & Fukunaga, T. 2007. Effects of plyometric and weight training on muscle-tendon complex and jump performance. Medicine and Science in Sports and Exercise 39 (10), 1801-1810.

Kubo, K., Ohgo, K., Takeishi, R., Yoshinaga, K., Tsunoda, N., Kanehisa, H. & Fukunaga, T. 2006. Effects of isometric training at different knee angles on the muscle-tendon complex in vivo. Scandinavian Journal of Medicine & Science in Sports 16 (3), 159-167.

Kubo, K., Kanehisa, H. & Fukunaga, T. 2005. Effects of cold and hot water immersion on the mechanical properties of human muscle and tendon in vivo. Clinical Biomechanics 20 (3), 291-300.

Kubo, K., Kanehisa, H., Azuma, K., Ishizu, M., Kuno, S. Y., Okada, M. & Fukunaga, T. 2003a. Muscle architectural characteristics in women aged 20-79 years. Medicine & Science in Sports & Exercise 35 (1), 39-44.

Kubo, K., Kanehisa, H., Miyatani, M., Tachi, M. & Fukunaga, T. 2003b. Effect of low-load resistance training on the tendon properties in middle-aged and elderly women. Acta Physiologica Scandinavica 178 (1), 25-32.

Kubo, K., Kanehisa, H., Azuma, K., Ishizu, M., Kuno, S. Y., Okada, M. & Fukunaga, T. 2003c. Muscle architectural characteristics in young and elderly men and women. International Journal of Sports Medicine 24 (2), 125-130.

Kubo, K., Kanehisa, H. & Fukunaga, T. 2001. Effects of different duration isometric contractions on tendon elasticity in human quadriceps muscles. The Journal of Physiology 536 (Pt 2), 649-655.

Kubo, K., Kawakami, Y. & Fukunaga, T. 1999. Influence of elastic properties of tendon structures on jump performance in humans. Journal of Applied Physiology 87 (6), 2090-2096.

Kuitunen, S., Ogiso, K. & Komi, P. V. 2011. Leg and joint stiffness in human hopping. Scandinavian Journal of Medicine & Science in Sports 21 (6), e159-67.

Kuitunen, S., Kyröläinen, H., Avela, J. & Komi, P. V. 2007. Leg stiffness modulation during exhaustive stretch-shortening cycle exercise. Scandinavian Journal of Medicine & Science in Sports 17 (1), 67-75.

Kuitunen, S., Komi, P. V. & Kyröläinen, H. 2002. Knee and ankle joint stiffness in sprint running. Medicine & Science in Sports & Exercise 34 (1), 166-173.

Kurokawa, S., Fukunaga, T. & Fukashiro, S. 2001. Behavior of fascicles and tendinous structures of human gastrocnemius during vertical jumping. Journal of Applied Physiology 90 (4), 1349-1358.

Kyröläinen, H. & Komi, P. 2011. Mechanical Efficiency of SSC Exercise. In P. Komi (Ed.) Neuromuscular Aspects of Sport Performance.Oxford, UK: Wiley-Blackwell.

Kyröläinen, H., Avela, J., McBride, J. M., Koskinen, S., Andersen, J. L., Sipila, S., Takala, T. E. & Komi, P. V. 2005. Effects of power training on muscle structure and neuromuscular performance. Scandinavian Journal of Medicine & Science in Sports 15 (1), 58-64.

Kyröläinen, H., Takala, T. E. & Komi, P. V. 1998. Muscle damage induced by stretch-shortening cycle exercise. Medicine and Science in Sports and Exercise 30 (3), 415-420.

Lanza, I. R., Towse, T. F., Caldwell, G. E., Wigmore, D. M. & Kent-Braun, J. A. 2003. Effects of age on human muscle torque, velocity, and power in two muscle groups. Journal of Applied Physiology 95 (6), 2361-2369.

LaRoche, D. P., Cremin, K. A., Greenleaf, B. & Croce, R. V. 2010. Rapid torque development in older female fallers and nonfallers: a comparison across lower-extremity muscles. Journal of Electromyography and Kinesiology 20 (3), 482-488.

Lichtwark, G. A., Bougoulias, K. & Wilson, A. M. 2007. Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running. Journal of Biomechanics 40 (1), 157-164.

Lichtwark, G. A. & Wilson, A. M. 2006. Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. Journal of Experimental Biology 209 (Pt 21), 4379-4388.

Lichtwark, G. A. & Wilson, A. M. 2005a. Effects of series elasticity and activation conditions on muscle power output and efficiency. The Journal of Experimental Biology 208 (Pt 15), 2845-2853.

Lichtwark, G. A. & Wilson, A. M. 2005b. In vivo mechanical properties of the human Achilles tendon during one-legged hopping. The Journal of Experimental Biology 208 (Pt 24), 4715-4725.

Liu, Y., Peng, C. H., Wei, S. H., Chi, J. C., Tsai, F. R. & Chen, J. Y. 2006. Active leg stiffness and energy stored in the muscles during maximal counter movement jump in the aged. Journal of Electromyography & Kinesiology 16 (4), 342-351.

Liu, Y., Schlumberger, A., Wirth, K., Schmidtbleicher, D. & Steinacker, J. M. 2003. Different effects on human skeletal myosin heavy chain isoform expression: strength vs. combination training. Journal of Applied Physiology 94 (6), 2282-2288.

Magnusson, S. P., Beyer, N., Abrahamsen, H., Aagaard, P., Neergaard, K. & Kjaer, M. 2003a. Increased cross-sectional area and reduced tensile stress of the Achilles tendon in elderly compared with young women. The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences 58 (2), 123-127.

Magnusson, S. P., Hansen, P., Aagaard, P., Brond, J., Dyhre-Poulsen, P., Bojsen-Moller, J. & Kjaer, M. 2003b. Differential strain patterns of the human gastrocnemius aponeurosis and free tendon, in vivo. Acta Physiologica Scandinavica 177 (2), 185-195.

Malatesta, D., Simar, D., Dauvilliers, Y., Candau, R., Borrani, F., Prefaut, C. & Caillaud, C. 2003. Energy cost of walking and gait instability in healthy 65- and 80-yr-olds. Journal of Applied Physiology 95 (6), 2248-2256.

Malisoux, L., Francaux, M., Nielens, H. & Theisen, D. 2006. Stretch-shortening cycle exercises: an effective training paradigm to enhance power output of human single muscle fibers. Journal of Applied Physiology 100 (3), 771-779.

McNeil, C. J., Vandervoort, A. A. & Rice, C. L. 2007. Peripheral impairments cause a progressive age-related loss of strength and velocity-dependent power in the dorsiflexors. Journal of Applied Physiology 102 (5), 1962-1968.

Mian, O. S., Thom, J. M., Ardigo, L. P., Minetti, A. E. & Narici, M. V. 2007. Gastrocnemius muscle-tendon behaviour during walking in young and older adults. Acta Physiologica 189 (1), 57-65.

Mian, O. S., Thom, J. M., Ardigò, ,L.P., Narici, M. V. & Minetti, A. E. 2006. Metabolic cost, mechanical work, and efficiency during walking in young and older men. Acta Physiologica 186 (2), 127-139.

Moritani, T., Oddsson, L. & Thorstensson, A. 1991. Phase-dependent preferential activation of the soleus and gastrocnemius muscles during hopping in humans. Journal of Electromyography and Kinesiology 1 (1), 34-40.

Morse, C. I., Thom, J. M., Birch, K. M. & Narici, M. V. 2005. Tendon elongation influences the amplitude of interpolated doublets in the assessment of activation in elderly men. Journal of Applied Physiology 98 (1), 221-226.

Morse, C. I., Thom, J. M., Davis, M. G., Fox, K. R., Birch, K. M. & Narici, M. V. 2004. Reduced plantarflexor specific torque in the elderly is associated with a lower activation capacity. European Journal of Applied Physiology 92 (1-2), 219-226.

Narici, M. V. & Maganaris, C. N. 2006. Adaptability of elderly human muscles and tendons to increased loading. Journal of Anatomy 208 (4), 433-443.

Narici, M. V., Maganaris, C. N., Reeves, N. D. & Capodaglio, P. 2003. Effect of aging on human muscle architecture. Journal of Applied Physiology 95 (6), 2229-2234.

Newton, R. U., Hakkinen, K., Hakkinen, A., McCormick, M., Volek, J. & Kraemer, W. J. 2002. Mixed-methods resistance training increases power and strength of young and older men. Medicine and Science in Sports and Exercise 34 (8), 1367-1375.

Norris, J. A., Granata, K. P., Mitros, M. R., Byrne, E. M. & Marsh, A. P. 2007. Effect of augmented plantarflexion power on preferred walking speed and economy in young and older adults. Gait & Posture 25 (4), 620-627.

Official Statistics of Finland (OSF)_A: Population projection [e-publication]. ISSN=1798-5153. 2012, Appendix table 1. Population by age 1900–2060 (years 2020 to 2060: projection). Helsinki: Statistics Finland [referred: 10.4.2014].
Access method:
http://www.tilastokeskus.fi/til/vaenn/2012/vaenn_2012_2012-09-28_tau_001_en.html.

Official Statistics of Finland (OSF)_B: Population projection [e-publication]. ISSN=1798-5153. Helsinki: Statistics Finland [referred: 11.4.2014]. Access method: http://tilastokeskus.fi/til/vaenn/tau_en.html.

Onambele-Pearson, G. L. & Pearson, S. J. 2012. The magnitude and character of resistance-training-induced increase in tendon stiffness at old age is gender specific. Age 34 (2), 427-438.

Panizzolo, F. A., Green, D. J., Lloyd, D. G., Maiorana, A. J. & Rubenson, J. 2013. Soleus fascicle length changes are conserved between young and old adults at their preferred walking speed. Gait & Posture 38 (4), 764-769.

Pearson, S. J., Burgess, K. & Onambele, G. N. 2007. Creep and the in vivo assessment of human patellar tendon mechanical properties. Clinical Biomechanics 22 (6), 712-717.

Peltonen, J., Cronin, N. J., Stenroth, L., Finni, T. & Avela, J. 2013. Viscoelastic properties of the Achilles tendon in vivo. SpringerPlus 2 (1), 212.

Peterson, D. S. & Martin, P. E. 2010. Effects of age and walking speed on coactivation and cost of walking in healthy adults. Gait & Posture 31 (3), 355-359.

Piirainen, J. M., Cronin, N. J., Avela, J. & Linnamo, V. 2014. Effects of plyometric and pneumatic explosive strength training on neuromuscular function and dynamic balance control in 60-70year old males. Journal of Electromyography and Kinesiology 24 (2), 246-252.

Piirainen, J. M., Avela, J., Sippola, N. & Linnamo, V. 2010. Age dependency of neuromuscular function and dynamic balance control. European Journal of Sport Science 10 (1), 69-79.

Pijnappels, M., Bobbert, M. F. & van Dieen, J. H. 2005a. Control of support limb muscles in recovery after tripping in young and older subjects. Experimental Brain Research 160 (3), 326-333.

Pijnappels, M., Bobbert, M. F. & van Dieen, J. H. 2005b. How early reactions in the support limb contribute to balance recovery after tripping. Journal of Biomechanics 38 (3), 627-634.

Portegijs, E., Rantakokko, M., Mikkola, T. M., Viljanen, A. & Rantanen, T. 2014. Association Between Physical Performance and Sense of Autonomy in Outdoor Activities and Life-Space Mobility in Community-Dwelling Older People. Journal of the American Geriatrics Society.

Rack, P. M. & Westbury, D. R. 1974. The short range stiffness of active mammalian muscle and its effect on mechanical properties. The Journal of Physiology 240 (2), 331-350.

Rantalainen, T., Hoffren, M., Linnamo, V., Heinonen, A., Komi, P. V., Avela, J. & Nindl, B. C. 2011. Three-month bilateral hopping intervention is ineffective in initiating bone biomarker response in healthy elderly men. European Journal of Applied Physiology 111 (9), 2155-2162.

Reeves, N. D., Spanjaard, M., Mohagheghi, A. A., Baltzopoulos, V. & Maganaris, C. N. 2009. Older adults employ alternative strategies to operate within their maximum capabilities when ascending stairs. Journal of Electromyography and Kinesiology 19 (2), 57-68.

Reeves, N. D., Narici, M. V. & Maganaris, C. N. 2004. Effect of resistance training on skeletal muscle-specific force in elderly humans. Journal of Applied Physiology 96 (3), 885-892.

Reeves, N. D., Maganaris, C. N. & Narici, M. V. 2003. Effect of strength training on human patella tendon mechanical properties of older individuals. The Journal of Physiology 548 (Pt 3), 971-981.

Roos, M. R., Rice, C. L. & Vandervoort, A. A. 1997. Age-related changes in motor unit function. Muscle & Nerve 20 (6), 679-690.

Rugg, S. G., Gregor, R. J., Mandelbaum, B. R. & Chiu, L. 1990. In vivo moment arm calculations at the ankle using magnetic resonance imaging (MRI). Journal of Biomechanics 23 (5), 495-501.

Savelberg, H. H., Verdijk, L. B., Willems, P. J. & Meijer, K. 2007. The robustness of age-related gait adaptations: can running counterbalance the consequences of ageing? Gait & Posture 25 (2), 259-266.

Scaglioni, G., Ferri, A., Minetti, A. E., Martin, A., Van Hoecke, J., Capodaglio, P., Sartorio, A. & Narici, M. V. 2002. Plantar flexor activation capacity and H reflex in older adults: adaptations to strength training. Journal of Applied Physiology 92 (6), 2292-2302.

Schmitz, A., Silder, A., Heiderscheit, B., Mahoney, J. & Thelen, D. G. 2009. Differences in lower-extremity muscular activation during walking between healthy older and young adults. Journal of Electromyography and Kinesiology 19 (6), 1085-1091.

Seidler, R. D., Alberts, J. L. & Stelmach, G. E. 2002. Changes in multi-joint performance with age. Motor Control 6 (1), 19-31.

Seynnes, O. R., Koesters, A., Gimpl, M., Reifberger, A., Niederseer, D., Niebauer, J., Pirich, C., Muller, E. & Narici, M. V. 2011. Effect of alpine skiing training on tendon mechanical properties in older men and women. Scandinavian Journal of Medicine & Science in Sports 21 Suppl 1, 39-46.

Shephard, R. J. 1997. Aging, Physical Activity and Health. Champaign, IL, USA: Human Kinetic.

Smith, J. L., Edgerton, V. R., Betts, B. & Collatos, T. C. 1977. EMG of slow and fast ankle extensors of cat during posture, locomotion, and jumping. Journal of Neurophysiology 40 (3), 503-513.

Sousa, F., Ishikawa, M., Vilas-Boas, J. P. & Komi, P. V. 2007. Intensity- and muscle-specific fascicle behavior during human drop jumps. Journal of Applied Physiology 102 (1), 382-389.

Stenroth, L., Peltonen, J., Cronin, N. J., Sipila, S. & Finni, T. 2012. Age-related differences in Achilles tendon properties and triceps surae muscle architecture in vivo. Journal of Applied Physiology 113 (10), 1537-1544.

Stevens, J. A. & Olson, S. 2000. Reducing falls and resulting hip fractures among older women. MMWR.Recommendations and reports : Morbidity and mortality weekly report. Recommendations and reports / Centers for Disease Control 49 (RR-2), 3-12.

Stosic, J. & Finni, T. 2011. Gastrocnemius tendon length and strain are different when assessed using straight or curved tendon model. European Journal of Applied Physiology 111 (12), 3151-3154.

Thompson, B. J., Ryan, E. D., Herda, T. J., Costa, P. B., Herda, A. A. & Cramer, J. T. 2014. Age-related changes in the rate of muscle activation and rapid force characteristics. Age 36 (2), 839-849.

Tracy, B. L. & Enoka, R. M. 2002. Older adults are less steady during submaximal isometric contractions with the knee extensor muscles. Journal of Applied Physiology 92 (3), 1004-1012.

van Dieen, J. H., Cholewicki, J. & Radebold, A. 2003. Trunk muscle recruitment patterns in patients with low back pain enhance the stability of the lumbar spine. Spine 28 (8), 834-841.

Welle, S., Totterman, S. & Thornton, C. 1996. Effect of age on muscle hypertrophy induced by resistance training. The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences 51 (6), M270-5.

Winter, D.A. 1990. Biomechanics and Motor Control of Human Movement.

John Wiley & Sons, Inc., Toronto.

Wren, T. A., Yerby, S. A., Beaupre, G. S. & Carter, D. R. 2001. Mechanical properties of the human achilles tendon. Clinical Biomechanics 16 (3), 245-251.

Yoon, S., Tauchi, K. & Takamatsu, K. 2007. Effect of ankle joint stiffness during eccentric phase in rebound jumps on ankle joint torque at midpoint. International Journal of Sports Medicine 28 (1), 66-71.

Young, W. 1995. Laboratory strength assessment of athletes. New Stud Athlete 10, 88-89–96.

Zajac, F. E. 1989. Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. Critical Reviews in Biomedical Engineering 17 (4), 359-411.

ORIGINAL PAPERS

I

AGE-RELATED NEUROMUSCULAR FUNCTION DURING DROP JUMPS

by

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Age-related neuromuscular function during drop jumps

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Hoffrén M, Ishikawa M, Komi PV. Age-related neuromuscular function during drop jumps. *J Appl Physiol* 103: 1276–1283, 2007. First published August 9, 2007; doi:10.1152/japplphysiol.00430.2007.—Muscle- and movement-specific fascicle-tendon interaction affects the performance of the neuromuscular system. This interaction is unknown among elderly and consequently contributes to the lack of understanding the age-related problems on neuromuscular control. The present experiment studied the age specificity of fascicle-tendon interaction of the gastrocnemius medialis (GM) muscle in drop jump (DJ) exercises. Twelve young and thirteen elderly subjects performed maximal squat jumps and DJs with maximal rebound effort on a sledge apparatus. Ankle and knee joint angles, reaction force, and electromyography (EMG) from the soleus (Sol), GM, and tibialis anterior (TA) muscles were measured together with the GM fascicle length by ultrasonography. The results showed that the measured ankle joint stiffness (AJS) during the braking phase correlated positively with the rebound speed in both age groups and that both parameters were significantly lower in the elderly than in young subjects. In both groups, the AJS correlated positively with averaged EMG (aEMG) in Sol during the braking phase and was further associated with GM activation ($r = 0.55$, $P < 0.01$) and TA coactivation (TA/GM $r = -0.4$ $P < 0.05$) in the elderly subjects. In addition, compared with the young subjects, the elderly subjects showed significantly lower GM aEMG in the braking phase and higher aEMG in the push-off phase, indicating less utilization of tendinous tissue (TT) elasticity. These different activation patterns are in line with the mechanical behavior of GM showing significantly less fascicle shortening and relative TT stretching in the braking phase in the elderly than in the young subjects. These results suggest that age-specific muscle activation patterns as well as mechanical behaviors exist during DJs.

stretch-shortening cycle; ultrasound; tendon

NORMAL LOCOMOTION INVOLVES use of stretch-shortening cycle (SSC) muscle action in which the active muscle is first stretched and subsequently shortened (see Ref. 23 for review). This definition applies to the entire muscle-tendon unit (MTU). However, the fascicle and tendon compartments inside MTU can behave differently in each functional phase of SSC (11, 14). This information of how muscle fascicles and tendons interact during human locomotion is very important for further understanding the muscle mechanics in real movement situations. For example, regulation of the fascicle length can play an important role in utilization of tendon elasticity during locomotion and can therefore influence the movement efficiency (11, 18).

Ultrasonographic scanning of muscle fascicles is currently a popular method to study the movement- and muscle-specific fascicle-tendon interaction, for example, in human walking, running, and jumping (34, 41). In addition to the action type-specific findings of these studies, it has been observed that there are also age-related differences in fascicle-tendon behavior during human walking (36). Higher compliance of tendon in elderly individuals may be the reason for the possible age-specific differences. In addition, the higher tendon compliance may explain the lower leg stiffness in elderly as estimated in countermovement jumps (35). However, both in walking and in countermovement jumps, the impact forces are relatively low, and the muscles demonstrate low activity during the braking phase of contact. Therefore, it remains unclear, how the fascicle-tendon interaction and consequently the tendon loading take place among elderly individuals at higher impact force conditions.

With aging humans, the fascicle length and pennation angle reportedly decrease (27, 39), and the tendon compliance increases (20, 29, 37). These changes may influence the force and power production not only in static but also in dynamic movements. Although it is not known in detail whether the muscle activation pattern in agonist muscles shows age-specific modifications, the measurements of antagonist coactivation have shown increased level of coactivation in elderly individuals (7, 15, 40). This increased coactivation may influence the joint stiffness, for example, in downward-stepping condition (17). On the other hand, high joint and/or leg stiffness in the braking phase has been suggested to be prerequisite for efficient SSC performance (3, 9, 12). Thus there is considerable need to explore whether there is age specificity in regulation of the fascicle-tendon interaction during SSC exercises. Such a knowledge can be helpful for planning and improving possible countermeasures for aging effects, for example, by building up the more specific training programs for elderly individuals.

Consequently, the purpose of the present study was to explore the age specificity of fascicle-tendon interaction in drop jump (DJ) exercises. These exercises were designed so that both young and elderly subjects were exposed to similar impact loads followed by maximal rebound (push-off). Considering that muscle activation profiles for both agonist and antagonist muscles may show age-specific differences, the fascicle-tendon interaction was expected to demonstrate reduced rebound performance among elderly compared with young individuals in these controlled situations. Special focus was placed on the calf muscles function because the ankle joint has been shown to play an important role in leg stiffness adjustment (1, 10).

METHODS

Subjects. Twelve young (5 men and 7 women; age 25.2 ± 2.5 yr, height 171.4 ± 7.4 cm, weight 66.8 ± 10.7 kg) and thirteen elderly

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adults (5 men and 8 women; age 69.0 ± 3.8 yr, height 168.0 ± 6.7 cm, weight 67.8 ± 9.8 kg) participated the study as subjects. Both groups were physically active. The young subjects were sport science students, and they exercised 6.3 ± 3.2 h/wk. The elderly subjects were recruited from a local senior gym, and they exercised 5.1 ± 1.8 h/wk. These volumes of physical activity did not differ between the age groups. Before measurements, the subjects were given an informed consent of the procedures and risks associated with the study, and they gave their written consent to participate. Medical screening was performed for the elderly subjects. Exclusion criteria included coronary artery disease, neurological diseases, and current lower extremity and low back pain as well as previous injuries in leg joints. The recommendations contained in the Declaration of Helsinki were followed, and the study was approved by the local ethics committee.

Experimental procedure. The subjects performed the maximal squat jump (SJ) and DJs bilaterally on a sledge apparatus (19). In the DJs, the following dropping heights were chosen: 10 cm, 15 cm, and 20 cm above standing height (DJ10cm, DJ15cm and DJ20cm, respectively). These heights are low for the normal subjects (24), but for safety reasons the elderly subjects could not be dropped from higher heights. The jumps were performed in randomized order. Five accepted trials were required for averaging. Before the measurements, the subjects were asked to perform a 10-min warm-up on a bicycle ergometer and then to perform several DJs to determine the lowest position of the sledge seat for each subject (knee angle 34.4 ± 8.2°; 0° full extension). In DJs, the subjects were instructed to jump with as little knee bending as possible, and this predetermined position was monitored and checked in each trial. The inclination of the sledge was 18° from the horizontal position.

Data recordings. Reaction forces (F_z; perpendicular to the movement plane of the sledge seat), sledge displacement, velocity of the sledge displacement and electromyogram (EMG) activity from the gastrocnemius medialis (GM), soleus (Sol), and tibialis anterior (TA) muscles in the right leg were stored simultaneously to a personal computer through an analog-to-digital converter (sampling rate 2 kHz; Power 1401, Cambridge Electronics Design). Bipolar miniature-size surface electrodes (diameter 6 mm, interelectrode distance 21 mm; Blue Sensor N-00-S/25, Medicotest, Olstykke, Denmark) were used for EMG recording (bandwidth 10 Hz to 1 kHz per 3 dB; model 16-2, EISA, Freiburg, Germany). Before electrode placement, the skin was shaved, abraded, and cleaned with alcohol to secure an interelectrode resistance value below 5 kΩ. The electrode placement followed the procedures used in our laboratory's earlier experiments (see Ref. 41).

All jumps were video recorded with a high-speed video camera at 200 frames/s (Peak Performance) from the right side perpendicular to the line of motion. Reflective markers were placed on trochanter major, the center of rotation of the knee, lateral malleolus, heel, and fifth metatarsal head. These points were then digitized automatically and filtered with Butterworth fourth-order filter (cutoff frequency 8 Hz) using Motus software (Peak Performance) to calculate knee and ankle joint angles.

Longitudinal images of GM muscle of the right leg were recorded (young $n = 12$, elderly $n = 12$) during all movements using a B-mode ultrasonography (model SSD-5500, Aloka) (for details see Ref. 41) with 6-cm linear-array probe (scanning frequency of 7.5 MHz). The images were obtained at 50 images/s. The probe was fixed securely with a special support device made of polystyrene. The superficial and deep aponeuroses and GM fascicle were digitized and tracked from each image. GM fascicle length was defined as the length of the fascicle line between the superficial and deep aponeuroses, and pennation angle was defined as the angle of fascicle line and the deep aponeurosis.

An electronic pulse was used to synchronize the kinetic, kinematic, EMG and ultrasonographic data.

Analyses. The model of Grieve et al. (13) was used to calculate GM MTU length changes. MTU data were resampled at 50 Hz to match the time scale of the ultrasound data. The length of the GM tendinous tissue (TT; free tendon and aponeuroses) was calculated by subtracting the horizontal length part of the fascicle from the MTU length as follows (33):

$$L_{TT} = L_{MTU} - L_{fa}\cdot\cos\alpha,$$

where L_{TT} is the TT length, L_{MTU} is the MTU length, L_{fa} is the fascicle length, and α is the fascicle angle between fascicle line and the aponeurosis.

Table 1. *Measured and estimated mechanical parameters*

			DJ10cm	DJ15cm	DJ20cm
Take-off speed, ms	b	Young	1.38±0.23	1.42±0.24	1.46±0.24[d]
		Elderly	1.05±0.21	1.11±0.23[d]	1.13±0.22[d]
Rel peak F_z (to bw)	c	Young	2.41±0.26	2.60±0.25[d]	2.74±0.31[e,f]
		Elderly	1.78±0.38	1.92±0.40[d]	2.11±0.44[d]
Contact time, ms	b	Young	365±42	348±30	335±30[d]
		Elderly	439±61	430±71	418±56
Braking phase, ms	$P = 0.055$	Young	170±37	156±26	152±24[d]
		Elderly	190±41	193±47	184±37
Push-off phase, ms	c	Young	195±17	192±17	183±18[e,f]
		Elderly	249±33	236±30[e]	234±25
AJS, N·m deg	a	Young	8.5±5.7	6.9±4.2	6.2±3.6
		Elderly	4.5±2.0	3.8±1.9	3.8±1.7

Values are means ± SD for 12 young and 13 elderly subjects. Rel peak F_z is vertical ground reaction force relative to body weight (bw); AJS is ankle joint stiffness during the braking phase; DJ10cm, DJ15cm, DJ20cm are dropping conditions for drop jumps 10 cm, 15 cm, and 20 cm above standing height, respectively. [a]Elderly significantly different from young, $P < 0.05$. [b]Elderly significantly different from young, $P < 0.01$. [c]Elderly significantly different from young $P < 0.001$. [d]Significantly different from DJ10cm, $P < 0.05$. [e]Significantly different from DJ10cm, $P < 0.01$. [f]Significantly different from DJ15cm, $P < 0.05$.

