Foot anatomy specialization for postural sensation and control

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Foot anatomy specialization for postural sensation and control. J Neurophysiol 107: 1513–1521, 2012. First published December 7, 2011; doi:10.1152/jn.00256.2011.—Anthropological and biomechanical research suggests that the human foot evolved a unique design for propulsion and support. In theory, the arch and toes must play an important role, however, many postural studies tend to focus on the simple hinge action of the ankle joint. To investigate further the role of foot anatomy and sensorimotor control of posture, we quantified the deformation of the foot arch and studied the effects of local perturbations applied to the toes (TOE) or 1st/2nd metatarsals (MT) while standing. In sitting position, loading and lifting a 10-kg weight on the knee respectively lowered and raised the foot arch between 1 and 1.5 mm. Less than 50% of this change could be accounted for by plantar surface skin compression. During quiet standing, the foot arch probe and shin sway revealed a significant correlation, which shows that as the tibia tilts forward, the foot arch flattens and vice versa. During TOE and MT perturbations (a 2- to 6-mm upward shift of an appropriate part of the foot at 2.5 mm/s), electromyogram (EMG) measures of the tibialis anterior and gastrocnemius revealed notable changes, and the root-mean-square (RMS) variability of shin sway increased significantly, these increments being greater in the MT condition. The slow return of RMS to baseline level (>30 s) suggested that a very small perturbation changes the surface reference frame, which then takes time to reestablish. These findings show that rather than serving as a rigid base of support, the foot is compliant, in an active state, and sensitive to minute deformations. In conclusion, the architecture and physiology of the foot appear to contribute to the task of bipedal postural control with great sensitivity.

foot deformation; proprioception; human posture control

THE HUMAN FOOT IS A UNIQUE structure, formed by numerous bones and joints and fastened by the three layers of ligaments. Human foot bones are arranged to form three strong arches: two length ways and one across the foot. Ligaments bind the foot bones together along with the tendons of foot muscles. This helps to hold our foot bones firmly in the arched position but still allows some give and springiness. It is known that during locomotion (especially in running), the foot arch is subjected to considerable deformations, resulting in elastic energy storage in the longitudinal foot arch for propulsion. From the biomechanical viewpoint, the foot is typically considered as a “functional unit” with two important aims: to support the body weight (static foot) and to serve as a lever to propel the body forward in walking and running (dynamic foot; Bramble and Lieberman 2004; Ker et al. 1987; Morton 1935; Ridola and Palma 2001). However, support of the body weight in the erect posture involves not only the counterbalancing of the gravitational load, but also equilibrium maintenance, which is dynamic in nature.

The inverted pendulum is often used as a model of bipedal human posture (Clifford and Holder-Powell 2010; Fitzpatrick et al. 1994; Gatev et al. 1999; Maurer et al. 2006; Morasso and Schieppati 1999; Vette et al. 2010; Winter et al. 2001). A multijoint plant for posture control also typically implies a rigid foot body (Kiemberl et al. 2008). Yet, the two areas, arch structure and toes, which have been identified as critical in gait because of the large range of motion displayed in the ankle and proximal interphalangeal joint, are also involved in posture. Furthermore, there are additional sources of deformation that are of similar magnitude as in the ankle and toes during quiet standing (QS). For example, there are the longitudinal and transverse arches as well as the soft tissue on the plantar surface both under forefoot and calcaneus (Hicks 1955; Scott and Winter 1993). Accordingly, somatosensory information on local foot deformations can be provided from numerous receptors in the foot arch ligaments, joint capsules, intrinsic foot muscles, and cutaneous mechanoreceptors on the plantar soles (Fallon et al. 2005; Gimmon et al. 2011; Kavounoudias et al. 1998; Magnusson et al. 1990; Meyer et al. 2004; Schieppati et al. 1995).

