Stable human standing with lower-limb muscle afferents providing the only sensory input

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1. This study investigated the sources of sensory information upon which normal subjects' ability to stand depends.
2. An 'equivalent body' was used to simulate the physical properties of each subject's body during standing. The modulation of ankle torque required to support the equivalent body in an upright position was similar to that required to support the subject's own body when standing. However, when balancing the equivalent body, vestibular inputs were excluded from directing the appropriate changes in ankle torque. Thus, stability of stance could be studied with (normal stance) and without (balancing equivalent body) modulation by vestibular inputs. Vision could be excluded by closing the eyes. Sensory input from the feet and ankles could be removed by local anaesthesia from prolonged ischaemia, induced by occluding blood flow with inflated pneumatic cuffs just above the ankles. With vestibular, visual and peripheral sensory inputs negated, standing could rely only upon remaining sensory inputs, notably those from sensory receptors in the leg muscles.
3. Unlike the human body, the equivalent body used to negate vestibular inputs is not segmented. Therefore, the effects on stability of having a segmented body were determined by splinting subjects during standing so that only ankle movement was possible. This was done in the presence and absence of visual stabilization.
4. For each experimental task, either standing or balancing the equivalent body, sway was recorded while posture was unperturbed. Root mean square values of sway amplitude and power spectra were used to compare conditions.
5. Every subject could balance the equivalent body in a stable way when the eyes were closed, and when the feet were anaesthetized. Therefore, they could perform a task that was equivalent to standing but when only sensory information from the leg muscles was available to detect the sway. However, although subjects were stable, sway was greater than when they were standing normally with all sensory inputs available.
6. In all situations, sway increased significantly when the eyes were shut, or when splinting prevented the movement of body segments above the ankles. In contrast, there was a small increase in sway when sensory inputs from the feet and ankles were excluded. Sway was similar for standing with the body splinted (vestibular inputs available) and for balancing the equivalent body (vestibular inputs excluded).
7. It is concluded that, for normal subjects: (i) proprioceptive signals from receptors in the leg muscles are sufficient to maintain a stable upright stance; (ii) visual inputs are necessary for maximal stability; (iii) the effect of the segmented body is to significantly improve stability; (iv) sensory information from the feet and ankles has a smaller but significant effect on stability; and (v) during normal standing, vestibular inputs are not responsible for modulating activity in the leg muscles to assist stability.

Stable human standing is usually considered to depend on an integrated reflex response to vestibular, visual and somatosensory inputs. Stretch reflexes play a major role in the control of muscles throughout the body and proprioceptors within muscles provide the nervous system with information about joint position and movement. However, the role of muscle spindles and stretch reflexes in the regulation of standing is unclear.

During standing, activity in soleus is continuous and can be modulated to compensate for postural disturbances (Joseph & Nightingale, 1952; Fitzpatrick, Gorman, Burke & Gandevia, 1992*a*). The human soleus has a high density of muscle spindles (Levy, 1963) and a powerful tendon jerk. However, experiments suggest that short-latency stretch reflexes have a minimal role in postural compensation (Gurfinkel, Lipshits & Popov, 1974; Nashner, 1976; Allum & Büdingen, 1979). Furthermore, soleus monosynaptic Ia responses are suppressed during standing (Katz, Meunier & Pierrot-Deseilligny, 1988), the tonic vibration reflex cannot be elicited during standing (Eklund, 1972), and the transmission of signals from muscle afferents to cortical centres is attenuated during standing (Applegate, Gandevia & Burke, 1988).

Other evidence indicates that significant postural reflexes may originate from receptors in the legs. In standing subjects, rapid rotation of the ankles evokes a negligible short-latency response in the leg muscles followed by a much larger response at a latency of 65–120 ms (Nashner, 1976; Diener, Bootz, Dichgans & Bruzek, 1983; Dietz, Quintern & Sillem, 1984). The later response(s) is considered to provide a more powerful postural correction. However, in a highly non-linear system, it is unlikely that responses to impulsive physical or electrical disturbances reflect the steady-state operation of reflex mechanisms during quiet standing. If a stochastic postural disturbance is used, rather than an impulsive one, the reflex transmission characteristics cannot be explained on the basis of a response with a fixed latency (Fitzpatrick *et al.* 1992*a*). The α–γ motoneuron coactivation during standing also suggests a high level of neural integration. Experiments that have attempted to exclude selectively afferents from the leg muscles with an ischaemic block at the level of the thighs reveal a characteristic 1 Hz body sway if the eyes are shut, which is not present when the block is at ankle level (Aggashyan, Gurfinkel, Mamasakklisov & Elner, 1973; Mauritz & Dietz, 1980; Diener, Dichgans, Guschlbauer & Mau, 1984; Horak, Nashner & Diener, 1990). While it cannot be assumed that such ischaemia did not induce changes at least in part due to block of motor nerves or loss of muscle function, the finding suggests that information from the larger Ia and Ib afferents from leg muscles may contribute to stability at this frequency and that responses based on vestibular inputs are inadequate to stabilize sway at this frequency.