The ankle joint moment was estimated from the F_z and kinematics similarly to Kawakami et al. (21). The quotient of change in ankle joint moment generated by a right leg (from contact to peak) divided by change in ankle joint angle (from contact to minimum) (31) was used as a value of ankle joint stiffness (AJS) during the braking phase. It must be noted that the peak ankle joint moment and the minimum ankle joint angle do not necessarily occur at the same time. Originally, we calculated the AJS in two ways: with minimum ankle joint angle and peak ankle joint moment and also with minimum ankle joint angle and corresponding moment. Because the results were similar, it was decided to use the peak ankle joint moment for AJS calculations.

EMG signals were first full-wave rectified and then low-pass filtered at 50 Hz. The filtered EMG signals were integrated and then averaged (aEMG) in the following three phases: preactivation, braking, and subsequent push-off phases. The preactivation phase was defined as the 100-ms period preceding the ground contact (25). The transition from the braking to the push-off phase was determined while the sledge was at its lowest position. EMG activities during DJs were normalized to maximal SJ push-off phase aEMG. Force and EMG-data were resampled at 50 Hz to match the time scale of kinematics and ultrasound data.

TA muscle serves as an antagonist to plantar flexors during the contact phase of DJs. To obtain the TA activation during the braking phase more accurately, the braking phase was divided into two halves, and TA aEMGs were calculated separately for those two halves. After that, the activation relative to TA preactivation was defined (change in activation in relation to preactivation value). These calculations were done only for the two highest dropping conditions because the 10-cm dropping height was so low that it was initiated with greater dorsiflexion by some subjects and therefore higher TA preactivation.

Statistics. The results are presented as means ± SD. ANOVA for repeated measurements on two factors was used to test the main effects of dropping condition and age as well as the interactions on different parameters. When applicable, the ANOVA for repeated

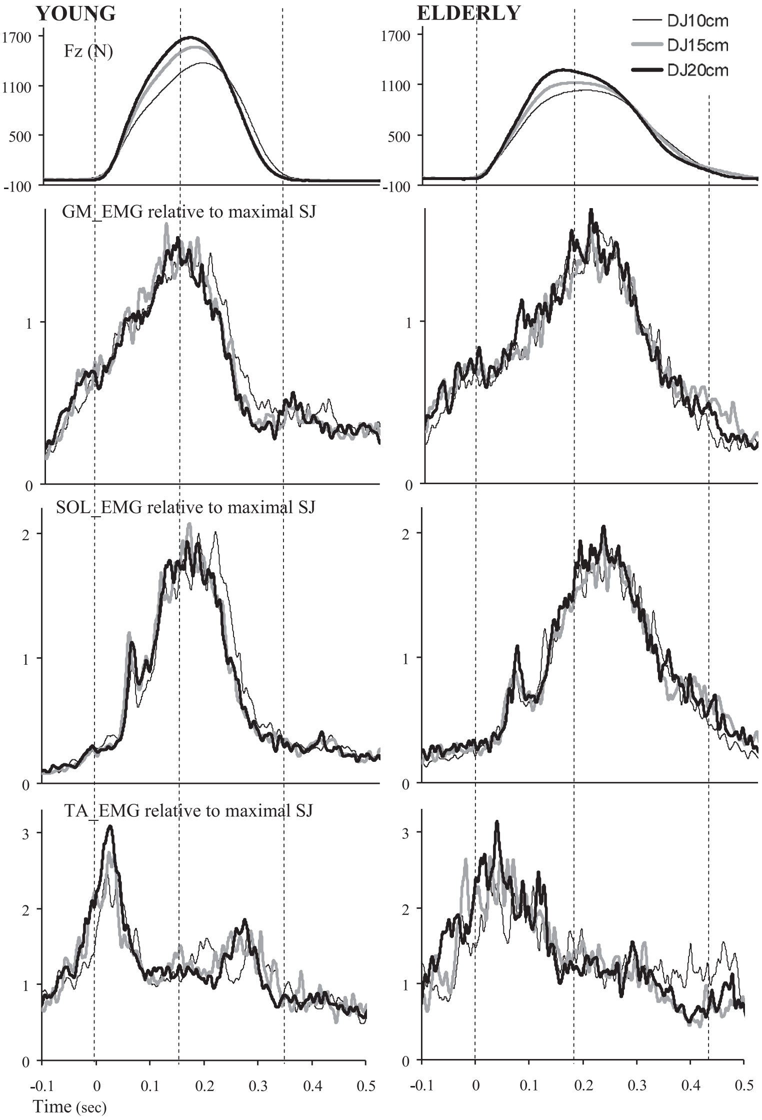

Fig. 1. Averaged force-time and electromyograph (EMG)-time curves for the young and elderly subjects in different drop jump (DJ) conditions [dropping heights 10 cm, 15 cm, and 20 cm above standing height (DJ10cm, DJ15cm and DJ20cm, respectively)]. F_z, vertical ground reaction force; GM, gastrocnemius medialis; Sol, soleus; TA, tibialis anterior. Vertical lines denote the contact moment, the transition point from the braking to push-off phase, and the take-off moment. EMG is normalized to maximal squat jump (SJ) push-off phase average EMG.

measurements on one factor and post hoc Bonferroni were used to determine the significant differences between dropping height conditions separately in young and elderly. Relationships between variables were investigated using Pearson's product-moment correlation coefficient. The level of statistical significance was set at $P < 0.05$.

RESULTS

Mechanical parameters. Sledge take-off speed was used to determine the jumping performance. Take-off speed increased significantly with increasing dropping height in both age groups ($P < 0.01$; Table 1). As expected, the young subjects showed significantly higher values than the elderly subjects in all conditions: in SJ ($P < 0.001$) and in all three DJs ($P < 0.01$).

The elderly subjects had longer total contact time than the young subjects in all jumping conditions (SJ $P < 0.001$, DJs $P < 0.01$). Total contact time decreased with increasing dropping height in the young ($P < 0.05$) but not in the elderly subjects. Also, the duration of the braking phase decreased with increasing dropping height in the young ($P < 0.05$) but not in the elderly subjects. The push-off phase time decreased with increasing dropping height both in the young ($P < 0.01$) and in elderly ($P < 0.01$). The elderly had a significantly longer push-off phase than the young subjects ($P < 0.001$).

Although the absolute dropping heights were the same in both groups, the relative peak F_z (per body weight) was lower in the elderly than in the young subjects ($P < 0.001$). Peak force increased from SJ to DJs ($P < 0.001$ in both groups) and with increasing dropping height (young $P < 0.01$, elderly $P < 0.05$).

EMG activation. The averaged EMG patterns for the young and elderly subjects in different DJ conditions is shown in Fig. 1. Clear preactivation of GM and Sol muscles was followed by the increasing activity in the braking phase and by decreasing activity toward the late push-off.

The young and elderly subjects showed different activation patterns. The young subjects activated their GM muscles more in the braking phase than the elderly subjects ($P < 0.05$). Thereafter, the elderly subjects had higher activation in the push-off phase in both GM and Sol muscles compared with the young subjects ($P < 0.05$). When EMG ratio of braking phase aEMG divided by push-off phase aEMG was calculated, the young subjects showed higher values in both muscles ($P < 0.05$; Fig. 2).

GM preactivity increased with increasing dropping height both in the young ($P < 0.05$) and in elderly subjects ($P < 0.05$). In addition, a significant age × dropping height interaction was observed in the push-off phase activities of GM and Sol muscles ($P < 0.05$ in both muscles): with increasing dropping height the GM and Sol push-off phase aEMGs increased in the elderly but decreased in the young subjects.

Activation of TA muscle, which serves as an antagonist to plantar flexors during the contact phase of DJs, decreased in the braking phase rapidly after the contact in the young subjects (Fig. 1). However, in the elderly subjects, the TA activation remained higher during the braking phase. Therefore, the elderly subjects had higher TA activation than the young subjects during the first half of the braking phase ($P < 0.05$). Also, when coactivation was calculated for both age groups, the elderly subjects showed higher values in TA/Sol activation during the whole braking phase ($P < 0.05$) (Fig. 2).

AJS. The elderly subjects had lower AJS during the braking phase of DJs than the young subjects ($P < 0.05$; Table 1). There was a positive correlation between AJS and jumping performance both in the young and elderly subjects (Table 2). In both age groups, the AJS correlated positively with Sol

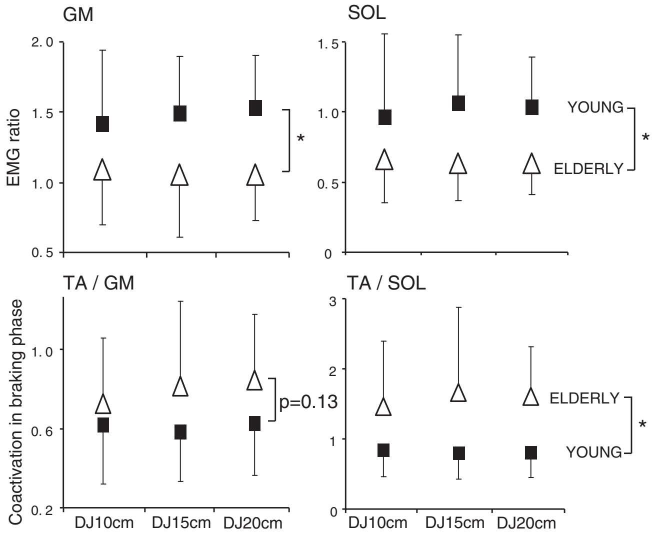

Fig. 2. EMG ratio and coactivation during the braking phase of DJs. EMG ratio was calculated by dividing the braking phase average EMG (aEMG) by the push-off phase aEMG. TA/GM and TA/Sol coactivations during the whole braking phase were calculated by dividing the TA aEMG by the GM or Sol aEMG, respectively. *Elderly significantly different from young subjects, $P < 0.05$.

Table 2. *Correlation coefficients between the selected parameters and AJS (N·m/deg) during the whole braking phase*

	Take-off Speed (ms)	GM aEMG (mV)	Sol aEMG (mV)	TA aEMG (mV)	TA/GM Activation (unitless)	TA/Sol Activation (unitless)	TT/MTU Stretch (unitless)
Young	0.54†	0.06	0.60†	−0.19	−0.30	−0.52†	0.48†
Elderly	0.63‡	0.55†	0.63‡	0.009	−0.40*	−0.62‡	0.77‡

Values are for 12 young and 13 elderly subjects with three dropping conditions. GM, gastrocnemius medialis; Sol, soleus; TA, tibialis anterior; aEMG, averaged electromyography; TT, tendinous tissue; MTU, muscle-tendon unit. $^*P < 0.05$. $†P < 0.01$. $‡P < 0.001$.

braking phase aEMG and the relative TT stretch (TT/MTU stretch) and negatively with TA/Sol EMG during the braking phase. In the elderly subjects, there was also a positive correlation between GM braking phase EMG and AJS and negative correlation between TA/GM EMG and AJS, but those were not observed in the young subjects.

Mechanical behavior of GM. The braking phase was characterized by stretch of MTU and TT, whereas the fascicles shortened. Then, in the push-off phase, MTU as well as TT and fascicles shortened. The age comparison showed slight differences in this behavior (Fig. 3).

First, the elderly subjects had shorter GM fascicle length than the young subjects at the contact moment (5.4 ± 0.9 cm in young vs. 4.5 ± 0.7 cm in elderly; $P < 0.01$). Total fascicle shortening during the contact phase was also less in the elderly than in young subjects (2.0 ± 0.4 cm in young vs. 1.4 ± 0.5 cm in elderly; $P < 0.01$). This was due to less shortening of fascicle in braking phase in the elderly subjects ($P < 0.05$; Fig. 4) because the shortening amplitude in push-off phase was similar between the groups (1.2 ± 0.4 cm in young vs. 0.9 ± 0.5 cm in elderly).

Second, the lengthening of MTU and TT in the braking phase increased with increasing dropping height both in the young (MTU $P < 0.01$, TT $P < 0.05$) and in the elderly subjects (MTU $P < 0.001$, TT $P < 0.01$; Fig. 4). Although there was a trend for greater MTU stretch in the elderly compared with the young subjects ($P = 0.07$), the absolute stretching amplitudes of MTU and TT did not show significant differences between the age groups. However, when TT stretch was calculated in relation to MTU stretch (TT/MTU stretch), the elderly subjects showed lower values ($P < 0.05$; Fig. 4). TT/MTU stretch ratio also decreased with increasing dropping height in the elderly ($P < 0.01$) but not in the young subjects.

Finally, in the push-off phase, there were no significant differences in shortening amplitudes of either MTU, TT or fascicle between the age groups. However, with increasing dropping height, the recoil amplitude of TT increased (2.7 ± 1.0 cm in DJ10cm vs. 3.1 ± 1.1 cm in DJ20cm; $P < 0.05$) and shortening of fascicle decreased (1.4 ± 0.4 cm in DJ10cm vs. 1.1 ± 0.4 cm in DJ20cm; $P < 0.01$) in the young but not in the elderly subjects. Therefore, TT/MTU shortening ratio increased with increasing dropping height in the young (0.64 ± 0.10 in DJ10cm vs. 0.72 ± 0.12 in DJ20cm, $P < 0.05$) but not in the elderly subjects.

DISCUSSION

As expected, the results demonstrated that the elderly had clearly lower performance than the young subjects, as measured by the take-off velocity. Interestingly the elderly had also lower AJS compared with the young subjects. These two parameters were also interrelated, and the age groups showed different activation patterns on the sledge DJs. However, both groups showed similar peak EMG activation levels during the braking phase of DJ relative to SJ. The results therefore suggest that the elderly subjects utilize tendon elasticity less

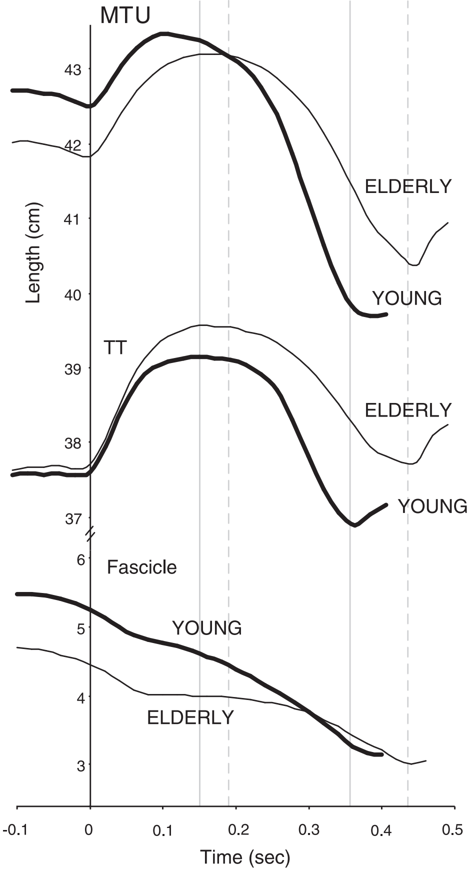

Fig. 3. Averaged length-time curves for GM muscle-tendon unit (MTU), tendinous tissue (TT), and fascicle in the young and in elderly subjects in DJ15cm. *Time 0* is the contact moment. Vertical lines (dotted for the elderly subjects) denote the transition point from the braking to push-off phase and the take-off.

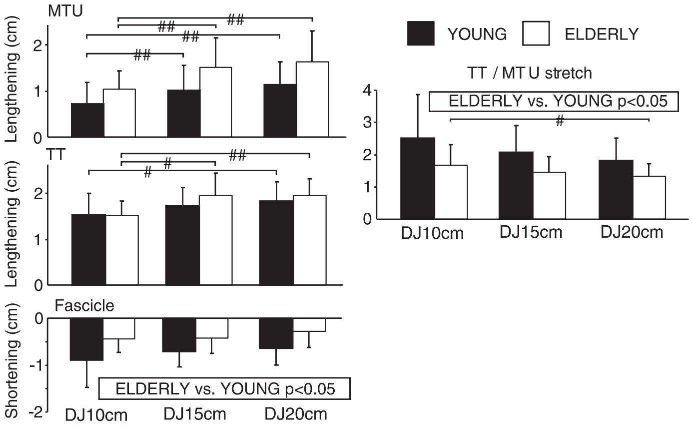

Fig. 4. Length changes of GM MTU, TT and fascicle in the braking phase of DJs in the young and elderly subjects. Lengthening of MTU and TT was calculated from contact moment to peak length. Fascicle length changes were calculated from contact to the end of the braking phase. #Significant difference between the conditions, $P < 0.05$. ##Significant difference between the conditions, $P < 0.01$.

efficiently than their younger counterparts because of the age specificity in activation patterns.

In order for the SSC exercise to be efficient, the high joint stiffness in the braking phase is needed (16, 43). That can be achieved by high activation of agonist muscles in the preactivation and early braking phases (3, 9, 43). In the present study, the DJ performance in the young subjects resembled the more efficient SSC exercise than in the elderly subjects: they had higher AJS (Table 1) and higher GM activation in the braking phase (Fig. 1) than the elderly subjects and thus better jumping performance (Table 1). This higher activation in the braking phase affects also the mechanical behavior of the muscle because the fascicle shortened more in the young subjects in the braking phase, and therefore they had higher TT/MTU stretch ratio than the elderly subjects (Fig. 4).

The AJS correlated positively with jumping performance also in elderly (Table 2). This indicates that those elderly subjects who had higher agonist activation in the braking phase and thus higher AJS jumped better. In general, however, the elderly subjects activated their muscles less in the braking phase than the young subjects and thereafter had more activation in the following push-off phase (Fig. 1). According to previous studies (2, 3, 5), this activation pattern in elderly individuals reflects decreased efficiency to utilize the stored negative work. Interestingly, the activation pattern of the elderly subjects in the present study resembles that of young individuals after excessive SSC exercises (marathon running and DJs) (26, 32). Although the mechanisms in these situations can be totally different, it may be suggested that in both situations (in fatigued marathon runners and in elderly individuals) the impact loads are not sufficiently tolerable. This comparison suggests, however, that there may be room for the proper training to possibly modify the activation pattern and/or joint stiffness among elderly individuals so that they would resemble closer to those of young individuals.

In addition to differences in agonist activation, the elderly showed also greater coactivation of TA muscle during the braking phase of DJs than the young subjects (Fig. 2). High coactivation is reportedly associated with increased joint stiffness in stabilizing actions (4, 42). However, in SSC exercise, like DJ in the present study, it is likely that increased antagonist coactivation makes the ankle joint more compliant in the braking phase (Table 2). Although it is not easy to understand why elderly had higher coactivation, it may be related to the strategy to reduce joint stiffness and lower the impact loads during the braking phase. Even if this were true, it still remains open whether this happens purposely or unconsciously.

Contrary to many animal experiments (see Ref. 22 for review), the human studies have suggested that tendon stiffness may decrease with aging (20, 29, 37). Although the stiffness was not calculated in the present study, its decrease would increase the tendon strain for a given load and therefore could be advantageous in utilization of elastic energy in SSC exercises (9, 28, 30). However, the present study suggests that elderly individuals utilize tendon elasticity less efficiently than young individuals. This is likely to be due to the observed

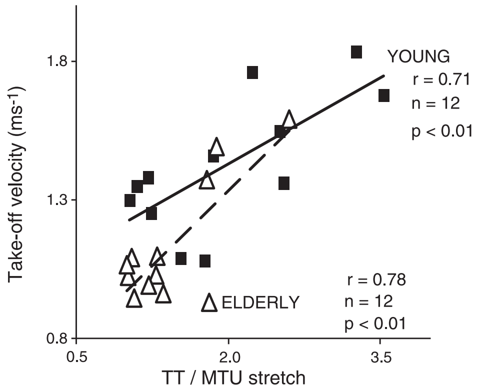

Fig. 5. Influence of TT/MTU stretch on jumping performance in the young and in elderly subjects in DJ15cm.

lower muscle activation in the braking phase among elderly individuals and consequently their less ability to stiffen the fascicles and ankle joints resulting in lower TT/MTU stretch ratio. In line with this suggestion, TT/MTU stretch ratio and jumping performance intercorrelated positively in both age groups (Fig. 5). This would mean that those elderly subjects who could shorten the fascicle more in the braking phase and thus had higher TT/MTU stretch ratio jumped better. A more compliant tendon could also increase the TT/MTU stretch ratio under high agonist activation, that would allow the adequate joint stiffness.

Because we were only examining calf muscles in the present study we do not know whether similar findings could be observed, for example, for thigh muscles. It can also be argued whether the present study design, that uses the same absolute dropping heights (stretch levels), is appropriate when measuring two age groups with obviously different neuromuscular characteristics. It is generally known that the optimal dropping height varies between the individuals and also between the age groups (6). The highest dropping height used was closer to the optimal dropping height for elderly subjects and was very much in the ascending phase in the dropping height vs. rebound height curve for young subjects. However, to use relatively similar stretch levels, the maximum stretch level have to be measured first, which is challenging and certainly risky, when measuring elderly subjects. On the other hand, we believe that it is not totally wrong to use the same stretch levels because the requirements and challenges that young and elderly individuals have to encounter in natural locomotion and in activities of daily living are also similar in absolute level. To confirm the results of the present study, it would be beneficial to study also the relatively similar stretch levels in young and elderly subjects while staying still in the submaximal level.

An important question that remains, however, is whether the present results can be explained *1*) by the influence of reduced physical activity with increasing age and/or *2*) by the aging process itself. With regard to physical activity level, the both age groups had similar habitual physical activity level in hours per week. Consequently the major cause for differences may be the aging process itself. On the other hand, elderly do not usually utilize high-intensity loads in daily activities (8, 38), and the present study made no effort to quantify the possible differences in exercise-intensity levels. Thus to separate the roles of changes in physical activity and the aging process itself may not be so simple.

Finally, the present study gives an impression that elderly individuals perform DJ in a way that it resembles damping in a landing type of movement followed by the increased activation in the less economical push-off phase. Consequently, the resulting lower AJS in the elderly subjects in the braking phase is characterized by lower agonist activation and higher antagonist coactivation. Differences in muscle activation also affect the mechanical behavior of the GM muscle, resulting in lower TT/MTU stretch ratio in the elderly subjects. Therefore, this study suggests that elderly individuals utilize tendon elasticity less efficiently than young individuals.

GRANTS

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REFERENCES

1. **Arampatzis A, Schade F, Walsh M, Bruggemann GP.** Influence of leg stiffness and its effect on myodynamic jumping performance. *J Electromyogr Kinesiol* 11: 355–364, 2001.
2. **Asmussen E.** Positive and negative muscular work. *Acta Physiol Scand* 28: 364–382, 1953.
3. **Asmussen E, Bonde-Petersen F.** Storage of elastic energy in skeletal muscles in man. *Acta Physiol Scand* 91: 385–392, 1974.
4. **Baratta R, Solomonow M, Zhou BH, Letson D, Chuinard R, D'Ambrosia R.** Muscular coactivation. The role of the antagonist musculature in maintaining knee stability. *Am J Sports Med* 16: 113–122, 1988.
5. **Bosco C, Ito A, Komi PV, Luhtanen P, Rahkila P, Rusko H, Viitasalo JT.** Neuromuscular function and mechanical efficiency of human leg extensor muscles during jumping exercises. *Acta Physiol Scand* 114: 543–550, 1982.
6. **Bosco C, Komi PV.** Influence of aging on the mechanical behavior of leg extensor muscles. *Eur J Appl Physiol* 45: 209–219, 1980.
7. **Burnett RA, Laidlaw DH, Enoka RM.** Coactivation of the antagonist muscle does not covary with steadiness in old adults. *J Appl Physiol* 89: 61–71, 2000.
8. **Candow DG, Chilibeck PD.** Differences in size, strength, and power of upper and lower body muscle groups in young and older men. *J Gerontol A Biol Sci Med Sci* 60: 148–156, 2005.
9. **Cavagna GA.** Storage and utilization of elastic energy in skeletal muscle. *Exerc Sport Sci Rev* 5: 89–129, 1977.
10. **Farley CT, Houdijk HH, Van Strien C, Louie M.** Mechanism of leg stiffness adjustment for hopping on surfaces of different stiffnesses. *J Appl Physiol* 85: 1044–1055, 1998.
11. **Fukunaga T, Kubo K, Kawakami Y, Fukashiro S, Kanehisa H, Maganaris CN.** In vivo behaviour of human muscle tendon during walking. *Proc Biol Sci* 268: 229–233, 2001.
12. **Gollhofer A, Strojnik V, Rapp W, Schweizer L.** Behaviour of triceps surae muscle-tendon complex in different jump conditions. *Eur J Appl Physiol* 64: 283–291, 1992.
13. **Grieve D, Pheasant S, Cavanagh PR.** Prediction of gastrocnemius length from knee and ankle joint posture. In: *International Series on Biomechanics,*edited by Asmussen E and Jorgensen K. Baltimore, MD: University Park Press, 1978, vol. 2A, p. 405–412.
14. **Griffiths RI.** Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *J Physiol* 436: 219–236, 1991.
15. **Häkkinen K, Alen M, Kallinen M, Izquerdo M, Jokelainen K, Lassila H, Mälkiä E, Kraemer WJ, Newton RU.** Muscle CSA, force production, and activation of leg extensors during isometric and dynamic actions in middle-aged and elderly men and women. *J Aging Phys Act* 6: 232–247, 1998.
16. **Horita T, Komi PV, Nicol C, Kyrolainen H.** Stretch shortening cycle fatigue: interactions among joint stiffness, reflex, and muscle mechanical performance in the drop jump. *Eur J Appl Physiol* 73: 393–403, 1996.
17. **Hortobagyi T, DeVita P.** Muscle pre- and coactivity during downward stepping are associated with leg stiffness in aging. *J Electromyogr Kinesiol* 10: 117–126, 2000.
18. **Ishikawa M, Komi PV, Finni T, Kuitunen S.** Contribution of the tendinous tissue to force enhancement during stretch-shortening cycle exercise depends on the prestretch and concentric phase intensities. *J Electromyogr Kinesiol* 16: 423–431, 2006.
19. **Kaneko M, Komi PV, Aura O.** Mechanical efficiency of concentric and eccentric exercises performed with medium to fast contraction rates. *Scand J Sports Sci* 6: 15–20, 1984.
20. **Karamanidis K, Arampatzis A.** Mechanical and morphological properties of different muscle-tendon units in the lower extremity and running mechanics: effect of aging and physical activity. *J Exp Biol* 208: 3907–3923, 2005.
21. **Kawakami Y, Muraoka T, Ito S, Kanehisa H, Fukunaga T.** In vivo muscle fibre behaviour during counter-movement exercise in humans reveals a significant role for tendon elasticity. *J Physiol* 540: 635–646, 2002.
22. **Kjaer M.** Role of extracellular matrix in adaptation of tendon and skeletal muscle to mechanical loading. *Physiol Rev* 84: 649–698, 2004.
23. **Komi PV.** Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. *J Biomech* 33: 1197–1206, 2000.

