**Effects of triceps surae muscle strength and tendon stiffness on the reactive dynamic stability and adaptability of older female adults during perturbed walking**

Epro G1,2, McCrum C3,4, Mierau A5,6, Leyendecker M5, Brüggemann G-P2,7, Karamanidis K1

1Sport and Exercise Science Research Centre, School of Applied Sciences, London South Bank University, United Kingdom; 2Institute of Biomechanics and Orthopaedics, German Sport University Cologne, Germany; 3NUTRIM School of Nutrition and Translational Research in Metabolism, Maastricht University Medical Centre+, Department of Human Movement Science, Maastricht, The Netherlands; 4Institute of Movement and Sport Gerontology, German Sport University Cologne, Germany; 5Institute of Movement and Neurosciences, German Sport University Cologne, Germany; 6Department of Exercise and Sport Science, LUNEX International University of Health, Exercise and Sports, Differdange, Luxembourg; 7Cologne Center for Musculoskeletal Biomechanics, Medical Faculty, University of Cologne, Cologne, Germany

**Corresponding Author:**

Gaspar Epro

Sport and Exercise Science Research Centre

School of Applied Sciences, London South Bank University

103 Borough Road, London SE1 0AA, United Kingdom

E-mail: g.epro@lsbu.ac.uk

Tel: +44 20 7815 7935

**Keywords:** aging, falls, margin of stability, muscle strength, tendon stiffness

**Running title**: Triceps surae properties and gait stability in older adults

**New & Noteworthy:** Triceps surae muscle weakness and a more compliant Achilles tendon partly limit older adults’ ability to effectively enlarge the base of support and recover dynamic stability after an unexpected perturbation during walking, increasing their fall risk. However, the degeneration in muscle strength and tendon stiffness may not inhibit the ability of the locomotor system to adapt the reactive motor response to repeated perturbations.

# Abstract

This study aimed to examine whether the triceps surae (TS) muscle-tendon unit (MTU) mechanical properties affects gait stability and its reactive adaptation potential to repeated perturbation exposure in older adults. Thirty-four older adults each experienced eight separate unexpected perturbations during treadmill walking, while a motion capture system was used to determine the margin of stability (MoS) and base of support (BoS). Ankle plantarflexor muscle strength and Achilles tendon (AT) stiffness were analysed using ultrasonography and dynamometry. A median split and separation boundaries classified the subjects into two groups with GroupStrong (n=10) showing higher ankle plantarflexor muscle strength (2.26±0.17 Nm·kg-1 vs. 1.47±0.20 Nm·kg-1; *P<*0.001) and AT stiffness (544±75 N·mm-1 vs. 429±86 N·mm-1; *P*=0.004) than GroupWeak (n=12). The first perturbation caused a negative ΔMoS (MoS in relation to unperturbed baseline walking) at touchdown of perturbed step (PertR), indicating an unstable position. GroupStrong required four recovery steps to return to ΔMoS zero level, while GroupWeak was unable return to baseline within the analysed steps. However, after repeated perturbations, both groups increased ΔMoS at touchdown of PertR with a similar magnitude. Significant correlations between ΔBoS and ΔMoS at touchdown of the first recovery step and TS MTU capacities (0.41<r<0.57; 0.006<*P*<0.048) were found. We concluded that older adults with TS muscle weakness have a diminished ability to control gait stability during unexpected perturbations, increasing their fall risk, but that degeneration in muscle strength and tendon stiffness may not inhibit the ability of the locomotor system to adapt the reactive motor response to repeated perturbations.

# Introduction

Aging is associated with a gradual decline in the capacities of the entire neuro-motor system, which lead to diminished mobility and reduced gait performance and hence, to a decreased ability to produce effective and safe gait patterns during daily life. This can directly or indirectly lead to falls, which can have severe consequences such as adverse clinical conditions or even mortality (53). Approximately one third of older adults fall at least once a year and these occur most frequently during locomotion, usually due to tripping or slipping (4, 51). As well as daily life falls, deficient stability control has also been demonstrated in laboratory settings using mechanical gait perturbations (e.g. sudden surface changes and trips) in older adults (7, 42, 49).

Gait stability can be controlled via reactive (feedback-driven) or predictive (feedforward-driven) adjustments (5, 8, 9, 25, 30, 32). Predictive adjustments are made based on prior experience and knowledge about potential changes in the external environment, whereas reactive adjustments rely on the real-time sensory feedback received during movement (5, 8, 9, 29, 38, 40). Older adults, in comparison to younger adults, show less effective reactive adjustment in dynamic stability, mainly due to a reduced ability to effectively increase the base of support (BoS) following a gait perturbation (49). Given the importance of these predictive and reactive mechanisms for maintaining stability, it is promising that these mechanisms show improvement in response to repeated mechanical perturbations in healthy older adults (7, 8, 9, 12, 30, 33, 37, 39). However, the rate of the adaptive improvement (at least in feedforward adaptation), seems to be diminished in older adults (12, 30). Therefore, the assessment of adaptation to repeated perturbations may provide useful insight into gait stability control in groups with reduced neuro-motor capacities.

The age-related degeneration of the muscle-tendon unit (MTU) capacities, primarily the declined muscle strength and reduced tendon stiffness (14, 20, 26, 35, 48), are often linked to the reduced locomotor capacities. For instance, the age-related deterioration in muscle strength has been associated with diminished mobility in older populations (3, 24), as well as with a decreased ability to recover following a loss of balance (18, 23, 44, 45). In particular, inadequate recovery responses after tripping have been linked to age-related deficits in the ankle plantarflexion moment during the push-off phase (41–43). Older fallers show lower rates of torque development in all the support limb joints and a lower peak ankle moment, which contribute to an insufficient reduction of the angular momentum during push-off and creates less proper placement of the recovery limb after induced tripping when compared to younger or older non-fallers (42, 43). Furthermore, it has been shown that lower leg-extensor muscle strength and tendon stiffness are associated with deficits in balance recovery following a forward loss of balance in older adults (21, 23). These results imply that the triceps surae (TS) muscle-tendon unit (MTU) mechanical properties in particular, play an essential role in the recovery response to sudden gait disturbances, indicating that greater ankle plantarflexor muscle strength and AT stiffness may be beneficial for gait stability in the elderly.

