Differences in muscle synergies among recovery responses limit inter-task generalisation of stability performance

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Abstract

Generalisation of adaptations is key to effective stability control facing variety of postural threats during daily life activity. However, in a previous study we could demonstrate that adaptations to stability control do not necessarily transfer to an untrained motor task. Here, we examined the dynamic stability and modular organisation of motor responses to different perturbations (i.e. unpredictable gait-trip perturbations and subsequent loss of anterior stability in a lean-and-release protocol) in a group of young and middle-aged (n = 57; age range 19-53 years) to detect potential neuromotor factors limiting transfer of adaptations within the stability control system. We hypothesized that the motor system uses different modular organisation in recovery responses to tripping and lean-and-release, which may explain lack in positive transfer of adaptations in stability control. After eight trip-perturbations participants increased their dynamic stability during the first recovery step ($p < 0.001$), yet they showed no significant improvement to the untrained lean-and-release transfer task compared to controls who did not undergo the perturbation exposure ($p = 0.44$). Regarding the neuromuscular control of responses, lower number of synergies (3 vs. 4) were found for the lean-and-release compared to gait-trip perturbation task, revealing profound differences in both the timing and function of the recruited muscles to match the biomechanical specificity of different perturbations. Our results provide indirect evidence that the motor system uses different modular organisation in diverse perturbation responses, what possibly inhibits inter-task generalisation of adaptations in stability control.

Keywords: Locomotion, muscle synergy, perturbation training, dynamic stability, motor control

1 Introduction

Daily life locomotion is a challenging task facing countless situations that can interrupt movement consistency and stability. Thus, to maintain its integrity when confronted by unpredictable perturbations, the central nervous system is constantly required to modulate its motor output and hence increase the system's robustness to similar future perturbations (Kitano, 2004; Santuz, Ekizos, Eckardt, & Kibele, 2018). Since postural threats are highly variable in nature, transfer of learned recovery mechanisms to new challenges appears as particularly important for effective stability control (Poggio & Bizzi, 2004).

Positive transfer of adaptations between different conditions of the same perturbation has been reported previously, i.e. from treadmill gait-slips to a 'novel' overground slip, or from training gait-slips on a moveable platform to an untrained slip on an oily surface (Bhatt & Pai, 2009; A. Lee, Bhatt, Liu, Wang, & Pai, 2018; Parijat & Lockhart, 2012; Wang et al., 2019; Yang, Bhatt, & Pai, 2013; Yang, Cereceres, & Qiao, 2018). In a recent study (König, Epro, Seeley, Potthast, & Karamanidis, 2019) we demonstrated that repeated exposure to anteriorly-directed gait perturbations lead to remarkable improvements in recovery responses. Based on earlier findings these are governed most likely by the rapid increase of anteroposterior base of support at the time of touch down (Epro, McCrum, et al., 2018; Süptitz, Catalá, Brüggemann, & Karamanidis, 2013), a key control mechanism for dynamic stability both in tripping and slipping (Hof, Gazendam, & Sinke, 2005; Maki & McIlroy, 2006). However, the improved skills could not be transferred to the recovery response in a similar large mechanical perturbation (i.e. high centre of mass displacement) in the anterior direction during a simulated forward fall (lean-and-release task). This is surprising, as the ability to effectively increase the base of support was found to be key to recover stability also for this task (Arampatzis, Karamanidis, & Mademli, 2008; Karamanidis, Arampatzis, & Mademli, 2008).-These findings suggest that, despite the apparent similarity in the two perturbation tasks, critical task parameters (e.g. sensory input, muscle activity patterns, muscle-tendon-unit length and body dynamics) may differ based on the specific biomechanical constraints, presumably resulting in different neuromotor control of responses. Thus generalisation of adaptation is in principle possible within the human stability control system. However, it may be limited if factors other than shared limb mechanics discriminate perturbation responses in different motor tasks.

Muscle synergies have been increasingly employed over the last years for providing indirect evidence of a simplified, modular control of motor output (Bizzi, Cheung, d'Avella, Saltiel, & Tresch, 2008; Bizzi, Mussa-Ivaldi, & Giszter, 1991; Lee, 1984; Mussa-Ivaldi, Giszter, & Bizzi, 1994; Tresch, Saltiel, & Bizzi, 1999). By using few common activation patterns of functionally-related muscle groups or synergies, rather than muscle-specific commands, the neuromotor system may overcome the overwhelming amount of degrees of freedom available for accomplishing targeted movement (Bernstein, 1967; d'Avella & Bizzi, 2005; d'Avella, Saltiel, & Bizzi, 2003). However, 'task-specific' motor modules may occur when biomechanical demands are altered or perturbations added (Munoz-Martel, Santuz, Ekizos, & Arampatzis, 2019). Mixture of shared and specific synergies has been reported previously across different postural responses, e.g. stepping vs. non-stepping (Chvatal, Torres-Oviedo, Safavynia, & Ting, 2011; Torres-Oviedo & Ting, 2010) or walking and standing perturbation responses as well as unperturbed walking (Chvatal & Ting, 2013) that mirror the reportedly limited correlations between different types of stability performance (Kiss, Schedler, & Muehlbauer, 2018). Together, these findings indicate that profound biomechanical, and hence neuromotor task specificity may subsequently interfere with positive transfer of adaptations from one perturbation task to another. Results from visuomotor skill adaptations provide evidence to this hypothesis, suggesting that generalisation of adaptations is maximised if the same synergy set involved in original, adapted and generalized movements fully overlaps, while if different synergies are recruited (i.e. as in case of big deviations in covered workspace), generalisation is reduced or even lost (De Marchis, Di Somma, Zych, Conforto, & Severini, 2018). Further, previous findings suggest rapid adaptability in basic activation patterns of the same synergies for robustness, as seen for the transition from unperturbed walking to walking on uneven or slippery ground (Martino et al., 2015; Santuz, Brüll, et al., 2020; Santuz, Ekizos, Eckardt, et al., 2018). Thus, while generalisation of adaptations between altered conditions of the same task may be driven by a high degree of similarity in shared sets of muscle synergies, the previously observed lack in transfer of adaptations between different perturbation responses (König, Epro, Seeley, Potthast, et al., 2019) may be explained mostly by different spatiotemporal motor entities.