24. **Komi PV, Bosco C.** Utilization of stored elastic energy in leg extensor muscles by men and women. *Med Sci Sports* 10: 261–265, 1978.
25. **Komi PV, Gollhofer A, Schmidtbleicher D, Frick U.** Interaction between man and shoe in running: considerations for a more comprehensive measurement approach. *Int J Sports Med* 8: 196–202, 1987.
26. **Komi PV, Hyvärinen T, Gollhofer A, Mero A.** Man-shoe-surface interaction: special problems during marathon running. *Acta Univ Oul A* 179: 69–72, 1986.
27. **Kubo K, Kanehisa H, Azuma K, Ishizu M, Kuno SY, Okada M, Fukunaga T.** Muscle architectural characteristics in women aged 20–79 years. *Med Sci Sports Exerc* 35: 39–44, 2003.
28. **Kubo K, Kanehisa H, Fukunaga T.** Effects of viscoelastic properties of tendon structures on stretch - shortening cycle exercise in vivo. *J Sports Sci* 23: 851–860, 2005.
29. **Kubo K, Kanehisa H, Miyatani M, Tachi M, Fukunaga T.** Effect of low-load resistance training on the tendon properties in middle-aged and elderly women. *Acta Physiol Scand* 178: 25–32, 2003.
30. **Kubo K, Kawakami Y, Fukunaga T.** Influence of elastic properties of tendon structures on jump performance in humans. *J Appl Physiol* 87: 2090–2096, 1999.
31. **Kuitunen S, Komi PV, Kyrolainen H.** Knee and ankle joint stiffness in sprint running. *Med Sci Sports Exerc* 34: 166–173, 2002.
32. **Kuitunen S, Kyrolainen H, Avela J, Komi PV.** Leg stiffness modulation during exhaustive stretch-shortening cycle exercise. *Scand J Med Sci Sports* 17: 67–75, 2007.
33. **Kurokawa S, Fukunaga T, Fukashiro S.** Behavior of fascicles and tendinous structures of human gastrocnemius during vertical jumping. *J Appl Physiol* 90: 1349–1358, 2001.
34. **Lichtwark GA, Wilson AM.** Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *J Exp Biol* 209: 4379–4388, 2006.
35. **Liu Y, Peng CH, Wei SH, Chi JC, Tsai FR, Chen JY.** Active leg stiffness and energy stored in the muscles during maximal counter movement jump in the aged. *J Electromyogr Kinesiol* 16: 342–351, 2006.
36. **Mian OS, Thom JM, Ardigo LP, Minetti AE, Narici MV.** Gastrocnemius muscle-tendon behaviour during walking in young and older adults. *Acta Physiol (Oxf)* 189: 57–65, 2007.
37. **Morse CI, Thom JM, Birch KM, Narici MV.** Tendon elongation influences the amplitude of interpolated doublets in the assessment of activation in elderly men. *J Appl Physiol* 98: 221–226, 2005.
38. **Morse CI, Thom JM, Davis MG, Fox KR, Birch KM, Narici MV.** Reduced plantarflexor specific torque in the elderly is associated with a lower activation capacity. *Eur J Appl Physiol* 92: 219–226, 2004.
39. **Narici MV, Maganaris CN, Reeves ND, Capodaglio P.** Effect of aging on human muscle architecture. *J Appl Physiol* 95: 2229–2234, 2003.
40. **Seidler RD, Alberts JL, Stelmach GE.** Changes in multi-joint performance with age. *Motor Control* 6: 19–31, 2002.
41. **Sousa F, Ishikawa M, Vilas-Boas JP, Komi PV.** Intensity- and muscle-specific fascicle behavior during human drop jumps. *J Appl Physiol* 102: 382–389, 2007.
42. **van Dieen JH, Cholewicki J, Radebold A.** Trunk muscle recruitment patterns in patients with low back pain enhance the stability of the lumbar spine. *Spine* 28: 834–841, 2003.
43. **Yoon S, Tauchi K, Takamatsu K.** Effect of ankle joint stiffness during eccentric phase in rebound jumps on ankle joint torque at midpoint. *Int J Sports Med* 28: 66–71, 2007.

II

AGE-RELATED MUSCLE ACTIVATION PROFILES AND JOINT STIFFNESS REGULATION IN REPETITIVE HOPPING

by

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TITLE

AGE-RELATED MUSCLE ACTIVATION PROFILES AND JOINT STIFFNESS REGULATION IN REPETITIVE HOPPING

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Keywords: aging; stretch-shortening cycle; neural control; stiffness control

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ABSTRACT

It is well documented that increasing effort during exercise is characterized by an increase in electromyographic activity of the relevant muscles. How aging influences this relationship is a matter of great interest. In the present study, nine young and twenty-four elderly subjects did repetitive hopping with maximal effort as well as with 50%, 65%, 75% and 90% intensities. During hopping joint kinematics were measured together with electromyographic activity (EMG) from the soleus, gastrocnemius medialis, gastrocnemius lateralis and tibialis anterior muscles. The results showed that agonist activation increased in both age groups with increasing intensity. The highest jumping efficiency (EMG ratio of the braking phase to the push off –phase activation) was achieved with moderate hopping intensities (65%-75%) in both the young and in the elderly. Age-comparison showed that elderly subjects had high agonist preactivation but thereafter lower activation during the braking phase. Antagonist coactivation was minimal and did not show age- or intensity-specificity. The elderly had more flexed knees at the instant of ground contact. When intensity increased, the elderly also plantarflexed their ankles more before ground contact. Ankle joint stiffness was lower in elderly subjects only in high hopping intensities (90% and Max). These results confirm that age-specific agonist muscle activation profiles exist during hopping even when exercise intensities are matched on the relative scale. The results suggest further that the elderly can adjust their reduced neuromuscular capacity to match the demands set by different exercise intensities.

INTRODUCTION

The weakness associated with aging is not only due to a decrease in the size of skeletal muscles (sarcopenia) but also related to impaired neural control of muscles (for review see e.g. [Enoka, 1997; Roos et al, 1997]). Movement patterns in the elderly are usually slow and characterized by excessive co-contraction of agonist and antagonist muscle pairs [Burnett et al, 2000; Häkkinen et al, 1998; Seidler et al, 2002]. This increased coactivation may have functional relevance in locomotion since it could partly explain the higher energy cost of walking in the elderly [Hortobágyi et al, 2009; Mian et al, 2006]. On the other hand, however, high coactivation during stabilizing actions (down-ward stepping) has been shown to increase joint stiffness in the elderly which may improve the stability and safety of locomotion [Hortobagyi and DeVita, 2000].

The recent study of our laboratory [Hoffren et al, 2007] with young and elderly subjects also showed that the tibialis anterior muscle was more coactivated in the elderly than in the young during the braking phase of drop jumps. However, it seems that in stretch-shortening cycle (SSC) exercises such as jumping and hopping, coactivation does not increase joint stiffness [Hobara et al, 2007; Yoon et al, 2007] and therefore is not beneficial for hopping performance where high joint stiffness is a prerequisite [Asmussen and Bonde-Petersen, 1974; Cavagna, 1977; Gollhofer et al, 1992]. To support this hypothesis, it was also found that coactivation was negatively correlated with ankle joint stiffness both in young and elderly subjects and therefore it seems that higher coactivation in the elderly is a safety strategy to reduce impact loads during drop jumps [Hoffren et al, 2007]. In addition, the age-specific comparison of agonist activation profiles showed less agonist activation in the braking phase in the elderly with subsequent higher activation in the push-off phase. This kind of agonist muscle activation profile suggests less efficient jumping performance in the elderly as compared to the young [Asmussen, 1953; Asmussen and Bonde-Petersen, 1974; Bosco et al, 1982].

However, the possible problem in this earlier study [Hoffren et al, 2007] as well as in some other aging studies (e.g. [Mian et al, 2007; Ortega et al, 2008]) is that the same absolute exercise intensities were used for two age groups with obviously different neuromuscular capacities. This makes interpretation of results difficult since it is known that movement efficiency (walking and hopping, for example) and therefore also neural activation are intensity specific in a non-linear fashion [Cavagna and Kaneko, 1977; Finni et al, 2001]. This means that efficient hopping or walking is achieved in moderate intensities. In lower and higher performance intensities the efficiency may be compromised [Cavagna and Kaneko, 1977; Finni et al, 2001]. When the same absolute exercise intensities are used for the young and the elderly, the chosen intensity is always closer to maximum for elderly subjects. Consequently, demonstration of the possible existence of age-specific muscle activation profiles during jumping or hopping would require use of the same relative exercise intensities (stretch levels) for young and elderly subjects. If age-specific muscle activation profiles truly exist in dynamic actions, this may then influence the fascicle behavior and fascicle-tendon interaction and finally utilization of elastic energy in a way already observed in young individuals [Ishikawa et al, 2006; Ishikawa et al, 2007].

It was therefore in our interest to examine how muscle activation of lower leg muscles is regulated when hopping intensity is changed from low to maximal levels both in young and elderly subjects. This comparison performed at the same relative exercise intensities (% max) was expected to clarify whether age-related muscle activation profiles truly exist and how this may influence muscle stiffness regulation.

METHODS

Subjects

Nine young (YOUNG) and twenty-four elderly (ELDERLY) men volunteered for the study as subjects. The background information of the subjects is presented in Table 1. ELDERLY were shorter ($p<0.05$) and they had higher body mass index (BMI) ($p<0.05$) as compared to YOUNG. Both groups were physically active. YOUNG were sport science students and ELDERLY were recruited from the local senior gym. The volumes of physical activity did not differ between the age groups. Before measurements the subjects were informed of the procedures and risks associated with the study and they gave their written consent to participate. Medical screening was performed for ELDERLY. Exclusion criteria included coronary artery disease, neurological diseases and current lower extremity and low back pain as well as previous injuries in the leg joints. The recommendations contained in the Declaration of Helsinki were followed and the study was approved by the local ethics committee.

Protocol

In the present study, subjects performed repetitive two-legged hopping on a piezoelectric force platform (Kistler® model 9281B, Kistler Instrumente AG, Winterthur, Switzerland, natural frequency ~600 Hz, Kistler amplifier model 9861A) first with maximal effort to determine the submaximal hopping intensities. Different submaximal hopping intensities were determined from the peak vertical ground reaction force (Fz) (50%, 65%, 75%, 90% Fz, respectively). The hopping duration at each intensity level was 10 seconds. This gave usually 15 to 20 repeatable hops. In submaximal hopping the subjects received visual feedback about their Fz levels from the monitor in front of them. Maximal hopping was measured also at the end of the protocol in order to examine the learning effect within the measurement session (maxafter in Results). In each hopping trial the subjects were asked to achieve the required hopping intensity with approximately five hops and then to maintain the required level for at least another five hops. The instruction was to jump with short contact time and with as little knee flexion as possible. Before the actual measurements, the subjects performed a 10-min warm-up on a bicycle ergometer followed by balance board exercises for three times 20 seconds and 10 heel raises on the edge of a stair. In addition, the subjects were allowed to familiarize themselves for jumping by performing a few submaximal jumping trials on the force plate.

Data recordings

During jumping electromyographic activity (EMG) was recorded from the soleus (SOL), gastrocnemius medialis (GaM), gastrocnemius lateralis (GaL) and tibialis anterior (TA) muscles of the right leg. These recordings were stored simultaneously with 3D reaction forces (Fz, Fy, Fx) to a personal computer through an AD converter (Power 1401, Cambridge Electronics Design Ltd, England) with a sampling frequency of 1 kHz. Bipolar miniature size surface electrodes (Blue Sensor N-00-S/25, diameter 6 mm; interelectrode distance 21 mm, Medicotest A/S, Olstykke, Denmark) were used for EMG recording (Glonner electronic, Munich, Germany; input impedance >25 MΩ, common mode rejection ratio >90 dB). Before electrode placement the skin was shaved, abraded and cleaned with alcohol in order to secure an inter-electrode resistance value below 5 kΩ. The electrode placement followed the SENIAM guidelines [Hermens et al, 1999] as accurately as possible.

All jumps were video-recorded with a high speed video camera at 200 fps (Peak Performance Inc, USA) from the right side perpendicular to the line of motion. Reflective markers were placed on trochanter major, the centre of rotation of the knee, lateral malleolus, heel and fifth metatarsal head. These points were then digitized automatically and filtered with a Butterworth fourth-order filter (cut-off frequency 10Hz) using Motus software (Peak Performance Inc, USA) in order to calculate knee and ankle joint angles in the sagittal plane (180 deg indicates full knee extension and ankle plantarflexion; measured angles are defined in the schematic figure 2). An increase in ankle angle indicates plantarflexion and a decrease in ankle angle indicates dorsiflexion. In knee angle an increase in value indicates knee extension and a decrease in value indicates knee flexion.

An electronic pulse from the force plate was used to synchronize the kinetic, kinematic and EMG data.

Analyses

EMG-signals were first band-pass filtered (10–500 Hz), full-wave rectified and then low-pass filtered at 75 Hz (Butterworth type 4th-order digital filter) in order to examine the EMG profiles. After these processes the root-mean-square values (RMS) were calculated for the following three phases; preactivation, braking and subsequent push-off phases. The preactivation phase was defined as the 100 ms period preceding the ground contact [Komi et al, 1987]. The transition from the braking to the push-off phase was marked, when the ankle joint angle was at its minimum (dorsiflexion). In general, four to five hops were averaged for each subject per intensity. When comparing the RMS values between the age groups in different functional phases of hopping, the RMS values were normalized relative to preactivation (100 ms) of maximal hopping. TA muscle serves as an antagonist to plantarflexors during the braking phase of hopping. Coactivation of the TA muscle during the braking phase was calculated by dividing TA RMS in the braking phase by SOL, GaM or GaL RMS in the braking phase (TA/SOL, TA/GaM and TA/GaL, respectively).

Ankle and knee joint moments (Nm) were calculated with inverse dynamics [Winter, 1990]. Masses of the foot and shank segments as well as the locations of center of masses and radius of gyrations of the segments were determined from anthropometric data according to Dempster [Winter, 1990]. The quotient of change in ankle or knee joint moment generated by a the right leg (from contact to peak) divided by change in ankle or knee joint angle (from contact to min) [Kuitunen et al, 2002] was used as a value of ankle joint stiffness (AJS) and knee joint stiffness (KJS), respectively, during the braking phase.

Statistics

The results are presented as means and standard deviations (SD). Differences in background information between age groups were tested using t-test for independent samples. Normality of the parameters was tested using the Shapiro-Wilk test and equality of variances with Levene's test. If either of these tests failed, the non-parametric Mann-Whitney U test was used to examine differences between age-groups. The ANOVA for repeated measurements on two factors was used to test the main effects of hopping intensity and age as well as the interactions on different parameters. When applicable, ANOVA for repeated measurements on one factor and post hoc bonferroni were used to determine significant differences between hopping intensities separately for YOUNG and ELDERLY. In addition, differences between YOUNG and ELDERLY at different exercise intensities were tested using t-test for independent samples. If normality or equality of variances failed, the non-parametric Mann-Whitney U test was used. Relationships between variables were investigated using Pearson's product-moment correlation coefficient. The level of statistical significance was set at $p < 0.05$.

RESULTS

Jumping height and contact times

As expected, as compared to ELDERLY, YOUNG jumped higher at all jumping intensities ($p<0.001$) with shorter total contact time ($p<0.01$) as well as its two parts, the braking phase ($p<0.01$) and push off –phase times ($p<0.01$) (figure 1). With increasing intensity, the jumping height increased in both age groups ($p<0.001$).

Total contact time, as well as braking and push off –phase times, decreased from 50% intensity to higher intensities both in YOUNG and in ELDERLY. Maximal hopping trials that were done at the beginning and at the end of the measurement session (Max and Maxafter, respectively in figure 1) did not differ significantly with regard to jumping height and contact time. Therefore, only results from the Maxafter conditon are presented for the parameters that follow.

Peak Fz during maximal hopping

As expected, and compared to YOUNG, ELDERLY had significantly lower maximal vertical ground reaction force (Fz) during maximal hopping ($p<0.001$) (4529 ± 666 N vs. 3131 ± 476 N, respectively) (figure 4). The difference remained similar after body weight (bw) was taken into account (relative peak Fz during maximal hopping YOUNG 6.2 ± 0.9 vs. ELDERLY 4.2 ± 0.7 times bw, $p<0.001$).

Kinematics

ELDERLY had more flexed knees at the instant of ground contact as compared to YOUNG ($p<0.01$) (fig 2A). Also the ankles were more flexed (dorsiflexion) in ELDERLY from low to moderate hopping intensities (50%-75%) (fig2A). There were no differences in minimum knee and ankle joint angles (at the end of the braking phase) between the age groups in any studied intensity. However, at take-off ELDERLY had more flexed knees ($p<0.01$) and ankles ($p<0.01$) at all jumping intensities.

Knee joint angle at the instant of ground contact decreased both in YOUNG ($p<0.05$) and ELDERLY ($p<0.001$) with increasing hopping intensity. Ankle joint angle at the contact instant increased (plantarflexion) with intensity in ELDERLY ($p<0.01$) but not in YOUNG. Knee and ankle joint angles at the lowest position (at the end of the braking phase) decreased and the angles at take-off increased with increasing intensity both in YOUNG and ELDERLY. Take-off knee and ankle angles were larger in maximal hopping as compared to submaximal hopping in both age groups.

Amplitudes of the joint displacements during the braking and push off –phases are summarized in figure 2B. Knee joint displacement in the braking phase did not change in either group with hopping intensity. In the ankle joint, however, it increased clearly in the braking phase in ELDERLY ($p<0.001$) as a function of increase in exercise intensity. This was not observed in YOUNG. In the push-off phase both the ankle and knee joint displacements increased with increasing intensity in YOUNG ($p<0.01$) and ELDERLY ($p<0.001$).

Ankle and knee joint stiffness

As compared to YOUNG, ELDERLY had significantly lower ankle joint stiffness (AJS) during the braking phase of hopping at high hopping intensities (90% and Maxafter) (figure 3). In YOUNG, AJS started to increase from 50% intensity to higher hopping intensities ($p<0.05$). In ELDERLY, AJS did not change with increasing intensity. A significant Age group x AJS interaction existed from 75% to 90 % intensity ($p<0.05$). The high AJS in elderly in maximal hopping was associated with a short contact time ($r=-0.61$, $p<0.01$, $n=24$). In addition, a low but still significant negative correlation was observed between contact time and performance (flight time) ($r=-0.44$, $p<0.05$, $n=24$).

Knee joint stiffness increased with increasing hopping intensity both in YOUNG ($p<0.01$) and in ELDERLY ($p<0.05$) (figure 3). There were no differences in knee joint stiffness between the age groups at any studied intensities.

EMG activation

The averaged relative EMG patterns of SOL, GaM, GaL and TA muscles during 50%, 75% and Maximal hopping are shown in figure 4 separately for YOUNG and ELDERLY. Clear preactivation of agonist muscles was followed by increasing activity in the braking phase and by decreasing activity towards the late push-off in both age groups.

There were some differences in relative EMG amplitudes between the age groups in different functional phases of hopping (figure 5). Preactivation of plantarflexor muscles increased with increasing hopping intensity in both age groups, except that SOL preactivation increased only in YOUNG ($p<0.05$). Similarly, in the braking phase, the activation of plantarflexor muscles increased with hopping intensity in both age groups. However, YOUNG had higher agonist braking phase activations as compared to ELDERLY (figure 5). Activation of the antagonist TA muscle in the braking phase increased only in YOUNG with increasing intensity ($p<0.05$). The activation of plantarflexor muscles increased also in the push off –phase with increasing intensity in both age groups. There were no differences in push off –phase activities between age groups in any muscles.

EMG ratio: Braking phase activation over push off –phase activation

YOUNG and ELDERLY showed some differences in muscle activation profiles during repetitive hopping. When the EMG ratio of braking phase RMS over push off –phase RMS was calculated for agonist muscles (SOL, GaM, GaL), ELDERLY showed typically lower values as compared to YOUNG especially in GaL muscle (figure 6). This EMG ratio showed an inverse parabolic shape and was lower in maximal hopping as compared to submaximal hopping. In addition, an Age group x Brak/Push -ratio interaction existed in the GaM and GaL muscles from 50% to 65% intensity ($p<0.05$): the ratio increased in YOUNG and did not change in ELDERLY.

The EMG ratio of braking phase RMS over push off –phase RMS of the agonist muscles (SOL, GaM and GaL) was positively associated with AJS in ELDERLY ($n=24$) in maximal hopping (figure 7). In addition, the EMG ratio of the antagonist TA muscle in maximal hopping was negatively correlated with AJS in ELDERLY. The correlations did not reach statistical significance in YOUNG ($n=8$).

Coactivation in the braking phase

Coactivation of the antagonist TA muscle during the braking phase of hopping was calculated by dividing TA RMS in the braking phase over SOL, GaM or GaL RMS in the braking phase (TA/SOL, TA/GaM and TA/GaL, respectively). There were no differences between the age groups in coactivation values of any examined muscle pairs and coactivation did not change with hopping intensity. TA/SOL coactivation in maximal hopping was negatively correlated with AJS in ELDERLY ($r=-0.48$, $p<0.05$, $n=24$).

DISCUSSION

The present study investigated the effects of aging on muscle activation profiles and joint stiffness regulation in repetitive hopping exercise at different intensities. The main findings were as follows: 1) Young and elderly subjects had different agonist muscle activation profiles despite similar relative exercise intensities. The elderly activated their agonist muscles less in the braking phase. 2) At the instant of ground contact the elderly had a more flexed knee joint position at all exercise intensities. Ankle joint angle at the instant of ground contact increased in the elderly with increasing intensity (more plantarflexion). These findings may have consequences for muscle and joint stiffness regulation in the elderly as well as for the utilization of tendon elasticity.

Firstly, activation of the plantarflexor muscles (SOL, GaM and GaL) increased with increasing intensity in all functional phases of hopping (preactivation, braking and push off-phase) in both age groups (figure 5). This increase in agonist muscle activation with increasing intensity supports earlier findings [Finni et al, 2001; Ishikawa and Komi, 2004; Komi et al, 1987]. However, one exception to this behavior should be highlighted: SOL preactivation was very prominent at low intensities in elderly subjects and it remained at the same level at all exercise intensities. This was not the case in the GaM and GaL muscles which showed increased activity with increasing intensity in the preactivation phase. This muscle specificity may imply already well documented difference between these two muscles regarding balance control where SOL plays a greater role (e.g. [Smith et al, 1977]). Low intensity hopping in the elderly does not include a long flight phase which therefore poses a challenge regarding balance control. Moritani et al. (1991) have showed similar high SOL preactivation in very fast short-contact hopping with low force and a mean jumping height of <1 cm.

Secondly, in a previous study of our group [Hoffren et al, 2007], we showed that the young and the elderly have different agonist muscle activation profiles in drop-jump exercise with the same absolute exercise intensities (dropping heights). The elderly had less agonist activation in the braking phase which resulted in lower braking phase to push off –phase activation ratios and therefore less efficient jumping performance. The present study supports those results although the difference was now smaller because exercise intensities were matched on the relative scale for the two age groups. This was expected since muscle activation profiles in hopping are intensity specific [Finni et al, 2001]. The present study confirms the findings of Finni et al. (2001) that there is a certain submaximal intensity (65-75%) in which the efficiency of hopping is highest. Both the young and the elderly followed the same "inverse parabolic" shape in the braking phase to push-off phase activation ratio. This means that the economy of hopping is compromised at maximal hopping intensity. Nonetheless, the lower braking phase to push-off activation ratios in elderly subjects suggest that hopping performance is less efficient in the elderly as compared to the young [Asmussen, 1953; Asmussen and Bonde-Petersen, 1974; Bosco et al, 1982].

Much to our surprise, coactivation of the TA muscle during the braking phase was very low in the present study. In this line it supports those papers that have investigated the relationship between leg stiffness or joint stiffness and coactivation in hopping [Hobara et al, 2007; Yoon et al, 2007]. Hobara et al. (2007) concluded that coactivation may not play a role in leg stiffness regulation during repetitive hopping by showing that coactivation decreased although leg stiffness increased from preferred contact time hopping to short contact time hopping. In the present study, as well as in our previous drop jump study [Hoffren et al, 2007], coactivation showed an inverse relationship with ankle joint stiffness among the elderly. Therefore it can be concluded that joint stiffness is downregulated with an increase in TA coactivation in short-contact hopping. Generally high coactivation especially during dynamic movements (drop jumps, squat jumps, walking, targeting movements) is linked to aging [Hoffren et al, 2007; Hortobágyi et al, 2009; Häkkinen et al, 1998; Seidler et al, 2002]. However, in the present study, coactivation did not differ between the age groups. It may be possible that because of the continuous hopping and therefore adaptation to the required stretch levels, elderly subjects could keep their TA activation low. Due to this adaptation, there is no need for increased coactivation as a safety strategy to reduce the impact loads (as compared to single drop jumps, for example). It has been shown that high AJS is needed in the braking phase in order to be able to jump properly [Asmussen and Bonde-Petersen, 1974; Cavagna, 1977; Gollhofer et al, 1992] and therefore low TA activation in the elderly is especially beneficial because their agonist activation is low. On the other hand it may simply be the case that because of similar relative exercise intensities for young and elderly subjects in the present study, the coactivation levels were also similar.

A kinematic comparison showed that the elderly had more flexed knees at the instant of ground contact at all hopping intensities. In addition, the ankle and knee joint angles at the contact instant were modified among the elderly so that the ankle angle increased (plantarflexion) and knee joint angle decreased when intensity increased. This age-specificity in kinematics supports the findings in walking [DeVita and Hortobagyi, 2000] and in stair ascent [Karamanidis and Arampatzis, 2009]. The change in kinematics further determines how moments (loads) are distributed in joints [DeVita and Hortobagyi, 2000; Karamanidis and Arampatzis, 2009]. The most probable explanation for differences in kinematics between age groups in the present study is that it is a safety strategy for the elderly to adjust plantarflexor muscles to a shorter length in order to absorb the impact forces and leave room for stretching in high impact force conditions. It has been shown by several recent studies already (e.g. [DeVita and Hortobagyi, 2000; Reeves et al, 2009; Savelberg et al, 2007]) that the neuromuscular system of the elderly is able to match the task demands with their reduced neuromuscular capacities. In this line, the present study showed that ankle joint stiffness was lower in the elderly than in the young only at high exercise intensities (90% and max). This is primarily because of modifications in ankle joint position at the instant of ground contact in elderly subjects that results in an increase of the joint displacement amplitude in the braking phase of these high exercise intensities. At the same time the knee joint stiffness is still high in the elderly and therefore the present study supports earlier observations that the elderly redistribute muscular output depending on task demands [DeVita and Hortobagyi, 2000; Reeves et al, 2009; Savelberg et al, 2007] and in this case shift the load to the knee and most probably also to hip joint muscles.

In conclusion, the present study demonstrated modifications in neural control which then leads to modifications in joint kinematics in the elderly as compared to the young in repetitive hopping exercise at different intensities. It was shown descriptively that the elderly had a more flexed knee joint position at the instant of ground contact at all exercise intensities. When intensity increased, the elderly also plantarflexed their ankles more at the instant of ground contact. Thereafter elderly as compared to young subjects showed less agonist activation in the braking phase. More mechanistically then this changed hopping strategy must have consequences to modify the regulation of joint stiffness so that the reduced neuromuscular capacity of elderly individuals can be adjusted to match the demands set by different exercise intensities.

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REFERENCES

Asmussen E. Positive and negative muscular work. Acta Physiol Scand 1953;28(4):364-382.

Asmussen E, Bonde-Petersen F. Storage of elastic energy in skeletal muscles in man. Acta Physiol Scand 1974;91(3):385-392.

Bosco C, Ito A, Komi PV, Luhtanen P, Rahkila P, Rusko H, Viitasalo JT. Neuromuscular function and mechanical efficiency of human leg extensor muscles during jumping exercises. Acta Physiol Scand 1982;114(4):543-550.

Burnett RA, Laidlaw DH, Enoka RM. Coactivation of the antagonist muscle does not covary with steadiness in old adults. J Appl Physiol 2000;89(1):61-71.

Cavagna GA. Storage and utilization of elastic energy in skeletal muscle. Exerc Sport Sci Rev 1977;5:89-129.

Cavagna GA, Kaneko M. Mechanical work and efficiency in level walking and running. J Physiol 1977;268(2):467--81.

DeVita P, Hortobagyi T. Age causes a redistribution of joint torques and powers during gait. J Appl Physiol 2000;88(5):1804-1811.

