Coordination of intrinsic and extrinsic foot muscles during walking

**Karl E. Zelik · Valentina La Scaleia · Yuri P. Ivanenko ·
Francesco Lacquaniti**

Abstract

Purpose The human foot undergoes complex deformations during walking due to passive tissues and active muscles. However, based on prior recordings it is unclear if muscles that contribute to flexion/extension of the metatarsophalangeal (MTP) joints are activated synchronously to modulate joint impedance, or sequentially to perform distinct biomechanical functions. We investigated the coordination of MTP flexors and extensors with respect to each other, and to other ankle–foot muscles.

K. E. Zelik · Y. P. Ivanenko · F. Lacquaniti
Laboratory of Neuromotor Physiology, IRCCS Santa Lucia
Foundation, Via Ardeatina 306, 00179 Rome, Italy

Y. P. Ivanenko
e-mail: y.ivanenko@hsantalucia.it

F. Lacquaniti
e-mail: lacquaniti@med.uniroma2.it

K. E. Zelik (✉)
Department of Mechanical Engineering, Vanderbilt University,
2400 Highland Avenue, Nashville, TN 37212, USA
e-mail: karl.zelik@vanderbilt.edu; kzelik@umich.edu

K. E. Zelik
Department of Physical Medicine and Rehabilitation, Vanderbilt
University, 2201 Children's Way, Nashville, TN 37212, USA

V. La Scaleia · F. Lacquaniti
Department of Systems Medicine, University of Rome Tor
Vergata, Via Montpellier 1, 00133 Rome, Italy
e-mail: v.lascaleia@hsantalucia.it

F. Lacquaniti
Centre of Space Bio-medicine, University of Rome Tor Vergata,
Via Montpellier 1, 00133 Rome, Italy

Methods We analyzed surface electromyographic (EMG) recordings of intrinsic and extrinsic foot muscles for healthy individuals during level treadmill walking, and also during sideways and tiptoe gaits. We computed stride-averaged EMG envelopes and used the timing of peak muscle activity to assess synchronous vs. sequential coordination.

Results We found that peak MTP flexor activity occurred significantly before peak MTP extensor activity during walking ($P < 0.001$). The period around stance-to-swing transition could be roughly characterized by sequential peak muscle activity from the ankle plantarflexors, MTP flexors, MTP extensors, and then ankle dorsiflexors. We found that foot muscles that activated synchronously during forward walking tended to dissociate during other locomotor tasks. For instance, extensor hallucis brevis and extensor digitorum brevis muscle activation peaks decoupled during sideways gait.

Conclusions The sequential peak activity of MTP flexors followed by MTP extensors suggests that their biomechanical contributions may be largely separable from each other and from other extrinsic foot muscles during walking. Meanwhile, the task-specific coordination of the foot muscles during other modes of locomotion indicates a high-level of specificity in their function and control.

Abbreviations

EDB	Extensor digitorum brevis
EHB	Extensor hallucis brevis
EHL	Extensor hallucis longus
EMG	Electromyographic, electromyogram
FDB	Flexor digitorum brevis
FDHL	Flexor digitorum longus and flexor hallucis longus

FDL	Flexor digitorum longus
FHL	Flexor hallucis longus
LG	Lateral gastrocnemius
MC	Maximum contraction
MG	Medial gastrocnemius
MTP	Metatarsophalangeal
PB	Peroneus brevis
PL	Peroneus longus
SOL	Soleus
TA	Tibialis anterior

Introduction

During gait the foot undergoes various deformations, including compression of the heel pad following foot-strike, elastic stretching and flattening of the foot arch during mid-stance, and then extension of the toes about the metatarsophalangeal (MTP) joints near the end of the stance. These complex deformations result from passive tissues such as the plantar fascia and ligaments (McKenzie 1955; Ker et al. 1987), as well as from contractions of intrinsic and extrinsic foot muscles, such as the toe flexors and extensors (Sheffield et al. 1956; Mann and Inman 1964). Sensory information from these passive and active structures is then relayed back to the central nervous system and used to control movement and posture (Sinkjær et al. 2000; Nurse and Nigg 2001; McKeon et al. 2014).

Advances in measurement and imaging modalities have enabled in vivo study of the human foot and provided new insights about the foot's adaptability, complexity and contributions during walking. However, the role of the toes and the function of the muscles acting on them is only partially understood (Reeser et al. 1983). Various functions have been proposed for the human foot muscles during walking, including stabilizing the foot during propulsion (Mann and Inman 1964), improving pressure distribution on the plantar surface (Rolian et al. 2009), supporting the longitudinal and transverse arches (Reeser et al. 1983; Fiolkowski et al. 2003; Soysa et al. 2012; McKeon et al. 2014; Kelly et al. 2014), and adapting to dynamic or postural load changes (McKenzie 1955; Kelly et al. 2012; Wright et al. 2012). Nevertheless, additional questions remain such as the degree to which foot muscles contract synergistically and whether the foot function improves or degrades economy of gait (Song and Geyer 2011).

Understanding the function of the toes during walking also has important clinical and technological implications. Assessment and treatment of conditions such as diabetic neuropathy (Severinsen and Andersen 2007), claw toe (Bus et al. 2009) and hallux valgus (Hutton and Dhanendran 1981; Soysa et al. 2012) rely on our fundamental knowledge of foot function. Furthermore, the development of assistive technologies such as prosthetic feet may benefit from a better understanding of the role of the toes. For instance, some evidence suggests that inclusion of biomimetic degrees-of-freedom at the mid-foot and MTP joints in a foot prosthesis may facilitate economical movement, and thus help reduce fatigue-related challenges experienced by amputees (Grabowski et al. 2010). Studying the foot muscles that control toe movement provides one way to further our understanding of the functional role of the toes during locomotion.