While it has been shown that the ability to generate appropriate joint moments in the support limb during push-off may influence stability recovery following gait perturbations (41, 42), it has not yet been thoroughly investigated if TS MTU mechanical properties are associated with gait stability and adaptability during repeated perturbations in older adults. In a previous study (16), we divided a group of older female adults into a strong and weak group according to their ankle plantarflexor muscle strength and showed that the stronger older adults also possessed a higher AT stiffness. In the current study, we analysed dynamic gait stability during perturbed walking in the same subject groups and thereby aimed to examine whether TS MTU mechanical properties are associated with the recovery responses and reactive adaptation potential in dynamic stability during perturbed walking in older adults. It was hypothesized that (i) a greater BoS and MoS at touchdown (TD) of the first recovery step would be associated with the TS MTU mechanical properties, (ii) that older adults with greater ankle plantarflexor muscle strength and AT stiffness would regain balance after a perturbation during walking more effectively, and (iii) that the stronger older adults would show more pronounced improvement in the reactive response following repeated exposure to unexpected perturbations than their weaker counterparts.

# Materials and Methods

## *Participants*

Thirty-four older female adults (mean ± standard deviation; age: 65±7 years; body mass: 65±9 kg; body height: 165±6 cm) from a large-scale knee osteoarthritis study (moderate unilateral knee osteoarthritis with KL-score 2-3; no pain during locomotion) voluntarily participated in the study. Exclusion criteria were any other neurological or musculoskeletal impairments of the lower limbs (e.g. joint pain during locomotion) which might influence the findings of the study. The subjects were generally healthy in comparison to normative age group data (SF-36 general health questionnaire average outcome of 73.5%; average single leg stance time of 39.6 s out of maximal 45 s test duration; mean timed up and go test result of 7.2 s). All participants received medical clearance from their general practitioners prior the measurements, and provided their written informed consent after the procedures and possible risks of the study were explained. The study was approved by the ethics committee of the German Sport University Cologne and met all requirements for human experimentation in agreement with the Declaration of Helsinki.

## *Analysis of ankle plantarflexor muscle strength and Achilles tendon stiffness*

The method used to examine the mechanical properties of the TS MTU *in vivo* has been previously described in detailed (16). Briefly, in order to determine ankle plantarflexor muscle strength, all subjects were placed in a seated position with their preferred leg for step initiation fixed, with ankle and knee joints flexed at 90° (thigh and foot perpendicular to the shank) and their feet placed on a custom-made strain gauge dynamometer (sampling frequency 1000 Hz; Precision Engineering and Electronics Department of the German Sport University Cologne). Following a standardized warm-up (27), which consisted of 10 submaximal and three maximal voluntary isometric ankle plantarflexion contractions (MVCs), the subjects performed six separate MVCs with verbal encouragement (3 contractions “as strong as possible” and 3 controlled ramp contractions). The resultant ankle joint moments were calculated using inverse dynamics by accounting for the gravitational moments using a passive measurement (16). The individual ankle plantarflexor muscle strength (maximal plantarflexion moment) was assessed by considering all six performed MVC plantarflexion contractions, and was normalized to the subject’s body mass (Nm·kg-1) to insure an appropriate comparison. The contributions of the other synergistic muscles or the antagonist dorsiflexors were not accounted for, thereby the resultant plantarflexion moment is an approximation of the moment produced by the TS muscle. The mean values of the three MVC ramp contractions were used to determine the force-length relationship of the AT. For each participant, the AT moment arm was individually assessed using the tendon excursion method with the aid of ultrasonography during passive ankle joint rotation (28). The displacement of the myotendinous junction (MTJ) of the m. gastrocnemius medialis (GM) during the passive movements and ramp contractions was analysed with a linear array ultrasound probe (frequency 29 Hz; ultrasound device: MyLabTMFive, Esaote; Genoa, Italy). The displacement of the MTJ in relation to a skin marker was manually digitized using the Simi Motion 5.0 video analysis software (SIMI Reality Motion System GmbH, Unterschleißheim, Germany). The effect of inevitable ankle joint angular rotation on the measured tendon elongation during each contraction was taken into account using a potentiometer located under the heel to calculate changes in the ankle joint angle as described previously (1, 16). Subsequently, the AT force was calculated by dividing the resultant ankle joint moment by the individual tendon moment arm. The stiffness of the AT was determined as the slope of the calculated tendon force and resultant tendon elongation between 50% and 100% of maximum tendon force using linear regression (16).

## *Analysis of the recovery response and reactive gait adaptation during perturbed walking*

On a second measurement day, a gait perturbation paradigm was applied while walking on a treadmill using a manually controlled custom-built pneumatic brake-and-release system, similar to the magnetic system described in previous studies (30, 32, 49), which applies and removes resistance (generating approximately 55 N, within about 20 ms) to the lower right limb during walking via an ankle strap and Teflon cable. A treadmill walking familiarization session was conducted for all subjects four to seven days prior to the measurement day. During the measurement, all subjects walked at 1.4 m·s-1 on a motor-driven treadmill (pulsar 4.0, h/p/cosmos; Nussdorf-Traunstein, Germany) and were secured with a safety harness connected to an overhead frame. In order to attain a natural gait pattern, all participants wore their own regular sports shoes. Similar to our previous protocols (30–32, 49), a separate baseline measurement (unperturbed walking) were recorded after four minutes walking (22) while wearing the ankle strap (with a negligible external resistance of about 0.1 N), from which twelve consecutive steps were used to determine the baseline parameters. Directly after this baseline measurement the external resistance (55 N) was applied unexpectedly during an entire swing phase of the right leg, provoking a gait perturbation (Fig. 1). The application of the resistance over the entire swing phase assured an individually standardized perturbation from the temporal perspective for each participant. This unexpected perturbation was repeated eight times (trials), separated by washout periods of unperturbed walking of varying lengths of approximately two to three minutes with the first (Trial 1), fourth (Trial 4) and eighth (Trial 8) trial being considered for further analysis (Fig. 2). The participants were not informed about the onset or removal of the resistance, but were aware that their gait was going to be perturbed at some point during walking.