This study used the muscle synergy concept to examine neuromotor correlates of responses to different types of perturbation, i.e. trip-like gait perturbations and sudden loss of stability in a lean-and-release protocol. The overall aim was to test our hypothesis that the lack in transfer within the stability control system comes along with a different modular organisation (i.e. different number and characteristics of muscle synergies) between different perturbation responses. Our results would provide indirect evidence that the fundamental synergies of motor responses may be one factor limiting inter-task generalisation of stability adaptations.

2 Methods

2.1 Participants and experimental design

Fifty-seven young and middle-aged adults (36 men; age range: 19 – 53 years) took part in this study. Exclusion criteria were any neurological or musculoskeletal impairments of the lower limbs (e.g. joint pain during locomotion). The participants were healthy and regularly active (with an average self-reported physical activity level of 6.5 ± 5.7 $h \cdot week^{-1}$). The study was approved by the ethics committee of the London South Bank University (approval code

SAS1826b) and met all requirements for human experimentation in accordance with the Declaration of Helsinki. All participants provided written informed consent after being informed about the procedures and possible risks of the study.

The participants took part in two different tasks – firstly a treadmill walking task and secondly a lean-and-release task (Fig. 1). Thirty-nine participants were randomly assigned to a single session treadmill perturbation group (eight separate unpredictable trip-like perturbations, PERT: age: 31 ± 9; body height: 177 ± 12 cm; body weight: 78 ± 15 kg; physical activity level: 5.7 ± 4.7 h·week^{-1}), and the remaining eighteen participants formed a control group (unperturbed walking, CTRL: 30 ± 10 years; 178 ± 9 cm; 79 ± 14 kg; 5.4 ± 3.9 h·week^{-1}). The two groups underwent equivalent periods of treadmill walking (20–25 min) with only PERT group experiencing unexpected perturbations in randomised time points. After treadmill walking all participants were exposed to a lean-and-release task. Both unexpected tripping and (subsequent) sudden loss of stability in the anterior direction reflect common hazards during daily-life locomotion (Luukinen et al., 2000). Notably, Carty et al. (2015) found that the recovery stepping performance after a simulated forward fall in the laboratory can predict future fall risk (Carty et al., 2015). Kinematics of the two tasks were recorded using an eight-camera optical motion capture system (120 Hz; QTM v2019.3; Qualisys, Gothenburg, Sweden). In order to examine the modular organisation of the recovery responses, the electromyographic (EMG) activity of 13 ipsilateral muscles was recorded only for group PERT (n = 39).

Insert Figure 1

2.2 Gait perturbation task

Trip-like gait perturbations were applied during treadmill walking using a manually-controlled custom-built pneumatic brake-and-release system, similar to the one described in our previous studies (Epro, McCrum, et al., 2018; Epro, Mierau, et al., 2018; König, Epro, Seeley, Catalá-Lehnen, et al., 2019; König, Epro, Seeley, Potthast, et al., 2019). To generate a trip, a constant restraining force of approximately 100 N (rise time about 20 ms) was applied to and removed from the lower left limb during swing phase via an ankle strap and Teflon cable. In more detail, the pulling force was activated during the stance phase of the left leg, just before the start of the swing phase and the force was first perceivable at toe-off of the perturbed leg. The pulling force was turned off during the next stance phase of the same foot. Accordingly, the duration of the perturbation was the entire swing phase of the right leg and thereby individually standardised for each participant. Treadmill-walking familiarisation took place for all participants about seven days prior to the training session. The protocol began with the participants walking at a standardized velocity of 1.4 $m \cdot s^{-1}$ on a treadmill (Valiant 2 sport XL; Lode B.V., Groningen, The Netherlands) while wearing an ankle strap at each leg and a full-body safety harness connected to an overhead frame. After four minutes of walking (Karamanidis, Arampatzis, & Bruggemann, 2003), 25 stride cycles of unperturbed walking were recorded, from which 12 consecutive steps were used to determine the baseline for all analysed parameters (Epro, Mierau, et al., 2018). Subsequently, the resistance was applied for one step (i.e. the perturbed step). The subsequent step with the contralateral right leg was defined as the first recovery step. The participants were not informed about the onset or removal of the resistance but were aware that walking 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 (Epro, McCrum, et al., 2018; Epro, Mierau, et al., 2018; König, Epro, Seeley, Potthast, et al., 2019; McCrum et al., 2014), with the *Trial 1* and *8* being considered for further analysis. These specific trials were considered as they represent the participants' initial and post-training performance. Note that the trial-to-trial changes within training have been reported previously in detail (König, Epro, Seeley, Potthast, et al., 2019; McCrum et al., 2014).

To assess dynamic stability during unperturbed and perturbed walking we used a reduced kinematic model (Süptitz et al., 2013), with five markers placed to the following anatomical landmarks: seventh cervical vertebra and the greater trochanter and forefoot of the left and right legs. A fourth-order digital Butterworth filter with cut-off frequency of 20 Hz was applied to the 3D coordinates of the five markers. The anteroposterior margin of stability (MoS; Hof et al., 2005), a valid measure for biomechanical stability of human gait (Bruijn, Meijer, Beek, & van Dieen, 2013) was determined at each foot touchdown during unperturbed walking, and at the foot touchdown of the perturbed step and following first six recovery steps after each perturbation. The MoS was defined as the difference between the extrapolated centre of mass and the anterior boundary of the base of support (anteroposterior position of the toe projection to the ground). The used reduced kinematic model has been previously demonstrated to be valid for dynamic stability assessment during trip-like perturbation to gait with the same age group and walking velocity as in the current study (with significant correlations with a full-body kinematic model of on average $r = 0.90$, $p < 0.01$ across steps; Süptitz et al., 2013).