What is the role of the vaulted configuration of the foot in the equilibrium maintenance? In a previous study (Gurfinkel et al. 1994), we showed that support surface or body inclinations by approximately 1–1.5° relative to the vertical were accompanied by not only the changes in the ankle joint angle, but also a noticeable plantar surface skin compression. The vertical displacements of the calcaneus recorded by means of a clamp rigidly fixed at the heel were 0.5 ± 0.3 mm° during body tilt in the anterior-posterior (A/P) direction, and the corresponding foot compliance was 0.04 ± 0.03/Nm (foot pitch tilt per unit torque change in the ankle joint), so that the actual changes in the ankle joint angle were estimated to be only half of those expected when considering the foot as a rigid body firmly attached to the ground (Gurfinkel et al. 1994).

It is also known that under limb loading, the height of the longitudinal foot arch decreases. In young adults, a navicular drop and medial longitudinal arch deformation during QS were 5.0 ± 2.2 mm and 3.5 ± 2.6°, respectively (Bandholm et al. 2008). The height of the dorsum changes by ~4 mm during changes in load from 10 to 90% body wt. In the study of McPoiil et al. (2008), the mean difference in dorsal arch height between nonweight bearing and weight bearing was even 10 mm. These values characterize foot arch deformations under significant changes in limb loading. However, it might be that during QS, the foot is also subjected to some deformations due to the center-of-body-mass (COM) displacements. The extent of deformations may, in fact, turn out to be not so negligible.
when taking into account the large body weight and, consequently, the large load on the feet. By visual observation alone, flattening of the foot arch during QS has been reported (Di Giulio et al. 2009). Therefore, even a small deformation could yield relatively large errors in the measured changes of the ankle joint angle. If so, what could be the functional significance of such deformations and their consequences?

To answer to these questions, it is important to ascertain the presence or absence of foot deformations under normal postural conditions. This was our first goal. In the case of the positive result and knowing the parameters of deformations, one might further question what the postural consequences of specially evoked deformations of the foot arch could be. To this end, in our study, we (1) quantified foot deformations in the sitting position under stationary foot loading corresponding approximately to the amplitude of postural foot pressure oscillations (protocol 1), (2) quantified foot deformations during QS (protocol 2), and (3) applied very small perturbations of the foot arch by elevating the metatarsals (MT) or toes during QS (protocol 3). The results are discussed in context of the contribution of foot deformations to the actual changes of the ankle joint angle and body sway during QS and their role in the posture control mechanisms.

METHODS

Subjects

Twelve healthy subjects (8 women and 4 men) between the ages of 26 and 44 (33 ± 5 yr), with an average height of 171.6 ± 7.9 cm, an average weight of 75.0 ± 15.5 kg, and no known neurological, vestibular, or neuromuscular impairments participated in this study. All subjects gave informed written consent to participate in the institutional review board-approved protocols conducted in this study, in accordance with local ethical regulations for human subjects studies and the Declaration of Helsinki.

Equipment and Experimental Paradigm

Protocol 1: quantification of foot arch deformation. To quantify foot arch deformation under stationary loading (Fig. 1A), subjects (n = 7) were seated on a stable armless chair. Its height was adjusted to keep the thigh approximately horizontal with knees and ankle slightly flexed past 90° so that the shank vertical orientation was about the same as that during normal upright standing. The subject was fully seated without back support with the feet in a natural, relaxed state, flat on a stable, fixed, horizontal surface (AMTI force plate, Watertown, MA). A linear displacement transducer (Series 200; Trans-Tek, Ellington, CT) was placed either on left foot dorsum (Fig. 1A) approximately over the cuneiform bones but avoiding dorsiflexor tendons (e.g., extensor hallucis longus) or at the head of the 1st MT (MT1; in separate trials). The force applied by the transducer was <0.1 N, and no subject was aware of changes in the skin pressure of the probe on the foot dorsum. This device was placed to measure changes in the height of the foot arch when loaded and unloaded with 10-kg weight on the knee. The rationale for using a 10-kg weight was that this load imitates approximately the amplitude of natural oscillations in the forefoot and heel loading during QS. We were interested here not in the deformations of the foot that occur due to large foot loadings (Bandholm et al. 2008; McPoil et al. 2008) but rather the deformations due to a redistribution of loading between anterior and posterior foot parts caused by displacements of the COM. Given that the center of pressure (COP) is located 4–5 cm in front of the ankle joint axis, redistribution of pressure does not exceed 4–8% body wt during QS. During loading, the weight was slowly placed (within ~1 s; Fig. 2A) on the knee by the experimenter (W. G. Wright). The subject was allowed to guide manually lateral stabilization of the weight during the load and hold period, but the full 10 kg was vertically loaded on the knee. The weight was then lifted off the knee. Loading and lifting was repeated at least three times. The mean value of the dorsum displacement in the vertical direction for the last 2 s of the trial was used to estimate foot deformations. Trials in which the transducer was placed over MT1, so that compression of the plantar surface could be measured during passive 10-kg knee loading, employed a similar measurement technique. The mean height change of the dorsum was significantly greater than at MT1 (P < 0.01; Fig. 2B).

