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Individual muscle responses to mediolateral foot placement perturbations during walking

Lydia G. Brough *, Richard R. Neptune

Walker Department of Mechanical Engineering, The University of Texas at Austin, Austin, TX, USA

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ABSTRACT

Walking requires active control of frontal plane balance through adjustments to mediolateral foot placement and ground reaction forces. Previous work on mediolateral balance perturbations and control of foot placement has often focused on the bilateral gluteus medius muscles. However, additional leg and trunk muscles can influence foot placement by transferring power to the foot and pelvis during swing. Thus, the purpose of this study was to determine individual muscle contributions to balance control following medial and lateral foot placement perturbations. Ten participants performed treadmill walking trials which included perturbations immediately before randomized heel strikes. Muscle contributions to foot placement, ground reaction forces, trunk power and frontal plane external moments during representative perturbed and unperturbed gait cycles were estimated using musculoskeletal modeling and simulation. Net muscle contributions to foot placement were 61 ± 50% more medial during the first recovery step following lateral perturbations and 28 ± 14% less medial in the second recovery step following medial perturbations. Following lateral perturbations, the swing gluteus medius performed 57 ± 50% more lateral work and the stance gluteus medius performed 61 ± 50% more medial work on the foot. Following medial perturbations, the erector spinae performed 39 ± 33% less lateral work on the foot. Changes in net muscle work on the foot were inconsistent with changes in step width, suggesting that changes in step width were not due to active muscle control but rather the mechanical effect of the perturbation. These outcomes provide a foundation for future studies analyzing balance control in populations at risk of falling.

1. Introduction

Walking requires the successful control of balance in the frontal plane, which is primarily accomplished via the generation of appropriate ground reaction forces (GRFs) and mediolateral foot placement (Bruijn and van Dieën, 2018; Neptune and McGowan, 2016). Previous work found that young healthy individuals react to an imposed error in foot placement with lateral hip and ankle strategies on the stance leg (Brough et al., 2021). After these initial stance leg responses, further corrections may take place by altering the subsequent swing leg mediolateral foot placement (Hof et al., 2010). Both strategies work to maintain a low net external moment about the body's center of mass (COM), and thus a low range of frontal plane angular momentum, which has been observed in healthy walking (Herr and Popovic, 2008). There is evidence that these responses are complementary strategies (van Leeuwen et al., 2021) since contributions to foot placement are produced by both stance and swing leg muscles (Roelker et al., 2019).

The stance leg gluteus medius muscles are primary contributors to mediolateral GRFs (John et al., 2012) and act to rotate the body toward the swing leg during stance (Neptune and McGowan, 2016). The swing and stance leg gluteus medius are also important contributors to foot placement (Roelker et al., 2019) and have been the focus of a number of perturbation studies (Afschrift et al., 2018; Hof and Duysens, 2013; Rankin et al., 2014). However, the stance leg plantarflexors, trunk muscles, and swing leg iliopsoas also play important roles in transferring power to the pelvis and foot during swing, both of which influence foot placement (Roelker et al., 2019). Thus, it is not clear how the swing and stance leg gluteus medius coordinates with other muscles to perform both the lateral hip strategy and control foot placement.

Due to the mechanical effects of a foot placement perturbation, it is difficult to differentiate between muscle responses to the perturbation versus passive mechanical effects. For example, an observed decrease in angular momentum following lateral foot placement perturbations was originally attributed to a decrease in medial GRFs modulated by hip

* Corresponding author at: Walker Department of Mechanical Engineering, The University of Texas at Austin, 204 E. Dean Keeton Street, Stop C2200, Austin, TX 78712-1591, USA.

E-mail address: lydia.brough@utexas.edu (L.G. Brough).

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abductor muscles (Miller et al., 2018), but was later determined to be caused by the perturbation itself (Brough et al., 2021). Likewise, changes to foot placement following a perturbation may be due to a combination of active and passive effects. Previous studies have attempted to separate passive and active responses by analyzing EMG (Hof and Duysens, 2013; Reimann et al., 2018), performing sensory perturbations (Reimann et al., 2018; Stokes et al., 2017) and using simulation approaches (e.g, Afschrift et al., 2018).

Previous simulation work has found that bilateral gluteus medius activity can explain changes in step width following medial and lateral treadmill perturbations at various points in the gait cycle (Afschrift et al., 2018). Similarly, mediolateral visual perturbations also produced a swing gluteus medius response and corresponding step width change, as well as increased activity from trunk muscles (Stokes et al., 2017). However, rotating visual perturbations simulating a lateral fall at heel strike triggered a foot placement response not caused by a change in gluteus medius activity (Reimann et al., 2018). Instead, participants increased the plantarflexion angle during perceived falls towards the stance leg and vice versa for perceived falls towards the swing leg (Reimann et al., 2018). While the stance leg plantarflexors can be important contributors to mediolateral foot placement (Roelker et al., 2019), there was no plantarflexion moment response following foot placement perturbations in healthy young adults (Brough et al., 2021). Together, these results highlight the specificity of balance responses to the type of perturbation. However, because these studies only examined a limited number of muscles, the contribution of other muscles to restore balance control following a perturbation is unclear.