**Insert Figure 1 and Figure 2**

In order to analyse dynamic stability during treadmill walking, a reduced kinematic model (adapted from reference #49) was used. Five retro reflective markers (radius 16 mm) attached to anatomical landmarks (seventh cervical vertebra (C7), greater trochanter of the left and right leg, left and right hallux) were tracked at a frequency of 120 Hz using a motion capture system (Nexus; Vicon Motion Systems, Oxford, UK). The 3D coordinates of the markers were smoothed using a fourth order digital Butterworth filter with a cut-off frequency of 20 Hz. Each foot TD was detected using two-dimensional accelerometers (ADXL250; Analog Devices, Norwood, MA, USA) placed on the tibias (50), whereas each foot toe-off (TO) was determined by using the trajectories of the foot markers (41). A valid method to analyse biomechanical stability of human walking (11), the margin of stability (MoS), was calculated in the anteroposterior direction during gait at each foot TD (Fig. 2) according to the extrapolated centre of mass concept (19), as the difference between the anterior boundary of the base of support (BoS; anteroposterior component of the toe projection to the ground) and the extrapolated centre of mass (XCoM), adapted for the simplified kinematic model based on Süptitz et al. (49):

$$X\_{CoM}=P\_{Tro}+ \frac{\frac{\left(v\_{Tro}+ v\_{C7}\right)}{2}+ \left|v\_{BoS}\right|}{\sqrt{\frac{g}{L}}}$$

where PTro is the average horizontal (anteroposterior) component of the projection of the trochanter markers to the ground, vTro is the average horizontal velocity of the trochanter markers, vC7 is the horizontal velocity of the C7 marker, vBoS the horizontal velocity of the anterior boundary of the base of support (roughly equivalent to the velocity of the treadmill, as it is the average velocity of the forefoot marker during the stance phase), g is the acceleration due to the gravity and L is the average distance between the trochanter and the ankle joint center of rotation of the left and right leg in the sagittal plane, measured in a standing reference position. This adapted reduced kinematic model (49) has been shown to be appropriate to assess dynamic stability parameters (XCoM, MoS and BoS) in a wide range of age groups with negligible differences to a full body kinematic model, thus reducing data analysis and data processing.

Furthermore, in order to evaluate task demand during walking at the selected velocity (1.4 m·s-1) during perturbations, we additionally determined maximal walking velocity for each participant during over ground walking over a 15 m walkway using the motion capture system (120 Hz) and two force plates (60 x 40 cm, 1080 Hz; Kistler, Winterthur, CH). The two force plates were used for a real time check of the double support phase. The left and right greater trochanter were tracked within a 3 m distance in the centre of the laboratory. The maximal value of the average horizontal velocity of the trochanter markers in five valid (double support present) walking trials was selected as the individual maximal walking velocity.

## *Analysis of the electromyographic activity of the ankle plantarflexors during perturbed walking*

The electromyographic (EMG) activity of m. soleus (SOL) and m. gastrocnemius medialis (GM) of the right limb were recorded at a sampling rate of 1080 Hz with adhesive bipolar surface Ag/AgCl electrodes (Blue Sensor; Ambu GmbH, Bad Nauheim, Germany) by using a telemetric EMG system (m320; myon AG, Schwarzenberg, Switzerland). The skin over the muscle belly was carefully shaved and cleaned with ethanol to reduce skin impedance. The electrodes were placed over the mid-point of the muscle belly, parallel to the assumed direction of the muscle fibres and further secured to the skin along with the transmitter using an elastic tape in order to minimize motion artefacts. The raw EMG signals were band pass filtered (10–500 Hz Butterworth fourth order recursive filter), full-wave rectified and smoothed with a root-mean-square envelope using a 20 ms moving window. The filtered EMG data was separated into ground contact phases (time period between the foot TD and TO) and normalized to the full length of the ground contact phase and to the maximal activation during six consecutive contacts in the baseline walking for each muscle (relative EMG activity; EMGnorm). As the joint moment generation at ankle joint during the PertR stance phase may be important determinants of the BoS at the first recovery step (Reco1L), the EMGnorm was analysed at baseline walking (average of six consecutive right foot contact phases) and during the contact phase of the perturbed right step (PertR) in the analyzed perturbation trials (Trial 1, Trial 4 and Trial 8; Fig. 3). In order to specifically examine the ankle push-off phase during walking, the mean EMGnorm from 50 to 100% of the ground contact phase was calculated. To assess the changes in relation to the baseline we subtracted the mean EMGnorm during unperturbed walking in both analyzed muscles (ΔEMGSOL and ΔEMGGM).

**Insert Figure 3**

## *Statistics*

The analysed older female adults were classified into two groups (GroupStrong and GroupWeak) based on their normalized maximal isometric ankle plantarflexion moment (Nm·kg-1) by using a median split and separation boundaries allowing for a minimum of 15% difference between the weakest subject of the GroupStrong and the strongest subject of the GroupWeak. Implementing this method lead to a decrease in the overall number of subjects (n=22), but allowed a clear separation between the groups. The distribution normality of all variables was checked before applying statistical analysis using Shapiro-Wilk-Test, which revealed normal distributions for all parameters (*P* > 0.05). Independent samples T-tests were used to examine possible differences between GroupStrong and GroupWeak in size (body height and mass), age, ankle plantarflexor muscle strength, AT stiffness and maximal walking velocity. Additional independent sample T-tests were implemented to determine potential differences in MoS and BoS during unperturbed baseline walking (average of 12 consecutive steps of unperturbed walking with the ankle strap) between the two subject groups. In order to examine the recovery response during perturbed walking, the MoS and BoS at TD of the perturbed right step (PertR) and of the following first six recovery steps (Reco1L, Reco2R, Reco3L, Reco4R, Reco5L and Reco6R) of the Trial 1 were investigated. Furthermore, in order to account for individual differences in walking stability, the change in the MoS and BoS relative to baseline unperturbed walking at PertR and the following 6 recovery steps was used (ΔMoS and ΔBoS), where negative ΔMoS and ΔBoS values indicate smaller MoS and BoS in relation to steady state (unperturbed) walking respectively. To identify potential differences in ΔMoS and ΔBoS, a two-way repeated measures analysis of variance (ANOVA) was implemented with the subject group (GroupStrong and GroupWeak; independent variable) and step (PertR, Reco1L, Reco2R, Reco3L, Reco4R, Reco5L and Reco6R; dependent variable) as factors. For the analysis of the adaptation potential of the reactive recovery response, the ΔMoS at TD of PertR were analysed in Trial 1, Trial 4 and Trial 8. Therefore, a two-way repeated measures ANOVA was implemented for ΔMoS at TD of PertR with subject group as an independent variable and the perturbation trial as the dependent variable. When a significant group, step, trial or interaction effect was detected by the ANOVAs, a Tukey’s post-hoc test was implemented for pairwise comparisons. Regarding the EMG activity of the PertR, further separate two-way repeated measures ANOVAs were performed with the mean EMGnorm during the second phase of the ground contact phase (push-off/propulsion phase) for both analysed muscle (ΔEMGSOL and ΔEMGGM) with the subject group (GroupStrong and GroupWeak; independent variable) and perturbation trial (Trial 1, Trial 4 and Trial 8; dependent variable) as factors. Furthermore, the Pearson product-moment correlation coefficient and a multiple regression analysis was implemented in order to identify the relationship between TS MTU capacities and dynamic stability control, by using the ankle plantarflexor muscle strength and AT stiffness, and the ΔMoS and ΔBoS at TD of the first recovery step (Reco1L) of the Trial 1 with the participants from the newly formed groups (n=22). All statistical analyses were performed using STATISTICA (version 10, StatSoft Inc., Tulsa, OK, USA). The significance level was set at α=0.05, with results in text and figures presented as mean and standard deviation (SD).