One of the major challenges to discerning the mechanistic function of the toes is a gap in knowledge about how foot muscle activations are coordinated during ambulation. Much of our understanding is derived from pioneering studies of the 1950s and 1960s (Suzuki 1956; Sheffield et al. 1956; Mann and Inman 1964; Sutherland 1966; Gray and Basmajian 1968). However, due to the measurement technology available, these findings were generally limited to simple phasic descriptions, identifying rough time intervals when the foot muscles were either "on" or "off". Based on these recordings it is unclear if the antagonistic MTP flexor and extensor muscles are co-activated during gait. Some early studies suggested that the muscles are synchronously activated during late stance (Mann and Inman 1964), while others reported sequential muscle activations (Sheffield et al. 1956). From a functional perspective, co-contraction of these antagonistic muscles might suggest that they modulate the impedance of the MTP joint, a strategy employed by the central nervous system for postural and movement stabilization (Hogan 1984). However, co-contraction is generally considered uneconomical during movement, and thus a sequential activation of the MTP extensors and flexors would suggest a different biomechanical function.

The main purpose of this study was therefore to address a simple, yet critical question related to foot function: do the antagonistic MTP flexor and extensor muscles activate synchronously during walking, or are they activated sequentially? As a secondary objective, we also sought to investigate if these MTP muscles activate synchronously with any other extrinsic foot muscles, specifically nearby muscles that contribute to ankle dorsi- or plantar-flexion. Finally, we sought to determine if subsets of MTP muscles, which we observed to activate synchronously during forward walking, continued to function synergistically during other gaits (e.g., sideways and tiptoe walking). To investigate these questions, we collected electromyographic (EMG) recordings from intrinsic and extrinsic foot muscles during walking and analyzed their temporal coordination patterns.

Methods

We principally studied foot muscle EMGs during level walking on a treadmill at 4 km/h in 7 healthy human

participants (3 males, 4 females, 25.9 $\pm$ 2.7 years, 1.76 $\pm$ 0.11 m, 74 $\pm$ 16 kg). Subjects also performed two additional locomotor tasks, tiptoe (digitigrade) and sideways walking, which were used to assess potential decoupling of specific foot muscle activations (as explained below). We analyzed 30s of walking data for each condition and participant. Walking was performed barefoot on a standard treadmill. The protocol was approved by the Ethics Committee of the Santa Lucia Institute and all subjects gave informed consent prior to participation.

Data collection

We recorded selected intrinsic and extrinsic foot muscle EMGs from the right limb of each participant using surface electrodes. Of particular interest during walking were muscles contributing to MTP flexion and extension. Given the complex structure of the foot (e.g., four plantar layers of foot muscles), a limited number of MTP muscles were accessible via surface electrodes. We recorded three extensors—extensor hallucis brevis (EHB), extensor digitorum brevis (EDB) and extensor hallucis longus (EHL)—and two flexors—flexor digitorum brevis (FDB) and flexor digitorum/hallucis longus (FDHL). The intrinsic MTP muscles (EHB, EDB and FDB) have both their origins and insertions in the foot, whereas the extrinsic muscles (EHL and FDHL) have origins in the leg and then long tendons that cross the ankle and MTP joints. FDHL and EHL muscles are biarticular, and therefore contribute to both ankle motion (plantarflexion/dorsiflexion) and MTP motion (flexion/extension). In addition to MTP flexors and extensors, we also recorded the following extrinsic foot muscles involved in ankle joint movement: medial (MG) and lateral gastrocnemius (LG), soleus (SOL), tibialis anterior (TA), peroneus longus (PL) and brevis (PB).

Surface electrodes were preferential for safely recording foot muscle activity during diverse locomotor tasks without risk of intramuscular wire breakage. The surface recordings provide a reference dataset that is broadly applicable to rehabilitation and locomotion research fields. However, the trade-off is that surface electrodes provide less spatial resolution compared to fine wire recordings and are more susceptible to cross-talk. As a result, the ability to separately record flexor digitorum longus (FDL) and flexor hallucis longus (FHL) using surface electrodes was precarious due to their close proximity. We therefore chose to report this measured muscle activity using the composite term FDHL. We note that the FDHL sensor location used in this study was consistent with the FHL electrode placement used by (Sheffield et al. 1956). For the purposes of this study, because FDL and FHL perform similar sagittal biomechanical functions (i.e., ankle and toe flexion), and because prior literature suggests that they exhibit similar EMG activation profiles during forward gait (Perry 1992), the distinction between FDHL, FDL and FHL was not considered critical.

We placed electrodes based on published recommendations (Hermens et al. 2000). For the MTP flexor and extensor muscles the electrodes were placed by palpating the muscle bellies during targeted contraction exercises and orienting the electrodes along the main direction of the fibers (Kendall 2005). The EDB and EHB muscles were recorded from the dorsal surface of the foot, EHL from the anterolateral aspect of the shank, FDB from the plantar aspect of the foot and FDHL just posterior and superior to the medial malleolus.

EMGs were recorded at 4,000 Hz using a wireless system (Delsys Trigno, Boston, MA, USA). The only exception was the FDB, which was recorded using a different, synchronized system (Delsys Bagnoli). Due to the FDB recording site on the plantar aspect of the foot the Trigno electrodes were too thick (15 mm), but lower profile Bagnoli electrodes (6 mm thick) allowed individuals to walk barefoot without discomfort. Both Trigno and Bagnoli electrodes had the same fixed contact spacing (i.e., interelectrode distance) of 10 mm. During the experiments a few EMG electrodes became fully or partially detached and were thus not usable. These were removed on a subject-specific basis (see Table 1). Each subject that we analyzed had usable muscle recordings from at minimum 2 MTP extensors and 1 MTP flexor.

