Improving trip and slip-resisting skills in older people: perturbation dose matters

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Abstract

Aging negatively affects balance recovery responses following trips and slips. We hypothesize that older people can benefit from brief treadmill-based trip and slip-perturbation exposure despite reduced muscular capacities, but with neuropathology their responsiveness to these perturbations will be decreased. Thus, to facilitate long-term benefits and their generalizability to everyday life, one needs to consider the individual threshold for perturbation dose.

Summary: Improving trip and slip-resisting skills in older people requires a consideration of individual thresholds for perturbation practice dose.

Key Words: Falls; Balance; Perturbation Training; Gait Stability; Neurological Disorders; Locomotion; Aged.

Key Points:
• Aging and neuropathology negatively affect balance recovery responses following sudden gait perturbations like trips and slips.
• Older adults can adapt and retain trip and slip-resisting skills through brief exposure to repetitive treadmill gait perturbations despite age-related muscular changes, but pathology of the sensory and neuromotor systems reduce the responsiveness to such practice.
• In order to facilitate trip and slip-resisting skills and long-term reduction in fall risk, there is a need to consider the individual threshold for practice dose (number of perturbations).
INTRODUCTION

Balance control during human biped locomotion in constantly changing environments requires a continuous correspondence between perceptual information and motor responses. This is achieved by the central nervous system governing the musculoskeletal system according to visual, vestibular and proprioceptive feedback received from the environment (e.g. terrain and walking surface) in which the movement occurs. Locomotor adaptability resulting from these systems is essential for successful and safe mobility. Although this process can be accomplished easily by healthy young adults, it becomes more demanding and less effective with increasing age, especially in the presence of neurological disorders (e.g. Parkinson’s, stroke, vestibulopathy), which coincides with the increased risk of falls in these groups (1). Environmental perturbation-related falls while walking due to trips or slips are responsible for about 60% of outdoor falls among older adults (2).

Long-term exercise interventions over several months aimed at increasing older adults’ balance and/or muscle strength have been shown to be effective in reducing fall risk (3). However, according to the concept of training specificity, the motor skills required for avoiding a trip- or slip-related fall may be improved most effectively and efficiently (within several training sessions) with skill-specific training (4), which represents a departure from conventional long-term fall-prevention interventions. Treadmill-based perturbation training using cable-trip systems (5–8) or belt accelerations/decelerations (9–11) can simulate slip- or trip-like perturbations and trigger error-driven motor learning in the control of postural balance. The perturbation-induced motor error stimulates the central nervous system via sensory feedback to adapt the motor programs relevant for gait and balance to increase the system’s robustness to similar future balance disturbances; a process that
includes acquisition, retention and generalization of the fall-resisting skills. This has been supported by evidence that treadmill-based trip-perturbation training targets specific balance recovery mechanisms that may be beneficial when an actual trip is experienced during daily life (12). An advantage of the treadmill in relation to overground setups, is that predicting when a perturbation will be applied is more difficult, which ensures that mainly reactive balance control strategies are involved. Furthermore, practice dose (defined as the total amount of perturbation trials experienced over a given exercise period) and perturbation intensity can be easily and quickly manipulated in a safe, controlled environment. This is of particular relevance for the conceptualization of fall prevention interventions because the hypothesis of the dose-response relationship implies that adaption may not be directly related to the applied practice dose (i.e. non-linear relationship) and that a dose threshold exists beyond which any additional stimuli may not induce further changes. Since there is a growing body of evidence that fall prevention interventions using treadmills to deliver large postural disturbances (relatively high perturbation magnitude) seem to be both effective and efficient for improving fall resisting skills, there is also a critical need to identify the most effective practice dose (4). It is quite likely that the extent for immediate (within the same training session) or long-term gains and, hence, the effectiveness of the applied practice dose will depend on the specific skills and neuromotor capacities of an individual or population.