2.3 Lean-and-release transfer task

Directly after treadmill walking (within 10-15 minutes), participants were exposed to a single trial of the lean-and-release protocol involving sudden anterior loss of stability in a separate laboratory setup. The same marker set as described above for trip perturbations was used. Arrangements to assess dynamic stability during a simulated forward fall has been described previously in detail (Karamanidis & Arampatzis, 2007; König, Epro, Seeley, Potthast, et al., 2019). Briefly, participants stood on a force plate (1080 Hz; 40 x 60 cm; Kistler, Winterthur, Switzerland) and, keeping their feet flat on the ground, were tilted forward via a horizontal inextensible cable attached at one end to a body harness and at the other end to a custom-built pneumatic release system (Do, Breniere, & Brenguier, 1982; Thelen, Wojcik, Schultz, Ashton-Miller, & Alexander, 1997). Once the targeted inclination was reached (i.e. 33 ± 3% of the individual body weight, recorded via a load cell placed in series with the cable) and any possible anticipatory behaviour had subsided (i.e. antero-posterior and medio-lateral weight shift regulation, recorded via centre of pressure under the feet), the cable was suddenly released after a random time interval of 10 to 30 s. The instructions given to the participants were as follows: "Aim to regain stability within a single large recovery step with your right leg when released from the forward-lean position". The foot thereby always landed on a second force plate (1080 Hz; 40 x 60 cm; Kistler, Winterthur, Switzerland) mounted in front of the first. The right limb was pre-selected as recovery limb for every participant to allow for comparability of data to the gait perturbation task (note that resistance was applied to the left limb and hence the first recovery step was performed with the right limb for the gait perturbation task). The exact forward lean was chosen based on previous data using the same experimental setup (Karamanidis et al., 2008), providing a challenging condition for stability of the younger adults. The anteroposterior MoS at foot touchdown of the recovery limb was calculated as described above for gait perturbations. No practice trials were conducted to avoid adaptations in dynamic stability parameters and ensure novelty of the task (König, Epro, Seeley, Potthast, et al., 2019; Ringhof, Arensmann, & Stein, 2019). Participants were secured by a full-trunk safety harness connected to an overhead track, allowing 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 measured MoS values were not affected by potential cable assistance (i.e. > 20% body weight placed on the safety device at touchdown of the recovery limb after the sudden release; Cyr & Smeesters, 2009).

2.4 Step cycle assessment

In order to compare the different motor tasks in group PERT, the first recovery step cycle was broken down into swing and early stance (i.e. energy absorption) by obtaining the foot toe-off, foot touchdown and minimum knee joint angle using kinematic, kinetic and accelerometer data. Foot toe-off during each task was estimated using the local maximum in the vertical acceleration of toe marker in relation to its minimum vertical position (Maiwald, Sterzing, Mayer, & Milani, 2009). Foot touchdown was obtained via two different approaches: (1) in treadmill walking task by using the impact peaks of two 2D accelerometers (1080 Hz; ADXL250; Analog Devices, Norwood, MA, USA) placed over the tibia of each leg (Süptitz, Karamanidis, Moreno Catalá, & Brüggemann, 2012) and (2) for the lean-and-release task by determining the first instant when the vertical ground reaction force exceeded a threshold value of 20 N using force plate data. To define the termination of energy absorption, the minimum knee joint angle was determined for the right limb as the first local minima after foot touchdown of the sagittal plane angle between the greater trochanter, lateral femoral epicondyle and lateral malleolus markers (Karamanidis & Arampatzis, 2007). The swing phase was then defined as the time period between foot toe-off and touchdown, and the early stance phase as the time period between the foot touchdown and the following minimum knee joint angle (Fig. 2).

Individual recovery step cycles were manually analysed by two independent examiners and trials were excluded from further analysis in at least one of the following cases to allow comparability of the data (either within the gait perturbation task or between different perturbation tasks): (i) the participant fell in one of the tasks or had to grasp the handrails of the treadmill in perturbed walking, (ii) elevating of the perturbed limb which itself counted as first recovery step in perturbed walking or use of the left leg as a recovery limb in the lean-and-release (iii) artefacts in the EMG signal. Then, for each of the three conditions, the remaining valid trials for unperturbed walking, perturbed walking and the lean-and-release–task were considered for further analysis (Fig. 1).