The purpose of this study was to investigate individual muscle contributions to balance recovery strategies following medial and lateral foot placement perturbations. Specifically, we determined individual muscle contributions to mediolateral COM acceleration during stance and foot placement during the perturbed stance phase and subsequent step. We also determined muscle contributions to the overall balance response by calculating their contributions to the whole-body external moment. We hypothesized that the stance gluteus medius would contribute to changes in foot placement, but contributions from the stance plantarflexors would be negligible. We also hypothesized that the stance gluteus medius would contribute to changes in mediolateral GRFs and frontal plane external moment following the perturbations.

2. Methods

2.1. Experimental data

Kinematic and kinetic data from ten young healthy participants (six female, mass = 64 ± 13 kg, age = 25.6 ± 3.8 years) were used to create the musculoskeletal models and simulations. Data collection methods are described in detail in Brough et al. (2021). All participants provided informed consent in accordance with the Institutional Review Board of the University of Texas at Austin. Each participant performed 10 treadmill walking trials which included two medial and two lateral perturbations of 15 N over 180 ms, produced by bursts of air exiting laterally and medially directed nozzles attached at the ankle. During randomized gait cycles, perturbations were applied to the left foot immediately before the estimated heel strike. Kinematic data were collected at 120 Hz using a 10-camera motion capture system (Vicon, Oxford, UK) and a full-body set of 65 reflective markers. Kinetic data were collected at 960 Hz from a split-belt instrumented treadmill (Motek, Amsterdam, NL). Kinematically representative medially perturbed, laterally perturbed and unperturbed gait cycles at each participant's self-selected speed (group average: 1.33 ± 0.14 m/s) were selected using a functional depth method (Sangeux and Polak, 2015) for further analysis, resulting in a total of thirty simulations.

Table 1
Muscle analysis groups.

Name	Abbreviation	Muscles Included
Iliopsoas	IL	Iliacus, Psoas
Adductors	ADD	Adductor Longus, Adductor Brevis, Pectineus, Quadratus Femoris, Superior, Middle and Inferior Adductor Magnus
Erector Spinae	ERSPIN	Erector Spinae
Internal Obliques	INTOB	Internal Obliques
Rectus Femoris	RF	Rectus Femoris
Gluteus Medius	GMED	Anterior and Middle Gluteus Medius, Anterior and Middle Gluteus Minimus, Posterior Gluteus Medius, Posterior Gluteus Minimus
Biarticular Hamstrings	HAM	Semimembranosus, Semitendinosus, Biceps Femoris Long Head, Gracilis
Gastrocnemius	GAS	Medial Gastrocnemius, Lateral Gastrocnemius
Soleus	SOL	Soleus, Tibialis Posterior, Flexor Digitorum Longus
Tibialis Anterior	TA	Tibialis Anterior
Vasti	VAS	Vastus Intermedius, Vastus Lateralis, Vastus Medialis
Tensor Fasciae Latae	TFL	Tensor Fasciae Latae

2.2. Musculoskeletal models and simulations

Simulations were performed in OpenSim 4.1, using a generic model with 23 degrees of freedom and 92 musculotendon actuators (Delp et al., 2007; Seth et al., 2018). The body segment and muscle–tendon lengths of the generic model were scaled to fit the anthropometry of each participant using the positions of markers on anatomical landmarks during a static trial (Delp et al., 2007). After model scaling, an inverse kinematics analysis determined joint angles by minimizing the difference between experimental marker data and model body segment markers. Experimental GRFs were applied to the calcaneus segments and a residual reduction algorithm (RRA) reduced dynamic inconsistencies between the model and experimental data (Delp et al., 2007). Static optimization was then used to estimate muscles forces that reproduced joint accelerations while minimizing the sum of muscle activations squared. Muscles were combined into groups with similar biomechanical functions for further analysis (Table 1).

2.3. Muscle contributions to balance strategies

To quantify muscle contributions to foot placement, a segment power analysis (Fregly and Zajac, 1996) was used to determine mediolateral musculotendon power delivered to the foot segment relative to the pelvis (Roelker et al., 2019), which was integrated over the first and second recovery swing phases following the perturbation (Fig. 1) to determine each muscle's net mechanical work done on the foot in each phase. To quantify muscle contributions to the mediolateral GRF, muscle contributions to COM mediolateral acceleration were calculated over stance. A segment power analysis was also used to determine muscle contributions to mediolateral power to control the trunk.

Muscle contributions to the net external moment in the frontal plane were calculated to determine their overall contribution to balance control as:

$$\dot{\vec{H}} = \vec{r} \times \vec{F}_{GRF} = \vec{M}_{EXT} \tag{1}$$

where $\dot{\vec{H}}$ is the time rate of change of whole-body angular momentum, $\vec{r}$ is the moment arm between the body COM and the center of pressure, $\vec{F}_{GRF}$ are the ground reaction forces, and $\vec{M}_{EXT}$ is the external moment (Neptune and McGowan, 2016). To help quantify changes in subsequent steps following the perturbations, spatiotemporal measures including stance time and step width were also calculated during the representative gait cycles.

