Tibialis anterior muscle fascicle dynamics adequately represent postural sway during standing balance

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Submitted 29 April 2013; accepted in final form 15 October 2013

Day JT, Lichtwark GA, Cresswell AG. Tibialis anterior muscle fascicle dynamics adequately represent postural sway during standing balance. J Appl Physiol 115: 1742–1750, 2013. First published October 17, 2013; doi:10.1152/japplphysiol.00517.2013.—To maintain a stable, upright posture, the central nervous system (CNS) must integrate sensory information from multiple sources and subsequently generate corrective torque about the ankle joint. Although proprioceptive information from the muscles that cross this joint has been shown to be vital in this process, the specific source of this information remains questionable. Recent research has been focused on the potential role of tibialis anterior (TA) muscle during standing, largely due to the lack of modulation of its activity throughout the sway cycle. Ten young, healthy subjects were asked to stand normally under varying conditions, for periods of 60 s. During these trials, intramuscular electromyographic (EMG) activity and the fascicle length of three distinct anatomical regions of TA were sampled synchronously with kinematic data regarding sway position. In the quiet standing conditions, TA muscle activity was unmodulated and fascicle length changes in each region were tightly coupled with changes in sway position. In the active sway condition, more EMG activity was observed in TA and the fascicle length changes were decoupled from sway position. No regional specific differences in correlation values were observed, contrasting previous observations. The ability of the fascicles to follow sway position builds upon the suggestion that TA muscle spindles may be well placed to provide accurate, straightforward sensory information to the CNS. As previously suggested, through reciprocal inhibition, afferent information from TA could help to regulate plantar flexor torque at relevant phases of the sway cycle. The proprioceptive role of TA appears to become complicated during more challenging conditions.

Postural sway; human balance; proprioception; electromyography; ultrasound

HUMAN UPRIGHT STANCE, despite requiring little cognitive attention to maintain, is a mechanically unstable posture (32). During normal, quiet standing, the central nervous system (CNS) must integrate sensory information from various sources and subsequently generate corrective torque about the ankle joint (35). This ongoing process results in postural sway which oscillates in both the sagittal and frontal planes (10). In this upright position, the body is often assumed to behave like a single inverted pendulum, where kinematic variables describing body position are coupled throughout the sway cycle and movement occurs about mainly the ankle joints (32, 35).

The three major sources of sensory information during standing are the somatosensory, visual, and vestibular systems (31). The CNS can dynamically adjust the weighting it places on each system based upon the situational context (2, 30, 31).

Under normal circumstances, healthy individuals generally rely heavily on the somatosensory system to maintain balance (15, 31). In particular, it has been traditionally thought that the muscle spindles of the plantar flexor muscles, which are integral in providing corrective torque during standing, are the main source of this somatosensory information (7–9, 29).

Recent evidence however suggests that series elasticity in the plantar flexors may render the proprioceptive task of these muscles complicated (23). A high short-range muscle stiffness, highly compliant tendon, and large amount of efferent activity modulation required to provide corrective torque lead to fascicle length changes that are decoupled from postural sway, commonly referred to as “paradoxical” muscle movement (6, 13, 19, 20, 23). Evidence has shown that passive, sway-driven changes in the plantar flexor fascicles may be at least an order of magnitude less than length changes driven by active modulation (20), suggesting the CNS would have a difficult task extracting an adequate control signal through fusimotor activity (6).

As such, it has recently been proposed that quiescent, unmodulated muscles may be better placed to provide proprioceptive input during quiet standing (6, 20). Of specific interest has been the potential sensory contribution of the primary dorsiflexor, the tibialis anterior (TA) muscle. This muscle is known to play a role in maintaining upright stance, highlighted by detrimental localized effects of vibration (3, 28, 34, 35) and fatigue (1, 10) on balance control. Despite providing some degree of ankle torque when balance is challenged (17, 35), during normal quiet standing the TA remains relatively quiet and unmodulated in activity throughout the sway cycle (6, 31). In the absence of active modulation, it is likely that the length of the contractile elements of TA may change in line with sway-related changes to the total muscle-tendon unit (MTU) length, commonly termed “orthodox” muscle movement (6, 21, 23). Preliminary evidence shows that in the deep proximal compartment of TA (TA PD), this behavior holds true, such that length changes in the fascicles are positively correlated with sway position (6), suggesting that TA PD spindles may be well placed to monitor ankle joint position during quiet standing (6).