Insert Figure 1

This review hypothesizes that older people can benefit from brief treadmill-based trip and slip-perturbation exposure despite reduced muscular capacities, but with neuropathology their responsiveness to these perturbations will be decreased, reflecting a rightwards shift in the practice dose-response relationship (Fig. 1). The
perturbation practice dose-response relationship here refers to the relationship between the number of perturbations and long-lasting changes in balance responses generalizable to daily life trip and slip situations, for which we propose that a critical threshold exists. Note that our hypothesis includes both middle-aged (i.e. about 40-59 y) and older adults (i.e. ≥60 y), covering the ages in which various age-related changes have been observed (we have used 60 years as a cutoff as this is deemed appropriate by the United Nations for classifying older adults in international contexts (13). Our recent data suggest that the potential for improvement following repeated perturbations is independent of changes in lower limb muscle-tendon unit capacities, and we hypothesize here that, as opposed to the general age-related decline in muscular capacities, neurological deterioration (often age-related) in which the sensory inflow or motor control is affected, may lead to a decreased responsiveness to treadmill-based perturbations (Fig. 1). As such, in neuropathology, lower practice doses possibly limit the retention and the generalizability of the beneficial adaptations (the extent to which adaptations are maintained over time and can be translated to improvements in performance in daily life trip and slip situations). This would support our view that disruptions in locomotor control, stability and learning (e.g. adaptation rate and magnitude) may be more apparent in sensory or neuromotor decline than in age-related deterioration of muscular capacities. Due to the majority of falls occurring as a result of trips and slips during walking, as well as the practical and feasibility-related advantages of a treadmill-based setup, this review focusses on information derived from studies of balance control and training from treadmill trip and slip perturbations, in both healthy adults as well as those with neurological disorders affecting the sensory or neuromotor systems.
MAINTAINING BALANCE FOLLOWING TRIPS AND SLIPS

Human walking is partly controlled by central pattern generators, which are spinal cord neurons, providing near autonomous control of basic locomotor rhythms (14). Afferent feedback to the spinal cord allows reactive adjustments whereas feedback to the supraspinal structures facilitates predictive adjustments in the locomotor patterns (14), potentially aiding postural balance and stability during locomotion. When gait stability is unexpectedly disturbed, the neuromotor system applies a series of reactive corrections to re-establish postural equilibrium. In mechanical terms according to Hof (15), this can be achieved by adjusting the application of force to the ground, by counter rotating body segments around the center of mass (CoM) or by applying forces other than the ground reaction force (e.g. by grasping a handrail).

In case of an unexpected slip or trip during gait, the relationship between the body’s CoM and the base of support is suddenly disrupted either by a disturbance of the swing limb (trip) or unwanted displacement of the stance limb (slip). Due to the high displacement of the CoM, it is not surprising that during tripping, a large anterior step is typically required to recover balance, either initiated by the perturbed leg when the disturbance occurs early in the swing phase (raising the perturbed limb over the obstacle; elevating strategy), or by the contralateral leg when the disturbance occurs later in swing (placing the perturbed limb quickly on the ground, aborting the step, and stepping with the unperturbed limb; lowering strategy; (16)). In both cases, the leg taking the compensatory recovery step needs to rapidly move forward (in particular via high moment generation by the hip flexors) to be able to generate a moment at landing to effectively counteract the forward angular momentum of the trunk (17). The joint moment generation of the support limb (trailing leg) also plays
an important role, as during the push-off, the moments generated by the ankle plantar flexors and knee extensors, as well as the hip extensors, provide enough time for clearance and positioning of the stepping limb (leading leg) and counteract the forward angular momentum of the CoM (18). In contrast, slipping can occur in multiple directions to one or both limbs. However, slips leading to an anteriorly-directed displacement of the stance limb resulting in a backwards loss of balance have been most often studied. Once a backward balance loss is initiated, the primary motor response is to act against the sliding motion of the foot by generating knee flexion and hip extension joint moments in the slipping (leading) limb to minimize the vertical descent of the body (19). In addition, a compensatory step by the trailing limb posterior to the CoM is required to recover balance (20), initiated after the onset of the slipping limb motor responses by generating an extension moment at the hip and flexion moment at the knee joint in the trailing limb in order to cause foot clearance and to interrupt the anterior displacement of the foot after toe-off, followed by an knee extension moment to lower the trailing limb onto the ground (21). It can be concluded that both slipping and tripping typically require the effective use of dynamic stability control mechanisms (i.e. counter rotation of body segments and adjusted application of ground reaction forces), although the contribution of each to balance recovery following trips and slips likely differ.

