Journal of Physiology (2002), **545.3**, *pp.* 1041–1053
DOI: 10.1113/jphysiol.2002.025049
www.jphysiol.org

Direct measurement of human ankle stiffness during quiet standing: the intrinsic mechanical stiffness is insufficient for stability

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During quiet standing the human 'inverted pendulum' sways irregularly. In previous work where subjects balanced a real inverted pendulum, we investigated what contribution the intrinsic mechanical ankle stiffness makes to achieve stability. Using the results of a plausible model, we suggested that intrinsic ankle stiffness is inadequate for providing stability. Here, using a piezo-electric translator we applied small, unobtrusive mechanical perturbations to the foot while the subject was standing freely. These short duration perturbations had a similar size and velocity to movements which occur naturally during quiet standing, and they produced no evidence of any stretch reflex response in soleus, or gastrocnemius. Direct measurement confirms our earlier conclusion; intrinsic ankle stiffness is not quite sufficient to stabilise the body or pendulum. On average the directly determined intrinsic stiffness is 91 ± 23 % (mean ± S.D.) of that necessary to provide minimal stabilisation. The stiffness was substantially constant, increasing only slightly with ankle torque. This stiffness cannot be neurally regulated in quiet standing. Thus we attribute this stiffness to the foot, Achilles' tendon and aponeurosis rather than the activated calf muscle fibres. Our measurements suggest that the triceps surae muscles maintain balance via a spring-like element which is itself too compliant to guarantee stability. The implication is that the brain cannot set ankle stiffness and then ignore the control task because additional modulation of torque is required to maintain balance. We suggest that the triceps surae muscles maintain balance by predictively controlling the proximal offset of the spring-like element in a ballistic-like manner.

(Received 23 May 2002; accepted after revision 8 October 2002; first published online 15 November 2002)
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In quiet standing, the body mass is generally regarded as being inherently unstable with the body centre of mass (CoM) maintained a few centimetres in front of the ankle joint. Close examination reveals quasi-random alternating movements of the centre of mass in the sagittal plane. The gravitational torque on the centre of mass is generally considered to increase linearly with ankle angle (Winter *et al.* 1998; Morasso & Schieppati, 1999) and we refer to this relationship as the toppling torque per unit angle. Forward collapse of the body is prevented by ankle torque produced by activity of the triceps surae muscles.

The activated triceps surae musculature generates an intrinsic mechanical stiffness across the ankle joint. Such stiffness provides an instant torque response to any change in ankle angle without any intervention required from the nervous system (Grillner, 1972; Horak & MacPherson, 1996; Winter *et al.* 1998). What is the extent of this free restoring force?

If the ankle stiffness is less than the toppling torque per unit angle then the body CoM is mechanically unstable and an active neural modulation of ankle torque is required to produce stability (Morasso *et al.* 1999; Morasso & Schieppati, 1999). Conversely, if the ankle stiffness is greater than the toppling torque per unit angle, the body CoM is in principle at least marginally stable. However, to account for the relatively high frequency of small sagittal oscillations which make up the sway pattern, stiffness would have to be greater still. Based on a mean frequency of 0.5 Hz, Morasso amd coworkers have suggested a value of 200 % relative to the toppling torque per unit angle (Morasso *et al.* 1999; Morasso & Schieppati, 1999). A similar value can be derived from Winter *et al.* (1998). Thus active neural modulation of ankle torque is still required if the intrinsic mechanical stiffness is less than 200 % of the toppling torque per unit angle.

In experiments where subjects balanced a human proportioned inverted pendulum (Loram & Lakie, 2002), ankle torque changes were shown to result from anticipatory neural modulation as well as the intrinsic mechanical ankle stiffness. Using a plausible model it was predicted that the intrinsic ankle stiffness was just insufficient to provide marginal stability of the real inverted pendulum or the body CoM in standing.

In this study we measured the intrinsic mechanical ankle stiffness using a method which allows the activity of standing quietly to continue undisturbed and which uses perturbations which are comparable to the ankle movements normally experienced in quiet standing. The essence of the technique is that it measures the intrinsic stiffness which is the stiffness before the nervous system has time to produce any change by reflex or other means. Gurfinkel *et al.* (1974) attempted something similar but it is not clear from their paper that their technique can precisely distinguish between the intrinsic and neurally generated stiffness. With subjects lying on their backs, ankle stiffness has been measured for a variety of torque levels using a pseudo-random binary sequence of relatively large perturbations (Hunter & Kearney, 1982; Mirbagheri *et al.* 2000; 5 deg and 1.7 deg, respectively). These measurements also showed that the ankle stiffness increased markedly as the size of the perturbation decreased (Kearney & Hunter, 1982) although the perturbation size was not decreased to values comparable with typical ankle deflections in quiet standing. Using a rapid release ergonometer, the series elastic stiffness of the triceps surae has been measured at different torque levels for subjects sitting (de Zee & Voigt, 2001) and for subjects standing with the availability of a bar (Hof, 1998). The size and speed of these releases were very large (30 deg at 860 deg s^{-1}, > 25 deg at 800 deg s^{-1}) and much greater than values encountered in normal standing movements. It has been claimed that the mechanical, series elastic ankle stiffness has been measured directly during standing using simple regression of ankle torque against ankle angle for an extended time period (Winter *et al.* 2001). However this, and the author's previous method (Winter *et al.* 1998) are invalid because they do not take into account the changes in torque caused by changes in muscle activation. For their claims to be true it is necessary to demonstrate that all the changes in ankle torque over an extended period of 10 s are caused by mechanical stretching of the muscle without any sway related neural modulation. Others have suggested that torque is generated as a result of reflex activity in standing and that the gain of these reflexes can be altered thus changing the effective stiffness (Fitzpatrick *et al.* 1992*a*,*b*, 1996).

The novel method presented in this paper uses a piezo-electric translator to apply small perturbations to the foot while the subject is standing freely or balancing an equivalent inverted pendulum. These perturbations are of similar size and velocity to the ankle movements that are normally encountered during this activity. As well as measuring the operative intrinsic, mechanical stiffness it also allows study of the reflex response relevant to the small, slow ankle movements that are normally present in quiet standing.

We address six questions. (1) What is the effective intrinsic, mechanical ankle stiffness during quiet standing and when balancing the inverted pendulum? (2) Is ankle stiffness a neurally controlled parameter or is it a biomechanical constant? (3) Can this stiffness be partitioned into foot and true ankle components? (4) Is there evidence of reflex activity during quiet standing? (5) In principle can stability be maintained with a low intrinsic ankle stiffness? (6) What mechanism for controlling the body CoM is suggested by these results?

METHODS

Subjects

Fifteen healthy people, eight male, aged between 20 and 68 years took part in this study. The subjects gave written informed consent, and the study was approved by the local human ethics committee and conformed to the principles of the Declaration of Helsinki.

Experimental protocol

Subjects performed three tasks and we measured the intrinsic mechanical ankle stiffness of the left leg during each activity. First, they stood freely and quietly with their eyes open for a minimum period of 200 s. Second, they were strapped to a fixed, vertical support and shown an oscilloscope displaying the level of torque they were generating. They were asked to maintain a constant level of torque for 40 s. This experiment was repeated for randomised, different, torque levels varying between 5 and 25 N m. Third, they were strapped to a fixed vertical support and asked to balance a human proportioned inverted pendulum for a minimum period of 200 s. Subjects could see the pendulum position displayed on the oscilloscope and were asked to maintain the pendulum at 3 deg so as to approximate the level of ankle torque applied during quiet standing. All subjects could perform this task after minimal familiarisation.

