Individual muscle contributions to lower-limb joint quasi-stiffness during steady-state healthy walking

Stephanie L. Molitor , Richard R. Neptune *

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

ARTICLE INFO

ABSTRACT

Maintaining appropriate lower-limb joint stiffness is critical for walking performance, as it facilitates tasks such as absorbing impact loading, maintaining balance, and providing body support and propulsion. Quasi-stiffness, an indirect measure describing the joint moment–angle relationship, is often used to assess joint stiffness during walking as it accounts for passive soft tissue stiffness and active muscle force generation. Thus, identifying the primary muscle contributors to joint moments and angles can elucidate how muscles are coordinated to maintain quasi-stiffness. However, determining individual muscle contributions experimentally is challenging. Therefore, the objective of this study was to use musculoskeletal modeling and simulation to identify individual muscle contributions to sagittal-plane quasi-stiffness during walking. Simulations of 15 healthy young adults were developed and individual muscle contributions to joint moments and angles were determined within discrete phases of the gait cycle. As expected, contributors to ankle, knee and hip moments were the primary dorsiflexors/plantarflexors, knee flexors/extensors, and hip flexors/extensors, respectively, as these muscles cross the joint and directly contribute to their respective joint moments. However, major contributors to the joint angles also included distant and contralateral muscles. Specifically, the hip extensors and ankle dorsiflexors were found to contribute to the knee angle (8.4–19.7% and 9.0–17.1% of total muscle contributions, respectively), while contralateral hip extensors were found to contribute (16.6–27.2%) to the hip angle. These results highlight the role of distant muscles in maintaining quasi-stiffness, and provide a foundation for developing rehabilitation strategies and assistive devices to target stiffness impairments in clinical populations.

1. Introduction

Maintaining sufficient joint stiffness is critical for successfully performing locomotor tasks, with healthy individuals able to modulate dynamic joint stiffness for different task demands (e.g., Bayram and Bayram, 2018; Collins et al., 2018; Kern et al., 2019). Previous research with lower-limb prostheses has further highlighted the influence of joint stiffness on specific biomechanical outcomes of walking. For example, studies have found that decreased prosthetic ankle–foot stiffness was associated with improved balance control during turning (Shell et al., 2017) and reduced impact loading during straight-line walking (Major et al., 2014). Others have likewise noted that individuals feel more stable during weight acceptance with a more compliant prosthesis (Perry et al., 1997). Previous studies have also identified prosthetic ankle–foot stiffness values that improve kinematic symmetry (Clites et al., 2021) and reduce metabolic cost (Zelik et al., 2011). Although

investigations of prostheses have elucidated the role of overall joint stiffness in locomotor performance, it is not clear how individual muscles modulate joint stiffness in healthy walking.

Previous studies have correlated muscle activity of the tibialis anterior, soleus and gastrocnemius with ankle quasi-stiffness during walking (e.g., Sekiguchi et al., 2018, Sekiguchi et al., 2015). However, surface electromyography (EMG) cannot elucidate causal relationships (Zajac et al., 2002) of how individual muscles contribute to quasi-stiffness. Furthermore, these studies did not explore distant and contralateral muscles, which can influence joint angles and resulting quasi-stiffness through dynamic coupling (Zajac and Gordon, 1989; Zajac et al., 2002).

Quasi-stiffness is an indirect, mechanics-based measure that is often used to assess dynamic joint stiffness during walking tasks (Collins et al., 2018; Crenna and Frigo, 2011; Gabriel et al., 2008; Hansen et al., 2004; Safaeepour et al., 2014; Shamaei et al., 2013a). Quasi-stiffness is

---

* 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: rneptune@mail.utexas.edu (R.R. Neptune).

determined experimentally by evaluating the slope of joint moment–angle loops during discrete phases of the gait cycle (Crenna and Frigo, 2011; Davis and DeLuca, 1996; Hansen et al., 2004; Shamaei et al., 2013a). As such, quasi-stiffness does not necessarily describe the capacity of the system to store elastic energy, but instead describes the resistance of the joint to motion in the presence of an applied force, which captures the combined resistance from passive soft tissues and active muscle force generation (Davis and DeLuca, 1996; Latash and Zatsiorsky, 1993; Rouse et al., 2013). Quasi-stiffness has been used in developing assistive devices (e.g., orthoses and prostheses) that augment or mimic biological joint mechanics (Au and Herr, 2008; Caputo and Collins, 2013; Nigro and Arch, 2023). Therefore, an increased understanding of how individual muscles contribute to quasi-stiffness during healthy walking can help inform the prescription of devices for individuals based on their specific muscle impairments. Furthermore, elucidating individual muscle contributions to quasi-stiffness during healthy walking can help identify how neuromuscular impairments may compromise quasi-stiffness and inform targeted rehabilitation strategies to restore healthy walking mechanics.

Previous forward dynamics simulations of walking with altered passive hip stiffness identified distant compensations such as increased work by the soleus to restore healthy gait patterns (Goldberg and Neptune, 2007). However, modifying passive joint stiffness alone does not account for altered muscle force generation (e.g., Lee et al., 2019), whereas quasi-stiffness captures joint-level mechanics that include both passive and active forces. Although it is important to recognize compensatory strategies that result from altered joint stiffness, it is not clear which muscles contribute to stiffness impairments, which would be useful for identifying targets to directly improve impaired joint mechanics rather than facilitating compensatory responses. Previous work investigating foot placement found that muscles on the contralateral limb contributed to foot trajectories (Roelker et al., 2019), suggesting that distant and contralateral muscles may likewise modulate quasi-stiffness through their influence on joint angles. Thus, more research is needed to determine 1) *which* muscles contribute to lower-limb joint quasi-stiffness, and 2) *how* agonist and antagonist muscles are coordinated to provide quasi-stiffness (e.g., through joint moment versus joint angle modulation).

Neuromusculoskeletal modeling and simulation provides a computational framework for estimating muscle forces and determining biomechanical functions that cannot be measured experimentally (e.g., Zajac et al., 2002, 2003; Seth et al., 2018). Musculoskeletal modeling not only allows identification of individual muscle contributions to the net joint moment (e.g., Kipp et al., 2022), but also individual muscle contributions to joint angles (Anderson et al., 2004), both of which are critical to determining contributions to quasi-stiffness. The objective of this study was to use modeling and simulation to determine individual muscle contributions to sagittal-plane ankle, knee and hip quasi-stiffness during healthy walking in order to help identify how specific muscle impairments may lead to dysregulated quasi-stiffness in clinical populations. While we expected that that the primary contributors to ankle, knee and hip quasi-stiffness would be the muscles that cross each joint and directly contribute to respective net joint moments, we also expected distant and contralateral muscles to contribute to quasi-stiffness by modulating joint angles through dynamic coupling. Understanding how lower-limb joint quasi-stiffness is modulated in healthy walking will establish a framework for future studies investigating contributions to quasi-stiffness for individuals with altered neuromotor control and during other locomotor tasks. Furthermore, this work will serve as a foundation for developing assistive devices and rehabilitation strategies to improve stiffness impairments in clinical populations.

2. Methods

2.1. Experimental data

Previously collected kinematic, kinetic and EMG data (for additional details, see Molina et al., 2023) were used to create musculoskeletal models and simulations. Fifteen healthy young adults (8 female; age: 25 $\pm$ 4 years; height: 169 $\pm$ 13 cm; mass: 69 $\pm$ 12 kg) completed 30-second walking trials on a split-belt instrumented treadmill while walking at their self-selected speed. Three-dimensional ground reaction forces (GRF) and full-body kinematic data were collected. EMG data were collected bilaterally from the following muscles: medial gastrocnemius, soleus, tibialis anterior, rectus femoris, vastus medialis, biceps femoris, semitendinosus and gluteus medius. For each subject, we determined a representative step (heel contact to ipsilateral toe-off; gait events determined using vertical GRFs) for the simulation analyses using a functional median depth method (Sangeux and Polak, 2015) based on GRF and kinematic profiles.