Enoka RM. Neural adaptations with chronic physical activity. J Biomech 1997;30(5):447-455.

Finni T, Komi PV, Lepola V. In vivo muscle mechanics during locomotion depend on movement amplitude and contraction intensity. Eur J Appl Physiol 2001;85(1-2):170-176.

Gollhofer A, Strojnik V, Rapp W, Schweizer L. Behaviour of triceps surae muscle-tendon complex in different jump conditions. Eur J Appl Physiol Occup Physiol 1992;64(4):283-291.

Häkkinen K, Alen M, Kallinen M, Izquerdo M, Jokelainen K, Lassila H, Mälkiä E, Kraemer WJ, Newton RU. Muscle CSA, force production, and activation of leg extensors during isometric and dynamic actions in middle-aged and elderly men and women. J Aging and Phys Act 1998(6):232-232-247.

Hermens HJ, Freriks B, Merletti R, Hägg G, Stegeman D, Blok Jea. SENIAM 8: European recommendations for surface electromyography 1999.

Hobara H, Kanosue K, Suzuki S. Changes in muscle activity with increase in leg stiffness during hopping. Neurosci Lett 2007;418(1):55-59.

Hoffren M, Ishikawa M, Komi PV. Age-related neuromuscular function during drop jumps. J Appl Physiol 2007;103(4):1276-1283.

Hortobágyi T, Solnik S, Gruber A, Rider P, Steinweg K, Helseth J, DeVita P. Interaction between age and gait velocity in the amplitude and timing of antagonist muscle coactivation. Gait Posture 2009;29(4):558-564.

Hortobagyi T, DeVita P. Muscle pre- and coactivity during downward stepping are associated with leg stiffness in aging. J Electromyogr Kinesiol 2000;10(2):117-126.

Ishikawa M, Komi PV. Effects of different dropping intensities on fascicle and tendinous tissue behavior during stretch-shortening cycle exercise. J Appl Physiol 2004;96(3):848-852.

Ishikawa M, Pakaslahti J, Komi PV. Medial gastrocnemius muscle behavior during human running and walking. Gait Posture 2007;25(3):380-384.

Ishikawa M, Komi PV, Finni T, Kuitunen S. Contribution of the tendinous tissue to force enhancement during stretch-shortening cycle exercise depends on the prestretch and concentric phase intensities. J Electromyogr Kinesiol 2006;16(5):423-431.

Karamanidis K, Arampatzis A. Evidence of mechanical load redistribution at the knee joint in the elderly when ascending stairs and ramps. Ann Biomed Eng 2009;37(3):467-476.

Komi PV, Gollhofer A, Schmidtbleicher D, Frick U. Interaction between man and shoe in running: considerations for a more comprehensive measurement approach. Int J Sports Med 1987;8(3):196-202.

Kuitunen S, Komi PV, Kyrolainen H. Knee and ankle joint stiffness in sprint running. Med Sci Sports Exerc 2002;34(1):166-173.

Mian OS, Thom JM, Ardigò ,L.P., Narici MV, Minetti AE. Metabolic cost, mechanical work, and efficiency during walking in young and older men. Acta Physiol Scand 2006;186(2):127-139.

Mian OS, Thom JM, Ardigo LP, Minetti AE, Narici MV. Gastrocnemius muscle-tendon behaviour during walking in young and older adults. Acta Physiol Scand 2007;189(1):57-65.

Ortega JD, Fehlman LA, Farley CT. Effects of aging and arm swing on the metabolic cost of stability in human walking. J Biomech 2008;41(16):3303-3308.

Reeves ND, Spanjaard M, Mohagheghi AA, Baltzopoulos V, Maganaris CN. Older adults employ alternative strategies to operate within their maximum capabilities when ascending stairs. J Electromyogr Kinesiol 2009;19(2):e57-68.

Roos MR, Rice CL, Vandervoort AA. Age-related changes in motor unit function. Muscle Nerve 1997;20(6):679-690.

Savelberg HH, Verdijk LB, Willems PJ, Meijer K. The robustness of age-related gait adaptations: can running counterbalance the consequences of ageing? Gait Posture. 2007;25(2):259-266.

Seidler RD, Alberts JL, Stelmach GE. Changes in multi-joint performance with age. Motor control 2002;6(1):19-31.

Smith JL, Edgerton VR, Betts B, Collatos TC. EMG of slow and fast ankle extensors of cat during posture, locomotion, and jumping. J Neurophysiol 1977;40(3):503-513.

Winter DA. Biomechanics and Motor Control of Human Movement. : John Wiley & Sons, Inc., Toronto, 1990.

Yoon S, Tauchi K, Takamatsu K. Effect of ankle joint stiffness during eccentric phase in rebound jumps on ankle joint torque at midpoint. Int J Sports Med 2007;28(1):66-71.

FIGURE LEGENDS

Figure 1. Jumping height and conctact times in maximal repetitive hopping in YOUNG and in ELDERLY. *, ** and ***: significant difference between YOUNG and ELDERLY (p<0.05, p<0.01 and p<0.001, respectively).

Figure 2. Knee and ankle joint angles at the contact instant of hopping with different intensities (A) and joint displacement amplitudes in the braking and push off –phases (B). *, ** and ***: significant difference between YOUNG and ELDERLY (p<0.05, p<0.01 and p<0.001, respectively). Joint displacement amplitudes in the braking phase were calculated from the angle at the instant of ground contact to the minimum angle and in the push off –phase from the minimum angle to the angle at take-off. 180 deg indicates full knee extension and ankle plantarflexion. An increase in ankle angle indicates plantarflexion and a decrease in ankle angle indicates dorsiflexion. In knee angle an increase in value indicates knee extension and a decrease in value indicates knee flexion.

Figure 3. Ankle joint stiffness and knee joint stiffness in hopping with different intensities in YOUNG and in ELDERLY. *, **: significant difference between YOUNG and ELDERLY (p<0.05, p<0.01, respectively).

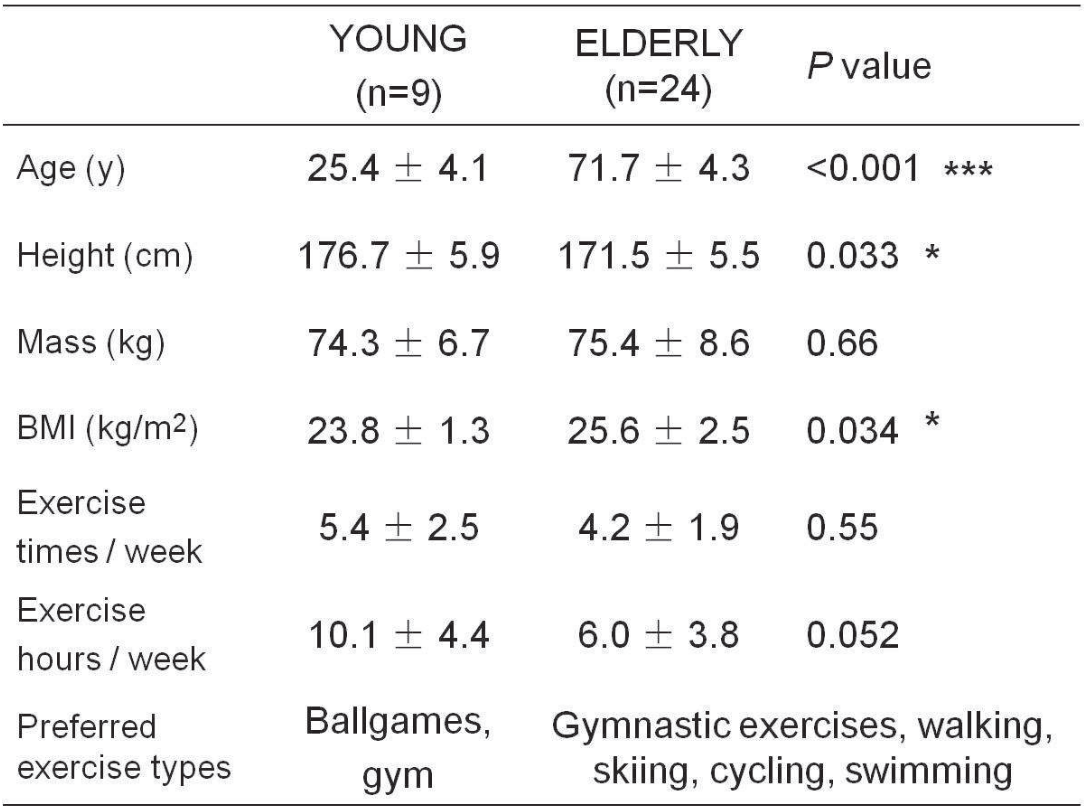
Figure 4. Averaged force-time and electromyograph (EMG)-time curves for YOUNG and ELDERLY in repetitive hopping with 50%, 75% and maximal hopping intensity. Fz, vertical ground reaction force; SOL, soleus; GaM, gastrocnemius medialis; GaL, gastrolateralis; TA, tibialis anterior. EMGs have been normalized for preactivation (100 ms) RMS of maximal hopping. Vertical lines denote the contact instant, the transition point from the braking to push-off phase (max intensity) and the take-off (max intensity), respectively.

Figure 5. Relative EMG activation (to Preactivation of Maximal hopping = 1) of plantarflexors and antagonist TA muscle in different functional phases of hopping. Different hopping intensities are on the X-axis. Preactivation was defined as 100 ms preceding the ground contact. SOL, soleus; GaM, gastrocnemius medialis; GaL, gastrolateralis; TA, tibialis anterior. 1= preactivation (100 ms) in maximal hopping. Please note that for better visual inspection the vertical axes are not scaled the same way in all cases.

Figure 6. EMG ratio of braking phase RMS over push off –phase RMS in repetitive hopping at different intensities in YOUNG and in ELDERLY. *: significant difference between YOUNG and ELDERLY (p<0.05).

Figure 7. Correlations of ankle joint stiffness (AJS) to EMG ratios of braking phase RMS over push off –phase RMS in SOL, GaM, GaL and GaL muscles in ELDERLY (n=24).

TABLE 1. Background information of the subject groups.



	YOUNG (n=9)	ELDERLY (n=24)	*P* value
Age (y)	25.4 ± 4.1	71.7 ± 4.3	<0.001 ***
Height (cm)	176.7 ± 5.9	171.5 ± 5.5	0.033 *
Mass (kg)	74.3 ± 6.7	75.4 ± 8.6	0.66
BMI (kg/m^2)	23.8 ± 1.3	25.6 ± 2.5	0.034 *
Exercise times / week	5.4 ± 2.5	4.2 ± 1.9	0.55
Exercise hours / week	10.1 ± 4.4	6.0 ± 3.8	0.052
Preferred exercise types	Ballgames, gym	Gymnastic exercises, walking, skiing, cycling, swimming	

FIGURE 1

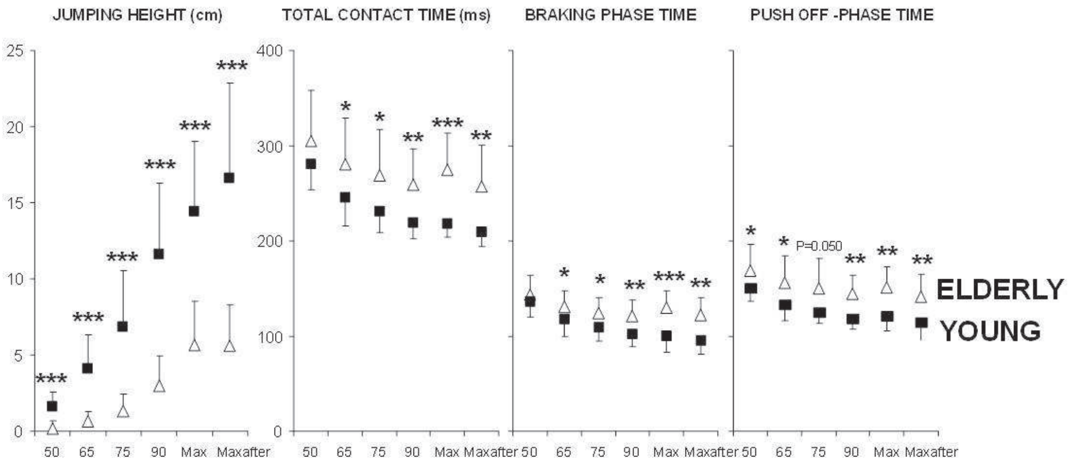
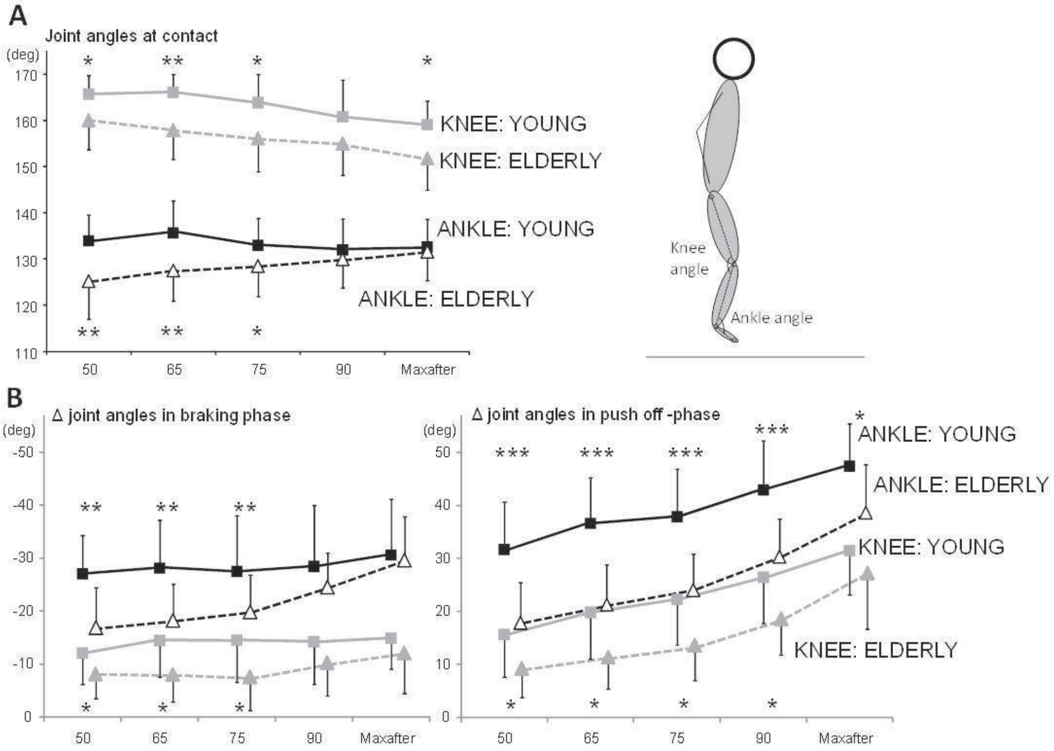

JUMPING HEIGHT (cm)
TOTAL CONTACT TIME (ms)
BRAKING PHASE TIME
PUSH OFF -PHASE TIME
25
20
15
10
5
0
400
300
200
100
0
50
65
75
90
Max
Maxafter
***
*
**
P=0.050
ELDERLY
YOUNG

FIGURE 2


A
Joint angles at contact
(deg)
170
160
150
140
130
120
110
50
65
75
90
Maxafter
*
**
*
*
**
**
*
KNEE: YOUNG
KNEE: ELDERLY
ANKLE: YOUNG
ANKLE: ELDERLY
Knee angle
Ankle angle
B
Δ joint angles in braking phase
(deg)
-50
-40
-30
-20
-10
0
50
65
75
90
Maxafter
**
**
**
*
*
*
Δ joint angles in push off -phase
(deg)
50
40
30
20
10
0
50
65
75
90
Maxafter
***
***
***
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*
*
*
*
*
ANKLE: YOUNG
ANKLE: ELDERLY
KNEE: YOUNG
KNEE: ELDERLY

FIGURE 3

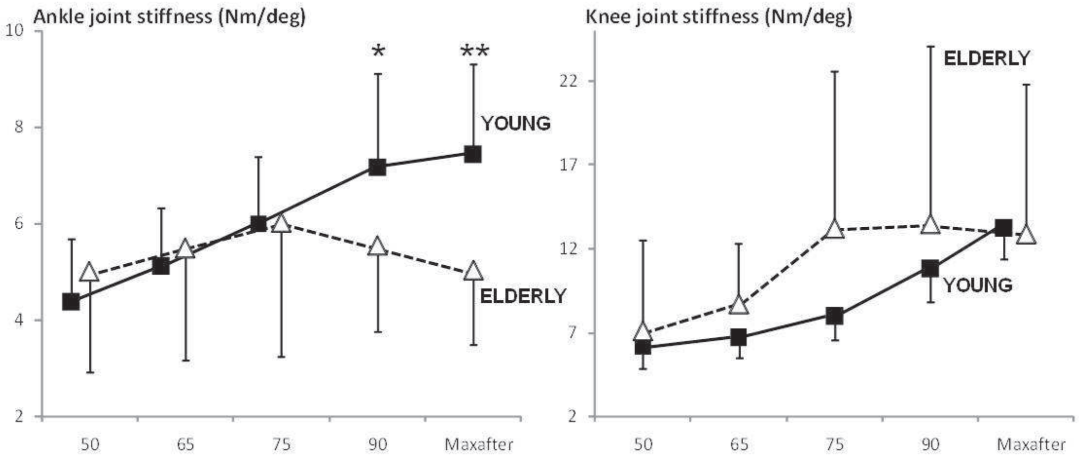

Ankle joint stiffness (Nm/deg)
10
8
6
4
2
*
**
YOUNG
ELDERLY
50
65
75
90
Maxafter
Knee joint stiffness (Nm/deg)
22
17
12
7
2
ELDERLY
YOUNG
50
65
75
90
Maxafter

FIGURE 4

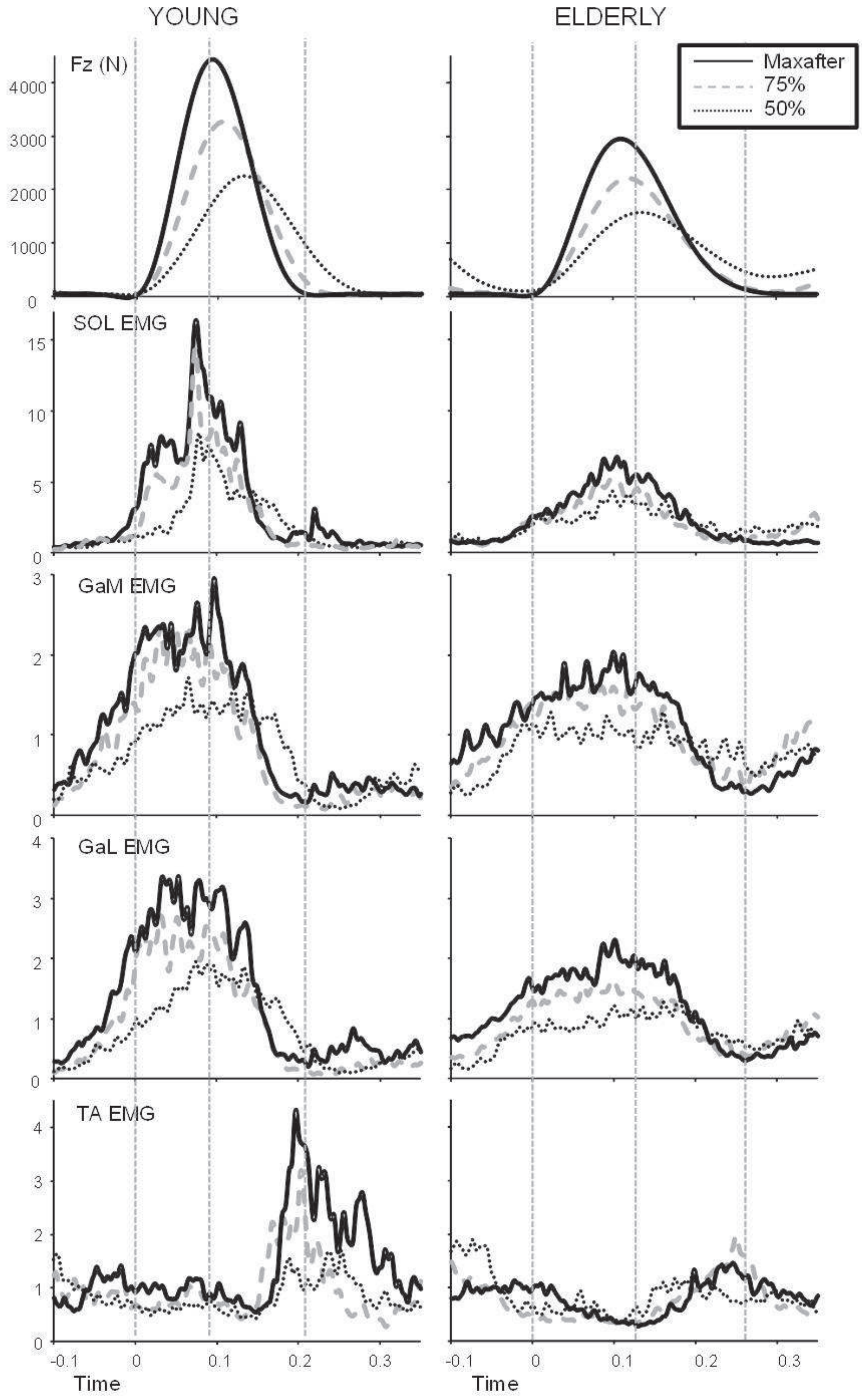

YOUNG
ELDERLY
Fz (N)
4000
3000
2000
1000
0
Maxafter
75%
50%
SOL EMG
15
10
5
0
GaM EMG
3
2
1
0
GaL EMG
4
3
2
1
0
TA EMG
4
3
2
1
0
-0.1
0
0.1
0.2
0.3
Time
-0.1
0
0.1
0.2
0.3
Time

FIGURE 5

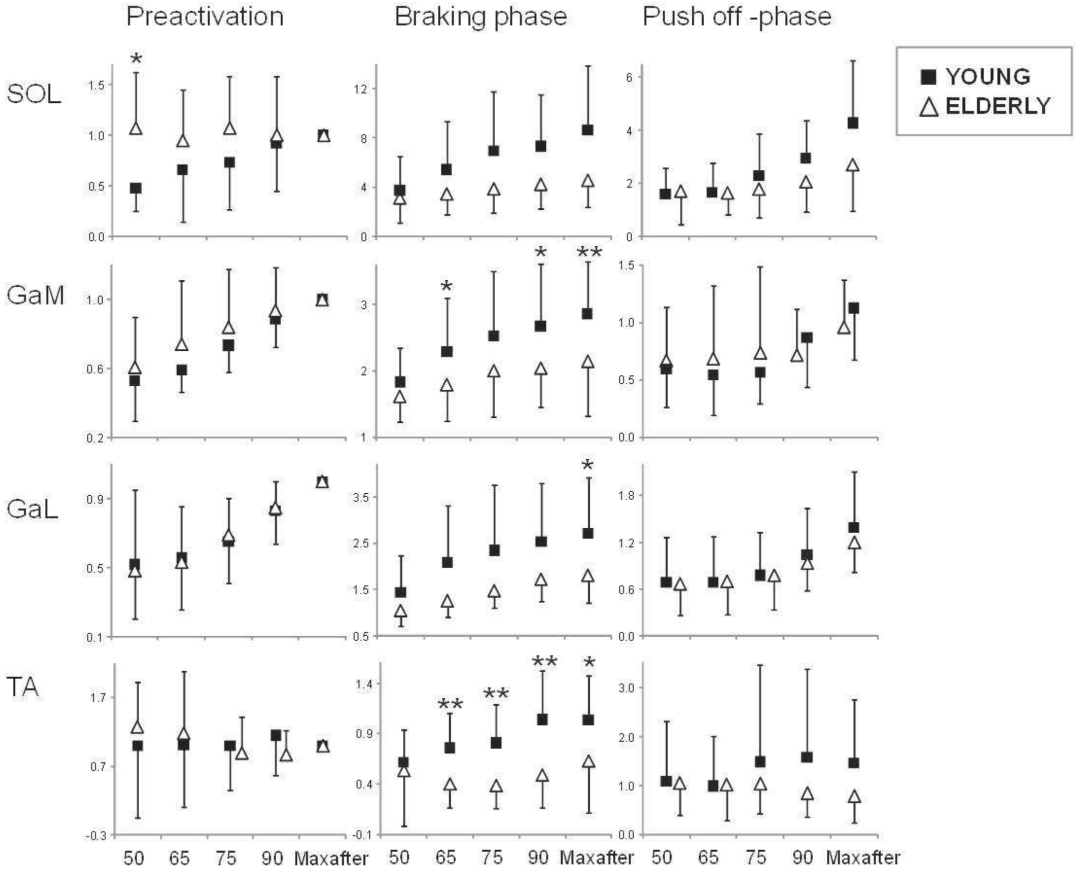

Preactivation
Braking phase
Push off -phase
■ YOUNG
△ ELDERLY
SOL
GaM
GaL
TA
*
*
**
*
*
**
**
**
*
1.5
1.0
0.5
0.0
12
8
4
0
6
4
2
0
1.0
0.6
0.2
3
2
1
1.5
1.0
0.5
0.0
0.9
0.5
0.1
3.5
2.5
1.5
0.5
1.8
1.2
0.6
0.0
1.7
0.7
-0.3
1.4
0.9
0.4
-0.1
3.0
2.0
1.0
0.0
50
65
75
90
Maxafter
50
65
75
90
Maxafter
50
65
75
90
Maxafter

FIGURE 6

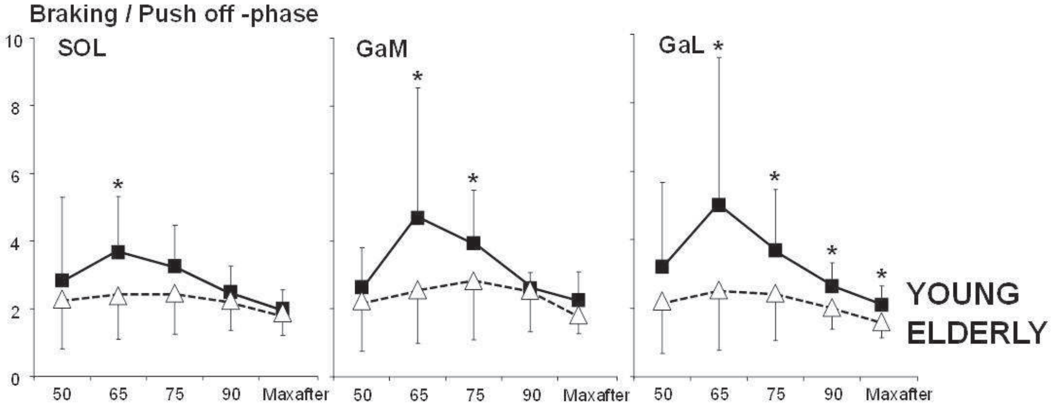
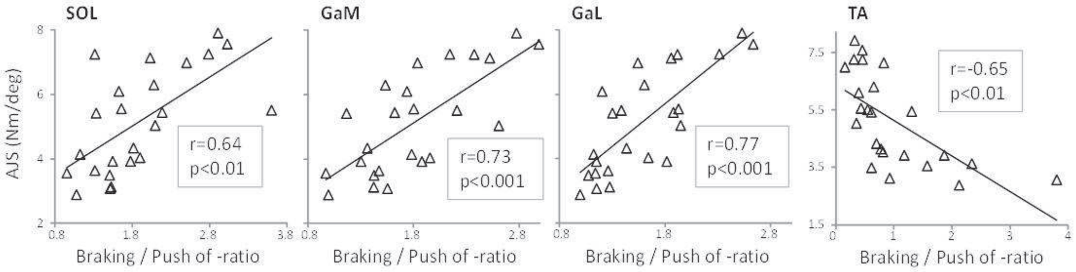

Braking / Push off -phase
SOL
GaM
GaL
10
8
6
4
2
0
50
65
75
90
Maxafter
*
YOUNG
ELDERLY

FIGURE 7


SOL
GaM
GaL
TA
AJS (Nm/deg)
8
6
4
2
0.8
1.8
2.8
3.8
r=0.64
p<0.01
r=0.73
p<0.001
r=0.77
p<0.001
7.5
5.5
3.5
1.5
0
1
2
3
4
r=-0.65
p<0.01
Braking / Push of -ratio
Braking / Push of -ratio
Braking / Push of -ratio
Braking / Push of -ratio

III

AGE-RELATED FASCICLE-TENDON INTERACTION IN REPETITIVE HOPPING

by

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ORIGINAL ARTICLE

Age-related fascicle–tendon interaction in repetitive hopping

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Abstract Increasing age can influence the interaction of muscle fascicles and tendon during dynamic movements. The object of the present study was to examine occurrence and possible reasons for the age-specific behavior of fascicles and tendons and their interaction during hopping with different intensities. Nine young and 24 elderly subjects performed repetitive hopping with maximal effort as well as with 50, 65, 75 and 90 % intensities. During hopping joint kinematics and ground reaction, forces were measured together with recordings of ultrasound images of both the fascicle and the muscle–tendon junction part of the gastrocnemius medialis (GaM) muscle. The results showed that fascicle behavior during the braking phase of hopping was clearly age specific in nature with more fascicle shortening in the young ($p < 0.001$). In addition, the fascicle shortening increased in young subjects with increasing intensity ($p < 0.05$). At the instant of ground contact, the elderly subjects demonstrated decreased fascicle length with increasing hopping intensity ($p < 0.01$). Thereafter in the braking phase, the elderly showed much smaller changes in fascicle length as compared to the young. In contrast to the fascicles, the GaM outer tendon did not show major age-specific differences in stretching and shortening amplitudes during hopping although the peak tendon forces were clearly lower in the elderly ($p < 0.001$). These results suggest that GaM outer tendon behavior is not influenced greatly with increasing age. It is further suggested that when aging modifies the fascicle–tendon interaction, it is primarily due to the age-specific difference in the fascicle level. This notion poses a question that as compared to the young, the elderly individuals may have a different fascicle behavior for optimal SSC locomotion such as hopping.

