Retention and generalizability of balance recovery response adaptations from trip-perturbations across the adult lifespan

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Abstract

For human locomotion, varying environments require adjustments of the motor system. We asked whether age affects gait balance recovery adaptation, its retention over months and the transfer of adaptation to an untrained reactive balance task. Healthy adults (26 young, 27 middle-aged and 25 older; average ages 24, 52 and 72 years respectively) completed two tasks. The primary task involved treadmill walking: either unperturbed (control; *n*=39) or subject to unexpected trip perturbations (training; *n*=39). A single trip perturbation was repeated after a 14-week retention period. The secondary transfer task, before and after treadmill walking, involved sudden loss of balance in a lean-and-release protocol. For both tasks the anteroposterior margin of stability (MoS) was calculated at foot touchdown. For the first (i.e. novel) trip, older adults required one more recovery step (*P*=0.03) to regain positive MoS compared to younger, but not middle-aged, adults. However, over several trip perturbations, all age groups increased their MoS for the first recovery step to a similar extent (up to 70%), and retained improvements over 14 weeks, though a decay over time was found for older adults (*P*=0.002; middle-aged showing a tendency for decay: *P*=0.076). Thus, although adaptability in reactive gait stability control remains effective across the adult lifespan, retention of adaptations over time appears diminished with aging. Despite these robust adaptations, the perturbation training group did not show superior improvements in the transfer task compared to aged-matched controls (no differences in MoS changes), suggesting that generalizability of acquired fall-resisting skills from gait-perturbation training may be limited.

New & Noteworthy

The human neuromotor system preserves its adaptability across the adult lifespan. However, although adaptability in reactive gait stability control remains effective as age increases,

retention of recovery response adaptations over time appears to be reduced with aging. Furthermore, acquired fall-resisting skills from single session perturbation training seem task-specific, which may limit the generalizability of such training to the variety of real-life falls.

Introduction

The aging human neuromotor system shows a gradual functional decline, which means a diminished ability to produce effective and safe gait patterns during daily life, resulting in higher fall risk. Falls in older adults can have severe functional consequences in the form of various clinical conditions, disability or even death (Burns and Kakara 2018; Terroso et al. 2014). Epidemiological studies indicate fall incidence increases by middle age, i.e. by about 50 years of age (Donaldson et al. 1990). Given the demographic transition to an expanded older population and higher life expectancy, the development of effective intervention strategies aimed at prevention of falls in populations at higher fall risk is vital for public health.

Most falls in older adults occur during walking and more than 30% of these result from a trip that causes sudden balance loss in the forward direction (Yang et al. 2018a). To ensure safe onward locomotion during such unexpected balance disturbances, rapid compensatory motor actions are required from the neuromotor system (Berger et al. 1984; Nashner 1980), but these become less effective with the onset of middle age (Süptitz et al. 2013). Hence older age groups are predisposed to higher fall risk. That being said, improvements in predictive and reactive balance control strategies can take place (Bhatt et al. 2006). It is promising that even in old age there is a capacity to enhance gait stability control following exposure to various laboratory-induced gait perturbations (e.g. sudden changes in the walking surface, slips or trips; Bierbaum et al. 2011; Epro et al. 2018a; Okubo et al. 2019; Pai et al. 2010; Wang et al. 2019a, 2019b; Yang and Pai 2013). Moreover, such experimental protocols have revealed retention of balance recovery response adaptations over prolonged time periods (i.e. several months to years), resulting from single-perturbation training sessions in middle-aged (König et al. 2019) and older adults (Bhatt et al. 2012; Epro et al. 2018b; Liu et al. 2017; Pai et al. 2014). These results provide evidence that even a very small number of external perturbations to gait can induce retainable task-specific balance control strategies in the aged neuromotor system. Therefore older adults' fall risk in daily life may possibly be reduced, at least for the practiced perturbation type (Rosenblatt et al. 2013).

In a previous study (Epro et al. 2018b) we found that adaptations in older adults' reactive recovery responses to a sudden trip were retained over 14 weeks, though these responses were significantly smaller than the acute effects from a single perturbation training session (i.e. there was partial retention). It is unclear, however, whether the decay in the retention of recovery response adaptations over time is dependent on the participants' age. Regarding this issue, Pai et al. (2010) showed more rapid reduction of improvements in balance recovery behaviour due to repeated slips in older compared to younger adults after merely a short wash-out period of unperturbed walking. Combining these results with earlier studies demonstrating that locomotor adaptations in general may be smaller and/or occur at a lower rate for older groups (Bierbaum et al. 2011; Bohm et al. 2012; Bruijn et al. 2012; McCrum et al. 2016), one might suggest that, although the capacity for adaptation in the human balance control system is preserved with increasing age, various aspects of learning (i.e. adaptation rate, retention) may be diminished.