In a recent study, it was shown that human standing can be maintained by reflexes that respond to sensory information from the legs in the absence of vestibular and visual reflexes (Fitzpatrick, Taylor & McCloskey, 1992*b*). The method used to show this involved a task that simulated standing but excluded changes in vestibular input as a possible contributor to the control process. During standing, movement occurs at all joints of the body. However, if 'body sway' is taken to mean the movement of the centre of gravity of the body then most of the sway in the sagittal plane occurs about the axis of the ankles, and must be controlled by a modulated contraction of the calf muscles. Muscles with a capacity to control lateral sway are the gluteal muscles, the hip adductors and the peroneal muscles (Day, Steiger, Thompson & Marsden, 1993). However, because these muscles are inactive during quiet stance (Joseph & Williams, 1957; Warwick & Williams, 1980), it seems that sway in the coronal plane is largely resisted by passive skeletal forces. Thus, the standing body was considered to behave as an inverted pendulum (Gurfinkel & Osevets, 1972) and an equivalent mechanical pendulum was matched to each subject. With the body and head immobilized, upright subjects used their feet to balance this 'equivalent body'. During this task, and during normal standing, the available lower-limb sensory information could originate from mechanoreceptors in the feet, joint receptors in the capsule of the ankle, cutaneous receptors adjacent to the ankles and from proprioceptors within the leg muscles. Because of the large mass of the body, small postural movements produce relatively large pressure changes under the feet so that receptors in the feet could provide significant information about body sway. There is some evidence that receptors in the feet may provide a significant sensory input to the control of standing (Magnusson, Enbom, Johansson & Pyykko, 1990).

The present work examined the ability of normal subjects to maintain a stable upright posture when relying only on proprioceptive information from the leg muscles. The significance of sensory information from the feet in controlling standing was determined in the presence, and absence, of visual and vestibular inputs. Because models of human standing (Gurfinkel & Osevets, 1972) and the experimental technique of this study consider the body as a rigid inverted pendulum rather than a segmented one, the effect of the segmented nature of the body on postural stability was also determined. Previously, it has been shown that reflex responses based on somatosensory inputs from the legs were sufficient to maintain standing (Fitzpatrick *et al.* 1992*b*) but the effects on stability of limiting sensory inputs were not determined. Therefore, in the present study, postural sway is measured as an indicator of stability.

METHODS

The initial experiment described here was designed to determine first, whether stable human standing can be maintained when sensory information about posture arises only from leg-muscle afferents and, second, the extent to which sensory information from the feet assists stability in the presence and absence of visual and vestibular inputs. The second experiment, which was instituted following observations made in the first, was designed to determine the extent to which the segmented nature of the body might assist stability. The subjects, who included the authors, were seven healthy adults of both sexes whose ages ranged from 24 to 50 years. Six subjects participated in each experiment and five participated in both. Four subjects had not previously participated in experiments that used this equipment. The experiments were approved by the Institute's human ethics committee and all subjects gave informed consent.

In both experiments, subjects either stood on a stable platform or performed a task that simulated standing but excluded changes in vestibular input as a possible source of information about sway. In both cases, subjects stood without shoes and with their feet separated by approximately 20 cm. In the 'equivalent task', each subject used the feet to balance an inverted pendulum that had the same mass and height of its centre of mass as the subject's body (see Fitzpatrick *et al.* 1992*b*). This pendulum rotated about the axis of the ankles and provided the same torque at the ankles as existed when the subject was standing (Fig. 1). Subjects were strapped to a rigid, upright support so that the body and the head were stationary. This ensured that vestibular input was unable to participate in directing the appropriate changes in leg-muscle activity required to balance the load.

