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Contributions of Muscles to Terminal-Swing Knee Motions Vary with Walking Speed

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Abstract

Many children with cerebral palsy walk with diminished knee extension during terminal swing, at speeds much slower than unimpaired children. Treatment of these gait abnormalities is challenging because the factors that extend the knee during normal walking, over a range of speeds, are not well understood. This study analyzed a series of three-dimensional, muscle-driven dynamic simulations to determine whether the relative contributions of individual muscles and other factors to angular motions of the swing-limb knee vary with walking speed. Simulations were developed that reproduced the measured gait dynamics of seven unimpaired children walking at self-selected, fast, slow, and very slow speeds (7 subjects $\times$ 4 speeds = 28 simulations). In mid-swing, muscles on the stance limb made the largest net contribution to extension of the swing-limb knee at all speeds examined. The stance-limb hip abductors, in particular, accelerated the pelvis upward, inducing reaction forces at the swing-limb hip that powerfully extended the knee. Velocity-related forces (i.e., Coriolis and centrifugal forces) also contributed to knee extension in mid-swing, though these contributions were diminished at slower speeds. In terminal swing, the hip flexors and other muscles on the swing limb decelerated knee extension at the subjects' self-selected, slow, and very slow speeds, but had only a minimal net effect on knee motions at the fastest speeds. Muscles on the stance limb helped brake knee extension at the subjects' fastest speeds, but induced a net knee extension acceleration at the slowest speeds. These data — which show that the contributions of muscular and velocity-related forces to terminal-swing knee motions vary systematically with walking speed — emphasize the need for speed-matched control subjects when attempting to determine the causes of a patient's abnormal gait.

Keywords

dynamic simulation; muscle function; gait; swing phase; cerebral palsy

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1. Introduction

Crouch gait, a common walking abnormality in children with cerebral palsy, is characterized by diminished knee extension during the terminal swing and stance phases. Individuals with crouch gait typically exhibit an abnormally short stride, and often walk more slowly than unimpaired children. Designing treatments to increase swing-limb knee extension, and thereby improve the mechanics of locomotion in these individuals, is challenging. Few studies have examined the biomechanical factors that influence terminal-swing knee motions (e.g., Arnold et al., in press), and none has evaluated whether the relative importance of these factors varies with walking speed.

Knee motions during swing are often attributed to the “passive dynamics” of the limb segments (e.g., McGeer, 1990; Mochon and McMahon, 1980), analogous to the passive motion of a multi-link pendulum. However, unimpaired persons can modulate speed, without compromising terminal-swing knee extension, by actively adjusting the excitation patterns of muscles. Understanding how muscles, gravity, and the passive dynamics of the body contribute to swing-limb knee motions during normal gait— at a range of speeds— is necessary to establish a scientific basis for identifying factors that limit knee extension in persons with neuromuscular disorders.

In a previous study (Arnold et al., in press), we evaluated the angular accelerations of the swing-limb knee induced by muscles and other factors in six unimpaired subjects walking at self-selected speeds. Our analysis revealed that the knee is accelerated toward extension by velocity-related forces (i.e., Coriolis and centrifugal forces) and by a number of muscles, notably passive forces generated by the vasti in mid-swing, the hip extensors in terminal swing, and the stance-limb hip abductors. Knee extension is decelerated in terminal swing by the stance-limb hip flexors. Whether these same factors are the predominant contributors to knee motions at faster or slower speeds, however, remains unclear.

In this study, we determined the angular accelerations of the swing-limb knee induced by individual muscles, gravity, and the passive dynamics of the body in unimpaired children walking at four different speeds. The velocity-related forces, which contribute to the passive dynamics of the swinging limb, increase with walking speed. The EMG activity of several swing-limb muscles also increase with speed, and the swing-limb hip and knee undergo larger angular excursions (e.g., Andersson et al., 1997; den Otter et al., 2004; Hof et al., 2002; Murray et al., 1984; Schwartz and Trost, 2006; Stansfield et al., 2006; van der Linden et al., 2002). Thus, we hypothesized that the relative contributions of the muscular and velocity-related forces to terminal-swing knee motions change with speed as well. We tested this hypothesis by analyzing a series of three-dimensional, muscle-driven simulations.

