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Generalization of motor module recruitment across standing reactive balance and walking is associated with beam walking performance in young adults

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ABSTRACT

Background: Recent studies provide compelling evidence that recruiting a common pool of motor modules across behaviors (i.e., motor module generalization) may facilitate motor performance. In particular, motor module generalization across standing reactive balance and walking is associated with both walking speed and endurance in neurologically impaired populations (e.g., stroke survivors and individual's with Parkinson's disease). To test whether this phenomenon is a general neuromuscular strategy associated with well-coordinated walking and not limited to motor impairment, this relationship must be confirmed in neurologically intact adults.
Research Question: Is motor module generalization across standing reactive balance and walking related to walking performance in neurologically intact young adults?
Methods: Two populations of young adults were recruited to capture a wide range of walking performance: professionally-trained ballet dancers (i.e., experts, n = 12) and novices (n = 8). Motor modules (a.k.a. muscle synergies) were extracted from muscles spanning the trunk, hip, knee and ankle during walking and multidirectional perturbations to standing. Motor module generalization was calculated as the number of modules common to these behaviors. Walking performance was assessed using self-selected walking speed and beam-walking proficiency (i.e., distance walked on a narrow beam). Motor module generalization between experts and novices was compared using rank-sum tests and the association between generalization and walking performance was assessed using correlation analyses.
Results: Experts generalized more motor modules across standing reactive balance and walking than novices ($p = 0.009$). Across all subjects, motor module generalization was moderately associated with increased beam walking proficiency ($r = 0.456$, $p = 0.022$) but not walking speed ($r = 0.092$, $p = 0.349$).
Significance: Similar relationships between walking performance and motor module generalization exist in neurologically intact and impaired populations, suggesting that motor module generalization across standing reactive balance and walking may be a general neuromuscular mechanism contributing to the successful control of walking.

1. Introduction

Maintaining balance is critical for well-coordinated walking and the neuromuscular control of walking and balance may therefore share common structure. Motor module (a.k.a. muscle synergy) analysis has frequently been used to investigate the structure of neuromuscular control underlying walking and balance performance. Motor modules are defined as groups of coactive muscles flexibly recruited over time to transform movement goals into biomechanical output [1]. Our recent studies provide novel and compelling evidence that recruiting a common set of motor modules across standing reactive balance and walking (i.e., motor module generalization) contributes to successful walking

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performance in neurologically impaired populations [2,3]. The similarity of motor modules across these two tasks suggests that the nervous system takes advantage of neuromuscular mechanisms for the automatic control of posture to enable the robust and automatic control of walking. If motor module generalization across these two tasks represents a general neuromuscular strategy important for the control of walking, then its relationship to walking performance should also be present among neurologically intact populations. The purpose of this study was therefore to identify whether motor module generalization across standing reactive balance and walking is related to walking performance in neurologically intact young adults.

The number of motor modules recruited during walking is frequently used as a measure of neuromuscular complexity, with higher complexity (i.e. more motor modules) associated with better walking performance. However, neuromuscular complexity during walking does not directly translate to a specific level of walking performance. Increased neuromuscular complexity is observed with motor development in infants [4] and with motor expertise in adults [5]. Conversely, neuromuscular complexity is reduced in many neurologically impaired populations that exhibit motor deficits and is associated with reduced walking speed and endurance [6–10]. Nevertheless, individuals with similar neuromuscular complexity during walking can exhibit very different levels of walking performance [3,6,9]. Further, improvements in walking performance, such as those due to rehabilitation in neurologically impaired populations or long-term training in neurologically intact populations, can occur without an increase in neuromuscular complexity [5,11,12].