Insert Figure 2

2.5 Modular organisation assessment

For each task, the EMG activity of the following 13 ipsilateral (right side) muscles was recorded at a sampling rate of 1080 Hz using bipolar surface electrodes with two synchronized 8-channel EMG systems (Bagnoli^{TM}; Delsys, Natick, MA, USA): *gluteus medius* (ME), *gluteus maximus* (MA), *tensor fasciæ latæ* (FL), *rectus femoris* (RF), *vastus medialis* (VM), *vastus lateralis* (VL), *semitendinosus* (ST), *biceps femoris* (long head, BF), *tibialis anterior* (TA), *peroneus longus* (PL), *gastrocnemius medialis* (GM), *gastrocnemius lateralis* (GL) and *soleus* (SO). The electrodes were placed over the midpoint of the muscle belly and further secured to the skin using an elastic tape to minimize motion artefacts. Before electrode placement, the skin over the muscle belly was carefully shaved and cleaned with ethanol to reduce skin impedance. Muscle synergies were extracted from each participant for unperturbed walking, eighth perturbed walking and lean-and-release through a custom script (R v3.6.3, R Core Team, 2020, R Foundation for Statistical Computing, Vienna, Austria) based on the R package "musclesynergies" version 0.7.1-alpha (Santuz, 2021) using the classical Gaussian non-negative matrix factorisation (NMF) algorithm (Lee & Seung, 1999; Santuz, Ekizos, Janshen, Baltzopoulos, & Arampatzis, 2017a). Note that only *Trial 8* of perturbed walking was considered for modular organisation analyses because this is the most relevant in terms of transfer, as it represents the 'adapted' post-training state. The raw EMG signals were band-pass filtered within the acquisition device (cut-off frequencies 20 and 450 Hz). The signals were high-pass filtered, full-wave rectified and lastly low-pass filtered using a 4th order IIR Butterworth zero-phase filter with cut-off frequencies 50 Hz (high-pass) and 20 Hz (low-pass for creating the linear envelope of the signal) as previously described (Santuz, Ekizos, Eckardt, et al., 2018). One randomly chosen unperturbed step cycle and the first recovery step cycle from the eighth perturbation trial and the lean-and-release trial were then selected for each participant. After subtracting the minimum, the amplitude of the EMG recordings obtained from the single trials was normalized to the maximum activation recorded for every individual muscle (i.e. every EMG channel was normalized to its maximum in every trial; Santuz, Ekizos, Eckardt, et al., 2018). Then, for each of the three conditions separately, every available cycle was concatenated (i.e. joined) to the others in a single EMG matrix. This was done in order to create one representative dataset per condition, containing all the available information we could record for that specific task. Each step cycle, one for every participant, was then time-normalized to 200 points, assigning 100 points to the swing (i.e. from lift-off of the right foot and until touchdown) and 100 points to the early stance phase (i.e. from touchdown and until the minimum of the knee joint angle; Santuz, Ekizos, Eckardt, et al., 2018; Santuz, Ekizos, Janshen, Baltzopoulos, & Arampatzis, 2017b; Santuz, Ekizos, Janshen, et al., 2018). The reason for this choice is twofold (Santuz, Ekizos, Janshen, et al., 2018). First, dividing the step cycle into two macro-phases helps the reader to understand the temporal contribution of the different synergies, diversifying between swing and stance. Second, normalising the duration of swing and stance to the same number of points for all participants makes the interpretation of the results independent from the absolute duration of the gait events. Synergies were then extracted through NMF as previously described (Santuz, Ekizos, Eckardt, et al., 2018). For the analysis, we considered the 13 muscles described above (ME, MA, FL, RF, VM, VL, ST, BF, TA, PL, GM, GL and SO). The $m = 13$ time-dependent muscle activity vectors of all participants were grouped for each of the three tasks separately in a matrix V with dimensions $m \times n$ (m rows and n columns). The dimension n represented the number of normalized time points (i.e. 200*number of participants). The matrix V was factorized using NMF so that $V \approx V_R = WH$. The new matrix V_R, reconstructed by multiplying the two matrices W and H, approximates the original matrix V. The motor primitives (Dominici et al., 2011; Santuz et al., 2017a) matrix H contained the time-dependent coefficients of the factorisation with dimensions $r \times n$, where the number of rows r represents the minimum number of synergies necessary to satisfactorily reconstruct the original set of signals V. The motor modules (Gizzi, Nielsen, Felici, Ivanenko, & Farina, 2011; Santuz et al., 2017a) matrix W, with dimensions m × r, contained the time-invariant muscle weightings, which describe the relative contribution of single muscles within a specific synergy (a weight was assigned to each muscle for every synergy). H and W described the synergies necessary to accomplish the required task (i.e. treadmill walking or lean-and-release). The quality of reconstruction was assessed by measuring the coefficient of determination R^2 between the original and the reconstructed data (V and V_R, respectively). The limit of convergence for each synergy was reached when a change in the calculated R^2 was smaller than the 0.01% in the last 20 iterations (Santuz et al., 2017a), meaning that with this amount of synergies, the signal could not be reconstructed any better. This operation was first completed by setting the number of synergies to 1. Then, it was repeated by increasing the number of synergies each time, until a maximum of 10 synergies. The number 10 was chosen to be lower than the number of muscles, since extracting a number of synergies equal to the number of measured EMG activities would not reduce the dimensionality of the data. Specifically, 10 is the rounded 75% of 13, which is the number of considered muscles (Santuz et al., 2019). For each synergy, the factorisation was repeated 10 times, each time creating new randomized initial matrices W and H, in order to avoid local minima (d'Avella & Bizzi, 2005). The solution with the highest R^2 was then selected for each of the 10 synergies. To choose the minimum number of synergies required to represent the original signals, the curve of R^2 values versus synergies was fitted using a simple linear regression model, using all 10 synergies. The mean squared error (Cheung, d'Avella, Tresch, & Bizzi, 2005) between the curve and the linear interpolation was then calculated. Afterwards, the first point in the R^2-vs.-synergies curve was removed and the error between this new curve and its new linear interpolation was calculated. The operation was repeated until only two points were left on the curve or until the mean squared error fell below 10^{-4}. This was done to search for the most linear part of the R^2-versus-synergies curve, assuming that in this section the reconstruction quality could not increase considerably when adding more synergies to the model.

The EMG dataset was created by joining together (i.e. concatenating) trials from different participants. The concatenation process suffers from a drawback: the order of the concatenated trials can influence the extracted synergies. To account for this potential issue, we used a bootstrapping approach to create 1000 concatenations, each with randomly chosen individual trials, picked from those available and resampled without replacement (meaning that the trial from the same participant could not be sampled more than once).