**BALANCE CONTROL DURING TRIPS AND SLIPS IN HEALTHY AGING AND NEUROPATHOLOGY**

It is widely acknowledged that the aging process leads to a general deterioration of the neuromuscular system, including a gradual loss in motor neurons and impaired muscle activation, leading to loss in muscle mass and decreases in strength and
power (22). These degradations are frequently related to diminished locomotor performance. Age-related deficiencies in the recovery from many kinds of sudden balance loss have been demonstrated, including tripping and slipping (5,23,24) and can already be detected in middle age (5). Epidemiological studies showing an increasing fall risk across the adult lifespan also highlight the need for targeted fall prevention strategies in these age groups (25). In previous studies, we found a significant but only moderate association between leg-extensor muscle-tendon unit capacities (muscle strength, tendon stiffness), in particular of the triceps surae muscle, and the ability to increase the base of support following a sudden anterior loss of balance from forward leaning positions and unexpected treadmill trip perturbations (7,26). These findings may provide an explanation for the reduced ability to generate a large anterior balance recovery step with aging (5) and align with other earlier studies showing that the diminished ability to regain stability during perturbed walking is related to older adults’ reduced ability to generate appropriate joint moments in the trailing limb during push-off (18). Like gait-trip perturbations, previous studies have demonstrated that muscle weakness of the lower limbs seems to be associated with the frequency of laboratory based slip-like falls in older adults (27).

Even though the muscle activity patterns (sequencing and timing) in the lower limbs following trip and slip perturbations are similar in young and older adults, the magnitude and rate of development of muscle activity is considerably lower in older adults (23,28), indicating deficits in the neuromuscular control and reactive response (including reaction time) in older adults during the recovery task. In line with this, Arampatzis *et al*. (29) demonstrated that a less effective motor response during the push-off phase of the trailing limb was related to unsuccessful recovery from a
forward fall, irrespective of leg-extensor muscle-tendon unit mechanical properties, which emphasizes the importance of neuromuscular control for balance. This supports our view that a disruption in key functions of locomotor control for maintaining stability in middle-aged and older adults may arise predominantly from neuromotor decline rather than from age-related muscular changes.

Successful recovery from balance loss not only requires precise neuromuscular control, but also requires accurate detection and processing of balance loss. One of the sensory systems providing important information for balance control is the vestibular system, which monitors angular and linear accelerations of the head in space (30). In our previous study in middle-aged adults, we exposed participants to trip-like perturbations via a cable system similar to our other studies (5,7,8,31). We found that, compared to healthy controls, people with unilateral vestibulopathy showed a diminished recovery response to the first unexpected perturbation and required at least six steps (versus four in controls) to recover stability (6); Fig. 2B). Thus, next to the above described alterations accompanied with aging (i.e. altered neuromuscular control) these results indicate a potential role of the vestibular apparatus in postural corrections during an unexpected perturbation to gait. Other studies using slightly different paradigms that still require the same recovery mechanisms (rapid increase of the base of support) also provide some insight. For example, Moreno Catalá et al. (32) found that people with Parkinson’s disease, as opposed to healthy controls, were not able to significantly increase their base of support after a sudden change in ground surface compliance during walking. In people with stroke, anterior surface translation perturbations (initiating backward balance loss similar to a slip) to stance result in more falls compared to age-matched controls and young healthy adults (71% of trials vs. 0% in the other groups) and
patients have poorer stability control during recovery, and require more recovery steps (33). In summary, aged populations and in particular multiple neurological patient groups appear to have a reduced ability to cope with a sudden, unexpected mechanical perturbation to balance and gait predominately due to their inability to rapidly increase the base of support.