Keywords Stretch–shortening cycle · Ultrasound · Gastrocnemius medialis

Introduction

During normal locomotion (walking, running and jumping, for example) muscles exhibit consecutive lengthenings and shortenings. This type of muscle behavior is called stretch–shortening cycle (SSC) and it has been shown to be beneficial in terms of economy and efficiency, as compared to pure concentric action alone (see Komi 2000 for review). Inside the muscle–tendon unit (MTU), however, the elastic tendon compartments and force-generating fascicle compartments can behave very differently from this basic mode of SSC (Griffiths 1991; Hoffer et al. 1989). The way that these structures interact during human locomotion influences movement efficiency (Fukunaga et al. 2001) and it has been shown to vary according to movement type (Ishikawa et al. 2007; Lichtwark et al. 2007), intensity (Ishikawa et al. 2006) and the muscle examined (Ishikawa et al. 2003; Sousa et al. 2007). In addition, recent studies suggest that increasing age influences the fascicle–tendon interaction during walking (Mian et al. 2007) and jumping (Hoffren et al. 2007).

Mian et al. (2007) observed increased tendinous tissue and decreased fascicle lengthening of the lateral gastrocnemius

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muscle in the elderly as compared to the young during the stance phase of walking. In the recent study of our laboratory (Hoffren et al. 2007), on the other hand, no differences were found in absolute tendinous tissue stretching amplitudes of the medial gastrocnemius muscle between young and elderly subjects in drop jumps. However, the stretching amplitude of tendinous tissue relative to that of MTU was less in the elderly due to smaller fascicle shortening in the braking phase. Neither one of these studies reported any differences in MTU, tendinous tissue or fascicle shortening amplitudes between age groups in the push-off phase.

The origin and reason of these age-specific differences in fascicle and tendon behavior especially during the braking phase of SSC are not clear at the moment. Tendon stiffness and material properties have been reported to decrease with increasing age in humans (Karamanidis and Arampatzis 2005; Kubo et al. 2003; Morse et al. 2005), although latest studies have not always supported the finding (Carroll et al. 2008; Couppe et al. 2009) and the majority of animal studies have shown stiffening of tendons with aging (see Kjaer 2004 for review). If tendon material properties change with aging, it naturally could affect the fascicle–tendon interaction since it is the difference in stiffness between these two structures that determines the amount of lengthening on them when force is applied. Since fascicle stiffness is controlled by neural activation, it is clear that age-specific differences in neural control of muscles may influence fascicle–tendon interaction. It has been shown that muscle activation profiles (both agonist and antagonist) are age-specific (Hoffren et al. 2007) and, therefore, when measuring fascicle and tendon behavior, type and magnitude of neural activation during different functional phases of SSC should be taken into account. In addition, because both neural activation and fascicle–tendon interaction are intensity-specific in a nonlinear fashion (Cavagna and Kaneko 1977; Finni et al. 2001), the measured exercise intensity may affect the results and interpretations, especially because the neuromuscular capacities of the young and the elderly are totally different. The earlier studies (Hoffren et al. 2007; Mian et al. 2007) that found age-specific differences in fascicle and tendon behavior during locomotion, examined only one exercise intensity (walking speed or dropping height) that was the same in absolute terms for both age groups. In order to be able to conclude that age-specific fascicle–tendon interaction truly exists during human locomotion, it is important that measurements are performed at various relatively matched intensities.

The purpose of this study was to examine the possible age-specific differences in fascicle and tendon behavior by measuring repetitive hopping with different intensities from low to maximal. By comparing the similar exercise intensities in relative scale for young and elderly subjects, it was aimed to exclude the role of subjective exercise intensity to fascicle–tendon interaction. In addition, it was of interest to examine the fascicle–tendon behavior in both young and elderly with increasing hopping intensity.

Methods

Subjects

Nine young (YOUNG: 25.4 ± 4.1 years, 176.7 ± 5.9 cm and 74.3 ± 6.7 kg) and 24 elderly (ELDERLY: 71.7 ± 4.3 years, 171.5 ± 5.5 cm and 75.4 ± 8.6 kg) men participated in the study as subjects. YOUNG subjects were sport science students and ELDERLY were recruited from the local senior gym. Present report is part of the larger study that examined also the neural control of muscles, and these results are reported elsewhere (Hoffren et al. 2011). Detailed characteristics of the subjects as well as data regarding jumping heights, contact times, muscle activation profiles and joint stiffness during hopping are presented in that report. Before measurements, the subjects were given an informed consent of the procedures and risks associated with the study and they gave their written consent to participate. Medical screening was performed for ELDERLY. Exclusion criteria included coronary artery disease, neurological diseases and current lower extremity and low back pain as well as previous injuries in the leg joints. The recommendations contained in the Declaration of Helsinki were followed and the study was approved by the local ethics committee.

Protocol

Subjects performed repetitive two-legged hopping on a piezoelectric force platform (Kistler® model 9281B, Kistler Instrumente AG, Winterthur, Switzerland, natural frequency ~600 Hz, Kistler amplifier model 9861A) first with maximal rebound effort. Individual determination of the submaximal hopping intensities (50, 65, 75, 90 %) was based on this maximal rebound test. These intensities were determined from the peak vertical ground reaction force (Fz) (50, 65, 75, 90 % Fz, respectively). The hopping duration at each intensity level was 10 s. This gave usually 15–20 repeatable hops. In submaximal hopping, the subjects received visual feedback about their Fz levels from the monitor in front of them. Maximal hopping was measured also at the end of the protocol to examine the learning effect within the measurement session (Maxafter in Results). However, the maximal hopping trials that were done in the beginning and at the end of the measurement session did not differ significantly with regard to jumping height and contact time (Hoffren et al. 2011). Therefore, only results from the Maxafter condition are presented for the parameters of the present study. In each hopping trial, the subjects were asked to achieve the required hopping intensity with approximately five hops and then to maintain the required level for at least another five hops. The instruction was to jump with short contact time and with as little knee bending as possible. Before the actual measurements, the subjects performed a 10-min warm-up on a bicycle ergometer followed by balance board exercises for three times 20 s and 10 heel raises on the edge of a stair. In addition, the subjects were allowed to familiarize themselves for jumping by performing a few submaximal jumping trials on the force plate. Immediately before the jumping measurements, the relaxed upright standing position of 10 s in duration was recorded to serve as a control trial to ultrasound analysis.

Data recordings

During hopping the ground reaction force components (Fz, Fy, Fx) were stored in a personal computer through an AD converter (Sampling rate 1 kHz; Power 1401, Cambridge Electronics Design Ltd, England). All jumps were video-recorded at 200 fps (Peak Performance Inc, USA) from the right side perpendicular to the line of motion. Reflective markers were placed on trochanter major, the approximate center of rotation of the knee, lateral malleolus, lateral side of the heel, fifth metatarsal head, behind the foot on top of the calcaneus and on calf under the ultrasound probes. The positions of markers on lower leg are shown in Fig. 1. These points were then digitized automatically and filtered with a Butterworth fourth-order filter (cut-off frequency 10 Hz) using Motus software (Peak Performance Inc, USA) to calculate knee and ankle joint angles and later gastrocnemius medialis (GaM) MTU length changes.

Longitudinal images of right leg GaM muscle–tendon junction (MTJ) were recorded during hopping using a B-mode ultrasonography (SSD-5500; Aloka, Japan) with 6 cm linear array probe (scanning frequency of 7.5 MHz). The recordings were obtained at 96 images s^{-1}. Similarly, longitudinal images of GaM muscle fascicles of the right leg were recorded using another B-mode ultrasonography (α10; Aloka, Japan) with 4 cm linear array probe (scanning frequency of 13 MHz). These images were obtained at 204 images s^{-1}. The two probes were fixed securely with a special support device made of polystyrene. The superficial and deep aponeuroses and GaM fascicle as well as GaM MTJ were digitized and tracked from each image.

An electronic pulse was used to synchronize the kinetic, kinematic and ultrasonographic data.

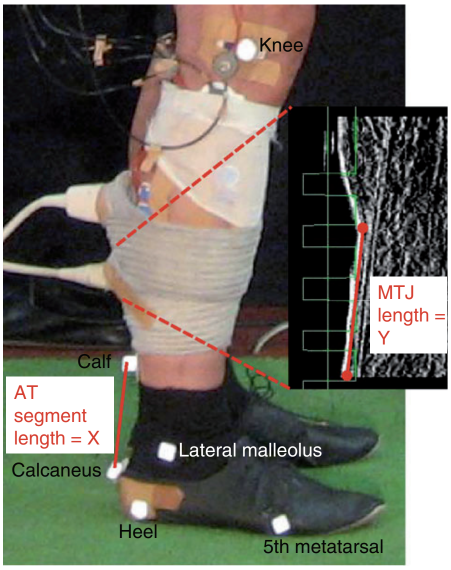

Fig. 1 Reflective markers of lower leg and parameters needed in gastrocnemius medialis (GaM) outer tendon length determination. *X* Achilles tendon (*AT*) segment length marked with reflective markers on calcaneus and under the ultrasound probes and analyzed from the kinematic data. *Y* GaM muscle–tendon junction (*MTJ*) length analyzed from ultrasound data

Analyses

The model of Hawkins and Hull (Hawkins and Hull 1990) was used to calculate GaM MTU length changes. Digitized GaM MTJ data were interpolated to 200 Hz to match the time scale of the kinematic data. The following equation was used to determine the GaM outer tendon length (L_{tendon}) changes during hopping (see also Fig. 1):

$$L_{\text{tendon}} = \left(X_{\text{hopping}} - X_{\text{standing}}\right) + \left(Y_{\text{hopping}} - Y_{\text{standing}}\right) + Z_{\text{standing}},$$

where X is the Achilles tendon (AT) segment length marked with reflective markers on calcaneus and under the ultrasound probes and analyzed from the kinematic data, Y is the GaM MTJ length analyzed from ultrasound data, and Z is the GaM tendon length from calcaneus to MTJ measured with measuring tape during standing before any measurement devices were attached to skin. The position of MTJ was determined with ultrasonography.

For simplicity, GaM outer tendon length is referred to as tendon length in the results section. It must be noted that the straight tendon model used in this study does not take into account the tendon curvature and, therefore, the results concerning tendon length may be slightly underestimated and tendon elongation and strain overestimated compared to curved tendon model (Stosic and Finni 2011).

GaM fascicle length was defined as the length of the fascicle line between the superficial and deep aponeuroses and pennation angle as the angle of fascicle line and the deep aponeurosis. Fascicle length was analyzed with three points: insertion to deep and superficial aponeuroses and one point in between them to take into account the fascicle curvature visible in some subjects. When fascicle length exceeded the analyzing window, the linear extrapolation of superficial aponeurosis and fascicle line was performed to determine the fascicle insertion to superficial aponeurosis and, therefore, the fascicle length.

Achilles tendon forces (ATF) (N) of the right leg were estimated by dividing the ankle joint moment, calculated with inverse dynamics (Winter 1990), over the Achilles tendon moment arm. Moment arm values were based on literature (Rugg et al. 1990) and the calculation took into account the change in moment arm length due to change in ankle joint angle. On average, the Achilles tendon moment arms during the peak ankle moments were 5.6 ± 0.2 cm and 5.4 ± 0.2 cm in 50 % and maximal hopping, respectively. Since there were no differences in ankle joint angles during the peak ankle moments between the age groups, it could be expected that no differences existed in the moment arm lengths either. Average tendon stiffness (N/mm) during the braking phase of hopping was calculated by dividing the peak ATF (N) over the GaM tendon stretch from contact to peak length (mm).

Hopping performance includes three functional phases with different purposes: preactivation, braking and push-off phase. Therefore, the parameters are presented separately for each of these phases. The preactivation phase was defined as the 100 ms period preceding the ground contact (Komi et al. 1987). The transition from the braking to the push-off phase was determined while the ankle joint angle was at its minimum position (dorsiflexion). On average, four to five hops were averaged for each subject per intensity. The criteria for choosing the hops were as follows: (1) the force level matched the required intensity, (2) balance during hopping was maintained and (3) the signals were free from noise.

Statistics

The results are presented as mean and standard deviations (SD). Differences in background information between age groups were tested using *t* test for independent samples. Normality of the parameters was tested using the Shapiro–Wilk test and equality of variances with Levene's test. If either of these tests failed, the non-parametric Mann–Whitney *U* test was used to examine differences between age groups. The ANOVA for repeated measurements on two factors was used to test the main effects of hopping intensity and age as well as the interactions on different parameters. When applicable, the ANOVA for repeated measurements on one factor and post hoc Bonferroni were used to determine the significant differences between hopping intensities separately for YOUNG and ELDERLY. In addition, differences between YOUNG and ELDERLY in different exercise intensities were tested using *t* test for independent samples. If normality or equality of variances failed, the non-parametric Mann–Whitney *U* test was used. The level of statistical significance was set at $a = 0.05$.

Results

Results section is organized to emphasize the major age-specific differences between the two groups of subjects, YOUNG and ELDERLY. In particular, this refers to differences in fascicle behavior. The minor differences between the age groups in the characteristics of the whole MTU and the tendon are presented shortly in the first parts of the section. Effects of hopping intensity are presented under each subtitle highlighting whether the regulation due to increasing intensity is similar in the two groups.

First of all, the peak ATF during maximal hopping were significantly higher in YOUNG than in ELDERLY (YOUNG 4,107 ± 986 N vs. ELDERLY 2,717 ± 581 N, $p < 0.001$). The force–time curves of Achilles tendon and length–time –curves of GaM MTU, tendon and fascicle at different hopping intensities are shown in Fig. 2 separately for YOUNG and ELDERLY.

GaM muscle–tendon unit behavior

When intensity increased from 50 % to maximum, GaM MTU length at the instant of ground contact clearly decreased in ELDERLY ($p < 0.001$). However, when the recording was taken during the braking phase (amplitude from contact to peak length), ELDERLY showed clear increase in MTU stretch with increasing intensity ($p < 0.001$). Neither of these modifications was seen in YOUNG. MTU shortening amplitude during the push-off phase increased with increasing intensity in both age groups (YOUNG $p < 0.01$ and ELDERLY $p < 0.001$).

The age comparison in MTU length at instant of ground contact showed that it was smaller in ELDERLY as compared to YOUNG only in maximal hopping ($p < 0.05$). MTU stretch during the braking phase was lower in ELDERLY at low intensities (50–75 %) but there were no differences at higher intensities (90 % and max). MTU shortening in push-off phase (amplitude from peak to take-off) was less in ELDERLY at all jumping intensities ($p < 0.001$).

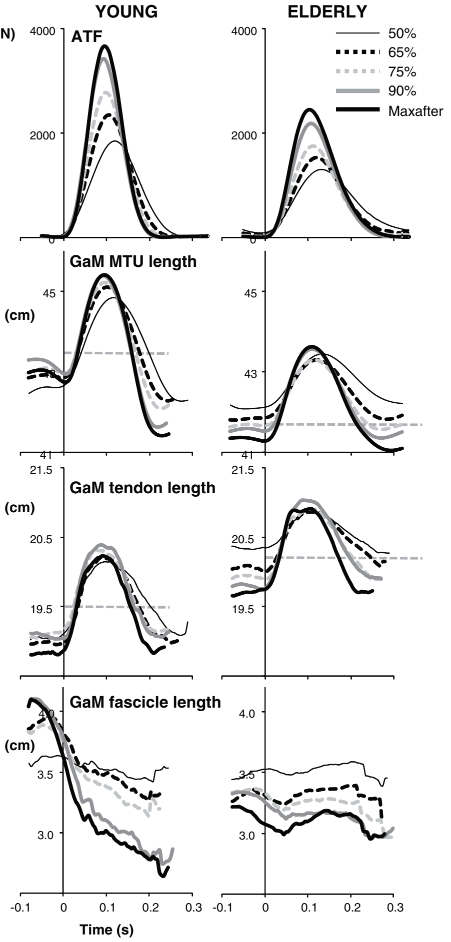

Fig. 2 Averaged Achilles tendon force (*ATF*)–time and gastrocnemius medialis (*GaM*) muscle–tendon unit (*MTU*), tendon and fascicle length–time curves for YOUNG and ELDERLY in repetitive hopping with different intensities. Time zero is the contact instant. The *dashed straight lines* in MTU and tendon length figures demonstrate shank and GaM tendon lengths, respectively, measured at relaxed upright standing position

Tendon behavior

When tendon was examined separately from the MTU, it was noted that the tendon stretch in the braking phase (amplitude from contact to peak length) was lower in ELDERLY at 50 % intensity ($p < 0.05$) but there were no differences between the age groups at higher intensities (65 % to Max) (Fig. 4a). That was because tendon stretch increased in ELDERLY with increasing hopping intensity ($p < 0.01$) but did not change in YOUNG. Tendon strain during maximal hopping was 7.6 ± 2.0 % in YOUNG and 7.1 ± 2.3 % in ELDERLY with no significant differences between age groups.

There were no differences in tendon shortening amplitudes in the push-off phase (amplitude from peak to take-off length) between the age groups (Fig. 4a). Shortening amplitude increased in ELDERLY with increasing intensity ($p < 0.01$) but did not change in YOUNG.

When tendon stretching and shortening amplitudes were related to MTU stretching and shortening amplitudes (tendon stretch/MTU stretch and tendon shortening/MTU shortening, respectively), there were no differences between the age groups at any studied intensity. In addition, these ratios did not change with change in hopping intensity. Tendon stretching accounted for 60.0 ± 20.5 % from the total MTU stretching amplitude. Similarly, tendon shortening accounted for 50.1 ± 16.6 % from the MTU shortening.

Tendon stiffness

Average GaM tendon stiffness during the braking phase of hopping was lower in ELDERLY than in YOUNG at 75 % to maximal hopping intensities (Fig. 3). Average tendon stiffness increased in YOUNG from low hopping intensities (50 and 65 %) to max hopping ($p < 0.05$) but did not change in ELDERLY.

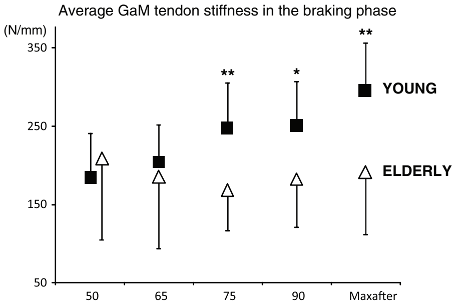

Fig. 3 Average GaM tendon stiffness during the braking phase of hopping in YOUNG and in ELDERLY. Significant difference between YOUNG and ELDERLY (*$p < 0.05$ and **$p < 0.01$, respectively). Stiffness is calculated by dividing the peak Achilles tendon force (N) over the tendon stretching amplitude during the whole braking phase (mm)

Fascicle behavior

When examining the differences in fascicle behavior between the two subject groups in dynamic hopping conditions, the reference values in relaxed state need to be reported. GaM fascicle length and pennation angle during relaxed standing were 7.3 and 7.4 %, respectively, lower in ELDERLY than in YOUNG but the differences did not reach statistical significance. Fascicle lengths during standing were 5.9 ± 0.8 cm and 5.5 ± 0.9 cm and pennation angles 20.7 ± 2.0 deg and 19.1 ± 3.2 deg in YOUNG and in ELDERLY, respectively.

When fascicle lengths were then compared at the instant of ground contact, again they did not show differences between YOUNG and ELDERLY (Fig. 2). In maximal hopping, the fascicle lengths at contact instant were 3.6 ± 0.9 cm in YOUNG and 3.1 ± 0.5 cm in ELDERLY (ns). Fascicle length at contact instant decreased in ELDERLY with increasing hopping intensity ($p < 0.01$) (Fig. 2).

However, the fascicle behavior during the braking phase of hopping clearly differed between the age groups (Fig. 2). Fascicles shortened less during the braking phase in ELDERLY ($p < 0.001$) (Fig. 4b). This difference was seen at all hopping intensities except at 50 % condition. In fact, in ELDERLY, fascicles maintained the same length in the braking phase when comparison was made between two points only (contact point and transition point from the braking to the push-off phase, Fig. 4b) without considering the possible, and also visible (see Fig. 2), changes between these two points. In fact, the early part of the braking phase showed shortening followed by stretching of the fascicles in ELDERLY. This was most prominent in maximal hopping condition but visible also at submaximal intensities. In maximal hopping, the fascicles in majority of elderly subjects were stretched also when values between contact point and transition point were compared. In YOUNG, fascicles constantly shortened (except for the rapid short-latency stretch shortly after the contact) in the braking phase at all intensities except at 50 % where the length did not change between the contact and transition points (Fig. 4b). Fascicle shortening in the braking phase increased with increasing hopping intensity in YOUNG ($p < 0.05$).

In the push-off phase, there were no statistically significant differences in fascicle lengths between the transition point and the take-off instant at most of the intensities. In some cases, the fascicles shortened slightly between these two points: significant shortening in YOUNG at 65 %

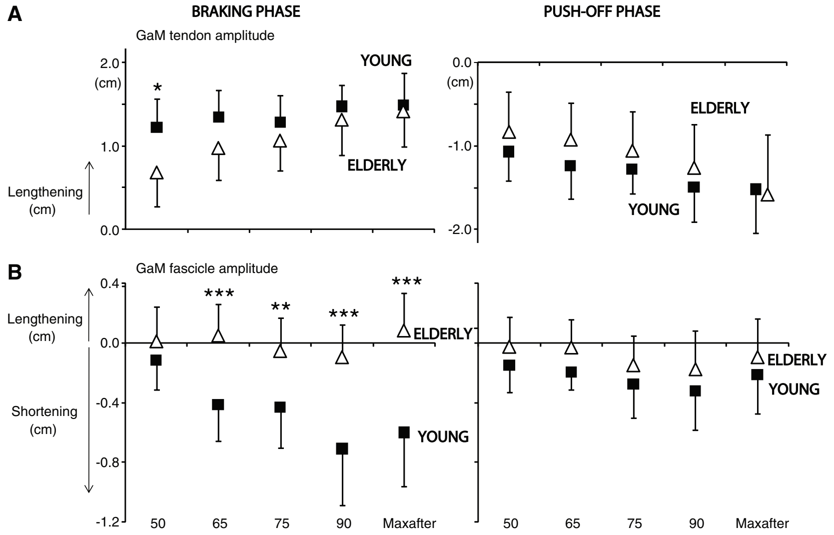

Fig. 4 GaM tendon (**a**) and fascicle (**b**) lengthening and shortening amplitudes in the braking and push-off phase in YOUNG and in ELDERLY when hopping with different intensities. Tendon amplitude in the braking phase was calculated from contact to the peak length and in the push-off phase from peak length to take-off. Fascicle amplitude in the braking phase was calculated from contact to the transition point from the braking to the push-off phase. Fascicle amplitude in the push-off phase was calculated from transition point to take-off. Tendon amplitudes $n = 8$ YOUNG, $n = 18$ ELDERLY. Fascicle amplitudes $n = 6$ YOUNG, $n = 17$ ELDERLY. Significant difference between YOUNG and ELDERLY (*$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$, respectively)

intensity ($p < 0.05$) and in ELDERLY at 75 % ($p < 0.05$) and 90 % intensities ($p < 0.05$). There were no differences in fascicle shortening amplitudes between the age groups in the push-off phase (Fig. 4b). In addition, the fascicle behavior in the push-off phase did not change with change in hopping intensity.

Discussion

The present study investigated the effects of aging on fascicle–tendon interaction of GaM muscle in repetitive hopping with different intensities. The main findings of the study were as follows: (1) Fascicle behavior in the braking phase showed clear age-specificity with more fascicle shortening in YOUNG. Fascicle shortening increased in YOUNG with increasing intensity. In ELDERLY, the fascicles demonstrated much smaller changes in length during the braking phase. (2) The outer tendon stretching and shortening amplitudes did not show major differences between the age groups although the peak tendon forces were clearly lower in ELDERLY.

With regard to the age-specific differences in fascicle behavior observed in the braking phase, the fascicles shortened more in the young at all other hopping intensities except at 50 % intensity. We have shown this same difference in fascicle behavior between the age groups also in drop–jump exercise performed with the same absolute dropping heights (Hoffren et al. 2007). Now, with the same relative exercise intensities in the present study, it can be concluded that age-specific fascicle behavior truly seems to exist during hopping action.

Isometric muscle action has been suggested to be more efficient as compared to concentric one since it reduces the active work done by the fascicles and, therefore, the energy cost (Hill 1938). Because of more constant fascicle lengths during the braking phase of hopping in the elderly as compared to the young, the fascicle function of elderly subjects could be considered more beneficial in terms of efficiency. This notion could open interesting discussion how the efficiency of locomotion can be influenced already at the fascicle level. It is well documented that the mechanical efficiency is different in two main types of muscle actions so that it is much higher in eccentric as compared to concentric action. And importantly, the speed plays a major role in efficiency values so that the increase in the speed of lengthening action (eccentric) increases the efficiency and the increase in the speed of shortening action (concentric) decreases the efficiency (see Kyrolainen and Komi 2011 for review). However, it is our understanding that the technology to record the instantaneous efficiency curves of fascicles in specific muscles has not yet advanced so that it could be applied during different kinds of human locomotion including the fascicle adaptation to training or aging. In addition, it must be noted that although there were no dramatic changes in fascicle length during the contact phase of hopping in the elderly, clear modifications seem to exist already before the contact instant when hopping intensity was changed from low to maximum (Fig. 2). Fascicle length at the contact instant shortened with increasing intensity in elderly subjects ($p < 0.01$) whereas the length remained unchanged in young subjects. It can be concluded that the young regulate their fascicle length in the braking phase whereas the regulation occurs already during the preactivation phase in the elderly. This regulation during the preactivation phase in the elderly is linked to kinematic modifications in knee and ankle joint angles (Hoffren et al. 2011) and, therefore, decreased MTU length at contact instant with increasing hopping intensity ($p < 0.001$) (see also Fig. 2). As we have discussed in our previous paper (Hoffren et al. 2011), the purpose of these modifications is likely to adjust plantar flexor muscles of elderly subjects to a shorter length to be able to absorb the impact forces and leave room for stretching in high impact force conditions.

