

Human balancing of an inverted pendulum: is sway size controlled by ankle impedance?

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1. Using the ankle musculature, subjects balanced a large inverted pendulum. The equilibrium of the pendulum is unstable and quasi-regular sway was observed like that in quiet standing. Two main questions were addressed. Can subjects systematically change sway size in response to instruction and availability of visual feedback? If so, do subjects decrease sway size by increasing ankle impedance or by some alternative mechanism?
2. The position of the pendulum, the torque generated at each ankle and the soleus and tibialis anterior EMG were recorded.
3. Results showed that subjects could significantly reduce the mean sway size of the pendulum by giving full attention to that goal. With visual feedback sway size could be minimised significantly more than without visual feedback. In changing sway size, the frequency of the sways was not changed.
4. Results also revealed that ankle impedance and muscle co-contraction were not significantly changed when the sway size was decreased. As the ankle impedance and sway frequency do not change when the sway size is decreased, this implies no change in ankle stiffness or viscosity.
5. Increasing ankle impedance, stiffness or viscosity are not the only methods by which sway size could be reduced. A reduction in torque noise or torque inaccuracy via a predictive process which provides active damping could reduce sway size without changing ankle impedance and is plausible given the data. Such a strategy involving motion recognition and generation of an accurate motor response may require higher levels of control than changing ankle impedance by altering reflex or feedforward gain.

In this study subjects balanced an artificial inverted pendulum equivalent in mass and inertia to a medium sized woman. Motion was restricted to one joint and one plane and sensory feedback could be limited to the proprioceptive system by eliminating visual feedback and preventing movement of the body. It provided a mechanically simple way of studying the ankle mechanisms employed in balancing which eliminated the multi-joint dynamics of real standing. Normal standing is a complex activity both mechanically and neurologically. Our approach was to reduce and simplify the complex system in order to gain an insight into the underlying principles. The inverted pendulum balancing task has previously been compared with normal standing (Fitzpatrick *et al.* 1992*a,b*, 1994*a,b*, 1996; Fitzpatrick & McCloskey, 1994). These authors concluded that the task was broadly equivalent to real standing.

In standing, the body has been considered as an inverted pendulum (Gurfinkel & Osevetz, 1972). Using a multi-target movement tracking system, Winter *et al.* (1998) recently validated the inverted pendulum model for

sagittal sway. While corroborating earlier observations that greater angular changes occur at the hip joint than the ankle (Day *et al.* 1993), Gatev *et al.* (1999), using a multi-camera system, have demonstrated that ankle mechanisms dominate in the sagittal plane with an almost synchronous sway of the body parts. Authors who work with more sophisticated models of standing still regard the inverted pendulum model as capable of capturing the gross dynamics of posture control (Nicholas *et al.* 1998).

It is evident that the extent of postural sway is not fixed. Some subjects sway more than others and in any one subject size of sway can be altered by changing sensory input (Paulus *et al.* 1984) or by volition (Fitzpatrick *et al.* 1992*a,b*). The role of joint stiffness in the maintenance of posture has been debated for some time (Grillner, 1972; Horak & MacPherson, 1996). There have been frequent suggestions that sway size is reduced by increasing ankle stiffness (Fitzpatrick *et al.* 1992*b*; Winter *et al.* 1998; Carpenter *et al.* 1999; Gatev *et al.* 1999).

Fitzpatrick *et al.* (1992*b*) applied slow, imperceptible perturbations to five subjects while standing or when

balancing an inverted pendulum. When subjects were instructed to stand still, or had more kinds of sensory feedback available, sway in response to perturbations was reduced and ankle stiffness was increased. The increased stiffness was attributed to increased reflex gain.

Winter *et al.* (1998) measured the centre of pressure and centre of mass oscillations of 10 quietly standing subjects. They argued that the relationship of these two parameters could be explained by a non-reactive, simple elastic model. With this model, sway size would be predicted to be inversely proportional to the square root of stiffness (K_e). Values for anterior/posterior (A/P) oscillations are not given, but in the medial/lateral (M/L) plane sway size was observed to be proportional to $K_e^{-0.55}$, which was close to their theory.

Gatev *et al.* (1999) demonstrated feedforward modulation of gastrocnemius activity with seven standing subjects. He hypothesised a central, predictive control of ankle stiffness working to restrict sway size with the activated gastrocnemius muscle working in a spring-like manner. Whereas Gatev *et al.* (1999) and Winter *et al.* (1998) found no effect of vision on quiet standing, Fitzpatrick *et al.* (1992*a,b*) and Carpenter *et al.* (1999) found conflicting evidence that vision does increase ankle stiffness.

Some experimenters have used relatively large and abrupt disturbances such as moving the platform on which the subject stands. Such experiments provide insight into the mechanisms which respond to a gross loss of balance (Horak *et al.* 1989; Bloem *et al.* 2000). Such events are rare in the usual experience of standing and do not illustrate the patterns of muscular activity that are repeated over and over in quiet standing. Fitzpatrick *et al.* (1992*b*) used small, slow perturbations to measure ankle stiffness while subjects maintained their own balance or balanced an inverted pendulum. These disturbances, which were not consciously detected by the subject, were comparable in size to normal sway and thus portrayed the standing process more closely.

We employed an alternative approach. In normal balancing there are frequent minor departures from equilibrium. By examining the response to these spontaneous departures from equilibrium the need for external perturbations is obviated. By detecting the losses of balance as they occur naturally, and by averaging many examples of the responses, the impedance of the ankles can be determined. (The impedance is to be preferred to stiffness as the resistance to motion at the ankles involves elastic and viscous components and is frequency dependent.)

The aim of this investigation was to address two main questions. Can subjects systematically reduce sway size through their own volition or by use of visual feedback? If so, do subjects reduce sway size by increasing ankle impedance?

METHODS

Subjects

Ten healthy people, of whom six were male, aged between 18 and 45 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.

Apparatus

Subjects were strapped round the pelvis to a vertical support that effectively eliminated their actual sway (Fig. 1). The subject stood on two footplates with his/her ankles positioned to be co-axial with the axis of rotation of an inverted pendulum. The footplates were exactly horizontal when the backward lean of the pendulum was 3 deg, thus approximating typical forward lean in standing. The pendulum had a mass of 61.65 kg with a centre supported 0.937 m from the axis of rotation (distance h). The subject balanced the inverted pendulum, which was free to move forwards and backwards, in a parasagittal plane while always tending to topple backwards. The same mass and distance h were used for all subjects. The constant static and dynamic properties of the pendulum presented each subject with an identical task. This allowed results from all subjects to be pooled. The toppling torque of the pendulum was measured to be 10.2 ± 0.4 N m deg⁻¹ (mean \pm s.d.). Using a spring of known stiffness and by recording the damped oscillations of the pendulum, the moment of inertia was determined to be 62.6 ± 2 kg m² (which included the contribution of the rod and other rotating parts), the viscous damping was 0.061 ± 0.02 N m s deg⁻¹ and friction was 0.045 ± 0.1 N m (means \pm s.d.).

The relative angular position of the pendulum was measured using a Hall effect precision potentiometer (with an effective range of 15 deg) (CP 2UTX, Midori Precision Company Ltd, Japan) and fixed gain amplifier. Absolute angular position was measured using an electronic inclinometer (Cline R1, Cline Labs Inc., USA), of resolution 0.001 deg, attached to the base of the pendulum. The angular velocity of the pendulum was measured using a piezoelectric vibrating gyroscope (range ± 90 deg s⁻¹) (ENV-05 A+C, Murata Co. Ltd, Japan) in conjunction with an instrumentation amplifier. The subject exerted torque on the pendulum via each footplate. The left and right torque signals were recorded using horizontally mounted miniature load cells (Sensotec model 31, Sensotec Inc., USA) followed by a two-channel bridge amplifier and low-pass filter (Sensotec UBP). The load cells were mounted in compression in the horizontal plane. One end of the transducer was rigidly bolted and the other made contact with a polished surface. This method of mounting effectively decoupled the load cells from off-axis loads and prevented the slight deflection of the structure caused by the subject's weight from producing a signal which would be falsely registered as a torque (Kelly, 1998). Electromyographic (EMG) activity from the right and left tibialis anterior and soleus muscles was recorded using home-constructed bipolar surface electrodes with encapsulated preamplifiers (Johnson *et al.* 1977). These signals containing the entire bandwidth were then amplified and passed through an analogue full-wave rectifier and r.m.s. averaging filter with a time constant of 100 ms. Data from all sensors were recorded by computer, and sampled at 25 Hz via an analog-to-digital converter (CED 1401, Cambridge Electronic Design, UK). The resolution of the recorded data was limited by input noise levels of less than 0.002 deg, 0.02 deg s⁻¹, 0.03 N m, 60 μ V for relative angular position, angular velocity, right or left torque and surface EMG, respectively.

Experimental protocol

The inverted pendulum apparatus has been designed to study the effect of limiting the kinds of sensory inputs influencing ankle

mechanisms used to control upright balance (Fitzpatrick *et al.* 1992*b*). Since the subjects themselves were prevented from swaying, vestibular feedback was not available to them. The pendulum mass and rod were screened from view, though an oscilloscope was available providing the option of visual feedback regarding the position of the pendulum. The oscilloscope was 1 m away from the subject and had a gain of 1 cm deflection per degree change in angular position. When visual feedback was not used, the oscilloscope was turned off though subjects still had their eyes open. Proprioceptive information from the legs was available to all subjects. Tactile information from the areas of the trunk in contact with the support was also available, but is likely to be inconsequential (Fitzpatrick *et al.* 1992*b*).

In four separate trials, subjects were asked to balance the inverted pendulum under differing instructions and visual conditions. The four trial conditions were (1) stand still using visual feedback, (2) stand easy using visual feedback, (3) stand still with no visual feedback and (4) stand easy with no visual feedback. The order in which the four conditions were carried out was randomised. The duration of each trial was 200 s. In all cases the subjects were asked to keep the pendulum between 0.5 and 5.5 deg from the vertical so as to approximate standing sway.

It was explained that 'stand still' meant to reduce the sway of the pendulum to an absolute minimum and to keep the pendulum at the same angle. Subjects were told that 'stand easy' meant to balance the pendulum while giving the least possible attention to the sway of the pendulum. When subjects were 'standing still' they were encouraged to give their full attention to the oscilloscope when that was turned on and to give full attention to what they could register through their legs when the oscilloscope trace was blanked. When subjects were 'standing easy' they were engaged in meaningful conversation to take their mind off the task as much as possible.

All subjects were given a preliminary experience of balancing the pendulum at different angles ranging from 1 to 5 deg using visual feedback from the oscilloscope. They also practised balancing the pendulum without the use of visual feedback. The subjects then reported the angle at which they preferred to balance the pendulum. This was around 3–4 deg for all subjects. For each trial, recording started with the pendulum at the preferred angle of the subject.