Apparatus

The subject stood on two footplates with the centre of their ankles approximately 22 cm apart. Their ankles were positioned to be co-axial with the axis of rotation of an inverted pendulum (Fig. 1*C*). The apparatus and sensor instrumentation for balancing the inverted pendulum has been reported fully elsewhere (Loram *et al.* 2001) and is shown in Fig. 1*C*. The left footplate was fitted with a piezo-electric translator (LVPZT P-840.60, PI, Germany) which applied a rotation to the footplate causing dorsiflexion of the ankle joint (Fig. 1*A*).

While standing, subjects stood freely without any mechanical contact or support and the pendulum and platform were locked to provide a horizontal surface. Subjects adopted their own standing position and their mean ankle angles ranged from 1.5 to 4 deg. While subjects generated constant levels of torque the pendulum and platform were locked and a vertical support was moved forwards so the subject could be strapped at their normal standing position. While balancing the inverted pendulum the subject was strapped to the same fixed back support while the pendulum and platform were free to move coaxially with the footplates and feet. An appropriate pendulum mass was used for each subject. This was usually 60 kg although 40 or 50 kg was used for smaller, lighter subjects. The distance of the pendulum centre of mass from the axis of rotation was 0.94 m.

The piezo-electric translator had a maximum throw of 100 μm and was positioned to give 0.055 deg of footplate rotation. The maximum throw was used for all experiments. For each

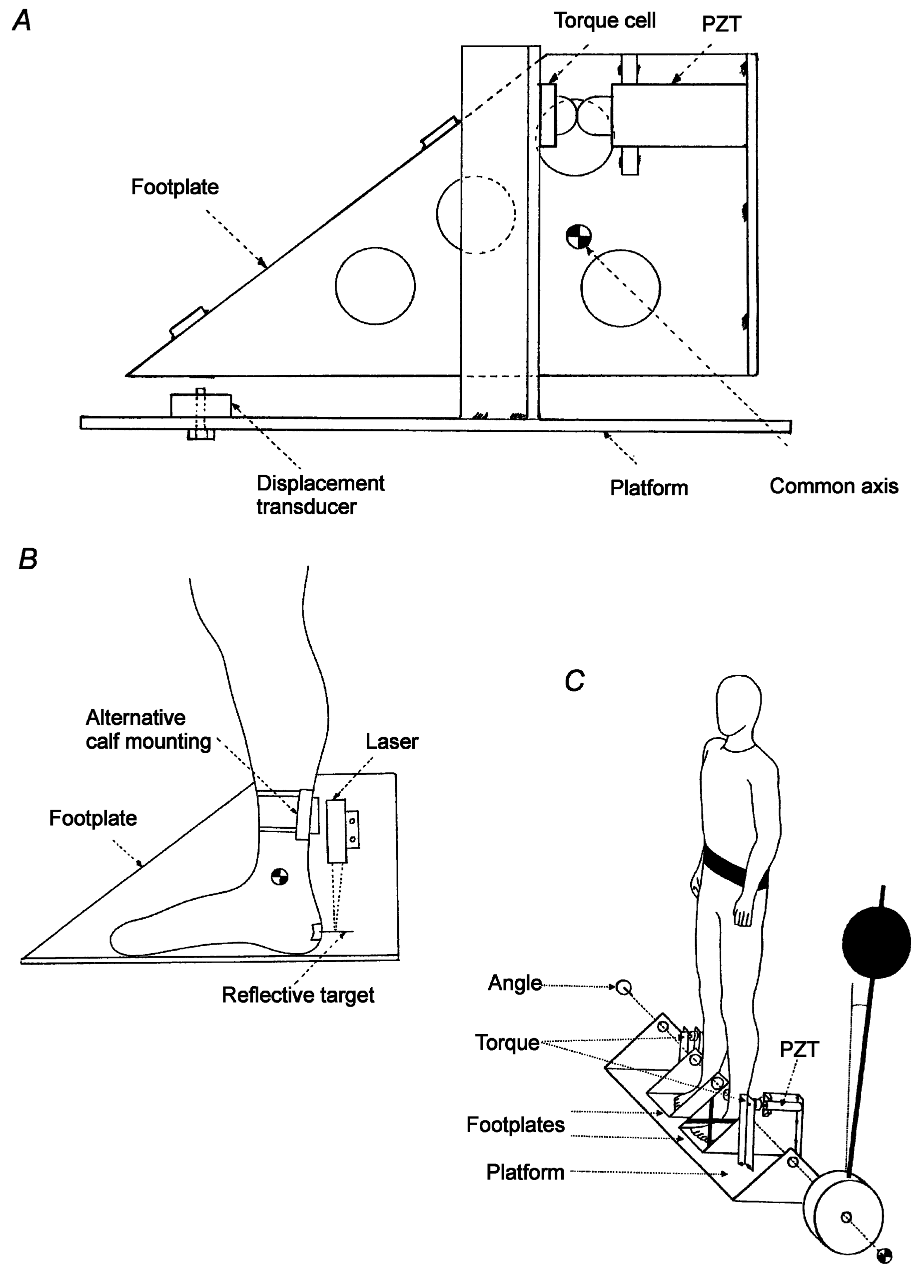

Figure 1. Ankle stiffness measuring apparatus

A, ankle stiffness measurement. The left footplate is constructed of aluminium alloy, lightened by holes and cross-braced for rigidity. A piezo-electric transducer (PZT) produces a translation which rotates the footplate relative to the platform. Lengthening of the element raises the toe end of the footplate. The footplate rotation is registered by the contactless displacement transducer. The resulting force change is recorded by the torque cell. The contact face of the PZT is spherical to minimise off-axis forces. *B*, ankle rotation. A miniature laser range-finder operating by triangulation and insensitive to rotation measures the linear distance to a target attached to a mount attached to the subject's heel with dental wax. The laser can be attached to the footplate as shown or alternatively mounted on a snugly fitting calf mould securely taped to the leg. *C*, general view. The subject stands on two footplates. Both footplates are coupled to the platform by horizontally mounted load cells which record ankle torque. The platform is rigidly coupled to a heavy inverted pendulum. A piezo-electric, vibrating gyroscope mounted under the platform measures angular velocity. In free standing the platform and pendulum are immobilised and the apparatus remains stationary while the subject sways. In the torque generation and pendulum balancing tasks the subject is strapped at pelvis height to a solid back support (not shown) that prevents body movement. During pendulum balancing the pendulum and platform sway while the subject is static. The backward lean of the pendulum mimics the normal forward inclination of the body and is measured by a contactless, precision potentiometer. The ankles, platform and footplates have a common axis. Alignment and support are provided by six precision ball races and a substantial steel framework (omitted here for clarity).

perturbation a raised cosine waveform was used to minimise footplate acceleration and the accompanying reactive inertial torques. This method works on the assumption that there is no responsive change in muscle torque during the perturbation. Isolated perturbations with a rise time of 70 ms and a period of 140 ms (7 Hz cosine wave) were used. The average speed of these perturbations is 0.7 deg s^{-1}. The effect of the piezo-electric translator is simultaneously to push the toe end of the footplate up and the pendulum or human centre of mass to a more upright angle. The inertia of the footplate and foot is less than 1/1000 times that of the pendulum or the human body so there is negligible deflection of the latter two during the perturbation. A few subjects could feel the perturbations clearly when they were standing freely and when they were strapped to the support generating low constant levels of ankle torque. Others were never able to perceive the perturbations. For all subjects, the perturbations merged into the background when ankle torque levels were high and when torque fluctuations were greater such as when balancing the pendulum. No auditory cues were perceptible.

A contactless variable reluctance displacement sensor (Model 502-F, NS020, EMIC, France) with a sensitivity of 1 mV μm^{-1} and response time of < 0.1 ms recorded rotation of the left footplate relative to the platform. A piezo-electric vibrating gyroscope measured velocity of the platform relative to the ground. A Hall effect precision potentiometer measured pendulum position and horizontally mounted miniature load cells recorded left and right ankle torque. The piezo-translator was mounted in series with the left torque cell. The footplate rotation and left torque were sampled at 1000 Hz. Other sensors were sampled at 25 Hz.