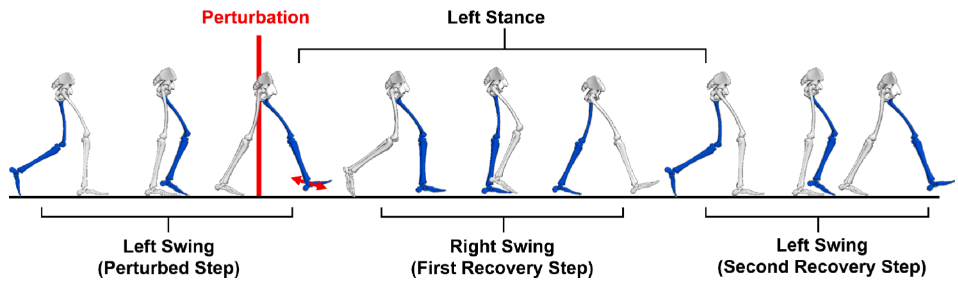

Fig. 1. Gait phases during and after the foot placement perturbation. The perturbed (left) leg is shaded. Muscle contributions to foot placement were analyzed during the first and second recovery steps after the perturbation, while muscle contributions to GRFs, torso power, and external moment were analyzed during the left stance phase following the perturbation.

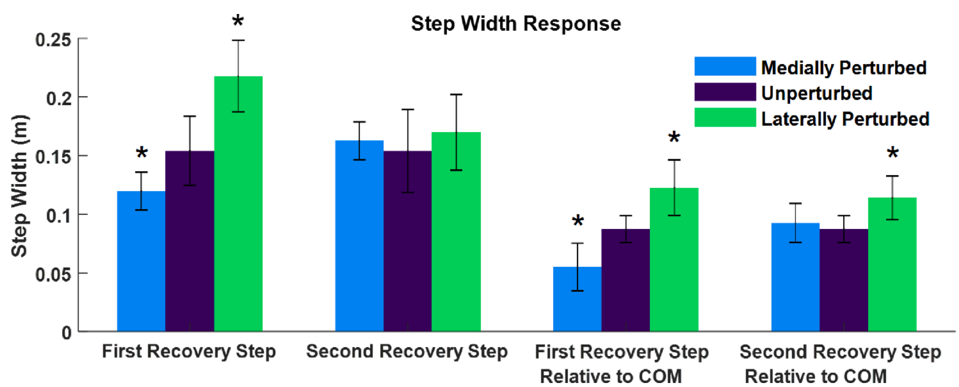

Fig. 2. Step widths in the first and second recovery steps after the perturbed step relative to the opposite foot and relative to the center of mass. '*' indicates that the step is significantly wider or narrower than unperturbed steps ($p < 0.025$).

2.4. Statistical analysis

Paired t-tests were used to assess changes in the summary dependent measures (step width, stance time, muscle work on foot placement) between unperturbed and medially perturbed gait cycles and between unperturbed and laterally perturbed gait cycles. Differences in continuous variables over time (muscle contributions to mediolateral GRFs, trunk power and frontal plane external moments) were assessed using one-dimensional statistical parametric mapping parallel of a paired *t*-test (Pataky, 2012), which identified normalized time points where variables from medial or laterally perturbed gait cycles differed significantly from the corresponding variables from unperturbed gait cycles. A Bonferroni correction was used to correct for multiple comparisons, resulting in a significance level of $\alpha = 0.025$.

3. Results

3.1. Spatiotemporal

Participants took a 3.4 ± 2.7 cm narrower step relative to the perturbed foot following medial perturbations ($p = 0.003$) and a 6.4 ± 3.3 cm wider step in the first recovery step following lateral perturbations ($p < 0.001$) compared to unperturbed steps (Fig. 2). Relative to the COM position, participants had a 3.2 ± 1.5 cm narrower step in the first recovery step following medial perturbations ($p < 0.001$) and a 3.5 ± 1.9 cm wider step following lateral perturbations ($p < 0.001$) compared to unperturbed steps (Fig. 2). In the second recovery step following medial perturbations, step width relative to the COM was not significantly different. However, in the second step following lateral perturbations foot placement relative to the COM was still 2.7 ± 2.3 cm wider compared to unperturbed steps ($p = 0.005$). Participants had a 32 ± 22 ms longer stance time following medial perturbations ($p = 0.001$) and 33 ± 19 ms shorter stance time following lateral perturbations ($p < 0.001$).

3.2. Muscle contributions to foot placement

3.2.1. Medial perturbations

Following medial perturbations, the swing gluteus medius did 15 ± 17% less lateral work on the foot relative to the pelvis only during the second recovery step (p < 0.001) (Fig. 3B). The swing erector spinae did 39 ± 33% and 37 ± 15% less lateral work on the foot during the first ($p = 0.01$) and second ($p < 0.001$) recovery steps, respectively (Fig. 3A & B). The stance iliopsoas did less 181 ± 118% less lateral work on the foot during the first recovery step ($p < 0.001$)(Fig. 3A). The stance erector spinae did 45 ± 26% and 27 ± 29% less medial work after the first ($p = 0.003$) and second ($p = 0.009$) recovery steps, respectively (Fig. 3A & B). No significant changes to work done by the swing internal obliques, tibialis anterior, iliopsoas, hamstrings, adductors, or stance gluteus medius were observed during either recovery step following medial perturbations (Fig. 3A & B). The net muscle work done on the foot relative to the pelvis was unchanged during the first recovery step and 28 ± 14% less medial during the second recovery step ($p = 0.006$) (Fig. 3A & B).