Our recent studies demonstrate that generalization of motor modules across gait and balance tasks may be another important neuromuscular mechanism underlying differences in walking performance. We found that motor module generalization across standing reactive balance and walking is reduced in individual's with neurological impairments, such as Parkinson's disease [2] and stroke [3]. In other words, few standing reactive balance modules were recruited during unperturbed walking. Many of these individuals were community-dwelling with high function and although their walking speed was slower than neurotypical controls, they did not exhibit reduced neuromuscular complexity (i.e., number of motor modules). Instead, a reduction in motor module generalization was associated with their slower walking speeds. Because the relationship between motor module generalization and walking speed was present in individuals who do not exhibit reduced neuromuscular complexity we reasoned that it might also explain differences in neurologically intact individuals. Although many of the motor modules recruited for standing reactive balance are also recruited during unperturbed walking in healthy young adults [13], the relationship between generalization and walking performance has not been tested.

In the present study, we analyzed electromyography (EMG) from muscles spanning the trunk, hip, knee, and ankle during overground walking and multidirectional perturbations to standing in healthy young adults. We recruited two populations of young adults to capture a wide range of walking performance: professionally trained ballet dancers (experts) and untrained novices. Two measures of walking performance were investigated: self-selected walking speed and beam-walking proficiency. Beam walking proficiency (i.e., walking on a narrow beam [14]) provides a challenge to walking balance that may better differentiate walking performance than walking speed. Based on our hypothesis that motor module generalization across standing reactive balance and walking is a general neuromuscular strategy contributing to the successful control of walking, we predicted that generalization across all subjects would be positively associated with our measures of walking performance.

2. Methods

2.1. Participants

Twelve experts (professionally-trained ballet dancers; 12 female, 22.0 ± 2.5 yrs old, 1.64 ± 0.06 m height, 54.3 ± 6.3 kg weight) and 8 sex, age, height, and weight-similar untrained novices (no dance or gymnastics training; 8 female, 21.9 ± 3.4 yrs old, 1.66 ± 0.06 m height, 66.1 ± 21.4 kg weight) participated in the experiment. Inclusion criteria for all participants was age greater than 18 yr. Experts were required to have at least 10 years of ballet training and were recruited from the professional development program of the Atlanta Ballet Center for Dance Education and the Company of the Atlanta Ballet. Novices were required to have no formal dance or gymnastic training. Exclusion criteria for both groups were self-reported medical conditions that could impair walking and balance. All participants provided written informed consent before participating according to protocols approved by the institutional review boards at Emory University and Georgia Institute of Technology.

2.2. Experimental procedures

All participants completed four walking conditions (narrow beam-walking, wide beam-walking, overground walking at slow speed, overground walking at preferred speed) and one standing reactive balance condition. Motor modules in beam-walking and overground walking at slow speed in these participants were previously analyzed in Sawers et al. [5]. Here, we focus on motor modules in standing reactive balance and overground walking at preferred speed.

- *Standing reactive balance*. Reactive balance performance was assessed through postural responses to ramp-and-hold translations of the support surface while subjects stood on an instrumented platform. The platform translated in 12 equally spaced directions in the horizontal plane (see Fig. 1B) with 13 cm displacement, 15 cm/s peak velocity, and 0.3 g acceleration. Three trials in each direction were collected in random order. Subjects were instructed to cross their arms and maintain balance without stepping or using their arms. Stance width was self-selected and enforced to be the same across all trials.
- *Overground walking at preferred speed*. Subjects were instructed to walk at their preferred speed over a 7.5 m distance while keeping their head up and looking straight ahead. Six trials were collected per subject.

2.3. EMG data collection and processing

Surface EMG activity was recorded at 1080 Hz from 16 muscles on the right leg and trunk of each participant: tibialis anterior (TA), peroneus longus (PERO), medial gastrocnemius (MGAS), soleus (SOL), vastus medialis (VMED), vastus lateralis (VLAT), biceps femoris long head (BFLH), semimembranosus (SEMM), gluteus maximus (GMAX), gluteus medius (GMED) rectus femoris (RFEM), tensor fasciae latae (TFL), adductor magnus (ADMG), rectus abdominus (REAB), external obliques (EXOB), and erector spinae (ERSP). EMG signals were high-pass filtered at 35 Hz (third order-Butterworth), de-meaned, rectified, and low-pass filtered at 40 Hz (third-order Butterworth) using custom Matlab routines. Subject-specific EMG data matrices for each condition (i.e., standing reactive balance and walking) were assembled as described below. The assembled EMG data matrices for each condition were then normalized to the maximum activation observed during walking at preferred speed.