An additional and crucial aspect of neuromotor capacity, which is generally assessed in relation to learning effects, is the ability to transfer the acquired adaptations from one situation to various alternative contexts, in this case to transfer the improvement in balance recovery mechanisms from perturbation training to different postural challenges. There is evidence to support such generalization of adaptations, at least between different conditions of the same task (e.g. from training gait-slips on the treadmill to a 'novel' overground slip, or from simulated slips on a moveable platform to an untrained slip on an oily surface; Bhatt and Pai 2009; Lee et al. 2018; Parijat and Lockhart 2012; Wang et al. 2019c; Yang et al. 2013, 2018b). It remains largely unknown, however, whether such adaptations are limited to a specific task or can improve recovery performance for other reactive balance tasks (inter-task transfer) and whether this is affected by age. This is of particular importance for the development of targeted fall prevention strategies in aged populations since real-life falls can result from a variety of postural threats.

The present study aimed to examine acute adaptations in reactive gait stability control due to repeated trip-like perturbations, the retention of those adaptations over several months and their transfer to an untrained reactive balance task (the lean-and-release task) in young, middle-aged and older adults. We hypothesised that older adults are capable of inducing long-term adaptation in their reactive gait stability control but that (i) the adaptation occurs at a lower rate, (ii) decays at a faster rate and (iii) transfers less effectively to an untrained task than for the young and middle-aged. The results of this study have significance for our understanding of the dynamics of the human neuromotor system in relation to both acute external influences (perturbations) and to longer-term internal (aging) constraints.

Methods

Participants

Twenty-six young (15 of them men; 24.1 ± 3.5 yr; mean and standard deviation), twenty-seven middle-aged (13 men; 52.4 ± 5.3 yr) and twenty-five older adults (11 men; 72.0 ± 4.4 yr) took part in this study. The height and body mass for each group were 176.8 ± 8.4 cm and 70.0 ± 11.0 kg for the young, 173.5 ± 11.0 cm and 78.3 ± 13.7 kg for the middle-aged, and 169.7 ± 7.9 cm and 75.3 ± 14.1 kg for the older adults respectively. People were excluded if they had any neurological or musculoskeletal impairments of the lower limbs (e.g. joint pain during locomotion). The participants were generally healthy and showed comparable self-reported physical activity levels (7.1 ± 3.4, 7.3 ± 4.3 and 6.5 ± 3.3 h week^{-1} for young, middle-aged and older adults respectively). The study was approved by the ethics committee of the German Sport University Cologne (ethical approval number 141/2017) and met all requirements for human experimentation in accordance with the Declaration of Helsinki. All participants provided written informed consent after initial briefing.

Reactive balance tasks

Our participants took part in two different tasks - a primary trip-perturbation task and a secondary lean-and-release transfer task. They were randomly assigned to one of two groups for treadmill walking (20-25 min each): to a control group (unperturbed walking only; 14 young, 13 middle-aged and 12 older adults) or to a perturbation training group (eight separate unexpected trip-like perturbations; 12 young, 14 middle-aged and 13 older adults). Before and after treadmill walking all participants were exposed to a secondary transfer lean-and-release task. In order to examine the extent of retention of recovery response adaptations from trip-perturbation and their variation across the adult lifespan, participants from the training group performed a single trip-perturbation trial after 14 weeks (see also Fig. 1). After the perturbation-training session and testing, participants experienced no other exposure to mechanically induced perturbations, but were allowed to continue with their normal physical activities.

Insert Figure 1

Analysis of gait stability after unexpected trip perturbation

The gait-perturbation task and paradigm have been described in detail previously (Epro et al. 2018a, 2018b; König et al. 2019). Briefly, trip-like gait perturbations were applied during treadmill walking using a manually-controlled custom-built pneumatic brake-and-release system, which generates a constant restraining force of approximately 55 N (rise time about 20 ms) to the swing phase of the lower right limb via an ankle strap and Teflon cable. Treadmill-walking familiarization took place for all participants about seven days prior to the training session. After the lean-and-release task (please see *Analysis of inter-task transfer* below) the protocol began with the participants walking at a standardised velocity of 1.4 m s^{-1} on a treadmill (pulsar 4.0, h/p/cosmos; Nussdorf-Traunstein, Germany) while wearing the ankle strap and a full-body safety harness connected to an overhead frame. The strap created a negligible resistance of about 0.1 N and this had no effect on sagittal plane joint kinematics at the instant of foot touchdown (TD; unpublished data). After four minutes of walking (Karamanidis et al. 2003), a baseline measurement (25 stride cycles of unperturbed walking) was recorded in each measurement session, from which baseline values of the analyzed parameters were determined as the average over twelve consecutive steps (Epro et al. 2018b; König et al. 2019). Following this baseline measurement, the resistance was applied at an unexpected point in time for one step and immediately removed. In the present study this specific step is referred to as the *perturbed step*. The pulling force was activated during the stance phase of the right limb, just before the start of the swing phase and turned off during the next stance phase of the same foot. Resistance was first perceivable at toe-off of the perturbed step. By applying the external resistance over the entire swing phase the perturbation was standardised from participant to participant. The onset and removal of the resistance were unexpected, but participants were aware that their gait was going to be perturbed at some points during walking. The perturbation was repeated eight times in total (eight *trials*), separated by uneven two- to three-minute washout periods of unperturbed walking, and was delivered only when participants' step length returned to individual baseline levels (checked in real-time through visualization of the anteroposterior trajectories of toe markers; Epro et al. 2018a, 2018b; König et al. 2019; McCrum et al. 2014). The *trials 1* and *8* of the training session and the retention test trial post 14 weeks were used for statistical analysis. These specific trials were considered to represent the participants' initial and post-training performance, including its retention. However, as it was the aim of this study to assess adaptation rate also, the trial-to-trial changes within the training session were examined via *trials 2, 4* and *6*.