**IMPROVING TRIP AND SLIP-RESISTING SKILLS**

It is well established that the human neuromotor system can adapt its motor behavior to intrinsic (e.g. growth, muscle fatigue) and extrinsic changes (e.g. changes in the mechanical environment), creating a complex interaction between sensory feedback information from the periphery and motor output (34). Unexpected perturbations to balance will provoke involuntary sensory prediction errors, which may not be mitigated solely by volitional corrective motor responses and hence stimulate the central nervous system to reorganize its internal representation of the body within the mechanical environment (35). Previous studies have indeed demonstrated significant improvements in reactive gait stability following repeated exposure to unexpected slip or trip-like perturbations (24 or 8 repetitions, respectively) not only in young and middle-aged adults (6,31), but even up to old age; i.e. 60-90 y (7,24). Notably, we recently found remarkable adaptations in reactive gait stability in healthy older adults (mean age and standard deviation: 65 ± 7 y) to eight repeated unexpected treadmill-based trip-perturbations due to a refined neuromuscular control (Fig. 2; (7)). Interestingly, participants’ adaptation potential to these perturbations was independent of their triceps surae muscle-tendon unit capacities (7) and similar to that reported for middle-aged in the same laboratory setup (31). These results support our hypothesis that an age-related degeneration of muscular capacities seems not to
affect one’s ability to adapt and improve such fall-resisting skills following repeated gait perturbations (7). Moreover, when considering the trial-to-trial adaptation over the eight trip perturbations we were able to demonstrate a gradual increase in reactive gait stability with increasing perturbation practice dose in middle-aged and older adults, with no further improvements after only four to five perturbation trials (6,7). Combined with the results seen for overground slip-perturbation training showing similar rapid improvement (i.e. ‘single trial effect’) and plateauing of training effects after merely a few slip trials in healthy young and older adults (24), these findings support the notion that a small number of slip or trip perturbation trials is sufficient to facilitate large refinements in the locomotor-balance control system, irrespective of age. Nevertheless, whether the adaptation rate and amount, and hence the perturbation dose-response relationship, are comparable across the adult lifespan remains unclear and needs further investigation and a lack of knowledge regarding the dose-response relationship in exercise based falls prevention has been highlighted recently (4,36).

*Insert Figure 2*

Given the fact that successful motor learning depends on the function of the neuromotor system, this review proposes the hypothesis that difficulties in improving fall-resisting skills will be seen when the normal flow of information within the nervous system is altered due to pathology (Fig. 1). In our previous study in unilateral vestibulopathy using eight repeated trip perturbations on a treadmill as described above, we found significant improvements in reactive gait stability during the perturbed step in healthy age-matched controls but not in the vestibulopathy patients (Fig. 2B; (6)). This suggests that a lack of accurate vestibular sensory feedback may result in diminished locomotor adjustments and may negatively affect
the modification of internal models of the external environment (35), which could lead to diminished corrections and adaptations of the reactive response to repeated perturbations. However, we found improvements in the number of steps required to recover balance in the vestibulopathy group, though not to the same extent as the healthy age-matched controls. Based on these findings, we propose that patients with vestibulopathy can still make improvements in their balance recovery responses, but an increased practice dose (by increasing the total amount of perturbation trials experienced over a given exercise period) may be needed. Looking beyond the sensory systems themselves, another structure that plays a critical role in motor control and sensory integration is the cerebellum. One study (37) examined how cerebellar lesion patients (n=5; age range 20 to 56 y) and age-matched controls deal with 60 repeated, sudden deceleration-acceleration perturbations during treadmill walking. In line with our observations in vestibulopathy, patients improved their response over time, with fewer multistep recoveries towards the end of the session, but these improvements were faster, less variable and more apparent in the healthy control group.