Protocol 2: correlating foot arch deformation and postural sway. To test the relation between A/P body sway and foot arch deformation during QS, subjects (n = 7) stood with eyes closed for 60 s on a fixed, horizontal AMTI force plate (Fig. 1, B and C) on which COP was measured. The onset of recording started 5–10 s after the subject closed his or her eyes in preparation for trial. A linear displacement transducer was placed on the dorsum of the left foot immediately over cuneiform bones but avoiding dorsiflexor tendons (e.g., extensor hallucis longus or in separate trials either at the head of MT1 or on the toe nail of the hallux). This device was used to measure changes in foot arch height during active postural control. An angular potentiometer attached to anterior fibia of the left leg was used to detect A/P change in tibial orientation (i.e., shin tilt). The shin tilt measurement device included a rigid metal arm (40 cm) connected to a sensitive CP-2UK-R250 potentiometer (Midori America, Fullerton, CA). The metal arm was linked to the lower leg using nonelastic thread attached to a flat mounting piece (6 × 1.5 cm) that was strapped around the lower leg. The lower leg attachment site was at the medial surface of the tibial shaft, 5–7 cm below the patella (planum tibia). The tibia at this site has a flat surface, and the thickness of a subcutaneous layer is small and thus minimizes unwanted shifting of the mounting piece, which therefore gives accurate measure of the tibia orientation. The thread linking the metal arm to the tibia was kept taut using the low restoring force of very thin elastic cords (0.5 mm) connected to the metal arm in a manner similar to symmetrical guy wires. The sensitivity of this sensor was found to be on the order of the force plate. Additionally, kinematic data using reflective markers attached to the skin overlying the ankle and knee joints were collected at 120 Hz using Motion Analysis (Santa Clara, CA) system cameras during QS trials to verify the accuracy of the shin tilt measurement device (Fig. 1B). Because of some intrinsic noise, the optoelectronic (Motion Analysis) system loses sensitivity below 0.2 mm, whereas the linear transducer was able to detect the correlation of foot dorsum motion with shin tilt at well below 0.1 mm. Although the shin tilt potentiometer was more sensitive than the camera system, the two devices showed highly significant correlation with each (r = 0.88–0.98, SD 0.049). Therefore, the data presented in RESULTS refer to those measures using the angular potentiometer.