To assess dynamic stability during treadmill walking a reduced kinematic model (Süptitz et al. 2013), consisting of five retro-reflective markers attached to anatomical landmarks (seventh cervical vertebra and the greater trochanter and forefoot of the left and right legs), was tracked using a 10-camera optical motion capture system (120 Hz; Nexus 2.6.1; Vicon Motion Systems, Oxford, UK). The 3D coordinates of the markers were smoothed using a fourth-order digital Butterworth filter (cut-off frequency 20 Hz). The anteroposterior margin of stability (MoS), as a valid measure for biomechanical stability of human walking (Bruijn et al. 2013), was calculated at each foot TD for baseline gait, the perturbed step and the first six recovery steps after each perturbation as the difference between the anterior boundary of the base of support (anteroposterior position of the toe projection to the ground) and the extrapolated center of mass (Hof et al. 2005). Furthermore, to account for inter-individual differences in gait stability, the change in MoS during the perturbed step and first two recovery steps relative to baseline walking during the same session was used to examine the recovery response during perturbed gait ($\Delta \mathrm{MoS}_{\mathrm{Step}} = \mathrm{MoS}_{\mathrm{Step}} - \mathrm{MoS}_{\mathrm{Base}}$, calculated for each individual; Epro et al. 2018a), with negative $\Delta \mathrm{MoS}_{\mathrm{Step}}$ values indicating a smaller MoS relative to baseline. Foot TD was detected using two 2D accelerometers (1080 Hz; ADXL250; Analog Devices, Norwood, MA, USA) placed over the tibia of each leg (Süptitz et al. 2012). The reduced kinematic model used here has been validated previously for the assessment of dynamic stability (i.e. MoS) during perturbed and unperturbed treadmill walking (Süptitz et al. 2013) with the same age groups, perturbation task and gait velocity as in the current study. There were significant correlations with a full-body kinematic model (on average $r = 0.90$, $P < 0.01$ across trials).

For evaluation of adaptations in dynamic stability control for *trial 2* and other even-numbered trials in the training session, we calculated the adaptation magnitude for MoS in a similar manner to Bierbaum et al. (2011) as follows:

$$\mathbf{Adaptation\ magnitude} = \left(1 - \frac{\boldsymbol{MoS_{AdaptPhase} - MoS_{Base}}}{\boldsymbol{MoS_{T1} - MoS_{Base}}}\right) \mathbf{x\ 100}$$

where $\mathrm{MoS}_{\mathrm{AdaptPhase}}$ is the MoS during the first recovery step in *trials 2*, *4*, *6* or *8*, $\mathrm{MoS}_{\mathrm{T1}}$ is the MoS during the first recovery step in *trial 1* of the training session and $\mathrm{MoS}_{\mathrm{Base}}$ represents baseline MoS, with positive magnitude values indicating a higher MoS relative to the first (i.e. novel) trip perturbation trial.

Analysis of inter-task transfer

Within a 10-to-15-minute period before and after treadmill walking and perturbation training, participants' dynamic stability was assessed in a separate laboratory via a single trial of the lean-and-release protocol involving sudden anterior balance loss. The same marker set as described above for trip perturbations was tracked by a 6-camera optical motion capture system (120 Hz; Nexus 2.6.1; Vicon Motion Systems, Oxford, UK). This secondary transfer task was conducted as described previously (Karamanidis and Arampatzis 2007). Briefly, participants stood on a force plate (1080 Hz; 60 x 90 cm; Kistler, Winterthur, Switzerland) and, keeping their feet flat on the ground, were tilted forward via a horizontal inextensible cable attached to a body harness until 23 ± 3% of their body weight (BW) was recorded on a load cell placed in series with the cable (see also Do et al. 1982; Thelen et al. 1997). After the given inclination was reached and any possible anticipatory behavior had subsided (i.e. antero-posterior and medio-lateral weight shift regulation, recorded via real-time cable force on the load cell and center of pressure on the force plate), the cable was suddenly released after a random time interval of 10 to 30 s using a custom-built pneumatic release system. Participants were instructed to attempt to restore stable stance within a single recovery step using the limb of their choice when released from the forward-leaning position (Madigan and Lloyd 2005). No practice trials were conducted to ensure novelty of the task. The exact forward lean was chosen according to the reduced ability of older individuals to regain stability with a single recovery step from greater cable loads than 23% BW (Karamanidis et al. 2008). The anteroposterior MoS was calculated at foot TD of the recovery limb after the sudden release as described above for gait perturbations. Foot TD was defined as the first instant when vertical ground reaction force exceeded a threshold level of 20 N determined by a second force plate (1080 Hz; 60 x 90 cm; Kistler, Winterthur, Switzerland) mounted in front of the first. Validity of our main outcome parameter MoS has been demonstrated in a previous study (Karamanidis et al. 2008), showing that MoS during the recovery step predicts the recovery behavior (i.e. single vs. multiple stepping) in about 96% of the cases for a large subject pool. In order to account for inter-individual differences in the recovery response to the untrained transfer task, the change in MoS during the first recovery step in the trial after the treadmill protocol relative to the first (i.e. novel) trial was used to examine inter-task transfer of training effects ($\Delta MoS_{Trial} = MoS_{PostTrial} - MoS_{PreTrial}$, calculated for each individual), with positive ΔMoS_{Trial} values indicating a higher MoS relative to the pre-trial. Participants were secured by a full-trunk safety harness connected to an overhead track that allowed for forward and lateral motion while preventing contact of the body with the ground (with exception of the feet). The safety harness suspension cable incorporated a second load cell to ensure that the measured MoS values were not affected by potential cable assistance (i.e. > 20% BW placed on the safety harness suspension cable at TD of the recovery limb after the sudden release; Cyr and Smeesters 2009).