2.2. Musculoskeletal model and simulation

We scaled a full-body musculoskeletal model with 23 degrees of freedom and 92 musculotendon actuators to fit the anthropometry of each participant using OpenSim 4.4 (Delp et al., 2007; Seth et al., 2018). An inverse kinematics (IK) analysis determined joint angles throughout the simulated step by solving a weighted least squares problem to minimize differences between experimental and model marker trajectories (average RMS error: 1.3 cm). We iteratively used a residual reduction algorithm (RRA) to make small adjustments to the center-of-mass position, segment mass distributions and kinematics from IK to reduce dynamic inconsistences with experimental GRF data (Delp et al., 2007), while ensuring that residual forces and kinematic errors were below recommended thresholds (Hicks et al., 2015).We then used computed muscle control (CMC) to estimate the muscle excitations that track the joint kinematics while applying the GRFs to the center-of-pressure of each foot (Thelen et al., 2003; Thelen and Anderson, 2006). Resulting simulated muscle activations from CMC were compared against experimental EMG data to ensure that the muscles were generating force at appropriate times. When necessary, excitation constraints (e.g., timing and/or magnitude bounds informed by the experimental EMG data) were added to the CMC actuators to better match the simulated muscle activity with the experimental EMG patterns.

Given that quasi-stiffness characterizes the relationship between the net joint moment and joint angle during discrete phases of the gait cycle, we determined individual muscle contributions to sagittal-plane ankle, knee and hip net joint moments as well as individual muscle contributions to the joint angles for previously defined quasi-stiffness phases (Table 1, Fig. 1).

Table 1

Muscle contributions to the net joint moment and angle were computed for previously-defined quasi-stiffness phases (Molitor and Neptune, 2024). Approximate timing for each phase is reported with respect to a full gait cycle (i. e., ipsilateral heel-contact to its subsequent heel-contact).

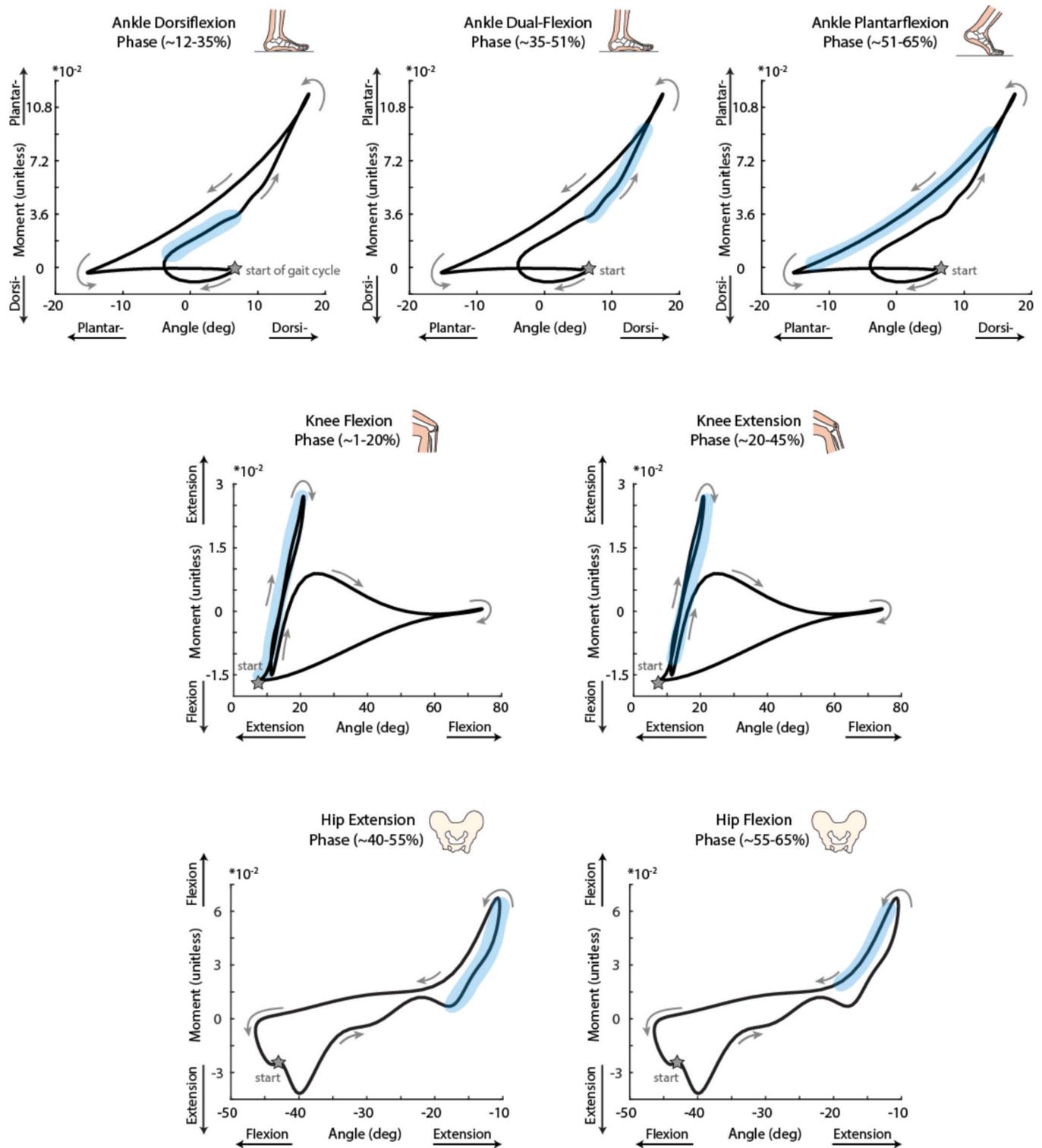| Joint	Phase	Approximate % Gait Cycle
Ankle	Dorsiflexion	12–35%
	Dual-Flexion	35–51%
	Plantarflexion	51–65%
Knee	Flexion	1–20%
	Extenison	20–45%
Hip	Extension	40–55%
	Flexion	55–65%

Fig. 1. Quasi-stiffness phases for the ankle (top row), knee (middle row) and hip (bottom row) as defined in Molitor and Neptune (2024).

2.3. Individual muscle contributions to net joint moments

To determine individual muscle contributions to sagittal-plane ankle, knee and hip net joint moments, we multiplied the instantaneous force generated by each muscle (estimated from CMC) by its instantaneous moment arm about the given joint (based on the kinematic state of the model) throughout each phase (Table 1) of the simulated walking step (Kipp et al., 2022). Using a custom MATLAB script, we summed individual muscle moments within functional groups (Table 2) to determine contributions of each group to the net joint moment. We also compared the summed muscle moments from all 92 musculotendon actuators against the net joint moments determined through an inverse dynamics analysis (error range: 1.38–2.49 Nm) to ensure the accuracy of the joint moment decomposition.

Table 2

Muscle group definitions. Individual muscle contributions to net joint moments and angles were combined within functional groups.

Muscle group	Muscles
GMAX	Superior, middle, and inferior gluteus maximus
GMED	Anterior, middle, and posterior gluteus medius
GMIN	Anterior, middle, and posterior gluteus minimus
RF	Rectus femoris
VAS	Vastus intermedius, vastus lateralis, vastus medialis
IL	Iliacus, psoas
TA	Tibialis anterior
SOL	Soleus
GAS	Lateral gastrocnemius, medial gastrocnemius
PER	Peroneus longus, peroneus brevis
HAM	Biceps femoris longus, semimembranosus, semitendinosus
BFsh	Biceps femoris short head

2.4. Individual muscle contributions to joint angles

To determine individual muscle contributions to sagittal-plane ankle, knee and hip joint angles, we applied an induced position analysis similar to Anderson et al. (2004). We first performed an induced acceleration analysis (IAA) to identify contributions to joint acceleration due to gravitational forces, velocity-dependent forces (i.e., Coriolis and centripetal) and muscle forces (Hamner et al., 2010). Using a custom MATLAB script, we then integrated the accelerations twice within each phase of the gait cycle to determine the joint angle as a function of the muscle and external forces as well as the initial conditions (Eq. 1; from Anderson et al., 2004).

$$\vec{q}(t) = \underbrace{\vec{q}_0}_{\text{initial position}} + \underbrace{\dot{\vec{q}}_0(t - t_0)}_{\text{changes in position due to initial velocity}} + \underbrace{\sum_i \vec{q}_i}_{\text{induced positions due to applied forces}}$$

(1)

Initial joint position and velocity for each phase were determined from the IK analysis. Contributions to joint angles from all 92 musculotendon actuators, gravitational forces, velocity-dependent forces and initial conditions were summed for each phase. To confirm the accuracy of individual muscle contributions, we verified that for all joints and phases, the summed contributions to joint angles were within five degrees (range: 0.59–4.46 degrees) of the joint angles derived from IK. Muscles within each functional group (Table 2) were combined to determine contributions of each group to the joint angle.