# Results

GroupStrong (n=10), in comparison to GroupWeak (n=12), had, on average, about a 43% higher maximal isometric ankle plantarflexion moment (2.26 ± 0.17 Nm·kg-1 vs. 1.47 ± 0.20 Nm·kg-1; *P <* 0.001) accompanied by a 24% higher AT stiffness (544 ± 75 N·mm-1 vs. 429 ± 86 N·mm-1; *P* = 0.004). Furthermore, GroupStrong demonstrated approximately 11% higher maximal walking velocity than GroupWeak (2.54 ± 0.15 m·s-1 vs. 2.27 ± 0.21 m·s-1; *P* = 0.003). There were no significant differences between the groups in age (GroupStrong: 64 ± 5 vs. GroupWeak: 65 ± 6 years), body mass (63 ± 11 vs. 68 ± 7 kg) and body height (166 ± 8 vs. 165 ± 5 cm).

**Insert Figure 4**

Regarding the gait stability parameters during baseline walking, no significant differences were found between the subject groups either in MoS (0.04 ± 0.03 m vs. 0.04 ± 0.04 m for GroupStrong and GroupWeak respectively) nor in BoS (0.63 ± 0.04 m vs. 0.65 ± 0.04 m). Concerning the analysis of the reactive recovery response during the first unexpected perturbation trial (Trial 1), the two-way repeated measures ANOVA revealed a statistically significant subject group and step interactionfor the ΔMoS, meaning the effect of subject group on dynamic stability control was step specific. The gait perturbation caused considerable decrease in MoS and BoS (Fig. 4) in both subject groups, with the post hoc tests revealing no significant group differences in ΔMoS or ΔBoS at TD of the PertR. GroupWeak demonstrated significantly lower ΔMoS (more negative values) in comparison to GroupStrong for the first four analysed recovery steps (0.034 < *P* < 0.043; Fig. 4). Following the perturbation, GroupStrong showed significantly higher ΔMoS values to PertR in all analyzed recovery steps (0.0001 < *P* < 0.004; Fig. 4), thereby requiring four recovery steps to return to MoS baseline (zero level). GroupWeak demonstrated significantly (*P* < 0.01; Fig. 4) higher ΔMoS values to PertR starting from the second recovery step (Reco2R), but failed to recover to MoS baseline within the observed six recovery steps (did not reach ΔMoS zero level). For the ΔBoS values, the two-way repeated measures ANOVA resulted in a group and step interaction. The post hoc comparison revealed a significantly (*P* < 0.001; Fig. 3) higher ΔBoS at TD of all recovery steps in comparison to PertR in both groups, with GroupStrong showing a significantly (*P* = 0.042) higher ΔBoS at TD of Reco1L than GroupWeak (0.10 ± 0.05 m vs. 0.03 ± 0.04 m; Fig. 4).

**Insert Figure 5**

Significant correlations were identified between the TS MTU mechanical properties and the ΔBoS at the TD of Reco1L (r = 0.57, *P* = 0.006 and r = 0.53, *P* = 0.012 with maximal isometric ankle plantarflexion moment and AT stiffness respectively; n = 22; Fig. 5) and for the ΔMoS at the TD of Reco1L (r = 0.50, *P* = 0.019 and r = 0.41, *P* = 0.048; n = 22; Fig. 5). The multiple regression analysis revealed a significant relationship between ankle plantar flexor muscle strength and AT stiffness and the stability measures, with ΔBoS at the TD of Reco1L (R2 = 0.37, P = 0.015; n = 22) as well as with ΔMoS at the TD of Reco1L (R2 = 0.27, P = 0.044; n = 22).

**Insert Figure 6**

Concerning the analysis of the repeated gait perturbations, the two-way ANOVA with subject group and perturbation trial (Trial 1, Trial 4, Trial 8) as factors revealed a significant perturbation trial effect on ΔMoS (*P <* 0.001), but no significant subject group effect or interaction (Fig. 6). The post hoc tests showed that repeating the gait perturbation resulted in a significant (*P <* 0.001) increase in the ΔMoS at the TD of the PertR in both GroupStrong and GroupWeak, with no between subject group differences (Fig. 6). No significant differences in the ΔMoS at TD of the PertR were found between Trial 4 and Trial 8, in either of the subject groups (no significant interaction effect).

**Insert Figure 7**

Regarding the mean EMGnorm during the second phase of the ground contact phase (50 to 100% of the ground contact phase) of the PertR in SOL and GM in Trial 1, Trial 4 and Trial 8, a significant subject group effect was determined for GM with higher (*P* = 0.038) ΔEMGGM for GroupStrong in comparison to GroupWeak, regardless of the analysed perturbation trial (Fig. 7). No significant group differences were found in the ΔEMGSOL during the the second phase of the ground contact phase (push-off phase) of the PertR.

# Discussion

This study aimed to examine whether TS MTU mechanical properties are associated with the recovery response and the reactive adaptation potential in dynamic stability during perturbed walking within a homogenous group of older adults. Our first hypothesis, that the BoS at TD of the first recovery step is associated with the TS MTU mechanical properties was partly confirmed with a moderate correlation. Further, the hypothesis that stronger older adults have a more effective recovery response than weaker older adults, could be likewise confirmed, as the stronger adults needed fewer recovery steps to regain dynamic stability after a sudden perturbation than their weaker counterparts. However, our third hypothesis, that older adults with greater ankle plantarflexor muscle strength and AT stiffness show more pronounced improvement in the reactive response following repeated exposure to unexpected perturbations than their weaker counterparts was rejected, as no differences in reactive adaptation potential were seen between the stronger and weaker groups of older adults.