For standing reactive balance, EMG data were analyzed during four time bins: one before the perturbation and three during the automatic postural response (APR; Fig. 1B) [13]. Specifically, mean muscle activity was calculated during a 280-ms background period that ended 140 ms before the perturbation and during each of three 75 ms bins beginning 100 ms after perturbation onset. Mean muscle activity values for each muscle during each bin for each trial were assembled to form an $m \times t$ data matrix, where m is the number of muscles (16) and t is the number of data points (3 trials × 12 directions × 4 time bins = 144).

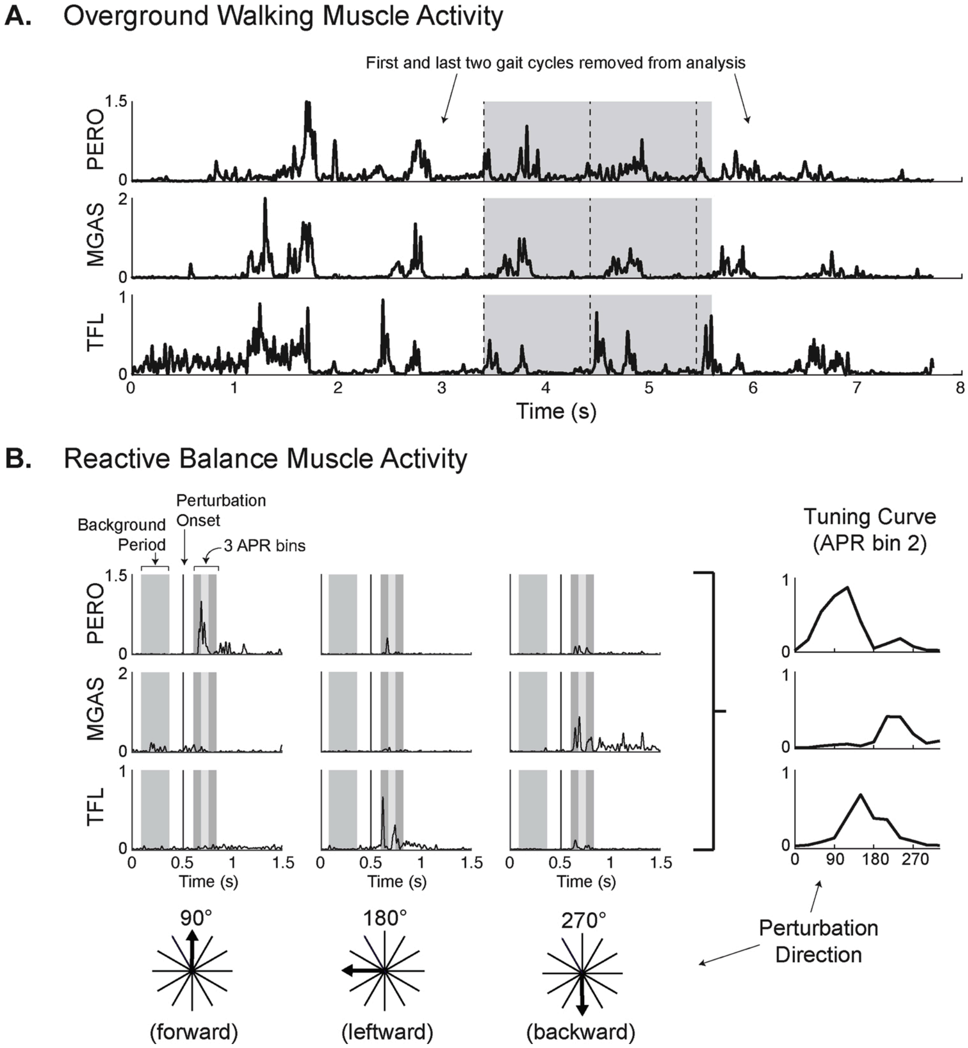

Fig. 1. Example processed EMG from select muscles during overground walking (A) and standing reactive balance (B). A: muscle activity for walking was recorded while participants walked overground at their self-selected speed for at least 6 trials of 7.5 m each. For each trial, the first and last two gait cycles were removed to avoid gait initiation and termination. Dashed lines represent right heel-strikes, and the shaded region represents the data analyzed for 1 trial. Data from all trials for a subject were concatenated before motor module extraction to form an m x t data matrix, where m is the number of muscles and t the number of time points across all trials. B: muscle activity for standing reactive balance was assessed through ramp-and-hold perturbations in 12 evenly spaced directions. *Left*: responses to forward, leftward, and backward perturbations are illustrated. EMG responses occurred −100 ms after perturbation onset (denoted by black vertical line). Mean EMG activity was calculated during a background period before the perturbation and three 75-ms time bins during the automatic postural response (APR). *Right*: tuning curves of mean muscle activity from perturbations as a function of perturbation directions for the second APR bin. Before motor module extraction, the tuning curves were assembled to form an m x t data matrix, where m is the number of muscles and t the number of data points (3 trials x 12 directions x 4 time bins = 144). (PERO, peroneus longus; MGAS, medial gastrocnemius; TFL, tensor fascia latae).

For consistency with reactive balance processing, EMG data for walking were averaged over 75 ms bins. Data from the first and last two steps were removed to avoid gait initiation and termination (Fig. 1A). Trials were concatenated end-to-end to form an $m \times t$ data matrix. The number of data points, t (trials × time bins), varied across subjects, with a minimum size of 121. There was no significant difference between groups (176.4 ± 39.3 for experts, 213.9 ± 47.9 for novices, $t(18) = 1.91$, $p = 0.10$).