Potentially complicating the proprioceptive role of TA muscle is the multiple anatomical regions that exist. In a previous balance study, the proximal superficial compartment of TA (TA PS) did not follow the same behavior as the TA PD compartment. Unlike the deep compartment, the fascicles of TA PS were in fact not synchronized with sway position, implying possible regional specific roles during standing (6). Further, a third distinct distal superficial region of TA (TA DS) also exists (36), the behavior of which has not been ascertained during quiet standing. The finding of regional specific differences between the deep and superficial compartments is surprising...
since generally the regions of the TA are considered homogeneous during a range of more intense contractions (26). The source of this difference is not yet understood (6). It also remains unclear if the behavior of each region changes as the postural standing task becomes more challenging, requiring larger activation of the TA to possibly contribute to the forces required to maintain balance.

The present study therefore aimed to progress this earlier study by Di Giulio et al. (6) by determining the activation and length change of the TA MTU (TA<sub>MTU</sub>) and its fascicles while standing under more diverse and challenging postural conditions, while also investigating surprising differences between the deep and superficial regions of the TA found in this study. Due to the possibility of regional differences, a third, distal TA region will be included in analysis, which was not investigated in the previous study. Based upon previous research into muscle behavior during TA contractions, it was hypothesized that during quiet standing, each region of TA would act similarly and orthodoxically, such that fascicle length changes would be positively correlated with ankle joint displacement (postural sway). In this sense, as subjects naturally swayed forward, TA fascicles would shorten, and vice versa. It was speculated that such positive coupling might be lost as postural conditions became more challenging, where a torque generated by TA might be required, and the elastic tendon tissues subsequently undergo stretch.

**METHODS**

**Participants.** Ten subjects (8 men, 2 women) participated in the study. The mean ± SD for age, height, and body mass was 25 ± 5 yr, 180 ± 10 cm, and 74 ± 15 kg, respectively. Subjects were recruited via word of mouth throughout the university. Subjects were physically active and did not report any disorders, injuries, and contraindications that would affect their ability to control standing posture or safely participate in the study. All participants gave written informed consent prior to participation. The study protocol and procedures were approved and endorsed by the university’s principal human ethics committee, which is registered with the Australian Health Ethics Committee as complying with the National Statement. The study was conducted in accordance with the Declaration of Helsinki.

**Protocol.** Prior to testing, subjects were asked to perform maximum voluntary efforts (MVE) in both plantar flexion and dorsiflexion for electromyography (EMG) normalization purposes. Subjects were then asked to stand in a comfortable position on a hard, flat surface. For standardization and repeatability purposes, each subjects’ feet were positioned with their heels approximately 14 cm apart and the location of both feet was traced on a piece of graph paper taped to the surface in order to ensure a similar standing position if the subject moved between trials. In this position, subjects completed two blocks of seven 60-s trials. During the first block of trials an ultrasound probe was positioned to record fascicle length from the two proximal regions of TA (TA<sub>PS</sub> and TA<sub>PD</sub>), while the length of the distal fascicles (TA<sub>DS</sub>) was recorded during the second block of trials. For each block, subjects completed four different balance conditions, presented in a pseudorandom order, designed to challenge balance at varying levels. The conditions included two trials each of quiet standing with either eyes open (EO) or eyes closed (EC), two trials varying levels. The conditions included two trials each of quiet standing with reduced base of support (RBOS), and one trial while standing with a reduced base of support (RBOS), and one trial of active sway, where the subject was asked to consciously control their sway. In the EO and EC conditions, subjects were asked to perform a simple arithmetic task aloud to shift the focus of their attention away from the postural control task. For the RBOS condition, subjects were asked to stand on a narrow beam (8.5 cm wide and 1.7 cm high) placed under the ball of the foot and aligned with the ML axis to increase AP sway. Subjects were instructed to keep both their toes and heel off the ground while standing on the wood. For the active sway condition, subjects were asked to sway in time with a metronome set at 0.2 Hz and a self-selected amplitude as close to the subject’s limits of stability as they could comfortably obtain. This condition was selected to observe TA behavior under voluntary control. During each trial, subjects had their arms positioned across their chest and, if required, their feet were repositioned to match the initial tracing. Subjects were given approximately 60 s of rest between each trial to avoid any effects associated with possible fatigue.