While not necessarily directly influencing sensory input, other neurological disorders that disrupt sensory integration or neuromotor control could be expected to influence the adaptation to perturbations such as in stroke. Nevisipour et al. (38) reported that, in people with stroke, a training session of 15 posterior treadmill translation perturbations during stance resulted in reduced trunk flexion during recovery from a similar but untrained perturbation, indicating a training-related improvement, but trunk flexion velocity, reaction time, step duration, step length and stability did not improve. Bhatt et al. (39) applied repeated anterior surface translation perturbation (initiating backward balance loss) to stance in people with stroke with both higher
and lower motor impairment. Both groups improved in their ability to cope with the perturbations (fewer falls and better stability control), but there was a slower rate of adaptation over the trials in people with more severe motor impairment. Consistent with our hypotheses, these data suggest that the response to training is affected by neuromotor function and that there is a need to consider the individual threshold for practice dose. While not applying trip or slip perturbations, both Moreno Catala et al. (32) and Martelli et al. (40) have demonstrated, a lack of improvement in the balance recovery responses of people with Parkinson’s disease following repeated perturbations (6 sudden surface compliance changes or 72 anteroposterior and mediolateral waist pulls, respectively) during gait. These findings indicate that with neurological disorders, it may be difficult to stimulate the improvements of fall-resisting skills that are commonly observed in healthy middle-aged and older adults as described above, at least within a single gait perturbation training session or with a similar number of perturbation trials. In summary, there are some early indications that slip or trip-like perturbations on the treadmill would potentially provide sufficient stimulus to trigger improvements in fall-resisting skills in middle-aged or older adults with stroke, vestibulopathy and cerebellar lesions, although impairment severity will likely influence both the tolerance to perturbations and the adaptive response to the perturbations. This suggests that the perturbation practice dose-response relationship is shifted to the right, but it could be harder to reach sufficient practice doses within single training sessions to trigger substantial adaptations (Fig. 1). Further investigation is needed to detect thresholds for practice dose required to induce robust gait modifications (indicated by a plateau in learning effects) as seen for healthy middle-aged and older adults, which also may have important consequences on their retention and/or generalizability to different conditions.
RETENTION AND GENERALIZABILITY OF IMPROVED TRIP AND SLIP-RESISTING SKILLS

It is well known that adaptation of locomotion in response to repeated perturbation exposure can occur quite rapidly in healthy middle-aged and older adults, even within a single treadmill perturbation training session consisting of only a few perturbation trials. Importantly, for overground walking previous slip-perturbation studies have demonstrated that the acute adaptations in reactive gait stability acquired during a single slip-perturbation training session (up to 24 slips) can be partly retained for both short-term (a few weeks) and long-term (up to 12 months) time periods by older adults in the same laboratory settings (41–43). One of our gait-trip treadmill perturbation studies (eight trips at baseline, eight trips at 14 weeks) supports these findings as we found that the improved recovery responses can be partly retained over 1.5 years in older adults (65 ± 7 y (8)), but that these improvements decay over time in this age group (Fig. 3). This suggests that even at a higher age, repeated exposure to gait perturbations that mimic real-life slips or trips seems to be an appropriate stimulus for the human central nervous system to improve and retain balance control strategies specific to the practiced perturbation type. Enhancing triceps surae muscle-tendon unit capacities through controlled resistance exercise over 1.5 years did not lead to further meaningful improvements in older adults’ recovery response following a trip (Fig. 3; (8)). Thus, older adults seem to benefit more from specific exposure to unexpected gait perturbations than from improving presumed fall risk-related factors (i.e. muscle strength), as this alone seems to result in sufficient improvement in performance of the targeted task.
The identified decay in reactive gait stability improvements over time (8) raises the question whether this decay is influenced by the person’s age. The comparison of different studies from our laboratory on retention over several months indicates lower retention of adaptations in older compared to middle-aged adults for the same treadmill trip perturbation paradigm (8,31). Future studies should therefore investigate whether long-term retention (i.e. several months or years) of exercise-induced improvements in gait stability control may diminish across the adult lifespan.

Insert Figure 3

Next to aging, the amount of practice seems to affect various aspects of learning. Specifically, there is a growing body of evidence that to achieve such long-lasting refinement of balance control strategies, certain practice doses may be required. For instance, even though experiencing only one overground-slip during walking can facilitate long-term retention of the acquired fall-resisting skills in older adults, these effects were approximately 50% less than after interventions with higher practice doses (i.e. 24 slip perturbations; (42)). Furthermore, specific ancillary ‘booster’ sessions consisting of only a single slip have been found to further aid to these superior retention effects (43). In agreement with these results, we recently found evidence of a critical threshold for the amount of treadmill-based trip-like perturbation trials required to provoke retainable adaptive changes in the human neuromotor system (31). Specifically, we found a retention of reactive gait adaptations over several months in healthy middle-aged adults only when they were exposed to repeated (eight) gait-trip perturbations and not if they only experienced a single perturbation (31). Thus, whereas brief exposure to treadmill-based gait perturbations appears to be sufficient to achieve acute improvements in fall-resisting
skills in aging, retention of learned skills seems to require a minimum perturbation practice dose facilitating robust gait modifications (i.e. reaching a plateau in the dose-response-relationship).