It must also be highlighted that specifically among elderly subjects, the great variability was observed in the braking phase fascicle behavior. This was true especially at maximal hopping intensity (Fig. 5). In some subjects, the fascicles shortened but in some cases lengthened. Fascicle shortening amplitude in the braking phase of maximal hopping was positively associated with ankle joint stiffness (AJS) in ELDERLY (Fig. 5). Those elderly who could shorten the fascicles in the braking phase (fascicle behavior similar to that of young subjects), had higher AJS.

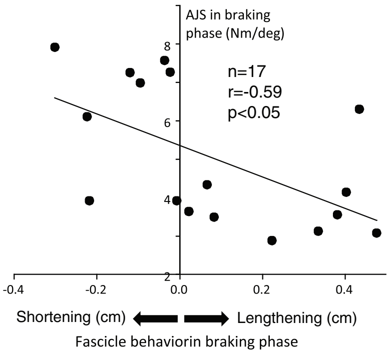

Fig. 5 Correlation between the fascicle behavior in the braking and ankle joint stiffness (AJS) in the braking phase in ELDERLY in maximal hopping. The data regarding AJS values are taken from Hoffren et al. (2011)

High joint stiffness has been known to be beneficial for good performance in this kind of short contact hopping (see Butler et al. 2003 for review). However, AJS has been shown to be lower in the elderly as compared to the young during high hopping intensities (Hoffren et al. 2011). It could be that especially at high hopping intensities the fascicles need to shorten in the braking phase to be able to produce high ATF, even if this may compromise movement efficiency. This behavior of increased fascicle shortening with increase in tendon forces is seen also when fascicle behavior in walking is compared to that in running (Ishikawa et al. 2007; Lichtwark et al. 2007). It must be noted that since the shortening speed of fascicles even in young subjects (in maximal hopping 2.7 ± 0.6 muscle lengths per second (Lo/s) when fascicle length during relaxed standing was used as a reference length) was still very low compared to maximal contraction speed of muscles (10 Lo/s in Zajac 1989), the energy cost due to concentric action may not be high. Regarding the noticed age-specific differences in fascicle function, it is not an easy task to identify the actual origins for this behavior. Differences in muscle activation levels provide one explanation since it is shown that the elderly activate their GaM muscles less in the braking phase of jumping and hopping as compared to the young (Hoffren et al. 2007, 2011). At maximal hopping intensity, in the present study, it is suggested that fascicles in the elderly cannot tolerate the impact forces and are, therefore, stretched after the initial shortening in the early braking phase. Most probably, this stretch is due to cross-bridge detachment because of high impact forces (Rack and Westbury 1974) and not due to eccentric action with attached cross-bridges. However, the cross-bridge detachment and, therefore, fascicle stretching in the elderly seems to happen only at maximal hopping intensity and, therefore, it does not explain the different behavior between the age groups also at lower exercise intensities. It may be true that because of lower ATF in the elderly as compared to the young, more isometric fascicle behavior is possible. On the other hand, different mechanical properties in tendons and other elastic structures in the elderly may favor different kind of muscle activation and fascicle behavior for optimal efficiency and power output in these age groups (Lichtwark and Wilson 2005).

It has been shown by several research groups using ultrasonography that tendon stiffness and Young's modulus decrease with aging (Karamanidis and Arampatzis 2005; Kubo et al. 2003; Morse et al. 2005). In the present study we calculated average GaM tendon stiffness in the braking phase of dynamic SSC–exercise. The method was similar to that used by Lichtwark and Wilson (2005), and values observed were also in a similar physiological range considering that GaM muscle was examined in the present study and GaL by Lichtwark and Wilson (2005) (interquartile range of 244-311 N/mm in maximal hopping in YOUNG vs. 145–231 N/mm in Lichtwark and Wilson 2005). However, the present study showed that average stiffness was lower in elderly subjects from moderate to high exercise intensities (75 %-Max). It was found that tendon stiffness in the braking phase increased with increasing hopping intensity in the young but did not change in the elderly. This result is puzzling and cannot be thoroughly explained at the moment. It has been suggested that stiffness of elastic structures may change with increase in muscle activity (Hof 1998, 2003) which may give a partial explanation since the young increase their plantar flexor activation more in the braking phase with increasing intensity as compared to the elderly (Hoffren et al. 2011). Increase in stretching velocity may also increase stiffness due to viscoelastic properties of the tendon (Butler et al. 1978). However, no difference was found in increase of peak tendon stretching velocity between the age groups (increase of 16 ± 12 cm/s in YOUNG vs. 19 ± 10 cm/s in ELDERLY from 50 % to Max intensity). One must notice, however, that in the present study the average tendon stiffness was calculated for the whole braking phase, which includes the toe region as well as the linear region of tendon force–length curve and no effort was made to distinguish between those two parts. If the elderly would indeed have more compliant tendon, it could imply better utilization of elastic energy (Ettema 2001) and, therefore, increase movement efficiency and possibly also allow less fascicle shortening in the braking phase, as shown in the present study.

Conclusions

When taken together the results from the fascicle and tendon compartments, this study suggests that GaM outer tendon behavior is not influenced greatly with increasing age. On the other hand major differences between the young and the elderly in fascicle–tendon interaction point of view seem to occur in the fascicle level. Fascicles showed only small changes in length during the braking phase in the elderly and fascicles were stretched after the initial shortening at higher exercise intensities. In young subjects, fascicles behaved more concentrically during the braking phase and fascicle shortening increased with increasing hopping intensity. Therefore, this study suggests that different kind of fascicle behavior may be optimal for the elderly as compared to the young. The results would imply the existence of the age specific differences in energetic behavior of the fascicles, the exact nature of which cannot be quantified based on the results of the present study.

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Conflict of interest The authors declare that they have no conflict of interest.

References

Butler DL, Grood ES, Noyes FR, Zernicke RF (1978) Biomechanics of ligaments and tendons. Exerc Sport Sci Rev 6:125–181

Butler RJ, Crowell HP 3rd, Davis IM (2003) Lower extremity stiffness: implications for performance and injury. Clin Biomech (Bristol, Avon) 18:511–517

Carroll CC, Dickinson JM, Haus JM et al (2008) Influence of aging on the in vivo properties of human patellar tendon. J Appl Physiol 105:1907–1915. doi:10.1152/japplphysiol.00059.2008

Cavagna GA, Kaneko M (1977) Mechanical work and efficiency in level walking and running. J Physiol 268:467–481

Couppe C, Hansen P, Kongsgaard M et al (2009) Mechanical properties and collagen cross-linking of the patellar tendon in old and young men. J Appl Physiol 107:880–886. doi:10.1152/japplphysiol.00291.2009

Ettema GJ (2001) Muscle efficiency: the controversial role of elasticity and mechanical energy conversion in stretch-shortening cycles. Eur J Appl Physiol 85:457–465

Finni T, Komi PV, Lepola V (2001) In vivo muscle mechanics during locomotion depend on movement amplitude and contraction intensity. Eur J Appl Physiol 85:170–176

Fukunaga T, Kubo K, Kawakami Y, Fukashiro S, Kanehisa H, Maganaris CN (2001) In vivo behaviour of human muscle tendon during walking. Proc Biol Sci 268:229–233

Griffiths RI (1991) Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. J Physiol (Lond) 436:219–236

Hawkins D, Hull M (1990) A method for determining lower extremity muscle-tendon lengths during flexion/extension movements (Une methode pour determiner les longueurs des muscles et tendons lors de mouvements de flexion extension du membre inferieur)

Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc R Soc Lond B Biol Sci 126:136–195

Hof AL (1998) In vivo measurement of the series elasticity release curve of human triceps surae muscle. J Biomech 31:793–800

Hof AL (2003) Muscle mechanics and neuromuscular control. J Biomech 36:1031–1038

Hoffer JA, Caputi AA, Pose IE, Griffiths RI (1989) Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat. Prog Brain Res 80:75–85

Hoffren M, Ishikawa M, Komi PV (2007) Age-related neuromuscular function during drop jumps. J Appl Physiol 103:1276–1283. doi:10.1152/japplphysiol.00430.2007

Hoffren M, Ishikawa M, Rantalainen T, Avela J, Komi PV (2011) Age-related muscle activation profiles and joint stiffness regulation in repetitive hopping. J Electromyogr Kinesiol 21:483–491. doi:10.1016/j.jelekin.2011.01.009

Ishikawa M, Finni T, Komi PV (2003) Behaviour of vastus lateralis muscle-tendon during high intensity SSC exercises in vivo. Acta Physiol Scand 178:205–213

Ishikawa M, Komi PV, Finni T, Kuitunen S (2006) Contribution of the tendinous tissue to force enhancement during stretch-shortening cycle exercise depends on the prestretch and concentric phase intensities. J Electromyogr Kinesiol 16:423–431

Ishikawa M, Pakaslahti J, Komi PV (2007) Medial gastrocnemius muscle behavior during human running and walking. Gait Posture 25:380–384

Karamanidis K, Arampatzis A (2005) Mechanical and morphological properties of different muscle-tendon units in the lower extremity and running mechanics: effect of aging and physical activity. J Exp Biol 208:3907–3923

Kjaer M (2004) Role of extracellular matrix in adaptation of tendon and skeletal muscle to mechanical loading. Physiol Rev 84:649–698

Komi PV (2000) Stretch-shortening cycle: a powerful model to study normal and fatigued muscle. J Biomech 33:1197–1206

Komi PV, Gollhofer A, Schmidtbleicher D, Frick U (1987) Interaction between man and shoe in running: considerations for a more comprehensive measurement approach. Int J Sports Med 8:196–202

Kubo K, Kanehisa H, Miyatani M, Tachi M, Fukunaga T (2003) Effect of low-load resistance training on the tendon properties in middle-aged and elderly women. Acta Physiol Scand 178:25–32

Kyrolainen H, Komi PV (2011) Mechanical efficiency of SSC exercise. In: Komi PV (ed) Neuromuscular aspects of sport performance. Wiley-Blackwell, Oxford

Lichtwark GA, Wilson AM (2005) Effects of series elasticity and activation conditions on muscle power output and efficiency. J Exp Biol 208:2845–2853. doi:10.1242/jeb.01710

Lichtwark GA, Bougoulias K, Wilson AM (2007) Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running. J Biomech 40:157–164. doi:10.1016/j.jbiomech.2005.10.035

Mian OS, Thom JM, Ardigo LP, Minetti AE, Narici MV (2007) Gastrocnemius muscle-tendon behaviour during walking in young and older adults. Acta Physiol (Oxf) 189:57–65

Morse CI, Thom JM, Birch KM, Narici MV (2005) Tendon elongation influences the amplitude of interpolated doublets in the assessment of activation in elderly men. J Appl Physiol 98:221–226

Rack PM, Westbury DR (1974) The short range stiffness of active mammalian muscle and its effect on mechanical properties. J Physiol 240:331–350

Rugg SG, Gregor RJ, Mandelbaum BR, Chiu L (1990) In vivo moment arm calculations at the ankle using magnetic resonance imaging (MRI). J Biomech 23:495–501

Sousa F, Ishikawa M, Vilas-Boas JP, Komi PV (2007) Intensity- and muscle-specific fascicle behavior during human drop jumps. J Appl Physiol 102:382–389

Stosic J, Finni T (2011) Gastrocnemius tendon length and strain are different when assessed using straight or curved tendon model. Eur J Appl Physiol 111:3151–3154. doi:10.1007/s00421-011-1929-9

Winter DA (1990) Biomechanics and motor control of human movement. John Wiley & Sons, Inc., Toronto

Zajac FE (1989) Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. Crit Rev Biomed Eng 17:359–411

IV

NEUROMUSCULAR MECHANICS AND HOPPING TRAINING IN ELDERLY

by

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TITLE

NEUROMUSCULAR MECHANICS AND HOPPING TRAINING IN ELDERLY

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Running head: Hopping training to neuromuscular function in elderly

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ABSTRACT

Purpose: The present study examined the effects of repetitive hopping training on muscle activation profiles and fascicle-tendon interaction in the elderly.

Methods: 20 physically active elderly men were randomly assigned for training (TG) and control groups (CG). TG performed supervised bilateral short contact hopping training with progressively increasing training volume. Measurements were performed before the training period (BEF) as well as after 2 weeks (2W) and 11 weeks (11W) of training. During measurements the gastrocnemius medialis –muscle (GaM) fascicle and its outer Achilles tendon length changes during hopping were examined by ultrasonography together with electromyographic (EMG) activities of calf muscles, kinematics, and kinetics.

Results: At 2W the ankle joint stiffness was increased by 21.0 ± 19.3 % and contact time decreased by 9.4 ± 7.8 % in TG. Thereafter, from 2-11W the jumping height increased 56.2 ± 18.1 % in TG. Simultaneously tendon forces increased 24.3 ± 19.0 % but tendon stiffness did not change. GaM fascicles shifted to shorter operating lengths after training without any changes in their length modifications during the contact phase of hopping. Normalized EMG amplitudes during hopping did not change with training.

Conclusions: The present study shows that 11 weeks of hopping training improves the performance of physically active elderly men. This improvement is achieved with shorter GaM operating lengths and therefore increased fascicle stiffness and improved tendon utilization after training. Based on these results hopping training could be recommended for healthy fit elderly to retain and improve rapid force production capacity.

Keywords: stretch-shortening cycle; aging; ultrasound; electromyography; tendon; gastrocnemius medialis

ABBREVIATIONS

AJS	Ankle joint stiffness
ATF	Achilles tendon force
BEF	Baseline (first) measurement session before training
CG	Control group
EMG	Electromyography
Fz	Vertical component of the ground reaction force
GaL	Gastrocnemius lateralis muscle
GaM	Gastrocnemius medialis muscle
GRF	Ground reaction force
KJS	Knee joint stiffness
MTU	Muscle-tendon unit
MTJ	Muscle-tendon junction
MVC	Maximal voluntary contraction
RMS	Root mean square
RSI	Reactive strength index
SOL	Soleus muscle
TA	Tibialis anterior muscle
TG	Training group
2W	Second measurement session after 2 weeks of training
11W	Third and last measurement session after 11 weeks of training

INTRODUCTION

When elderly people are compared with younger ones, they reportedly have different agonist and antagonist muscle activation profiles during dynamic movements (Hoffren et al. 2007; Hoffren et al. 2011; Hortobagyi and DeVita. 2000; Häkkinen et al. 1998). This age-related behavior may also be demonstrated in the adaptation of the muscle fascicle–tendon interaction in normal activities such as in walking (Mian et al. 2007; Panizzolo et al. 2013) and hopping in place (Hoffren et al. 2007; Hoffren et al. 2012), which are basic examples of the stretch-shortening cycle way of muscle function. Generally, the movements in elderly can be characterized as weak (Candow and Chilibeck. 2005; Norris et al. 2007), slow (Lanza et al. 2003; Norris et al. 2007) and less economical (Malatesta et al. 2003; Mian et al. 2006) when compared to those of the young. Part of these changes are due to the aging process itself (Pearson et al. 2002) but may be partly explained by the decrease in physical activity level that typically occurs with aging (Hunter et al. 2000), especially high intensity exercises that require rapid force production (Candow and Chilibeck 2005; Morse et al. 2004).

However, in order to be able to function independently and avoid falls, the elderly also should have a reserve for rapid force production, for example, in situations when balance needs to be corrected quickly after tripping. Ankle joint functional capacity (high rate of development in muscle activation and high plantarflexor moment) is important in regaining balance after tripping (Pijnappels et al. 2005a; Pijnappels et al. 2005b) and has been reported to have decreased in elderly fallers compared to non-fallers (LaRoche et al. 2010). In addition, ankle joint functional capacity is the weakest link in elderly during walking (Beijersbergen et al. 2013; Clark et al. 2013), which is a prerequisite for independent living and the most common form of physical activity among elderly. It thus appears that training of muscles that actuate the ankle joint could be expected to have functional relevance in the elderly.

It is currently unclear whether the activation patterns and fascicle and tendon function during dynamic movements could be modified among elderly by an appropriate exercise regime to resemble those of young individuals. It is well established that strength training improves maximal force and power in elderly and young adults alike (Newton et al. 2002, Reeves et al. 2003) and that during the early phase of training, the improvements in performance are due to neural adaptations (Hakkinen and Komi 1983). Therefore, it could be speculated that the elderly could change their muscle activation profiles with short term explosive type training. If training increases the agonist activation and / or decreases antagonist coactivation during the early part of contact (braking phase) in elderly, it would increase hopping efficiency (Bosco et al. 1982; Finni et al. 2001; Kuitunen et al. 2007; Kyrolainen et al. 1998) and leg / joint stiffness (Hoffren et al. 2007; Hoffren et al. 2011; Kuitunen et al. 2007; Yoon et al. 2007). At longer term, cyclic training that includes high-strains has been shown to change the tendon mechanical properties so that tendon stiffness has increased in young individuals (Arampatzis et al. 2007), but the effects of longer-term high strain cyclic training has not been investigated in the elderly. If training increases tendon stiffness in elderly, it would counteract the effects of aging. That is because tendon stiffness decreases with aging (Karamanidis and Arampatzis. 2005; Kubo et al. 2003; Morse et al. 2005). It is currently unclear to what extent potential training-induced changes in muscle activation profiles and tendon mechanical properties would affect the fascicle-tendon interaction and performance of elderly individuals during dynamic movement. In practical terms improvements in the rate of force development and balance control could positively affect the ability of an elderly individual to recover from a perturbation.

Consequently, the purpose of the present study was to examine the effects of short and longer term repetitive hopping training on muscle activation profiles and fascicle-tendon interaction in physically active elderly men. It was hypothesized that short term training in elderly men would lead to modulation of their muscle activation profiles (increased EMG ratio of braking phase activation to push-off phase activation) to more closely resemble those of young individuals. Our second hypothesis was that longer term hopping training would result in increased tendon stiffness in the elderly.

METHODS

Subjects

In total, 24 elderly subjects volunteered for the study. Twelve of them were randomly assigned to the training group (TG) and 12 to the control group (CG). The present report is part of a larger study that also examined the effects of hopping training on bone biomarker response and these results have been reported elsewhere (Rantalainen et al. 2011). Randomizing was performed with concealed envelopes executed by drawing lots blindly. Two trained subjects dropped out due to injury. One of them injured his leg outside of the training sessions and the other developed pain in the Achilles tendon possibly due to training (Achilles tendon tendinitis). One control subject dropped out because of illness and one did not perform the maximal hopping test of the last measurements because of a leg injury that was not related to measurements. Therefore 10 trained and 10 control subjects participated all of the measurements. Both groups were physically active. The volumes of physical activity did not differ between the groups (table 1). Before measurements the subjects were given an informed consent of the procedures and risks associated with the study and they gave their written consent to participate. Medical screening was performed for all subjects before the first measurements. Exclusion criteria included coronary artery disease, neurological diseases and current lower extremity and low back pain as well as previous injuries in the leg joints. The recommendations contained in the Declaration of Helsinki were followed and the study was approved by the local ethics committee.

Protocol for the measurements

Both groups participated in three measurement sessions: before training (BEF), after 2 weeks (2W), and after 11 weeks (11W). The subjects performed repetitive two-legged hopping on a piezoelectric force platform (Kistler® model 9281B, Kistler Instrumente AG, Winterthur, Switzerland, natural frequency ~600 Hz, Kistler amplifier model 9861A). A maximal rebound test was performed at first (PRE100%). Individual determination of the submaximal hopping intensities (50% and 75%) was based on peak vertical ground reaction force (Fz) of this PRE100% hopping test. The hopping duration at each intensity level was 10 seconds. This resulted in 15 to 20 repeatable hops. In submaximal hopping the subjects received visual feedback about their Fz levels from the monitor in front of them. Maximal hopping was measured also at the end of the protocol (POST100%) in order to examine the learning effect within the measurement session. However, the PRE100% and POST100% hopping tests did not differ significantly at BEF with regard to jumping height and contact time (Hoffren et al. 2011). Therefore, only results from the POST100% hopping test are presented for the parameters of the present study and for simplicity POST100% is referred as 100% hopping intensity in the Results and Discussion sections. In each hopping series, the subjects were asked to achieve the required hopping intensity with approximately five hops and then to maintain the required level for at least another five hops. The instruction was to jump with short contact time and with as little knee bending as possible. Before the actual measurements, the subjects performed a standardized warm-up with 10 minutes of cycling on a bicycle ergometer with a freely chosen cadence and resistance followed by balance board exercises for three times 20 seconds and 10 heel raises on the edge of a stair. In addition, the subjects were allowed to familiarize themselves for jumping by performing a few submaximal jumping series on the force plate. Immediately before the jumping measurements, the relaxed upright standing position of 10 seconds in duration was recorded to serve as a control series for ultrasound analysis. In order to record maximal muscle activation to normalize electromyographic (EMG) activities during hopping, maximal voluntary isometric plantarflexion and dorsiflexion contractions (MVC) were measured. During these measurements subjects lay prone on a measurement table with straight knees (180 deg) and the ankle joint of the right leg fixed at a 90 degree position and with hands gripping the sides of the table in order to restrict their bodies from moving. Then they either pushed (plantarflexion) or pulled (dorsiflexion) maximally against the strain gauge attached to their ball of the foot and held the force steady for at least for a few seconds.

Hopping training

TG performed 11 weeks of supervised training three times per week, on Monday, Wednesday, and Friday in an exercise laboratory. Training included the same standardized warm-up previously described. This was followed by repetitive series of submaximal bilateral hopping on the ball parts of the feet (hopping series) on a force platform. Maximal hopping was measured every 2 weeks for proper readjustment of submaximal intensity levels. One hopping series lasted for 10 seconds followed by intermediate resting periods of 1-5 min until the subjects' heart rate recovered to resting values. During hopping subjects got continuous visual feedback about their Fz levels from a monitor in front of them. On week 1, the subjects performed 4 hopping series with 75% intensity from peak Fz of PRE100% hopping test measured at BEF. Training volume was increased progressively by increasing the number of hopping series as well as the intensity (table 2). CG did not participate in the training sessions and was asked to continue their normal daily routines.

Data recordings

During hopping, the ground reaction force components (Fz, Fy, Fx) were stored in a personal computer through an AD converter (Sampling rate 1 kHz; Power 1401, Cambridge Electronics Design Ltd, England). All jumps were video-recorded at 200 fps (Peak Performance Inc, USA) from the right side perpendicular to the line of motion. Reflective markers were placed on trochanter major, the approximate centre of rotation of the knee, lateral malleolus, lateral side of the heel, fifth metatarsal head, behind the foot on top of the calcaneus and on the calf under the ultrasound probes.

EMG activity was recorded from the soleus (SOL), gastrocnemius medialis (GaM), gastrocnemius lateralis (GaL) and tibialis anterior (TA) muscles of the right leg. These recordings were stored simultaneously with 3D reaction forces (Fz, Fy, Fx) to a personal computer through an AD converter (Power 1401, Cambridge Electronics Design Ltd, England) with a sampling frequency of 1 kHz. Bipolar miniature size surface electrodes (Blue Sensor N-00-S/25, diameter 6 mm; interelectrode distance 20 mm, Medicotest A/S, Olstykke, Denmark) were used for EMG recording (Glonner electronic, Munich, Germany; input impedance >25 MΩ, common mode rejection ratio >90 dB). Before electrode placement, the skin was shaved, abraded, and cleaned with alcohol in order to secure an inter-electrode resistance value below 5 kΩ. The electrode placement followed the SENIAM guidelines (Hermens et al. 1999) as accurately as possible.

Longitudinal images of the right leg GaM muscle-tendon junction were recorded during hopping using B-mode ultrasonography (SSD-5500; Aloka, Japan) with a 6 cm linear array probe (scanning frequency of 7.5 MHz). The recordings were obtained at 96 images s^{-1}. Simultaneously, longitudinal images of GaM muscle fascicles of the right leg were recorded using another B-mode ultrasonography (α10; Aloka, Japan) with 4 cm linear array probe (scanning frequency of 13 MHz). These images were obtained at 204 images s^{-1}. The two probes were fixed securely with a special support device made of polystyrene. The superficial and deep aponeuroses and GaM fascicle as well as GaM mucle-tendon junction were digitized and tracked from each image.

An electronic pulse was used to synchronize the kinetic, kinematic and ultrasonographic data.

Data analyses

The points of reflective markers were digitized automatically and filtered with a Butterworth fourth-order filter (cut-off frequency 10Hz) using Motus software (Peak Performance Inc, USA) in order to calculate knee and ankle joint angles and then GaM muscle-tendon unit (MTU) length changes.

EMG-signals were first band-pass filtered (10–500 Hz), full-wave rectified and then low-pass filtered at 75 Hz (Butterworth type 4th-order digital filter) in order to examine the EMG profiles. After these processes, the root-mean-square values (RMS) were calculated for the following three phases; preactivation, braking, and subsequent push-off phases. The preactivation phase was defined as the 100 ms period preceding the ground contact (Komi et al. 1987). The transition from the braking to the push-off phase was marked, when the ankle joint angle was at its minimum (dorsiflexion). In general, four to five hops were averaged for each subject per intensity. The criteria for choosing the hops were as follows: 1) the force level matched the required intensity, 2) balance during hopping was maintained (stable force-time curves) and 3) the signals were free from noise.

In order to compare the EMG profiles over training groups and measurement time points, the EMG ratio of braking phase RMS over push-off phase RMS was calculated for agonist muscles. High braking over push-off phase EMG ratio resembles efficient jumping performance (Aura & Komi 1986, Kyröläinen et al. 1998). In addition, in order to compare EMG activities over training groups and measurement time points in different functional phases of hopping, RMS values during different functional phases were normalized to RMS activation during isometric MVCs. When doing that the RMS activations of plantarflexor muscles (SOL, GaM and GaL) during isometric plantarflexion MVC was used to normalize the EMGs of those muscles during hopping. Similarly, the RMS activation of TA during isometric dorsiflexion MVC was used to normalize TA EMG during hopping. TA muscle serves as an antagonist to plantarflexors during the braking phase of hopping. Coactivation indexes of different muscle pairs (TA/SOL, TA/GaM and TA/GaL) during the braking phase were calculated as follows:

$$\text{Coactivation index} = \frac{\text{Normalized TA RMS during the braking phase}}{\text{Normalized SOL,GaM or GaL RMS during the braking phase}}$$

The model of Hawkins & Hull (Hawkins and Hull 1990) was used to calculate GaM MTU length changes. Digitized GaM muscle-tendon junction data was interpolated to 200 Hz to match the time scale of the kinematic data. The following equation was used to determine the GaM outer tendon length (L_{tendon}) changes during hopping (Hoffren et al. 2012):

$L_{tendon} = (X_{hopping} - X_{standing}) + (Y_{hopping} - Y_{standing}) + Z_{standing}$, where

X = Achilles tendon segment length marked with reflective markers on calcaneus and under the ultrasound probes and analyzed from the kinematic data
Y = GaM muscle-tendon junction (MTJ) length analyzed from ultrasound data
Z = GaM tendon length from calcaneus to MTJ measured with measuring tape during standing before any measurement devices were attached to skin. The position of MTJ was determined with ultrasonography.