We compared motor primitives by evaluating the full width at half maximum (FWHM) and the centre of activity (CoA), two metrics useful to describe the timing of activation patterns (Cappellini et al., 2016; Cappellini, Ivanenko, Poppele, & Lacquaniti, 2006; Martino et al., 2014; Santuz, Ekizos, Eckardt, et al., 2018). The FWHM was calculated cycle-by-cycle as the number of points exceeding each cycle's half maximum, after subtracting the cycle's minimum and then averaged (Martino et al., 2014). The CoA was also calculated cycle-by-cycle as the angle of the vector in polar coordinates that points to the centre of mass of that circular distribution (Cappellini et al., 2016). The polar direction represented the cycle's phase, with angle $0 \leq \theta \leq 2\pi$. The FWHM and CoA were calculated only for the motor primitives relative to fundamental synergies. A fundamental synergy can be defined as an activation pattern whose motor primitive shows a single main peak of activation (Santuz, Ekizos, Eckardt, et al., 2018) and one meaningful set of flexor or extensor muscles in the relevant motor module. In a case of two or more fundamental synergies are blended into one (or when one synergy is split into one or more synergies), a combined synergy appears. Combined synergies usually constitute, in locomotion data, 10 to 30% of the total extracted synergies (Janshen, Santuz, & Arampatzis, 2020; Santuz, Ekizos, et al., 2020). While fundamental synergies can be compared given their similar function (i.e. motor primitives and motor modules are comparable since they serve a specific task within the step cycle), combined synergies often differ from one another making their classification impossible. Due to the lack of consensus in the literature on how to interpret them, we excluded the combined synergies from the FWHM analysis. The recognition of fundamental synergies was carried out by classifying motor primitives using a previously described unsupervised learning method (Santuz, Ekizos, et al., 2020). Briefly, by using NMF we clustered together those primitives that showed similar behaviour over time. These functionally-related primitives were then ordered based on their CoA, while unclassified primitives were labelled as combined.

2.6 Statistical analysis

Four young participants fell after gait perturbation was applied (none of the participants failed to cope with the lean-and-release). Further eight gait perturbation trials did not meet the criteria to assure comparability of the data (see *2.4 Step cycle assessment*). Hence, the participants were removed from the dynamic stability analysis (both tasks). Accordingly, twenty-seven participants of group PERT and eighteen CTRL remained for adaptation and generalisation analyses (Fig. 1). For the muscle synergy assessment from the PERT group 28 trials for unperturbed walking, 27 for perturbed walking and 39 for lean-and-release remained for further analysis (Fig. 1). To assess the recovery response to gait perturbation for both analysed trials (*Trial 1* and *Trial 8*), separate one-way ANOVAs were performed to compare the MoS during unperturbed walking to the perturbed and following six recovery steps. To assess adaptations in the recovery response to repeated gait perturbation exposure, a two-way repeated measures ANOVA, with gait event (perturbed step and recovery steps 1-6) and perturbation trial (*Trial 1* and *Trial 8*) was applied for MoS at foot touchdown. In a case of significant main effects or interactions Bonferroni *post-hoc* corrections were implemented. The effect of repeated gait perturbations on recovery performance for the lean-and-release task was assessed by comparing

MoS at touchdown of the recovery limb after sudden forward fall for groups PERT and CTRL using a *t*-test for independent samples. Further independent-samples *t*-tests were implemented to identify possible group-differences in age, body mass, body height and self-reported physical activity level. To evaluate differences in modular organisation of recovery responses for the two perturbations, we estimated the 95% confidence interval of the bootstrapped relevant parameters (i.e. factorisation rank, reconstruction quality, FWHM and CoA) using the 2.5% sample quantile as the lower bound and the 97.5% sample quantile as the upper bound. Ten thousand resamples with replacement for each parameter were used to estimate the confidence intervals (Santuz et al., 2019). Moreover, we calculated the effect size Hedges' g. The approximate distribution of the effect size g was calculated from the bootstrapped sample pairs and confidence intervals (CI) were taken from this distribution as described above. Differences were considered significant when the zero was lying outside each CI. The level of significance was set at $\alpha = 0.05$, with all results presented as mean and SD. All statistical analyses were conducted using custom R scripts or SPSS software (26.0; IBM, Armonk, NY, USA).

3 Results

3.1 Dynamic stability changes to different types of perturbation

No significant differences were detected in participants' age, body height, body weight or physical activity level between PERT and CTRL groups.

For both analysed gait perturbation trials, the unpredictable trip caused significantly lower (i.e. more negative; $p < 0.01$) MoS during the perturbed step compared to unperturbed walking (average value over 12 consecutive steps; Fig. 3), indicating less stable body configuration. In *Trial 1* the participants slowly increased their MoS (still different to unperturbed walking; $p < 0.05$) within the following three recovery steps and regained their MoS of the unperturbed state at touchdown of the fourth recovery step (Reco4; Fig. 3). In *Trial 8* the participants regained MoS of the unperturbed state already during the second recovery step (Reco2; Fig. 3). Assessment of adaptations in the recovery response to repeated gait perturbation exposure revealed a statistically significant trial x gait event interaction ($F[6,21] = 7.72$, $p < 0.001$). When comparing *Trial 8* with the first (i.e. novel) unpredictable perturbation, we found a significantly higher ($0.001 \leq p < 0.01$) MoS during the perturbed step and the following two recovery steps for all analysed participants (Pert and Reco1-2 respectively; Fig. 3), indicating smaller changes in MoS, and hence more complete recovery following repeated exposure to gait perturbations. The analysis of inter-task transfer of recovery response adaptations from repeated gait perturbation exposure revealed no statistically significant differences in MoS at touchdown of the recovery limb in the untrained lean-and-release transfer task between PERT and CTRL ($p = 0.44$; Fig. 3). Note that there was no difference in task demand on stability control (i.e. MoS at the instant of release) between groups.

Insert Figure 3

3.2 Modular organisation of recovery responses to different types of perturbation

The minimum number of synergies necessary to reconstruct the resampled concatenated EMG data (i.e. the NMF factorisation rank) for the analysed single step was 4.3 ± 0.5 for unperturbed walking, 3.6 ± 0.5 for perturbed walking and 3.3 ± 0.5 for lean-and-release, significantly different between unperturbed and perturbed walking (-15.1%, CI [-0.90%, -0.44%], g = -7.6), unperturbed walking and lean-and-release (-21.2%, CI [-1.20%, -0.75%], g = -12.2) and perturbed walking and lean-and-release (-7.1%, CI [-0.50%, -0.04%], g = -3.2). The average reconstruction quality (i.e. the R^2 or the EMG variability accounted for by the factorisation) was 0.658 ± 0.030, 0.595 ± 0.036 and 0.459 ± 0.039 for the analysed step in the three tasks, respectively, with significant differences between all three (-9.2%, CI [-0.1%, -0.05%], g = -9.9 between the two walking tasks; -29.2%, CI [-0.20%, -0.18%], g = -33.8 between unperturbed walking and lean-and-release; -22.0%, CI [-0.20%, -0.12%], g = -21.0 between perturbed walking and lean-and-release). The percentage of combined synergies was 8.2%, 0.3% and 10.8% for the three tasks, respectively.