Protocol 3: postural response to phalange and metatarsal perturbations. To examine postural effects after small perturbations to different parts of the forefoot (Fig. 1D), subjects (n = 12) stood with eyes closed with a majority of the posterior part of each foot on a stably fixed horizontal surface while a small part of the anterior portion of each foot was on a moveable platform. Specifically, in the MT condition, heads of the 1st and 2nd MT and the phalanges were placed on a flat moveable surface that delivered small upward translations while the posterior part of the foot remained on a stable, fixed platform. In the TOE condition, only the 1st 3 phalanges were on the anterior moveable platform, while the 1st and 2nd MT as well as the rest of the mid- and hind foot were on the fixed platform. It is worth noting that all our subjects had a classic (non-Morton) form of the foot, i.e., MT1 was equal or longer than the 2nd MT (Morton 1927). The anterior moveable platform and the posterior fixed platform abutted each other with no gap between the two. The surfaces were level with one another before upward displacements of the anterior platform. A motorized, torque-driven surface (Neurocom, Clackamas, OR), was used to deliver 10° upward angular impulses to the anterior moveable platform of 0.5° per impulse at 10 Hz. The motion of the anterior platform was measured using a triaxial, force plate (AMTI, Watertown, MA) placed over MT1, so that compression of the plantar surface could be measured during passive 10-kg knee loading, employed a similar measurement technique. The mean height change of the dorsum was significantly greater than at MT1 (P < 0.01; Fig. 2B).
OR) was used to deliver the small linear displacements upward such that the left and right feet received a symmetrical stimulus. In other words, subjects were perturbed along the A/P direction to induce sagittal plane postural responses while no stimulus asymmetry existed along the mediolateral (M/L) axis. To validate the absence of any systematic response asymmetry along the M/L axis, we performed analyses of the M/L COP as well. Full trials lasted 60 s, divided into 10 s of eyes-closed QS followed by 50 s of eyes-closed standing postperturbation. The preperturbation period was a variable length with 10 s before perturbation used as a baseline for comparison with the postperturbation period. Four displacement magnitudes of the anterior platform were 1.5, 3.0, 4.5, and 6.0 mm, which were randomly delivered at 2.5 mm/s. The 2.5 mm/s speed was chosen because it is in the range of normal COP velocity during QS. Although no earphones were used, ambient noise made it impossible to hear the perturbation since the perturbations were so small and the system is driven by very-low-noise motors. Often, the subject reported no conscious awareness that the stimulus had occurred.

The shin tilt measurement device described in protocol 2 was used to measure A/P postural responses. Because the majority of the foot was on the posterior fixed platform with only the forefeet on the moveable platform (Fig. 1D), during displacement of the anterior
platform the part of the subject’s weight was lifted off the posterior AMTI force plate. As a result, the COP showed an obvious posterior shift, since the AMTI force plate uses body weight (Fz) to calculate COP. An analysis of Fz revealed that 9.2 ± 2.1% in MT or 4.5 ± 1.5% in TOE was lifted off the AMTI force plate after the moveable platform lifted up the forefoot. In this case, COP is not representative of a postural response, rather it indicates the mechanical consequence of removing part of the Fz load from the posterior force plate onto the anterior force plate. Therefore, in this protocol, shin tilt was used as the kinematic measure of A/P postural response rather than COP. Analysis of these two variables conducted in protocol 2 showed significant correlation between A/P COP and shin sway (r = 0.84 ± 0.09, P < 0.00001), and thus this measure of A/P sway was highly reliable (Fig. 3).

A linear displacement transducer was placed on the hallux toenail in the TOE condition or on the foot dorsum on the head of MT1 in the MT condition. This was used to measure how much of the upward surface displacement was transferred through the fat padding on the plantar surface of the foot to the supporting musculoskeletal structure. Electromyogram (EMG) of tibialis anterior (TA) and lateral gastrocnemius (GAST) of the same leg as transducer and shin tilt were collected during perturbation trials. Surface electrodes were placed 5 cm apart to collect a differential EMG signal that was amplified 2,000–5,000 times, low-pass filtered below 30 Hz, and full-wave-rectified. All measurement devices were controlled by one central computer, which synchronized and collected the force plate, dorsum displacement, and shin tilt data at 120 Hz and EMG data at 1,000-Hz sampling rate.

**Data Analysis**

The shin tilt, displacement transducer, and COP data were filtered using a low-pass 4th order Butterworth filter with a 5-Hz cutoff frequency. Changes in TA and GAST activity were analyzed both relative to the baseline measure (before perturbation) and with regard to those in the antagonist muscle (see RESULTS). Descriptive statistics included means ± SD. Statistical comparisons included repeated-measures general linear models multivariate analysis of variance, paired t-tests, and Pearson correlation coefficients. The nonparametric Fisher exact test was used to make binomial comparisons. Significance was set at α ≤ 0.05, with Bonferroni corrections applied when multiple comparisons with the same time series were made.