For simplicity, GaM outer tendon length is referred to as tendon length in the results section. It must be noted that the straight tendon model used in this study does not take into account the tendon curvature and therefore the results concerning tendon length may be slightly underestimated and tendon elongation and strain overestimated when compared to the curved tendon model (Stosic and Finni 2011). MTU and tendon stretching amplitudes during the braking phase were calculated from the length during contact instant to the peak length and shortening amplitudes in the push-off phase from peak length to length at take-off instant.

GaM fascicle length was defined as the length of the fascicle line between the superficial and deep aponeuroses and pennation angle as the angle of the fascicle line and the deep aponeurosis. Fascicle length was analyzed along its path with three points: insertion to deep and superficial aponeuroses and one point in between them in order to take into account the fascicle curvature visible in some subjects. When fascicle length exceeded the analyzing window, a linear extrapolation of the superficial aponeurosis and fascicle line was performed in order to determine the fascicle insertion to the superficial aponeurosis and therefore the fascicle length. The fascicle lengths were digitized by two people so that both of them had equal number of subjects from TG and CG and the same person digitized all the hopping series from one individual. Intra-class correlation coefficients (ICC) and 95% confidence intervals (CI) were calculated for fascicle lengths measured at resting condition as well as at various points of 100% hopping for CG (n=10) between BEF and 2W. The values were the following: fascicle length measured at resting condition ICC of 0.831 (95% CI of 0.457-0.955), at contact instant of 100% hopping ICC of 0.735 (95% CI of 0.239-0.937), at transition point from braking to push-off phase ICC of 0.820 (95% CI of 0.431-0.952) and at the take-off instant ICC of 0.876 (95% CI of 0.579-0.968). Fascicle length change amplitude during the braking phase was calculated from the length at contact instant to the length at the transition point from braking to push-off phase and the amplitude during the push-off phase from the length at the transition point to length at take-off. MTU and tendon stretching amplitudes were calculated from length during contact instant to peak length and shortening amplitudes from peak length to length at take-off instant.

Ankle and knee joint moments were calculated with inverse dynamics (Winter. 1990). Masses of the foot and shank segments as well as the locations of centers of mass and radius of gyrations of the segments were determined from anthropometric data according to Dempster (Winter. 1990). The quotient of change in ankle or knee joint moment generated by the right leg (from contact to peak) divided by change in ankle or knee joint angle (from contact to min) (Kuitunen et al. 2002) was used as a value of ankle joint stiffness (AJS) and knee joint stiffness (KJS), respectively, during the braking phase.

Achilles tendon forces (ATF) of the right leg were estimated by dividing the ankle joint moment over the Achilles tendon moment arm. Moment arm values were based on literature (Rugg et al. 1990) and the calculation took into account the change in moment arm length due to the change in ankle joint angle. Average tendon stiffness during the braking phase of hopping was calculated by dividing the peak ATF over the GaM tendon stretch from contact to peak length. The reactive strength index (RSI) was calculated as flight time divided by contact time (Flanagan et al. 2008).

Statistics

The results are presented as means and standard deviations (SD). Differences in background information between the groups were tested using Student's t-test for independent samples. Normality of the parameters was tested using the Shapiro-Wilk test and equality of variances with Levene's test. If either of these tests failed, the non-parametric Kruskal–Wallis test was used to examine differences between TG and CG. The ANOVA for repeated measurements on two factors was used to test the main effects of training period (BEF, 2W, 11W) and group (TG, CG) as well as the interactions on different parameters. The ANOVA for repeated measurements on one factor and post hoc Bonferroni were used to determine the significant differences between measurement time points (BEF, 2W, 11W) separately for TG and CG. In addition, the difference between TG and CG in specific hopping intensity and measurement time point was tested with Student's t-test for independent samples. The same procedures with normality and homogeneity of variance were followed as with background information parameters. Relationships between variables were investigated using Pearson's product-moment correlation coefficient. The level of statistical significance was set at $p < 0.05$.

RESULTS

Background information

There were no differences in age, height, weight, body mass index, exercise times, or exercise hours between TG and CG (table 1).

TRAINING OUTPUT AT 100% HOPPING INTENSITY

Kinematics

At BEF there were no differences in knee and ankle joint angles at contact and take-off instants or at minimum joint angles during hopping between TG and CG. Training induced only minor changes to kinematics (figure 1).

Knee and ankle joint angle amplitudes during the braking and push-off phases did not differ at BEF between TG and CG. Knee and ankle joint angle amplitudes from contact instant to minimum angle decreased in TG from BEF-2W (both $p<0.05$). Ankle joint angle amplitude in TG decreased also during the push-off phase (from minimum angle to angle at take-off instantt) from BEF-2W ($p<0.01$) whereas no changes were observed at knee joint angle amplitude.

Jumping height

At BEF there were no differences in jumping height at 100% between TG and CG (4.9 ±3.1 cm vs. 6.7 ± 1.7 cm, respectively). There was significant interaction between study group (TG or CG) * jumping height from 2-11W ($p<0.05$) with opposite (but ns) trends of decrease and increase in jumping height in TG and CG, respectively. Therefore, at 2W CG jumped higher than TG (7.2 ± 1.6 cm vs. 3.9 ± 3.1 cm, respectively, $p<0.01$). Jumping height increased significantly in TG from 2-11W (56.2 ± 18.1 %, $p<0.01$) and did not change in CG (figure 2A).

Contact times

At BEF there were no differences in total contact time at 100% between TG and CG (272 ± 32 ms vs. 241 ± 35ms, respectively). In TG, contact time shortened from BEF-2W ($p<0.05$) (figure 2B). Thereafter, significant study group * contact time interaction existed from 2-11W ($p<0.05$) when the BEF contact time was used as a covariate with opposite (but ns) trends of decrease and increase in contact time in TG and CG, respectively.

Braking phase time at 100% did not differ between TG and CG at BEF (123 ± 21 ms vs. 112 ± 12 ms in TG and CG, respectively) or in any other measurement points. In addition, the braking phase time did not change in either group with training. Push-off phase time at BEF (148 ± 17 ms vs. 129 ± 24 ms in TG and CG, respectively) did not differ between the groups either. However, push-off phase time shortened in TG from BEF-2W ($p<0.05$). Thereafter, significant study group * push-off phase time interaction existed from 2-11W ($p<0.05$) with opposite (but ns) trends of decrease and increase in push-off phase time in TG and CG, respectively.

Reactive strength index (RSI)

At BEF CG had higher RSI than TG at 75% ($p<0.05$). RSI increased in TG from BEF-11W at 75% and 100% on average 62.5 ± 72.9 % (in CG 19.8 ± 42.4 %) and from 2-11W 55.3 ± 64.2 % (in CG 9.8 ± 31.3 %) (figure 3). In addition, significant training group * RSI interactions were observed from 2-11W at 50% ($p<0.05$) and 75% ($p<0.01$).

Peak Fz

At BEF peak Fz at 100% did not differ between TG and CG. Peak Fz increased in TG from BEF-11W ($p<0.05$) and from 2-11W ($p<0.01$) but did not change in CG (figure 2C). Significant study group * peak Fz interaction existed from 2-11W ($p<0.05$): Peak Fz increased in TG ($p<0.01$) and did not change in CG.

Joint stiffness

At BEF AJS and KJS during the braking phase of hopping did not differ between TG and CG at any intensity level. AJS increased at 100% from BEF-2W ($p<0.05$) and BEF-11W ($p<0.01$) in TG and did not change in CG (figure 2D). There were no training effects in AJS in submaximal level. Training did not have any effect on KJS values.

EMG ACTIVATION

When normalized EMG activities in different functional phases were compared between TG and CG, CG showed higher values at BEF in GaM pre- and braking phase activations at 75% and 100% (all $p<0.05$). Thereafter, at 11W TG had lower normalized TA activation in the braking phase at 100% as compared to CG ($p<0.05$). Other than these, no between groups differences existed. In addition, no within group changes or interactions due to training were found in normalized EMG activations.

Braking over push-off phase EMG ratios of plantarflexors did not differ between TG and CG at BEF. EMG ratios increased in TG from BEF-2W at 100% (SOL and GaM $p<0.01$, GaL $p<0.05$). For simplicity, these changes are presented in figure 4 only for GaM muscle. However, the EMG ratio decreased again in TG at 100% from 2-11W in GaM ($p<0.05$) and in SOL and GaL the trends were similar (SOL $p=0.084$ and GaL $p=0.111$, ns).

Coactivation

At BEF, as compared to CG, TG had higher TA/SOL and TA/GaM coactivation indexes during the braking phase of hopping at 50% (TA/SOL 17.4 ± 9.6 % vs. 8.7 ± 6.2 % and TA/GaM 19.1 ± 13.1 % vs. 8.4 ± 5.3 % in TG and CG, respectively, both $p<0.05$). Thereafter, significant training group * coactivation interactions were observed at TA/SOL and TA/GaL coactivations from 2-11W at 50% (both $p<0.05$): opposite (but ns) trends of decrease and increase in coactivation in TG and CG, respectively, although no within group changes were found in any intensity level when groups were examined independently.

GaM MECHANICAL BEHAVIOR

The average length change patterns of GaM muscle muscle-tendon unit (MTU), outer tendon and fascicle are presented in figure 5 separately for TG and CG at all measured time points and intensities. MTU and tendon length showed stretching followed by a shortening pattern whereas fascicle length did not change greatly during contact phase. The significant changes between TG and CG at different levels are presented in the paragraphs below.

Peak Achilles tendon force (ATF)

At BEF there were no differences in peak ATF values at 100% between TG and CG (2429.0 ± 531.3 N vs. 2864.3 ± 598.9 N, respectively). However, as compared to CG, TG had lower ATF values at 2W ($p<0.05$). Thereafter, peak ATF increased 24.3 ± 19.0 % in TG from 2-11W ($p<0.01$).

MTU length

At BEF there were no differences in GaM MTU lengths or amplitudes during hopping between TG and CG except that shortening amplitude in push-off phase was higher in CG as compared to TG at 75%. Training caused some changes to MTU function. The general trend in TG was that MTU stretching and shortening amplitudes first decreased from BEF-2W and then increased over the BEF level from 2-11W (figure 6A). Significant MTU shortening amplitude * training group interaction was observed at 75% from 2-11W ($p<0.05$).

Tendon length

GaM outer tendon lengths during relaxed upright standing position at BEF were 20.2 ± 3.0 cm vs 19.2 ± 2.1 cm in TG and CG, respectively, with no significant difference between groups. Training did not have any effect on tendon resting lengths.

At BEF there were no differences in GaM tendon stretching and shortening amplitudes between TG and CG. Following the change in MTU level, tendon stretching and shortening amplitudes increased from 2-11W in TG (figure 6B).

At BEF, the GaM tendon stretch relative to MTU stretch at 100% hopping was 56.1± 17.0 % vs. 62.9 ± 14.9 % in TG and CG, respectively, with no significant difference between the groups. The ratio did not change with training. At BEF the tendon shortening accounted on average for 44.3 ± 25.8 % vs. 60.7 ± 11.7 % of MTU shortening at 100% in TG and CG, respectively, with no significant difference between the groups. However, at 11W the tendon / MTU shortening at100% was higher in TG (58.3± 10.7 %) than in CG (46.7 ± 12.9 %) ($p<0.05$).

Tendon strain (relative to length during relaxed standing) during the braking phase of 100% hopping was at BEF 6.3 ± 2.5 % in TG and. 8.3 ± 2.5 % in CG with no significant difference between the groups and it did not change with training.

Tendon stiffness

At BEF the average GaM tendon stiffness during the braking phase of hopping was at 100% 210 ± 81 N / mm in TG and 190 ± 88 N / mm in CG with no significant change with training. Average tendon stiffness did not change with change in hopping intensity either.

Fascicle length

At BEF GaM fascicle lengths during the relaxed upright standing position were 5.1 ± 1.1 cm and 5.8 ± 0.7 cm in TG and CG, respectively, with no significant differences between the groups. The pennation angles were also similar with 19.6 ± 4.5 deg and 19.5 ± 2.0 deg in TG and CG, respectively. Training did not have an effect on these resting fascicle lengths and pennation angles.

When fascicle lengths were compared between contact instant, transition point from braking to push-off phase, and take-off instant, the only significant findings were observed in TG at 11W where the fascicles shortened in TG from transition point to take-off instant at 75% and 100% (both $p<0.05$). Other than that, the fascicles behaved isometrically during hopping in TG and CG.

At BEF, the fascicle lengths at contact instant, at transition point from braking to push-off phase and at take-off instant did not differ between TG and CG. Training had only a minor effect on fascicle behavior except for the shift of the fascicles to lower lengths at 11W in TG (figure 5). GaM fascicles were shorter in TG as compared to CG at 11W at contact instant, at transition point from braking to push-off phase as well as at take-off instant at 50% and 75% (all $p<0.05$). Except for an obvious shift of fascicles to a shorter length at 11W, there were no differences in fascicle length change amplitudes during the braking or push-off phases between TG and CG at any intensity level or measurement point. In addition, the length change amplitudes did not change with training in either group.

Correlations between hopping performance and muscle mechanical behavior

Correlations between the jumping height at 100% at 11W and selected muscle mechanical behavior parameters are presented in table 3. Those trained subjects that jumped the best at 11W had high ATF and MTU and tendon stretching and shortening amplitudes during hopping. In addition, their GaM fascicles did not shorten much in the push-off phase. These correlations were not found in CG.

Finally, those trained subjects that increased their jumping height the most from 2-11W had the highest increase in GaM MTU stretch (r=0.67, $p<0.05$, n=10) and tendon strain (r=0.79, $p<0.01$, n=10). Again these correlations were not found in CG.

DISCUSSION

This study measured the effects of shorter and longer term hopping training on muscle activation profiles and fascicle-tendon interaction in the elderly. The main findings of the study were that 1) hopping training was effective in improving the jumping height and reactive strength index in elderly from 2-11W, 2) GaM fascicles shifted to a shorter operating length after training with unchanged fascicle length change patterns during the contact phase of hopping and 3) increased tendon utilization was observed after training that was an important contributor to improved jumping height.

First of all, with two weeks of hopping training the elderly learned to concentrate on the use of ankle joints during hopping, which resulted in stiffer performance with increased AJS, shorter contact times, and decreased ankle and knee joint angle amplitudes during the braking phase. Due to that, there was a tendency for jumping height to decrease in TG from BEF-2W. This seems logical since the instruction was to jump with short contact time and as little knee bending as possible. Thereafter, with longer term training the contact time remained at a low level but jumping height and RSI increased in TG. The training effect in these parameters is similar to Taube et al. (2012) in young subjects with 4 weeks of drop jump training from 30cm dropping height except that only a trend for increased jumping height was observed in Taube et al. (2012) and a significant increase from 2-11W was observed at present study. This seems logical because of considerably shorter training period in Taube et al. 2012 as compared to present study.

In previous studies, the elderly when compared to the young have been shown to have lower AJS during the braking phase of hopping in high hopping intensities, lower braking over push-off phase EMG ratios in drop jumps and hopping due to less agonist activation in the braking phase and therefore less fascicle shortening (Hoffren et al. 2007; Hoffren et al. 2011; Hoffren et al. 2012). Since the elderly do not regularly perform this kind of exercise, it was important to be able to confirm that these differences are not due to unfamiliar exercise. The present study shows that with short term training the AJS during maximal hopping increased in TG from 5.0 ± 1.4 Nm/deg at BEF to 6.1 ± 2.1 Nm/deg at 2W. We compared this to our data from young individuals (7.6 ± 1.9 Nm/deg) and did not find a statistical significance (p=0.14, ns) anymore, although the values are still a bit lower in the elderly when compared to the young. Therefore, it may be that lower AJS values in the elderly in previous studies are because of safety strategy to reduce the impact loads or inability to load ankle joints due to unfamiliar exercise and thus is not actually an age-related phenomenon. However, the fascicle function during hopping was unchanged with training and therefore the clear age-related difference in fascicle behavior (Hoffren et al. 2007; Hoffren et al. 2012) exists during hopping even after elderly have trained.

Some researchers have suggested that the increase in jumping height after plyometric training in young individuals is due to enhanced neural control during hopping (Chimera et al. 2004; Taube et al. 2012; Van Cutsem et al. 1998). Since we have also reported lower EMG ratios of braking over push-off phase RMS during hopping in the elderly when compared to the young

(Hoffren et al. 2007; Hoffren et al. 2011) and since high EMG ratio is a characteristic of efficient hopping performance (Bosco et al. 1982; Finni et al. 2001; Kuitunen et al. 2007; Kyrolainen et al. 1998), it was hypothesized that with hopping training the EMG ratios would increase in the elderly to resemble a profile closer to that of the young. Indeed, the results supported our hypotheses since EMG ratios of SOL, GaM and GaL increased from BEF-2W at 100% intensity. However, although we found an increase in jumping height from 2-11W in TG, the EMG ratios returned to BEF levels between these time points. Therefore, it seems that this EMG profile is more natural / optimal for the elderly during hopping and age-related muscle activation profiles (Hoffrén et al. 2007 and 2011) exist even when the elderly have trained, at least in the time frame of 11 weeks. It is likely that the age-related motor unit remodeling (for review see Andersen. 2003) and changed tendon mechanical properties (Karamanidis and Arampatzis. 2005; Kubo et al. 2003; Morse et al. 2005) favor different kinds of muscle activation for optimal efficiency and power output in these two age groups (Lichtwark and Wilson. 2005b). To support the findings of Kubo et al. (2007) and Kyröläinen et al. (2004) and (2005) that also reported unchanged muscle activation after plyometric training, the present study suggests that the increase in jumping height with 11 weeks of hopping training in the elderly was not caused by increased neural control of muscles because no training induced changes in normalized EMG values were observed.

With training, the GaM fascicle length change pattern during the contact phase of hopping was unchanged but instead the whole fascicle shifted to shorter position (figure 5). This decrease in fascicle operating length cannot be explained by increased neural command since no changes in GaM preactivation due to training was observed. However, shorter fascicle position but unchanged length change pattern together with increased tendon forces suggest that fascicle stiffness increased after training since fascicles were not stretched under the increased force. No changes were observed in muscle architecture with training, which may suggest that muscle hypertrophy was not an explanation for this increased stiffness. However, higher fascicle stiffness could be achieved with shifted myosin-heavy-chain (MHC) isoform composition of muscle fibers from slow (I) to fast (IIa), as shown by Liu et al. (2003) with combined strength plus ballistic stretch-shortening type-of training. Unfortunately, passive twitch was not measured or muscle biopsies taken in the present study in order to confirm the speculation. Malisoux et al. (2006) found some evidence that SSC training could also increase the cross-bridge mechanics of fast twitch muscle fibers by reporting increased normalized peak power of type IIa muscle fibers after 8 weeks of SSC training. Whatever the mechanism, it is suggested that an increase in fascicle stiffness after training enables the tendon to utilize more elastic energy since it is the difference in stiffness between these two structures that determines the amount of lengthening on them when force is applied (Zajac 1989). In addition, the shift of fascicles to a shorter position after training may have other functional relevance in the tendon by removing the tendon slack before the ground contact and therefore enabling a faster tendon stretch.

Average GaM outer tendon stiffness during the braking phase of hopping was on average 211 ± 95 N / mm, which is within the physiological range reported in *in vivo* studies that measured Achilles tendon stiffness during isometric contractions (Peltonen et al. 2012; Peltonen et al. 2013) and during one-legged hopping (Farris et al. 2012; Lichtwark and Wilson. 2005a). Tendon stiffness did not change with changes in hopping intensity. This supports the idea that tendon stiffness is not significantly influenced by viscosity and thus independent of the loading rate (Peltonen et al. 2013). When compared to young, the elderly generally have lower tendon stiffness (Karamanidis and Arampatzis. 2005; Kubo et al. 2003; Morse et al. 2005) so if training increases stiffness, this would counteract the effects of aging. However, contrary to our original hypotheses, stiffness did not change with training. There are several studies that have found an increase in outer tendon / tendon-aponeurosis stiffness after strength training (Onambele-Pearson and Pearson. 2012; Reeves et al. 2003) or alpine skiing training (Seynnes et al. 2011) in the elderly as well as after strength training (Kubo et al. 2006; Kubo et al. 2007) or isometric cyclic training in young (Arampatzis et al. 2007). It has been shown that tendon requires high strains in order to adapt (Arampatzis et al. 2007). Arampatzis et al. 2007 found increase in GaM tendon-aponeurosis stiffness after 14 weeks (4 days per week) of isometric cyclic training that caused high tendon strains (4.7%) but not with low strain (2.97%) training. Hopping training in the present study was performed with 75% and 90% intensities from peak Fz and the average tendon strain during those intensities was 5.1 ± 2.3 % (relative to length during relaxed standing) which is considered very high in relation to the reported maximal physiological tendon strain values (Wren et al. (2001) reported failure strain value of 7.5 ± 1.1 % for human Achilles tendon substances) as well as with high strain rate of 43.0 ± 19.6 % / s. Therefore, the training intensity was probably as high as it could safely be. The training group performed on average 134 ± 28 jumps per training session and in total 4268 ± 638 jumps over the 11 week training period. There are several other studies that found unchanged tendon stiffness after plyometric training (Hansen et al. 2003; Houghton et al. 2013; Kubo et al. 2007) and Kubo et al. (2007) found that tendon stiffness increased after strength training but not after plyometric training. Lack of tendon adaptation after plyometric training as compared to that after strength training may suggest that in addition to high loading magnitude, a high loading duration per contraction is required for tendon adaptation, as suggested also by Arampatzis et al. (2010) and Kubo et al. (2001). In addition, it can be argued that since tendon stiffness is closely related to strength level (Stenroth et al. 2012), calf muscle strength may not have changed much with hopping training (Kyrolainen et al. 2005; Piirainen et al. 2014) and therefore also the stiffness remains unchanged. On the other hand, it must be noted here that the GaM outer tendon was measured in the present study, whereas most of the studies have measured the combined stiffness of the tendon-aponeurosis structure (e.g. Arampatzis et al. 2007; Kubo et al. 2006). Since it is known that the outer tendon and aponeurosis have different mechanical properties (Finni et al. 2003; Kubo et al. 2005; Magnusson et al. 2003), it may be that their adaptability also differs and therefore it can be speculated that adaptation might have occurred at the aponeurosis level, which was not investigated at the present study. Similar conclusions have been suggested before (Kubo et al. 2006). Another possibility is that a longer training period would be required for elderly tendon to increase its stiffness due to longer adaptation period to correct loading technique although changes have been observed in young individuals two months after the start of strength training (Kubo et al. 2012).

Although tendon stiffness remained unchanged with training, some training induced adaptations were observed in tendon function. First of all, tendon stretching and shortening amplitudes followed the changes in the MTU level and in tendon force and increased with training from 2-11W (figure 6). In addition those trained subjects that increased their jumping height the most from 2-11W also increased their tendon strain thus highlighting the importance of tendon function during this kind of short contact hopping. Finally, the tendon seemed to adapt beyond the level of MTU since tendon recoil relative to MTU shortening was higher in TG as compared to CG at 11W.

A few limitations of the present study must be highlighted. First of all, it must be noted that although the subjects of this study were randomly assigned for TG and CG, the groups were not perfectly similar at baseline. Although the difference in 100% jumping height was not statistically significant, there was a tendency for CG to jump better than TG at BEF. CG were also few years younger and had a trend for lower BMI as compared to TG (table 1). This difference between the subject groups at BEF is minor but is seen in many variables and somewhat complicates the results and interpretations although we believe that it does not affect the overall picture. Secondly, the superimposed twitch was not measured during MVCs and therefore it is not known whether the capacity to voluntarily activate calf muscles improved with training. If activation capacity was insufficient at BEF, this would cause us to overestimate the normalized EMG values of BEF condition and therefore possibly hide the improved neural drive due to training. However, the activation capacity of calf muscles during maximal plantarflexion has been shown to be high in the elderly (Barber et al. 2013) and therefore it is not expected to change greatly with training. Finally, had passive twitch been measured, it could have been used as an indicator of possible changes in MHC isoforms with training.

Why should the elderly perform hopping training?

When considering aging, it is known that force production capacity declines and movements become slower (Candow and Chilibeck, Lanza et al. 2003; Norris et al. 2007). Part of these changes are due to the aging process itself and part is due to a decrease in physical activity level, especially exercises that include rapid force production (Candow and Chilibeck. 2005; Morse et al. 2004). However, in order to be able to function independently and avoid falls, the elderly should also have a reserve for rapid force production in situations when balance needs to be corrected quickly after tripping. The present study showed that hopping training improved rapid force production in the elderly by decreasing the contact time and increasing the ground reaction force and RSI. Therefore, hopping training could possibly help elderly to retain and improve some rapid force production capacity. In addition, the short contact hopping performed in the present study that loads mainly the ankle joints could also help walking ability in elderly since the ankle joints are reported to be the weakest link during walking in elderly (Beijersbergen et al. 2013).

CONCLUSIONS

In conclusion, the present study suggests that an 11 week repetitive hopping training intervention can improve the jumping height and RSI in physically active elderly men. The improvement in performance was achieved with shorter GaM operating lengths after training and therefore increased fascicle stiffness and improved tendon utilization. Based on results of the present study, hopping training could be recommended for at least healthy fit elderly in order to retain and improve their rapid force production capacity.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

REFERENCES

Andersen JL (2003) Muscle fibre type adaptation in the elderly human muscle. Scand J Med Sci Sports 13:40-47

Arampatzis A, Peper A, Bierbaum S, Albracht K (2010) Plasticity of human Achilles tendon mechanical and morphological properties in response to cyclic strain. J Biomech 43:3073-3079. doi:10.1016/j.jbiomech.2010.08.014; 10.1016/j.jbiomech.2010.08.014

Arampatzis A, Karamanidis K, Albracht K (2007) Adaptational responses of the human Achilles tendon by modulation of the applied cyclic strain magnitude. J Exp Biol 210:2743-2753. doi:10.1242/jeb.003814

Aura O, Komi PV (1986) Effects of prestretch intensity on mechanical efficiency of positive work and on elastic behavior of skeletal muscle in stretch-shortening cycle exercise. Int J Sports Med 7:137-143. doi:10.1055/s-2008-1025751

Barber LA, Barrett RS, Gillett JG, Cresswell AG, Lichtwark GA (2013) Neuromechanical properties of the triceps surae in young and older adults. Exp Gerontol 48:1147-1155. doi:10.1016/j.exger.2013.07.007; 10.1016/j.exger.2013.07.007

Beijersbergen CM, Granacher U, Vandervoort AA, DeVita P, Hortobagyi T (2013) The biomechanical mechanism of how strength and power training improves walking speed in old adults remains unknown. Ageing Res Rev 12:618-627. doi:10.1016/j.arr.2013.03.001; 10.1016/j.arr.2013.03.001

Bosco C, Ito A, Komi PV et al (1982) Neuromuscular function and mechanical efficiency of human leg extensor muscles during jumping exercises. Acta Physiol Scand 114:543-550

Candow DG, Chilibeck PD (2005) Differences in size, strength, and power of upper and lower body muscle groups in young and older men. J Gerontol A Biol Sci Med Sci 60:148-156

Chimera NJ, Swanik KA, Swanik CB, Straub SJ (2004) Effects of Plyometric Training on Muscle-Activation Strategies and Performance in Female Athletes. J Athl Train 39:24-31

Clark DJ, Manini TM, Fielding RA, Patten C (2013) Neuromuscular determinants of maximum walking speed in well-functioning older adults. Exp Gerontol 48:358-363. doi:10.1016/j.exger.2013.01.010; 10.1016/j.exger.2013.01.010

Farris DJ, Trewartha G, McGuigan MP (2012) The effects of a 30-min run on the mechanics of the human Achilles tendon. Eur J Appl Physiol 112:653-660. doi:10.1007/s00421-011-2019-8; 10.1007/s00421-011-2019-8

Finni T, Hodgson JA, Lai AM, Edgerton VR, Sinha S (2003) Nonuniform strain of human soleus aponeurosis-tendon complex during submaximal voluntary contractions in vivo. J Appl Physiol 95:829-837. doi:10.1152/japplphysiol.00775.2002

Finni T, Komi PV, Lepola V (2001) In vivo muscle mechanics during locomotion depend on movement amplitude and contraction intensity. Eur J Appl Physiol 85:170-176

Flanagan EP, Ebben WP, Jensen RL (2008) Reliability of the reactive strength index and time to stabilization during depth jumps. J Strength Cond Res 22:1677-1682. doi:10.1519/JSC.0b013e318182034b; 10.1519/JSC.0b013e318182034b

Häkkinen K, Alen M, Kallinen M et al (1998) Muscle CSA, force production, and activation of leg extensors during isometric and dynamic actions in middle-aged and elderly men and women. Journal of Aging and Physical Activity :232-232-247

Hakkinen K, Komi PV (1983) Electromyographic changes during strength training and detraining. Med Sci Sports Exerc 15:455-460

Hansen P, Aagaard P, Kjaer M, Larsson B, Magnusson SP (2003) Effect of habitual running on human Achilles tendon load-deformation properties and cross-sectional area. J Appl Physiol (1985) 95:2375-2380. doi:10.1152/japplphysiol.00503.2003

Hawkins D, Hull M (1990) A method for determining lower extremity muscle-tendon lengths during flexion / extension movements (Une methode pour determiner les longueurs des muscles et tendons lors de mouvements de flexion extension du membre inferieur).