**Motion capture.** An eight-camera, three-dimensional (3D) optoelectronic motion capture system (Oqus, Qualisys AB, Gothenburg, Sweden) was used to measure body position while standing and subsequently estimate various kinematic variables relating to postural sway. Eleven spherical reflective markers (38 mm in diameter) were attached to each subject’s right-sided foot, shank, and thigh using double-sided tape. The configuration of the marker placement was adapted from a previous study (18) and consisted of markers at the heads of the first and fifth metatarsals, the navicular tuberosity, the base of the fifth metatarsal, the calcaneus, the medial and lateral malleoli, 2-mm clusters on the shank, and lateral condyles, the tibial tuberosity, and the greater trochanter. In addition, three rigid lightweight clusters (~5 × 10 cm) of three or four spherical reflective markers were secured to the right-sided foot, shank, and thigh using double-sided tape. The position data were sampled at 200 Hz using specific motion analysis hardware and software (QTM, Qualisys AB, Gothenburg, Sweden) prior to being exported for offline analysis in commercially available software (Visual 3D, C-Motion, Kingston, Canada). Prior to testing, a static standing trial was completed to assist in the development of a lower-limb model, after which the specific markers were removed, leaving only the three clusters on the respective segments during testing trials.

**Electromyography.** Pairs of single-strand, teflon-coated, stainless steel wire (75 µm bare, 140 µm coated, half hard, A-M Systems, WA) were used to record intramuscular EMG from three distinct regions of the TA muscle (TA<sub>PS</sub>, TA<sub>PD</sub>, and TA<sub>DS</sub>). Approximately 2 mm of insulation was removed from each wire to produce an active recording site. Wires were then inserted into the lumen of a single-use hypodermic needle (0.5 × 38 mm, BD Technologies) and bent to produce a hook before being sterilized. The site and required depth of each electrode pair were identified using ultrasound (Echochamber, 128, UAB, Telemed, Vilnius, Lithuania) prior to the skin being shaved, cleaned, and disinfected. Electrodes were needle delivered into the muscle so that the tips of the wires were approximately 5 mm apart. The needles were then carefully removed leaving the hooked wires remaining in the muscle. The location of the tips of the wires was again verified using ultrasound. A surface reference electrode (1.5-cm diameter, Ag/AgCl, Covidien, Mansfield, MA) was placed over the right patella after cleaning and lightly abrading the skin. Intramuscular signals were amplified 350–2,000 times (MA300, Motion Lab Systems) depending on signal strength, and band-pass filtered between 30 Hz and 5 kHz, prior to being sampled at 10 kHz using a 16-bit Power 1401 and Spike2 data collection system (Cambridge Electronics Design, Cambridge, UK).

**Muscle fascicle visualization.** The ultrasound system used for electrode insertion was also used to record TA muscle fascicle length changes at a sampling frequency of 40 Hz. A flat, 96-element, linear, multifrequency probe (LVT7.5/60/96, Telemed, Vilnius, Lithuania) was used in B-mode with a frequency of 6 MHz, a field of view of 65 mm, and a focus range of 18–26 mm to visualize TA fascicles.