**RESULTS**

**Foot Arch Deformation Measures**

In protocols 1 and 2, the measures from the linear displacement transducer showed changes in the foot arch height with weight loading in a passive state (sitting posture) and their correlation with changes in kinetic (COP) and kinematic (shin tilt) measures during active postural control. Specifically, in protocol 1, loading and unloading a 10-kg weight on the knee lowered and raised the foot arch, respectively, on average 1.3 ± 0.47 mm. Placement of the transducer on the foot dorsum at the head of MT1 allowed measurements to be taken at this location to rule out plantar skin compression as the cause for the change in foot arch height (Fig. 2B). Loading of the knee would presumably compress the plantar pads under the extra weight, however, our measures revealed that <50% of the magnitude of the foot arch height change could be accounted for by skin compression.

In protocol 2, we characterized natural foot arch deformations during QS. The amplitude (peak-to-peak) of foot dorsum
displacements was approximately 0.2–0.9 mm across subjects (Fig. 3B) and that of the shin tilt was 1.5–4.1°. Analysis of the foot arch deformation and the shin sway revealed a significant correlation between the two measures ranging from \( r = 0.70 \) to 0.90, with an average \( r = 0.81 \pm 0.07 \) \((P < 0.0001)\) during QS with eyes closed. Anterior shin tilt correlated with flattening of the foot arch and posterior tilt with the foot arch rising (Fig. 3). Correlations with similarly high significance were found between foot arch displacements and A/P COP \((r = 0.70 \pm 0.09, P < 0.0001; \text{Fig. 3})\). Correlations of M/L COP with foot arch displacements were weak ranging from \( r = -0.36 \) to 0.04 with an average of \( r = -0.14 \) (Fig. 3A, bottom curves).

**Postural Response to Surface Perturbations of the Foot**

In protocol 3, perturbed standing showed measurable changes in the shin tilt and EMG (TA and GAST), corresponding to the displacement onset of the anterior platform. Overall, the lift of the platform resulted in greater mean values of the lift of the phalanges in the TOE condition than the phalanges and MT in the MT condition. For instance, a 3-mm perturbation resulted in 1.84 ± 0.27° and 2.46 ± 0.29-mm vertical displacements in the MT and TOE condition, respectively. Thus more compression of the plantar surface skin occurred in MT than in TOE, which means on average the toes were displaced by the stimulus more during TOE than MT perturbations. Despite this, however, postural responses were significantly more pronounced in the MT compared with the TOE conditions. The postural response occurred <600 ms after perturbation onset on average. A 3-s window was chosen that represents a period greater than long-latency postural phasic responses and 1 s greater than the slowest responses observed across trials (latencies ranged from 0.3 to 2.1 s). The 10 s of QS preceding the perturbation was divided into three 3-s windows excluding the first second and then averaged to ensure that variability measures were not biased by the length of the window. The average shin tilt variability during the 9 s of QS preceding the perturbation was 0.31°. The average shin tilt variability during 3 s immediately after the perturbation was 0.50 ± 0.45° in MT and 0.24 ± 0.29° in TOE. As perturbation magnitude increased from 1.5 to 6 mm, the magnitude of the shin tilt response also increased, however, this change was not significant in either the MT \((P > 0.10)\) or TOE conditions \((P > 0.5; \text{Fig. 4B})\).

The shin tilt measure showed different outputs depending on the foot perturbation condition, MT or TOE. In the MT conditions, an initial passive response to surface perturbation was typically evident whereby the shin tilted backward as MT1 was pushed upward. This was considered to be a passive, mechanical response and was evident in the 87% of the trials, whereas in the TOE condition a clear passive response was evident in only 33% of the trials. After the initial passive response, the subject either responded with a compensatory anterior shin tilt or continued backward typically at a different rate than during the passive response. In the MT condition, 30% of the responses resulted in posterior shin tilt, and 59% were anterior compensatory responses, whereas 11% showed no clear directional shin tilt. In the TOE condition, 30% were posteriorly directed responses, 49% were anterior compensatory responses, and 35% showed no clear shin tilt response. Many of the trials showing no response in shin tilt occurred
during low amplitude surface perturbations (i.e., 1.5 and 3 mm) in the TOE condition.