The positions of the right heel (calcaneus) and fifth metatarsal joint were recorded synchronously at 100 Hz using a 9-camera Vicon-612 motion capture system (Vicon, Oxford, UK) and used to define individual stride cycle events. Maximum forward excursion of the heel marker was defined as the start and end of each stride. This event occurs just prior to ipsilateral foot-strike (typically <5 % of the stride cycle in normal forward walking) and was selected as a robust method for dividing gait cycles for various modes of locomotion (Zelik et al. 2014). For graphical presentation purposes, we also approximated stance and swing phases within the stride cycle from foot kinematics. The beginning of stance phase was estimated from the decreasing vertical height of the heel marker (at the end of leg swing) for forward and sideways gait, and from the vertical height of the fifth metatarsal for tiptoe walking. The beginning of leg swing was approximated as the time of maximum backward excursion of the heel during each stride, which was a convenient estimate for treadmill walking.

Data analysis

We processed EMGs using common filtering and rectifying techniques, as described below. Raw EMGs were

Table 1 Muscles analyzed from each participant

Subject	LG	MG	SOL	PL	PB	FDHL	FDB	EHB	EDB	EHL	TA
1	X	X	X	X	X	X	–	X	X	X	X
2	X	X	X	X	X	–	X	X	X	X	X
3	X	X	X	X	X	X	X	X	–	X	X
4	X	X	X	X	X	X	X	X	X	X	X
5	X	X	X	X	X	–	X	X	X	X	X
6	X	X	X	X	X	X	X	X	X	X	X
7	X	X	X	X	X	X	–	X	X	–	X
Total	7	7	7	7	7	5	5	7	6	6	7

de-meaned and then filtered. We applied a 30-Hz high-pass filter, followed by a 50-Hz notch filter (to remove 50-Hz power-line artifacts), then rectified the signal and finally applied a 10-Hz low-pass filter (all filters, zero-lag 3rd order Butterworth). Some subjects exhibited artifacts in the MTP flexor and extensor muscles and in the peroneus muscles, roughly linked to the timing of foot-strike and foot-lift, similar to artifacts observed in prior literature (Sheffield et al. 1956). To remove these artifacts, we applied an additional 150-Hz high-pass filter to these muscle data, which has been suggested to improve measurement of electrophysiological processes, and thus the mapping of EMG to muscle force production (Potvin and Brown 2004). Next, we normalized the EMGs by each muscle's maximum contraction (MC) magnitude, computed from walking trials and a set of quasi-static exercises (Zelik et al. 2014). This normalization was not necessary to assess the temporal activation profiles, but since μV magnitudes can vary markedly between muscles (La Scaleia et al. 2014) this was useful for depicting and differentiating relatively large vs. small activations. We then divided the filtered and normalized EMGs into gait cycles based on foot kinematics and averaged across strides.

We investigated whether the MTP flexor muscles (FDB and FDHL) and MTP extensor muscles (EHB, EDB and EHL) activated synchronously with each other, or with other extrinsic foot muscles (MG, LG, SOL, PL, PB and TA). We examined the period from early stance to late swing (20–90 % of the gait cycle) to avoid muscle activations and transients around foot-strike. Because of the commonly reported burst-like patterns of lower-limb EMGs during gait (e.g., Winter and Yack 1987), we chose to quantify activations by computing the peak timing of muscle activity, which provides a simple, albeit imperfect, summary measure of the muscle activity. In this study, peak timing was preferable to estimating muscle onset activation (and offset deactivation) because we were interested in the functional contributions of various muscles to gait, and EMG magnitude generally scales with and provides an indirect indication of relative muscle force (Lippold 1952; Walmsley et al. 1978). Inter-subject mean, minimum and

maximum peak timing values are reported for each muscle as a percentage of the stride cycle. We then compared each muscle's peak activation timing to that of the other measured ankle and foot muscles. Statistical analysis was performed using repeated measures ANOVA with Sidak–Holm step-down correction, significance level of 0.05, and mean substitution to account for the small number of missing EMGs (Table 1).

We also performed a secondary analysis of relative muscle activation timing by cross-correlating EMGs. For each muscle pairing, we computed the relative time lead/lag of maximum correlation. Similar to the methods described previously, in order to avoid muscle activations and transients around foot-strike, we examined the period from early stance to late swing (20–90 % of the gait cycle) and limited the cross-correlation time shift to ±30 % of the gait cycle. This secondary analysis provided a complementary summary measure that also captured the relative timing of EMG bursts, without depending solely on peak activation timing.