Rotation of the footplate produces deformation of the foot and rotation of the ankle joint (Fig. 7*A*). In order to measure the relative contributions of each it is necessary to measure either lengthening of the Achilles' tendon or deformation of the foot relative to the heel. To assess whether the Achilles' tendon was being stretched by the perturbations a laser range finder (YP05MGVL80, Wenglor Sensoric, Germany) with a resolution of < 2 μm and a response time of 5 ms was used to measure vertical changes in distance 'y' between the heel and the calf. The laser was strapped to the back of the lower leg approximately 10–15 cm above the heel and reflected off a small metal plate firmly attached to the back of the heel close to the calcanean tuberosity (Fig. 1*B*). Each heel plate was individually fitted using a dental wax moulding. The approximate horizontal distance 'x' between the ankle joint and the point of reflection of the laser behind the heel was measured. The variation in ankle angle, 'θ', was calculated using $\theta = y/x$. There was some inevitable uncertainty in determining the exact position of the ankle axis of rotation. The absolute accuracy of θ is limited by the absolute accuracy of x to ± 20 %. To measure deformation of the foot, the laser was fixed to the footplate and reflected off the same heel plate. This measured deflection of the heel relative to the footplate resulting from deformation of the foot. The measurement assumes that the body centre of mass is not raised while the footplate rotates. Rather, the heel is left behind by the downward movement of the footplate underneath it. The laser signal was sampled at 100 Hz. The loss of ankle rotation caused by foot deformation was calculated by dividing the variation in heel height by x as above.

EMG activity was recorded on the left leg from soleus, tibialis anterior, gastrocnemius medialis and gastrocnemius lateralis using bipolar surface electrodes with encapsulated pre-amplifiers. These signals containing the entire bandwidth were then amplified and passed through an analogue full-wave rectifier. During preliminary trials these signals were sampled at 1000 Hz. During later experiments they were passed through a r.m.s. averaging filter with a time constant of 100 ms and then sampled at 25 Hz. The sampled EMG level corresponding to the 'noise floor' was 0.04 V.

Methods of data analysis

Perturbations were usually given regularly at rates of approximately 0.8 Hz. Experiments showed that giving perturbations irregularly made no difference. Perturbations were then averaged as shown in Fig. 2. Figure 2*A* shows the averaged footplate rotation and Fig. 2*B* shows the velocity of the perturbation.

During standing, the torque response to individual perturbations is less than the natural fluctuations in ankle torque which are associated with balance (Fig. 2*C*). Averaging reduces the size of the unrelated fluctuations relative to the mechanical response to the perturbation (Fig. 2*D*). Typically for standing or balancing the pendulum 200 perturbations were averaged. When the subject was generating a constant torque 30 perturbations were averaged.

Next the small torque response of the footplate is subtracted (Fig. 2*D*). This eliminates the inertia, viscosity and gravitational moment of the footplate itself. Some high frequency vibration at around 100 Hz remains which we attribute to resonance of the apparatus. For the 140 ms duration of the perturbation from 0.4 to 0.54 s we need to separate the mechanical torque response to the perturbation from the unrelated changes in ankle torque. By eye we draw a line between the left ankle torque at 0.4 s to the torque at 0.54 s as shown in Fig. 2*D*. Mathematically we use cubic spline interpolation to draw the line because a cubic spline matches both the value and the gradient at the two end points. A complication is that the remaining noise and 100 Hz vibration can throw out the gradient of the spline at the end points. So some smoothing is needed before applying the spline. First the left torque record in Fig. 2*D* was replaced by a linear interpolation between 0.4 and 0.54 s. Then the torque was low pass filtered at 7 Hz. Then the values between 0.4 and 0.54 s were replace by a cubic spline interpolation. The result is the dash–dot line shown in Fig. 2*D* and this is our estimate of the changes in ankle torque unassociated with the mechanical response to the perturbation. This estimate was subtracted from the torque record in Fig. 2*D* to give the mechanical response to the perturbation, as shown in Fig. 2*E*.

The mechanical response to the footplate rotation was modelled as having elastic, viscous and inertial components according to the equation $T = KA + Bv + I\,\mathrm{accel}$ (Fig. 2*E*). T is the mechanical torque response, A is the angle, v is the angular velocity and accel is the angular acceleration. Linear least squares regression was used to estimate the parameters K, B and I which are the stiffness, viscosity and moment of inertia, respectively. On average the percentage variance accounted for by this model (% VAF) was 99.0 % and the torque response was predominantly elastic. The parameters K, B and I can be estimated with a high degree of certainty. The mean 95 % confidence intervals were ± 1, 2 and 20 %, respectively. These confidence intervals do not reflect the true uncertainty of the parameters because the torque response to which the parameters have been fitted is itself uncertain due to the interpolation procedure. We estimated that uncertainty by applying our interpolation procedure to the right ankle torque which is known throughout the perturbation (0.4 to 0.54 s). We calculated the difference between the known right torque and the interpolated right torque. We added this difference to the mechanical response of the left ankle torque in Fig. 2*E* to assess the effect of this uncertainty on the elastic, viscous and inertial parameters. The elastic, viscous and inertial parameters changed on average by 4, 5 and 89 %. The uncertainty in the inertial parameter is high because the inertial component is a small part of the mechanical response and indeed is only of minor interest in this study.

A 30th order linear phase FIR filter was used to differentiate the averaged footplate position and then to differentiate the velocity record. Using the Parks-McClellan algorithm, the filter was designed to differentiate the signal up to frequencies of 300 Hz (Ingle & Proakis, 1997). The differentiation was followed by a low pass FIR filter with a pass band of 100 Hz.

The averaged records of footplate rotation, platform rotation and laser deflection also contained some residual variation unassociated with piezo-electric translation. These variations were subtracted using the same interpolative method as for the averaged torque record. A very small movement of the platform was subtracted from the rotation of the footplate relative to the platform to calculate the true rotation of the footplate relative to the ground. The torque response to true ankle rotation was modelled using the laser measurements from the back of the heel (mean % VAF = 99.5 %). Likewise, the foot stiffness was modelled from the heel deflection relative to the footplate measured using the laser (mean % VAF = 95.5 %).

For each subject the approximate toppling torque per unit angle of the CoM was calculated using $m \times g \times h$, where m is the mass of the subject above the ankles, g is the gravitational field strength and h is the height of the CoM above the ankles (Table 1). Each subject was weighed and a corrective fraction of 0.029 (Patla *et al.* 2002) corresponding to the mass of the feet was subtracted. The approximate position of the centre of mass was measured by lying subjects on a horizontal board and measuring the moment produced across a pivot (Page, 1978). The height of the ankles above the ground was subtracted from the height of the centre of mass.

During free standing, an estimate of the CoM angle was calculated from the ankle torque record using a low pass filter with a frequency cut off of 0.5 Hz (Caron *et al.* 1997). We replaced the filter of Caron *et al.* with a 1st order Butterworth filter since verification with real inverted pendulum data shows that this provides an improved estimate (I. D. Loram, unpublished observations).