The onset of ultrasound recording was used to synchronize all data signals to a common start time.

**Data and statistical analysis.** A 3D multisegment model with foot, shank, and thigh segments was scaled and fitted to the kinematic marker data using inverse kinematics (24). TA<sub>MTU</sub> length was estimated by creating a virtual muscle from digitized landmarks from the origin (inferior lateral corner of tibial tuberosity) to the insertion point.
The position of the greater trochanter marker was also sampled as an estimate of center of mass position (COM\textsubscript{est}). The calculated AA contained movements in three anatomical planes. Since TAMTU length can be driven by both plantar/dorsiflexion and inversion/eversion of the ankle, a multiple linear regression model was used to assess the amount of TAMTU length accounted for by each of these movements. Using Matlab (Mathworks, R2011a, Natick, MA), four separate regression models were calculated for each muscle region and the total TAMTU length. The three dimensions of ankle movement (dorsiflexion/plantar flexion, inversion/eversion, and internal/external rotation) were used as explanatory variables, and then either fascicle length from a region of the TA (deep, superficial, distal) or TAMTU length calculated from the 3D motion capture system were used as dependent variables. Normalized beta weight and R-squared values were obtained and grouped by condition.

EMG data were processed offline using scripts written in commercially available software (Spike2, Cambridge Electronics Design, Cambridge, UK). The root-mean-square (RMS) amplitude was calculated from the detrended EMG signal sampled during the MVE and for all test trials. EMG data from the trial conditions was then normalized to the EMG values obtained during MVE.

Ultrasound images were exported from the collection software as a video file for analysis by custom-written tracking algorithms implemented in Matlab, described in detail elsewhere (5, 11). To summarize, the muscle region of interest and fascicle end points were manually selected in the first frame of the trial. The tracking algorithm then automatically tracked the movement of the region of interest using a least squares fit of an affine transformation and applies the movement to the two end points of the muscle fascicle with submillimeter accuracy. The instantaneous fascicle length and pennation angle values for the respective fascicle were calculated based on the line between the two fascicle end points at each frame throughout the trial.

All data were imported into Matlab as time-series data for further analysis. Using custom-written scripts, each signal was filtered using a zero-phase, fourth-order, low-pass Butterworth filter with a cut-off frequency of 6 Hz to remove unwanted high-frequency components. For each trial, the total angular distance traveled and SD of the AA signal were calculated. The SD of the fascicle length signals was also calculated to assess the variability of the changes in the fascicle lengths over the trial.

The AA position signal was then cross-correlated with the respective fascicle length for each TA region. Prior to cross-correlation analysis, the two previously detrended signals were resampled to a common frequency of 100 Hz. At a range of temporal time shifts, a cross-correlation coefficient was calculated such that signals were iteratively shifted with respect to each other in steps of 1 ms up to a maximum temporal time shift of ±1.5 s. For each condition and ultrasound location pair, the cross-correlation time series was combined to provide a mean cross-correlation curve. This was plotted with standard error of the mean (SEM) to visually represent the mean cross-correlation output of the group. The absolute maximum value and the respective time-shift of this curve were then found as an indication of the average relationship between the relevant variables for the particular condition and location pair. The same cross-correlation analysis was completed between the AA signal and the previously rectified, detrended and RMS smoothed EMG signal from each region. The cross-correlation analysis used in this study was taken across the whole trial. Although previous studies have used smaller windows to provide an estimate of time spent within certain behaviors (6), we found this was highly sensitive to the window size chosen, and as such, have only considered the whole trial signal.