2.4. Motor module analysis

Motor modules for each subject were extracted separately from EMG data matrices derived from standing reactive balance and walking using non-negative matrix factorization (NNMF; [15]). NNMF decomposes the recorded EMG according to EMG = W×C, where W is an $m \times n$ matrix with n motor modules and C is an $n \times t$ matrix of motor module activation coefficients. To ensure equal weight of each muscle during the extraction process, each row in the EMG data matrices (i.e. each muscle) was scaled to unit variance before motor module extraction and rescaled to original units afterward.

Motor module number in each condition (n_{walk}, $n_{balance}$) was chosen as described previously [2,3]. Briefly, 1−16 motor modules (W) were extracted from each EMG data matrix. Goodness of fit between actual and reconstructed EMG was evaluated with variability accounted for (VAF), defined as 100 × squared uncentered Pearson's correlation coefficient [16]. The 95 % confidence intervals (CI) on VAF were calculated using a bootstrapping procedure where EMG datasets were resampled 250 times with replacement and VAF of the reconstructed EMG was recalculated after each resampling. n was chosen such that the lower bound of the 95 % VAF CI exceeded 90 %. We compared n_{walk} *and* $n_{balance}$ between groups using separate two-tailed Wilcoxon Rank Sum tests (H_0: experts = novices; H_1: experts ≠ novices).

Motor module generalizability, n_{shared}, was defined as the number of motor modules shared between standing reactive balance and walking [2,3,13] and identified using Pearson's correlation coefficients. A pair of motor modules were considered shared if $r>0.623$, which corresponds to the critical value of r^2 for 16 muscles at $\alpha = 0.01$. To account for the fact that each subject recruited a different number of total motor modules, motor module generalization was also expressed as a percentage: % $n_{shared} = 100 \times [n_{shared}/(n_{walk}+n_{balance}-n_{shared})]$. To determine if experts generalized more motor modules across standing reactive balance and walking, we compared n_{shared} and %n_{shared} between groups using a one-sided Wilcoxin rank sum test and t-test, respectively (H_0: experts = novices; H_1: experts > novices).