2.5. Statistical analyses

Muscle moments were normalized by participant height and weight, and angles were converted to radians. We then rank-ordered each muscle group for its contribution (averaged across all subjects) to the net joint moment and angle components of quasi-stiffness for each phase of the gait cycle. Refer to the Supplementary Data for group-level descriptive statistics (mean ± standard deviation) and individual subject results. Primary muscle contributors to the net joint moments and angles were considered to be those that account for at least 5% of the total muscle contribution for each respective measure. Primary contributors are discussed (for muscle contributions below the 5% threshold, refer to the Supplementary Data).

3. Results

3.1. Muscle contributions to net joint moments and angles

3.1.1. Ankle

During the ankle Dorsiflexion (12–35% gait cycle), Dual-Flexion (35–51%) and Plantarflexion (51–65%) phases, the largest contributors to the net ankle moment and angle were the primary plantarflexors (SOL, GAS) and dorsiflexors (TA) (Figs. 2-4). Other notable contributors

to the ankle angle during all three phases were PER and GMED. During both the Dual-Flexion and Plantarflexion phases, IL was also a notable contributor to the ankle angle (Fig. 2B-C, Fig. 4).

3.1.2. Knee

During the Knee Flexion (1–20% gait cycle) and Extension phases (20–45%), VAS, RF and HAM were major contributors to the knee moment (Fig. 3&5). GAS also contributed to the knee moment for both phases, although its contribution was more notable during the Knee Extension phase. For both phases, VAS, GMAX, IL, TA and SOL were all notable contributors to the knee angle (Figs. 4-5). During the Knee Flexion phase, contralateral GMED and contralateral IL also contributed to the knee angle, as did ipsilateral HAM and PER (Fig. 5A). During the Knee Extension phase, ipsilateral GMED, GAS and BFsh contributed to the knee angle (Fig. 5B).

3.1.3. Hip

During the Hip Extension (40–55% gait cycle) and Flexion phases (55–65%), primary contributors to both the net hip moment and angle were IL and GMED (Figs. 3-4, Fig. 6). RF and HAM also contributed to the hip moment. For both phases, contralateral HAM and contralateral IL contributed to the hip angle. Ipsilateral SOL also contributed to the hip angle for the Hip Extension phase (Fig. 6A) while contralateral GMAX and ipsilateral VAS contributed to the hip angle for the Hip Flexion phase (Fig. 6B).

4. Discussion

The objective of this study was to determine how individual muscles contribute to sagittal-plane ankle, knee and hip quasi-stiffness during healthy walking. We expected that the primary contributors to ankle, knee and hip quasi-stiffness would be the muscles that cross each joint and directly contribute to its joint moment, but we also expected that distant and contralateral muscles would contribute to quasi-stiffness through dynamic coupling and joint angle modulation. As expected, primary contributors to ankle, knee and hip quasi-stiffness were the ankle dorsiflexors/plantarflexors, knee flexors/extensors, and hip flexors/extensors, respectively, but contributions to quasi-stiffness were also present from distant and contralateral muscles at all three joints.

4.1. Muscle contributions to net joint moments and angles

4.1.1. Ankle

Ankle plantarflexors (SOL, GAS) and dorsiflexors (TA) were primary contributors to the ankle moment for the Dorsiflexion, Dual-Flexion and Plantarflexion phases of the gait cycle. During all three phases, the summed plantarflexor moment contributions were greater than the dorsiflexor contributions, which aligns with the overall net plantarflexor ankle moment that exists throughout these phases of the gait cycle (Molitor and Neptune, 2024). The ankle plantarflexors and dorsiflexors were also the primary contributors to the ankle angle during all three phases. However, muscles that cross the hip joint (GMED, IL) also contributed to the ankle angle through dynamic coupling. These results suggest that the increased soleus work seen in the case of increased passive hip joint stiffness (Goldberg and Neptune, 2007) may reflect a compensatory strategy to not only aid in hip extension (Arnold et al., 2005), but also to regulate ankle quasi-stiffness in response to distant neuromuscular changes.

4.1.2. Knee

Knee flexors (HAM, GAS) and extensors (VAS, RF) were primary contributors to the knee moment for the Knee Flexion and Extension phases of the gait cycle. In addition to its contribution to the knee moment, VAS was also a primary contributor to the knee angle during both phases. Interestingly, the other major contributors to the knee angle differed from the major contributors to the knee moment. During
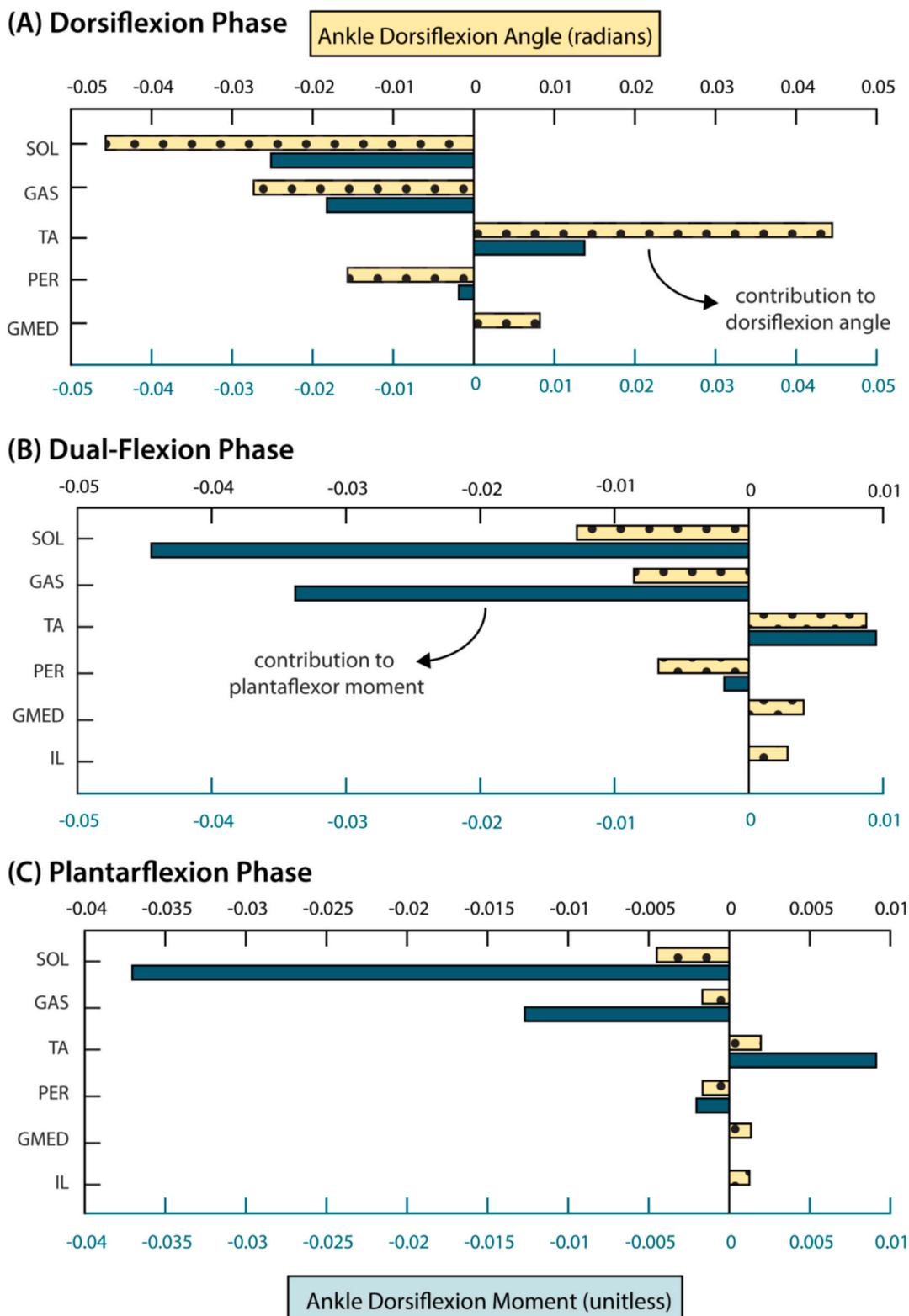
Fig. 2. Primary muscle contributors to the ankle angle (dotted) and moment (solid) during the Dorsiflexion (A), Dual-Flexion (B), and Plantarflexion (C) phases.