RESULTS

When a dorsiflexion of 0.055 deg is applied to the foot, approximately 70 % of that rotation is transmitted through the foot and ankle joint to the distal end of the Achilles' tendon and thereafter to the triceps–surae muscle–tendon complex (Fig. 2*A*). The true angular deflection of the ankle shown in Fig. 2*A* has been calculated from the change in length between the laser on the back of the lower leg and the plate attached to the heel. During the perturbation itself the angular deflection of the CoM is negligible (Fig. 2*A*). This means that

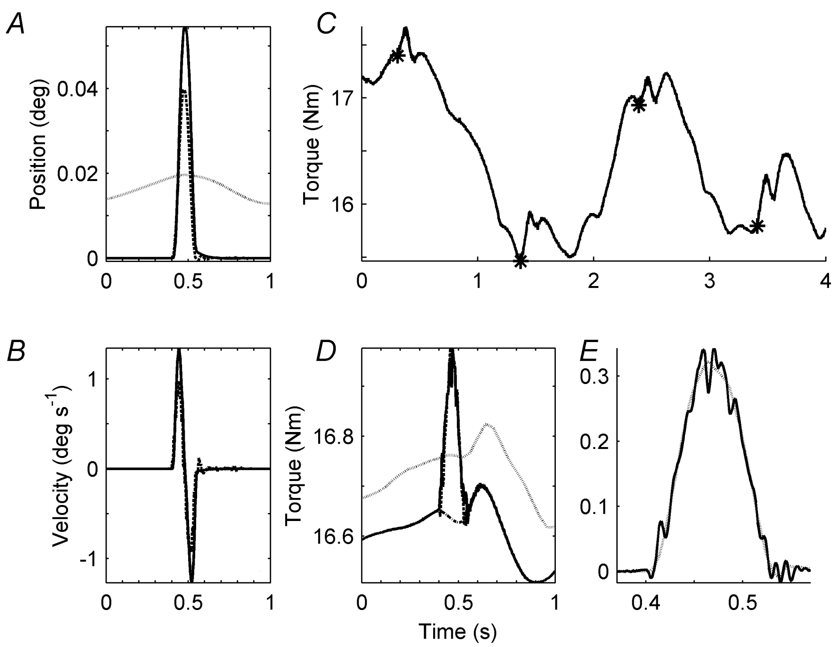

Figure 2. Averaging and calculation of mechanical response

For one representative standing subject, *A* shows the averaged footplate rotation (continuous), rotation of heel (calcanean tuberosity) about the ankle measured using the laser (dashed), and movement of the body CoM (dotted). The zero degree position is arbitrary. The footplate rotation starts at 0.4 s. *B,* the averaged velocity of the footplate (continuous trace) and the heel about the ankle (dashed trace). *C,* the unaveraged time record of left ankle torque. The asterisks mark the beginning of footplate rotations. *D,* the averaged record of left torque (continuous trace), left torque after subtraction of footplate component (dashed trace), the interpolated background torque during the perturbation (dot-dashed trace) and the right torque (dotted trace). *E*, the averaged mechanical response to the footplate rotation (continuous trace) and the torque computed from the elastic, viscous, inertial model (dotted trace).

approximately 30 % of the footplate rotation is absorbed in the foot and is not transmitted to the ankle joint.

For an ankle stretch reflex, raw gastrocnemius EMG would have a latency of ~40 ms and the torque response would have an onset latency of ~75 ms reaching a peak value after ~170 ms (Stein & Kearney, 1995). The response would be in one leg only. The perturbations that we applied produced no evidence of a stretch reflex either during preliminary trials when the raw EMG was sampled at 1000 Hz or in subsequent trials when EMG was integrated and sampled at 25 Hz. Figure 3*B* shows averaged integrated EMG records while subjects were strapped to the fixed vertical support and were generating constant levels of ankle torque. In the left leg there was no unambiguous EMG response in soleus, gastrocnemius medialis, gastrocnemius lateralis or tibialis anterior. There was also no evidence of any neural modulation of torque occurring solely in the left leg (Fig. 3*A*). However, in both the right and left legs there is evidence of a small, damped oscillatory variation in torque. This fluctuation in torque may be a small vibration transmitted through the apparatus or it may be an attenuated version of the balancing reaction described below. When the subjects were standing freely there was evidence of a small reaction in left soleus, gastrocnemius medialis and possibly tibialis anterior (Fig. 3*D*). In the integrated EMG record this reaction starts approximately 100 ms after the start of the dorsiflexion and reaches a peak approximately 200 ms after the start of the dorsiflexion. For the standing activity there was a corresponding torque reaction in both the right and left leg (Figs 3*C* and 2*D*). Because the reaction occurs in both legs it is not a stretch reflex. The onset and peak of the torque reaction are ~140 and ~270 ms after the start of the perturbation, respectively. It can be seen that the neurally modulated torque response begins as the mechanical response from the perturbation finishes and does not interfere with the calculation of the intrinsic mechanical stiffness. This reaction is inappropriate as it has a destabilising effect on the CoM which is accelerated to a more vertical position as seen in Fig. 2*A*. The same EMG and torque reaction is seen when balancing the pendulum. The reaction is therefore present only when the intention is to balance an unstable load.

The accuracy of the measurement method was assessed by measuring the stiffness of a calibrated spring. The toe end of the footplate was fastened to the platform by a tension spring. Manual static displacement of the spring through small, calibrated distances provided an estimate of the angular spring stiffness using readings from the load cell and footplate rotation sensor. Measurement of the stiffness using the piezo-electric translator produced a value (4.6 ± 0.2 N m deg^{-1}, mean ± S.D.) that was 18 % higher than the static stiffness of the spring (3.9 ± 0.05 N m deg^{-1}, mean ± S.D.). The coefficient of variation, 5 %, was calculated by taking repeated measurements of the same spring. Using this spring a

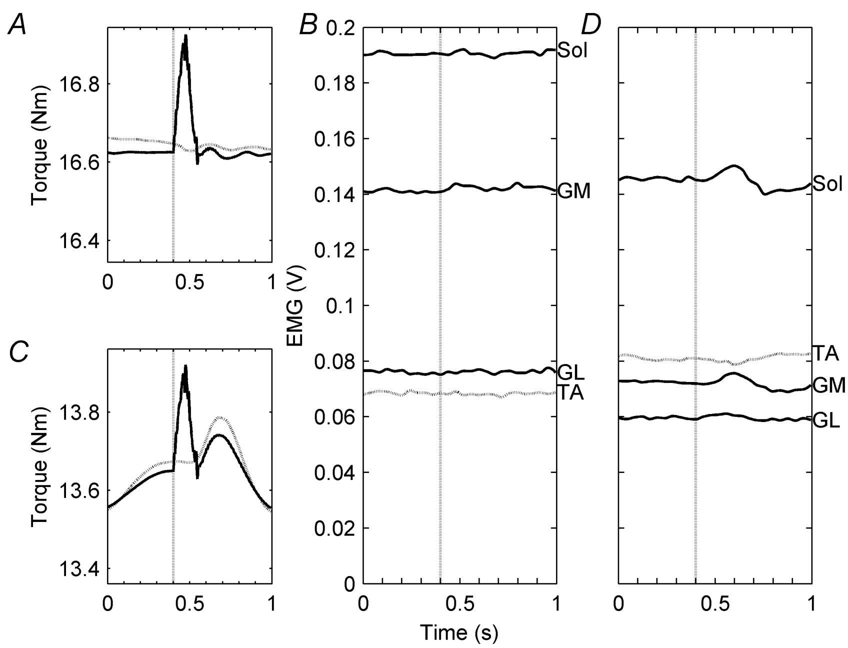

Figure 3. Neurally modulated responses to perturbation

A, left torque (continuous trace) and right torque (dotted trace) record averaged from nine subjects while they maintained a variety of constant torque levels. *B*, the corresponding averaged integrated EMG records from soleus (Sol), gastrocnemius medialis (GM), gastrocnemius lateralis (GL) and tibialis anterior (TA) for the left leg. For the same nine subjects, *C* shows the averaged torque records while standing freely and *D* shows the corresponding averaged EMG records. The perturbations start at 0.4 s.