2. Methods

Simulations of the swing phase were generated that reproduced the measured gait dynamics of seven typically-developing children walking at a range of speeds. The subjects' ages ranged from 10-14 yrs (mean 12.2 yrs). Each subject was instructed to walk comfortably at his/her self-selected speed, and at fast, slow, and very slow speeds (Fig. 1) during a single session. The subjects' self-selected speeds ranged from 1.0-1.4 m/s (mean 1.24 m/s). The subjects' fast speeds ranged from 120-140% of their self-selected speeds (mean 1.55 m/s), their slow speeds from 60-75% of their self-selected speeds (mean 0.86 m/s), and their very slow speeds from 40-60% of their self-selected speeds (mean 0.62 m/s).

Each subject underwent gait analysis at the Gillette Children's Specialty Healthcare, St. Paul, MN. A twelve-camera system (Vicon Motion Systems, Lake Forest, CA) was used to record the three-dimensional locations of markers secured to the torso, pelvis, and lower extremities

during static and walking trials. Markers were placed over skeletal landmarks according to a standard clinical protocol (Davis et al., 1991), supplemented with torso markers at the seventh cervical vertebra and distal to the clavicles. The subjects' hip and knee centers were estimated using functional techniques (Schwartz and Rozumalski, 2005), and their joint angles were computed (e.g., Kadaba et al., 1990). Surface EMG (Motion Lab Systems, Baton Rouge, LA) was recorded bilaterally from the medial hamstrings, biceps femoris long head, rectus femoris, gastrocnemius, and anterior tibialis following SENIAM conventions (www.seniam.org). These data were sampled at 1080 Hz, band-pass filtered between 20 and 400 Hz, rectified, and low-pass filtered at 10 Hz, yielding EMG envelopes for comparison with the simulations. Four force plates (AMTI, Watertown, MA) were used to record the ground reaction forces and moments. These data were sampled at 1080 Hz and low-pass filtered at 20 Hz. One trial with consecutive force plate strikes, per subject and speed, was selected for analysis. All subjects and/or their parents provided informed consent for the collection of these data. Analyses of the data were performed in accordance with the regulations of all participating institutions.

A dynamic model of the musculoskeletal system was used, in conjunction with the data obtained from gait analysis, to create a simulation of each subject's swing phase at each of the four speeds (7 subjects $\times$ 4 speeds = 28 simulations; Fig. 2). Our model and procedure for creating the simulations is described in detail elsewhere (Arnold et al., in press; Thelen and Anderson, 2006). Briefly, we scaled a musculoskeletal model with 21 degrees of freedom and 92 muscle-tendon actuators to each subject's anthropometric dimensions. We then solved for a set of muscle excitations which, when applied to the model along with the subject's measured ground reaction forces and moments, reproduced the subject's measured kinematics. In most cases, our tracking algorithm produced excitations that were similar to the subjects' measured EMG patterns and to EMG on/off times published in the literature. In some cases, however, one or more of the muscles were excited at inappropriate times unless we constrained the solution of the algorithm, forcing those muscles to be inactive at those times. We implemented the necessary constraints for each simulation, solved for a refined set of muscle excitations, and verified that the resulting coordination patterns were plausible (e.g., Fig. 3). We compared the simulations at the different walking speeds, and we confirmed that the magnitudes of the excitations generally scaled with speed as reported in the literature (e.g., den Otter et al., 2004; Hof et al., 2002; Murray et al., 1984; Schwartz and Trost, 2006). We also verified that the joint angles of each simulation matched the subject's measured joint angles to within a few degrees, and that the joint moments were consistent with the moments computed from the experimental data (e.g., Arnold et al., in press).