In order to have a beneficial impact on daily life, these treadmill-based perturbation training paradigms must result in fall-resisting skills that can positively benefit recovery from an actual trip or slip. At least partial generalizability of adaptations to repeated treadmill-delivered trip or slip perturbations to the recovery response following an untrained trip/slip during overground walking has been reported (9,44). Moreover, one study could show reductions in trip-related falls incidence (but not all cause falls) during everyday life after experiencing over a two weeks period four sessions of treadmill-based trip perturbation training (12). When combining these results with recent findings in younger adults (10,11) indicating an increased generalizability of treadmill perturbation training effects (i.e. improved transfer to overground slips) with higher practice dose, it can be suggested that one primary driver of a person’s ability to cope with gait perturbations during everyday life may be the total amount of perturbation trials experienced in the laboratory. However, there seems to be a certain threshold for perturbation practice dose (>24 perturbation trials) beyond which additional stimuli do not further increase transfer to the overground condition in healthy older adults (45), indicating a critical optimum in the perturbation practice dose-response relationship for generalizability to daily life situations.

It is important to highlight that there is currently very little information in the literature regarding the retention and generalizability of fall-resisting skills in neurological populations. Using multidirectional perturbations to stance, Van Duijnhoven et al. (46) found that people with stroke could improve the percentage of
trials recovered in a single step over five weeks of training, an effect that was retained 6 weeks post-intervention. These findings indicate an intact ability of retaining perturbation exposure mediated adaptations in people with stroke if the number of practice sessions are sufficiently high enough, supporting our proposed hypothesis. In line with this, some preliminary studies on long-term perturbation training over several months in Parkinson’s and stroke have shown promising (but often not significant, potentially due to small samples) effects on daily life falls incidence, implying a longer benefit and generalizability of the training (for a review see (47)), but no study known to the authors has directly assessed this in a similar manner to the studies discussed above in healthy middle-aged and older adults.

Given the potential deficits in gait stability and adaptability in response to repeated perturbations in neurological populations (rightwards shift in the practice dose-response relationship), it is reasonable to assume that retention and generalizability of such improvements will also be negatively affected (Fig. 1).

Our proposed hypothesis of a minimum required perturbation practice dose to most effectively facilitate learning (i.e. adaptation, retention and generalizability) in the reactive balance control system requires consideration of the tolerability of training for older adults. It may be that the minimum required dose exceeds the tolerance threshold of participants, leading to anxiety or inability to physically cope with the perturbations. This may be of particular importance when using this training approach with frail or clinical people or groups. One possible solution might be to progressively increase the complexity, unexpectedness or magnitude of perturbations to initially increase training tolerance so that the minimum required dose can be achieved after a certain period. Such approaches have recently been shown to induce
significant improvements in reactive stability control in community-dwelling older adults (48,49).

One obvious limitation for the field is that conducting large enough trials to have enough statistical power to detect the effects of such training on daily life falls incidence will need high financial and high time commitments. The required sample size would increase even further if researchers wished to reliably evaluate the effects on specific types of falls (e.g. falls due to slips or trips), to increase the number of the specific type of fall of interest in the assessed sample. But it is this information that would provide more definitive answers to questions regarding the most effective interventions. For instance, whereas remarkable reductions in trip-related falls incidence (but not all cause falls) after experiencing four sessions of treadmill-based trip perturbation training within a 2 weeks training period have been observed by one study (12), this task specific transfer to everyday life could not be observed in slipping (50) potentially due to the low statistical power for this outcome of the study. In this context, it is important to note that the present review does not allow for a general conclusion regarding the optimum number of perturbations needed in order to facilitate retainable and transferable fall resisting skills in older adults, as differences in perturbation paradigms (i.e. perturbation types and magnitude) may also affect the dose-response-relationship. For these reasons, steps towards aligning and standardizing perturbation training protocols and methodologies, as well as assessment methods are critical to facilitate larger, multicenter, collaborative studies.