2.5. Walking performance metrics

1. Preferred walking speed: Walking speed for each trial was defined as the average velocity of the C7 marker in the middle of the walkway and was then averaged across all trials for each subject.
2. Beam-walking proficiency: Participants walked in a heel-to-toe pattern along a narrow beam (3.8 cm wide, 3.25 cm high, and 3.66

m long) six times while keeping their arms crossed over their chest. Participants were instructed to stop if they uncrossed their arms or stepped off the beam (i.e., failure). Beam-walking proficiency was defined as a normalized distance walked, calculated as the ratio of the sum of the distance walked across all six trials and the total possible distance [14]. Perfect performance – i.e., no failures – equals 1.0.

Differences in preferred walking speed and beam-walking proficiency were compared between experts and novices using two-sided t-tests. To test our prediction that motor module generalization is positively associated with walking performance, one-tailed Pearson's correlations (H_0: $r = 0$, H_1: $r>0$) were performed to relate each metric of motor module generalizability (n_{shared}, $\%n_{shared}$) to each metric of walking performance (walking speed, beam-walking proficiency).

3. Results

Motor module number (Fig. 2B) did not differ between experts and novices in either walking (p = 0.299) or standing reactive balance (p = 0.497). The median number of motor modules recruited for walking was 7 in experts (range: 5–8) and 6 for novices (range: 5–9). The median number of motor modules recruited in standing reactive balance was 6 in experts (range: 4–7) and 6 for novices (range: 4–8).

Motor module generalization (Fig. 2C) was higher in experts compared to novices (n_{shared}: p = 0.009, $\%n_{shared}$: p = 0.010). The median number of motor modules shared across standing reactive balance and walking was 3 in experts (range: 1–4) and 2 in novices (range: 1−3). These numbers correspond to an average percentage of motor modules shared across conditions of 30.9 ± 11.2 % in experts and 18.2 ± 10.1 % in novices.

Beam-walking proficiency but not preferred walking speed differed between experts and novices, with better beam-walking proficiency associated with higher levels of motor module generalization (Fig. 3). Average preferred walking speed was 1.16 ± 0.18 m/s in experts and 1.08 ± 0.16 m/s in novices (p = 0.303). Beam walking proficiency was 0.76 ± 0.20 in experts and 0.59 ± 0.20 in novices (p = 0.037). Across all subjects we identified a significant moderate positive relationship between beam walking proficiency and number of motor modules generalized across conditions (r = 0.46, p = 0.022) and a similarly sized positive relationship with the percentage of modules shared across conditions that did not quite reach significance level of α = 0.05 (r = 0.34, p = 0.072). No significant relationship between motor module generalization and preferred walking speed was identified (n_{shared}: r = 0.09, p = 0.349; $\%n_{shared}$: r = 0.19, p = 0.205).

4. Discussion

Accumulating evidence suggests that motor module generalization across standing reactive balance and walking, defined as recruiting a common set of motor modules across both tasks, may help to distinguish differences in walking performance. Here, we demonstrate that motor module generalization across these two tasks is positively associated with the ability to perform a challenging beam-walking task in neurotypical adults. This corroborates our prior studies in stroke survivors and individuals with Parkinson's disease demonstrating a positive relationship between motor module generalization and measures of walking performance such as speed and endurance. Taken together, these studies add to our understanding of how walking is controlled and provide compelling evidence that motor module generalization with standing reactive balance may be a neuromuscular strategy utilized during walking in both healthy and motor-impaired populations. In particular,