3.2.2. Lateral perturbations

Following lateral perturbations, the swing gluteus medius did 57 ± 50% and 55 ± 27% more lateral work on the foot relative to the pelvis during the first ($p = 0.004$) and second ($p < 0.001$) recovery steps, respectively (Fig. 3A & B). The swing erector spinae did 22 ± 38% more lateral work on the foot only during the first recovery step ($p = 0.01$) (Fig. 3A). The internal obliques did 28 ± 37% and 38 ± 65% more lateral work during the first ($p = 0.001$) and second ($p = 0.025$) recovery steps, respectively (Fig. 3A & B). The swing tibialis anterior did 121 ± 186% more lateral work only during the second recovery step ($p = 0.009$)(Fig. 3B). The swing hamstrings did 30 ± 55% more medial work during the second recovery step ($p = 0.017$) (Fig. 3B). The swing adductors performed 7 ± 30% and 17 ± 19% more medial work during the

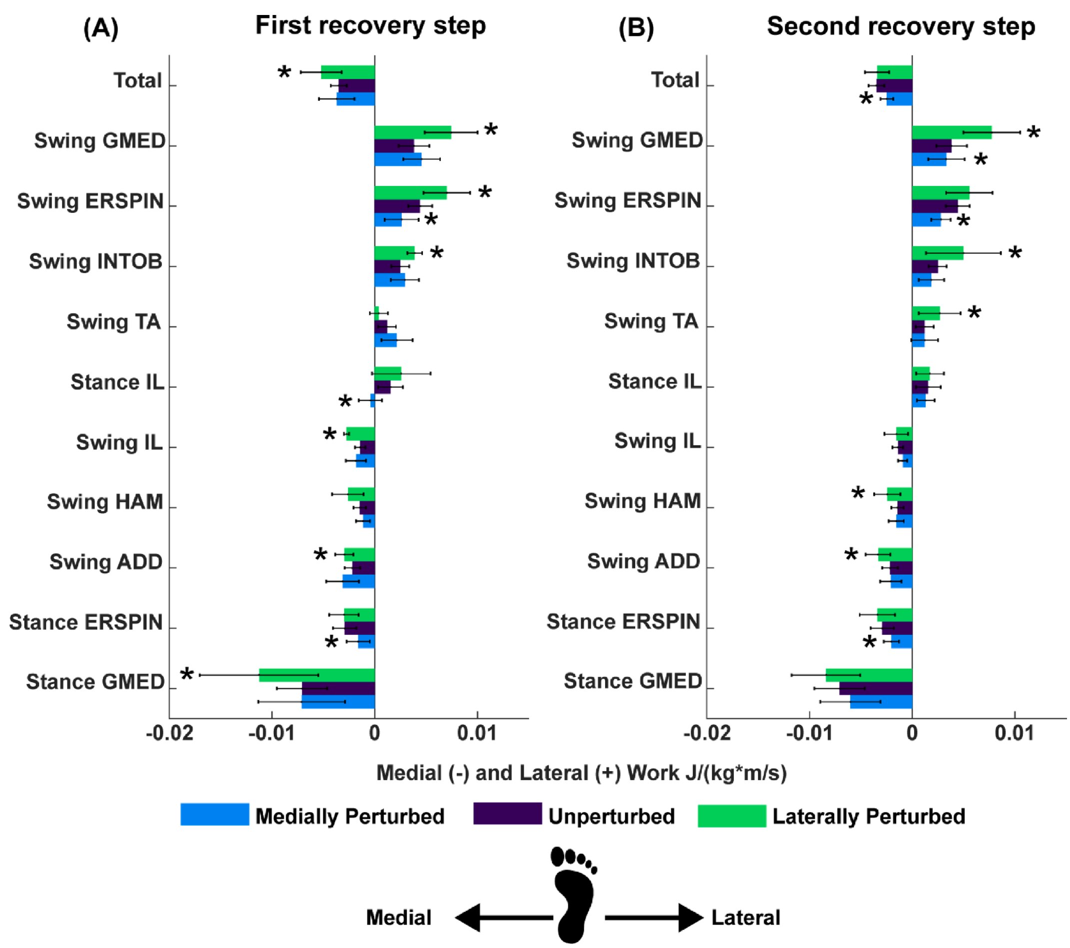

Fig. 3. Primary contributors to muscle work on medial (−) and lateral (+) foot placement relative to the pelvis during swing. Error bars represent one standard deviation. Muscles are ordered from most medial to most lateral work on average from all the gait cycles analyzed. Stance muscles are on the stance leg side, while all other muscles are on the swing leg side. '*' indicates a significant difference between the perturbed and unperturbed condition ($p < 0.025$).