**CONCLUSION**

Healthy middle-aged and older adults can benefit from specific treadmill slip and trip perturbation training interventions triggering large balance recovery responses (i.e.
high perturbation magnitudes), regardless of lower limb muscle-tendon unit capacities. Neuropathology in aging appears to disrupt locomotor control, stability and learning, leading to a higher risk of falls in these populations, and more notably, resulting in a decreased responsiveness to treadmill-based perturbations. We propose that a critical threshold for perturbation dose (number of perturbation trials) exists to facilitate long-term adaptive changes and their generalizability to everyday life situations in older adults. This implies that retention of adaptations to perturbation exposure in older people with neuropathology can be achieved if the number of perturbation trials or training sessions fulfill their increased need for training exposure, due to a rightwards shift in the practice dose-response relationship. As such, a longer period of perturbation training will be required to stimulate beneficial improvements in fall-resisting skills in older adults with neurological impairments.

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**FIGURE CAPTIONS**

**Figure 1:** Schematic illustration of the proposed hypothesis: A brief exposure to high magnitude gait perturbations, which mimic real-life slip or trip-like perturbations (Task-specific training), can stimulate long-term adaptive changes (Long-term retention) within the locomotor system. These changes lead to improved resistance to treadmill trips/slips and reduced incidence of trip/slip-falls in daily life situations in older adults, given that a critical threshold (dark circle) for perturbation practice dose (number of perturbation trials) is reached. These improvements in fall-resisting skills can be partly retained in healthy older adults over several months up to years without additional training (Post-Training Retention). In neuropathology, in which the sensory systems or motor control are affected, it is proposed that, due to a rightwards shift in the practice dose-response-relationship for perturbation training, a greater
total amount of perturbation trials experienced over a given exercise period will be
required to reach the critical practice dose threshold to stimulate beneficial
improvements in fall-resisting skills. Experiencing perturbation practice dose below
the critical threshold will lead to a lower improvement and generalization of the fall-
resisting skills, whereas additional stimuli beyond this threshold have no further
benefit (steady state).

**Figure 2:** A: Electromyographic (EMG) activity of m. gastrocnemius medialis (GM)
and m. soleus (SOL) during the ground contact phase during unperturbed walking
and of the perturbed step (trailing limb) during first (T1) and eighth (T8) perturbation
trial of a single perturbation training session in a group of healthy older adults (n =
22). EMG activity was normalized to the maximal activity during unperturbed
walking for the corresponding muscle. B: Margin of stability (MoS; means and SD)
at touchdown (TD) of the perturbed leg in the first (T1) and eighth trial (T8) of a
single perturbation training session in a group of healthy older adults (OLD; n = 22)
and middle-aged unilateral peripheral vestibular disorder patients (UPVD, n = 13).
Note that whereas healthy middle-aged adults show rapid adaptation to the repeated
perturbation exposure, these adaptations seem dependent on an intact sensory inflow.

*aStatistically significant difference between groups OLD and UPVD (P < 0.05);
bStatistically significant difference to T1 for group OLD (P < 0.05). (Adapted from
Epro et al. (7) and McCrum et al. (6)).

**Figure 3:** Margin of stability (MoS; means and SD) at touchdown (TD) of the
perturbed leg during first (T1) and eighth (T8) perturbation trial of a single
perturbation training session (8 unexpected gait-trip perturbations) at baseline (Base),
post 14 weeks (Post 14w) and post 1.5 years (Post 1.5y) measurement time points in a group of older female adults experiencing trip-gait perturbation training (PERT group; n = 13) and a second group of older female adults, who in addition underwent a triceps surae muscle-tendon unit (MTU) specific exercise over 1.5 years (MTU group; n = 12). Note that the training-induced enhancement of the triceps surae MTU capacities did not benefit the recovery response from a sudden trip. \(^a\)Statistically significant difference to T1Base (P < 0.05); \(^b\)Statistically significant difference to T8Base (P < 0.05); \(^c\)Statistically significant difference to T1Post14w (P < 0.05); \(^d\)Statistically significant difference to T8Post14w (P < 0.05); \(^e\)Statistically significant difference to T1Post1.5y (P < 0.05). (Adapted from Epro et al. (8)).