both phases, GMAX was a primary contributor to knee extension angle while TA and IL were primary contributors to knee flexion angle. During the Knee Flexion phase, contralateral IL also contributed to knee flexion angle, with approximately equal magnitude to that of the ipsilateral IL (7.9% and 7.8%, respectively). These findings are consistent with Anderson et al. (2004) who found that VAS, TA and IL were major contributors to knee flexion angle, albeit their analysis was during the

swing phase. During the Knee Extension phase, SOL and GMED also contributed to the knee extension angle. Similar to the ankle joint, many of the contributors to the knee angle were muscles that do not cross the knee joint, further highlighting the role of dynamic coupling in modulating joint angles and thus quasi-stiffness.

For the muscle groups that contributed to both the knee moment and angle, the direction of their contribution to the knee moment did not

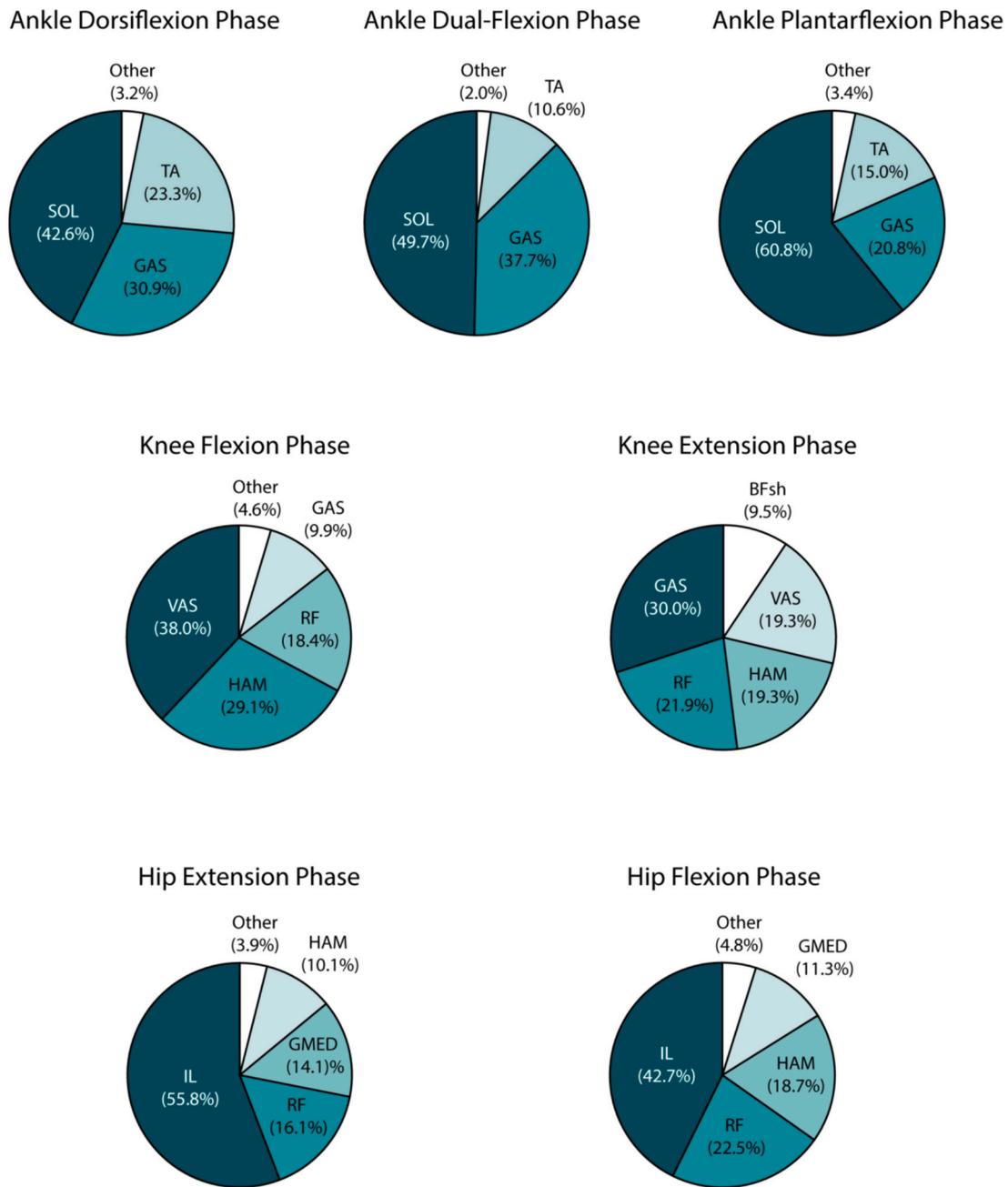# Percent of Total Muscle Contribution to Net Joint Moments

Fig. 3. Distributions of individual muscle contributions to the ankle, knee and hip moment during each quasi-stiffness phase.

always align with the angle contribution. The direction of the knee moment and angle contributions matched for uniarticular groups (i.e., VAS, BFsh). However, biarticular HAM contributed to the knee *flexion moment* but *extension angle* for both Knee Flexion and Extension phases. Previous studies (e.g., Arnold et al., 2005) have similarly noted that the simultaneous knee flexion moment and hip extension moment by HAM can result in net knee acceleration towards extension. The opposing directionality of the moment and angle at the knee demonstrate the effect of dynamic coupling and concurrent action on adjacent joints (Arnold et al., 2005; Neptune et al., 2004). Furthermore, the opposing directionality of HAM contributions to moment and angle elucidates a potential target for better understanding the increased knee quasi-stiffness seen in individuals with knee osteoarthritis or ACL

reconstruction (Dixon et al., 2010; Garcia et al., 2023; Zeni and Higginson, 2009). Despite reduced quadriceps strength and insufficient knee extensor moments present for these groups (Garcia et al., 2023), HAM may be acting to increase knee quasi-stiffness and restore knee stability by reducing knee flexion angles. Thus, it may be advantageous for rehabilitation strategies to target both the quadriceps and hamstrings for these individuals to restore healthy knee mechanics and prevent further injury.

4.1.3. Hip

Hip flexors (IL, RF) and extensors (HAM) were the primary contributors to the hip moment during the Hip Extension and Flexion phases. Hip abductors (GMED) also contributed to the hip extension