We analyzed the contributions of individual muscles to the accelerations of the swing-limb knee using a perturbation technique (Liu et al., 2006). At each 10 ms time step in each simulation, for each muscle in the model, we introduced a 1 N perturbation in the muscle's force. All other muscles were constrained to apply the same force trajectories that they applied in the unperturbed simulation. We integrated the equations of motion over a 20 ms interval to determine the changes in the accelerations of the swing-limb segments and joints per unit force. We then scaled these accelerations by the muscle's average force over the perturbation interval to determine the net accelerations attributable to that muscle, independent of other factors such as gravity. Interactions between the stance-limb foot and the ground were characterized by a set of rotational and translational spring-damper units (Arnold et al., in press). Hence, the ground reaction forces and moments were allowed to change in response to the perturbations in force. Analogous methods were used to determine the knee motions induced independently by gravity and velocity-related forces (i.e., Coriolis and centrifugal forces).

To compare the actions of the muscles and other factors across speeds, we calculated the average acceleration of the swing-limb knee induced by each factor over the “extension” and “braking” phases (Fig. 4). One-way analysis of variance with repeated measures was performed

(SPSS Inc., Chicago, IL) to determine whether these average accelerations varied significantly with speed. For each test, there was one within-subjects factor with four levels (speed), and one between-subjects factor representing the independent measure of interest.

3. Results

During normal gait, the knee is rapidly accelerated toward flexion during pre-swing. The knee reaches its peak flexion velocity near toe-off and its peak flexion angle between 20-40% of the swing phase, depending on walking speed (Fig. 4A). After reaching its peak flexion velocity, the knee is accelerated toward extension (Fig. 4B, *extension phase*), then toward flexion (Fig. 4B, *braking phase*) as the knee's extension motion is slowed prior to foot contact. These knee accelerations increased with speed (Fig. 4B and Fig. 5, *black bars*) throughout the extension [$F(3, 18) = 41.8, p < 0.001$] and braking phases [$F(3, 18) = 27.7, p < 0.001$].

In our simulations, muscles generated 50-70% of the knee extension acceleration during the extension phase (Fig. 5A, *dark grey bars*); velocity-related forces also contributed substantially (Fig. 5A, *light grey bars*). The knee extension acceleration induced by the velocity-related forces was diminished at the subjects' slower speeds. As a result, the relative contribution (i.e., average induced acceleration normalized to the total acceleration) of the muscles to knee extension was greater when the subjects walked slower [$F(3, 18) = 22.7, p < 0.001$], even though the net knee acceleration induced by the muscles was less. During the braking phase, muscles generated nearly all of the knee flexion acceleration that slowed the knee's motion prior to foot contact (Fig. 5B, *dark grey bars*).

During the extension phase, muscles on the stance limb made the largest net contribution to extension of the swing-limb knee at all speeds examined (Fig. 6A, *dark grey bars*). This occurred because the stance-limb hip abductors and extensors generated forces in early stance that accelerated the pelvis upward and rotated the pelvis posteriorly, and this acceleration of the pelvis induced reaction forces at the swing-limb hip that powerfully extended the knee (Fig. 7). Passive forces produced by the swing-limb vasti and residual forces produced by the uniarticular ankle plantarflexors, remaining from their activity in pre-swing, also opposed knee flexion in our simulations (Fig. 7). However, the net action of muscles on the swing limb was to accelerate the knee toward flexion (Fig. 6A, *light grey bars*); this result was consistent across subjects and speeds. The swing-limb hip flexors, biceps femoris short head, and ankle dorsiflexors all contributed to knee flexion during the extension phase (Fig. 7).

During the braking phase, the net contributions of swing-limb muscles and stance-limb muscles to motions of the swing-limb knee varied systematically with walking speed (Fig. 6B). Muscles on the stance limb powerfully flexed the knee at the subjects' fastest speeds, but induced a net knee extension acceleration at the slowest speeds (Fig. 6B, *dark grey bars*). This change in the muscle actions with speed [$F(3, 18) = 33.9, p < 0.001$] was observed in all subjects (Fig. 8B). Muscles on the swing limb decelerated knee extension at the subjects' self-selected, slow, and very slow speeds (Fig. 6B, *light grey bars*), but had only a minimal net effect on knee motion at the fastest speeds. This trend with speed [$F(3, 18) = 11.2, p < 0.001$] was also observed in all subjects (Fig. 8A).