Principles and methods of data analysis

During balancing, the pendulum sways to and fro in a quasi-regular fashion. We identified the times at which the pendulum reversed direction by interpolating between the data points when the velocity changes sign. The unidirectional movement between one turning point and the next was categorised as a sway. For any trial, the mean sway size was the average magnitude of the sways. Mean sway frequency was calculated as the total number of sways (positive and negative) divided by 2 and divided by the trial duration.

Gravity exerts a torque on the inverted pendulum given by $T_g = K_u \sin \theta \approx K_t \theta$, where K_t is the gravitational toppling torque per unit angle. At any angle θ from the vertical, this formula defines the ankle torque that is required to balance exactly the pendulum. (Dynamic torques due to frictional and viscous damping of the pendulum are very small.) On a plot of torque *vs.* angle this formula defines a line of unstable equilibrium (which has also been called the load stiffness of the pendulum; Fitzpatrick *et al.* 1992*b*). To keep the sway size between certain limits, the ankle torque must be repeatedly alternated above and below this line. Line crossings represent repeated events around which data can be averaged and from which ankle impedance at equilibrium can be measured.

Using Savitzky-Golay filters, the position data were double differentiated to produce a record of acceleration (Press *et al.* 1999).

From Newton's second law of motion the angular acceleration is zero at equilibrium. Equilibrium points represent moments at which the subject perfectly balances the static and dynamic torques exerted on them via the pendulum. We identified those equilibrium points when zero acceleration was crossed by interpolating between the data points when the acceleration changes sign.

In each unidirectional sway a spring-like equilibrium occurs at least once. This is represented by a positive gradient of torque *vs.* angle crossing the line of equilibrium. These equilibria were identified by an acceleration changing from positive to negative while the pendulum was falling, or negative to positive while the pendulum was rising. The data surrounding these equilibrium points were averaged to show the mean responses. The impedance at these averaged equilibrium points was calculated as the regression value for

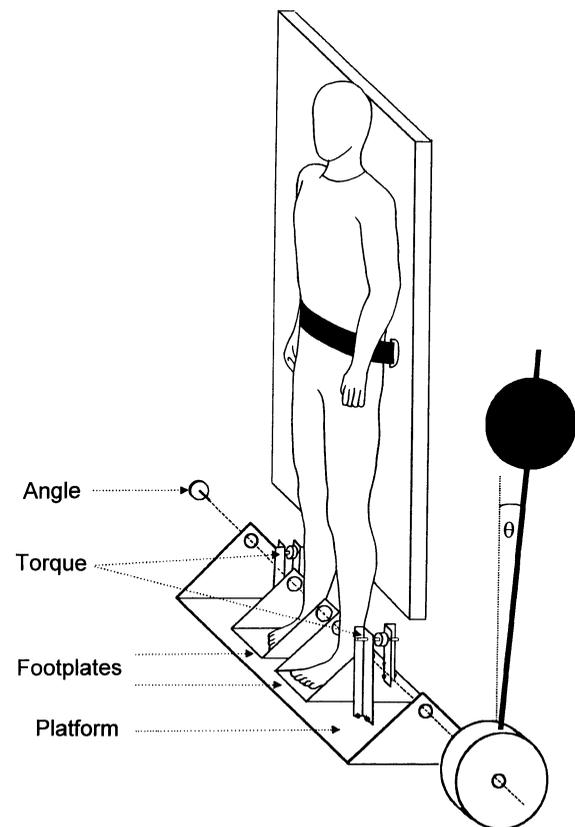


Figure 1. Inverted pendulum apparatus

Subjects balanced a backward-leaning, real inverted pendulum of mass and inertia equivalent to a medium sized woman. The subjects were unable to sway since they were strapped round the pelvis to a fixed vertical support. The axis of rotation of the pendulum, platform and footplates was co-linear with the subject's ankles. Force exerted by the subject's ankle musculature onto each footplate was transmitted by horizontally mounted load cells. These measured the torque that each leg applied to the pendulum via the rigidly attached platform. The footplates and the platform were independently mounted on precision ball races. A precision potentiometer measured sway of the pendulum. Absolute angle of the pendulum (θ) and angular velocity were measured by an electronic inclinometer and a solid state gyroscope (not shown).

Δ torque/ Δ angle encompassing one data point (40 ms) either side of the equilibrium. This method of identifying equilibrium points, sampling around these points and averaging is illustrated in Fig. 2.

This line crossing impedance is a biased measure in that the ankle impedance of high frequency sways will be greater than that for low frequency sways. So, to investigate the effect of frequency, we have grouped the line crossing equilibria into frequency bins and then separately averaged the line crossings for each frequency category. The appropriate frequency bin for each line crossing was determined from the duration between the nearest reversal points surrounding the line crossing, using the formula: frequency = $1/(2 \times \text{inter-reversal duration})$.

The position and velocity records possess small, relatively high frequency variations of the same magnitude and frequency as the noise that is recorded when a subject is not standing on the footplate to balance the pendulum. Given the large inertia of the pendulum, these variations are taken to be a noise product of the measuring and recording process and were eliminated by smoothing as part of the

differentiation process. A Savitzky-Golay filter algorithm was used, which assumes that the noise is normally distributed and independent of the slowly changing variable and that a moving polynomial can be fitted to the data (Gander & Hrebicek, 1997; Press *et al.* 1999). This algorithm was effectively used as a low-pass filter with a bandwidth of 3 Hz and zero phase shift. Data from the velocity and position sensors were cross-checked to corroborate the differentiation and smoothing process.

Modelling

We wanted to know the effect of ankle stiffness, viscosity and noise on our line crossing measure of ankle impedance, on sway size and on sway frequency. A second-order model of the inverted pendulum was constructed for simulation purposes as described in Appendix. Torque generated at the ankles was modelled as having a stiffness component, a viscous component and a noise component as described by Winter *et al.* (1998). Results generated from this model were subjected to the same analysis procedures used for real data.

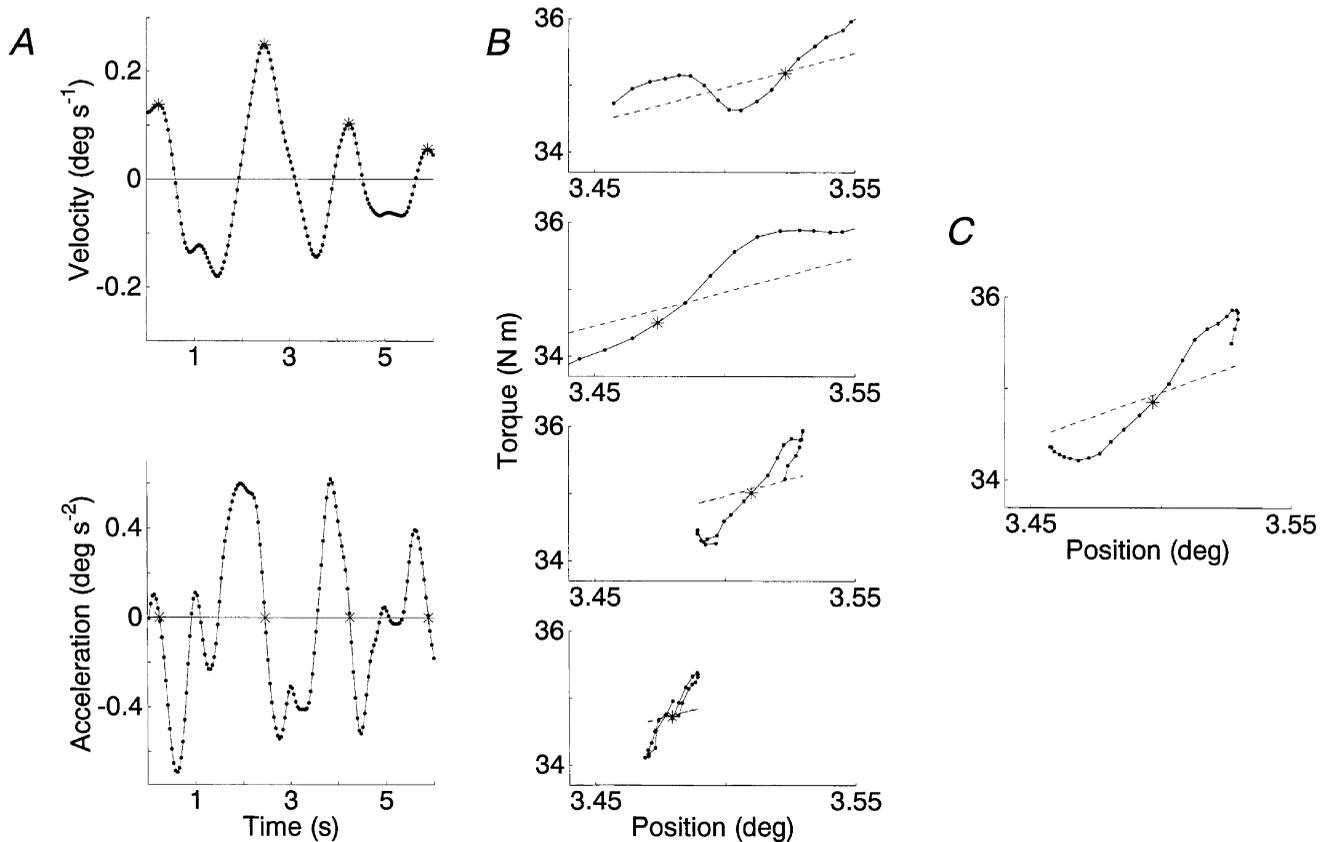


Figure 2. Illustration of the line crossing averaging process

A, a 6 s record of angular velocity and angular acceleration against time for a representative subject. Equilibrium times are identified by interpolating between the pairs of acceleration data points that cross zero. From these equilibrium times are selected those that occur while the acceleration is passing from positive to negative and while the velocity is positive (i.e. the pendulum is falling). These equilibrium times are shown as an asterisk. Ankle torque and pendulum position records are sampled at 0.04 s intervals for up to 5 s before and after these selected equilibrium times. The four selected equilibrium times in A are shown in B, together with ± 0.48 s of surrounding data, plotted as ankle torque against pendulum position. The straight dashed lines represent the line of equilibrium, $T_g = K_v \sin \theta$ (load stiffness). The selected equilibria represent falling (increasing angle), spring-like (positive gradient) line crossings with an ankle impedance (Δ torque/ Δ angle) greater than the load stiffness. The four 0.96 s records shown in B are averaged to produce the record shown in C. The rising, positive gradient line crossings are selected and averaged in an analogous manner.

RESULTS

All the subjects could balance the pendulum for an adequate period after minimal familiarisation although some found the task easier than others.