Descriptive statistics and cross-correlation measures were grouped according to trial condition prior to statistical analysis using commerc-

Fig. 1. A 60-s sample from an eyes open trial from a representative subject showing estimated center of mass position (COM\textsubscript{est}), ankle angle (AA), length of the tibialis anterior (TA) muscle-tendon unit (TAMTU), and the length of the fascicles in the proximal, superficial compartment of the TA muscle (TAPS FL). Forward sway is indicated by the direction of the arrow and is associated with a decrease in COM\textsubscript{est} position.
cally available software (Prism 5, Graphpad Software, La Jolla, CA). For the kinematic and fascicle length descriptive statistics, either a one-way analysis of variance (ANOVA), with a condition (EO vs. EC vs. RBOS vs. Active) factor, or a two-way ANOVA, with condition (EO vs. EC vs. RBOS vs. Active) and muscle region (TAPS vs. TAPD vs. TADS) as factors, were performed. All grouped data are reported as means ± SD unless otherwise stated, while figures are reported as means ± SEM for clarity. Statistical significance was set as \( P \leq 0.05 \). The mean cross-correlation coefficients for each variable pair were assessed using the scale described by Cohen (4) as a guide: small relationship (0.1–0.3), moderate relationship (0.3–0.5), or large relationship (0.5–1.0).

RESULTS

Inspection of three kinematic variables relating to postural sway (AA, COM\textsubscript{st} and TA\textsubscript{MTU}) revealed a strong coupling between all measures during the EO (Fig. 1), EC, and active sway trials. Analysis of the contribution of the three anatomical ankle movements on TA\textsubscript{MTU} length revealed that the majority of TA\textsubscript{MTU} length change, calculated from the lower leg model, was driven by plantar flexion/dorsiflexion motion. For EO, EC, and RBOS trials, the majority of TA\textsubscript{MTU} length change (normalized beta weight of \(~0.8\)) or fascicle length (normalized beta weight of \(~0.4\)) can be explained by plantar/dorsiflexion, with lower beta weights for both inversion/eversion and internal/external rotation. As such, AA changes in the inversion/eversion plane were discounted from further analyses, with AA in the plantar/dorsiflexion plane subsequently chosen as the best parameter to describe sway. This was done under the assumption that subjects exhibited motion in line with a single-inverted pendulum model during these trials. For the RBOS condition, subjects exhibited more complex, multi-segment strategies, involving movement at the knee and hip joints, and as such, other kinematic measures have been used to describe movement during this condition.

Two separate one-way ANOVAs revealed a significant main effect of condition for both AA SD \([F(3,136) = 53.56; P \leq 0.01]\) and AA amplitude \([F(3,136) = 16.49; P \leq 0.01]\), such that an increase in both measures was found with increasing postural demand. Specifically, post hoc analysis highlighted that each measure was similar between the EO and EC trials, but were significantly larger during both the RBOS and active sway conditions (see Fig. 2A, \( P \leq 0.05 \)). Further, for the RBOS condition, large movements were observed at the knee joint, which were not apparent for the other conditions. This suggests that both RBOS and active sway were effective in inducing postural sway beyond normal values.

In analyzing movement of the fascicles in each region, a two-way ANOVA revealed there was no significant main effect for each muscle region or condition; however, significant interaction effect between muscle region and condition was found for both fascicle length change SD \([F(6,192) = 2.91; P \leq 0.05]\; Fig. 2] and fascicle length change amplitude \([F(6,192) = 2.57; P \leq 0.05]\; Fig. 2]. Similar to postural sway measures, post hoc analyses revealed that fascicle length amplitude and SD during normal standing (EO and EC) was significantly less \((P \leq 0.05)\) than during both RBOS and active sway, suggesting the difficulty in balance highlighted through ankle angle changes was also reflected at a neuromuscular level. The only significant difference between muscle regions occurred during the RBOS condition, where fascicle length amplitude and SD were smaller for the TADS in comparison to the two proximal regions (TAPS and TAPD, \( P \leq 0.05 \)).