Examination of the knee motions induced by individual muscles provided additional insight into the source of these speed-related changes. For example, in our simulations of the subjects' faster trials, the stance-limb hip flexors were highly activated during late stance, generating forces that accelerated the pelvis backward, rotated the pelvis anteriorly, and accelerated the swing-limb hip and knee toward flexion (Figs. 9A and 10A). In the slower trials, however, the knee flexion acceleration induced by the hip flexors was reduced (Figs. 9B and 10B). This change shifted the net knee acceleration induced by stance-limb muscles toward extension at

the slower speeds. Swing-limb muscles also showed speed-related trends. For instance, in our simulations of the subjects' faster trials, the hip flexors and ankle dorsiflexors accelerated the knee toward flexion, while the hip extensors accelerated the knee toward extension (Figs. 9A and 11A). In the slower trials, however, the knee flexion accelerations induced by the hip flexors and ankle dorsiflexors were increased, while the knee extension accelerations induced by the hip extensors were decreased (Figs. 9B and 11B). These changes shifted the net knee acceleration induced by swing-limb muscles toward flexion at the slower speeds.

4. Discussion

Several investigators have shown that EMG activity, joint angles, and joint moments during walking vary systematically with walking speed (e.g., Andersson et al., 1997; den Otter et al., 2004; Hof et al., 2002; Murray et al., 1984; Schwartz and Trost, 2006; Stansfield et al., 2006; van der Linden et al., 2002). However, few studies have examined whether the functions of individual muscles during walking also change with speed (e.g., Sasaki and Neptune, 2006). In this study, we evaluated the angular accelerations of the swing-limb knee induced by individual muscles, gravity, and the passive dynamics of the body in seven children walking at four different speeds. We showed that both muscular and velocity-related forces make important contributions to knee extension at speeds ranging from 0.5 to 1.75 m/s, consistent with our earlier analysis at speeds near 1.3 m/s (Arnold et al., in press). We also demonstrated that the relative contributions of swing-limb muscles, stance-limb muscles, and other factors to terminal-swing knee motions vary significantly and systematically with speed, which has not been reported previously.

During the extension phase (Fig. 4B) at self-selected speeds, the knee was accelerated toward extension in our simulations by velocity-related forces and by several muscles, notably the vasti, the uniarticular ankle plantarflexors, and the stance-limb hip abductors. At the subjects' faster speeds, the velocity-related forces, and their induced knee extension accelerations, were greater (Fig. 5A). Forces produced by the swing-limb vasti (passive) and the uniarticular ankle plantarflexors (resulting from their activity in pre-swing) also accelerated the knee toward extension more when walking faster (Fig. 7). The vasti generated larger passive forces at the subjects' faster speeds, and thus larger knee extension accelerations, because the subjects' knee flexion angles were greater (e.g., Fig. 4A). The plantarflexors also generated larger forces at the faster speeds, consistent with the subjects' increased EMG activity prior to toe-off and published EMG data (den Otter et al., 2004; Murray et al., 1984). Hence, changes in the actions of the muscles and velocity-related forces with speed, as identified from our simulations, were generally consistent with changes in the subjects' measured gait data.

Extension of the swing-limb knee was opposed in our simulations by the swing-limb hip flexors and ankle dorsiflexors (Fig. 7). These muscles produced forces in early swing that accelerated the knee toward flexion, and these accelerations were increased when the subjects walked faster (Fig. 7). The hip flexors generated larger forces at the faster speeds, and thus larger knee flexion accelerations, consistent with studies that have documented an increase in hip flexion moment with speed during pre-swing (Schwartz and Trost, 2006; van der Linden et al., 2002). The ankle dorsiflexors in our simulations also generated larger forces at the faster speeds.