Statistics

To examine the recovery response adaptations to the trip-perturbation task amongst the three age groups (young, middle-aged and older), separate one-way ANOVAs were used to compare the number of recovery steps needed to regain positive MoS (in the present study defined as a criterion for a “stable” body configuration) in *trial 1* and *8* of the training session. For the analysis of the adaptation potential, the adaptation magnitude for MoS during the first recovery step was analyzed in *trials 2*, *4*, *6* and *8* of the training session. To assess the effect of age and perturbation trial on adaptation magnitude we used a two-way repeated-measures ANOVA with age group and trial as factors [hypothesis (i)]. The effect of age on the retention of recovery response adaptations was assessed by means of a two-way repeated measures ANOVA with age group and perturbation trial (*trial 8* of the perturbation-training session, retention test trial) as factors applied separately for $\Delta \mathrm{MoS}_{\mathrm{Step}}$ (MoS referenced to baseline) during the perturbed step and first two recovery steps [hypothesis (ii)]. For baseline MoS (average of 12 consecutive steps of unperturbed walking with ankle strap attached, assessed prior to the first perturbation trial of each measurement session), a further two-way repeated measures ANOVA with factors age group and time point (perturbation-training session, retention test) was implemented. For the analysis of inter-task transfer we calculated $\Delta \mathrm{MoS}_{\mathrm{Trial}}$ as the absolute change in dynamic stability after a sudden forward fall from before to after treadmill walking, and for the control group. To assess the effect of age and treadmill perturbation training on $\Delta \mathrm{MoS}_{\mathrm{Trial}}$ we used a two-way ANOVA with age group and intervention group (training, control) as factors [hypothesis (iii)]. In a case of significant main effects or interactions Duncan *post-hoc* corrections were applied pairwise. The level of significance was set at $\alpha = 0.05$, with all results presented as mean and SD. All statistical analyses were conducted using Statistica software (Release 10.0; Statsoft Inc, Tulsa, OK, USA).

Results

Changes in gait stability control to repeated trip perturbations

Four participants (one middle-aged and three older adults) had to grasp the handrails of the treadmill to cope with the tripping task and were removed from the analysis (none of the younger adults failed to cope with the task). Accordingly, 26 young, 27 middle-aged and 22 older adults were considered for the statistical analyses.

Assessment of dynamic stability during treadmill walking revealed positive MoS during baseline walking (average value over twelve consecutive steps) for all analyzed participants with no statistically significant age group or time point effects (perturbation-training session vs. retention test; Fig. 2). The unexpected gait perturbation caused a considerable decrease in MoS (lower values compared to baseline) in all age groups (Fig. 2), indicating less stable body positions. For the recovery response to the first (i.e. novel) unexpected perturbation, we found a statistically significant age effect [$F(2,32) = 2.99$, $P = 0.05$] with the older adults requiring on average one more recovery step to regain positive MoS compared to younger adults ($P = 0.03$; Fig. 2). Although not significant ($P = 0.085$), there was a tendency to require a higher number of recovery steps also in middle-aged compared to younger adults. After experiencing eight trip perturbations, there were no statistically significant differences in the required number of recovery steps to attain positive MoS amongst the three age groups (Fig. 2).

Insert Figure 2

We found a significant trial effect [$F(3,96) = 4.35$, $P = 0.01$] for the adaptation magnitude (*trial 2* vs. *trials 4*, *6* and *8;* $0.01 \leq P \leq 0.02$), indicating smaller changes in MoS, and hence more complete recovery, during the first recovery step in *trials 2*, *4*, *6* and *8* relative to *trial 1* of the training session (Fig. 3). However, no significant trial by age group interaction was found, which refutes our first hypothesis.