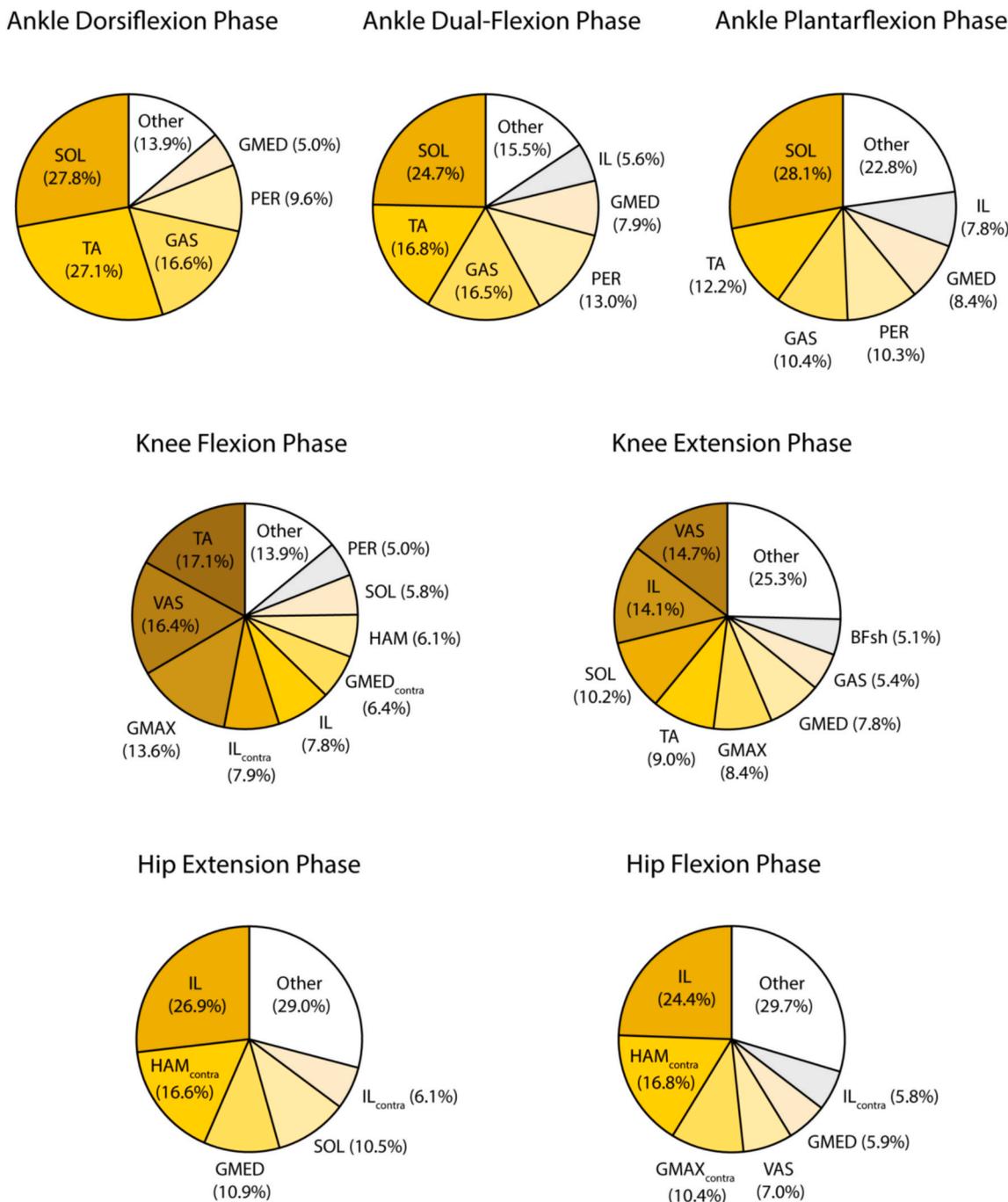## Percent of Total Muscle Contribution to Joint Angles

Fig. 4. Distributions of individual muscle contributions to the ankle, knee and hip angle during each quasi-stiffness phase.

moment in both phases. The primary contributor to the hip angle was IL for both phases, accounting for approximately 25% of all muscle contributions for each phase. As a primary hip flexor, IL contributed to hip flexion angle to help initiate leg swing during these phases (Hall et al., 2011; Neptune et al., 2008, Neptune et al., 2004). Interestingly, the second largest contributor to the hip angle was the contralateral HAM (16.6-16.8% of all muscle contributions), which contributed to hip extension angle. During this time, the contralateral HAM acts to decelerate leg swing (Neptune et al., 2008, Neptune et al., 2004) and prepare for heel-strike. As the swing leg progresses forward, the stance-leg hip must extend to accommodate the movement of the swing leg and overall

body center-of-mass (Hall et al., 2011). Previous work has similarly noted that contralateral muscles have a significant role in modulating ipsilateral limb trajectories (e.g., Roelker et al., 2019). On the ipsilateral side, HAM was a small contributor to the hip angle (2.6% contribution for both phases) although it was a major contributor to the hip moment (10.1% and 18.7% contribution to Hip Extension and Hip Flexion phases, respectively). During the Hip Extension Phase, GMED and SOL also contributed to the hip extension angle, which was consistent with others (Arnold et al., 2005; Neptune et al., 2004). Compared to the knee and ankle, hip quasi-stiffness was most influenced by contralateral muscle contributions, emphasizing the need to consider both limbs when
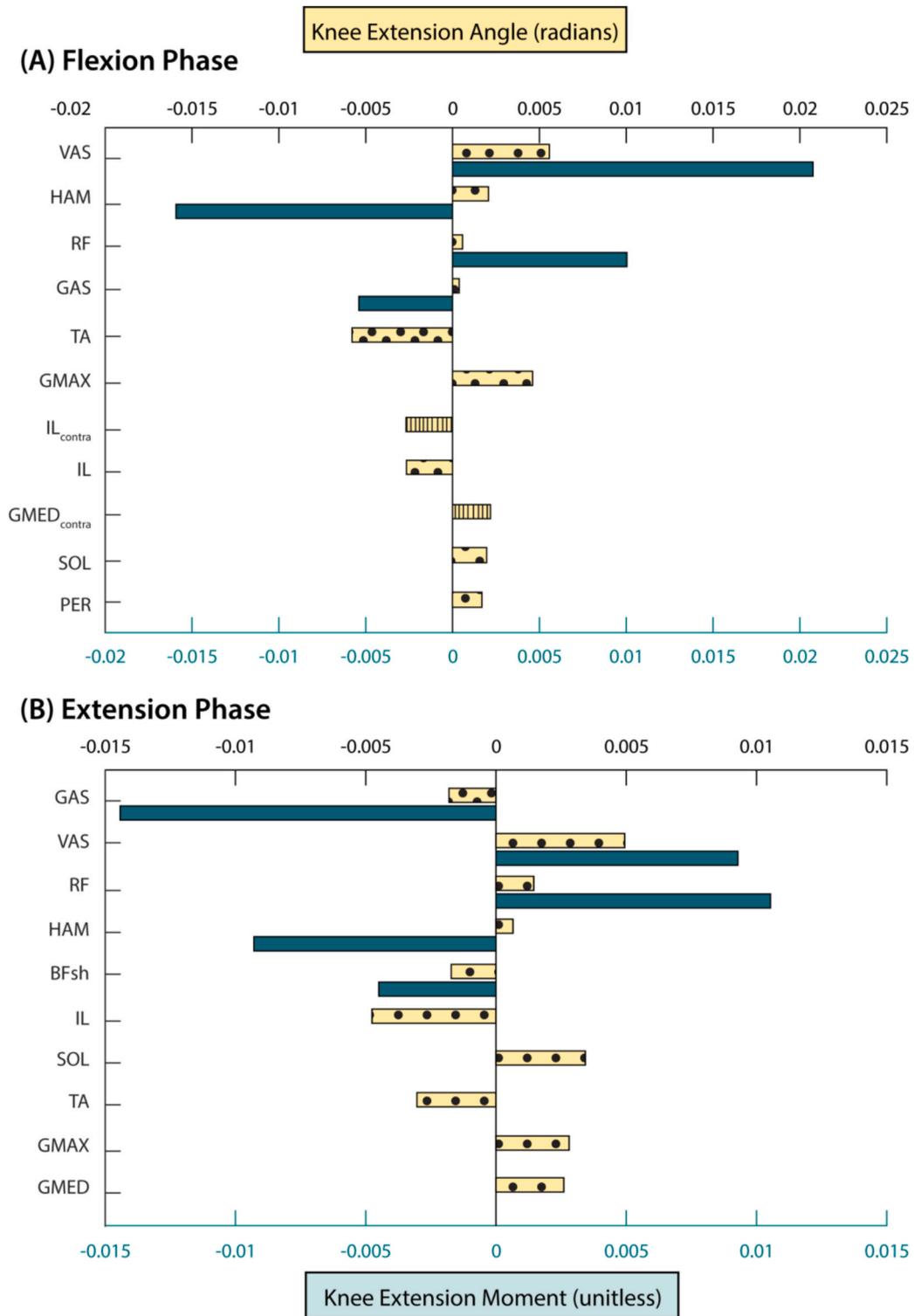
Fig. 5. Primary muscle contributors to the knee angle (ipsilateral dotted; contralateral striped) and moment (solid) during the Knee Flexion (A) and Knee Extension (B) phases.

delivering assistance through hip exoskeletons or similar devices (Malcolm et al., 2018; Pan et al., 2023).