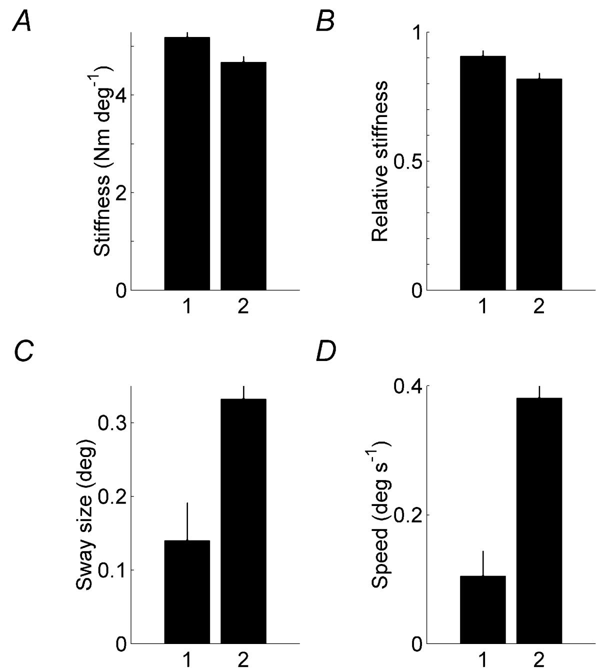

Figure 4. Stiffness during standing and balancing the pendulum

The intrinsic, mechanical left ankle stiffness, averaged from 15 subjects while they stood freely (1) and balanced the pendulum (2) is shown in *A*. *B*, combined stiffness of both legs relative to the toppling torque per unit angle of (1) the body CoM while standing (2) the pendulum CoM while balancing the inverted pendulum. A sway is defined as a unidirectional movement from one reversal point to the next. The median sway size and median sway speed, averaged from 13 subjects are shown in *C* and *D*, respectively, for standing (1) and balancing (2). The uncertainty bars represent standard errors in the mean values.

viscosity of 0.04 N m s deg^{-1} was measured which should be attributed to the apparatus. For four subjects the consistency of their ankle stiffness was assessed by repeating measurements after an interval of 6 months. For the quiet standing activity, their mean difference in ankle stiffness was 10 % or 0.5 N m deg^{-1}.

For fifteen subjects, the mean intrinsic mechanical ankle stiffness for the left leg during quiet standing and balancing the pendulum is 5.2 ± 1.2 and 4.7 ± 1.0 N m deg^{-1} (mean $\pm$ S.D.), respectively (Fig. 4*A*). The difference in stiffness between these tasks is significant but small (unbalanced two way ANOVA, $n = 48$, $F = 11.6$,

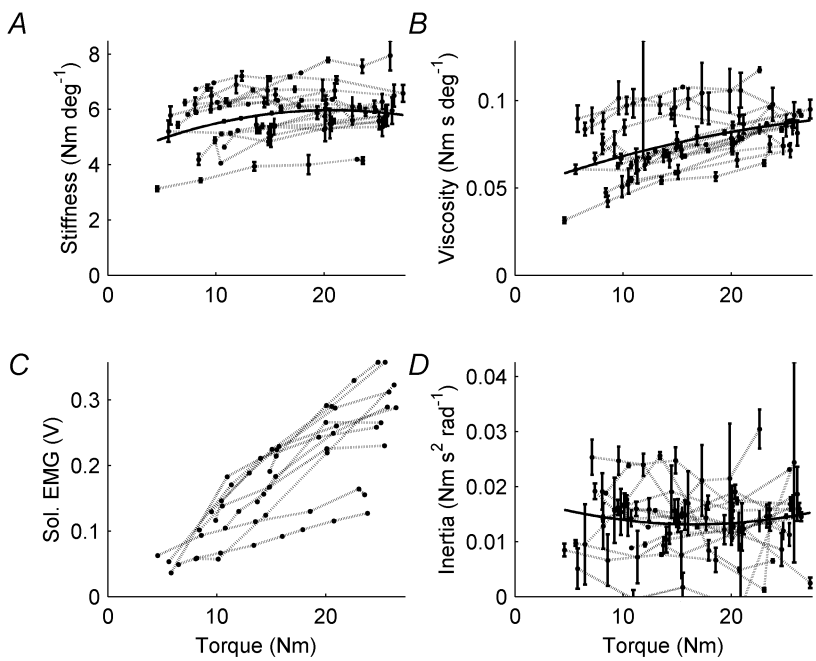

Figure 5. Variation of stiffness with ankle torque

For 15 subjects, the variation of intrinsic mechanical left ankle stiffness with ankle torque is shown in *A*. *B* and *D* show the variation with ankle torque of viscosity (ankle and apparatus) and inertia (foot), respectively. The error bars show the uncertainty associated with estimating the background torque during the perturbation. The continuous lines represent the mean quadratic line of best fit. *C* shows the variation of soleus EMG with ankle torque for 11 of the 15 subjects. For these experiments subjects were strapped at their normal standing ankle angle to a fixed vertical support. Subjects maintained constant ankle torque using visual feedback from an oscilloscope and repeated this at different levels of torque.

$P = 0.002$). By assuming both ankles have the same stiffness, we have calculated the combined ankle stiffness relative to the static toppling torque per unit angle of the body CoM or the pendulum CoM. The mean relative stiffnesses are 91 ± 23 and 80 ± 19 % (mean ± S.D.), respectively, for standing and balancing the pendulum (Fig. 4*B*). The individual subject values of body mass, body height, height of CoM above ankle joint (h), toppling torque per unit angle (mgh), left ankle stiffness and combined relative ankle stiffness are shown in Table 1. For thirteen subjects the mean sway size and sway speed are shown (Fig. 4*C* and *D*). For standing, the footplate rotation caused by the translator is 40 % of the mean subject sway size and the mean footplate rotation speed is 5 times faster than the mean sway speed. While balancing the pendulum the sway size and speed are 2.5 times larger than while standing. Averaging over all subjects, the footplate rotations are larger than 29 % of sways in quiet standing and are faster than all sways in quiet standing.

Measurement of the intrinsic ankle stiffness while subjects maintained a variety of constant torque levels showed only very slight variation of stiffness with ankle torque (Fig. 5*A*). As ankle torque is increased from 5 to 25 N m, the mean ankle stiffness rises from 5 to 6 N m deg^{-1} at around 20 N m and then slightly decreases. The large increase in muscle activation shown in Fig. 5*C* is unable to produce much change in intrinsic mechanical ankle stiffness. For this reason, the ankle stiffness measured is not attributed to muscle fibre stiffness. The source of the measured stiffness is more likely to be the combination of aponeurosis, tendon and foot which will not change greatly with muscle activation. The measured viscosity increases slightly with ankle torque from 0.06 to 0.09 N m s deg^{-1} (Fig. 5*B*). Up to 0.04 N m s deg^{-1} is likely to result from the apparatus and not the subject's ankles. The inertia of the foot showed little variation with ankle torque as would be expected (Fig. 5*D*). The mechanical response was mostly elastic. For each parameter and for all parameters combined the mean percentage variance accounted for (% VAF) was 90 (elastic), 9(viscous) 0 (inertial) and 99 % (combined). The inertial component of our mechanical response is very low. As described in Methods, estimates of the moment of inertia have a high relative error of 89 % and are included to show an