Insert Figure 3

Retention of improvement in gait stability control over 14 weeks

The retention test trial was performed on average 98 (± 4) days after the perturbation-training session and revealed an improved recovery response compared to the first (novel) trip-perturbation trial for all age groups (Fig. 2). The specific comparison of ΔMoS_{Step} (MoS referenced to baseline) during the perturbed step in *trial 8* of the training session and the retention test trial revealed a statistically significant trial effect [$F(1,32) = 18.01$, $P < 0.001$], showing lower ΔMoS_{Step} values (more negative, $P < 0.001$) after 14-weeks and hence only partial retention of recovery response adaptations, independent of age group (Fig. 4). However, when considering the same comparison for the first two recovery steps after perturbation a statistically significant trial by age interaction for both analyzed steps was found [$F(2,32) = 3.37$, $P = 0.05$ and $F(2,32) = 1.30$, $P = 0.05$ for the first and the second recovery steps respectively]. This means that the effect of single session perturbation training on long-term retention in training effects was age specific. Specifically, a significant decrease ($0.002 \leq P \leq 0.01$) in ΔMoS_{Step} during the first two recovery steps after 14 weeks (retention test trial vs. *trial 8* of the perturbation-training session) could be observed for the older but not for the young and middle-aged adults (Fig. 4), supporting our second hypothesis. Note that, although non-significant, there was a tendency ($P = 0.076$) for middle-aged adults also to have lower ΔMoS_{Step} values in the retention test trial compared to *trial 8* of the perturbation-training session (Fig. 4). Consequently, older adults showed lower ($0.03 \leq P \leq 0.04$) ΔMoS_{Step} values during the second recovery step in the retention test trial compared to the two younger age groups (Fig. 4).

Insert Figure 4

Dynamic stability changes for the lean-and-release task

All age groups improved their recovery response to the sudden forward fall in the second trial compared to the first (i.e. novel) trial as indicated by the positive ΔMoS_{Trial} values (Fig. 5). However, contrary to our third hypothesis, the analysis of inter-task transfer of recovery response adaptations from a single trip-perturbation training session revealed no statistically significant main effects or interaction (i.e. intervention vs. control group) for ΔMoS_{Trial} for the first recovery step in the transfer lean-and-release task ($P = 0.98$ for the age group by intervention group interaction; Fig. 5).

Insert Figure 5

Discussion

We aimed to examine acute adaptations of reactive gait stability control due to repeated trip-like perturbations, the retention of those adaptations over several months and transfer to an untrained reactive balance (lean-and-release) task in young, middle-aged and older adults. Our first hypothesis that adaptation to repetitive perturbation exposure would occur at a lower rate in old age was rejected since all age groups rapidly, and to a similar extent, improved their reactive gait stability control to the perturbation task (i.e. no differences in the trial-to-trial adaptation were found). However, our second hypothesis was confirmed in that older adults demonstrated a significant decrease in retention of acquired recovery response adaptations after 14 weeks (lower recovery performance in the retention test trial vs. *trial 8* of the training session), which was not observed for younger adults (though with a tendency for a decrease in the middle-aged group). Finally, despite robust gait adaptations, the perturbation training group did not show superior improvements in the untrained transfer task in comparison to aged-matched controls (no differences in ΔMoS_{Trial}). Hence, while the capacity for adaptation in reactive gait stability control remains high as people age and the acquired changes appear limited in their generalizability independent of age, retention of adapted stability improvements over a prolonged time seems reduced with aging.

Balance recovery response and its adaptability to trip perturbation

In *trial 1* of the perturbation-training session older adults needed more recovery steps (3 vs. 2) to regain positive MoS values compared to younger adults (Fig. 2), which is in line with previously reported deficiencies in the recovery response from sudden balance loss with aging (Karamanidis and Arampatzis 2007; Pai et al. 2010; Pavol et al. 2002; Süptitz et al. 2013). Note that for this study, and similar to previous work (Süptitz et al. 2013), we found a tendency for middle-aged adults to require one more recovery step to regain positive MoS compared to young adults (a difference that did not, however, reach statistical significance: $P = 0.085$), potentially indicating that the ability to cope with a sudden trip has already begun to deteriorate by middle age. The diminished recovery from tripping with increasing age has previously been associated with reduced ankle push-off for older adults (Pijnappels et al. 2005). Moreover, Epro et al. (2018a) recently found that in older adults higher triceps surae muscle strength and tendon stiffness contribute to enhanced recovery responses to an unexpected trip, highlighting a potential role in gait stability control for general age-related degeneration in leg-extensor muscle-tendon unit capacities (Karamanidis and Arampatzis 2006; Onambele et al. 2006).