5. Clinical implications

Results from this study identified the muscle coordination needed to modulate joint quasi-stiffness during walking and may provide insight into targeted rehabilitation strategies to promote healthier gait patterns.

For example, previous work found that individuals with Cerebral Palsy rely more on muscle forces, rather than skeletal and passive structures, to maintain joint and leg stiffness compared to healthy controls (Wang et al., 2015). Based on results from this study, strengthening the ankle plantarflexors, hip flexors, and hip abductors may be advantageous for these individuals to improve leg stiffness and associated body support, as these muscles were primary contributors to quasi-stiffness for all three lower-limb joints during healthy walking. Further recommendations can
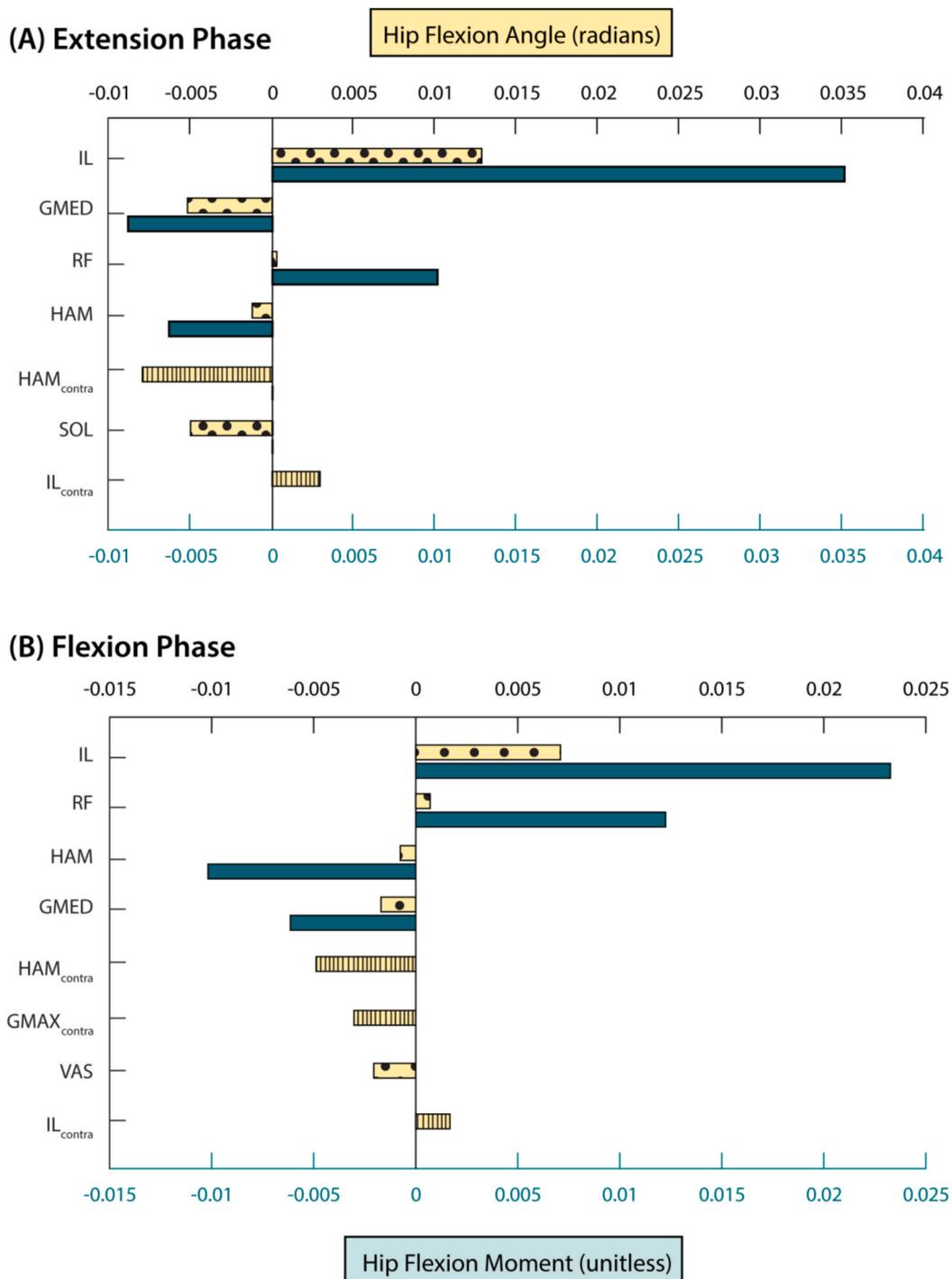
Fig. 6. Primary muscle contributors to the hip angle (ipsilateral dotted; contralateral striped) and moment (solid) during the Hip Extension (A) and Hip Flexion (B) phases.

be made to target improvements in specific joint mechanics based on the respective primary contributors. Results from this study also highlight distant and contralateral muscle influences through joint angle modulation. For example, hip flexors and abductors had notable impacts on the ankle angle and resulting quasi-stiffness. Similarly, contralateral IL contributed to knee flexion angle and contralateral HAM contributed to hip extension angle. The observed contributions of distant and contralateral muscles to quasi-stiffness highlight the role of dynamic coupling (Zajac et al., 2002; Zajac and Gordon, 1989) and the need for holistic clinical gait evaluations. Not accounting for distant and contralateral muscles when attempting to replicate biological quasi-stiffness with

assistive devices may result in reduced potential of the device and/or unnatural compensations. For example, a previous study on individuals post-stroke observed that increased ankle–foot orthosis (AFO) stiffness resulted in compensations at the knee joint at heel-strike due to plantarflexor weakness (Singer et al., 2014). Conversely, prescribing subject-specific AFO stiffness values based on individual stiffness deficits reduced knee and hip compensations (Arch and Reisman, 2016). As such, rehabilitation programs and assistive devices should consider all muscle contributors when training or mimicking the function of a particular joint.

6. Limitations

In this study, we evaluated the role of individual muscles in modulating quasi-stiffness. While quasi-stiffness is commonly used to describe joint "stiffness" during dynamic tasks, it is an indirect measure that evaluates discrete phases of the gait cycle and does not capture continuous changes in joint stiffness. As such, quasi-stiffness, and its decomposition to assess individual muscle contributions, are sensitive to gait phase definitions. In this study, we used phase definitions that have been previously established and accepted based on characteristic kinematic, kinetic and GRF events (Crenna and Frigo, 2011; Shamaei et al., 2013a, 2013b, 2013c). Furthermore, a sensitivity analysis shifting phase timing by ± 2–5% of the gait cycle confirmed the interpretation of our results is robust to these timing variations. In addition, this study used CMC, which accounts for muscle–tendon dynamics to estimate muscle excitations; however, it is important to acknowledge underlying model assumptions that may affect the accuracy of estimated muscle excitations and forces. The model (Gait 2392) was based on cadaveric data and scaled to match anatomical landmarks between the model and experimental data. However, subject-specific musculotendon stiffness properties may differ from the generalized model. Furthermore, the model assumes separate tendons for each musculotendon actuator whereas multiple muscles can attach to a single tendon *in vivo*. In light of these assumptions, we validated our estimates of muscle excitations by comparing the timing of experimental EMG signals to simulated muscle activations. In addition, we performed indirect validation of generated muscle forces by comparing simulated joint angles and moments to the experimentally measured values as recommended in Hicks et al. (2015). By using CMC, which closely tracks the experimental kinematics, we also ensured the state of the system was accurate throughout the gait cycle, which is critical for the induced position analysis.