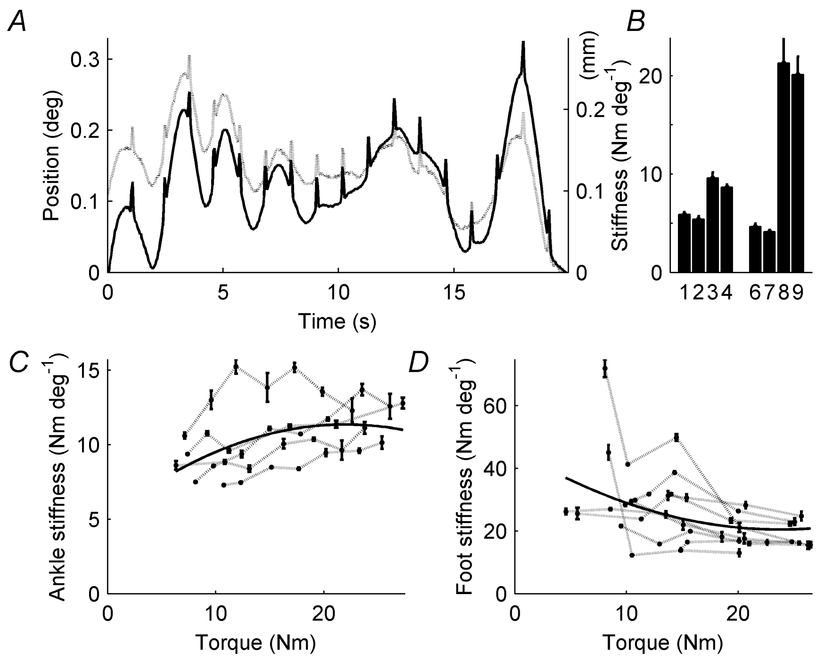

Figure 6. Partitioning stiffness into ankle and foot components

For one representative subject balancing the inverted pendulum, *A* shows the unaveraged record of footplate angle (continuous trace) and heel rotation about the ankle measured using the laser (dotted trace). The left axis scale shows angular changes of the footplate and heel in degrees about an arbitrary zero and the right axis scale shows linear movements of the heel relative to the calf in millimetres. *B*, for six subjects the mean, intrinsic, overall ankle stiffness while standing (1), and balancing the pendulum (2) is shown. The true ankle stiffness measured using the laser is shown for standing (3) and balancing the pendulum (4). For nine subjects the overall ankle stiffness while standing (6) and balancing the pendulum (7) is shown. The foot stiffness measured using the laser is shown for standing (8) and balancing the pendulum (9). For five subjects, *C* shows the variation of true ankle stiffness with ankle torque. *D* shows the variation of foot stiffness with ankle torque for nine subjects. For *C* and *D* the error bars show the uncertainty associated with estimating the background torque during the perturbation. The continuous lines represent the mean quadratic line of best fit.

Table 1. Subject values of toppling torque per unit angle and ankle stiffness

Subject	Mass (kg)	Height (m)	*h* (m)	*mgh* (N m deg^{-1})	Left leg stiffness (N m deg^{-1})	Combined relative stiffness
JH	78.0	1.83	0.97	12.63	5.6	0.89
NH	69.1	1.82	0.93	10.69	5.9	1.11
LT	77.4	1.62	0.86	11.11	4.9	0.87
NC	72.6	1.80	0.96	11.58	6.5	1.13
JR	70.9	1.60	0.87	10.20	1.9	0.37
MK	86.5	1.72	0.93	13.34	5.3	0.80
FO	83.1	1.73	0.96	13.30	5.0	0.75
DG	81.5	1.66	0.92	12.48	4.0	0.63
MH	80.4	1.71	0.90	11.96	6.0	1.01
JHa	73.5	1.65	0.89	10.81	5.0	0.92
KW	59.1	1.67	0.88	8.67	4.4	1.02
JW	60.5	1.74	0.88	8.87	6.0	1.35
SP	79.5	1.73	0.91	12.01	5.0	0.84
IL	69.4	1.78	0.97	11.18	5.8	1.03
ML	90.9	1.85	0.97	14.70	6.5	0.88
Mean	75.5	1.73	0.92	11.57	5.2	0.91
S.D.	8.9	0.08	0.04	1.64	1.2	0.23

approximate value for the foot. The larger elastic component has a small relative error of 4 %.

Figure 6*A* shows that the perturbations are a sizeable fraction of the normal sway size during pendulum balancing and thus also during the smaller sways of quiet standing (Fig. 4*C*). It can also be seen that most of the perturbation is transmitted to the distal end of the Achilles' tendon though some is lost in the foot. The torque resulting from rotation of the footplate allows the calculation of the overall or combined stiffness. The overall stiffness is usually (as here) referred to as ankle stiffness. Figure 7 and the explanatory legend should be consulted for a definition of terms. Rotation of the footplate results in a sum of foot deformation and rotation at the ankle joint. The true ankle rotation is less than the footplate rotation because of the foot deformation. Depending on the position of the laser, the laser measurements can be used to calculate foot stiffness or the true ankle stiffness. For nine subjects where the laser measured deflection of the heel from the footplate, the foot stiffness is around

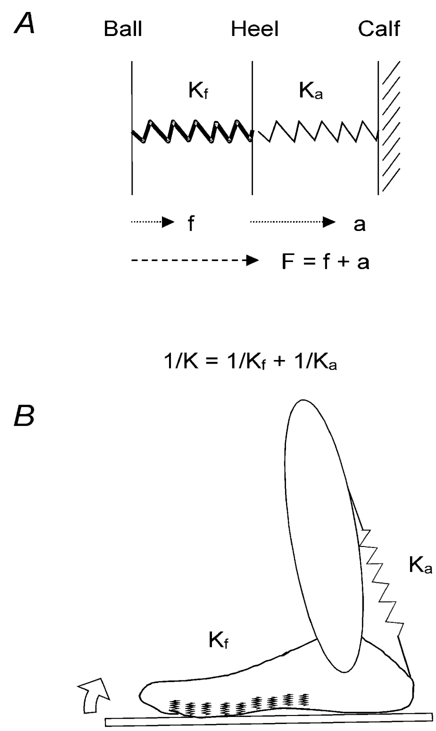

Figure 7. Stiffness and compliance of the foot and ankle

A, rotation of the footplate relative to the calf (*F*) is taken up by angular deformation of the ball of the foot relative to the heel (*f*) and rotation of the heel relative to the calf (*a*) such that $F = f + a$. It is assumed that the calf does not move during the applied rotation of the footplate. The stiffness of the foot (K_f) can be thought of as being in series with the stiffness of the ankle (K_a). In both series elements, the torque (*T*) is the same. The foot stiffness is calculated from the torque increment per unit foot deformation, $K_f = \Delta T/\Delta f$. Likewise the ankle stiffness is the torque increment per unit ankle rotation, $K_a = \Delta T/\Delta a$. The combined stiffness (*K*) is the torque increment per unit footplate rotation, $K = \Delta T/\Delta F$. Compliance is the inverse of stiffness. The combined compliance ($1/K$) is the sum of the foot compliance ($1/K_f$) and ankle compliance ($1/K_a$) so $1/K = 1/K_f + 1/K_a$. Accordingly, *K* of the two series springs is less than the weakest spring in the chain. Usually researchers do not partition footplate rotation into foot and ankle components. *K* is usually regarded as ankle stiffness. So that we may compare our results with previous work we will refer to the combined stiffness (*K*) as the ankle stiffness and we refer to the stiffness related purely to ankle rotation (K_a) as the true ankle stiffness. *B*, we think K_f most likely resides in the soft tissues of the foot as well as the arch. The true ankle stiffness (K_a) includes all components acting in parallel at the ankle joint.