Additional walking conditions

As a follow-up to forward walking, we analyzed two additional ambulation tasks for all subjects ($N = 7$). During forward gait the MTP flexors (FDHL and FDB) exhibited synchronous peak activations, followed by synchronous peak activations of the intrinsic MTP extensors (EHB and EDB, see "Results" for full details). The purpose of studying additional conditions was to determine if the grouped MTP flexor muscles and the grouped MTP extensor muscles continued to activate synergistically, or if these muscle activations differentiated during other gaits. We predicted that dynamic tasks, which placed differing biomechanical demands on the foot muscles, might decouple activations (either in timing or magnitude). To assess the synchronicity of EHB vs. EDB activations, we studied participants walking sideways, which introduced differential mechanical demands on the medial (EHB) vs. lateral (EDB) sides of the foot. We sought to determine if these muscles exhibited temporal differences in their peak activations. We did not have analogous hallucis

(medial) vs. digitorum (lateral) recordings for the MTP flexors measured in this study. Therefore, to assess FDHL vs. FDB we analyzed tiptoe (digitigrade) walking. The plantarflexed configuration of the ankle during tiptoe gait causes the FDHL to slacken but not FDB, and thus we compared the increase in EMG magnitudes for FDB vs. FDHL (relative to their peak EMGs during normal forward walking). Tiptoe walking was performed at 4 km/h (the same speed as the forward walking condition), but sideways walking was performed at 3 km/h because several subjects had difficulty maintaining a higher speed during this task. Sideways gait was performed walking to the left such that the trailing limb never crossed ahead of the leading limb. Statistical comparisons between EHB vs. EDB (during sideways gait) and FDHL vs. FDB (during tiptoe) were performed using two-tailed *t* tests with significance level of 0.05.

Cross-talk validation tests

We recorded surface EMGs from relatively small foot muscles that were in close proximity to each other and to larger muscle groups. Although surface electrodes have previously been used to record various foot muscles during locomotion (Sheffield et al. 1956; Kayano 1986; Arinci Incel et al. 2003), they are susceptible to cross-talk (Farina 2006; Hug 2011). In order to assess potential cross-talk interference, we performed additional validation analyses. First, we performed a validation test on the forward walking EMGs of each subject ($N = 7$) by computing the Pearson correlation of high-pass filtered signals (at 150 Hz). Correlation coefficients >0.2 have previously been used as an indication of potential cross-talk (Yang et al. 2005). Second, based on the EMGs observed during walking the main question we needed to address was: might the MTP flexor activity simply originate from cross-talk of the triceps surae muscles (which had somewhat similar peak activation timings during forward walking, Fig. 1)? We had two participants perform further tests. While seated, participants were instructed to perform a sequence of toe flexion contractions (i.e., flex then relax), without ankle flexion. Next, participants performed similar ankle plantarflexion contractions, in the absence of toe flexion. All contractions were performed with visual feedback from the SOL, MG, LG, FDHL and FDB muscles, and several 10-s trials were recorded for each individual. We used these data to assess our ability to independently record ankle plantarflexion vs. toe flexion muscle activity.

Results

We found that the intrinsic and extrinsic foot muscles exhibited bursts of activity around the stance-to-swing transition during forward walking (Fig. 1; Table 2). In all
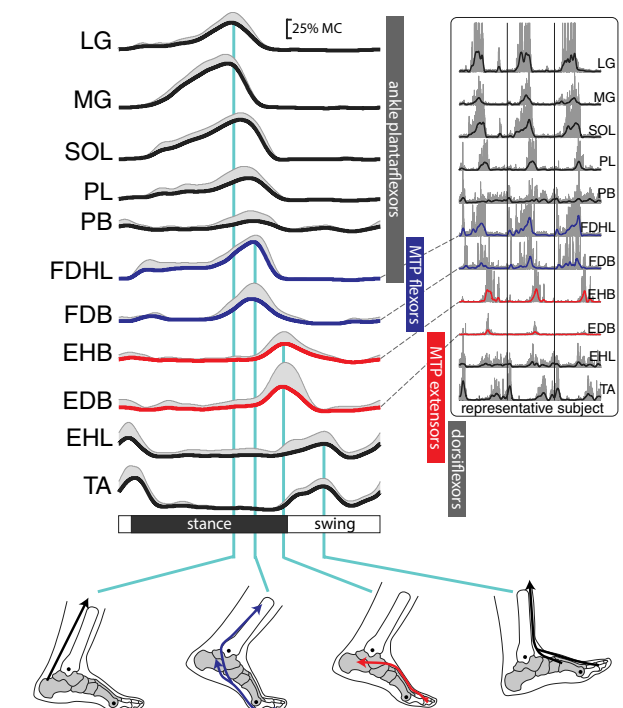

Fig. 1 Progression of foot muscle activity during forward walking. Mean inter-subject EMGs and standard deviations are shown for one stride cycle ($N = 7$). Muscles depicted are: *LG* lateral and *MG* medial gastrocnemius, *SOL* soleus, *PL* peroneus longus and *PB* brevis, *FDHL* flexor digitorum/hallucis longus, *FDB* flexor digitorum brevis, *EHB* extensor hallucis brevis, *EDB* extensor digitorum brevis, *EHL* extensor hallucis longus and *TA* tibialis anterior. Biomechanical muscle functions are shown graphically as *arrows* overlaying the foot skeleton, for the: (1) main ankle plantarflexors (LG/MG/SOL); (2) metatarsophalangeal (MTP) flexors (FDHL/FDB); (3) intrinsic MTP extensors (EHB/EDB); and (4) ankle dorsiflexors (EHL/TA). For clarity, these biomechanical illustrations are depicted sequentially to roughly correspond to peak EMG activity of these muscle groups. But, as evident in the EMG waveforms, burst-like activations were often observed to partially overlap between the groups. *Vertical lines* indicate approximate timing of peak activity for each aforementioned group of muscles, although intra-group peak EMG timing differences were also observed (e.g., between the ankle plantarflexors). EMGs are scaled as a % of *MC* maximum contraction magnitude. *Inset* depicts rectified data with EMG envelope overlaid for three stride cycles of a representative subject

seven subjects we observed that groups of muscles exhibited peak activations in a consistent order: (1) MG/LG/SOL; (2) FDB/FDHL; (3) EHB/EDB, and then (4) TA (Figs. 1, 2). These muscle activations roughly correspond to generation of the following joint torques: ankle plantarflexion, MTP flexion, MTP extension, and ankle dorsiflexion, respectively. Although muscle activations were sequential in terms of peak activity, the burst-like EMGs often overlapped between groups (e.g., MTP flexor burst began before ankle plantarflexor activity had returned to baseline). Other foot muscle activations (PL, PB and EHL) exhibited more variable, subject-dependent timings.