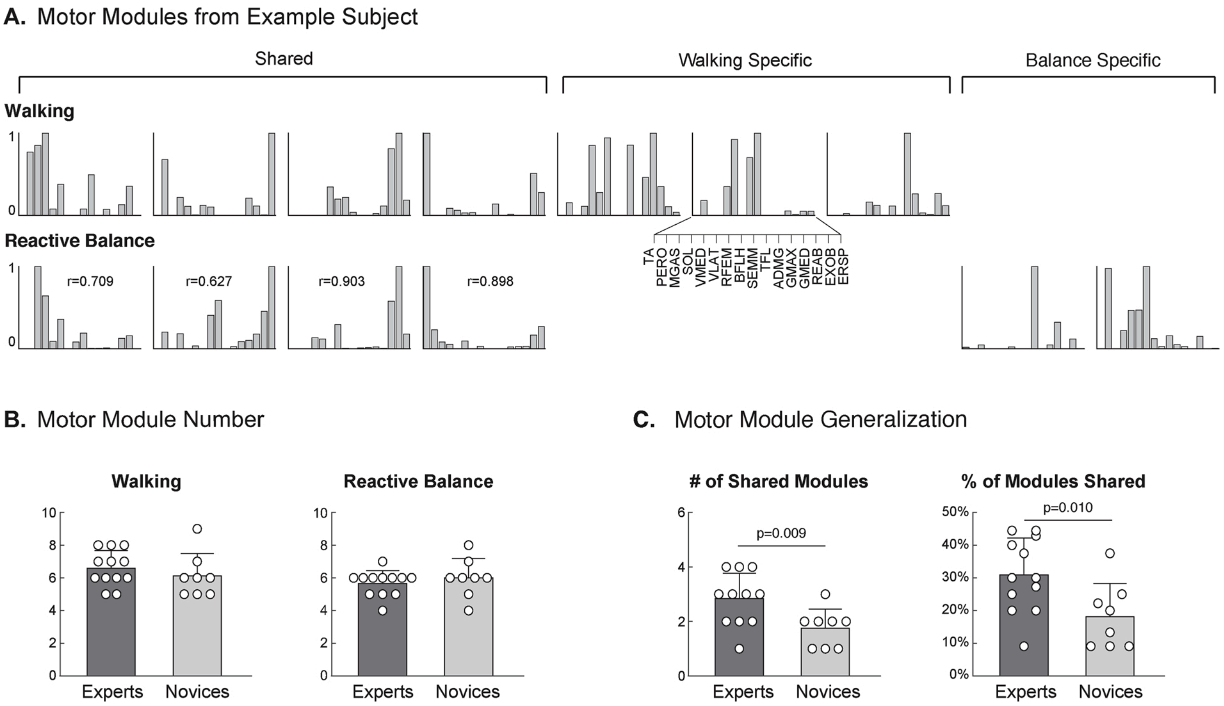

Fig. 2. Motor module number and generalization across walking and reactive balance. A: representative motor modules from an expert subject during walking and standing reactive balance. Motor modules were extracted from each behavior independently and identified as shared across behaviors if r > 0.623. 4 out of 9 motor modules, or 44.4 %, were shared across conditions in the example subject. B: The number of motor modules recruited during overground walking (left) and standing reactive balance (right) did not differ between experts (n = 12, dark gray) and novices (n = 8, light gray). C: Both the number (left) and percentage (right) of shared modules was decreased in novices compared to experts. White circles in B and C represent individual values for each subject. (TA, tibialis anterior; PERO, peroneus longus; MGAS, medial gastrocnemius; SOL, soleus; VMED, vastus medialis; VLAT, vastus lateralis; RFEM, rectus femoris; BFLH, biceps femoris long head; SEMM, semimembranosus; TFL, tensor fascia latae; ADMG, adductor magnus; GMAX, gluteus maximus; GMED, gluteus medius; REAB, rectus abdominus; EXOB, external obliques; ERSP, erector spinae).