The complex variation of ankle torque with pendulum angle for a representative subject over a 12 s period is plotted in Fig. 3. As seen from the 'line crossings', there was no one position of equilibrium though the irregular sway was confined to a small range of angles. At all angles the ankle torque stayed close to the line of equilibrium (approximately ± 1 N m). The torque alternated above and below that required for equilibrium. A given sway size of the pendulum can be maintained by the subject exerting an ankle torque close to the equilibrium line for a long time or far from the equilibrium line for a short time. The torque *vs.* angle gradient (instantaneous ankle impedance) was usually steeper than the equilibrium line (load stiffness) and appeared to have some consistency. The equilibrium line was sometimes crossed with a negative gradient, which permitted sustained positional drift while maintaining balance.

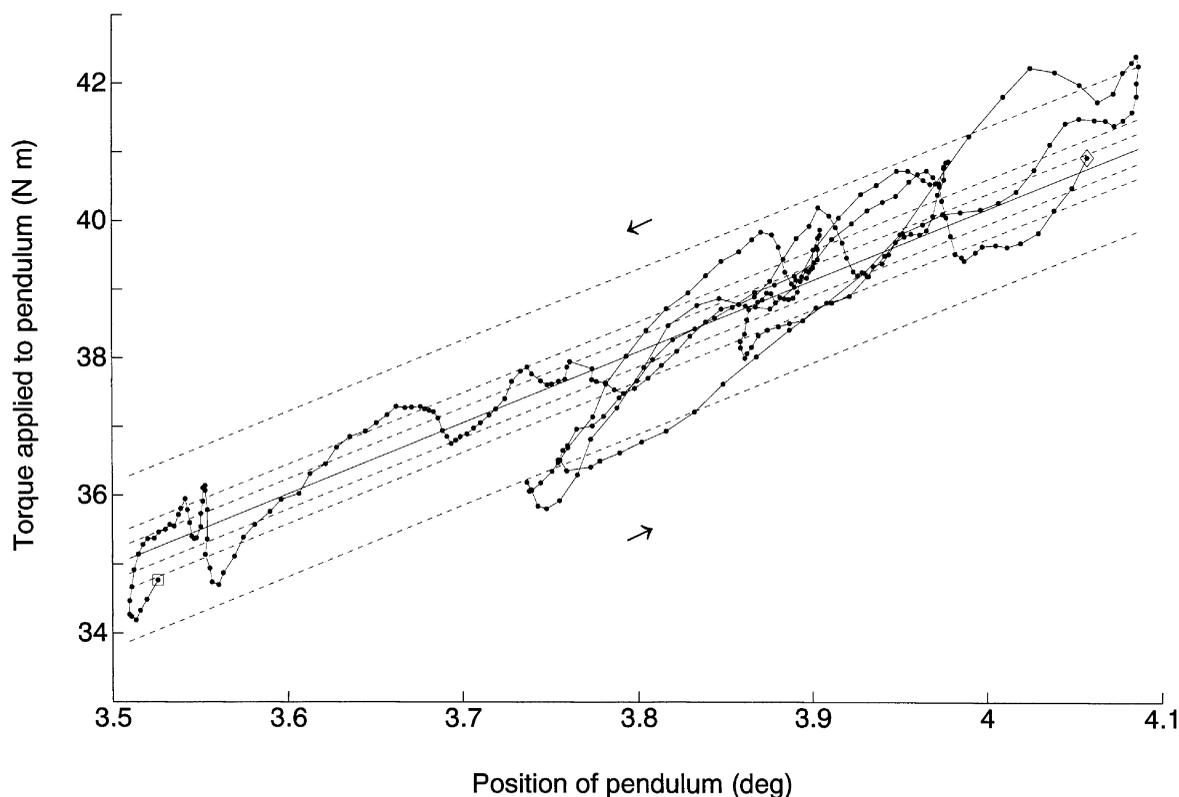


Figure 3. Representative sway of one subject

A 12 s record from one subject is plotted as combined ankle torque against pendulum position. Data points are at 40 ms intervals. The starting point, \diamond , and finishing point, \square , are indicated. The line of equilibrium, load stiffness ($T_g = K_{tt}\sin\theta$), is shown as a continuous straight line. Dashed lines parallel to this represent lines of constant torque error. Torque error produces a directly proportional acceleration of the pendulum in the direction indicated by the arrows. The inertia of the pendulum effectively 'absorbs' the torque; even with the largest torque error shown it will take 0.6 s for the deflection of the pendulum to reach 0.3 deg (this trial's average sway size) from rest. The smaller and smallest torque errors are associated with times of 1.0 and 1.4 s, respectively.

Figure 4 shows that the conditions of the trial did make a difference to the sway size. Figure 4A shows a histogram of sway sizes for a representative subject recorded under each of the four trial conditions. For each condition, most sways were small. There were fewer large sways and more small sways when the subject was attempting to stand still rather than stand easy (1 *vs.* 2 and 3 *vs.* 4) and sways were slightly smaller when visual feedback was allowed (1 *vs.* 3 and 2 *vs.* 4).

Figure 4B shows that there was a significant difference in sway size between the four trial conditions (two-way ANOVA, $N = 2040$, $F = 41.4$, $P < 0.001$). The mean trial sway size from the first 51 sways of each trial was averaged over 10 subjects for each of the four conditions. Subjects could significantly minimise their sway size when 'standing still' as opposed to 'standing easy' (1 *vs.* 2 and 3 *vs.* 4, 95% simultaneous confidence intervals (SCI) used for *post hoc*, Tukey, pairwise comparisons). Subjects could minimise their sway size significantly more with visual feedback (1 *vs.* 3, 95% SCI). Visual feedback made less difference to the sway size when subjects were 'standing easy', i.e. giving minimal attention to sway (2

vs. 4). Interestingly, the trial conditions caused no significant change in the sway frequency (Fig. 4C; two-way ANOVA, $N = 40$, $F = 0.89$, $P = 0.46$). This implies that the amplitude but not the duration of the sways is being changed by the intent or visual conditions of the subject.

Ankle impedance was not changed to bring about a reduction in sway size (Fig. 5). Figure 5A shows representative data for one subject in each of the four trial conditions. Data were averaged from 1.3 s before to 1.3 s after all positive gradient 'line crossings' while the pendulum was falling. Data points are shown at 40 ms intervals. The same basic pattern of torque *vs.* angle is seen for each condition. The width of the pattern, e.g. inter-reversal change in position (0.07, 0.23, 0.09, 0.34 deg, respectively), ranks in the same order as mean trial sway size. The 'line crossing' impedance was approximately the same for each condition. The velocity at equilibrium was less when the sway size was less and the stationary points (a, b) were closer to equilibrium (less torque error) when the sway size was less.

The detailed shape of the curves in Fig. 5A gives several interesting insights into the balancing process. Unlike undamped simple harmonic motion, the pattern of ankle torque *vs.* angle was not a straight line. Indeed the pattern is not strictly an oscillation with the same starting and finishing point: it shows a net change in position of equilibrium which can be thought of as a positional step. The torque did not always change in phase with angle. This indicates modulation of ankle torque that does not depend solely on elastic forces and which is partly in phase with velocity with a consequent energy absorbing effect. The average velocity of the preceding and subsequent equilibrium ('line crossing') was reduced (almost zero for 'stand still'), which illustrates the effect of damping. However, there was no increase in gradient at maximum velocity (equilibrium), which shows that this is not simple viscous damping. This same pattern was repeated when the pendulum was rising rather than falling. No difference from this pattern has been seen in any trial.

Figure 5B shows there was no significant difference in ankle impedance between the conditions of the four trials

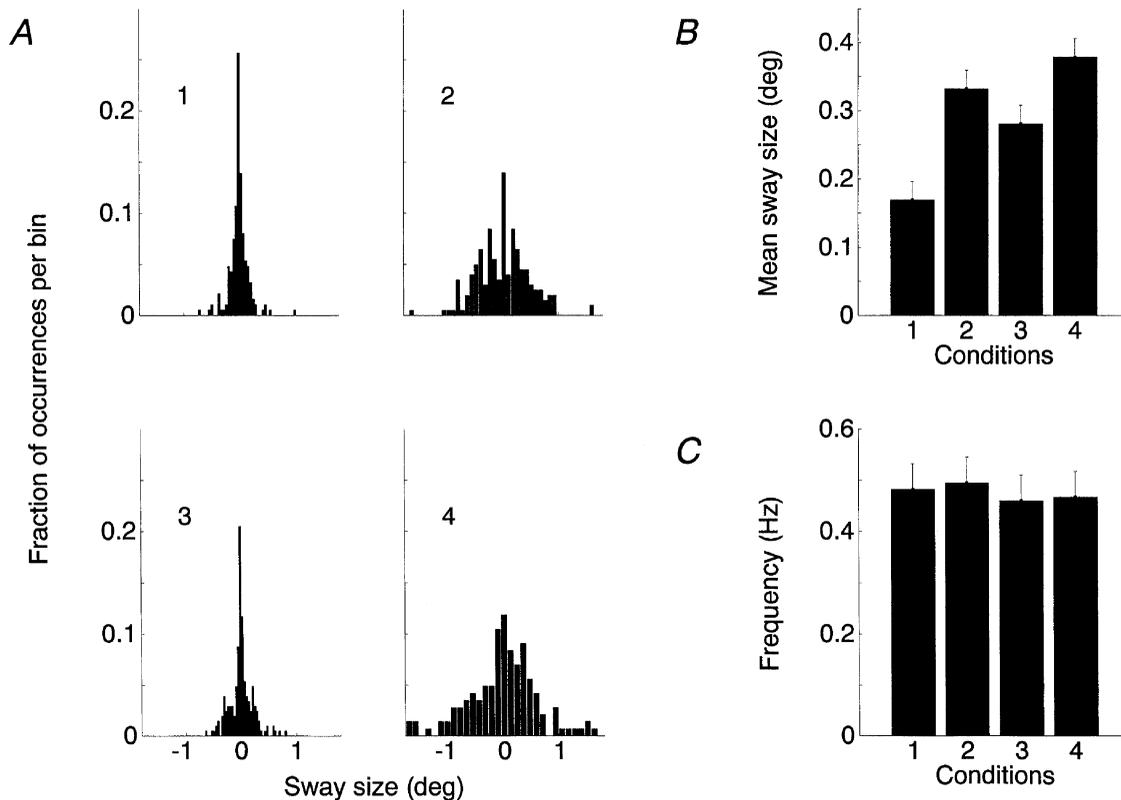


Figure 4. Effect of trial conditions on sway size

A, distributions of sway sizes for one subject under each of four trial conditions labelled 1, 2, 3 and 4 as described in Methods. Each trial lasted 200 s. A sway size was the angular displacement between successive turning points of the pendulum. Trial conditions were (1) stand still with visual feedback, (2) stand easy with visual feedback, (3) stand still with no visual feedback and (4) stand easy with no visual feedback. For each trial condition, B shows the mean, trial sway size and C shows the mean sway frequency. For both panels, values were averaged over 10 subjects for each of the four trial conditions. Error bars show 95% confidence intervals for the mean values.