Table 2 Timing of peak muscle activity during forward walking

Muscle	Average	Minimum	Maximum
LG	42.8	40.6	44.8
MG	41.1	37.6	44.1
SOL	47.8	45.1	53.1
PL	50.3	42.3	55.8
PB	58.0	35.9	79.5
FDHL	51.4	47.4	54.3
FDB	51.9	48.5	58.3
EHB	65.6	59.6	72.5
EDB	64.3	60.2	73.6
EHL	67.9	54.5	78.3
TA	77.1	68.2	79.8

Inter-subject mean, minimum and maximum values are reported as percentage of gait cycle (where 0 % corresponds to maximum forward excursion of the heel)

The MTP flexor and extensor activations appeared distinct from most other foot muscles. FDHL and FDB exhibited similar peak activation timings around 52 % of the gait cycle. These were on average within 1 % of the gait cycle of each other (Table 2), a difference that was not statistically significant ($P = 0.89$). However, FDB and FDHL peak activity followed the peak activations of the triceps surae muscles (MG, LG and SOL) by about 3–11 % of the gait cycle, and preceded the MTP extensors and the TA by about 13 and 25 %, respectively. These differences in timing were significant for EDB, EHB, EHL and TA ($P < 0.001$). FDHL and FDB activation timings were not found to be statistically different (after Holm–Sidak

correction) from the remaining triceps surae or peroneus muscles, although several marginal trends were observed (e.g., $P = 0.019$ for FDHL vs. LG, $P = 0.005$ for FDB vs. MG, $P = 0.013$ for FDB vs. LG).

The intrinsic MTP extensor muscles (EHB and EDB) were observed to activate together during walking, with peak activity at about 65 % of the gait cycle (Fig. 1, $P = 0.71$). In 5 out of the 6 subjects with usable recordings from both intrinsic MTP extensor muscles, this difference in peak activation timing was less than 1.5 % of the stride cycle. On average, EHB and EDB peak activation occurred about 16–24 % of the gait cycle after the triceps surae muscles, 13 % after the MTP flexors and 12 % before the TA. Both EHB and EDB peak timings were significantly different from all other ankle and foot muscles ($P < 0.006$), with the exception of the PB ($P > 0.03$) and EHL ($P > 0.31$), both of which exhibited high inter-subject variability. Also, the EHB vs. TA peak timing difference fell just short of significance after step-down correction ($P = 0.002$). The extrinsic MTP extensor (EHL) exhibited more variable peak activation timing, but frequently aligned closely with the TA (Fig. 1). Peak EHL activity occurred significantly later than most ankle plantarflexors (MG, LG, SOL, PL, FDHL and FDB, $P < 0.001$). Peak EHL activity was also, on average, later than the remaining ankle and foot muscles, but these timing differences did not reach statistical significance.

In terms of the EMG activation sequence, cross-correlation analysis yielded results (Table 3) that were qualitatively similar to the peak EMG timing results reported above (Table 2). During forward walking, the time lead/lag at maximum EMG correlation indicated that the burst

Fig. 2 Subject-specific MTP flexor and extensor EMGs. Peak MTP flexor activations (FDHL and FDB) were consistently observed to occur before MTP extensors (EHB and EDB), although there was substantial inter-subject variability in the relative timings and magnitudes of these activations. Approximate stance and swing phases within each stride cycle are depicted as *black* and *white boxes*, respectively
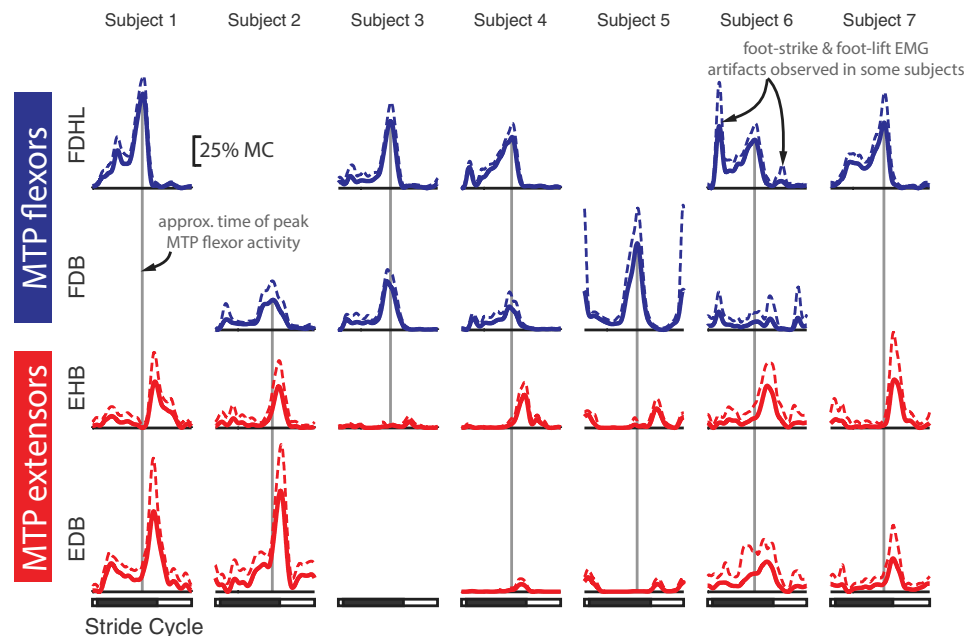
Table 3 Time shift at maximum EMG correlation, relative to MTP flexor and extensor muscles