Set-up

Experiment 1: effects of sensory inputs. Initially, four experimental conditions were tested for each subject and the sequence was randomized between subjects. The conditions were: trial A, standing with eyes open on a stable platform, a condition which made vestibular, visual and proprioceptive inputs available; trial B, standing similarly but with eyes shut so that only vestibular and proprioceptive inputs were available (Fig. 1*A*); trial C, balancing the equivalent body (see above) with the aid of a visual target so that visual and lower-limb proprioceptive inputs were available while vestibular inputs were excluded; and trial D, balancing the equivalent body with the eyes shut so that only lower-limb proprioceptive inputs were available (Fig. 1*B*). In trial C, a small brightly coloured target was supported by a bar that was rigidly attached to the equivalent body and extended 1·5 m in front of the subjects at eye level. Subjects could detect movements of the equivalent body by looking at the target or at the bar.

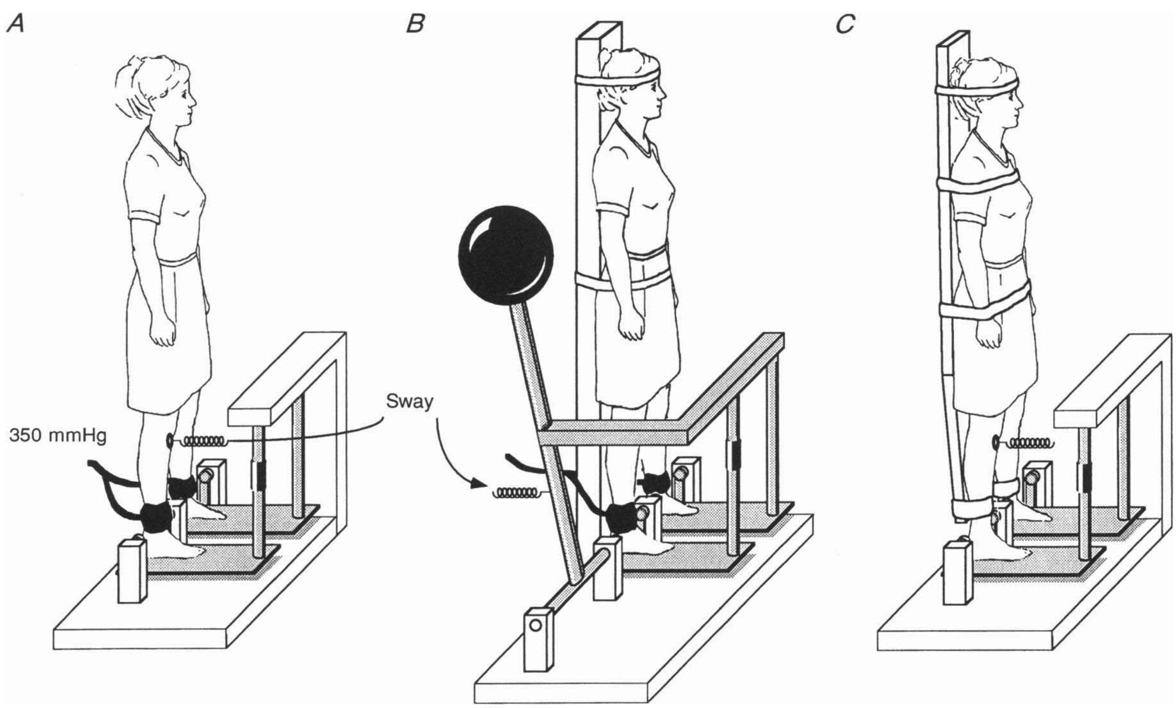

Figure 1. Experimental set-up

A, subjects stood on a stable platform with their eyes either open or shut. Sway was measured by attaching a very weak spring from the tibial tuberosity to an isometric strain gauge. Pneumatic cuffs were placed above the ankles and below soleus and inflated to 350 mmHg for approximately 1 h to cause anaesthesia of the feet and ankles. *B*, this set-up removed vestibular inputs related to sway. If the eyes were shut, sway would only activate receptors in the leg muscles and feet or, if the feet were anaesthetized, only in the leg muscles. The body was prevented from swaying by a rigid support and, by using the feet, subjects balanced a load that was matched to the physical properties of their own bodies during standing. The sway of this 'equivalent body' was measured. *C*, a rigid splint, shaped like an inverted Y, was strapped to the back of subjects at the head, chest, pelvis and above the ankles. This prevented movement at all joints other than the ankles and so resembled the rigid 'equivalent body' (*B*), except that when subjects were standing and splinted, vestibular inputs would be available to control posture.