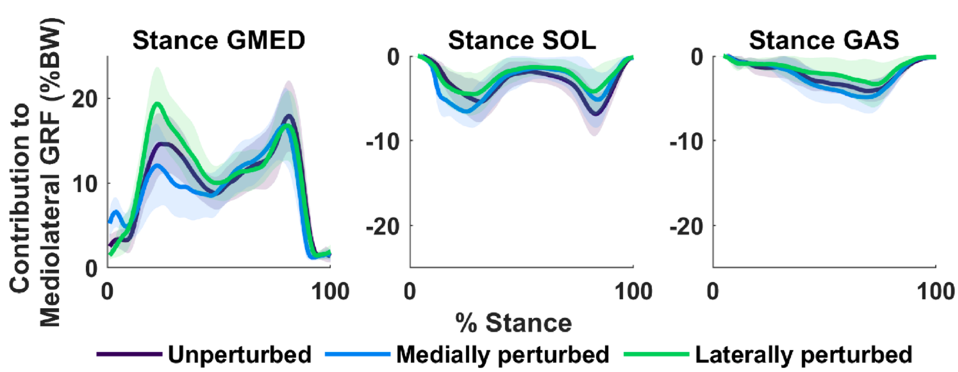

Fig. 4. Muscle contributions to the mediolateral GRFs during the stance phase immediately following the medial and lateral perturbations for the three major contributors to the mediolateral GRF.

first ($p = 0.025$) and second ($p < 0.001$) recovery steps, respectively (Fig. 3A & B). Finally, the stance gluteus medius performed 61 ± 50% more medial work on the foot only during the first recovery step ($p = 0.018$)(Fig. 3A). There were no changes in work performed by the stance erector spinae. The net muscle work done on the foot relative to the pelvis was 47 ± 37% more medial during the first recovery step and unchanged during the second recovery step (Fig. 3A & B). For all muscle contributions to foot placement, see Table A1 in the Appendix.

3.3. Muscle contributions to mediolateral GRFs

There were no differences in muscle contributions to mediolateral GRFs in the stance phase following medial or lateral perturbations from the major muscle contributors (Fig. 4).

3.4. Muscle contributions to mediolateral trunk power

The stance leg soleus power delivered to the trunk increased briefly in early stance following medial perturbations ($p < 0.001$) and swing

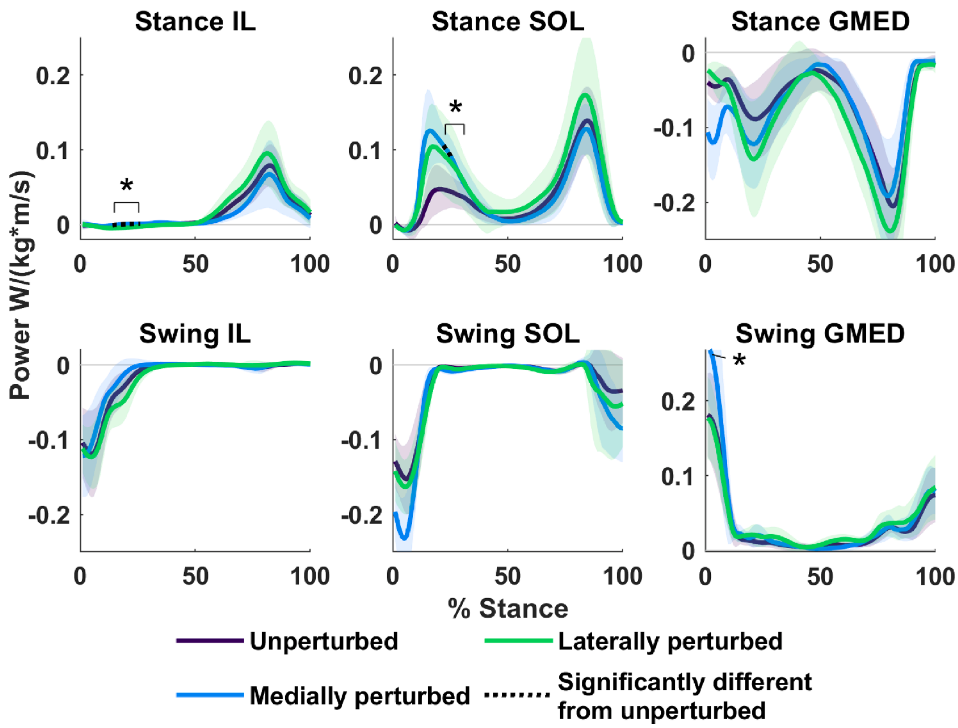

Fig. 5. Individual muscle power delivered to the torso during the stance phase following medial and lateral perturbations from the six primary contributors to torso power. '*' and a dotted line indicate the period where the power after medial or lateral perturbations is significantly different from the unperturbed power ($p < 0.025$).