	FDHL	FDB	EHB	EDB
LG	−5.9 (1.7)	−9.5 (3.2)	−23.5 (3.7)	−21.4 (4.6)
MG	−8.8 (3.0)	−11.5 (4.4)	−26.3 (4.0)	−23.8 (4.2)
SOL	−2.2 (1.8)	−6.5 (4.5)	−20.7 (4.6)	−18.1 (5.5)
PL	1.2 (2.7)	−2.2 (5.1)	−16.2 (6.0)	−15.1 (7.7)
PB	12.3 (14.6)	2.7 (15.0)	−7.5 (14.0)	−5.2 (18.6)
FDHL	0	−0.8 (1.5)	−15.2 (2.2)	−12.4 (0.6)
FDB	0.8 (1.5)	0	−14.5 (6.4)	−12.6 (6.5)
EHB	15.2 (2.2)	14.5 (6.4)	0	0.7 (1.5)
EDB	12.4 (0.6)	12.6 (6.5)	−0.7 (1.5)	0
EHL	17.2 (14.2)	15.9 (11.3)	6.1 (8.6)	8.6 (9.7)
TA	27.3 (2.6)	24.2 (3.6)	10.1 (4.3)	12.8 (5.3)

Inter-subject mean (and standard deviation) is reported as percentage of gait cycle (%)

Cross-correlation was performed between each pair of muscle EMGs (i.e., column vs. row headings)

Positive and negative values represent the time lead and lag, respectively, of the column-header EMG relative to the row-header EMG, when these EMG waveforms were maximally correlated

of triceps surae activity was generally shifted about 2–12 % earlier in the gait cycle relative to the FDHL and FDB muscle activity. EHB and EDB activity was then shifted about 12–14 % of the gait cycle after the MTP flexors, with the TA activity another 10–13 % later.

Functionally similar foot muscles that activated simultaneously during forward walking were observed to dissociate during other tasks (Fig. 3). For instance, peak activation of EHB was found to shift later than EDB during sideways gait ($P = 0.006$). In 5 out of the 6 subjects (with recordings from both intrinsic MTP extensors), we observed a time shift between EHB and EDB greater than 1.5 % during sideways walking; and for 3 subjects this shift was greater than 9 %. In contrast, during forward walking only a single subject exhibited a peak timing difference greater than 1.5 % for EHB vs. EDB. Meanwhile, MTP flexor muscles (FDHL and FDB) were observed to dissociate in activation amplitude during tiptoe gait. FDB activation magnitude increased 5 times more than FDHL (compared to their magnitudes during forward walking, Fig. 3). FDHL and FDB did not, however, differ significantly in peak activation timing ($P = 0.69$).

We carried out additional tests to assess potential cross-talk between the recorded MTP muscle EMGs and other surrounding muscles. We found that the MTP flexors (FDHL and FDB) exhibited little activity during quasi-static ankle plantarflexion, and the triceps surae muscles exhibited negligible activity during toe flexion (Fig. 4). Also, from pairwise comparison of EMGs recorded during forward walking, we found correlation coefficients to
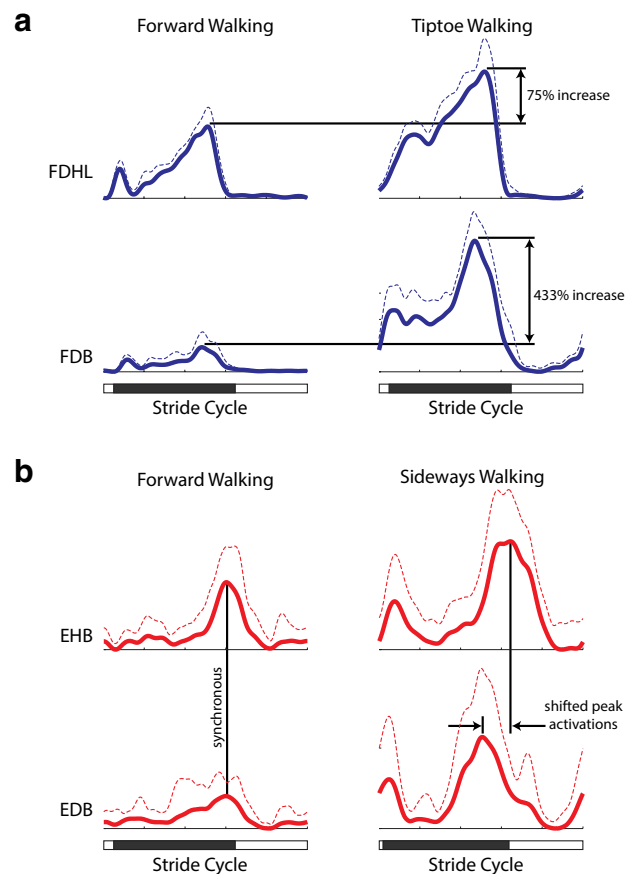

Fig. 3 Decoupling of MTP muscle activations. Mean inter-subject EMGs and standard deviations are depicted ($N = 7$). We observed **a** a differential increase in FDB vs. FDHL EMG magnitude during tiptoe gait (compared to forward walking), **b** a temporal shift in EHB vs. EDB peak activation during sideways gait. Approximate stance and swing phases within each stride cycle are depicted as *black* and *white boxes*, respectively

be less than 0.2, a threshold previously used for identifying potential cross-talk (Yang et al. 2005). Only two exceptions were observed: we found correlations >0.2 between PB and EHL for a single subject, and between PL and EHL in another subject.