One final potential limitation is that we presented results from contributions to joint moment and angles independently, with the assumption that the muscles which contribute the most to the individual components of quasi-stiffness are also the primary contributors to overall quasi-stiffness. However, it may not be intuitive to predict how a particular muscle group impacts joint quasi-stiffness based on its contribution to the moment or angle alone since quasi-stiffness characterizes moment–angle interactions. We chose to explore the contributions to joint moments and angles separately because individual muscle "stiffness contributions" (i.e., dividing each muscle moment by its contribution to the angle) are not directly additive to produce overall quasi-stiffness. Furthermore, distant and contralateral muscles contribute to quasi-stiffness through angle modulation; however, the role of these muscles would be occluded when calculating individual muscle "stiffness contributions" due to their zero moment contributions.

7. Conclusion

This study aimed to identify how individual muscles contribute to sagittal-plane ankle, knee and hip quasi-stiffness in healthy walking. Through analyzing individual muscle contributions to net joint moments and angles during specific quasi-stiffness phases of the gait cycle, we determined that in addition to the muscles that cross each joint, distant and contralateral muscles were major contributors to quasi-stiffness through joint angle modulation. These results highlight the effects of dynamic coupling and the role of distant muscles in modulating quasi-stiffness, and provide insight for rehabilitation targets and assistive device prescription to address quasi-stiffness impairments. Future work should similarly quantify muscle contributions to quasi-stiffness for individuals with altered neuromuscular control to assess how specific muscle impairments impact quasi-stiffness. Furthermore, an investigation of how assistive devices impact muscle responses and quasi-stiffness at the non-targeted joints could be useful to better understand compensatory mechanisms associated with inappropriate device prescription.

CRediT authorship contribution statement

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.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jbiomech.2025.112851.

References

Anderson, F.C., Goldberg, S.R., Pandy, M.G., Delp, S.L., 2004. Contributions of muscle forces and toe-off kinematics to peak knee flexion during the swing phase of normal gait: an induced position analysis. J. Biomech. 37, 731–737. https://doi.org/10.1016/j.jbiomech.2003.09.018.

Arch, E.S., Reisman, D.S., 2016. Passive-dynamic ankle-foot orthoses with personalized bending stiffness can enhance net plantarflexor function for individuals poststroke. JPO 28, 60. https://doi.org/10.1097/JPO.0000000000000089.

Arnold, A.S., Anderson, F.C., Pandy, M.G., Delp, S.L., 2005. Muscular contributions to hip and knee extension during the single limb stance phase of normal gait: a framework for investigating the causes of crouch gait. J. Biomech. 38, 2181–2189. https://doi.org/10.1016/j.jbiomech.2004.09.036.

Au, S.K., Herr, H.M., 2008. Powered ankle-foot prosthesis. IEEE Rob. Autom. Mag. 15, 52–59. https://doi.org/10.1109/MRA.2008.927697.

Bayram, H.A., Bayram, M.B., 2018. Dynamic Functional Stiffness Index of the Ankle Joint during Daily living. J. Foot Ankle Surg. 57, 668–674. https://doi.org/10.1053/j.jfas.2017.11.034.

Caputo, J.M., Collins, S.H., 2013. An experimental robotic testbed for accelerated development of ankle prostheses. In: 2013 IEEE International Conference on Robotics and Automation. Presented at the 2013 IEEE International Conference on Robotics and Automation, pp. 2645–2650. https://doi.org/10.1109/ICRA.2013.6630940.

Clites, T.R., Shepherd, M.K., Ingraham, K.A., Wontorcik, L., Rouse, E.J., 2021. Understanding patient preference in prosthetic ankle stiffness. J. Neuroeng. Rehabil. 18, 128. https://doi.org/10.1186/s12984-021-00916-1.

Collins, J.D., Arch, E.S., Crenshaw, J.R., Bernhardt, K.A., Khosla, S., Amin, S., Kaufman, K.R., 2018. Net ankle quasi-stiffness is influenced by walking speed but not age for older adult women. Gait Posture 62, 311–316. https://doi.org/10.1016/j.gaitpost.2018.03.031.

Crenna, P., Frigo, C., 2011. Dynamics of the ankle joint analyzed through moment–angle loops during human walking: Gender and age effects. Hum. Mov. Sci. 30, 1185–1198. https://doi.org/10.1016/j.humov.2011.02.009.

Davis, R.B., DeLuca, P.A., 1996. Gait characterization via dynamic joint stiffness. Gait Posture 4, 224–231. https://doi.org/10.1016/0966-6362(95)01045-9.

Delp, S.L., Anderson, F.C., Arnold, A.S., Loan, P., Habib, A., John, C.T., Guendelman, E., Thelen, D.G., 2007. OpenSim: open-source software to create and analyze dynamic simulations of movement. IEEE Trans. Biomed. Eng. 54, 1940–1950. https://doi.org/10.1109/TBME.2007.901024.

Dixon, S.J., Hinman, R.S., Creaby, M.W., Kemp, G., Crossley, K.M., 2010. Knee joint stiffness during walking in knee osteoarthritis. Arthritis Care Res. 62, 38–44. https://doi.org/10.1002/acr.20012.

Gabriel, R.C., Abrantes, J., Granata, K., Bulas-Cruz, J., Melo-Pinto, P., Filipe, V., 2008. Dynamic joint stiffness of the ankle during walking: Gender-related differences. Phys. Ther. Sport 9, 16–24. https://doi.org/10.1016/j.ptsp.2007.08.002.

Garcia, S.A., Johnson, A.K., Brown, S.R., Washabaugh, E.P., Krishnan, C., Palmieri-Smith, R.M., 2023. Dynamic knee stiffness during walking is increased in individuals with anterior cruciate ligament reconstruction. J. Biomech. 146, 111400. https://doi.org/10.1016/j.jbiomech.2022.111400.

Goldberg, E.J., Neptune, R.R., 2007. Compensatory strategies during normal walking in response to muscle weakness and increased hip joint stiffness. Gait Posture 25, 360–367. https://doi.org/10.1016/j.gaitpost.2006.04.009.

Hall, A.L., Peterson, C.L., Kautz, S.A., Neptune, R.R., 2011. Relationships between muscle contributions to walking subtasks and functional walking status in persons with post-stroke hemiparesis. Clin. Biomech. 26, 509–515. https://doi.org/10.1016/j.clinbiomech.2010.12.010.

Hamner, S.R., Seth, A., Delp, S.L., 2010. Muscle contributions to propulsion and support during running. J. Biomech. 43, 2709–2716. https://doi.org/10.1016/j.jbiomech.2010.06.025.

Hansen, A.H., Childress, D.S., Miff, S.C., Gard, S.A., Mesplay, K.P., 2004. The human ankle during walking: implications for design of biomimetic ankle prostheses. J. Biomech. 37, 1467–1474. https://doi.org/10.1016/j.jbiomech.2004.01.017.

Hicks, J.L., Uchida, T.K., Seth, A., Rajagopal, A., Delp, S.L., 2015. Is my model good enough? Best practices for verification and validation of musculoskeletal models and simulations of movement. J. Biomech. Eng. 137. https://doi.org/10.1115/1.4029304.

Kern, A.M., Papachatzis, N., Patterson, J.M., Bruening, D.A., Takahashi, K.Z., 2019. Ankle and midtarsal joint quasi-stiffness during walking with added mass. PeerJ 7, e7487.

Kipp, K., Kim, H., Wolf, W.I., 2022. Muscle-specific contributions to lower extremity net joint moments while squatting with different external loads. J. Strength Cond. Res. 36, 324. https://doi.org/10.1519/JSC.0000000000003874.

Latash, M.L., Zatsiorsky, V.M., 1993. Joint stiffness: Myth or reality? Hum. Mov. Sci. 12, 653–692. https://doi.org/10.1016/0167-9457(93)90010-M.

Lee, S.S.M., Jakubowski, K.L., Spear, S.C., Rymer, W.Z., 2019. Muscle material properties in passive and active stroke-impaired muscle. J. Biomech. 83, 197–204. https://doi.org/10.1016/j.jbiomech.2018.11.043.

Major, M.J., Twiste, M., Kenney, L.P.J., Howard, D., 2014. The effects of prosthetic ankle stiffness on ankle and knee kinematics, prosthetic limb loading, and net metabolic cost of trans-tibial amputee gait. Clin. Biomech. 29, 98–104. https://doi.org/10.1016/j.clinbiomech.2013.10.012.