Four fundamental synergies were clustered in both walking conditions, while three were clustered for the lean-and-release (Fig. 4, Fig. 5). In walking, the first synergy functionally referred to the early swing, with a major involvement of the foot dorsiflexors to counteract the plantarflexion at heel strike and the mediolateral foot stabilisers. The second synergy was associated with the late swing, highlighting the relevant influence of knee flexors in unperturbed walking and of the foot dorsiflexors and the hip abductors and flexors in perturbed walking. The third synergy identified the body weight acceptance and showed the involvement of the knee and hip extensors in both walking conditions with the addition of the knee flexors in perturbed walking. The fourth and last synergy reflected the propulsion phase, highlighting the relevant influence of the foot plantarflexors. In the lean-and-release task, the first two synergies covered the early and late swing phase, respectively. The early swing was predominantly characterised by the contribution of foot dorsiflexors and hip abductors and flexors, similarly to what we found in the late swing phase of perturbed walking. The late swing saw the contribution of almost all recorded muscles. Note that the spatiotemporal characteristics of this specific synergy do not reflect the typical patterns of a late swing synergy, since the primitive expands temporally well after touchdown, with a negligible contribution of foot dorsiflexors and hip flexors and comparably high contribution of plantarflexor muscles. The third and last synergy, namely weight acceptance, included the contribution of knee and hip extensors, similarly to the weight acceptance synergy of the walking tasks. The synergy-by-synergy variability of individual bootstrapped motor modules is reported in Table 1, where it is possible to appreciate the influence of concatenation order on the factorisation outcomes (in case the concatenation order would not play a role, this table would be filled with zeroes). Variability across different trials is depicted in Fig. 4, where it is possible to recognize the different timewise strategies adopted by every participant in each of the three tasks. FWHM and CoA results are reported in Table 2 and Table 3. When comparing unperturbed and perturbed walking, all primitives were narrower (i.e. lower FWHM) in the latter. In perturbed walking, the CoA shifted later in time in both swing primitives earlier in both the stance-related ones (i.e. weight acceptance and propulsion; Tab. 2, Fig. 4, Fig. 5). The primitives of the lean-and-release task were all wider than those of perturbed walking. The early swing primitive was shifted later and the remaining two earlier in time when compared to perturbed walking (Fig. 5).

Insert Figure 4 and 5

Insert Tables 1, 2 and 3

4 Discussion

This study used the muscle synergy concept to detect potential neuromotor factors limiting inter-task generalisability of fall-resisting skills. We found no benefit of improved stability control from repeated gait perturbations for the recovery performance in an untrained lean-and-release task. Profound differences in the spatiotemporal organisation of muscle activation patterns indicated a diverging modular control to the different perturbations. These results confirm our hypothesis in that a lack of transfer of adaptations to stability control comes along with differences in muscle synergies for the perturbation recovery responses.

Repeated exposure to sudden gait perturbations led to a significant improvement of reactive stability control mechanisms, providing evidence to the hypothesis that changes in the natural environment stimulate our neuromotor system to rapidly adapt its motor output relevant for stability control, and hence increase the system’s robustness to similar future perturbations

(Santuz, Brüll, et al., 2020; Santuz, Ekizos, Eckardt, et al., 2018). While generalisation of adaptations in stability control between different conditions of the same perturbation (e.g. from treadmill gait-slips to a 'novel' overground slip; Lee et al., 2018; Wang et al., 2019; Yang et al., 2013, 2018) have been reported quite frequently in the past, this does not seem to be the case with all kinds of daily life postural threats. In line with our previous study (König, Epro, Seeley, Potthast, et al., 2019), no benefit from repeated gait perturbation exposure could be observed for the recovery performance in an untrained reactive stability task, instability levels (i.e. MoS prior to recovery stepping for different perturbation; Fig. 3). To further prove comparability of applied tasks, we analysed both the base of support and also its rate of increase for both perturbation responses, showing significantly larger values for both kinematic variables for the recovery step after the first gait perturbation or sudden forward fall compared to 'normal', i.e. unperturbed walking (base of support unperturbed walking: 0.68 ± 0.03 m; gait perturbation: 0.78 ± 0.12 m; lean-and-release: 0.97 ± 0.15 m; $0.001 \leq p \leq 0.002$; rate of increase in base of support: 1.78 ± 0.05 m/s vs. 2.50 ± 0.50 m/s vs. 4.58 ± 0.54 m/s; $p \leq 0.001$). In other words, unpredictable tripping and sudden release from a forward inclined position inherently require rapid base of support increment in the anterior direction, hence sharing the same mechanism for stability recovery. However, critical components in neuromotor control (e.g. module composition and time-coordinated recruitment of motor modules) due to different biomechanical task constraints (e.g. sensory input, muscle activity patterns, muscle-tendon-unit length and body dynamics) may still discriminate perturbation types, possibly explaining the discrepancy between findings for generalisation of adaptations from repeated gait perturbation exposure. Thus, although generalisation is in principle possible within the human stability control system, it requires a certain degree of similarity, if not consistency, between tasks which may be determined by factors other than shared limb mechanics seen at the macro level.