23 ± 13 N m deg^{-1} (mean ± S.D.) compared with their overall stiffness of 4.7 ± 1.2 N m deg^{-1} (mean ± S.D.) (Fig. 6*B*). For six subjects where the laser measured deflection of the calcanean tuberosity relative to the calf, the true ankle stiffness during quiet standing is around 9.6 ± 1.3 N m deg^{-1} (mean ± S.D.) compared to their overall stiffness of 5.9 ± 0.6 N m deg^{-1} (mean ± S.D.) (Fig. 6*B*). Both foot stiffness and true ankle stiffness show some dependency on ankle torque. The true ankle stiffness increases with ankle torque from 8 N m deg^{-1} at 5 N m to a peak and plateau of approximately 11 N m deg^{-1} at around 25 N m (Fig. 6*C*). Conversely, the foot stiffness decreases with ankle torque plateauing at a mean value of 21 N m deg^{-1} at around 20 N m (Fig. 6*D*). During standing the foot stiffness is approximately twice as much as the true ankle stiffness. If the overall ankle stiffness is a series combination of foot and true ankle stiffness, then approximately one-third of the compliance occurs in the foot and two-thirds of the compliance occurs in the Achilles' tendon and associated muscle.

DISCUSSION

In order of discussion we are considering six questions. (1) Is there evidence of reflex activity during quiet standing? (2) What is the intrinsic mechanical ankle stiffness during quiet standing and balancing the inverted pendulum? (3) Is this stiffness a neurally controlled parameter or is it a biomechanical constant, and how does it compare with previous measurements? (4) How does this stiffness partition into 'true ankle' and foot components? (5) Can balance be maintained with a low intrinsic stiffness? (6) What mechanisms of human balance are implied by these results?

Is there evidence of reflex activity during quiet standing?

Studies of reflex activity in the ankle joint musculature have commonly used perturbations that are large and rapid compared with movements that are normally encountered during quiet standing (Stein & Kearney, 1995; Mirbagheri *et al.* 2000). Although the perturbations used in these experiments were smaller than a typical ankle movement during quiet standing they were approximately five times faster. Accordingly they might be expected to elicit reflex responses. In all experimental conditions we found no EMG or torque evidence of a stretch reflex in all 15 of our subjects and thus conclude that stretch reflexes are probably not relevant to quiet standing (Fig. 3). Further investigation of the size and velocity thresholds required to elicit the reflex is necessary to consolidate this conclusion. Our results are consistent with previous research (Gurfinkel *et al.* 1974). These authors used perturbations up to 0.2 deg at 0.6 deg s^{-1} and from visual inspection of the raw EMG they also found no evidence of stretch reflexes.

However, when subjects were standing or balancing the inverted pendulum but not when strapped and maintaining constant levels of torque, there was a very interesting longer latency reaction in triceps surae and tibialis anterior (Fig. 3*C* and *D*). The reaction appears to be 'approved or sanctioned' by the decision to balance (Berthoz, 2000) and is not a reflex in the classic Sherringtonian sense. This response was transmitted to both legs and given the latency is possibly of central origin. It was also inappropriate and destabilising causing the CoM to sway to the upright. It might have been a response to the proprioceptive illusion of falling generated by the increased pressure on the sole of the left foot and the dorsiflexion of the left ankle. The vestibular or visual senses would not have been stimulated because only the foot was moved. If the angular movement about the ankle joint corresponded to a head movement below the visual and vestibular thresholds then the movement was open to misinterpretation by the nervous system. It is a useful reminder of how balancing reactions can be inappropriate and destabilising (Diener *et al.* 1984) and a source of sway generally (Loram & Lakie, 2002).

The intrinsic mechanical ankle stiffness during quiet standing and balancing the pendulum

During the 140 ms period of the perturbation, there was no neural modulation of ankle torque and thus this technique measures the intrinsic, mechanical stiffness of the ankle. This stiffness is assumed to include components from the foot, the parallel elastic stiffness of the ankle, the Achilles' tendon and the triceps surae musculature.

In quiet standing the ankle stiffness is approximately 91 % of the static toppling torque per unit angle of the CoM (Fig. 4) and is thus insufficient to stabilise the human 'inverted pendulum'. This conclusion is valid whether or not human standing is in fact a true, rigid inverted pendulum provided that for the body CoM (i) the vertical acceleration is negligible, (ii) the angular acceleration about the ankles is proportional to the horizontal acceleration and (iii) the moment of inertia of the body about the ankles is constant (Morasso *et al.* 1999). Essentially the same ankle stiffness was found when subjects were balancing the human proportioned inverted pendulum and this was 80 % of that required for minimal stability of the pendulum used, although of course this comparison is dependent on the size of the pendulum used. The viscous component was found to be a very small part of the total response.

While stability and positional control are not provided by the intrinsic ankle stiffness alone, there is some useful instant mechanical torque response to any perturbation or change of ankle angle. In effect the action of gravity on the CoM is nearly cancelled out and so a reduced balancing problem is presented to the central nervous system. Although the system is still unstable and the nervous system has to generate an appropriate ankle torque for every ankle angle, errors in torque are not subjected to so much destabilising positive feedback. The situation is equivalent to having to balance an inverted pendulum of approximately 9 % the actual toppling torque per unit angle although the inertia of the system is unchanged.

Is this stiffness a neurally controlled parameter or is it a biomechanical constant?

It has been argued that the nervous system sets or modulates ankle stiffness to control body sway (Winter *et al.* 1998; Carpenter *et al.* 1999; Gatev *et al.* 1999). According to our measurements the intrinsic stiffness changes little with ankle torque despite a large change in muscle activation and so muscle fibre stiffness is unlikely to be the source of stiffness (Fig. 5*A* and *C*). This leaves the aponeurosis, tendon, and foot as the likely sources of stiffness in standing. We have found that it is remarkably difficult to bring about any significant change in the intrinsic mechanical ankle stiffness. Our conclusion is that in quiet standing intrinsic ankle stiffness is not under neural control but is a biomechanical constant so far as the nervous system is concerned.

Comparison of our stiffness values with previous measurements

Our values of intrinsic stiffness increase from 5 N m deg^{-1} at 5 N m ankle torque to a broad maximum of 6 N m deg^{-1} at 20–25 N m torque (Fig. 5*A*). Using perturbations, others have measured this stiffness over the same range of ankle torques (Hunter & Kearney, 1982; Mirbagheri *et al.* 2000). They give values increasing from 2 and 3 N m deg^{-1} respectively at 5 N m ankle torque to 5 and 6 N m deg^{-1} at 25 N m ankle torque. Also most recent measurement of the triceps surae series elastic stiffness which, excludes the parallel ankle stiffness, shows an increase from 2 N m deg^{-1} at 5 N m to 4.5 N m deg^{-1} at 25 N m (de Zee & Voigt, 2001).

At low torques our values are higher than those previously measured using perturbations and while our values follow the same increasing trend with ankle torque our trend is less pronounced and has a slight plateau or decrease at the higher torque values. Why has this difference in results occurred? An important explanation is that these authors used substantially larger and faster perturbations than we have used. Their earlier measurements have indicated that ankle stiffness increases substantially as perturbation size decreases though their measurements did not extend to the movement range experienced in quiet standing (Kearney & Hunter, 1982). There was the possibility that the small movements occurring in quiet standing are subjected to high short range stiffness caused by the friction-like and stiction-like properties of passive joint complexes (Winters *et al.* 1988). Our perturbations were 40 % of the median ankle movement during standing and are thus appropriate for measuring the stiffness encountered during quiet standing. Our results give weight to the idea that ankle stiffness is higher when the ankle movements are smaller and slower. This idea is illustrated by the fact that while standing the intrinsic ankle stiffness is 10 % higher than while balancing the inverted pendulum (Fig. 4*A*). Balancing the pendulum was associated with greater ankle movement (Fig. 4*C*) and was not even remotely associated with any corresponding changes in ankle torque, EMG or ankle angle. Based on our absolute accuracy check using a calibrated spring, a second explanation of the difference between our measurements and previous measurements is that our values could be 18 % too high though this would not account for the lack of dependency on ankle torque.