Malcolm, P., Galle, S., Van den Berghe, P., De Clercq, D., 2018. Exoskeleton assistance symmetry matters: unilateral assistance reduces metabolic cost, but relatively less than bilateral assistance. J NeuroEng. Rehab. 15, 74. https://doi.org/10.1186/s12984-018-0381-z.

Molina, L.K., Small, G.H., Neptune, R.R., 2023. The influence of step width on balance control and response strategies during perturbed walking in healthy young adults. J. Biomech. 157, 111731. https://doi.org/10.1016/j.jbiomech.2023.111731.

Molitor, S.L., Neptune, R.R., 2024. Lower-limb joint quasi-stiffness in the frontal and sagittal planes during walking at different step widths. Journal of Biomechanics 162, 111897. https://doi.org/10.1016/j.jbiomech.2023.111897.

Neptune, R.R., Sasaki, K., Kautz, S.A., 2008. The effect of walking speed on muscle function and mechanical energetics. Gait Posture 28, 135–143. https://doi.org/10.1016/j.gaitpost.2007.11.004.

Neptune, R.R., Zajac, F.E., Kautz, S.A., 2004. Muscle force redistributes segmental power for body progression during walking. Gait Posture 19, 194–205. https://doi.org/10.1016/S0966-6362(03)00062-6.

Nigro, L., Arch, E.S., 2023. Design and mechanical testing of a novel dual-stiffness ankle-foot orthosis. J. Med. Devices 17. https://doi.org/10.1115/1.4062864.

Pan, Y.-T., Kang, I., Joh, J., Kim, P., Herrin, K.R., Kesar, T.M., Sawicki, G.S., Young, A.J., 2023. Effects of bilateral assistance for hemiparetic gait post-stroke using a powered hip exoskeleton. Ann. Biomed. Eng. 51, 410–421. https://doi.org/10.1007/s10439-022-03041-9.

Perry, J., Boyd, L.A., Rao, S.S., Mulroy, S.J., 1997. Prosthetic weight acceptance mechanics in transtibial amputees wearing the single axis, seattle lite, and flex foot. IEEE Trans. Rehabil. Eng. 5, 283–289. https://doi.org/10.1109/86.650279.

Roelker, S.A., Kautz, S.A., Neptune, R.R., 2019. Muscle contributions to mediolateral and anteroposterior foot placement during walking. J. Biomech. 95, 109310. https://doi.org/10.1016/j.jbiomech.2019.08.004.

Rouse, E.J., Gregg, R.D., Hargrove, L.J., Sensinger, J.W., 2013. The difference between stiffness and quasi-stiffness in the context of Biomechanical modeling. IEEE Trans. Biomed. Eng. 60, 562–568. https://doi.org/10.1109/TBME.2012.2230261.

Safaeepour, Z., Esteki, A., Ghomshe, F.T., Abu Osman, N.A., 2014. Quantitative analysis of human ankle characteristics at different gait phases and speeds for utilizing in ankle-foot prosthetic design. Biomed. Eng. Online 13, 19. https://doi.org/10.1186/1475-925X-13-19.

Sangeux, M., Polak, J., 2015. A simple method to choose the most representative stride and detect outliers. Gait Posture 41, 726–730. https://doi.org/10.1016/j.gaitpost.2014.12.004.

Sekiguchi, Y., Muraki, T., Owaki, D., Honda, K., Izumi, S.-I., 2018. Regulation of quasi-joint stiffness by combination of activation of ankle muscles in midstances during gait in patients with hemiparesis. Gait Posture 62, 378–383. https://doi.org/10.1016/j.gaitpost.2018.03.042.

Sekiguchi, Y., Muraki, T., Tanaka, N., Izumi, S.-I., 2015. Relationship between activation of ankle muscles and quasi-joint stiffness in early and middle stances during gait in patients with hemiparesis. Gait Posture 42, 348–353. https://doi.org/10.1016/j.gaitpost.2015.04.020.

Seth, A., Hicks, J.L., Uchida, T.K., Habib, A., Dembia, C.L., Dunne, J.J., Ong, C.F., DeMers, M.S., Rajagopal, A., Millard, M., Hamner, S.R., Arnold, E.M., Yong, J.R., Lakshmikanth, S.K., Sherman, M.A., Ku, J.P., Delp, S.L., 2018. OpenSim: simulating musculoskeletal dynamics and neuromuscular control to study human and animal movement. PLoS Comput. Biol. 14, e1006223. https://doi.org/10.1371/journal.pcbi.1006223.

Shamaei, K., Sawicki, G.S., Dollar, A.M., 2013a. Estimation of quasi-stiffness and propulsive work of the human ankle in the stance phase of walking. PLoS One 8, e59935. https://doi.org/10.1371/journal.pone.0059935.

Shamaei, K., Sawicki, G.S., Dollar, A.M., 2013b. Estimation of quasi-stiffness of the human hip in the stance phase of walking. PLoS One 8, e81841. https://doi.org/10.1371/journal.pone.0081841.

Shamaei, K., Sawicki, G.S., Dollar, A.M., 2013c. Estimation of quasi-stiffness of the human knee in the stance phase of walking. PLoS One 8, e59993. https://doi.org/10.1371/journal.pone.0059993.

Shell, C.E., Segal, A.D., Klute, G.K., Neptune, R.R., 2017. The effects of prosthetic foot stiffness on transtibial amputee walking mechanics and balance control during turning. Clin. Biomech. (Bristol, Avon) 49, 56–63. https://doi.org/10.1016/j.clinbiomech.2017.08.003.

Singer, M.L., Kobayashi, T., Lincoln, L.S., Orendurff, M.S., Foreman, K.B., 2014. The effect of ankle–foot orthosis plantarflexion stiffness on ankle and knee joint kinematics and kinetics during first and second rockers of gait in individuals with stroke. Clin. Biomech. 29, 1077–1080. https://doi.org/10.1016/j.clinbiomech.2014.09.001.

Thelen, D.G., Anderson, F.C., 2006. Using computed muscle control to generate forward dynamic simulations of human walking from experimental data. J. Biomech. 39, 1107–1115. https://doi.org/10.1016/j.jbiomech.2005.02.010.

Thelen, D.G., Anderson, F.C., Delp, S.L., 2003. Generating dynamic simulations of movement using computed muscle control. J. Biomech. 36, 321–328. https://doi.org/10.1016/S0021-9290(02)00432-3.

Wang, T.-M., Huang, H.-P., Li, J.-D., Hong, S.-W., Lo, W.-C., Lu, T.-W., 2015. Leg and joint stiffness in children with spastic diplegic cerebral palsy during level walking. PLoS One 10, e0143967. https://doi.org/10.1371/journal.pone.0143967.

Zajac, F.E., Gordon, M.E., 1989. Determining muscle's force and action in multi-articular movement. Exerc. Sport Sci. Rev. 17, 187.

Zajac, F.E., Neptune, R.R., Kautz, S.A., 2003. Biomechanics and muscle coordination of human walking: Part II: Lessons from dynamical simulations and clinical implications. Gait Posture 17, 1–17. https://doi.org/10.1016/S0966-6362(02)00069-3.

Zajac, F.E., Neptune, R.R., Kautz, S.A., 2002. Biomechanics and muscle coordination of human walking: Part I: Introduction to concepts, power transfer, dynamics and simulations. Gait Posture 16, 215–232. https://doi.org/10.1016/S0966-6362(02)00068-1.

Zelik, K.E., Collins, S.H., Adamczyk, P.G., Segal, A.D., Klute, G.K., Morgenroth, D.C., Hahn, M.E., Orendurff, M.S., Czerniecki, J.M., Kuo, A.D., 2011. Systematic variation of prosthetic foot spring affects center-of-mass mechanics and metabolic cost during walking. IEEE Trans. Neural Syst. Rehabil. Eng. 19, 411–419. https://doi.org/10.1109/TNSRE.2011.2159018.

Zeni, J.A., Higginson, J.S., 2009. Dynamic knee joint stiffness in subjects with a progressive increase in severity of knee osteoarthritis. Clin. Biomech. 24, 366–371. https://doi.org/10.1016/j.clinbiomech.2009.01.005.