After experiencing eight trip perturbations, all age groups improved their recovery response and needed fewer steps to regain positive MoS values following the trip-perturbation task (Fig. 2). More interestingly, we found no age-related differences in adaptation magnitude with respect to dynamic stability irrespective of perturbation trial with a plateau in improvement after only four perturbation trials (Fig. 3). Our results align with previous findings that show remarkable improvements in stability control after merely a single perturbation exposure (König et al. 2019; Marigold and Patla 2002; Owings et al. 2001) and similarly rapid recovery response adaptations to repetitive gait-slip perturbations for young and older adults (Pai et al. 2010). These results together suggest that although aging may reduce one’s ability to cope with sudden perturbations to gait, older adults remain capable of developing robust balance control strategies after merely a few gait perturbations, which seems promising for application of trip/slip training to frail, clinical populations or groups limited in their tolerance of higher perturbation doses.

One might argue, however, that our perturbation paradigm may not permit a general conclusion regarding the effect of age on the adaptability of the human balance control system since task demand may have differed between age groups. Supporting this, we found remarkably lower MoS values during the first recovery step for older compared to middle-aged and younger adults in *trial 1* of the training session (-0.10 ± 0.10 m, -0.06 ± 0.03 m and -0.03 ± 0.05 m respectively; see also Fig. 2). To deal with this issue a subgrouping of data was arranged with young and older adults equal in MoS during the first recovery step in the initial perturbation trial. These stability-matched subgroups consisted of eight young and eight older adults with respectively the lowest and highest MoS values for the first recovery step (young, -0.06 ± 0.03 m; old, -0.06 ± 0.04 m). The subgroups still showed no differences in adaptation magnitude for dynamic stability irrespective of adaptation phase (P = 0.75). Thus our current perturbation paradigm revealed no evidence for age in having a negative effect on the rate of adaptation in reactive gait stability control, though the issue of (initial) task demand and its possible effects on adaptability should be examined in more detail in future investigations.

Given such rapid recovery response adaptations after merely a single perturbation trial, it seems reasonable to suggest that the observed improvements may be driven foremost by the central nervous system. Our perturbation paradigm consisted of repeated trip-like perturbations at unexpected times, provoking involuntary prediction errors that may stimulate the central nervous system to reorganise the motor programs relevant for stability control and hence increase the system's robustness to similar future perturbations. Data from our previous study (Epro et al. 2018a) using the same setup does indeed indicate that the observed recovery response adaptations to the tripping task are accompanied by a refined neuromuscular control of the perturbed step. These may benefit performance during the subsequent recovery steps. That being said, it cannot be determined from the current findings whether the observed reactive adjustments to the external perturbation occur solely at a spinal level as in previous observations of motor output modulation, for example to repeated stumbling in complete low-thoracic spinal cats (Zhong et al. 2012) or in human infants prior to independent walking (Lam et al. 2003; Pang et al. 2003). Descending influence of supraspinal structures may also be involved (Dietz et al. 1985; Dimitrov et al. 1996; Jacobs and Horak 2007; Mochizuki et al. 2009; Wittenberg et al. 2017).

Retention of recovery response adaptations after single-session perturbation training

Aside from these short-term training effects, fall prevention strategies should target long-term retention of the acquired recovery-response adaptations. Previous studies demonstrated meaningful retention of improvements in reactive gait stability control over prolonged time periods (i.e. several months up to years) following exposure to a single session of gait perturbation in middle-aged (König et al. 2019) and older adults (Bhatt et al. 2012; Epro et al. 2018b; Pai et al. 2014). Nevertheless, after quite short periods of time (i.e. several minutes to days) gait adaptive changes have been shown to wane more rapidly in older compared to younger adults (Krishnan et al. 2018; Malone and Bastian 2016; Pai et al. 2010; Sombric et al. 2017). This provides evidence that, next to short-term adaptation, long-term retention of recovery response adaptations may be diminished, to some degree, by aging.

As expected, all age groups showed a retention in training effects from the single perturbation training session over 14 weeks as indicated by the improved recovery response in the retention test trial compared to the first novel trip perturbation trial (Fig. 2). However, whereas we found a minor but significant decrease in stability measures over time (*trial 8* of the training session vs. the retention test trial; Fig. 4) for the perturbed step for all age groups, only older adults demonstrated a significant drop in dynamic stability after the 14-week retention period for the first two recovery steps. Together these results indicate that, independent of age, single-session perturbation training leads to a partial retention in recovery response adaptations over several months, with a more prominent decay over time with aging. This was supported by a trend for a reduction in ΔMoS_{Step} over 14 weeks during the first recovery step for middle-aged but not younger adults ($P = 0.076$). One might argue that our result of a diminished ability to retain acquired recovery response adaptations with aging may be of limited importance in view of its marginal significance level ($P = 0.05$). Additional support for our main finding was, however, achieved when considering only young and older adults in our analysis since we found a highly significant trial by age interaction at $P = 0.01$. In order to investigate this further we analyzed additionally the recovery stepping behavior in the retention test trial, finding that older adults on average required one more recovery step to regain positive MoS compared to younger and middle-aged adults ($0.01 \leq P \leq 0.05$; note that there were no age-related differences in the number of recovery steps in *trial 8* of the training session). Therefore our results clearly suggest that although all age groups were able to adapt rapidly their reactive response to the trip-perturbation task to a similar extent (as indicated by the plateau in learning effects, Fig. 3), retention in those improvements over prolonged time seems diminished with aging. The ability to retain a learned motor skill has been shown previously to involve a distributed network within the central nervous system including the primary motor cortex (Cantarero et al. 2013; Centeno et al. 2018; Hadipour-Niktarash et al. 2007), and different to that engaged in motor task acquisition (Galea et al. 2011; Shadmehr and Holcomb 1997). Thus one possible explanation for the observed deterioration in the ability of older adults to retain perturbation training-induced adaptations may be inhomogeneous changes in brain function with aging (e.g. due to non-uniform regional brain changes; Raz et al. 2005), possibly affecting motor memory more than the ability to adapt motor behavior rapidly.