With a combined relative stiffness of 91 %, the partial stabilisation achieved by the intrinsic, mechanical ankle stiffness is greater than has been predicted (Morasso *et al.* 1999; Morasso & Schieppati, 1999). These authors have argued, rightly in our view, in favour of active stabilisation mechanisms. However we think they have tended to overestimate the human toppling torque per unit angle (Table 1). They also underestimated the intrinsic ankle stiffness by neglecting the fact that people have two legs.

In a similar experiment to our own Gurfinkel *et al.* (1974) estimated the mean intrinsic ankle stiffness of five subjects to be 7.6 N m deg^{-1} per leg. These gave a combined stiffness of 112 % relative to the toppling torque per unit angle of their subjects. Subjects were standing on a force platform which was rotated toes upwards at 0.6 degs s^{-1} by up to 0.2 deg. These unidirectional perturbations are the same order of magnitude as movements which occur naturally in quiet standing and like our own experiments the perturbations appear to have allowed the standing process to continue. Perturbations were averaged and ankle stiffness was calculated from the change in ankle torque divided by the change in ankle angle measured over an unspecified period up to 0.3 s following the perturbations. Our reservation about this work is that from their Fig. 1 the subjects were clearly thrown backwards by the perturbation. This can be seen from the difference between the platform rotation and the change in ankle angle. The modulation of ankle torque associated with the change in position of the body centre of mass was not subtracted from the total change in ankle torque. In fact it is not clear that the change in torque was wholly mechanical, especially given the unspecified duration of the measuring period, the movement of the body centre of mass, the unidirectional nature of the perturbations and the raw EMG records shown in Fig. 1. If these factors were included the estimate of stiffness would be reduced but we cannot say by how much.

Recently it has become possible by using dynamic ultrasonography to measure tendon stiffness *in vivo* without using perturbations. Measurement of the gastrocnemius tendon gives a mean stiffness of 3.4 N m deg^{-1} rising to a value of 6.5 N m deg^{-1} near maximum voluntary contraction of the muscle (Maganaris, 2002). These values exclude other parallel components to ankle stiffness such as other tendons (particularly the soleus tendon) and connective tissue. It is therefore expected that the mean value will be lower than our value for quiet standing.

Partitioning of compliance into foot and ankle components

Our laser measurements of foot deflection and true ankle rotation allow us to partition the ankle stiffness into foot and true ankle components. Our finding for quiet standing that approximately one-third of the angular compliance occurs in the foot and two-thirds occurs at the ankle joint is in good agreement with a previous study of this question (Gurfinkel *et al.* 1994). These authors found similar values of foot stiffness and a similar partition ratio for larger ankle displacements including up to 2 deg.

The source of intrinsic ankle stiffness

Our direct measurements of ankle stiffness confirm our previous model based predictions showing that the intrinsic ankle stiffness is insufficient to provide stability of the human or the artificial, human proportioned inverted pendulum (Loram & Lakie, 2002). It is important to be clear what we mean by intrinsic ankle stiffness. It is the instantaneous mechanical stiffness provided by the combination of active muscle, tendon, connective tissue and foot. When one is measuring the stiffness combination of springs in series such as the muscle fibres and the tendon, the value of stiffness is limited by the weakest spring. It is a common misconception (initially shared by ourselves) that the tendon has greater stiffness than the muscle. The misconceived idea is of an actuator (the muscle) connected to a lever (the heel of the foot) by a steel wire (the tendon). In the context of quiet standing, it seems from the lack of change in stiffness with ankle torque and muscle activation, that the combined inactive components of tendon, aponeurosis and foot are less stiff than the muscle fibres. The tendon and connective tissue thus provide the weakest member in the series chain and they effectively set the value of the intrinsic ankle stiffness. It makes mechanical sense for the tendon to be more compliant than the muscle fibres for large as well as small movements. If the tendon and foot were stiffer than the muscle fibres then a sudden, forceful deflection of the foot, such as when walking up a step onto the ball of the foot, might provide a rapid, damaging pull on the muscle fibres. A more compliant tendon would buffer the muscle fibres from the perturbation by reducing the sudden lengthening of the muscle. The situation is different at much higher force levels where the increased tendon stiffness must be adequate to transmit the large torques generated during running and jumping (Hof, 1998; de Zee & Voigt, 2001).

Response to the criticism that the CoM cannot be stabilised with a low intrinsic ankle stiffness

It has been claimed that stability cannot be maintained unless the intrinsic ankle stiffness is greater than the gravitational spring (mgh) (Winter *et al.* 1998, 2001). These authors argue that the nervous system sets the muscle tone sufficiently high to create muscle stiffness safely greater than the gravitational spring and they also maintain that the nervous system then leaves the intrinsic stiffness to do its job. Our results do not support these assertions because even at ankle torques higher than those encountered in quiet standing the measured intrinsic stiffness is too low. An alternative theoretical possibility would be co-contraction of the ankle musculature, but there is little evidence of this when the ankle strategy is used to balance an inverted pendulum (Loram *et al.* 2001; Loram & Lakie, 2002).

We agree with Winter *et al.* (1998, 2001) that on average the instantaneous rate of change of ankle torque with CoM angle must be greater than mgh to maintain stability. However, as stated by Roberts, changes in torque with angle can result from changes in spring offset as well as from intrinsic, spring stiffness (Stein, 1982). Modulation of the offset is ignored in the analysis of Winter *et al.* (1998, 2001). Stability of the CoM can be maintained with low intrinsic ankle stiffness so long as there is an alternative neural mechanism for modulating ankle torque. Our favoured possible mechanism is active and appropriately phased, neural modulation of the series elastic offset. This mechanism would be consistent with our previous hypothesis of intermittent, ballistic-like control of the CoM (Loram & Lakie, 2002).

A proposed mechanism of balance control

Our measurements and reasoning suggest a simple model of standing. They suggest that the muscle fibres act as a stiff actuator which has the ability to change its length as a result of neural modulation. This actuator transmits torque to the ankle joint via a relatively weak spring. The spring has its length and tension altered by changes in position which occur at the distal end (the heel) and the proximal end (the tendo-muscular junction). The triceps surae muscle controls the position of the proximal end of the Achilles' tendon and thereby controls the tension in the spring and indirectly the position of the body CoM. Our conclusion is that the horizontal projection of the centre of mass is controlled by a spring offset control mechanism, not by a stiffness control mechanism. This mechanism requires that the proximal end of the weak spring (length of muscle fibres) be controlled in an anticipatory manner by the nervous system. It may be significant that the muscle spindles are well positioned to register the length of the muscle fibres and thus the spring offset. This idea and its physiological implications will be discussed more fully in the future.

A caveat

Compliance of the foot means that the axis of rotation of the body CoM is not a fixed centre through the ankle joint. As visual observation will confirm, the axis of rotation moves forward as the body sways forward and more torque is transmitted through foot. This may mean that for small sways close to the vertical the toppling torque per unit angle is less than it would be if the centre of rotation did not move. Thus for such sways the intrinsic mechanical stiffness could confer more stability than our calculations show. This possibility requires further investigation.

Conclusion

In conclusion, we find that in quiet standing the intrinsic, mechanical ankle stiffness is around 5 N m deg^{-1} per leg which for both legs amounts to 91 % of the static toppling torque per unit angle of the body CoM. This stiffness is relatively constant and is not under neural control. One-third of the compliance occurs in the foot and two thirds occurs at the ankle joint. We predict that the body CoM is controlled by anticipatory modulation of the proximal offset position of the weak spring which is the Achilles' tendon. Our evidence is that stretch reflexes are not relevant to quiet standing.

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Acknowledgements

The apparatus, which was funded by a grant from the Sir Jules Thorn Charitable Trusts, was constructed by Mr Steve Allen. We would like to thank the subjects for participating in these experiments.