Following the unexpected gait perturbation, GroupStrong was able to produce a larger first recovery step in the anterior direction (higher ΔBoS) than GroupWeak (Fig. 4). As a result, GroupStrong could create a more advantageous body position at the first recovery step than GroupWeak, thereby influencing the dynamic stability control in the following recovery steps. Consequently, the stronger older female subjects returned to the ΔMoS baseline (zero ΔMoS) at the fourth recovery step following the perturbation, whereas the weaker group showed a less effective recovery behaviour and did not return to baseline ΔMoS within the observed six recovery steps (Fig. 4). Similar decreased ability to recover following a loss of balance due to age-related deterioration in the MTU capacities has been identified in various perturbations (slips and trips) or in sudden forward falls from an inclined position in older compared with younger adults (18, 23, 42-44, 49). Similar to the current study, these contrasts were mainly attributed to a reduced ability to effectively increase the BoS following a gait perturbation, which highlights the role age-related degeneration of the MTU capacities may play in recovery from unexpected perturbations. Despite the fact that the sample was intentionally homogenous (group of older female adults), and thus the variability relatively low, we found significant positive correlations between ΔBoS at TD of the first recovery step and TS MTU capacities (r = 0.57 and r = 0.53, for the ankle plantarflexor muscle strength and AT stiffness respectively), as well as with the ΔMoS at TD of the first recovery step (r = 0.50 and r = 0.41), meaning that approximately 30% and 21% of the variability in ΔBoS and ΔMoS during Reco1L can be related to the variance in the TS muscle strength and AT stiffness within the examined group of older female adults (Fig. 5). Moreover, the multiple regression analysis demonstrated that the ankle plantarflexor muscle strength and AT stiffness contributed from 27 to 37% to the MoS (R2 = 0.27) and and BoS (R2 = 0.37). However, one might argue if these static measures can truly show the importance of TS MTU in recovering from sudden perturbations and whether the trip perturbation causes one to generate higher plantarflexion moments for creating a large anterior step and thereby increasing the BoS in response to a sudden perturbation to recover the dynamic gait stability. Due to the lack of direct joint moment assessment during the perturbation trials while walking on treadmill, therefore we analysed the EMG activity of two major plantarflexors (GM and SOL). When considering all subjects (n=22) in the analysis of mean EMGnorm during the ankle push-off phase (50 to 100% of the ground contact phase) of the PertR and comparing the perturbation trials with the baseline walking (please see Fig. 3), both GM and SOL showed a significantly higher mean EMGnorm during the push-off in Trial 1 (GM baseline vs. PertR in Trial 1: 0.36 ± 0.09 vs. 0.76 ± 0.41, *P* = 0.007 and SOL: 0.38 ± 0.08 vs. 0.67 ± 0.33, *P* = 0.005). Furthermore, when comparing the two subject groups, GroupStrong in comparison to the GroupWeak demonstrated a higher ΔEMGGMduring the ankle push-off phase of the PertR for the throughout all the analysed perturbation trials. Accordingly, it could be suggested that the observed greater TS muscle strength and higher AT stiffness in the stronger group may facilitate the generation of higher magnitudes and rates of ankle plantarflexion push-off moments, thereby creating more effective placement of the recovery limb following tripping. Previous studies using trip perturbations with younger and older adults seem to support this notion, because even though the muscular activity patterns (i.e. EMG trajectories over time) are similar between the different age-groups, older adults seem to show a lower magnitude and rate of development of muscle activity (43) as well as lower ankle plantarflexion moment generation during the push-off phase (42) than their younger counterparts. Therefore, according to the current findings, the reduced ability to rapidly enlarge anterior recovery step and effectively increase the BoS following gait perturbations seen in the elderly (49) may be more pronounced in weaker older adults, and this could be mainly due to lower ankle plantarflexion moment generation.

After repeating the unexpected gait perturbation, both groups (GroupStrong and GroupWeak) showed significantly higher ΔMoS at TD of PertR and Reco1L in the Trial 4 and Trial 8, compared to Trial 1 (Fig. 6). This confirms earlier findings that adaptability to repeated perturbations seems to be preserved with human ageing (2, 10, 13, 15, 30, 40). Based on the absence of warning about the perturbation and a very short duration between the onset of the perturbation and TD of the PertR, it can be suggested that the adaptation seen at TD of the PertR was primarily a result of reactive, feedback-driven adaptation. Therefore, these findings confirm previous reports (8, 40) that healthy older adults can adapt their reactive recovery response to repeated perturbations. Interestingly, despite the weaker subjects demonstrating significantly lower MoS values at TD for the analysed recovery steps following the first perturbation trial (Trial 1) in comparison to the stronger subjects, both groups increased their MoS at TD of PertR with a similar magnitude (Fig. 6) after repeated exposure to the mechanical perturbation (no significant differences between subject groups). Therefore, even though subjects with greater ankle plantarflexor muscle strength and AT stiffness display more effective stability recovery during an unexpected perturbation, this seems not to affect the ability to adapt the reactive recovery response to repeated gait perturbations. Therefore, it can be assumed that even if TS MTU mechanical properties are important for the recovery from gait perturbations, they seem not to be the only major contributors to the plasticity of the reactive response during perturbation exposure. This is an important finding for clinical settings, as it can be suggested that older adults could benefit from perturbation training, despite the age-related degenerations in the TS MTU capacities.

The outcomes of the current study may partly explain why exercise interventions (even if using combined strength and balance exercises) to date have resulted only in modest (~15%) improvements in falls incidence (17, 47). In the current study, significantly different recovery responses following an unexpected trip perturbation were identified between two groups of older adults with substantial differences in TS MTU mechanical properties (43% and 24% in maximal isometric ankle plantarflexion moment and AT stiffness respectively). Accordingly, one might suggest that the exercise-induced improvements in the lower extremity MTUs in earlier exercise interventions may have been insufficient and that increases beyond a certain threshold have to occur in order to cause notable changes in stability. The fact that experiencing just few slip-perturbations can result in long-term (up to 12 months) retention of the improvements in the reactive recovery response obtained in the acquisition session (5, 6, 39) as well as reduce daily life falls up to 50% (36) and that an additional session can augment these retention effects (6) may explain why exercise programmes that are more specific in challenging balance and use higher dose may have larger effects in falls prevention (46). Accordingly, improving not only the TS muscle strength but also the recovery mechanisms via more specific tasks to balance recovery responses may be beneficial for falls reduction and prevention.