During the braking phase (Fig. 4B) at subjects' self-selected speeds, the knee was decelerated by muscles on both the swing limb and stance limb muscles in our simulations (Fig. 6). An important finding of this study is that the contributions of these muscles to terminal-swing knee motions varied significantly with walking speed. The stance-limb hip flexors, for example, decelerated the swing-limb knee more at the subjects' faster speeds (Fig. 9). The subjects took longer steps when walking faster, and achieved greater hip extension in stance. This

necessitated a greater hip flexion moment (Schwartz and Trost, 2006; Stansfield et al., 2006), inducing a greater flexion acceleration of the swing-limb knee.

The swing-limb hip flexors and ankle dorsiflexors also decelerated the knee during the braking phase. However, in contrast to the stance-limb hip flexors, these muscles decelerated the knee more when walking slower (Fig. 9). The swing-limb hip flexors were excited more, and generated larger forces at the slower speeds, possibly to assist with forward advancement of the limb. The ankle dorsiflexors were not excited more, but the muscles' *potential* to decelerate the knee (i.e., induced acceleration per unit force, which depends on the muscle's moment arms and the configuration of the body as described by Arnold et al., 2005) was increased at slower speeds in most subjects. Thus, the net action of the swing-limb muscles was to decelerate the knee more at the slower speeds (Figs. 6,8). The swing-limb hip extensors contributed further to this trend. These muscles were activated less, and accelerated the knee toward extension less when walking slower (Fig. 8), consistent with EMG data (Murray et al., 1984) and with studies that have documented a decrease in the hip extension moment at slower speeds (Schwartz and Trost, 2006; van der Linden et al., 2002).

It is important to acknowledge that our estimates of the knee motions induced by muscles depend on the forces applied by the muscles during the simulations. We fine-tuned the timing of the muscle excitations based on detailed comparisons with measured and published EMG recordings, and we verified that the simulations accurately reproduced the subjects' measured gait dynamics; thus, we believe that the forces generated by most muscles in our simulations are reasonable. Nevertheless, the forces produced by some muscles remain questionable. In particular, our tracking algorithm chose not to excite the vasti in terminal swing, inconsistent with EMG recordings, because these muscles were shortening too rapidly to generate much force. If the vasti had generated more force, then they would have made larger contributions to terminal-swing knee extension. The gluteus medius in our simulations exhibited prolonged excitation during stance as compared to EMG data. Hence, our analysis may have exaggerated the contribution of the stance-limb hip abductors to swing-limb knee extension, particularly in the late extension phase. Our tracking algorithm chose not to increase the excitation of tibialis anterior in late swing, also inconsistent with EMG data. If tibialis anterior had generated more force, then its ability to decelerate the knee would have been greater.

It has been reported that rectus femoris contributes substantially to knee extension during swing (e.g., Piazza and Delp, 1996), and its EMG activity is known to increase with walking speed (Murray et al., 1984; Nene et al., 2004; Schwartz and Trost, 2006). However, rectus femoris provided only small contributions to knee extension in our simulations (Fig. 7). This is different from the muscle's actions reported by Piazza and Delp (1996), but is consistent with the actions reported by Anderson et al. (2004). Our explanation for the discrepancy is two-fold. First, Piazza and Delp prescribed the motions of the pelvis in their simulations, and they only considered muscles on the swing limb. If we had analyzed a simpler model consisting of only the swing limb, in which the pelvis trajectory was prescribed, then we, too, would likely have attributed different actions to the muscles (Chen, 2006). Second, in our simulations (and in the one analyzed by Anderson et al.), the rectus femoris was not highly activated after toe-off. This may reflect a limitation of our tracking algorithm, or it may be that the subjects were not walking fast enough to elicit such activity (e.g., Nene et al., 2004). If rectus femoris had been activated more, then it would have generated larger forces, and larger knee extension accelerations, during early swing.