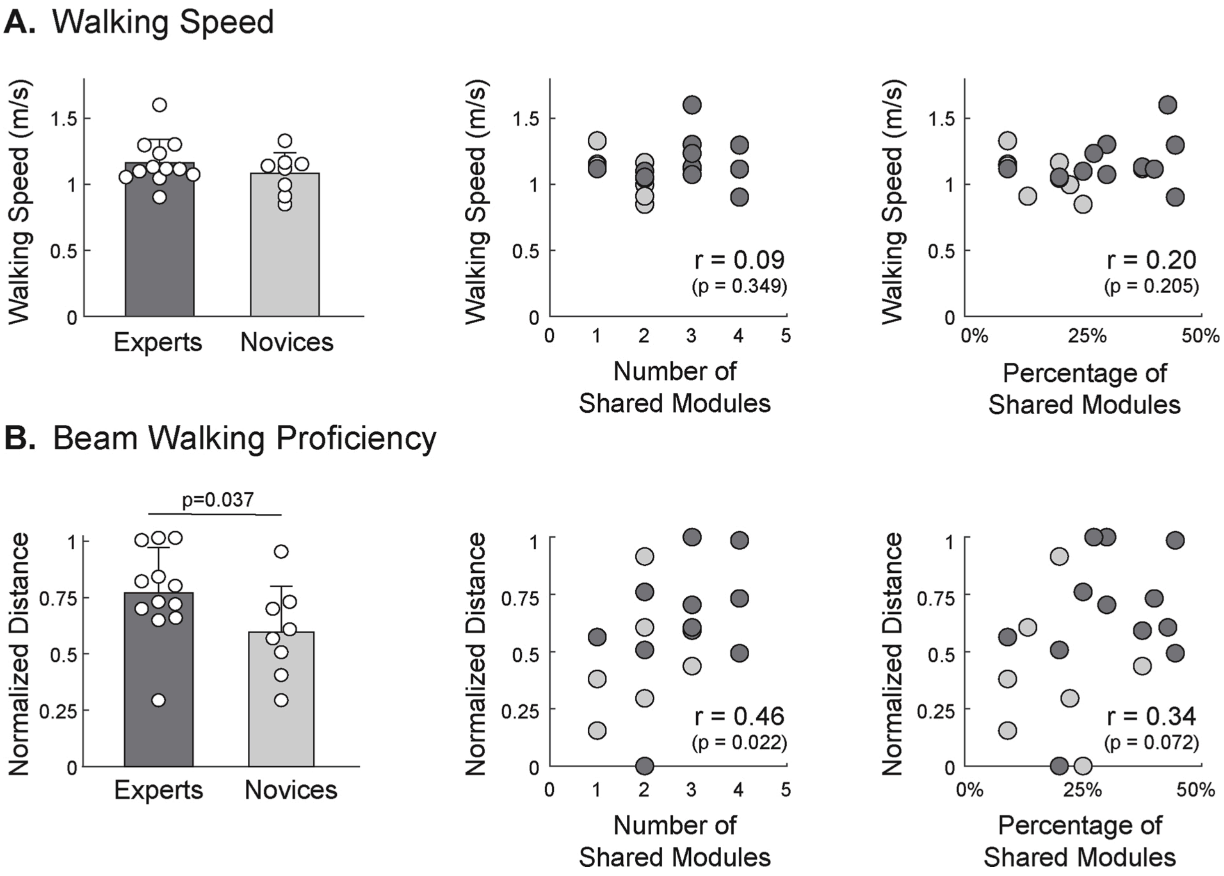

Fig. 3. Walking performance metrics. A: Self-selected walking speed did not differ between experts and novices (left panel) and was not associated with the number (center panel) or percentage (right panel) of motor modules shared across standing reactive balance and walking. B: The normalized distance walked on a narrow balance beam was higher in experts compared to novices (left panel) and was positively associated with both the number (center panel) and percentage (right panel) of motor modules shared across standing reactive balance and walking. Experts are denoted in dark gray and novices in light gray. Circles represent individual values for each subject.

this strategy may co-opt the neuromuscular control important for automatic postural responses to enable the robust and automatic control of balance during walking.