Hermens HJ, Freriks B, Merletti R, Hägg G, Stegeman D, Blok Jea (eds) (1999) SENIAM 8: European recommendations for surface electromyography. Roessingh Research and Development bv

Hoffren M, Ishikawa M, Avela J, Komi PV (2012) Age-related fascicle-tendon interaction in repetitive hopping. Eur J Appl Physiol 112:4035-4043. doi:10.1007/s00421-012-2393-x; 10.1007/s00421-012-2393-x

Hoffren M, Ishikawa M, Rantalainen T, Avela J, Komi PV (2011) Age-related muscle activation profiles and joint stiffness regulation in repetitive hopping. J Electromyogr Kinesiol 21:483-491. doi:10.1016/j.jelekin.2011.01.009

Hoffren M, Ishikawa M, Komi PV (2007) Age-related neuromuscular function during drop jumps. J Appl Physiol 103:1276-1283. doi:10.1152/japplphysiol.00430.2007

Hortobagyi T, DeVita P (2000) Muscle pre- and coactivity during downward stepping are associated with leg stiffness in aging. J Electromyogr Kinesiol 10:117-126

Houghton LA, Dawson BT, Rubenson J (2013) Effects of plyometric training on achilles tendon properties and shuttle running during a simulated cricket batting innings. J Strength Cond Res 27:1036-1046. doi:10.1519/JSC.0b013e3182651e7a; 10.1519/JSC.0b013e3182651e7a

Hunter SK, Thompson MW, Adams RD (2000) Relationships among age-associated strength changes and physical activity level, limb dominance, and muscle group in women. J Gerontol A Biol Sci Med Sci 55:B264-73

Karamanidis K, Arampatzis A (2005) Mechanical and morphological properties of different muscle-tendon units in the lower extremity and running mechanics: effect of aging and physical activity. J Exp Biol 208:3907-3923

Komi PV, Gollhofer A, Schmidtbleicher D, Frick U (1987) Interaction between man and shoe in running: considerations for a more comprehensive measurement approach. Int J Sports Med 8:196-202

Kubo K, Ikebukuro T, Maki A, Yata H, Tsunoda N (2012) Time course of changes in the human Achilles tendon properties and metabolism during training and detraining in vivo. Eur J Appl Physiol 112:2679-2691. doi:10.1007/s00421-011-2248-x; 10.1007/s00421-011-2248-x

Kubo K, Morimoto M, Komuro T et al (2007) Effects of plyometric and weight training on muscle-tendon complex and jump performance. Med Sci Sports Exerc 39:1801-1810. doi:10.1249/mss.0b013e31813e630a

Kubo K, Ohgo K, Takeishi R et al (2006) Effects of isometric training at different knee angles on the muscle-tendon complex in vivo. Scand J Med Sci Sports 16:159-167. doi:10.1111/j.1600-0838.2005.00450.x

Kubo K, Kanehisa H, Fukunaga T (2005) Effects of cold and hot water immersion on the mechanical properties of human muscle and tendon in vivo. Clin Biomech 20:291-300

Kubo K, Kanehisa H, Miyatani M, Tachi M, Fukunaga T (2003) Effect of low-load resistance training on the tendon properties in middle-aged and elderly women. Acta Physiol Scand 178:25-32

Kubo K, Kanehisa H, Fukunaga T (2001) Effects of different duration isometric contractions on tendon elasticity in human quadriceps muscles. J Physiol 536:649-655

Kuitunen S, Kyrolainen H, Avela J, Komi PV (2007) Leg stiffness modulation during exhaustive stretch-shortening cycle exercise. Scand J Med Sci Sports 17:67-75

Kuitunen S, Komi PV, Kyrolainen H (2002) Knee and ankle joint stiffness in sprint running. Med Sci Sports Exerc 34:166-173

Kyrolainen H, Avela J, McBride JM et al (2005) Effects of power training on muscle structure and neuromuscular performance. Scand J Med Sci Sports 15:58-64. doi:10.1111/j.1600-0838.2004.00390.x

Kyrolainen H, Avela J, McBride JM et al (2004) Effects of power training on mechanical efficiency in jumping. Eur J Appl Physiol 91:155-159. doi:10.1007/s00421-003-0934-z

Kyrolainen H, Takala TE, Komi PV (1998) Muscle damage induced by stretch-shortening cycle exercise. Med Sci Sports Exerc 30:415-420

Lanza IR, Towse TF, Caldwell GE, Wigmore DM, Kent-Braun JA (2003) Effects of age on human muscle torque, velocity, and power in two muscle groups. J Appl Physiol (1985) 95:2361-2369. doi:10.1152/japplphysiol.00724.2002

LaRoche DP, Cremin KA, Greenleaf B, Croce RV (2010) Rapid torque development in older female fallers and nonfallers: a comparison across lower-extremity muscles. J Electromyogr Kinesiol 20:482-488. doi:10.1016/j.jelekin.2009.08.004; 10.1016/j.jelekin.2009.08.004

Lichtwark GA, Wilson AM (2005a) In vivo mechanical properties of the human Achilles tendon during one-legged hopping. J Exp Biol 208:4715-4725. doi:10.1242/jeb.01950

Lichtwark GA, Wilson AM (2005b) Effects of series elasticity and activation conditions on muscle power output and efficiency. J Exp Biol 208:2845-2853. doi:10.1242/jeb.01710

Liu Y, Schlumberger A, Wirth K, Schmidtbleicher D, Steinacker JM (2003) Different effects on human skeletal myosin heavy chain isoform expression: strength vs. combination training. J Appl Physiol (1985) 94:2282-2288. doi:10.1152/japplphysiol.00830.2002

Magnusson SP, Hansen P, Aagaard P et al (2003) Differential strain patterns of the human gastrocnemius aponeurosis and free tendon, in vivo. Acta Physiol Scand 177:185-195

Malatesta D, Simar D, Dauvilliers Y et al (2003) Energy cost of walking and gait instability in healthy 65- and 80-yr-olds. J Appl Physiol 95:2248-2256

Malisoux L, Francaux M, Nielens H, Theisen D (2006) Stretch-shortening cycle exercises: an effective training paradigm to enhance power output of human single muscle fibers. J Appl Physiol (1985) 100:771-779. doi:10.1152/japplphysiol.01027.2005

Mian OS, Thom JM, Ardigò ,L.P., Narici MV, Minetti AE (2006) Metabolic cost, mechanical work, and efficiency during walking in young and older men. Acta Physiol (Oxf) 186:127-139

Mian OS, Thom JM, Ardigo LP, Minetti AE, Narici MV (2007) Gastrocnemius muscle-tendon behaviour during walking in young and older adults. Acta Physiol (Oxf) 189:57-65

Morse CI, Thom JM, Birch KM, Narici MV (2005) Tendon elongation influences the amplitude of interpolated doublets in the assessment of activation in elderly men. J Appl Physiol 98:221-226

Morse CI, Thom JM, Davis MG, Fox KR, Birch KM, Narici MV (2004) Reduced plantarflexor specific torque in the elderly is associated with a lower activation capacity. Eur J Appl Physiol 92:219-226. doi:10.1007/s00421-004-1056-y

Newton RU, Hakkinen K, Hakkinen A, McCormick M, Volek J, Kraemer WJ (2002) Mixed-methods resistance training increases power and strength of young and older men. Med Sci Sports Exerc 34:1367-1375

Norris JA, Granata KP, Mitros MR, Byrne EM, Marsh AP (2007) Effect of augmented plantarflexion power on preferred walking speed and economy in young and older adults. Gait Posture 25:620-627. doi:10.1016/j.gaitpost.2006.07.002

Onambele-Pearson GL, Pearson SJ (2012) The magnitude and character of resistance-training-induced increase in tendon stiffness at old age is gender specific. Age (Dordr) 34:427-438. doi:10.1007/s11357-011-9248-y; 10.1007/s11357-011-9248-y

Panizzolo FA, Green DJ, Lloyd DG, Maiorana AJ, Rubenson J (2013) Soleus fascicle length changes are conserved between young and old adults at their preferred walking speed. Gait Posture 38:764-769. doi:10.1016/j.gaitpost.2013.03.021; 10.1016/j.gaitpost.2013.03.021

Pearson SJ, Young A, Macaluso A et al (2002) Muscle function in elite master weightlifters. Med Sci Sports Exerc 34:1199-1206

Peltonen J, Cronin NJ, Stenroth L, Finni T, Avela J (2013) Viscoelastic properties of the Achilles tendon in vivo. Springerplus 2:212. doi:10.1186/2193-1801-2-212

Peltonen J, Cronin NJ, Stenroth L, Finni T, Avela J (2012) Achilles tendon stiffness is unchanged one hour after a marathon. J Exp Biol 215:3665-3671. doi:10.1242/jeb.068874

Piirainen JM, Cronin NJ, Avela J, Linnamo V (2014) Effects of plyometric and pneumatic explosive strength training on neuromuscular function and dynamic balance control in 60-70year old males. J Electromyogr Kinesiol 24:246-252. doi:10.1016/j.jelekin.2014.01.010; 10.1016/j.jelekin.2014.01.010

Pijnappels M, Bobbert MF, van Dieen JH (2005a) How early reactions in the support limb contribute to balance recovery after tripping. J Biomech 38:627-634. doi:10.1016/j.jbiomech.2004.03.029

Pijnappels M, Bobbert MF, van Dieen JH (2005b) Control of support limb muscles in recovery after tripping in young and older subjects. Exp Brain Res 160:326-333. doi:10.1007/s00221-004-2014-y

Rantalainen T, Hoffren M, Linnamo V et al (2011) Three-month bilateral hopping intervention is ineffective in initiating bone biomarker response in healthy elderly men. Eur J Appl Physiol 111:2155-2162. doi:10.1007/s00421-011-1849-8; 10.1007/s00421-011-1849-8

Reeves ND, Maganaris CN, Narici MV (2003) Effect of strength training on human patella tendon mechanical properties of older individuals. J Physiol 548:971-981. doi:10.1113/jphysiol.2002.035576

Rugg SG, Gregor RJ, Mandelbaum BR, Chiu L (1990) In vivo moment arm calculations at the ankle using magnetic resonance imaging (MRI). J Biomech 23:495-501

Seynnes OR, Koesters A, Gimpl M et al (2011) Effect of alpine skiing training on tendon mechanical properties in older men and women. Scand J Med Sci Sports 21 Suppl 1:39-46. doi:10.1111/j.1600-0838.2011.01340.x; 10.1111/j.1600-0838.2011.01340.x

Stenroth L, Peltonen J, Cronin NJ, Sipila S, Finni T (2012) Age-related differences in Achilles tendon properties and triceps surae muscle architecture in vivo. J Appl Physiol (1985) 113:1537-1544. doi:10.1152/japplphysiol.00782.2012; 10.1152/japplphysiol.00782.2012

Stosic J, Finni T (2011) Gastrocnemius tendon length and strain are different when assessed using straight or curved tendon model. Eur J Appl Physiol 111:3151-3154. doi:10.1007/s00421-011-1929-9

Taube W, Leukel C, Lauber B, Gollhofer A (2012) The drop height determines neuromuscular adaptations and changes in jump performance in stretch-shortening cycle training. Scand J Med Sci Sports 22:671-683. doi:10.1111/j.1600-0838.2011.01293.x; 10.1111/j.1600-0838.2011.01293.x

Van Cutsem M, Duchateau J, Hainaut K (1998) Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. J Physiol 513 (Pt 1):295-305

Winter DA (1990) Biomechanics and Motor Control of Human Movement. John Wiley & Sons, Inc., Toronto

Wren TA, Yerby SA, Beaupre GS, Carter DR (2001) Mechanical properties of the human achilles tendon. Clin Biomech (Bristol, Avon) 16:245-251

Yoon S, Tauchi K, Takamatsu K (2007) Effect of ankle joint stiffness during eccentric phase in rebound jumps on ankle joint torque at midpoint. Int J Sports Med 28:66-71. doi:10.1055/s-2006-923903 [doi]

Zajac FE (1989) Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. Crit Rev Biomed Eng 17:359-411

FIGURE LEGENDS

Figure 1. Ankle and knee joint angles at contact instant, minimum angle and angle at take-off instant at BEF, 2W and 11W at 100% hopping intensity. # and ##; 11W significantly different from 2W ($p<0.05$ and $p<0.01$, respectively)

Figure 2. Changes (%) from BEF in A) jumping height, B) contact time, C) peak Fz and D) AJS at 100% hopping. * and **; significant training effect ($p<0.05$ and $p<0.01$, respectively), # and ##; significant group effect ($p<0.05$ and $p<0.01$, respectively)**.** AJS was calculated as the change in ankle joint moment (from contact to peak) generated by the right leg divided by change in ankle joint angle (from contact to min).

Figure 3. Reactive strength index (flight time divided by contact time) at different intensity levels at BEF, 2W and 11W. * and **; significantly different from BEF ($p<0.05$ and $p<0.01$, respectively). ##; significantly different from 2W ($p<0.01$).

Figure 4. GaM braking over push-off phase EMG ratios in hopping with different intensities at BEF, 2W and 11W. * and **: significant training effect ($p<0.05$ and $p<0.01$, respectively). ¤: significant difference between training and control groups ($p<0.05$).

Figure 5. The length-time curves of GaM MTU, outer tendon and fascicle as well the ATF-time curves during hopping with different intensities in TG and CG at BEF, 2W and 11W.

Figure 6. GaM A) MTU and B) outer tendon lengthening and shortening amplitudes during hopping with different intensities. Stretching amplitudes are calculated from length during contact instant to peak length and shortening amplitudes from peak length to length at take-off instant.* and **: significantly different from 2W ($p<0.05$ and $p<0.01$, respectively).

FIGURES AND TABLES

Figure 1

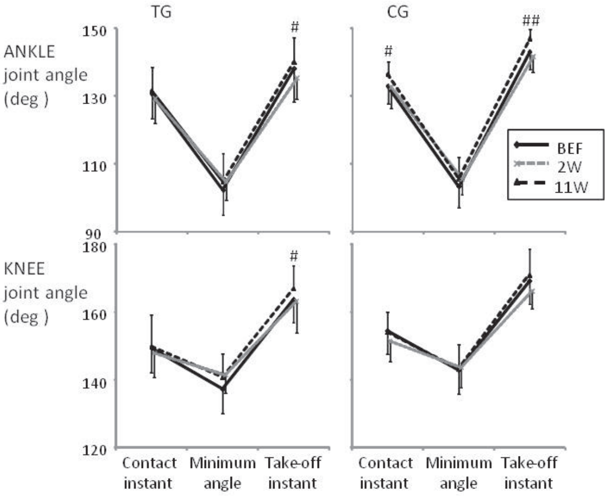

Figure 2

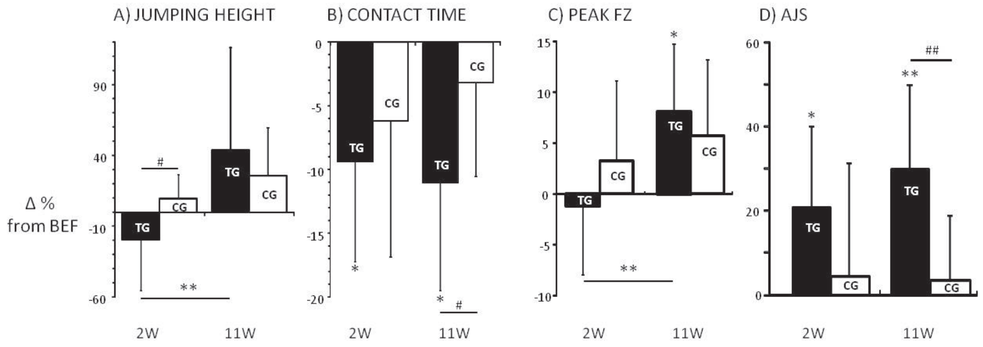
A) JUMPING HEIGHT
B) CONTACT TIME
C) PEAK FZ
D) AJS
Δ %
from BEF
90
40
-10
-60
0
-5
-10
-15
-20
15
10
5
0
-5
-10
60
40
20
0
TG
CG
#
##
*
**
2W
11W

Figure 3

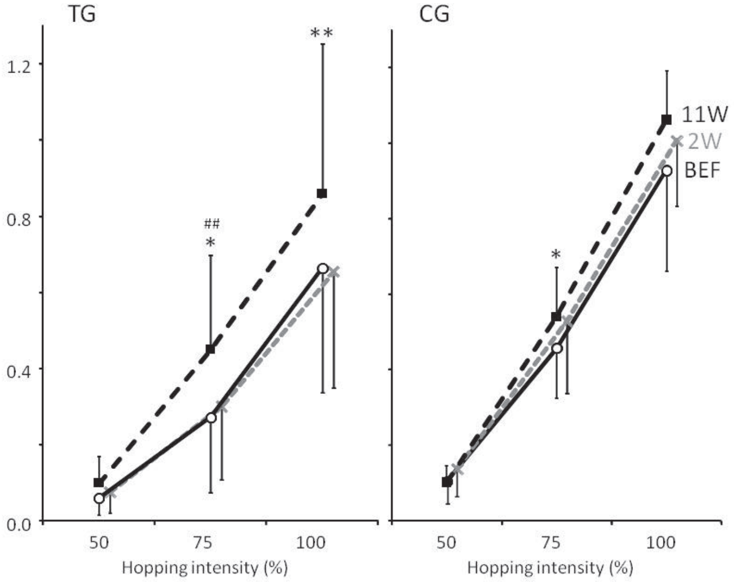
TG
CG
1.2
0.8
0.4
0.0
**
##
*
*
11W
2W
BEF
50
75
100
Hopping intensity (%)
50
75
100
Hopping intensity (%)

Figure 4

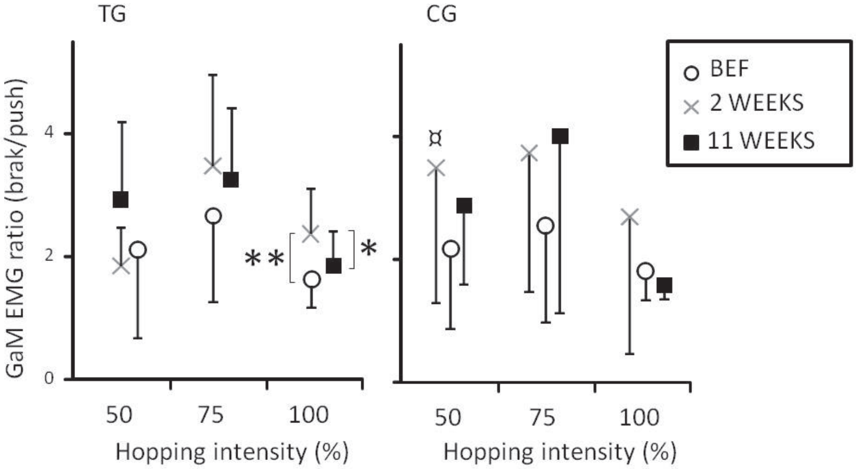
TG
CG
GaM EMG ratio (brak/push)
0
2
4
50
75
100
Hopping intensity (%)
50
75
100
Hopping intensity (%)
**
*
¤
BEF
2 WEEKS
11 WEEKS

Figure 5

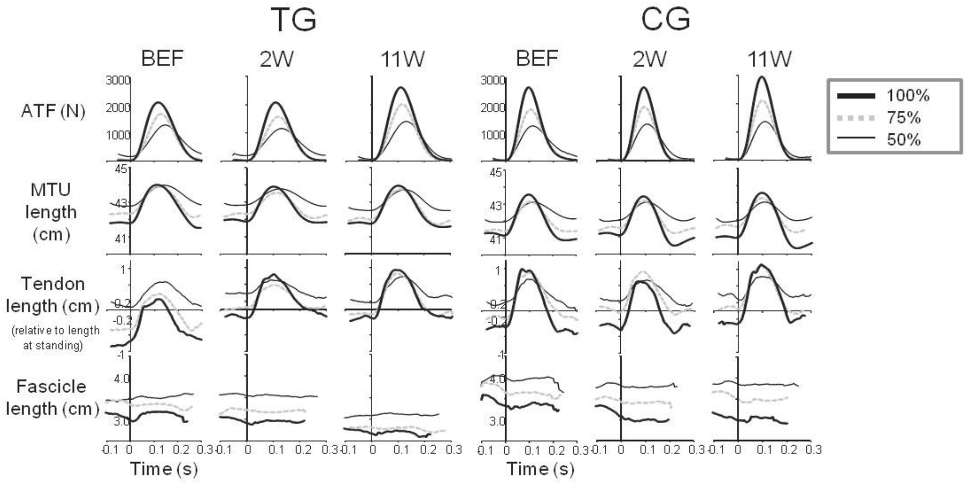
TG
CG
BEF
2W
11W
BEF
2W
11W
ATF (N)
MTU length (cm)
Tendon length (cm)
(relative to length at standing)
Fascicle length (cm)
3000
2000
1000
45
43
41
1
0.2
-0.2
-1
4.0
3.0
-0.1
0
0.1
0.2
0.3
Time (s)
100%
75%
50%

Figure 6

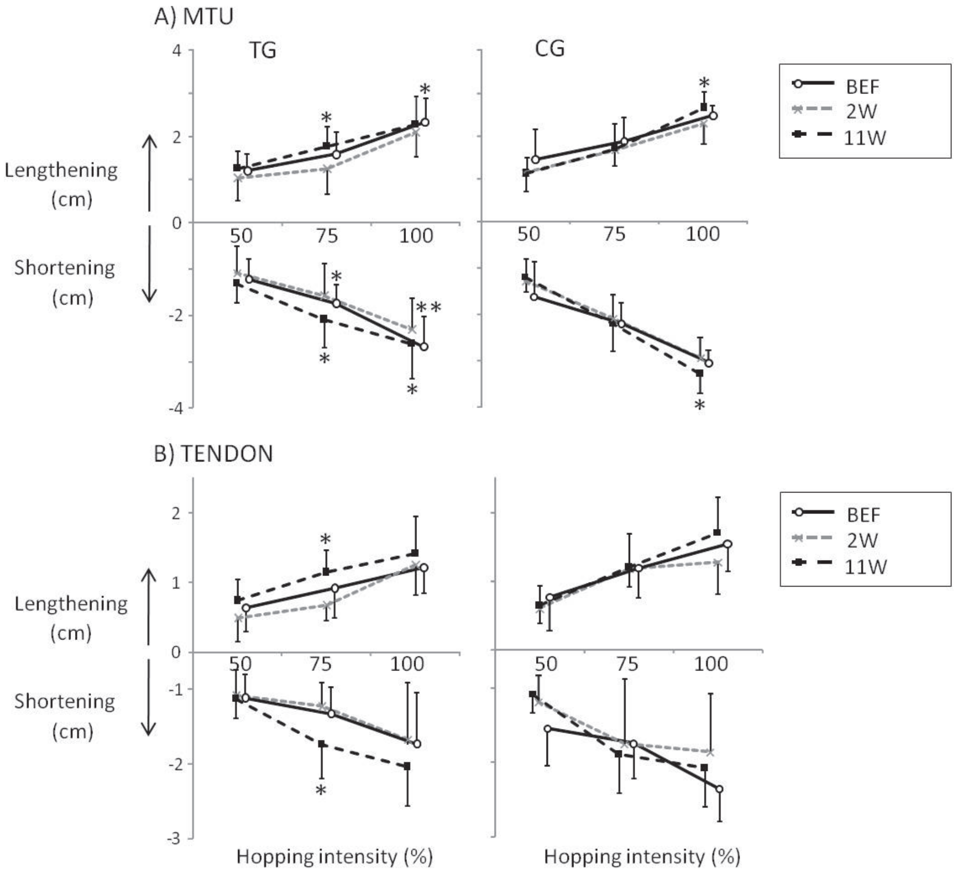
A) MTU
TG
CG
BEF
2W
11W
Lengthening (cm)
Shortening (cm)
4
2
0
-2
-4
50
75
100
*
**
B) TENDON
2
1
0
-1
-2
-3
Hopping intensity (%)
Hopping intensity (%)

Table 1. Background information of the subject groups. [#)] Supervised training means training with the supervisor outside the present study e.g. in local senior gym. *) Exercise types are listed in the order the subject groups reported they performed them.

	TG (n=10)	CG (n=10)	*P* value
Age (y)	73.1 ± 4.4	70.9 ± 4.4	0.28
Height (cm)	170.5 ± 7.4	171.9 ± 3.9	0.61
Weight (kg)	76.8 ± 9.2	73.4 ± 8.7	0.40
BMI (kg/m^2)	26.4 ± 2.5	24.8 ± 2.4	0.16
Exercise times / week	4.5 ± 1.8	3.6 ± 1.2	0.21
Exercise hours / week	7.4 ± 5.4	4.8 ± 2.2	0.24
Participation in supervised training [#)]	6/10	9/10	0.13
Preferred exercise types *)	Walking, skiing, gymnastic exercises	Gymnastic exercises, walking, cycling	

Table 2. Progression of the exercise intervention (adopted from Rantalainen et al. 2011).

Week	1	2	3	4	5	6	7	8	9	10	11
Sets * Intensity (% of maximal GRF)	4*75	2*75 3*90	1*75 4*90	1*75 4*90	1*75 4*90	2*75 5*90	2*75 5*90	2*75 5*90	2*75 5*90	2*75 5*90	2*75 5*90

Table 3. Correlation coefficients between the selected parameters and maximal jumping height (cm) at 11 WEEK measurements in trained and in controls. n= 10 trained, n= 10 controls. * and **: p<0.05 and p<0.01, respectively.

	Peak ATF	GaM fascicle shortening in push-off phase	GaM MTU stretch	GaM MTU shortening	GaM tendon strain	GaM tendon shortening
TG	0.86 **	-0.66 *	0.74 *	0.76 *	0.64 *	0.66 *
CG	-0.35	-0.22	-0.50	-0.31	-0.33	-0.10