Discussion

We found that groups of intrinsic and extrinsic foot muscles exhibited peak activations in a consistent progression during forward walking. The period around stance-to-swing transition could be roughly characterized by sequential peak muscle activity from the ankle plantarflexors, MTP flexors, then MTP extensors and finally ankle dorsiflexors. We did not observe evidence of substantial MTP flexor and extensor co-activation in late stance. The distinct peak activations of the MTP flexors vs. MTP extensors suggest that
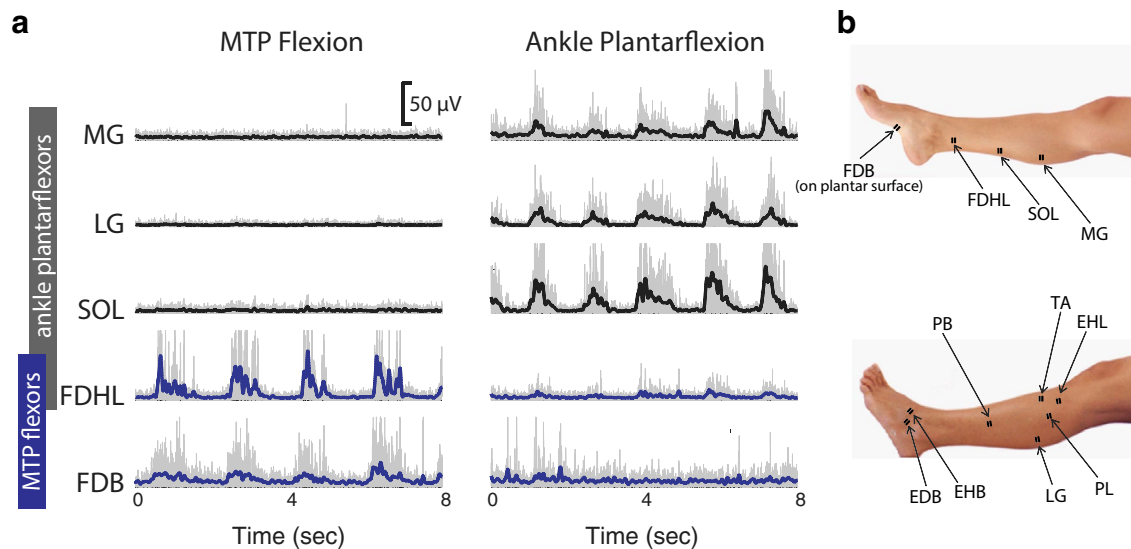
Fig. 4 Cross-talk assessment. **a** Representative data from a single subject demonstrating the ability of surface EMGs to differentiate muscle activations during MTP flexion and ankle plantarflexion with little cross-talk. Rectified data are shown with EMG envelope overlaid. **b** Diagram of surface electrode placement, adapted from La Scaleia et al. (2014)

their biomechanical contributions may be largely separable from each other, and from other extrinsic foot muscles during walking. We also found that the MTP muscles that activated synchronously during forward walking tended to dissociate during the other ambulatory tasks. For instance, peak activation timings of EHB and EDB were observed to decouple during sideways gait, indicating specificity in their function and control. These findings add to a growing body of knowledge related to the behavior of the foot muscles during locomotion. Understanding the general sequence of muscle activity (and the resultant joint kinetics) may be useful for development of assistive and rehabilitative technologies (Zhu et al. 2014), musculoskeletal simulations (Saraswat et al. 2010) and robotic foot emulators (Kirane et al. 2008).

We observed a progression of proximal to distal muscle activity in late stance, followed by a distal to proximal progression during swing (Fig. 1). Functionally, this muscle activation sequence represents contributions to the ankle plantarflexion kinetics, which help redirect the body's center of mass during push-off (Donelan et al. 2002; Zelik and Kuo 2010), followed by an MTP flexion moment near terminal stance phase. The MTP flexor activity has been suggested to support and stabilize the foot arch (Reeser et al. 1983; Fiolkowski et al. 2003), but the muscle–tendon unit may also perform negative work against the extending joint (Siegel et al. 1996). This latter behavior is particularly intriguing because the muscle–tendon unit appears to be absorbing energy, which may detract from the positive work performed by the ankle plantarflexors during push-off (Takahashi and Stanhope 2013). Further study is warranted

to better understand the functional contributions of these MTP flexors. Following the ankle and MTP flexor contractions, the EHB and EDB muscles activate to produce an MTP extension moment around foot-lift, followed by an ankle dorsiflexion moment from the TA activation. Both these actions presumably contribute to foot clearance during leg swing. We note that, due to the time delay between EMG onset and muscle force production (Inman et al. 1952; Cavanagh and Komi 1979), the peak MTP extensor activation appears slightly before the stance to swing (foot-lift) transition in Fig. 1.