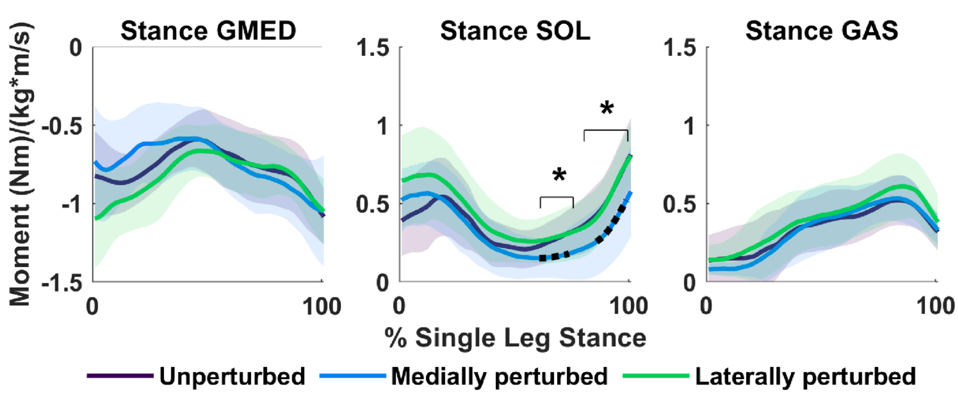

Fig. 6. Individual muscle contributions to the frontal plane external moment during the stance phase immediately following medial and lateral perturbations for the three primary contributors to frontal plane angular momentum. '*' and a dotted line indicate a period where the external moment after medial or lateral perturbations is significantly different from the unperturbed external moment ($p < 0.025$).

leg gluteus medius power increased briefly during the first double support phase ($p = 0.012$) (Fig. 5).

3.5. Muscle contributions to frontal plane external moment

Following medial perturbations, there was a decrease in soleus contributions to the frontal plane external moment during the second half of single leg stance compared to unperturbed steps ($p < 0.001$) (Fig. 6). There were no changes in muscle contributions to the frontal plane external moment between laterally perturbed and unperturbed steps.

4. Discussion

The purpose of this study was to investigate individual muscle contributions to balance control and recovery strategies following medial and lateral foot placement perturbations. Specifically, we determined muscle contributions to foot placement, mediolateral GRFs, trunk mechanical power and the frontal plane external moment after medially and laterally perturbed steps compared to unperturbed steps.

4.1. Muscle contributions to foot placement during swing

Participants took narrower and wider steps following medial and lateral perturbations, respectively (Fig. 2), which is consistent with previous work using similar foot placement perturbations (Segal and Klute, 2014). However, the net muscle work done on the foot during swing was more medial after lateral perturbations during the first recovery step, and less medial after medial perturbations during the second recovery step (Fig. 3), suggesting that changes in step width were not due to active muscle control. Alternatively, because foot placement control depends on trailing leg position relative to the COM (Rankin

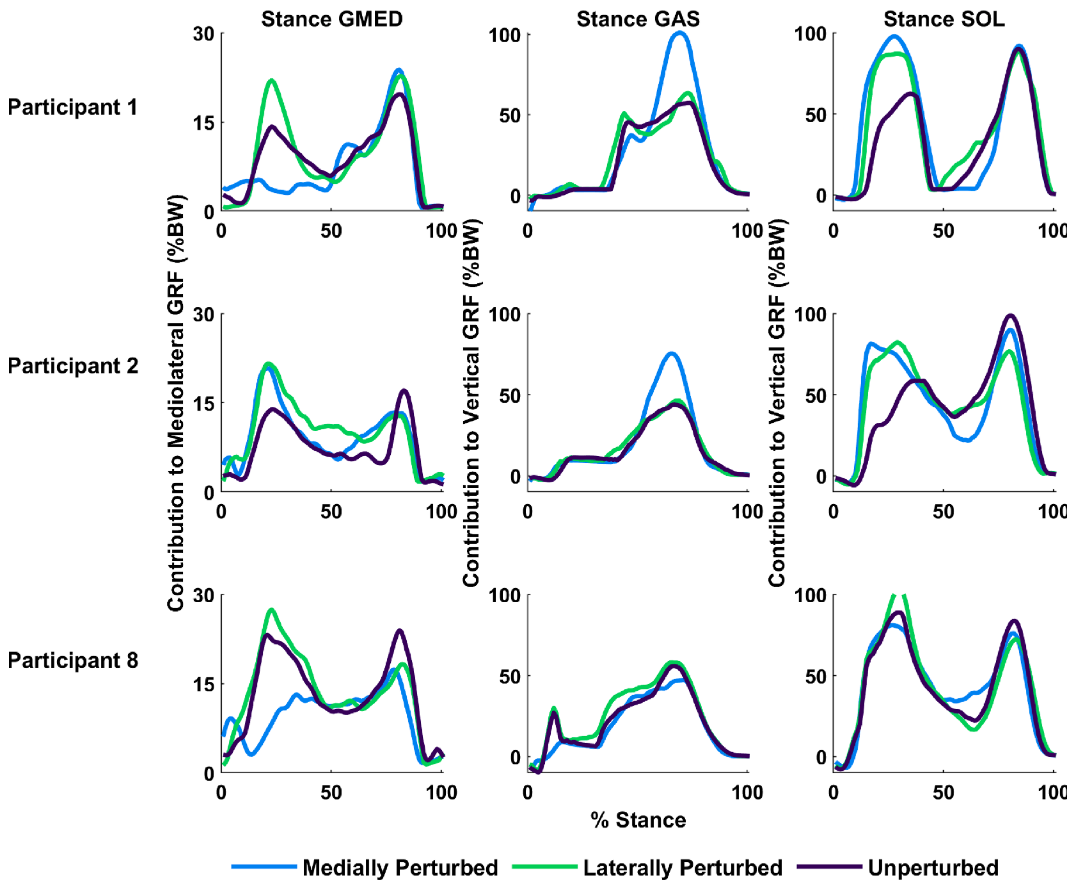

Fig. 7. Muscle contributions to mediolateral and vertical GRFs from primary muscle contributors for three participants with different balance response strategies.

et al., 2014), small changes to mediolateral COM position caused by the perturbations may cause muscles to bring the swing leg more medial after lateral perturbations and more lateral after medial perturbations.