For TA intramuscular EMG RMS, a significant main effect was found for condition \([F(3,387) = 32.32; P \leq 0.05]\), but no region main effect was observed, suggesting that there were no differences between activation levels in regions of the muscle. When the data were averaged between TA muscle regions (Fig. 3), post hoc analysis revealed that activity levels were

Fig. 2. Grouped mean ± SE bars of selected kinematic signals depicting sway and muscle movement. Data are grouped according to trial condition: eyes open (EO; open bar), eyes closed (EC; closed bar), reduced base of support (RBOS; light gray bar), and active sway (Active; dark gray bar). The specific signals variables shown are ankle angle standard deviation (AA SD) (A), ankle angle amplitude (AA amp) (B), fascicle length standard deviation of the proximal superior region of the TA (FL\textsubscript{ps} SD) (C), and fascicle length amplitude of the proximal superior region of the TA (FL\textsubscript{ps} amp) (D). *Significant difference between values. Differences that are nonsignificant are indicated by NS.
revealed that, during quiet standing, there was no clear correlation between variables for any condition or TA muscle region. This is likely due to the low level of TA activation and lack of modulation in its activity during the EO, EC, and RBOS condition, and an activation pattern during active sway that was not consistent between subjects, albeit relatively large in amplitude.

In contrast, clear correlations were observed between soleus EMG and AA (Fig. 5). In both EO and EC, there was a peak negative cross-correlation (−0.35 and −0.39, respectively) that was observed at a slight negative time shift (−0.26 and −0.15 s, respectively), indicating that the soleus EMG activity was at its greatest just before the most forward point in the sway cycle. A similar, but stronger, relationship was seen for active sway (−0.54), although the time shift was not present. For the RBOS condition, this relationship was opposite, with peak positive correlation (0.30) occurring with a slightly negative time shift (−0.32 s), indicating that the soleus EMG was at its greatest just before the AA reached its most forward position.

**DISCUSSION**

The purpose of this study was to determine and compare the activation and length change of the TA muscle and its fascicles within three distinct regions while standing under a range of postural conditions. It was hypothesized that during normal quiet standing, the contractile element of the TA would be tightly coupled to sway related changes in AA, and as such, the fascicles would be well placed to give sensory information regarding sway, which has been previously observed in the deep TA compartment (6). Further to this, it was proposed that there would be no distinct differences between the type of behavior (paradoxic or orthodoxical) exhibited by each of the three anatomical regions. Last, it was thought that as the postural task became more difficult, and the contraction levels required by the TA were greater, this orthodoxical relationship would be lost.

The results of the present study support each hypothesis. Orthodox behavior, whereby the fascicles of the TA follow sway related changes in total MTU length, was observed for all muscle regions during both quiet standing conditions, where TA activation levels were relatively low (−4% of MVE). Surprisingly, this orthodoxical behavior also existed for the challenging RBOS condition, where a larger activation of the TA was required (−7% of MVE), which we initially hypothesized would act to decouple fascicle length changes from postural sway-driven AA changes. Such decoupling was confirmed in the active sway condition, where the activation observed was significantly larger again (−18% of MVE), and a consistent relationship (orthodoxical or paradoxic) between fascicle length and AA was not found.

**Proprioceptive potential of the TA muscle.** Notwithstanding differences between regions, the present study builds upon the proposition put forward by Di Giulio et al. (6) that the deep compartment of the TA could provide accurate proprioceptive information to the CNS regarding sway. The information presented here suggests that perhaps a broader and more general role could exist throughout the whole muscle. As has been argued previously, it is likely that the CNS would preferentially select the simplest source of sensory feedback during

![Fig. 3. Grouped mean ± SE bars of the electromyography (EMG) root mean squared (RMS) from the pooled intramuscular EMG from each region of the TA muscle (A) and the surface EMG of the soleus (SOL) muscle (B). EMG levels are reported as a percentage of the respective maximal voluntary effort (MVE) EMG of the specific muscle. Data are grouped according to trial condition: EO, open bar; EC, closed bar; RBOS, light gray bar; active sway, dark gray bar. *Significant difference between conditions, indicating that TA remained relatively quiet during quiet standing. Differences between the former three conditions were not significant.](http://jappl.physiology.org/doi/10.1152/japplphysiol.00517.2013/fig-3)
sway (6). Despite having a long, compliant tendon and apo-
neurosis (27), the lack of active modulation during quiet
standing means that sway-driven changes in the total MTU are
reflected in proportional length changes of its contractile fibers.
With these fascicles acting homogeneously throughout the
whole muscle, as observed in the present study, this task seem-
ingly becomes simpler for the CNS, suggesting that the proprio-
ceptive role may be more likely than initially thought (6).