Another measure of postural response that showed clear changes was the root-mean-square (RMS) of shin tilt, pre- and postperturbation. The shin tilt RMS increased significantly in both the TOE \((F_{3,25} = 20.5, P < 0.0002)\) and the MT conditions \((F_{3,25} = 39.8, P < 0.00001)\) compared with baseline variability during QS. However, the increase in RMS was significantly greater in the MT condition \((P < 0.009)\). Furthermore, on average, shin tilt RMS did not return to baseline level for at least 30 s (Fig. 5, shin tilt traces).

**EMG Response to Surface Perturbations of the Foot**

EMG measures of the TA and GAST revealed measurable changes in muscle activity corresponding to the perturbation...
onset, which significantly correlated with A/P sway direction (Fig. 5A). On average, the absolute change in EMG activity was 43.1% relative to the 10-s baseline measure of EMG activity before surface perturbation in each trial. For each muscle, this percentage change was normalized as a ratio of the mean EMG activity (\( \mu_{\text{mmg}} \)) during the 3-s (\( t_1 = 10 \text{ s} \) to \( t_2 = 13 \text{ s} \)) postperturbation minus the mean activity during the 10-s (\( t_0 \) to \( t_1 \)) baseline QS before perturbation and then divided by the baseline QS activity. The ratio was multiplied by 100 to give the outcome as a percentage (Eq. 1).

\[
\delta_{\text{mmg}} = 100 \times \frac{\mu_{\text{mmg}}(t_2 - t_1)}{\mu_{\text{mmg}}(t_1)}
\]

With the median absolute change in EMG activity found to equal 25%, this was used as a threshold for a reliable leg muscle response to the surface perturbation. Among the trials that showed a clear EMG response, the anterior and posterior leg muscles sometimes worked reciprocally, i.e., when the TA increased, GAST decreased or vice versa, however (see also Di Giulio et al. 2009), we also observed trials with little or no response in the agonist as well as coactivation resulting in a net increase in leg muscle activity. An analysis of A/P shin tilt response relative to the difference in GAST and TA (\( \text{Diff}_{\text{mmg}} \)) revealed a highly significant correlation (\( r = 0.65, P < 0.00001 \)) with forward shin tilt corresponding to increasing GAST and/or decreasing TA. Specifically, the \( \text{Diff}_{\text{mmg}} \) between GAST and TA muscle activity (Eq. 2) in the no-response trials could have reached a maximum of 50% if one muscle increased by 25%, whereas the other decreased by 25%. However, the average of the absolute differences (\( \text{AbsDiff}_{\text{mmg}}, \text{Eq. 3} \)) was only 13% for no-response trials compared with 160% in the GAST and TA response trials (where \( n \) equals either the number of trials found with significant TA and GAST responses or the number of no-response trials).

\[
\text{Diff}_{\text{mmg}} = \delta_{\text{GAST}} - \delta_{\text{TA}}
\]

\[
\text{AbsDiff}_{\text{mmg}} = \frac{\sum_{i=1}^{n} |\delta_{\text{GAST}} - \delta_{\text{TA}}|}{n}
\]

The above evidence suggests that small surface perturbations elicited an EMG response in the legs in both MT and TOE conditions. Further analysis of the two surface conditions, MT and TOE, revealed significant differences in their EMG responses. First, as mentioned above, a significant correlation (\( r = 0.65 \)) exists between A/P sway and leg muscle activity,
Diff_{\text{emg}} (Eq. 2), however, in the MT condition, this correlation was \( r = 0.75 \) (\( P < 0.0000 \)), whereas in the TOE condition, a weaker correlation of \( r = 0.31 \) (\( P = 0.02 \)) was observed. A comparison of the absolute change in EMG activity revealed significantly more activity following MT perturbation than TOE perturbation (\( F_{1,23} = 7.73, P = 0.01 \)). In other words, the sum of absolute EMG change (\( |b_{\text{CAST}}^1 + b_{\text{TA}}^1| \)) was greater in MT than TOE trials. Finally, using the 25% threshold for no-response trials and performing a nonparametric analysis of the number of above threshold responses vs. no-response trials showed that 33% were above threshold in the TOE condition trials, whereas in the MT condition, 56% were above threshold, a significantly higher EMG response rate (Fisher exact test, \( P = 0.01, 1\)-tailed).