We hypothesized that the stance gluteus medius but not the stance plantarflexors would contribute to changes in foot placement following the perturbations. This hypothesis was partially supported. As hypothesized, the stance plantarflexors did not contribute to changes in foot placement while the stance gluteus medius did more medial work on the foot after lateral perturbations. However, there were no changes from the stance gluteus medius after medial perturbations (Fig. 3A). The swing leg gluteus medius also did more lateral work on the foot after lateral perturbations. These results align with other studies demonstrating the importance of the swing and stance gluteus medius in controlling foot placement during swing (Afschrift et al., 2018; Hof and Duysens, 2013; Rankin et al., 2014; Stokes et al., 2017).

A noteworthy result was the role of the trunk muscles in modulating foot placement during swing (Fig. 3). A lack of trunk control predicts poor balance and walking performance (Verheyden et al., 2006), and because of the significant trunk mass, trunk movement accounts for a large portion of whole-body angular momentum (e.g. Begue et al., 2021). However, it appears that trunk control also influences balance control by affecting foot placement. Previous work found increases in trunk muscle activity along with concurrent increases in gluteus medius activity after mediolateral perturbations to optical flow, suggesting that a postural adjustment was made by the trunk muscles, and the gluteus medius then compensated for changes in foot placement caused by the postural adjustment (Stokes et al., 2017). Our results support the existence of a concurrent trunk and foot placement response, as there were changes in the work done by trunk muscles on the foot following the perturbations, but not always in the direction of the net change in muscle work. Thus, other muscles may have coordinated a response with the trunk muscles to facilitate appropriate foot placement.

In agreement with previous work (Roelker et al., 2019), the swing gluteus medius, erector spinae and internal obliques were primary contributors to lateral work on the foot relative to the pelvis and the stance gluteus medius and erector spinae were primary contributors to medial work on the foot relative to the pelvis. However, unlike Roelker et al. (2019), we found that the stance leg plantarflexors performed very little work on the foot and the swing iliopsoas was also a relatively small contributor. Differences between these studies may be attributed to participant age (25.6 ± 3.8 versus 53.7 +/- 8.7 years) and walking speed (1.33 ± 0.14 m/s versus to 0.8 +/- 0.3 m/s), as we found that these results did not depend on whether static optimization (present study) or computed muscle control (Roelker et al., 2019) methods estimated muscle activations. In addition, there was considerable variability in stance plantarflexor contributions to mediolateral foot work among the participants in Roelker et al. (2019), with some having low contributions similar to the present study.

4.2. Muscle contributions to mediolateral GRF during stance

We hypothesized that the stance leg gluteus medius would contribute to changes in the mediolateral GRF following perturbations. We found that the stance gluteus medius, gastrocnemius and soleus were primary contributors to mediolateral GRFs in agreement with previous work (John et al., 2012; Pandy et al., 2010). However, while the gluteus medius contributions to mediolateral GRFs trended lower after medial perturbations and higher after lateral perturbations in early single leg stance as expected (Fig. 4), these reactions were not statistically significant and there was substantial variability between participants. We also considered changes in muscle contributions to trunk power, which like mediolateral GRFs, were largely insignificant. Thus, while we

Table A1
Muscle mechanical work done on medial and lateral foot placement relative to the pelvis during swing in J/(kg*m/s) × 10^{-3}. Medial work relative to the pelvis is negative and lateral work relative to the pelvis is positive. Significant differences between perturbed and unperturbed steps are bolded.