Here, we demonstrate that while the two walking conditions showed a comparable modular organisation as evidenced by similar amounts and characteristics of fundamental synergies, the lean-and-release task had one less synergy and a profound reorganisation of the remaining three. In addition to limited similarity in modular control between walking and lean-and-release, for the latter we found an increased variability of the bootstrapped motor modules of the late swing and weight acceptance synergies. Thus, while the ability to choose from abundant 'motor-equivalent' solutions reflects the adaptability or robustness of biological systems (Kitano, 2004; Ting et al., 2015), it may further aid to adapt the modular control to different perturbations.

Muscle synergies represent coordinated muscle activation patterns for functional movement (Bizzi et al., 2008, 1991; Lee, 1984; Mussa-Ivaldi et al., 1994; Tresch et al., 1999). While it is reasonable to suggest that the neuromotor system uses common sets of synergies to effectively and flexibly construct movement (d'Avella & Bizzi, 2005; d'Avella et al., 2003), also task-specific motor modules may occur when challenged with diverse biomechanical demands or perturbations (Chvatal & Ting, 2013; Chvatal et al., 2011; Munoz-Martel et al., 2019; Torres-Oviedo & Ting, 2010). The most important phase for stability recovery performance during the lean-and-release is the one from release until foot touchdown, because the MoS at touchdown determines the stability during stance (Arampatzis et al., 2008; Karamanidis et al., 2008). Therefore, the ability to generate a hip joint moment in an appropriate temporal framework in the beginning of the swing phase is very important (Arampatzis, Peper, & Bierbaum, 2011). This biomechanical requirement is visible in the early swing synergy of the lean-and-release, showing a dominant contribution hip- and ankle flexor muscles. Therefore, we argue that this synergy was the most important for the successful recovery of stability in the lean-and-release task from a neuromechanical point of view. In fact, the bootstrapped motor modules of this pivotal synergy showed a variability similar to that found in both unperturbed and perturbed walking, testifying how the relative muscle contributions were constrained across different participants in order to comply with the specific biomechanical requirement mentioned above. However, the two subsequent synergies showed a variability of the bootstrapped motor modules 1.2 to 3.6 times larger than that of perturbed walking. This outcome proves that the strategies required to complete the task after the early swing were much more flexible and variegated across participants than in perturbed walking. In addition to the reasons mentioned above, this is also likely to be due to the different requirements at the end of the task: while during walking the goal was to continue locomotion after perturbation, in the lean-and-release there were no further steps after recovery and this justifies the absence of a propulsion synergy. The observed discrepancies in the spatiotemporal organisation of the motor system reflected the neuromotor specificity of perturbed walking and lean-and-release and may, therefore, explain the absent performance transfer between tasks. In other words, the observed lack of generalisable may have been driven by the scarce similarity between neuromuscular responses to perturbations, visible in the different number and characteristics of muscle synergies.

Perturbation to gait was applied to unpredictable time points, affecting the normal locomotor pattern. Whilst both unperturbed and perturbed walking showed a similar modular organisation, there was a substantial shift in time-dependent activation signals evoked by the perturbation. Specifically, we found a delay in the CoA of both swing synergies and earlier CoA in the weight acceptance and propulsion synergies when comparing perturbed with unperturbed walking, indicating that the timing of the perturbation was largely unpredictable, characteristic that promoted reactive stability control mechanisms for quicker step execution. This might explain also the lower FWHM in perturbed as compared to unperturbed walking possibly due to a bigger signal-to-baseline ratio in perturbed walking. These results align with the changes in activation signals but preserved motor modules during the unperturbed recovery step in unexpected slipping (Oliveira, Gizzi, Kersting, & Farina, 2012), providing evidence to the hypothesis that the central nervous system flexibly modulates the temporal activation pattern of a retained set of motor modules via descending commands (Santuz, Brüll, et al., 2020; Santuz, Ekizos, Eckardt, et al., 2018; Yokoyama et al., 2019; Zandvoort, van Dieen, Dominici, & Daffertshofer, 2019), to respond to altered conditions of the same motor task.

A potential limitation of the present design may be the concatenation of trials from different participants because the order of the concatenated trials influences the extracted synergies (see Table 1). One possibility to overcome this issue in future studies would be to extract synergies from individual recovery steps. A solution that would not assume similar strategies across different participants and/or trials. While the reconstruction quality can appear relatively lower than that reported other locomotion studies, this cannot come as a surprise considering that the current data set was generated by concatenating cycles from different participants. Moreover, this approach unavoidably deals with the discontinuities at every new cycle beginning due to the considered locomotor cycle not being whole, since the segmentation was done from the toe-off to the minimum of the knee joint angle. Finally, the relatively low number of controls (*n* = 18) may foster inter-subject variability in recovery responses to the novel transfer perturbation task, and thereby reduce the potential for determining statistically significant generalisation. However, we found similar variability levels in MoS for group PERT (Fig. 2) though the group was quite large in size, and hence the size of the investigated sample may not be the primary driver for failure of generalisation from repeated gait perturbation exposure.

5 Conclusions

While generalisation of adaptation is in principle possible within the human stability control system, it seems limited if neuromotor factors discriminate perturbation responses in different motor tasks. Here, using the muscle synergies concept we investigated potential factors limiting inter-task generalisation within the stability control system. The profound differences detected in the synergistic spatiotemporal organisation of muscle activations indicate a diverging modular response to different perturbations, seemingly covered by the same main mechanism for stability control (i.e. rapid increase of base support). Hence, our results provide indirect evidence that the transfer of adaptations in stability control between different reactive stability tasks may be inhibited by differences in muscle synergies in the perturbation recovery responses.

6 Conflict of Interest

The authors declare no competing interests.

7 Author contributions

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

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10 Figure legends

Figure 1: Experimental design. Thirty-nine participants were randomly assigned to a single session treadmill perturbation group (eight separate unpredictable trip-like perturbations; PERT), and the remaining eighteen participants formed a control group (unperturbed walking only; CTRL). Trials were excluded from the analysis, in case of (i) a fall of the participant in

one of the tasks or if the participant had to grasp the handrails of the treadmill in perturbed walking, (ii) elevation of the perturbed limb which itself counted as first recovery step in perturbed walking or the use of the left leg as a recovery limb in the lean-and-release task, or (iii) artefacts in the EMG signal. N: Number of randomised participants; n: number of analysed trials per group.