Transfer of recovery response adaptations to the untrained lean-and-release task

Although a vital aspect of neuromotor capacity is the ability to apply acquired adaptations from one situation to various contexts, the topic of inter-task transfer has rarely been investigated to date. In the present study we investigated potential transfer of balance recovery response adaptations after a single perturbation training session to the recovery from a sudden forward fall. The perturbation and lean-and-release tasks were chosen based on their shared stability control mechanisms (i.e. establishing a new base of support in the anterior direction and reducing the anterior velocity of the center of mass), possibly facilitating transfer of adaptations. However, despite such task similarities and the meaningful improvements (~70%) in reactive gait stability control following repeated exposure to unexpected gait-trip perturbations, participants from the perturbation-training group did not show superior adaptations to the untrained lean-and-release task compared to age-matched controls (no perturbation training, Fig. 5), meaning that inter-task transfer of acquired fall-resisting skills (at least from single-session treadmill-perturbation training) may be limited. We acknowledge that this might be achieved if the number of perturbation-training sessions were increased, though the dose-response relationship for generalizability of training effects from treadmill-perturbation training needs to be examined in future investigations. Further, given the slightly higher stability adaptations to the lean-and-release task in older adults compared to the two younger age groups (Fig. 5), one might argue that exposure to the novel transfer task required older adults to adapt more to the sudden balance loss due to possible age-related differences in task demand. Indeed we found negative MoS values during the recovery step only in the majority of older adults (whereas middle-aged and younger adults regained positive MoS already by the first step; data not shown). This is in line with our results for the trip-perturbation task. However, when excluding young and middle-aged adults from our transfer analysis we still found no differences in the stability improvements between the training and the control group ($t(73) = 0.24$; $P = 0.82$). Thus this single trial effect confirmed the above findings of a high adaptation potential of the human balance control system irrespective of age. One may conclude that the observed improvements for the perturbation training group in the ‘untrained lean-and-release task can be associated with rapid adaptability rather than transfer in recovery response adaptations from a single perturbation training session.

Transfer of acquired motor behavior across tasks has been associated previously with similarity in motor programs (i.e. the relative timings and weightings of muscle activity; Manoel et al. 2002). This is supported by the notion that generalizability of recovery response adaptations has been found for different conditions of the same task (e.g. from gait-slips on a moveable platform to an untrained slip on an oily surface; Bhatt and Pai 2009; Parijat and Lockhart 2012) assisted possibly by a more robust motor output (Santuz et al. 2018). Thus one might argue that despite certain task similarities, critical task parameters (e.g. muscle activity patterns, muscle-tendon unit lengths, body dynamics), and hence modular organization of motor output, still differ, thereby limiting inter-task transfer of training effects. A study of Rosenblatt et al. (2013) showed reductions in older adults’ trip-related, but not all-cause, falls after four sessions of treadmill trip-perturbation training. Combining those results with ours points to the need for more-specific exercise-based fall prevention training if fall risk in aged populations is to be reduced (Grabiner et al. 2014). Therefore one potential avenue of research may be to explore the neuronal correlates determining generalizability of adaptations to the balance control system in order to provide more closely targeted fall-prevention strategies. In summary, we put forward the hypothesis that motor task acquisition is rapid, task-specific and independent of age, but retention of these learning effects is age-dependent (Fig. 6).

Insert Figure 6

Limitations

With regard to the applied perturbation paradigm, one might argue that the participants may have anticipated the perturbation onset after repeated practice of the task and thereby *predictively* modified their gait, favouring increased effectiveness of the recovery response (Pater et al. 2015). On account of this, trip perturbation was delivered only when participants' step length returned to individual baseline levels. Hence we observed no significant differences in MoS during the step prior to the perturbation (about 200 ms before perturbation) compared with baseline. That being said, while we argue that the perturbed step is primarily feedback-driven due to the short time window for possible predictive adjustments to gait after onset of the perturbation, adaptations in the subsequent recovery steps may be partially predictive. Thus we cannot fully exclude the possibility that laboratory settings involving perturbations may lead to a heightened state of awareness supporting (undetected) predictive adjustments of gait. Another potential limitation relates to a validity constraint of the MoS calculation (Hof et al. 2005), in that pendulum length (distance between axis of rotation and center of mass) may not always remain constant during perturbed walking due to possible knee joint angle changes during the ground contact phase. However, in our earlier trip perturbation studies (McCrum et al. 2014; Süptitz et al. 2013) we found no substantial changes in pendulum length during the trip perturbation trials, whereas intra and inter-individual variability in the recovery responses was large. Further, one might argue that generalizability of perturbation training effects cannot be disentangled from a 'single trial effect' to the transfer task which may vary between participants. However, the training and control groups were relatively large and homogeneous in their initial performances and therefore inter-subject variability is unlikely to have a significant effect on our main findings.