**DISCUSSION**

Overall, the results confirmed our hypothesis with respect to the presence of significant foot deformations (Figs. 2–3). Taking into account very small body oscillations during QS, these deformations are remarkable (\( \sim 0.5–1 \) mm) and might significantly affect the afferent outflow from the foot mechanoreceptors (and about the ankle joint angle in particular) during maintenance of orthograde posture. Furthermore, a very small perturbation to either the phalanges or MT evoked noticeable changes in the EMG activity and postural sway (Figs. 3–5). Interestingly, these changes could exceed the duration of perturbation by tens of seconds (see Fig. 5, shin tilt traces), suggesting a potential disturbance of the postural reference.

**Postural Foot Deformations**

Under full limb loading, the height of the foot dorsum decreases by a few millimeters (Bandholm et al. 2008; McPoil et al. 2008). It is worth emphasizing, however, that during normal standing, a relatively small redistribution of loading between forefoot and heel occurs due to A/P COM displacements. Here, we quantified variations in the height of the foot dorsum under relatively small changes in limb loading comparable with positional adjustments. In sitting position, loading the 10-kg weight on the knee lowered the foot arch by about 1–1.5 mm (Fig. 2). More than 50% of this change could be accounted for by the foot arch deformation and the rest by plantar surface skin compression (by skin compression, we imply pressing out and changing the shape of the foot soft tissues, since the body liquid per se is incompressible). Also, although we assumed that the foot behaves as an elastic body, it could not be ruled out that a part of the foot deformation was due to its plasticity (e.g., that of the soft tissues of the sole).

During standing, the foot arch probe and shin sway revealed a significant correlation, which shows that as the tibia tilts forward, the foot arch flattens and vice versa (Fig. 3). It is unlikely that changes in the linear displacement transducer height were simply due to compression of dermal padding on plantar surface of the feet (Gurfinkel et al. 1994), for a few reasons. The transducer was placed at a point between the anterior and posterior parts of the foot (i.e., the cuneiform bones). Thus, when the A/P COP shifts from front to back, this will compress the calcaneal fat pad while reducing compression of the forefoot fat pad, so measurement at the fulcrum of this lever-like action would not show a change at the midfoot dorsum. However, if the foot height changes were due to conformational changes of the foot arch as A/P sway occurs, then a net change in foot dorsum height would be expected.

Most work uses ankle joint angles determined from optoelectronic systems. Our findings clearly show that, depending on the marker position, the drop in the foot arch or deformation of soft tissues may have significant influence on the actual measured ankle angle. Moreover, taking into account very small changes in the ankle joint angle and a distributed or nonuniform deformation of different parts of the foot during standing (see Fig. 6 with a schematic foot model), one cannot be sure that the actual ankle joint angle is being measured. Furthermore, different muscles of the ankle joint or even different compartments of the same muscle may show counterintuitive changes in muscle length during postural body tilts due to the different attachment geometry and flattening of the foot (Di Giulio et al. 2009). There might also be large interindividual differences in the degree of deformation of the soft tissues of the foot (Gurfinkel et al. 1994). Moreover, such interindividual differences in foot compliance may affect postural responses to support surface perturbations (Gurfinkel et al. 1994). Further investigations are needed to determine the exact mechanism of these differences and the extent of foot compliance changes in different populations as well as adaptations throughout development (for instance, due to soft tissue distribution and foot shape in infants; Bertsch et al. 2004; Hallemans et al. 2006).