With regard to our analysis of gait stability, one might argue that the subjects may have anticipated the onset of the perturbation and predictively adjusted their gait, thereby influencing the recovery performance. However, when analysing the step prior to perturbation (TD of the left leg) for all eight perturbation trials, no clear predictive adjustments were observed (no significant differences in the MoS or BoS in comparison to baseline level) for either subject group. Despite the above arguments, however, the observed improvements in the recovery behaviour may not be completely attributed to reactive, feedback-driven motor adjustments, because experiencing the perturbation task may alter and support (potentially undetected) feedforward adjustments, which are predominantly controlled by the cerebellum (34). Moreover, we cannot exclude that the improved reactive recovery response due to repeated practice was partly attributed to a heightened state of awareness and concentration in lab settings where perturbations occur. One might argue, that the velocity of the treadmill (1.4 m·s-1) was not individually normalized, and that the perturbation may possibly not have been equal for each participant. However, as no differences were found in the stability parameters (MoS or BoS) in the baseline walking or in their change due to perturbation (ΔMoS or ΔBoS) at TD of PertR between the groups, we believe that the selected velocity (equal to about 60% of maximal walking velocity) was appropriate to use in both groups of older adults, even if there was about 11% difference in the groups’ average maximal walking velocities (2.54 ± 0.15 m·s-1 vs. 2.27 ± 0.21 m·s-1 for GroupStrong and GroupWeak respectively). Furthermore, it is important to note that, in comparison to our previous studies (30–32, 49), the change in MoS at TD of the PertR relative to baseline (ΔMoS) was slightly lower in absolute terms (‒0.15 ± 0.05 m in current study vs. approximately ‒0.20 m in 30–32, 49). This can be related to the specific perturbation systems (custom-built pneumatic brake-and-release system instead of earlier magnetic system) and hence to the resultant differences in perturbation magnitudes. Lastly, as noted in the “Materials and Methods” section, all participants had unilateral knee osteoarthritis (KL-score 2-3; no pain during locomotion), but were generally healthy in comparison to normative age group data. Considering that no differences were found in BoS, MoS or temporal parameters of gait (contact times, swing times) in the baseline unperturbed walking when comparing the legs (affected and non-affected), as well as the fact that the participants did not have pain during the perturbation trials, we believe that the participants were a representative sample and would not perform differently from older adults of the same age group without knee osteoarthritis, and therefore the findings of the current study could not be influenced by this drawback.

In conclusion, the results from the current study provide evidence that TS muscle weakness and a more compliant AT partly limit older adults’ ability to effectively enlarge the BoS and recover dynamic stability after an unexpected perturbation during walking, increasing their fall risk. However, independent from TS MTU mechanical properties older adults seem to be able to adapt their reactive response following repeated exposure to gait perturbations. Thus, in order to improve the ability to cope with unexpected gait perturbations and potentially reduce falls risk, older adults may benefit from both, from interventions targeting to increase the ankle plantarflexor muscle strength and AT stiffness, as well as reactive recovery responses using repeated gait perturbations.

# Author contributions

G.E., G-P.B. and K.K. conception and design of research; G.E., A.M., M.L., and K.K. performed experiments; G.E., C.M. and K.K. analyzed data; G.E., C.M., G-P.B. and K.K interpreted results of experiments; G.E. and K.K. prepared figures; G.E. and K.K. drafted manuscript; G.E., C.M., A.M., M.L., G-P.B. and K.K. edited and revised manuscript; G.E., C.M., A.M., M.L., G-P.B. and K.K. approved final version of manuscript.

# Conflict of Interest Statement

The authors declare no conflicts of interest.

# Acknowledgements

This work was supported by the Forschungsservicestelle, German Sport University Cologne (Hochschulinterne Forschungsförderung and Graduate Scholarship in Natural Science) and was rewarded with the Young Investigator Award by the German Society for Biomechanics. CM was funded by the Kootstra Talent Fellowship awarded by the Centre for Research Innovation, Support and Policy (CRISP) and by the NUTRIM Graduate Programme, both of Maastricht University Medical Center+.