(two-way ANOVA, $N=40$, falling $F=1.67$, $P=0.20$; rising $F=1.13$, $P=0.35$). The impedance at equilibrium was averaged over 10 subjects for each of the four trial conditions. We draw the important conclusion that reduced mean sway size was not caused by increased ankle impedance. If anything, there was a slight tendency for higher impedance when standing easy as opposed to standing still (2 *vs.* 1 and 4 *vs.* 3). It is clear from EMG recordings that, as a result of the trial conditions, there were no significant changes in mean activation levels of tibialis anterior (two-way ANOVA, $N=40$, $F=1.61$, $P=0.21$) or soleus (two-way ANOVA, $N=40$, $F=1.27$, $P=0.30$) (Fig. 5C). This implies that co-contraction of muscles about the ankle joint was not a factor in bringing about changes in sway size.

Grouping the equilibrium line crossings according to the duration of the sway they occur in shows that high frequency sways are associated with increased line crossing ankle impedance (Fig. 6A). However, investigation of the

relationship between sway frequency and ankle impedance shows that the intent of the subject or the availability of visual feedback makes no significant difference to the ankle impedance at all frequencies (Fig. 6C). Five sway frequency categories were used. For each frequency category and for each trial record, the line crossings were averaged and the rising and falling line crossing impedances calculated. These impedances were then averaged over 10 subjects for each of the four trial conditions (Fig. 6B). Figure 6A shows that the ankle impedances for each of the four trial conditions are very similar across the frequency range of 0.1–1.5 Hz. As in Fig. 5, there is a slight tendency for the ‘stand still’ impedances to be lower than the ‘stand easy’ impedances. For the frequency range 0.1–0.7 Hz, the ankle impedance was relatively frequency insensitive. This implies that any change in frequency at the low end of the range will make little difference to the ankle impedance. These ankle impedances are always higher than the pendulum impedance which is also shown. Figure 6B shows that for

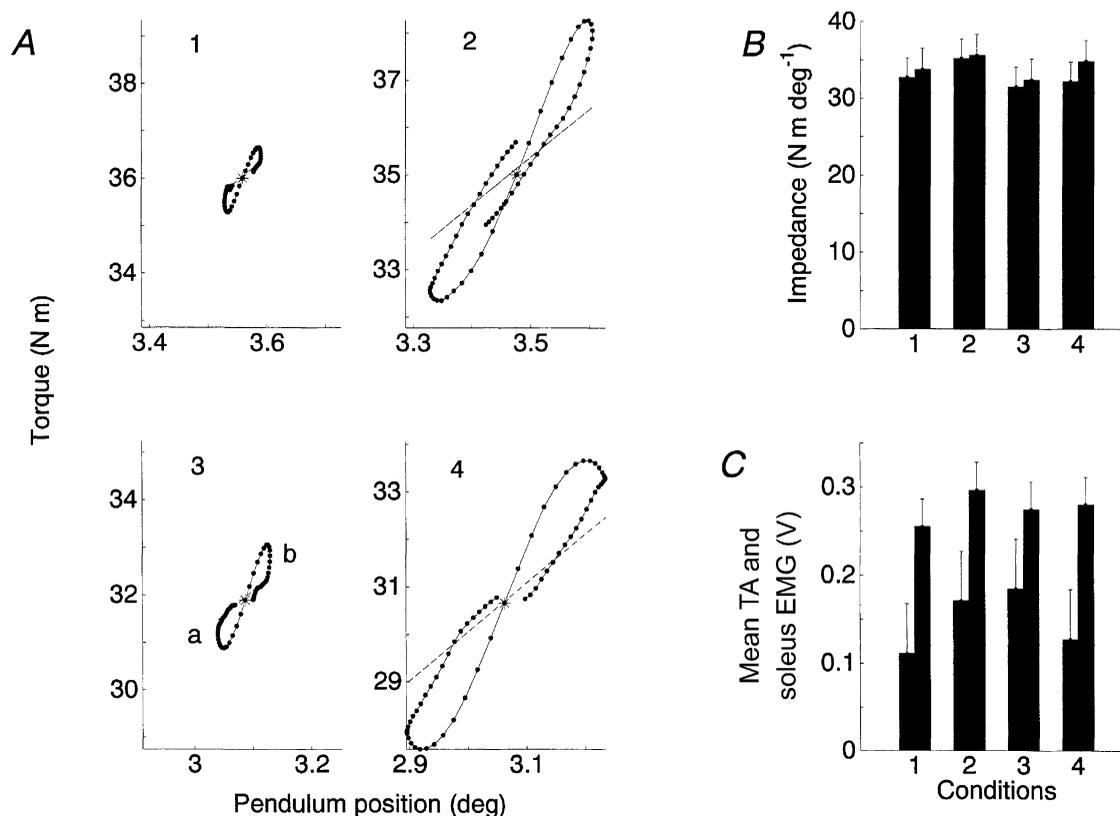


Figure 5. Effect of trial conditions on ankle impedance

A shows data averaged from 1.3 s before to 1.3 s after each positive gradient, equilibrium line crossing while the pendulum was falling. This is for one representative subject under each of four trial conditions labelled 1, 2, 3 and 4. Combined ankle torque is plotted against pendulum position with the same scaling for each graph. Trial conditions are the same as Fig. 3. Data points are at 40 ms intervals and proceed from label ‘a’ to ‘b’. The line of equilibrium (ignoring pendulum friction) is shown as a dashed line. The asterisk marks the point of equilibrium and maximum velocity. For each trial condition, B shows the mean, positive gradient, line crossing impedance (left bar, pendulum falling; right bar, pendulum rising) and C shows the mean EMG activity summed over both legs (left bar, tibialis anterior; right bar, soleus). For both panels, values were averaged over 10 subjects for each of the four trial conditions. Error bars show 95% confidence intervals for the mean values.

each frequency category, and for both the rising and falling line crossing impedances, there are no significant changes caused by the four trial conditions.

Due to the inertia of the pendulum, most of the pendulum sways occur in the 0.1–0.7 Hz range as seen in Fig. 6C. Thus we cannot say what happens to ankle impedance during sways of higher frequency and our conclusions are concerned with low frequency sway control. In any case, filtering of our data would have precluded observations

at frequencies greater than 3 Hz. The subject's intent and use of visual feedback make little difference to the frequency distribution of sways as well as no significant difference to the mean sway frequency (Fig. 4C). For each frequency category there is no significant change in the number of sways except the 0.4 Hz category. The intention to 'stand still' using visual feedback results in slightly more sways in the 0.2 Hz category at the expense of the 0.4 Hz category. This slight non-significant reduction in sway frequency when 'standing still' would

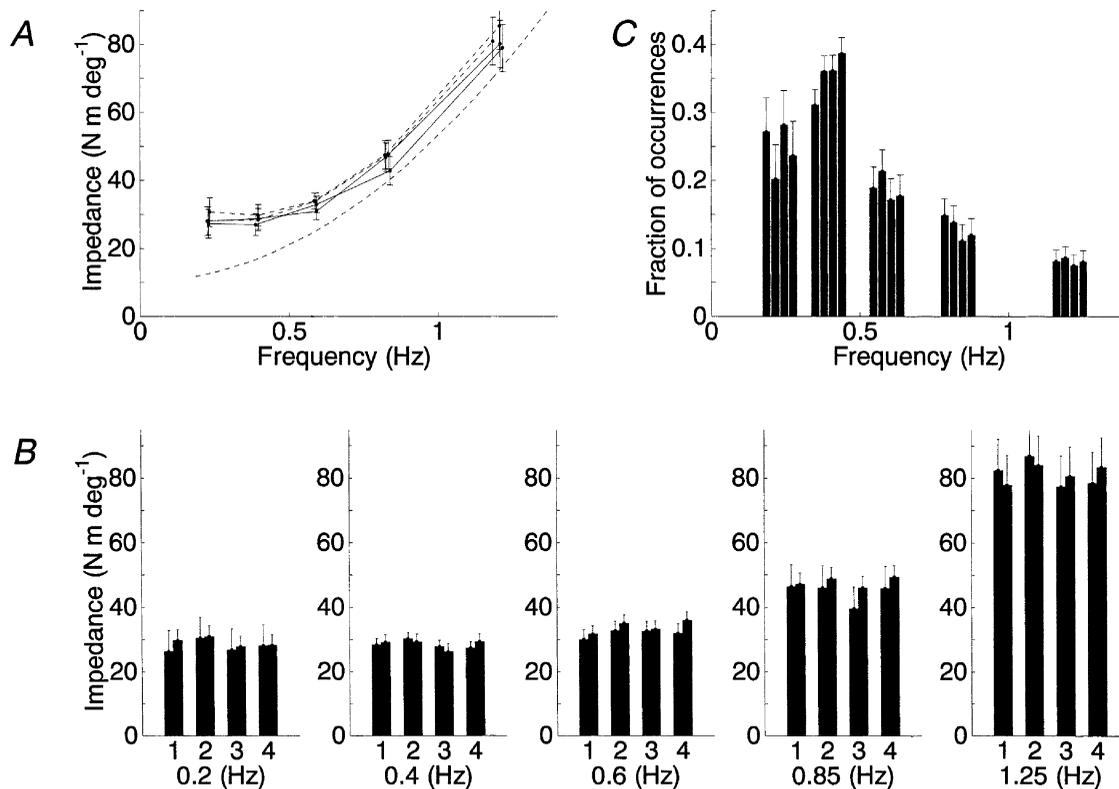


Figure 6. Relationship between ankle impedance and frequency

The pendulum falling and pendulum rising, positive gradient, line crossing equilibria were separately grouped into five frequency bins of 0.10–0.29, 0.30–0.49, 0.50–0.69, 0.70–0.99 and 1.00–1.50 Hz. The frequency for each line crossing was calculated from the duration of the associated sway. For each frequency bin for each trial, the mean falling and rising line crossing impedances, and the mean frequency associated with the line crossings, were calculated. The impedances were averaged over 10 subjects for each of the trial conditions. *A*, the mean line crossing impedance for each of the four trial conditions plotted against mean binned frequency. (For this plot the rising and falling impedances have been combined and the points have been plotted at the mean frequencies rather than the central bin frequencies.) The stand still conditions are plotted as continuous lines and the stand easy conditions are plotted as dashed lines. The lowest dashed line is the load impedance. The load impedance was calculated using the formula $Z = \text{complex modulus of } (I(j\omega)^2 - K_{tt} + b j\omega)$ where I is the pendulum moment of inertia, K_{tt} is the load stiffness, b is the viscous drag of the pendulum, ω is the angular frequency and j is the square root of -1 (Schwarzenbach & Gill, 1992). For each frequency bin and for each trial condition, *B* shows the mean, positive gradient, line crossing impedance (left bar, pendulum falling; right bar, pendulum rising). Two-way ANOVA, $N = 40$, $P = 0.80, 0.20, 0.54, 0.42, 0.48$ for the falling impedances in order of increasing bin frequency and $P = 0.52, 0.2, 0.1, 0.51, 0.75$ for the rising impedances in order of increasing bin frequency. *C*, the fraction of occurrences populating each bin for each trial condition. A group of four trial conditions are shown (order 1, 2, 3, 4 from left to right) with the group centred at the mean frequency for each bin. Two-way ANOVA, $N = 80$, $P = 0.11, 0.0004, 0.24, 0.13, 0.81$ for the five bins in order of increasing frequency. For all three panels, the error bars show the 95% simultaneous confidence intervals in the mean values.

be consistent with the slight non-significant reduction in ankle impedance.