The observed foot dorsum displacements (\( \sim 0.5 \) mm; Fig. 3) are not negligible. Taking into consideration a short distance between the transducer and the ankle joint (5–7 cm; Fig. 1B), the estimated errors in the ankle joint angle due to foot deformations (\( \sim 0.5/50 \) mm = 0.01 rad or 0.6°) are in fact of the same order as angular oscillations of an inverted pendulum (about 0.5–1°) that is often used as a model representing bipedal posture (Fitzpatrick et al. 1994; Gatev et al. 1999; Maurer et al. 2006; Morasso and Schieppati 1999; Winter et al. 2001). Given also a plantar surface skin compression that further attenuates the actual changes in the ankle joint angle by...
a factor of almost two (Gurfinkel et al. 1994), the hypothetical ankle joint angle oscillations and the corresponding changes in the calf muscle length may be minute if any (or even opposite in sign) during normal A/P postural body displacements. Furthermore, high tendon compliance (Rack et al. 1983) and “paradoxical” calf muscle lengthening/shortening during undisturbed human standing (Loram et al. 2007, 2009) also question the usage of a simple control scheme of human standing based on the stretch reflex in the ankle joint muscles. Therefore, sensory input arising from notable deformations of the foot arch and soft tissues may provide important (or at least complimentary) information about postural body sway and/or postural reference.

**Postural Responses to TOE and MT Perturbations**

It is worth stressing that the foot represents an important receptive field, formed by numerous skin, joint, tendon, and muscular receptors (including intrinsic foot muscles), and it has long been recognized that damage to the foot, be it either by sensorineural loss or physical damage to the muscles, bones, or supporting tissues, changes posture and gait stability. A number of cutaneous and load-related reflexes may participate in the fine control of posture or foot positioning during walking (Abbruzzese et al. 1996; Aniss et al. 1992; Duyssens et al. 2000; Ivanenko et al. 2002; Kavounoudias et al. 1998; Nardone et al. 2000; van Wezel et al. 1997; Yang and Stein 1990). For instance, loss of cutaneous sensation may lead to less stable posture and locomotion (Courtemanche et al. 1996; Dingwell and Cavanagh 2001; Meyer et al. 2004; Perry et al. 2000; Taylor et al. 2004). In addition, support surface may also be included as a component of our ego space in a similar way as external objects and tools can be included in our body scheme (Iriki et al. 1996; Ivanenko et al. 1997; Pearson and Gramlitch 2010; Solopova et al. 2003; Wright and Horak 2007). The tactile information from the main supporting areas of the foot is also used by the brain for perceptual purposes and can evoke strong kinesthetic illusions (Roll et al. 2002), vibrotactile thresholds being lower in the ball and arch of the sole than in the heel and toe regions (Gravano et al. 2011; Inglis et al. 2002).

Here, we found that perturbing MT or toes affects human posture (Fig. 4), consistent with the previous studies that input from the foot helps in the control of upright human balance (Fujiwara et al. 2003; Ivanenko et al. 1997; Kavounoudias et al. 2001; Priplata et al. 2006). Perturbing MT affected posture more than perturbing toes. The slow return to baseline posture after a very small perturbation to the phalanges or the 1st and 2nd MT may be due to a change in the surface reference frame. Subsequent to a change in the surface reference frame, it takes time to reestablish the new frame of reference. These findings suggest that the entire neurophysiology and anatomic architecture of the foot are uniquely designed for and integral to performing the complex task of bipedal postural control, a fact overlooked by some ankle-axis inverted pendulum models and postural control theories that focus suprapedally.

**Conclusions**

With over 100 muscles, tendons, and ligaments, 26 separate bones, and 33 joints, the foot and specifically the arch likely evolved for a role as specialized as the thumb and fingers did for fine manual control (Rolian et al. 2010). Despite this, many postural studies tend to focus on the simple hinge action of the ankle joint without taking into account the distributive nature of foot deformations. Here, we show that the foot, rather than serving as rigid base of support, is in an active, flexible state and is sensitive to minute perturbations even if the entire hind and midfoot is stably supported and the ankle joint is unperturbed. We also found that perturbing MT affects posture more than perturbing toes. The slow return to baseline posture after a small perturbation to the phalanges or the 1st and 2nd MT may be due to a change in the surface reference frame. Subsequent to a change in the surface reference frame, it takes time to reestablish the new frame of reference. These findings suggest that the entire neurophysiology and anatomic architecture of the foot are uniquely designed for and integral to performing the complex task of bipedal postural control, a fact overlooked by some ankle-axis inverted pendulum models and postural control theories that focus suprapedally.

**REFERENCES**


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