If the equivalent body swayed backwards, the torque at the ankles increased and the visual target approached the subject, both of which are analogous to forward sway during standing. During each trial, subjects were asked to minimize the sway of either the body or of the equivalent body for a period of 85 s. Subjects were seated for 5 min between trials to avoid fatigue.

Following the initial four trials, pneumatic cuffs were placed above each ankle and below the calf muscles and inflated to 350 mmHg. Total anaesthesia below the cuffs was achieved after 50–75 min. This was verified by clinical tests for cutaneous and deep pressure sensation and the inability to detect abduction of the toes. After a further period of approximately 10 min, the four experimental trials were repeated while the cuffs remained inflated (trials E, F, G and H). During these trials, the lower-limb sensory inputs would not include information from the anaesthetized regions below the level of the cuffs.

To avoid prolonged ischaemia in all subjects, two additional control experiments were performed with one of the authors as the subject. The first control was designed to exclude the possibility that skin and tendon sensation adjacent to the cuffs signalled information about ankle movement. Pneumatic cuffs (350 mmHg) were inflated around each thigh after the ankle cuffs had produced complete anaesthesia of the feet. The ankle cuffs were removed and the anaesthesia was maintained by the thigh cuffs while the subject balanced his equivalent body. This was done before the leg muscles were affected by ischaemia. The second control experiment was designed to determine whether reflex responses (rather than volitional responses) based on sensory input from the leg muscles alone are sufficient to correct perturbations of the equivalent body. The technique used here is described in an earlier study (Fitzpatrick *et al.* 1992*b*). A linear servomotor was attached through a weak spring (approximately 5 N m^{-1}) to the equivalent body, and the motor pulled with a slow, constant velocity for 3 s in the direction that would dorsiflex the ankles. The velocity of the motor was adjusted so that the subject could not perceive any movement that might arise. Ankle stiffness was calculated by linear regression of the torque *versus* angle data from the first 1·5 s of the pull. Average ankle stiffness for twenty perturbations was calculated. The 'load stiffness' of the equivalent body, which had been matched to the load stiffness of the subject's own body, was calculated from the slope of the torque *versus* angle relationship when the subject made the bar sway slowly.

Finally, each subject was asked to stand and sway voluntarily but not to the extent of stumbling. This provided an approximate measure of the amount of sway that might be considered clinically as unstable and which could be compared with documented recordings of the centre of foot pressure (stabilography) for unstable patients.

Experiment 2: effects of the segmented body. Each subject was tested with six experimental conditions that were presented in a randomized order. Four conditions were identical with those of Experiment 1 in which the feet were not anaesthetized. When standing with eyes open on a stable platform (trial A) and standing with eyes shut (trial B) movements of body segments were unrestricted experimentally and could theoretically influence stability, but when balancing their equivalent mechanical bodies with eyes open (trial C) and eyes shut (trial D), segmental movements were excluded because the experimental arrangement involved strapping the subject's body upright to a rigid support. To exclude the effects of segmental movements during standing, a rigid splint that had two 'legs' like an inverted Y was firmly strapped to the subject at the forehead, chest, pelvis and above each ankle (Fig. 1*C*). When splinted, subjects stood with their eyes open (trial E) or shut (trial F). Again, subjects were asked to minimize sway of either the body or equivalent body for the 85 s duration of each trial.

Data measurement and analysis

In this study, ankle movement ('sway') in the sagittal plane was used as the measure of stability rather than ankle torque or the related 'centre of foot pressure'. Sway measures the output of the postural control system and avoids the inclusion of dynamic responses which include the forces produced as a result of stabilizing reflexes (Gurfinkel, 1973).

For the freely standing and splinted-standing trials, a very weak spring (0·1 N m^{-1}), attached between the subjects right tibial tuberosity and a fixed strain gauge, was used to measure ankle movements (Fig. 1). When subjects balanced their equivalent mechanical bodies, ankle movements were measured by attaching the spring and strain gauge to the upright pendulum. The transducer had a noise level equivalent to 2×10^{-5} rad of ankle rotation whereas the measured range of ankle movements was approximately 4×10^{-2} rad. The weak spring had a fundamental frequency of 20 Hz – well above the frequencies considered in the analysis.