Our results are consistent with our prior studies in neurologically impaired populations [2,3], suggesting that recruiting reactive balance motor modules during walking may be a general neuromuscular strategy for well-coordinated walking regardless of motor ability. We found that motor module generalization across standing reactive balance and walking but not motor module number in either task differed between young adult experts and novices (Fig. 2). As both groups were young adults with no motor deficits it was not surprising that a similar number of motor modules were identified between groups in each task. However, the generalization of motor modules across standing reactive balance and walking differentiated the neuromuscular control structure between these two groups. Interestingly, the amount of motor module generalization that we observed previously in different group of young adults (37.4 ± 23.4 %) [13] was higher than the novices studied here ($p = 0.03$, t-test) but similar to experts ($p = 0.42$). This discrepancy could be due to lower motor ability of the novices studied here versus the young adults in the prior study, where we did not control for expertise [13]. Additionally, the perturbations to standing were of lower velocity and acceleration in this study (15 cm/s versus 35 cm/s velocity and 0.3 g compared to 0.5 g acceleration), which also could have altered the number and/or structure of motor modules recruited in reactive balance.

Recruiting standing balance motor modules during walking may contribute to the maintenance of walking balance. Our prior studies revealed that motor module generalization across these two tasks was associated with overground walking performance in motor impaired populations (i.e., speed and endurance) [2,3]. Unsurprisingly, we did not find a similar relationship with overground walking in healthy young adults in the current study. In contrast to motor impaired populations, overground walking does not provide a challenge to young adults and therefore we also included a beam-walking task. This beam-walking task was specifically designed to provide a challenge to walking balance and we previously found that it could differentiate walking balance ability in young adults [5,14]. Here, we expand upon our prior study and find that performance on the beam-walking task in the same cohort of young adults is positively associated with motor module generalization across standing reactive balance and overground walking. That this relationship only emerged when balance is challenged (i.e., overground walking in stroke survivors [3] and beam-walking in young adults) suggests that generalization across these two tasks represents a neuromuscular strategy for maintaining balance while walking. Given that this relationship is of only a fairly moderate strength ($r = 0.46$), this neuromuscular strategy should be placed in context as one of multiple concurrent strategies likely contributing to walking balance.

Motor module generalization across standing reactive balance and walking may also contribute towards the automatic control of walking. Responding to discrete perturbations, such as those experienced by participants in the current study in the standing reactive balance paradigm, requires rapid changes in the coordination of muscle recruitment. These rapid changes are typically thought to be mediated by brainstem circuits [17], although more voluntary contributions can play a role in the later response. Recruiting a common set of motor modules across standing reactive balance and walking suggests a convergence on this automatic recruitment of motor modules important for the maintenance of balance. That such convergence is increased (i.e. more common modules) in the expert group is consistent with prior evidence suggesting that automaticity and movement efficiency is increased with expertise [18–20]. These results are also consistent with our prior studies in stroke survivors and Parkinson's disease [2,3] in which reduced gait automaticity is common [21–25] and we found that motor module generalization across standing reactive balance and walking was reduced. Further, improvements in walking function in Parkinson's disease were accompanied by increased motor module generalization due to the walking motor modules becoming more similar to the standing reactive balance motor modules. Taken together, these results suggest a potential relationship between gait automaticity and motor module generalization that is common to both neurologically impaired and intact populations. Future work is needed to directly test this putative relationship.

5. Conclusions

We identified a positive relationship between beam-walking performance and motor module generalization across standing reactive balance and walking in young neurotypical adults. This relationship is consistent with our prior studies in individuals with Parkinson's disease [2] and stroke survivors [3]. Although the sample sizes in each study were small (between 6 and 11 per group), taken together these studies provide compelling evidence that recruiting reactive balance motor modules during unperturbed walking may be a general neuromuscular strategy that contributes to the maintenance of balance during walking.

Author contributions

A.S. and L.H.T conception and design of research; A.S. performed experiments; J.L.A. and H.D.C. analyzed data; J.L.A, H.D.C, L.H.T., and A.S. interpreted results of experiments; J.L.A. prepared figures; J.L.A. drafted manuscript; all authors edited and revised the manuscript and approved the final version.

Declaration of Competing Interest

The authors report no declarations of interest.

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