It is frequently presumed that the hamstrings are activated more when walking faster to restrain hip and knee flexion in preparation for foot contact (e.g., Gage, 2004). In our simulations of subjects' faster speeds, the hamstrings were activated more, and produced larger forces, consistent with the subjects' EMG activity and published EMG data (den Otter et al., 2004;

Murray et al., 1984; Schwartz and Trost, 2006). However, these increases did *not* cause the hamstrings to flex the knee more (Fig. 9). This was due to dynamic coupling: the hamstrings' knee flexion moment accelerated the knee toward flexion, but the hamstrings' hip extension moment accelerated the knee toward extension. Further analysis revealed that the hamstrings decelerated the forward motion of the swing-limb shank at all speeds examined.

The results of this study offer several clinically-relevant insights. First, it is important to recognize that motions of the swing-limb knee are sensitive to the forces generated by stance-limb hip muscles over a range of speeds. This suggests that the diminished knee extension exhibited by some patients may be caused by impaired hip muscles on the stance limb that result in abnormal accelerations of the pelvis. Our analysis also confirms that velocity-related forces make substantial contributions to knee extension, but only at speeds approaching 1 m/s or faster. At slower speeds, the knee motions are more dependent on muscles. This suggests that some patients may achieve greater knee extension if they are enabled to walk faster. The gastrocnemius and soleus contribute substantially to forward progression during normal gait (Liu et al., 2006; Neptune et al., 2001), so strengthening these muscles may be particularly beneficial in patients with weak calf muscles who walk slower than normal. Lastly, this work emphasizes the need to analyze data from speed-matched control subjects when attempting to determine the causes of a patient's abnormal gait.

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Figure 1. Fast, self-selected, slow, and very slow walking speeds of the subjects in this study. Simulations were created that reproduced the gait dynamics of each subject at each speed.

Figure 2.

Muscle-driven simulations of swing phase that reproduce the gait dynamics of a 13-year-old subject, Subject 7, walking at fast (1.4 m/s), self-selected (1.0 m/s), slow (0.7 m/s), and very slow (0.5 m/s) speeds. To create these simulations, a musculoskeletal model with 21 degrees of freedom and 92 muscles was scaled to the subject's mass (41.6 kg) and height (1.6 m). Each simulation is shown at the instants just prior to toe-off (*left*), just prior to initial contact (*right*), and at peak swing-phase knee flexion (*center*).

Figure 3.

Activation patterns for 10 of the 92 muscle-tendon actuators on the swing limb (*left*) and stance limb (*right*) used to drive the simulations of an 11-year-old subject, Subject 4, at fast, self-selected, slow, and very slow walking speeds (*darker lines correspond to faster speeds*). Note that our model has the isometric force-generating capacity of an adult, while the subject has the mass (31.7 kg) and height (1.4 m) of a child. The magnitudes of the muscle activations, therefore, reflect the relatively small activations (and forces) needed to track the subject's gait dynamics. Corresponding EMG on/off times published by Perry (1992) are overlaid for comparison (solid bars; the thinner bars indicate inconsistencies in EMG timing as documented

by Perry), and are scaled to the subject's measured stance and swing phases at the self-selected speed.

Figure 4.

Knee flexion angle (*A*) and angular acceleration (*B*) during the swing phase as determined experimentally for a 14-year-old subject, Subject 5, walking at fast (1.5 m/s), self-selected (1.1 m/s), slow (0.7 m/s), and very slow (0.5 m/s) speeds. Prior to toe-off, the knee is rapidly accelerated toward flexion. Near toe-off, the knee stops accelerating toward flexion and starts accelerating toward extension due to the actions of muscles and velocity-related forces. In late swing, the knee stops accelerating toward extension and starts accelerating toward flexion due to the actions of muscles. The *extension phase* is defined as the interval during which the knee is accelerated toward extension; the *braking phase* is defined as the interval during which the knee is accelerated toward flexion.

Figure 5. Angular acceleration of the swing-limb knee induced by gravity, velocity-related forces, and muscles, averaged over the extension phase (A) and the braking phase (B), at fast, self-selected, slow, and very slow walking speeds. Each bar represents the mean + 1 SD for the seven subjects in this study.

Figure 6.