The results in Fig. 7 were generated using the model described in Appendix. They reveal how independent changes in ankle stiffness, ankle viscosity and noise power would be reflected in our measures of 'line crossing' impedance, sway size and sway frequency. Figure 7A shows that, in conjunction with an appropriate noise source, typical values of ankle stiffness and viscosity for A/P standing sway (Winter *et al.* 1998) can produce a pattern similar to that seen in Fig. 5, except that the gradient increases at equilibrium (maximum velocity) due to linear viscosity in the model. Figure 7B compared with 7A shows that a reduction in stiffness causes a decrease in

sway frequency, an increase in sway size, a decrease in 'line crossing impedance' and a more apparent viscous increase in gradient at equilibrium. Figure 7C compared with 7A shows that decreasing the viscosity produces an increase in sway frequency, an increase in sway size and a decrease in 'line crossing impedance'. Figure 7D when compared to 7A shows that a fourfold increase in torque noise power produces no change in sway frequency and doubles the sway size without changing the 'line crossing impedance'. From the three factors which affect sway size (stiffness, viscosity and noise), a change in noise power, i.e. torque error, gives the most comparable results to our sway size, sway frequency and ankle impedance data of Figs 4 and 5.

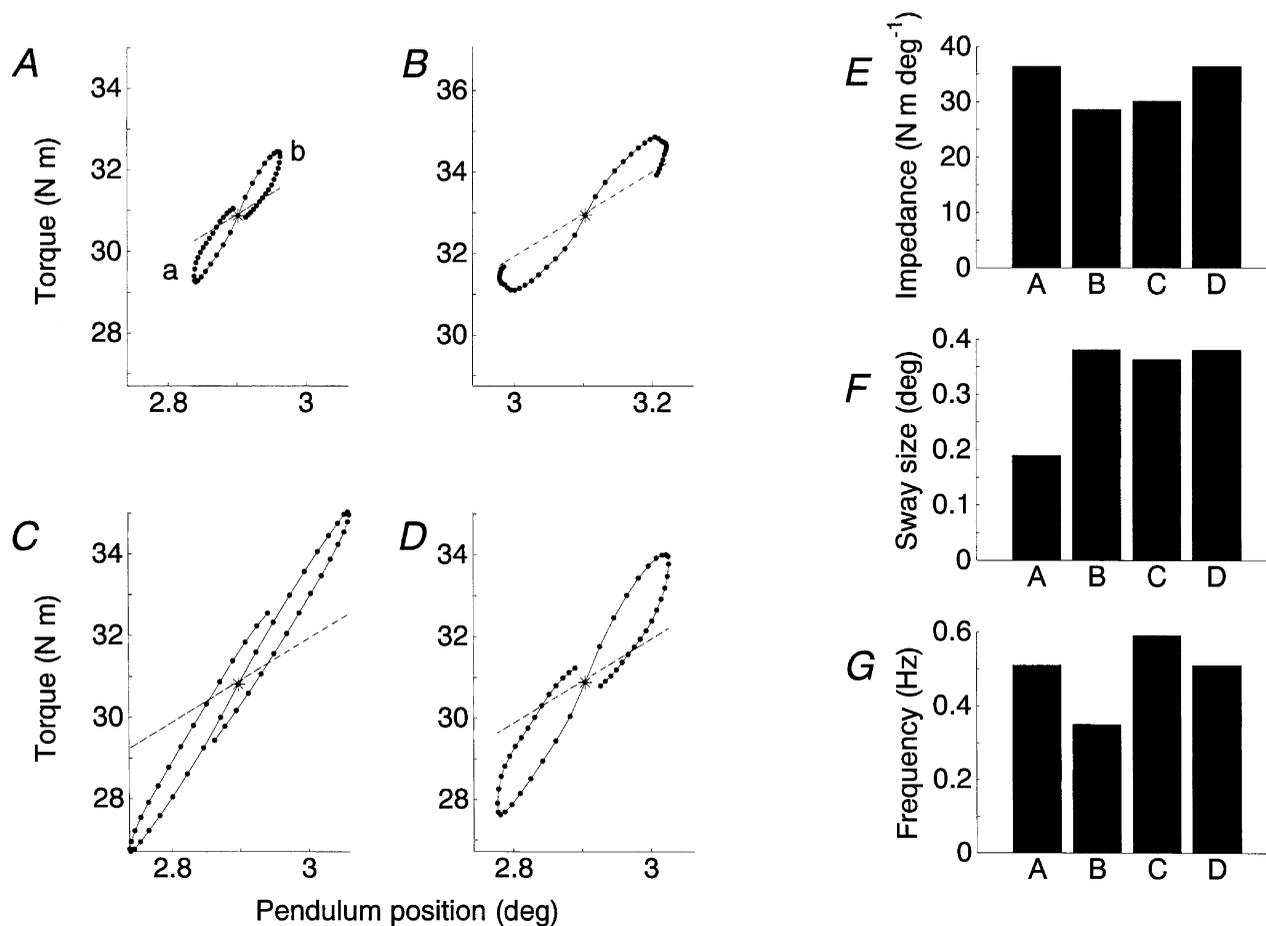


Figure 7. Effect of ankle stiffness, viscosity and torque noise on sway

These results were generated using the model described in Appendix. A–D, data averaged from 1 s before to 1 s after each falling, positive gradient, equilibrium line crossing. The same scaling is used for each graph. Data points are at 40 ms intervals and proceed from label 'a' to 'b'. The line of equilibrium (ignoring pendulum friction) is shown as a dashed line. The asterisk marks the point of equilibrium and maximum velocity. A has normal values for ankle stiffness and viscosity for A/P sway taken from Winter *et al.* (1998) ($K = 1440 \text{ N m rad}^{-1} = 25.1 \text{ N m deg}^{-1}$, $B = 350 \text{ N m s rad}^{-1} = 6.11 \text{ N m s deg}^{-1}$). B, reduced stiffness ($K = 600 \text{ N m rad}^{-1} = 10.5 \text{ N m deg}^{-1}$) compared to A. C, reduced viscosity ($B = 100 \text{ N m s rad}^{-1} = 1.75 \text{ N m s deg}^{-1}$) compared to A. D shows four times the torque noise power as A. E, the measured 'line crossing gradients' for the simulated trials shown in A–D. These line crossing gradients are inevitably higher than the stiffness as the impedance includes a viscous and noise component. F, the mean sway size; G, the mean sway frequency for the same simulated trials A–D.

DISCUSSION

The questions we are pursuing are (i) whether or not subjects can systematically reduce the sway size of the pendulum by their intention and/or use of visual feedback, and (ii) whether ankle impedance, ankle stiffness or ankle viscosity is the means used to change sway size or whether an alternative mechanism must be sought.

We found unambiguously that subjects could systematically control mean pendulum sway size (Fig. 4). Giving full attention to minimising sway ('standing still') was effective whether or not visual feedback was available. When subjects were 'standing still', visual feedback enabled sway size to be reduced more than without visual feedback. This result agrees with that of Fitzpatrick *et al.* (1992*b*) although the effect of vision need not be to increase reflex gain in the manner they suggested. Visual feedback made less difference to sway size when subjects were giving minimal attention to their sway ('stand easy'). This result may be relevant to work which showed that visual input had little effect or contradictory effects on sway (Fitzpatrick *et al.* 1992*b*; Collins & De Luca, 1995; Winter *et al.* 1998). If subjects are not intending to stand still, vision may have little effect on standing sway.

How do subjects achieve this systematic reduction in sway size? A crucial element of the answer is that in minimising sway size, subjects did not change the mean sway frequency (Fig. 4*C*). The second element of the answer concerns the ankle impedance. The simple result here is that ankle impedance was not changed by the subject's intent or use of visual feedback (Fig. 5*B*). However, this result is complicated by the fact that the line crossing impedance is a biased measure that is sensitive to frequency as shown in Fig. 6. Impedance increases with frequency although at the low end of the frequencies encountered the effect is slight. In comparing the degree of frequency bias between the four trial conditions we note (i) the mean sway frequency did not change and (ii) that subjects did not alter the distribution of frequencies with which line crossings are associated (apart from the 0.4 Hz category where there is little sensitivity to frequency anyway) (Fig. 6*C*). Thus the frequency bias did not change between the four trial conditions and it is reasonable to compare the averaged line crossing impedances in the manner shown in Fig. 5*B*. Moreover, by comparing the line crossing ankle impedance between the trial conditions at each frequency category, we could see that at all sway frequencies the ankle impedance is not changed by the intent of the subject to minimise sway, or by the use of visual feedback from the oscilloscope (Fig. 6). This confirms that changing ankle impedance was not the means used to alter sway size.

In theory, alteration of stiffness, viscosity and torque noise are three methods that could be used to control sway size. Our modelling results illustrate the effect of

independent changes in these parameters on sway size, line crossing impedance and sway frequency (Fig. 7). (i) Control of sway size by stiffness alone requires an ankle stiffness that is greater than the toppling torque per unit angle of the pendulum (K_{tt}). As the ankle stiffness is increased the sway size would decrease. If there is no damping, then the sway size is proportional to $K_e^{-0.5}$ where K_e is effective stiffness (ankle stiffness minus K_{tt}). Sway frequency would increase with stiffness. In our experiments we found no change in sway frequency between trial conditions so control of sway size by stiffness alone is ruled out. (ii) By increasing ankle viscosity alone, the sway size could be reduced without changing ankle stiffness. If viscous ankle torques were significant, the impedance (gradient on an ankle torque *vs.* angle plot) would increase at equilibrium ('line crossing gradient' where the velocity is greatest) and sway frequency would decrease. In our results sway frequency did not change when sway size was systematically reduced so viscous changes alone are not the cause of the reduction in sway size. Furthermore, the line crossing gradient was not velocity dependent (Fig. 5*A*). (iii) If ankle torque noise power alone were decreased, sway size would be decreased with no change in impedance or sway frequency, which is what we observed.