During each 85 s trial, ankle movement was sampled at 25 Hz by an analog-to-digital interface and stored for computer analysis. To remove effects of aliasing and DC shifts, the data were digitally bandpass filtered to accept frequencies of 0·05–10 Hz. Root mean square (r.m.s.) values were calculated from this data. Power spectra were calculated using a fast Fourier transform. The r.m.s. estimates were then averaged across subjects, and analysed by analysis of variance (ANOVA) with: (i) vision; (ii) anaesthesia of the feet; and (iii) task (own body, equivalent body, splinted body) as factors.

RESULTS

Experiment 1: effects of sensory inputs

Without prior training, all subjects were able to balance loads that were equivalent to their own bodies in a situation where visual and vestibular information were unavailable and proprioceptive information from the feet and ankles was removed by ischaemic anaesthesia. Recordings of sway in the sagittal plane from a typical subject (Fig. 2*A*) showed that, with only sensory input from the leg muscles available (Muscle), (i) the amplitude of sway was similar to that of normal standing (Muscle, feet, ears and eyes), and (ii) there were no abrupt postural corrections as might be seen in a stumbling reaction.

As sensory input was successively removed, first by eye closure, then by balancing the equivalent body to exclude vestibular inputs, and finally anaesthetizing the feet, the excursions of sway increased. When only sensory information from the leg muscles was available, the average r.m.s. estimate of sway was 2·4 times its value when standing with the eyes open (Fig. 3A, compare 'Ears, eyes and legs, normal sensation' with 'Legs, anaesthetized feet'). However, in all situations, sway was of the order of 1 deg, whereas when subjects were asked to sway voluntarily to simulate an unstable posture, excursions of more than 5 times this amplitude were maintained without falling, and the r.m.s. estimate of sway was more than 10 times greater (Fig. 3A, right Y-axis).

For one subject, anaesthesia of the feet was maintained by pneumatic cuffs around the thighs and the cuffs were removed from the ankles. This removed the possibility that signals related to ankle movement may come from receptors in the skin and tendons adjacent to the ankle cuffs. In this situation and with eyes shut, the subject balanced the load without marked instability. Sway was similar (r.m.s. = 2·6) to when the cuffs were at the ankles (r.m.s. = 2·8). For that subject in the same situation, the average ankle stiffness measured during twenty imperceptible perturbations was 539 N m rad^{-1}, 31% greater than the measured 'load stiffness' of the equivalent body (412 N m rad^{-1}) which had been matched to the subject's own body (390 N m rad^{-1}). Without a volitional response based on perception of the perturbation, the ankles were stiffer than the stiffness of the load that they were supporting. Thus, ankle stiffness generated by reflex mechanisms is sufficient to correct perturbations of the equivalent body (Fitzpatrick et al. 1992b).

To determine whether the loss of sensory input introduced instabilities at specific frequencies, power spectra were calculated from the recordings of sway (Fig. 2B). In each situation there was negligible sway at