		First recovery step				Second recovery Step			
Muscle	Unperturbed	Medially Perturbed	*p-value*	Laterally Perturbed	*p-value*	Medially Perturbed	*p-value*	Laterally Perturbed	*p-value*
Stance GMED	−6.5 ± 2.3	−6.6 ± 3.9	0.955	−10.4 ± 5.5	**0.018**	−5.7 ± 2.8	0.280	−7.9 ± 3.2	0.075
Stance ERSPIN	−3.0 ± 1.2	−1.6 ± 1.1	**0.003**	−3.0 ± 1.4	0.942	−2.1 ± 0.8	**0.009**	−3.5 ± 1.7	0.253
Swing ADD	−2.2 ± 0.8	−3.1 ± 1.6	0.120	−3.0 ± 0.9	**0.025**	−2.1 ± 1.0	0.689	−3.4 ± 1.2	**0.000**
Swing HAM	−1.5 ± 0.6	−1.1 ± 0.7	0.105	−2.6 ± 1.5	0.033	−1.6 ± 0.7	0.557	−2.5 ± 1.3	**0.017**
Swing IL	−1.4 ± 0.5	−1.8 ± 1.0	0.176	−2.7 ± 0.2	**0.000**	−1.0 ± 0.5	0.034	−1.6 ± 1.2	0.609
Stance INTOB	−1.2 ± 0.6	−1.0 ± 0.5	0.458	−1.8 ± 1.4	0.105	−0.9 ± 0.3	0.080	−1.2 ± 0.5	0.730
Swing SOL	−0.8 ± 0.6	−1.5 ± 1.2	0.129	−0.3 ± 0.6	0.079	−0.8 ± 0.9	0.848	−1.9 ± 1.7	**0.018**
Swing RF	0.7 ± 0.3	0.6 ± 0.5	0.738	1.0 ± 0.6	0.164	0.6 ± 0.4	0.434	1.1 ± 0.4	**0.000**
Stance GAS	1.0 ± 1.1	1.3 ± 1.5	0.430	2.1 ± 2.0	**0.011**	1.5 ± 1.3	0.321	0.5 ± 1.2	0.382
Stance IL	1.6 ± 1.2	−0.4 ± 1.1	**0.000**	2.6 ± 2.8	0.125	1.3 ± 0.9	0.586	1.7 ± 1.4	0.669
Swing TA	1.2 ± 0.9	2.2 ± 1.5	0.119	0.4 ± 0.9	0.084	1.2 ± 1.3	0.993	2.7 ± 2.0	**0.009**
Swing INTOB	2.5 ± 0.9	2.9 ± 1.4	0.355	3.9 ± 0.7	**0.001**	1.9 ± 1.3	0.056	5.1 ± 3.7	**0.025**
Swing ERSPIN	4.5 ± 1.2	2.6 ± 1.7	**0.010**	7.0 ± 2.3	**0.001**	2.8 ± 1.0	**0.000**	5.6 ± 2.3	0.028
Swing GMED	3.3 ± 1.4	4.1 ± 1.7	0.288	6.4 ± 2.5	**0.004**	3.0 ± 1.7	0.156	7.4 ± 2.9	**0.000**

previously found a clear decrease in mediolateral GRFs following medial perturbations and increase after lateral perturbations (Brough et al., 2021), individual muscle contributions to changes in mediolateral GRFs were not as clear.

4.3. Muscle contributions to frontal plane external moment

While contributions from the stance leg gluteus medius to the external moment (i.e., the time rate of change of whole-body angular momentum) in the frontal plane trended towards decreasing after medial perturbations and increasing after lateral perturbations during single leg stance, which mirrored their contributions to the mediolateral GRF, these results were not significant and not all participants used this response (Fig. 6). Interestingly, only the soleus had a significantly different contribution to the external moment following medial perturbations. This was despite the altered mediolateral moment arm resulting from both medial and lateral perturbations, possibly because after corresponding center of pressure and COM adjustments, the moment arm was similar to that of unperturbed walking.

4.4. Individual responses

Previously, we showed that on average, participants responded to medial perturbations with lateral ankle and hip strategies and lateral perturbations with a lateral ankle strategy, but neither perturbation produced a significant plantarflexor strategy (Brough et al., 2021). However, in a post-hoc analysis we observed distinct balance recovery strategies that did not conform to the average responses. For example, Subject 1 used the expected hip adduction strategy after medial perturbations to reduce the mediolateral GRF, but also increased the gastrocnemius contribution to the vertical GRF and also demonstrated a hip response after lateral perturbations (Fig. 7). Subject 2 did not use the expected hip strategy after medial perturbations, instead increasing the gastrocnemius contribution to the vertical ground reaction force. Subject 8 demonstrated the expected response of a hip adduction strategy after medial perturbations and minimal stance leg changes after medial perturbations. Subjects 1 and 2 also had increased soleus contributions to the vertical GRF after both medial and lateral perturbations during early stance, which may reflect a reflex response to stiffen the joint. Future work is needed to further understand why young, healthy participants would choose different balance recovery strategies, as we found they were not predicted by subject mass or walking speed.

4.5. Limitations

A limitation to this study is that the generalizability of our results is limited by the number of subjects and steps analyzed per subject. Despite choosing kinematically representative gait cycles for each participant, there was significant variability in outcome measures between and within participants. A post hoc analysis of additional perturbed gait cycles for one participant suggested that while outcome measures follow similar trends across gait cycles, the same participant may not always use the same balance recovery strategies. However, even with only one gait cycle per participant per condition (30 simulations total), we were able to identify clear and statistically significant trends in the data. Another limitation is that the low number of trunk muscles in this model limits our ability to deduce the individual roles of trunk muscles in foot placement and balance control. However, like previous work on muscle contributions to trunk acceleration (Klemetti et al., 2014), we can interpret the roles of the internal obliques and erector spinae as the net effect of all the trunk muscles. Finally, while scaling generic models from marker data can affect the accuracy of muscle moment arms, the functional roles of muscles during walking simulations are robust to moment arm errors (Correa et al., 2011). Thus, we do not believe that limitations in model scaling influenced our conclusions.

5. Conclusions

In summary, muscle work on the foot was less medial during the second recovery step following medial foot placement perturbations and more medial during the first recovery step following lateral perturbations, despite opposite changes in foot placement. There were no significant changes in muscle contributions to mediolateral ground reaction forces, trunk power, or frontal plane external moment, although we observed a number of different balance recovery strategies among participants. These results suggest that changes in foot placement were not due to active muscle control alone, and that the trunk muscles play a multifaceted role in maintaining balance.

CRediT authorship contribution statement

Lydia G. Brough: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Richard R. Neptune:** Conceptualization, Supervision, Resources, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing .

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Table A1.

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