What can we conclude regarding ankle stiffness and viscosity? Sway size was systematically reduced with no increase in average 'line crossing gradient'. The simplest explanation of this is that ankle stiffness and viscosity do not change. However, it is possible that a simultaneous decrease in ankle stiffness and increase in viscosity could have produced a reduction in sway size with no change in ankle impedance. We reject this possibility because a decrease in ankle stiffness and an increase in ankle viscosity would each have caused a decrease in sway frequency whereas no significant change in sway frequency was observed. A possible increase in ankle stiffness and decrease in viscosity is also rejected because again there was no change in sway frequency. Moreover, these possibilities are unlikely since one would expect position gain and velocity gain to vary together. Changes in noise power do affect changes in sway size, but do not affect the sway frequency or the line crossing impedance. For this reason we suggest changes in torque noise are the most likely cause of changes in sway size.

How do our conclusions correspond with those of other authors? Our 'line crossing' measure of impedance relates the repeated changes in torque to the changes in position that occur during unperturbed balancing of the pendulum. These changes in torque are taken to be the result of mechanical, reflex and feedforward (predictive) components though the extent of each component is unknown. Our results apparently differ from those of Fitzpatrick *et al.* (1992*b*) who claimed that task-dependent and sensory-dependent increases in ankle (reflex) stiffness changed the amount of sway in response to perturbation. Fitzpatrick and colleagues' measure of

stiffness relates the average change in ankle position to the average change in ankle torque induced by a slow perturbation. The ankle mechanisms used to regulate balance were averaged out by their method of analysis and the position maintaining stiffness remained.

Since subjects maintain equilibrium by balancing both the gravitational torque and the perturbation torque, the stiffness measured by Fitzpatrick *et al.* (1992*b*) (K_F) depends on the perturbation torque (ΔT_p), the toppling torque per unit angle of the pendulum (K_{tt}) and the angle through which the subjects are deflected (ΔA) such that $K_F = \Delta T_p / \Delta A + K_{tt}$ (M. Lakie, unpublished observations). The stiffness, K_F , describes the resistance to perturbation but gives no information on the mechanism used to produce that resistance. It does not discriminate between mechanisms based on stiffness control, viscous control, predictive momentum absorption or noise reduction. A predictive, active adjustment of torque to reduce deflection can be achieved without any increase in mechanical stiffness, reflex stiffness or line crossing impedance. Therefore it is potentially misleading to interpret the reduced deflection under slow perturbation as an increased ankle stiffness. The stiffness measured by Fitzpatrick *et al.* (1992*b*) describes the end result of the processes resisting a change in position, though it does not describe the ankle mechanisms used to resist the change in position. If the source of ankle impedance is mechanical, the ankles have one impedance only and our results are incompatible with those of Fitzpatrick *et al.* (1992*b*). However, if the nervous system is regulating one impedance associated with balance and a different impedance or gain associated with position maintenance, then our procedure provides a measure of the former and the procedure of Fitzpatrick *et al.* (1992*b*) may provide a measure of the latter. We agree with Fitzpatrick *et al.* that changes in sway size were not caused by alterations in muscle co-contraction (Fig. 5*C*).

Our results differ from the conclusions of Winter *et al.* (1998) who produced evidence that M/L sway in standing was inversely proportional to the square root of the ankle stiffness. However, it is clear from Winter and colleagues' own data that there was substantial damping present. Using their typical A/P measurements of effective stiffness, K_e , viscosity, B , and moment of inertia, I , we calculate a damping ratio of $B/\sqrt{4IK_e} = 0.76$ and successive sway amplitude ratio of $A_{n+1}/A_n = 0.0006$ ($K_e = 850 \text{ N m rad}^{-1}$, $B = 350 \text{ N m s rad}^{-1}$, $I = 62 \text{ kg m}^2$; Winter *et al.* 1998; Kreyszig, 1999). This calculation suggests that sagittal oscillations are not 'severely underdamped approaching the undamped condition' as Winter *et al.* (1998) claim. Rather, this measurement agrees with our findings that preceding and subsequent oscillations have small or negligible average velocity (Fig. 5*A*, especially 1 and 3). The data of Winter *et al.* (1998) and our graphs indicate that damping of sway is highly effective. We think this degree of damping is unlikely to be mechanical/reflex in origin. The shape of

our graphs does not indicate a simple damper where viscous torque is proportional to velocity. Also for small oscillations reflexly active cat soleus has a small damping ratio ($\xi < 0.1$) (Lin & Rymer, 2000). Damping produced by an active, predictive modulation of torque would seem more likely.

Our data are consistent with the feedforward modulation of ankle torque as shown by Gatev *et al.* (1999). Our graphs in Fig. 5*A* would illustrate their idea that ankle torque changes with angle in a spring-like manner though the muscle activity is modulated predictively. Our data do not support their hypothesis that ankle stiffness is controlled centrally so as to reduce sway size.

Since changes in sway size are not produced by changes in impedance, stiffness or viscosity (Figs 5, 6 and 7), an alternative mechanism must be sought. A predictive method with momentum absorption is plausible (Morasso & Schieppati, 1999) and feedforward control is likely (Fitzpatrick *et al.* 1996; Gatev *et al.* 1999). Below we sketch a broad outline of the processes involved in controlling the pendulum.

Balance of the inverted pendulum is unstable and uncorrected errors in ankle torque grow until a sizeable sway results. In effect the pendulum is either dropped or thrown by too little or too much ankle torque. A planned impulsive pattern of torque is then used in an attempt to arrest the motion of the pendulum. The pendulum is caught. The torque error when the pendulum is caught causes the next sway. The drop and catch or throw and catch process repeats over and over. The equilibrium position of the pendulum is not fixed (unlike stiffness control) and each drop (throw) and catch results in a change in position of equilibrium. This drop and catch process appears more complex than the simple regulation of a gain (or impedance). We suggest that mechanical stiffness may provide some stabilisation, that mechanical/reflex viscosity is rather insignificant and that torque is actively controlled to achieve final control.

Reduction of sway depends on the following processes: (1) registering quickly and accurately when position has changed, and velocity and acceleration have increased; (2) judging torque impulses accurately to arrest the motion and return to balance; and (3) accurately maintaining the torque close to that required for balance. These processes require fine control of muscular effort. Any random noise in the nervous activation of the muscle will tend to a loss of balance and an increase in sway. The accuracy or lack of noise with which torque can be delivered will provide a limit on reducing sway size. The sensory threshold for sway detection may also provide a limit on reducing sway size. We agree with Fitzpatrick *et al.* (1992*b*) that the task does not require complex volitional modulation of muscle activity since the task can be performed quite easily while the subject is distracted or engaged in conversation. In seeking to

‘stand still’ rather than ‘stand easy’, the ratio of active to passive processes may be increased.

Our results are for balancing an inverted pendulum which is not the same thing as standing, yet we have compared our results with those concerning quiet standing. In standing the effect of multi-segmentation is to reduce sway (Fitzpatrick *et al.* 1994*b*). The involvement of the vestibular apparatus in the fine regulation of quiet standing is not thought to be significant (Fitzpatrick *et al.* 1994*b*). Since pendulum sways occur at low frequencies, our method necessarily gives information about low frequency sway control. Our investigation shows that ankle impedance is not increased to reduce sway size. We deduce that ankle stiffness and viscosity are also not changed to control sway size. A reduction in torque noise via an active, predictive process, which provides damping, is more likely to be the cause of reduction in sway size.

APPENDIX

A model of the pendulum and the ankle torque applied to the pendulum has been constructed to assess the effect of changes in ankle stiffness, ankle viscosity and ankle torque noise on sway size, sway frequency and our measure of ankle impedance. The pendulum is modelled

as a second-order differential equation:

$$I d^2\theta/dt^2 + b d\theta/dt - K_{tt} \sin\theta = T_{\text{ankle}},$$

where I is the inertia, b is the viscous damping and K_{tt} is the gravitational toppling torque per unit angle of the pendulum. Values used were those for our own pendulum: $I = 62.6 \text{ kg m}^2$, $b = 0.061 \text{ N m s deg}^{-1}$, $K_{tt} = 10.3 \text{ N m deg}^{-1}$. θ is the pendulum angle and T_{ankle} is the ankle torque applied to the pendulum.

The ankle torque generated by the subject was modelled as having a stiffness, viscous and noise component:

$$-T_{\text{ankle}} = K(\theta - \theta_0) + B d\theta/dt + w,$$

where K and B are the ankle stiffness and viscosity, respectively. θ_0 is the offset angle for the ankle stiffness and w is the ankle torque noise. Typical values of K and B for A/P standing sway are taken from Winter *et al.* (1998): $K = 850 + K_{tt} = 1440 \text{ N m rad}^{-1} = 25.1 \text{ N m deg}^{-1}$, $B = 350 \text{ N m s rad}^{-1} = 6.11 \text{ N m s deg}^{-1}$.