# References

1. **Ackermans TMA, Epro G, McCrum C, Oberländer KD, Suhr F, Drost MR, Meijer K, Karamanidis K.** Aging and the effects of a half marathon on Achilles tendon length-tension properties. *Eur J Appl Physiol* 116: 2281–2292, 2016.
2. **Barrett RS, Cronin NJ, Lichtwark GA, Mills PM, Carty CP.** Adaptive recovery responses to repeated forward loss of balance in older adults. *J Biomech* 45: 183–187, 2012.
3. **Beijersbergen CMI**, **Granacher U**, **Vandervoort AA**, **DeVita P**, **Hortobágyi T**. The biomechanical mechanism of how strength and power training improves walking speed in old adults remains unknown. *Ageing Res Rev* 12: 618–627, 2013.
4. **Berg WP**, **Alessio HM**, **Mills EM**, **Tong C**. Circumstances and consequences of falls in independent community-dwelling older adults. *Age Ageing* 26: 261–268, 1997.
5. **Bhatt T**, **Wening JD**, **Pai Y-C**. Adaptive control of gait stability in reducing slip-related backward loss of balance. *Exp Brain Res* 170: 61–73, 2006.
6. **Bhatt T, Feng Y, Yi-Chung P.** Learning to resist gait-slip falls: Long-term retention in community-dwelling older adults. *Arch Phys Med Rehabil* 93: 557–564, 2012.
7. **Bierbaum S**, **Peper A**, **Karamanidis K**, **Arampatzis A**. Adaptational responses in dynamic stability during disturbed walking in the elderly. *J Biomech* 43: 2362–2368, 2010.
8. **Bierbaum S**, **Peper A**, **Karamanidis K**, **Arampatzis A**. Adaptive feedback potential in dynamic stability during disturbed walking in the elderly. *J Biomech* 44: 1921–1926, 2011.
9. **Bohm S**, **Mersmann F**, **Bierbaum S**, **Dietrich R**, **Arampatzis A**. Cognitive demand and predictive adaptational responses in dynamic stability control. *J Biomech* 45: 2330–2336, 2012.
10. **Bohm S, Mademli L, Mersmann F, Arampatzis A.** Predictive and Reactive Locomotor Adaptability in Healthy Elderly: A Systematic Review and Meta-Analysis. *Sport Med* 45: 1759–1777, 2015.
11. **Bruijn SM**, **Meijer OG**, **Beek PJ**, **Dieën JH Van**. Assessing the stability of human locomotion: a review of current measures. *J R Soc Interface* 10: 20120999, 2013.
12. **Bruijn SM**, **Van Impe A**, **Duysens J**, **Swinnen SP**. Split-belt walking: adaptation differences between young and older adults. *J Neurophysiol* 108: 1149–1157, 2012.
13. **Carty CP, Cronin NJ, Lichtwark GA, Mills PM, Barrett RS.** Mechanisms of adaptation from a multiple to a single step recovery strategy following repeated exposure to forward loss of balance in older adults. *PLoS One* 7: 3–8, 2012.
14. **Csapo R**, **Malis V**, **Hodgson J**, **Sinha S**. Age-related greater Achilles tendon compliance is not associated with larger plantar flexor muscle fascicle strains in senior women. *J Appl Physiol* 116: 961–969, 2014.
15. **Dijkstra BW, Horak FB, Kamsma YPT, Peterson DS.** Older adults can improve compensatory stepping with repeated postural perturbations. *Front Aging Neurosci* 7: 1–8, 2015.
16. **Epro G**, **Mierau A**, **Doerner J**, **Luetkens JA**, **Scheef L**, **Kukuk GM**, **Boecker H**, **Maganaris CN**, **Bruggemann G-P**, **Karamanidis K**. The Achilles tendon is mechanosensitive in older adults: adaptations following 14 weeks versus 1.5 years of cyclic strain exercise. *J Exp Biol* 220: 1008–1018, 2017.
17. **Gillespie LD, Robertson MC, Gillespie WJ, Lamb SE, Gates S, Cumming RG, Rowe BH**. Interventions for preventing falls in older people living in the community. *Cochrane Database Syst Rev* 2, 2012.
18. **Grabiner MD**, **Owings TM**, **Pavol MJ**. Lower extremity strength plays only a small role in determining the maximum recoverable lean angle in older adults. *J Gerontol A Biol Sci Med Sci* 60A: 1447–1450, 2005.
19. **Hof AL**, **Gazendam MGJ**, **Sinke WE**. The condition for dynamic stability. *J Biomech* 38: 1–8, 2005.
20. **Karamanidis K**, **Arampatzis A**. Mechanical and morphological properties of human quadriceps femoris and triceps surae muscle-tendon unit in relation to aging and running. *J Biomech* 39: 406–417, 2006.
21. **Karamanidis K**, **Arampatzis A**. Age-related degeneration in leg-extensor muscle-tendon units decreases recovery performance after a forward fall: Compensation with running experience. *Eur J Appl Physiol* 99: 73–85, 2007.
22. **Karamanidis K**, **Arampatzis A**, **Brüggemann G-P**. Symmetry and reproducibility of kinematic parameters during various running techniques. *Med Sci Sports Exerc* 35: 1009–1016, 2003.
23. **Karamanidis K**, **Arampatzis A**, **Mademli L**. Age-related deficit in dynamic stability control after forward falls is affected by muscle strength and tendon stiffness. *J Electromyogr Kinesiol* 18: 980–9, 2008.
24. **Kulmala J**, **Korhonen MT**, **Kuitunen S**, **Suominen H**, **Heinonen A**, **Mikkola A**, **Avela J**. Which muscles compromise human locomotor performance with age? *J. R. Soc. Interface* 11: 20140858, 2014.
25. **MacLellan MJ**, **Patla AE**. Adaptations of walking pattern on a compliant surface to regulate dynamic stability. *Exp Brain Res* 173: 521–530, 2006.
26. **Mademli L**, **Arampatzis A**. Mechanical and morphological properties of the triceps surae muscle-tendon unit in old and young adults and their interaction with a submaximal fatiguing contraction. *J Electromyogr Kinesiol* 18: 89–98, 2008.
27. **Maganaris CN**. Tendon conditioning: artefact or property? *Proc Biol Sci* 270 Suppl: S39–S42, 2003.
28. **Maganaris CN**, **Baltzopoulos V**, **Sargeant AJ**. In vivo measurements of the triceps surae complex architecture in man: Implications for muscle function. *J Physiol* 512: 603–614, 1998.
29. **Marigold DS**, **Patla AE**. Strategies for dynamic stability during locomotion on a slippery surface: effects of prior experience and knowledge. *J Neurophysiol* 88: 339–353, 2002.
30. **McCrum C**, **Epro G**, **Meijer K**, **Zijlstra W**, **Brüggemann G-P**, **Karamanidis K**. Locomotor stability and adaptation during perturbed walking across the adult female lifespan. *J Biomech* 49: 1244–1247, 2016.
31. **McCrum C**, **Eysel-Gosepath K**, **Epro G**, **Meijer K**, **Savelberg HHCM**, **Brüggemann G-P**, **Karamanidis K**. Associations between bipedal stance stability and locomotor stability following a trip in unilateral vestibulopathy. *J Appl Biomech* 33: 112-117, 2017.
32. **McCrum C**, **Eysel-Gosepath K**, **Epro G**, **Meijer K**, **Savelberg HHCM**, **Brüggemann G-P**, **Karamanidis K**. Deficient recovery response and adaptive feedback potential in dynamic gait stability in unilateral peripheral vestibular disorder patients. *Physiol Rep* 2: e12222–e12222, 2014.
33. **McCrum C**, **Gerards MHG**, **Karamanidis K**, **Zijlstra W**, **Meijer K**. A systematic review of gait perturbation paradigms for improving reactive stepping responses during walking and reducing falls in older people. *Eur Rev Aging Phys Act* 14: 3, 2017.
34. **Morton SM**, **Bastian AJ**. Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. *J Neurosci* 26: 9107–9116, 2006.
35. **Onambele-Pearson GL**, **Narici MV**, **Maganaris CN**. Calf muscle-tendon properties and postural balance in old age. *J Appl Physiol* 100: 2048–2056, 2006.
36. **Pai YC, Bhatt T, Yang F, Wang E.** Perturbation training can reduce community-dwelling older adults' annual fall risk: a randomized controlled trial. *J Gerontol A Biol Sci Med Sci* 69: 1586–1594, 2014.
37. **Pai Y-C**, **Bhatt T**, **Wang E**, **Espy D**, **Pavol MJ**. Inoculation Against Falls: Rapid Adaptation by Young and Older Adults to Slips During Daily Activities. *Arch Phys Med Rehabil* 91: 452–459, 2010.
38. **Pai Y-C**, **Wening JD**, **Runtz EF**, **Iqbal K**, **Pavol MJ**. Role of feedforward control of movement stability in reducing slip-related balance loss and falls among older adults. *J Neurophysiol* 90: 755–762, 2003.
39. **Pai Y-C**, **Yang F**, **Bhatt T**, **Wang E**. Learning from laboratory-induced falling: long-term motor retention among older adults. *Age (Dordr)* 36: 9640, 2014.
40. **Pavol MJ**, **Runtz EF**, **Pai Y-C**. Young and older adults exhibit proactive and reactive adaptations to repeated slip exposure. *Journals Gerontol Ser A Biol Sci Med Sci* 59: 494–502, 2004.
41. **Pijnappels M**, **Bobbert MF**, **Van Dieën JH**. Contribution of the support limb in control of angular momentum after tripping. *J Biomech* 37: 1811–1818, 2004.
42. **Pijnappels M**, **Bobbert MF**, **Van Dieën JH**. Push-off reactions in recovery after tripping discriminate young subjects, older non-fallers and older fallers. *Gait Posture* 21: 388–394, 2005.
43. **Pijnappels M**, **Bobbert MF**, **Van Dieën JH**. Control of support limb muscles in recovery after tripping in young and older subjects. *Exp Brain Res* 160: 326–333, 2005.
44. **Pijnappels M**, **Reeves ND**, **Maganaris CN**, **Van Dieën JH**. Tripping without falling; lower limb strength, a limitation for balance recovery and a target for training in the elderly. *J Electromyogr Kinesiol* 18: 188–196, 2008.
45. **Schultz AB**. Muscle function and mobility biomechanics in the elderly: an overview of some recent research. *J Gerontol A Biol Sci Med Sci* 50A: 60–63, 1995.
46. **Sherrington C, Michaleff ZA, Fairhall N**, **Paul SS, Tiedemann A, Whitney J, Cumming RG, Herbert RD, Close JCT, Lord SR.** Exercise to prevent falls in older adults: An updated systematic review and meta-analysis. *Br J Sports Med* 51: 1749–1757, 2017.
47. **Sherrington C, Whitney JC, Lord SR, Herbert RD, Cumming RG, Close JCT.** Effective exercise for the prevention of falls: A systematic review and meta-analysis. *J Am Geriatr Soc* 56: 2234–2243, 2008.
48. **Stenroth L**, **Peltonen J**, **Cronin NJ**, **Sipilä S**, **Finni T**. Age-related differences in Achilles tendon properties and triceps surae muscle architecture in vivo. *J Appl Physiol* 113: 1537–44, 2012.
49. **Süptitz F**, **Catalá MM**, **Brüggemann G-P**, **Karamanidis K**. Dynamic stability control during perturbed walking can be assessed by a reduced kinematic model across the adult female lifespan. *Hum Mov Sci* 32: 1404–1414, 2013.
50. **Süptitz F**, **Karamanidis K**, **Catalá MM**, **Brüggemann G-P**. Symmetry and reproducibility of the components of dynamic stability in young adults at different walking velocities on the treadmill. *J Electromyogr Kinesiol* 22: 301–307, 2012.
51. **Talbot LA**, **Musiol RJ**, **Witham EK**, **Metter EJ**. Falls in young, middle-aged and older community dwelling adults: perceived cause, environmental factors and injury. *BMC Public Health* 5: 86, 2005.