As suggested previously, providing that extrafusal fibers
within the muscle follow the movement of fascicle length
changes, the Ia afferent signals from the TA could be used to
shape specific and precise control signals to the plantar flexor
muscles at relevant positions throughout the phase cycle in
order to appropriately modulate activity and generate necessary
corrective torque (6). In anesthetized cats, spindle activity from
the lower leg muscles has been shown to be directionally tuned
and highly sensitive to small balance disturbances (14), partic-
ularly after a period of relative constant muscle length, such as
would occur in normal standing (16). It has also been shown
that reciprocal inhibition from unmodulated antagonist mus-
cles can be utilized to alter the persistent inward current from
the brain stem, such that specific control patterns targeting the
agonist muscles can be generated (12). This would explain
observations of the ability to maintain a stable posture using
only ankle proprioception (8) and H-reflex modulation in the
soleus pathway at different sway positions (33). Nonetheless, it
should be noted the actual drive from the TA muscle spindles,
and how this information is modulated and used by the CNS,
are well out of reach of the present study. As such, it should be
stressed that this study only shows that the conditions for
acting as a quiet listener are favorable in the TA; we cannot
ascertain directly if this role is actually performed.

**Effect of task difficulty.** While the observation of orthodox
behavior during quiet standing was expected, it was thought
that as the standing task became more demanding, and required
larger activation of the muscle, the fascicles of the TA would

Fig. 4. Grouped mean (solid line) ± SE of the mean (dotted line) cross-correlation signals for a range of TA regions and trial conditions. The cross correlations were calculated between the fascicle length and ankle angle signals during each 60-s trial. The cross-correlation coefficient (r) is located on the y-axis and ranges from −1 to +1. The temporal time shift in seconds is located on the x-axis and ranges from −1.5 to +1.5 s. The graphs are grouped vertically by muscle region and horizontally by trial condition. The muscle regions of the TA were the proximal, superficial (TAps; left), proximal, deep (TAPd; middle), and distal, superficial (TADS; right). Trial conditions were EC (A), EO (B), RBOS (C), and active sway (D).
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Fig. 5. Grouped mean (solid line) ± SE of the mean (dotted line) cross-correlation signals \( r \) calculated between the soleus electromyography (EMG) and ankle angle signals during each 60-s trial. The cross-correlation coefficient \( r \) is shown on the y-axis, ranging from −1 to +1 in value. The temporal time shift in seconds is located on the x-axis and ranges from −1.5 to +1.5 s. The four graphs are grouped by conditions, specifically EC (A), EO (B), RBOS (C), and active sway (D).

The tendon leads to overall length changes in the total MTU that are largely taken up by the tendon rather than the fascicles (13, 22, 23). As such, despite the total MTU length of the TA being positively correlated with AA, the high activity required in this voluntary, active sway task prevents fascicle length changes, and potentially TA spindle activity, from accurately indicating postural sway position. Instead, in this situation it is likely that the CNS preferentially uses other sources of sensory systems such as vestibular, visual, or other somatosensory systems (31).

For the RBOS condition, contrary to our initial expectations, subjects generally showed an orthodox behavior, with tight coupling between the fascicle length changes and AA displacement. In this condition, despite larger amounts of AA movement compared with normal standing, there was only a small, nonsignificant increase in TA activity for each region. Further inspection of other kinematic variables showed that subjects generally used a multisegment strategy to maintain balance, whereby movements of the hip and knee joints, as well as upper limb and trunk movement, occurred in combination with AA changes, rendering the inverted pendulum model invalid. As such, interpretation of the fascicle length movement became difficult. It is likely, since these multisegment movements involved large muscle groups, that significant TA torque production was not required and that the fascicles remained well placed to indicate AA position. This is supported by our EMG data, which suggest that the TA activity in the RBOS condition was not significantly different from that during quiet standing conditions with the eyes open or closed. It remains questionable however whether this signal is meaningful to the CNS since AA no longer can give an accurate indication of the COM position.

