### TITLE

AGE-RELATED MUSCLE ACTIVATION PROFILES AND JOINT STIFFNESS REGULATION IN

REPETITIVE HOPPING

Hoffrén Merja<sup>a</sup>, Ishikawa Masaki<sup>b</sup>, Rantalainen Timo<sup>a,c,d</sup>, Avela Janne<sup>a</sup> & Komi Paavo V<sup>a</sup>.

<sup>a</sup> Neuromuscular Research Center, Department of Biology of Physical Activity, University of Jyväskylä,

Finland.

<sup>b</sup>Osaka University of Health and Sport Sciences, Kumatori-cho, Sennan-gun, Osaka, Japan.

<sup>c</sup> Department of Mechanical Engineering, Lappeenranta University of Technology, Finland.

<sup>d</sup> Department of Health Sciences, University of Jyväskylä, Finland.

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

Correspondence to:

Merja Hoffrén

Neuromuscular Research Center

Department of Biology of Physical Activity,

University of Jyväskylä

Phone. +358-14-2602074

Fax +358-14-2602071

merja.hoffren@sport.jyu.fi

### **ABSTRACT**

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

22

23

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. Agecomparison 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 M $\Omega$ , 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

 $k\Omega$ . 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).

1 2

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

7 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 1 intensities both in YOUNG and in ELDERLY. Maximal hopping trials that were done at the beginning and at 2 3 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 4

6

5

7

8

9

10

11

13

14

15

16

17

18

Peak Fz during maximal hopping

presented for the parameters that follow.

As expected, and compared to YOUNG, ELDERLY had significantly lower maximal vertical ground reaction force (Fz) during maximal hopping (p<0.001) (4529  $\pm$  666 N vs. 3131  $\pm$  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  $\pm$  0.9 vs. ELDERLY 4.2  $\pm$  0.7 times bw, p<0.001).

12

- 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.

submaximal hopping in both age groups.

19

20

21

22

23

24

25

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

1 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).

7 Ankle and knee joint stiffness

2

3

4

5

6

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

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,
- 2 the activation of plantarflexor muscles increased with hopping intensity in both age groups. However, YOUNG
- 3 had higher agonist braking phase activations as compared to ELDERLY (figure 5). Activation of the antagonist
- 4 TA muscle in the braking phase increased only in YOUNG with increasing intensity (p<0.05). The activation of
- 5 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.

7

6

8

10

11

12

13

14

15

17

18

19

21

23

24

25

26

- EMG ratio: Braking phase activation over push off -phase activation
- 9 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.
- 16 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].

,

1

2

3

4

5

6

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

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.

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

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.

#### ACKNOWLEDGMENTS

- 2 The authors acknowledge the valuable contribution of Ms. P. Puttonen, Ms. S. Roivas and Mr. M. Ruuskanen
- 3 for technical assistance and help with data analysis.

4

5

6

7

8

10

11

12

14

15

16

17

18

19

20

1

GRANTS

This study was supported by grant #123757 from the Academy of Finland.

9

#### 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
- 13 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
- 21 1977;268(2):467--81.
- DeVita P, Hortobagyi T. Age causes a redistribution of joint torques and powers during gait. J Appl Physiol
- 23 2000;88(5):1804-1811.
- Enoka RM. Neural adaptations with chronic physical activity. J Biomech 1997;30(5):447-455.
- 25 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.

- 1 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.
- 3 Häkkinen K, Alen M, Kallinen M, Izquerdo M, Jokelainen K, Lassila H, Mälkiä E, Kraemer WJ, Newton RU.
- 4 Muscle CSA, force production, and activation of leg extensors during isometric and dynamic actions in
- 5 middle-aged and elderly men and women. J Aging and Phys Act 1998(6):232-232-247.
- 6 Hermens HJ, Freriks B, Merletti R, Hägg G, Stegeman D, Blok Jea. SENIAM 8: European recommendations
- 7 for surface electromyography 1999.
- 8 Hobara H, Kanosue K, Suzuki S. Changes in muscle activity with increase in leg stiffness during hopping.
- 9 Neurosci Lett 2007;418(1):55-59.
  - Hoffren M, Ishikawa M, Komi PV. Age-related neuromuscular function during drop jumps. J Appl Physiol
- 11 2007;103(4):1276-1283.

10

13

14

15

16

17

18

19

20

21

- 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 1 2 2002;34(1):166-173. Mian OS, Thom JM, Ardigò, L.P., Narici MV, Minetti AE. Metabolic cost, mechanical work, and efficiency 3 during walking in young and older men. Acta Physiol Scand 2006;186(2):127-139. 4 5 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. 6 Ortega JD, Fehlman LA, Farley CT. Effects of aging and arm swing on the metabolic cost of stability in human 7 walking. J Biomech 2008;41(16):3303-3308. 8 Reeves ND, Spanjaard M, Mohagheghi AA, Baltzopoulos V, Maganaris CN. Older adults employ alternative 9 strategies to operate within their maximum capabilities when ascending stairs. J Electromyogr Kinesiol 10 2009;19(2):e57-68. 11 Roos MR, Rice CL, Vandervoort AA. Age-related changes in motor unit function. Muscle Nerve 12 13 1997;20(6):679-690. Savelberg HH, Verdijk LB, Willems PJ, Meijer K. The robustness of age-related gait adaptations: can running 14 counterbalance the consequences of ageing? Gait Posture. 2007;25(2):259-266. 15 Seidler RD, Alberts JL, Stelmach GE. Changes in multi-joint performance with age. Motor control 16 2002;6(1):19-31. 17 Smith JL, Edgerton VR, Betts B, Collatos TC. EMG of slow and fast ankle extensors of cat during posture, 18 locomotion, and jumping. J Neurophysiol 1977;40(3):503-513. 19 Winter DA. Biomechanics and Motor Control of Human Movement. : John Wiley & Sons, Inc., Toronto, 1990. 20 21 Yoon S, Tauchi K, Takamatsu K. Effect of ankle joint stiffness during eccentric phase in rebound jumps on 22 ankle joint torque at midpoint. Int J Sports Med 2007;28(1):66-71.

23

24

#### FIGURE LEGENDS

- 2 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).

4

5

6

7

8

9

10

12

13

15

16

17

18

19

1

3

- 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.

11

- 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).

14

- 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.

20

21

22

23

24

- 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.

25

26

27

- 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).

28

29

30

- 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)	<i>P</i> value
Age (y)	$25.4 \pm 4.1$	$71.7 \pm 4.3$	<0.001 ***
Height (cm)	$176.7 \pm 5.9$	171.5 $\pm$ 5.5	0.033 *
Mass (kg)	$74.3 \pm 6.7$	75.4 $\pm$ 8.6	0.66
BMI (kg/m²)	$23.8 \pm 1.3$	$25.6 \pm 2.5$	0.034 *
Exercise times / week	5.4 ± 2.5	4.2 ± 1.9	0.55
Exercise hours / week	10.1 ± 4.4	$6.0\pm3.8$	0.052
Preferred exercise types	Ballgames, gym	Gymnastic exercises, walking, skiing, cycling, swimming	