# Figure legends

**Figure 1:** A typical recovery response to the trip perturbation in one participant. The pull from the pneumatic brake-and-release system was activated (Onset resistance) during the support phase of the right leg and deactivated (Offset resistance) during the following support phase of the same leg, thereby the subject only experienced the pull during the swing phase of that leg. This caused a reduction in the base of support at foot touchdown (TD PertR) and a more anterior position and higher forward velocity of the centre of mass in relation to unperturbed walking (TD PreR), hence leading to a decreased margin of stability. In order to maintain dynamic stability, the base of support needed to be increased in the following recovery step (TD Reco1L).

**Figure 2:** Margin of stability (MoS) trajectories of one subject during 5 steps before (Pre Pert) and 5 steps after (Post Pert) the unexpected perturbation (PertR) in the first (Trial 1), fourth (Trial 4), eighth (Trial 8) gait perturbation trial. The circles represent the MoS values at the instances of touchdown (TD) of the corresponding leg.

**Figure 3:** Electromyographic (EMG) activity of m. soleus (SOL) and m. gastrocnemius medialis (GM) during the ground contact phase of the right limb during unperturbed walking (BaselineR) and of the perturbed right step (PertR) in all three analysed perturbation trials (Trial 1, Trial 4 and Trial 8; n = 22). EMG activity data were normalized to the maximal EMG activity determined of the corresponding muscle during unperturbed walking.

**Figure 4:** Change relative to baseline unperturbed walking in base of support (ΔBoS) and margin of stability (ΔMoS) at touchdown (TD) of the perturbed step (PertR), and at TD of the first six recovery steps following the perturbation (Reco1L−Reco6R) in the stronger (GroupStrong, n = 10) and weaker (GroupWeak, n = 12) groups in the first perturbation trial (Trial 1). All values are expressed as means with SD (error bars).

\*: Statistically significant difference between GroupStrong and GroupWeak (*P <* 0.05).

#: Statistically significant difference to PertR for GroupStrong (*P <* 0.05).

†: Statistically significant difference to PertR for GroupWeak (*P <* 0.05).

**Figure 5:** *Top*: Relationship between the change in base of support (ΔBoS) at touchdown (TD) of the first recovery step (Reco1L) and maximal ankle plantarflexor moment (Max. PF moment) and Achilles tendon (AT) stiffness (n=22). *Bottom*: Relationship between the change in margin of stability (ΔMoS) at TD of the Reco1L and Max. PF moment and AT stiffness (n=22).

**Figure 6:**

Change relative to baseline unperturbed walking in margin of stability (ΔMoS) at touchdown (TD) of the perturbed step (PertR) and in the first recovery step (Reco1L) in the first (Trial 1), fourth (Trial 4) and eighth (Trial 8) perturbation trial for the stronger (GroupStrong) and weaker (GroupWeak) subject groups. All values are expressed as means with SD (error bars).

\*: Statistically significant differences to Trial 1 (*P <* 0.05).

**Figure 7:** Change relative to baseline unperturbed walking in electromyographic activity of m. soleus (ΔEMGSOL) and m. gastrocnemius medialis (ΔEMGGM) during the push-off phase (defined by examining 50 to 100% of the ground contact phase) of the perturbed step (PertR) in the analysed perturbation trials (Trial 1, Trial 4 and Trial 8).

\*: Statistically significant difference between GroupStrong and GroupWeak (*P <* 0.05).