Simulink (The MathWorks, Inc.) was used to solve the equations and the model is shown in Fig. 8. θ_0 was chosen to give a mean equilibrium position of 3 deg. A low frequency or band-limited white noise with a sizeable (a few newton metres) random step change in torque every 0.4 s produces records similar to real data. Band-limited

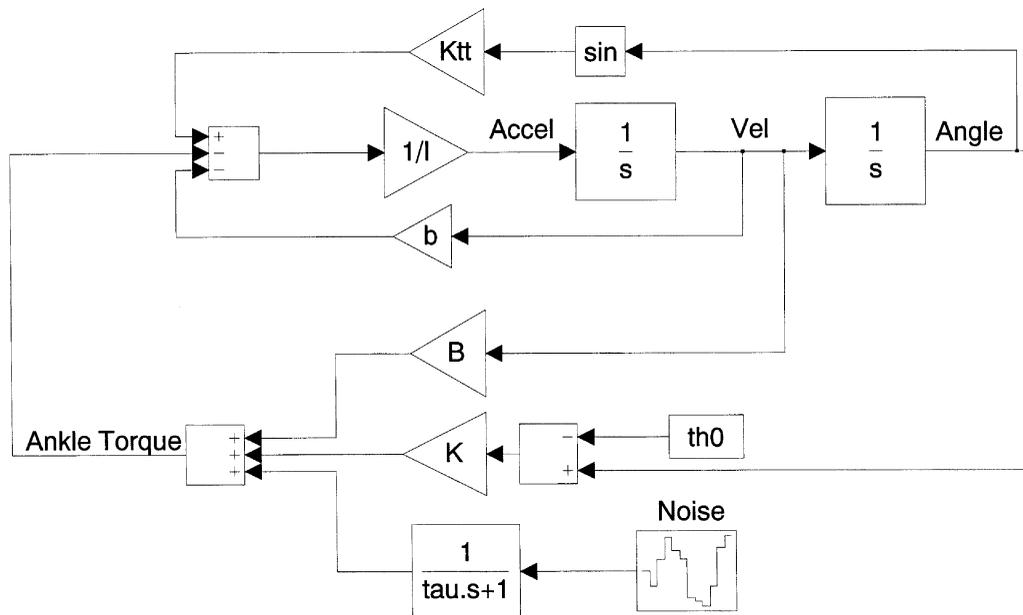


Figure 8. Model of inverted pendulum and ankle torque

The Simulink model used to represent the pendulum and the ankle torque is shown. I , pendulum moment of inertia; b , viscous damping; K_{tt} , gravitational toppling torque per unit angle of the pendulum. Values used were those for our own pendulum. $I = 62.6 \text{ kg m}^2$, $b = 0.061 \text{ N m s deg}^{-1}$, $K_{tt} = 10.3 \text{ N m deg}^{-1}$. K and B are the ankle stiffness and viscosity, respectively. θ_0 is the offset angle for the ankle stiffness. Typical values of K and B for A/P standing sway are taken from Winter *et al.* (1998). $K = 850 + K_{tt} = 1440 \text{ N m rad}^{-1} = 25.1 \text{ N m deg}^{-1}$; $B = 350 \text{ N m s rad}^{-1} = 6.11 \text{ N m s deg}^{-1}$. Band-limited white noise was used in conjunction with a first-order low-pass filter, $1/(1 + \tau s)$ (where s is the Laplace variable) to reduce the step-like nature of the noise. A noise sampling time $t_{\text{sample}} = 0.4 \text{ s}$, a noise power of 6.4, and a filter time constant $\tau = 0.5 \text{ s}$ were used.

white noise was used in conjunction with a first-order low-pass filter, $1/(1 + \tau s)$ (where s is the Laplace variable) to reduce the step-like nature of the noise. A noise sampling time $t_{\text{sample}} = 0.4$ s, a noise power of 6.4, and a filter time constant $\tau = 0.5$ s were used. We investigated the effect of varying the ankle stiffness K , ankle viscosity B , and torque noise power. Simulation data were subjected to the same analysis procedures as real data. Selected simulation results are shown in Fig. 7.

This model is essentially that described by Winter *et al.* (1998), although we have given more prominence to the effect of noise. The ankle stiffness and viscosity could represent mechanical values as suggested by Winter *et al.* (1998). The model could not represent reflex values of ankle stiffness and viscosity because there is no incorporation of a time delay, though the model could represent feedforward values in which it is assumed that time delays have been perfectly eliminated.

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Understanding standing

Standing is something we do without conscious thought, but it is a complex task involving the nervous system, muscles and tendon properties - and anticipation! Martin Lakie and Ian Loram explain



Martin Lakie (top) and Ian Loram (above) propose that the increased force that is required to prevent collapse is associated with active shortening of the muscles

In standing the body's centre of mass (the imaginary point at which the mass of the body can be considered to be concentrated, approximately in the small of the back) is usually slightly forward of the ankle joint which forms the axle on which the body rotates (Fig. 1A). So it is literally true to say that we are all inclined to fall on our faces. Why does this catastrophe not occur? The answer is that calf muscles, gastrocnemius and soleus are responsible (Fig. 1B). Gravity pulls us down and consequently forward and these muscles pull us up and consequently back. The more we lean forward the harder they have to work. Studies have shown that for most people the angle of forward lean is about 3 degrees. At this angle the mean force in the calf muscles of each leg is about 500 N, which is about 12% of the maximal force that can be produced by a single soleus muscle (figures from Hoy *et al.* 1990). Due to the muscular activity the total metabolic energy needed to stand is about 25 W greater than for lying supine (Davidson & Passmore, 1966). Although the anatomy seems simple, the problem that has intrigued neurophysiologists for many years is precisely how

standing people unconsciously regulate the activity of the calf muscles in response to the gravitational requirement.¹

The inverted pendulum

In attempts to answer this question, researchers have used a simplified model to represent human standing. The concept is shown in Fig. 1B. At the outset, it must be admitted that this model does not preserve all the normal features of standing. An assumption is made that all the motion occurs solely at the ankles – i.e. there is no other movement of the limbs or between different segments of the body. Also, it is usual to consider movement in only the forward – back (antero-posterior) plane whereas there is also the problem of side-to-side motion of the body to be considered. Furthermore, the model assumes that the two ankles share a common axis. Observation will show that this is not the way that most people stand. Nevertheless, since its introduction by Smith in 1957 (Smith was a lecturer in Anatomy at the University of St Andrews) the inverted pendulum concept has been a powerful stimulus to explaining how standing works. It is a good example of a reductionist approach where, in order to understand a complicated system, we

may remove some of its complex features and study a simplified version. Many studies have confirmed that the fundamental problem in standing is balancing an inverted pendulum. Although human standing is something that we mainly take for granted it is a complex activity that takes all of us about a year of life to accomplish. It is a reasonable hope that by understanding how the inverted pendulum is balanced we will be able to understand how standing in particular, and other aspects of postural maintenance in general, are controlled.

Sounding sway – a new technique for observing muscles in action

A number of measurements have conventionally been made on standing subjects in attempts to understand the standing process. It is universally agreed that in standing the body is not static. The human inverted pendulum is inherently unstable and small slow irregular sways are continually observed. Thus, body angle, torque and EMG continually fluctuate. It is comparatively easy to measure the muscle forces (or more precisely their close relative the ankle torques). With a little more difficulty the change in body angle can be measured. As far as

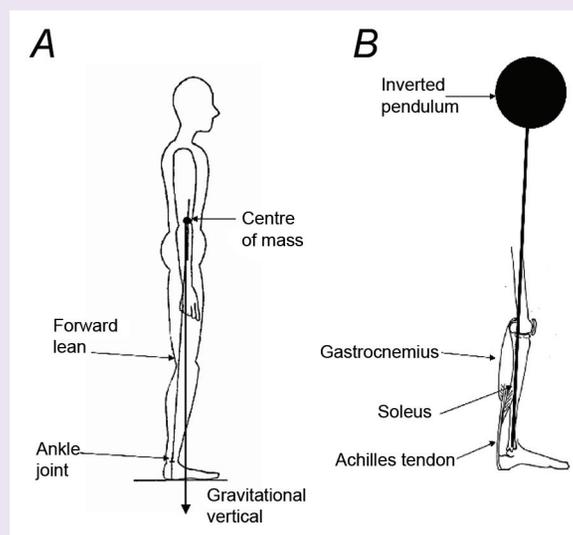


Figure 1. A The standing human. The centre of mass is normally forward of the axis of rotation (the ankles). Consequently the body tends to topple forward. B Collapse is prevented by the activity of the soleus and gastrocnemius muscles. The anterior compartment muscles (principally the tibialis anterior) are generally silent in quiet standing. Movement is assumed to occur only at the ankles and the body can therefore be considered as an inverted pendulum. (Fig. 1a adapted from Winter *et al.* 2001)

¹For simplicity, we mention only forward sway (falls) in this article. Backward sway (throws) are an identical process, with the signs of the movements reversed.

the muscles themselves are concerned it has previously only been possible to record their EMG. This enables one to see how their activity is varying, but it does not let one see what they are actually doing. In this article we describe a new technique which allows us to observe the tiny movements of calf muscles in standing subjects. The new information obtained by this technique suggests that many current ideas about standing require revision.

Our approach to the problem has been the use of dynamic ultrasonography with computerized image analysis (Loram *et al.* 2004). The work was done in collaboration with Constantinos Maganaris at Manchester Metropolitan University. Ultrasound is strongly reflected by collagen fibres. The collagen in tendons shows up clearly and collagen also demarcates many of the muscle fibres. This technique has previously been quite extensively used to make static measurements of muscle and tendon lengths. The pointwise resolution of the technique depends on a number of factors including the frequency of the ultrasound and is typically about 0.5 mm.

However, the ultrasound image has the properties of an array of detectors. This considerably increases the resolving power of the technique. As a simple analogy the human eye will struggle to see a dot of 10 mm diameter

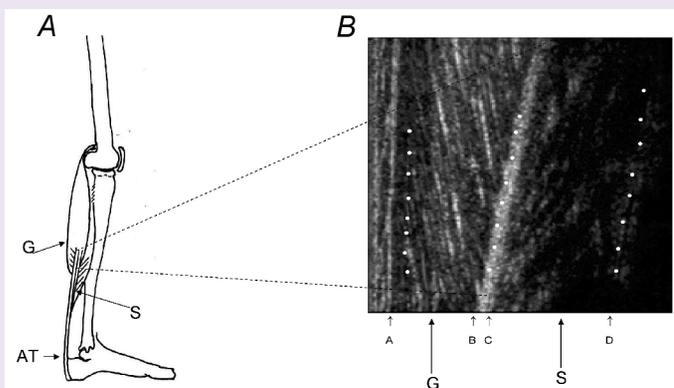


Figure 2. A static ultrasound image. A The calf muscles gastrocnemius (G) and soleus (S) and the Achilles tendon (AT) showing the approximate point at which a parasagittal plane image was obtained by ultrasonography using a dynamic ultrasound scanner (ATL, HDI 3000). B The resulting image which was approximately 7 cm square. A is the proximal aponeurosis (thin sheet of inextensible connective tissue linking muscle and tendon) of gastrocnemius muscle and B the distal aponeurosis of gastrocnemius. C is the distal aponeurosis of soleus and D is the proximal aponeurosis of soleus. The white streaks within the muscle are collagen fibres which demarcate some of the muscle fibres. Movements of the muscle fibres were recorded by automatically tracking eight pairs of markers (white dots) using 2-D cross correlation analysis on successive frames. Vector analysis was used to resolve the movement of the markers into length changes of the muscles. Adapted from Loram *et al.* (2004).

at 6 metres range – stretch the dot out into a long line 10 mm wide (power cable) and it may be seen at several kilometers. We have used computerized image analysis to take advantage of this fact. It is possible to resolve muscle fibre length changes of as little as 10 µm in the calf. A typical static image of the calf muscles is shown in Fig. 2.

What might happen in standing – orthodox views

Consider Fig. 1B. As the body sways forwards the muscles are stretched.