Figure 2: Step cycle assessment. In both tasks (perturbed walking and lean-and-release) the first recovery step cycle was broken down into swing and early stance phase (i.e. energy absorption) based on the foot toe-off, foot touchdown and minimum knee joint angle. The swing phase was defined as the time period between toe-off and touchdown, and the early stance phase as the time period between touchdown and the following minimum knee joint angle.

Figure 3: Margin of stability (MoS) during repeated gait perturbations and lean-and-release. MoS is presented for foot touchdown during unperturbed walking (Unpert), perturbation (Pert), and the following 6 recovery steps after perturbation (Reco1-Reco6) in Trial 1 and Trial 8 for the PERT group. Data of the lean-and-release task is given for the time points of release and foot touchdown of the control (CTRL) and PERT groups. Values are displayed as mean with SD as error bars. † statistically significant ($p < 0.05$) difference between Trial 1 and unperturbed walking; * statistically significant ($p < 0.05$) difference between Trial 8 and unperturbed walking. $^{\#}$ statistically significant ($p < 0.05$) difference between Trial 1 and Trial 8.

Figure 4: Bootstrapped motor modules and motor primitives of the fundamental synergies for unperturbed walking, perturbed walking and lean-and-release. For a clearer presentation, the motor modules are shown on a normalised y-axis base with each muscle contribution within one synergy ranging from 0 to 1 and each point representing the average of the nearest 10 runs obtained from the 1000 bootstrapped trials. For the motor primitives, the x-axis full scale represents the averaged step cycle (with swing and stance until the minimum of

the knee angle normalised to the same amount of points and divided by a vertical line) and the y-axis the normalised amplitude. The standard deviation of the obtained 1000 bootstrapped primitives for each synergy is shown as a light grey band. Muscle abbreviations: ME = *gluteus medius*, MA = *gluteus maximus*, FL = *tensor fasciæ latæ*, RF = *rectus femoris*, VM = *vastus medialis*, VL = *vastus lateralis*, ST = *semitendinosus*, BF = *biceps femoris*, TA = *tibialis anterior*, PL = *peroneus longus*, GM = *gastrocnemius medialis*, GL = *gastrocnemius lateralis*, SO = *soleus*.

Figure 5: Comparison of motor modules and motor primitives of the fundamental synergies for unperturbed walking, perturbed walking and lean-and-release task (see caption of Fig. 4 for details).

11 Tables

Table 1: Variability, reported as the average standard deviation of all 13 muscle contributions, of the motor modules for unperturbed and perturbed walking, and lean-and-release across the 1000 bootstrapped trials. This table shows that the order of concatenation has an influence on the factorisation outcomes.

	Average variability		
Motor module	Unperturbed walking	Perturbed walking	Lean-and-release
Early swing	0.047	0.048	0.047
Late swing	0.059	0.075	0.089
Weight	0.053	0.030	0.109

acceptance			
Propulsion	0.044	0.025	Not present

Table 2: Comparing bootstrapped full width at half maximum (FWHM) and centre of activity (CoA) of motor primitives for unperturbed and perturbed walking. Data are reported as percentage differences between unperturbed and perturbed walking ($\Delta_{U,P}$ ± standard deviation). Positive differences ($\Delta_{U,P} > 0$) denote bigger values in perturbed walking, whereas negative differences imply the contrary. The Hedges' g effect size shows the bias-corrected standardised differences between unperturbed and perturbed walking means. Asterisks highlight the 95% confidence intervals (CI) which do not contain the zero.

	FWHM		CoA	
Motor primitive	$\Delta_{U,P}$	95% CI	$\Delta_{U,P}$	95% CI
Early swing	-41.3% ± 1.3%	[-24.3%, -21.5%]* (g = -45.5)	+4.1% ± 0.8%	[2.7%, 6.2%]* (g = 6.9)
Late swing	-33.4 ± 2.8%	[-16.9%, -12.1%]* (g = -17.0)	+29.0% ± 3.4%	[36.6%, 58.5%]* (g = 12.0)
Weight acceptance	-34.6% ± 1.1%	[-27.4%, -24.1%]* (g = -43.1)	-9.0% ± 0.4%	[-13.2%, -11.3%]* (g = -36.0)
Propulsion	-39.5% ± 1.6%	[-24.3%, -20.7%]* (g = -35.2)	-11.1% ± 0.6%	[-21.2%, -17.2%]* (g = -27.1)

Table 3: Comparing bootstrapped full width at half maximum (FWHM) and centre of activity (CoA) of motor primitives for perturbed walking and lean-and-release. Data are reported as percentage differences between perturbed walking and lean-and-release ($\Delta_{P,L}$ ± standard deviation). Positive differences ($\Delta_{P,L} > 0$) denote bigger values in lean-and-release, whereas negative differences imply the contrary. The Hedges' g effect size shows the bias-corrected standardised differences between perturbed walking and lean-and-release means. Asterisks highlight the 95% confidence intervals (CI) which do not contain the zero.

	FWHM		CoA	
Motor primitive	$\Delta_{P,L}$	95% CI	$\Delta_{P,L}$	95% CI
Early swing	+33.9% ± 1.7%	[16.6%, 20.3%]* (g = 27.9)	+12.2% ± 1.7%	[11.3%, 19.9%]* (g = 10.1)
Late swing	+63.3% ± 2.8%	[52.5%, 62.4%]* (g = 32.1)	-22.6% ± 3.5%	[-48.0%, -25.7%]* (g = -9.2)
Weight acceptance	+29.3% ± 1.9%	[18.7%, 24.1%]* (g = 22.2)	-2.9% ± 1.0%	[-5.9%, 1.3%]* (g = -4.3)
Propulsion	Not present in lean-and-release			