Regional specific observations. This study falls in line with previous investigations into regional areas of the TA which suggest homogeneous behavior throughout the muscle (25), although this is in contrast to the regional differences observed by Di Giulio et al. (6). In this previous study, differences between the deep and superficial TA compartments were attributed to slight differences in anatomical structure, underlying differences in activity or issues with the orientation of the probe (6). That these results were not replicated in the present study, nor in other TA investigations, suggests that the anatomical explanations for the opposing behavior are unlikely, although they cannot be ruled out by the present study. Interestingly, in the present study, there was a difference found between the distal fascicle length amplitude and SD compared with the other compartments during the RBOS condition, although the orthodoxal relationship with sway was maintained.

A more likely explanation for the different regional results to that of Di Giulio et al. (6) is differences in the methods applied to measure and calculate muscle length changes as well as determine the relationship to sway cycles. The primary difference between our ultrasound techniques and those reported previously are 1) the tracking algorithm and measurement; and 2) the ultrasound setup. A preliminary analysis comparing the results of using our method to track fascicle length changes versus the cross-correlation technique to track net longitudinal length changes between the superficial and deep aponeurosis of both compartments demonstrated very similar length changes for the same trial (see Supplementary Video, available with the online version of this article). Hence we believe that the differences are more likely related to how the transducer is

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attached to the leg and potential changes in orientation of the probe that cause regional differences in the track muscle positions. Our flat-shaped transducer eliminates much of this potential movement as it ensures the image is always perpendicular to the skin, regardless of leg position.

Finally, the correlation method of binning the signals of interest used in the previous study (6) rather than using a more common cross-correlation technique may lead to incorrect interpretations of relationships between the variables. We have found theoretically, by using sine waves with similar characteristics to postural sway, that this analysis is highly sensitive to 1) the window size chosen, 2) any time shift between the two signals, and 3) any changes to the relationship between the signals over the course of the trial. In this analysis, the contextual significance of a time shift between two signals (highly common in biological signals) is lost and simply seen as an increase in “negative” correlation. This is discussed briefly in the previous study whereby a range of bin sizes was trialed to choose the most meaningful size (6); however, we feel that choosing a bin size for the whole trial is difficult for postural sway, which tends to vary in characteristics over the long term. If there were differences between the deep and superficial signals relating to the probe and/or tracking algorithm, this type of analysis may have exacerbated them.

Conclusion. The present study builds upon evidence that the TA is well placed to act as a listener of postural sway during quiet standing. Due to its low, unmodulated activity during normal standing, TA fascicles throughout the muscle change length in line with sway-driven AA changes, allowing its spindles to accurately convey sway position. This behavior holds true for each region of the muscle, which, unlike a previous study, suggests a broad, simplistic proprioceptive role for the TA muscle. It is likely that Ia-afferent activity from TA spindles is subsequently used by the CNS to help monitor and maintain balance, and could potentially be used via reciprocal inhibition as a method of modulating plantar flexor activity at relevant phases in the sway cycle. In tasks of increasing postural demand, where greater TA activation is required, the orthodromic relationship of fascicle length change with sway position can be lost and is likely due to the increased contractile stiffness in the muscle, which sees most of the MTU length change take place in the compliant tendon, thereby rendering the proprioceptive function of the TA spindles less effective.

ACKNOWLEDGMENTS

We acknowledge the contribution of S. Brennan, who assisted with data collection and data processing.

GRANTS

This study was not funded by any granting agency. Infrastructure support came from The University of Queensland. J. T. Day is supported by an Australian Postgraduate Award.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS


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