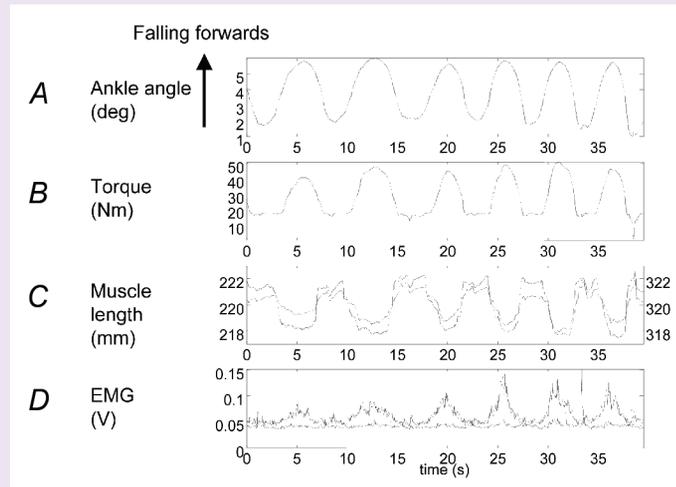


Figure 3. Slow voluntary sways of a typical subject. Measurements were made on the left leg. Ankle angle is shown in (A) and ankle torque in (B). As is anticipated, torque rises as the subject leans forwards. (C) shows the changes in length for gastrocnemius muscle (continuous line) and soleus muscle (dotted line). Muscle lengths are expressed relative to typical mean muscle lengths of 320 mm and 220 mm for soleus and gastrocnemius respectively. Both muscles shorten as the subject leans forward. (D) Integrated EMG for gastrocnemius (continuous line) and soleus (dotted line). An increase of EMG is associated with muscle shortening and rise in torque. Adapted from Loram *et al.* (2004).

Ankle torque (muscle force) rises (it has to or you fall down). One school of thought (e.g. Winter *et al.* 2001) has long maintained that the active muscles produce the force automatically as a direct consequence of the stretch because they have spring-like properties. If the spring stiffness is adequate, the force that can be generated by muscle stretch will suffice to prevent a fall. The job of the nervous system is simply to set the resistance to stretch of the muscles to a sufficiently high value; then no further neural intervention is needed. This *mechanical tonus* theory could be stated as ‘increased force is generated by muscle stretch’. Others have maintained that the mechanical tone of the muscles is inadequate to produce stability. They also observe that forward sway is associated with an increased EMG in the muscles (e.g. Morasso & Sanguineti, 2001; Fitzpatrick *et al.* 1994). Accordingly, they suggest that stretching the active muscle will generate stretch reflexes that raise tone by increasing activation of the stretched muscle. This *reflex tonus* view, summarised by the Sherrington School in the ‘little red book’ (Creed *et al.* 1932), is that ‘increased force is produced by muscle stretch plus reflex activity’. Both theories assume that the muscle will be lengthened by forward sway.

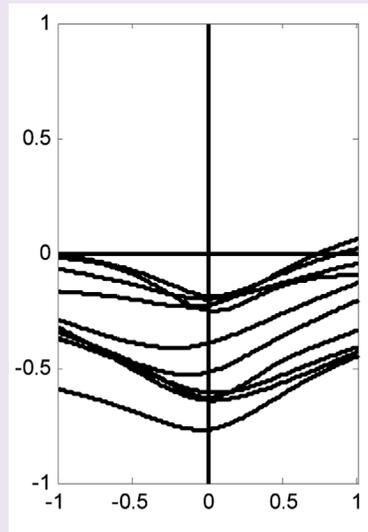


Figure 4. Cross correlation of soleus muscle length against ankle angle for eleven subjects standing normally. The tiny movements of the soleus muscle are on average in the opposite direction to that of the body. If they were a perfect mirror image the value of the cross correlation would be -1.0 and the delay zero. They are in fact an approximation to a mirror image. The closest approximation occurs in subjects where the intrinsic ankle stiffness is lowest in relationship to their size and mass. Loram & Lakie (unpublished results).

What does happen in standing – paradoxical muscle movements revealed by ultrasonography

However, Fig. 3 shows that forward sway is in fact associated with a shortening of the muscle! Torque rises, EMG increases but the muscle shortens. The rise in force cannot be due to muscle tone or muscle reflexes. The muscles and the load generally move in opposite directions.

This might at first seem not just counterintuitive, but quite impossible. How can it happen? The answer is that the stiffness of the Achilles' tendon and foot is not very great at the low forces that are involved in standing. (It is much greater for the large forces involved in running and jumping.) The tendon and the foot together form a spring-like buffer that decouples the muscle and the load (the body). This spring stiffness is not itself sufficient to permit standing. In direct measurements using a piezoelectric stretcher, we have measured the overall stiffness of the ankle. That is, we have abruptly stretched the series combination of the foot, the tendon and the muscle and measured the resulting force increment. This combination (inevitably limited by the weakest link) defines the intrinsic stiffness of the ankle. It represents the intrinsic

stiffness because the value is obtained before the nervous system has time to alter the state of the muscle. For 10 subjects the average intrinsic ankle stiffness was only 91% of that necessary for standing (Loram & Lakie, 2002a). Using rather bigger stretches, Morasso's group (Casadio *et al.* 2004) have recently obtained an even lower average value of 64%. What this means in effect is that if the muscle remained stationary then stretch of the foot and tendon caused by a sway would generate only 64-91% of the force that is necessary to prevent falling. In order to supply the deficiency, additional stretch of the tendon and foot must be generated. This can only be produced by active shortening of the muscle. Thus, forward sway of the body stretches the tendon – foot spring. Muscle shortening also simultaneously stretches it. These two features acting in concert produce the necessary force for standing. Muscle movement is absolutely necessary and the job cannot be done statically. Figure 3 was obtained from a subject who was voluntarily making large sways. The same process has been observed in subjects standing normally. The body and muscle movements are naturally much smaller but they are clearly on average in the opposite sense (Fig. 4). We have called this process of control

by active alterations in muscle length *the ballistic bias mechanism* (Loram & Lakie, 2002b).

It might seem that the shortfall in stiffness that must be made up by this mechanism is only 9-36%. However, the 100% figure applies to sways that are of infinite duration. For sways that take the times commonly observed in standing (usually ~ 0.8 s for a unidirectional sway) calculation and experiment suggest that a value of close to 200% is necessary (this figure represents what is often called the *effective* stiffness). Thus, the intrinsic stiffness of the ankle and the ballistic bias mechanism make a quantitatively approximately equal contribution to the effective stiffness. The intrinsic stiffness almost cancels the force due to gravity and the fine tuning is done by the active process. This probably means that the job of the nervous system is made easier.

Ballistic bias in action – acting on impulse

In an attempt to demonstrate the ballistic bias mechanism we have described some simple experiments in which subjects balance a large inverted pendulum by hand (Lakie *et al.* 2003). The pendulum represents the body. The hand represents the calf muscles. The hand is connected to the pendulum by a steel spring which defines the intrinsic stiffness. It can be set to any desired value. With values ~ 70 -100% subjects can easily balance the pendulum by active hand movements although none of them were able to describe exactly how they did it. Analysis clearly showed that on average the hand and pendulum moved in opposite directions. However, at any instant the movements are not an exact mirror image. Like the body, the pendulum sways rather slowly with an average duration between turning points of ~ 0.8 s. The hand movements are faster and intermittent (occurring approximately every 0.3 s). Each hand movement is a ballistic bias adjustment (impulse).

The most basic behaviour of such a system would be a form of oscillation where each impulse violently catches

and reverses a fall, throwing the pendulum transiently more upright in the manner of someone balancing on a pogo stick or keeping a tennis ball in the air with a racquet. In reality, depending on the complexity of the task and the sensory information available to the subject, there are generally 2-4 bias adjustments per unidirectional sway. The impulses are smaller and more sophisticated than those made on a pogo stick – consequently they are not all successful (they may merely slow the pendulum but not reverse it).

This is a good strategy because by making the adjustments as small as possible the acceleration, and hence sway size, of the pendulum is minimized. The large inertia of the pendulum buys time for the process to be tried again. The duration of the pendulum sway can therefore be explained as a consequence of an intermittent impulsive discrete motor act taking about 0.3 s and usually needing repetition one or more times per pendulum sway in order to reverse it. It also suggests a plausible mechanism by which any preferred standing position may be preserved. The pendulum or body is moved to, and maintained at, a new position by a series of nudges. As the impulses involve active muscle length changes which are on average in the opposite direction to those that would be passively produced, they must be driven by a signal which anticipates pendulum movement. Muscle activity cannot be a simple reaction to muscle length or tension (if it were it would produce bi-stable or ‘toggle’ action in

the muscle). Ballistic bias requires a higher level of control than has commonly been assumed for standing. We have recently been able to observe these ballistic bias adjustments of the calf muscles in normally standing subjects. They are very much smaller than the hand movements, but they have remarkably similar features.

Conclusion

Conventional views assume that the increased force that is required to prevent collapse is produced by stretching the active muscles. In opposition to this view we propose that the force is associated with active shortening of the muscles.

Furthermore, this is not a continuous type of feedback control arising from the muscles, but an impulsive controller which acts intermittently and anticipatorily. Many years ago, Craik showed that individually judged outputs of the nervous system could only be made at a low rate of 2-3 per second (Craik, 1947). The requirement for an anticipatory controller suggests a level of sophistication that is greater than the simple mechanical/reflex ideas that have been commonly proposed.

The place of standing in the hierarchy of motor control requires revision. In standing, cause and effect may have been confused; postural sway is actually generated by anticipatory neural activity whereas it has previously been assumed that neural activity is a reaction to postural sway.

Also, these observations suggest that the behaviour of muscles in other postural tasks assumed to be reflex

should be investigated. ‘Static’ postural control may be a myth.

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The Journal of Physiology symposia

The Journal of Physiology will sponsor two symposia at the IUPS meeting to be held in San Diego, CA, USA from 31 March to 5 April, 2005.

PDZ domain scaffolding proteins and their functions in polarized cells, will take place on Monday, 4 April 2005 from 0800-1000 and speakers will include Mark Donowitz, Sharon L Milgram, Heini Murer and Edward Weinman. This symposium is

organised by Mark Donowitz and Yoshihisa Kurachi on behalf of the Editorial Board of *The Journal*.

TRP channels: physiological genomics and proteomics, is scheduled for 1515-1715 on Tuesday, 5 April. Bernd Nilius, Wolfgang Liedtke, Viet Flockerzi and Craig Montell will speak, with Stewart Sage and Bernd Nilius acting as organisers.

The proceedings of the 2004 *Journal* symposia – *Structure/function correlates in neurons and networks: a symposium in honour of the late Eberhard H Buhl** held in Leeds, UK on 10 September, and *The Senses*, held in San Diego, CA, USA on 22 October – will be published in *The Journal of Physiology* early in 2005.

**See p. 37 for a report on the Leeds Symposium*