Angular acceleration of the swing-limb knee induced by swing-limb muscles and stance-limb muscles, averaged over the extension phase (A) and the braking phase (B), at fast, self-selected, slow, and very slow walking speeds. Each bar represents the mean + 1 SD for the seven subjects in this study. The net knee accelerations induced by all muscles (swing-limb muscles, stance-limb muscles, and back muscles) are shown for comparison.

Figure 7.

Angular acceleration of the swing-limb knee induced by individual muscles or groups of muscles on the swing limb (*light grey bars*) and on the stance limb (*dark grey bars*), averaged over the extension phase at fast (A) and very slow speeds (B). *DF*, the ankle dorsiflexors, includes tibialis anterior, extensor digitorum longus, extensor hallucis longus, and peroneus tertius. *HipFlx*, the hip flexors, includes iliacus, psoas, tensor fasciae latae, and sartorius. *BFSH* is the biceps femoris short head. *RF* is the rectus femoris. *VAS* includes vastus medialis, vastus intermedius, and vastus lateralis. *UPF*, the uniarticular ankle plantarflexors, includes soleus, tibialis posterior, flexor digitorum longus, flexor hallucis longus, peroneus longus, and peroneus brevis. *HipExt*, the stance-limb hip extensors, includes gluteus maximus, hamstrings, and adductor magnus. *HipAb*, the stance-limb hip abductors, includes gluteus medius and gluteus minimus. *Other* includes all other muscles of the corresponding limb in the model.

Figure 8.

Angular acceleration of the swing-limb knee during the braking phase induced by swing-limb muscles (A) and stance-limb muscles (B), expressed as a percentage of the total knee acceleration and plotted vs. walking speed. Data for each of the seven subjects are shown. Swing-limb muscles exert a greater net influence on the knee motions at slow speeds, while stance-limb muscles exert a greater net influence on the knee motions at fast speeds.

Figure 9.

Angular acceleration of the swing-limb knee induced by individual muscles or groups of muscles on the swing limb (*light grey bars*) and on the stance limb (*dark grey bars*), averaged over the braking phase at fast (*A*) and very slow speeds (*B*). *DF*, the ankle dorsiflexors, includes tibialis anterior, extensor digitorum longus, extensor hallucis longus, and peroneus tertius. *HipFlx*, the hip flexors, includes iliacus, psoas, tensor fasciae latae, and sartorius. *HAMS*, the hamstrings, includes semimembranosus, semitendinosus, and biceps femoris long head. *VAS* includes vastus medialis, vastus intermedius, and vastus lateralis. *UPF*, the uniarticular ankle plantarflexors, includes soleus, tibialis posterior, flexor digitorum longus, flexor hallucis longus, peroneus longus, and peroneus brevis. *HipExt*, the swing-limb hip extensors, includes gluteus maximus and adductor magnus. *HipAb*, the stance-limb hip abductors, includes gluteus medius and gluteus minimus. *Other* includes all other muscles of the corresponding limb in the model.

A) Stance-Limb Muscles, Fast

B) Stance-Limb Muscles, Very Slow

Figure 10.

Motions of the pelvis and swing limb induced by all stance-limb muscles during the braking phase at fast (A) and very slow speeds (B). Straight arrows represent translational accelerations, and curved arrows represent angular accelerations. All arrows are scaled proportional to their magnitudes. Accelerations of the thigh are calculated relative to the pelvis. Stance-limb muscles accelerated the model's center of mass (*not shown*) upward and forward during the braking phase, consistent with previous studies (Liu et al., 2006).

A) Swing-Limb Muscles, Fast

B) Swing-Limb Muscles, Very Slow

Figure 11.

Motions of the pelvis and swing limb induced by all swing-limb muscles during the braking phase at fast (A) and very slow speeds (B). Straight arrows represent translational accelerations, and curved arrows represent angular accelerations. All arrows are scaled proportional to their magnitudes. Accelerations of the thigh are calculated relative to the pelvis, and accelerations of the shank are calculated relative to the thigh.