There are several caveats to the simplified activation sequence described above. First, some muscles exhibited progressive activation patterns that distinguished them from other EMGs with similar peak timing. For instance, the gradual activation of the FDHL (Fig. 1), beginning from early stance, was generally not evident in the FDB muscle, despite their similar peak activation times. The more gradual activation of FDHL (compared to FDB) may be due to the biarticular nature of these muscles, specifically the contributions to ankle plantarflexion. EMG waveform differences were also observed when comparing activity from the two heads of the gastrocnemius (MG vs. LG). Second, muscles such as the TA and EHL have another major activation peak around foot-strike, consistent with prior literature (Winter and Yack 1987). These foot-strike-related activations were not analyzed in this study. Third, some muscles were grouped together for discussion purposes (e.g., triceps surae). While these muscles serve related biomechanical functions during forward walking, they nonetheless display relative differences in their activation

profiles and durations. Thus, the simplified description in Fig. 1 is only intended to characterize the general progression of peak muscle activity around the stance-to-swing transition, and leaves open the study and interpretation of more subtle differences in the EMG waveforms. Furthermore, MTP muscles that were observed to activate concomitantly during forward gait were also found to dissociate in activation timing and magnitude during other level-ground locomotor tasks (Fig. 3). Finally, we observed substantial inter-subject variability in precise activation timings (Fig. 2; Table 2), as well as in magnitude, similar to what has been reported in previous studies of the foot (De Carvalho et al. 1967; Reeser et al. 1983). Nonetheless, we did find that each individual subject demonstrated the same sequence of muscle-group activity during forward walking. This sequential progression refers to peak EMG activity, and we did observe partial overlap in the burst-like activity between muscle groups.

These findings may also be relevant to the ongoing discussion of modularity within the field of neuromotor control (Tresch and Jarc 2009; Lacquaniti et al. 2013). It has previously been hypothesized that a task-invariant modular strategy, in which the nervous system activates muscles in fixed groups (often termed synergies), may simplify neural control of movement by reducing the dimensionality of neural outputs (Tresch et al. 1999; Ting and Macpherson 2005; Tresch and Jarc 2009). However, the empirical results here indicate that various muscles which appear synergistic in one task, actually dissociate in other tasks. In particular, observations of sideways and tiptoe gaits indicated a high-level of control specificity in individual foot muscles during level-ground locomotion. For example, the EDB and EHB peak activations, which were synchronous during forward walking, were observed to temporally shift (relative to each other) during lateral movement (Fig. 2). Similarly, differences in the activation magnitudes of FDHL and FDB during tiptoe gait suggest a decoupling in the control of these muscles. Dissociation of functionally synergistic foot muscle activations has also previously been observed during stair ascent/descent (Mann and Inman 1964) and curvilinear walking (Courtine et al. 2006). A more comprehensive investigation and discussion of neural modularity is presented in our prior publication (Zelik et al. 2014). The control specificity of the foot muscles during locomotion is somewhat reminiscent of the fine motor control of the hand. It has been postulated that precise control of leg movements is evolutionarily and neurophysiologically linked to the control of arm reaching in mammals (Georgopoulos and Grillner 1989), and morphological observations have suggested the coevolution of the hands and feet (Rolian et al. 2010). Specificity of foot muscle activity has also been observed in rhesus primates (Courtine et al. 2005) and cats (Carlson-Kuhta et al. 1998) during quadrupedal terrestrial locomotion. Our results provide further support for the notion that the foot, rather than acting as a passive base of support, is a flexible and adaptive body segment with precise active control (Wright et al. 2012).

There are various limitations to our study. We recorded a limited subset of intrinsic and extrinsic foot muscles that were accessible via surface EMG recordings, and muscle activity was interpreted as representative of the primary muscles contributing to ankle and MTP flexion–extension. We focused on the sagittal plane, but the foot muscles also contribute to frontal and transverse plane biomechanics (Murley et al. 2014). The use of surface electrodes required tasks to be performed barefoot, and thus it is unclear how EMGs change with footwear. We did not account for individual differences in foot morphology, although all subjects were healthy with no known foot abnormalities or neurological disorders. For clarity, we also limited our study to a temporal analysis of foot muscle coordination. Given the burst-like muscle activations that are typical during walking (Winter and Yack 1987), we chose to use peak timing as a simple metric for assessing coordination. Various other quantification techniques have been proposed to evaluate muscle coordination and/or co-activation (e.g., Rudolph et al. 2001). We have presented one such complementary measure (based on cross-correlation, Table 3), and demonstrated that it yielded results similar to those obtained from quantifying peak EMG timing. Finally, we assessed EMG activity, which is associated with muscle force production, but does not capture muscle contraction dynamics or the behavior of the long elastic tendons in series, both of which require additional measurement modalities to investigate.

A challenge in this study was evaluating the potential issue of cross-talk on surface EMG recordings. It was impossible to completely remove cross-talk interference or to explore each possible source, but the additional validation tests provided evidence in support of muscle recordings with acceptable levels of cross-talk for the purposes of this study. Nevertheless, we note that the FDB recordings may have been affected by cross-talk from the muscles in the deeper plantar layers of the foot; however, since these muscles are also principally MTP flexors, their interference would not be expected to confound the MTP flexor vs. extensor coordination timing question studied here. Intramuscular electrodes would be superior to surface electrodes for further assessing this limitation, but such recordings may also be restrictive on the types of locomotor tasks that can be safely studied.

Conclusions

In summary, we observed a coordinated sequence of foot muscle activations during walking. The progression of

muscle activity involved unique activation of the MTP flexor muscles, followed by the MTP extensors. We did not find evidence of substantial MTP flexion–extension co-activation, suggesting sequential rather than synergistic functional contributions from these muscle groups. Furthermore, the subsets of MTP muscles that did activate together during forward walking were then found to dissociate during other ambulatory tasks. Collectively, these findings provide additional evidence for the actively coordinated participation of the foot muscles during locomotion.

Conflict of interest The authors declare that they have no conflict of interest.

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