Conclusions

The present results indicate that although adaptability in reactive gait stability control remains effective across the adult lifespan, the retention of recovery response adaptations over time appears to diminish with aging, suggesting that initial adaptations to reactive gait stability control may not necessarily predict their long-term retention for different age groups. Moreover, these robust adaptations to trip-perturbation training did not further improve the performance in an untrained reactive balance task compared to age-matched controls. Therefore the generalizability of acquired fall-resisting skills from gait-perturbation training may be limited.

Disclosure of Interest

The authors report no conflicts of interest.

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Author contributions

M.K. and K.K. conceived and designed the research; M.K. and G.E. performed the experiments; M.K., G.E. and K.K. analyzed data; M.K., G.E., J.S., W.P. and K.K. interpreted the results of experiments; M.K. and K.K. prepared figures; M.K. and K.K. drafted the manuscript; M.K., G.E., J.S., W.P. and K.K. edited and revised the manuscript; M.K., G.E., J.S., W.P. and K.K. approved the final text.

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Figure legends

Figure 1: Experimental protocol of the two reactive balance tasks. Treadmill gait-perturbation training consisted of eight trials (T1-T8) of a trip-perturbation task, separated by uneven two- to three-minute washout periods of unperturbed walking. Before and after treadmill walking the participants were exposed to a transfer lean-and-release task. Retention of adaptations in reactive gait stability control was analyzed 14 weeks later by means of a single retention test trial (RET) of the trip-perturbation task.

Figure 2: Margin of stability (MoS) measurements for the trip-perturbation training session and the retention test. Data are given for baseline walking (Base), for touchdown at perturbation (Pert) and for the following six recovery steps after the perturbation (Reco1-Reco6) in young (*n* = 12), middle-aged (*n* = 13) and older adults (*n* = 10). Values represent the first (T1), second (T2) and subsequent alternate trials (T4, T6 and T8) of the trip-perturbation training session and the retention trip trial (RET), and are expressed as means with SD error bars.

Figure 3: Adaptation magnitudes for the initial trip-perturbation training session. Values represent the adaptation in the margin of stability at touchdown for the first recovery step for the second (T2) and subsequent alternate trials (T4, T6 and T8) referenced to the first trip-perturbation trial in young (YA; n = 12), middle-aged (MA; n = 13) and older adults (OA; n = 10). Values are expressed as means with SD error bars. ⁎ represents a statistically significant difference with respect to T2 ($P < 0.05$).

Figure 4: Margin of stability changes ($\Delta \mathrm{MoS}_{\mathrm{Step}}$) for *trial 8* of the initial perturbation training session (T8) and the retention trial (RET). $\Delta \mathrm{MoS}_{\mathrm{Step}}$ values are referenced to baseline walking. Data are given for touchdown at perturbation (Pert) and for the following two recovery steps (Reco1 and Reco2) in young (YA; n = 12), middle-aged (MA; n = 13) and older adults (OA; n = 10). Values are expressed as means with SD error bars. Statistically significant differences at the level $P < 0.05$: ‡ = older compared to young and middle-aged adults; ⁎ = compared to *trial 8* of the initial perturbation training session. (t) = tendency to significance, *trial 8* of the perturbation-training session compared to the retention test trial ($P = 0.076$).

Figure 5: Margin of stability changes ($\Delta \mathrm{MoS}_{\mathrm{Trial}}$) for touchdown of the recovery limb for the transfer lean-and-release task. $\Delta \mathrm{MoS}_{\mathrm{Trial}}$ values are referenced to the first lean-and-release trial (i.e. before treadmill walking). Data are given for young (YA), middle-aged (MA) and older adults (OA) of the control group [unperturbed treadmill walking; n = 39 (14 young, 13 middle-aged and 12 older)] and perturbation-training group [single trip-perturbation session; n = 35 (12 young, 13 middle-aged and 10 older)]. Values are expressed as means with SD error bars.

Figure 6: A schematic illustration of the adaptability of the human balance control system to trip perturbations. (a) While motor task acquisition may be independent of age as indicated by

the observed similar rates and magnitudes of balance recovery response adaptations due to trip-perturbation training in young (YA), middle-aged (MA) and older adults (OA) (Training), retention of learning may diminish with increasing age (Detraining). (b) Although we observed meaningful reactive response adaptations to gait-trip perturbation training, we found no evidence for transfer of training effects to an untrained reactive balance task (the lean-and-release task), despite the similarity of the dynamic stability control mechanisms (i.e. establishing a new base of support in the anterior direction and reducing the anterior velocity of the center of mass). This suggests limited generalizability of acquired fall-resisting skills due to a single perturbation-training session.