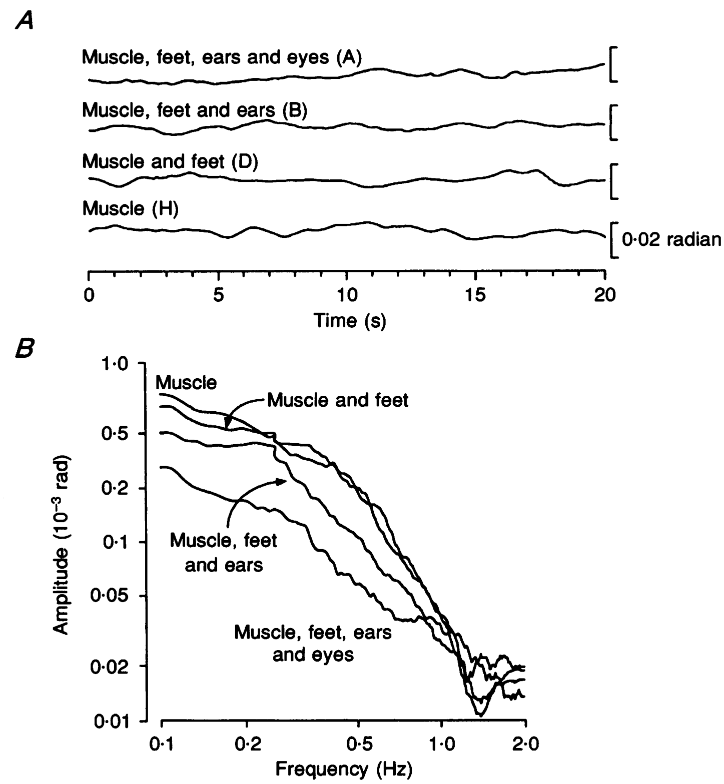

Figure 2. Sway when different sensory inputs were available

A, for one subject, recordings of sway are shown when standing with eyes open (top trace), when standing with eyes shut (2nd), when balancing the equivalent body with eyes shut (3rd) and when balancing the equivalent body with the feet and ankles anaesthetized (lower trace). The category of experimental trial (see Methods), and the sources of sensory information that were available are indicated. In each situation, the excursions of sway are similar (approximately 0·02 rad or 1 deg), and when only proprioceptive input from the leg muscles was available (Muscle) there was no marked instability. B, averages (geometric) of the sway spectra for 5 subjects as sensory input is successively removed. The square root of power is plotted so that the ordinate displays the mean amplitude of sway according to frequency. In each case there was negligible sway above 1 Hz. As each sensory input is removed, sway increases at frequencies below 1 Hz without large resonant peaks developing.

frequencies above 1 Hz. With successive removal of sensory modalities there was an increase in sway and this occurred at frequencies below 1 Hz without instability being introduced at a specific frequency.

Effects of anaesthesia of the feet and ankles

For each experimental condition – that is, standing with eyes open or shut and balancing the body with eyes open or shut – anaesthetizing the feet increased the group average r.m.s. estimate of sway (Fig. 3*A*). On average, sway increased by 17% ($P = 0.03$, three-way ANOVA). However, these differences were small, not consistent between subjects and did not reach statistical significance by Student's paired t test for any set of conditions.

Effects of vision

When standing and when balancing the equivalent body, either with or without the feet anaesthetized, eye closure increased sway (Fig. 3). With vision removed, the mean r.m.s. estimate of sway increased by 48% ($P < 0.001$, three-way ANOVA) and for each set of conditions was significant by Student's paired t test ($P < 0.05$ for each).

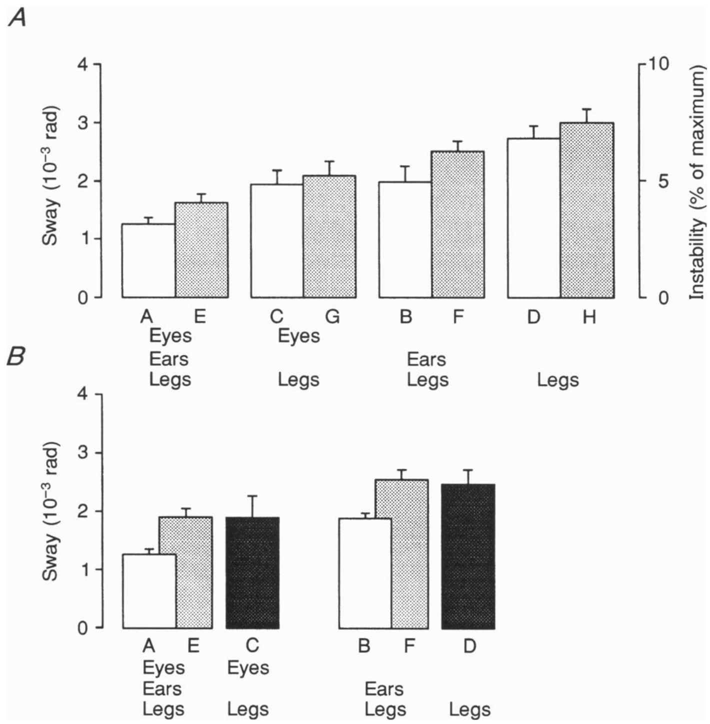

Figure 3. Average r.m.s. estimates of sway for 5 subjects during different experimental conditions

The category of experimental trial and sources of available sensory input are indicated below each column. The r.m.s. value is a least-squares estimate of the deviation from the mean standing position during the period of the recording. The error bars represent 1 S.E.M. The Y-axis on the right shows the recorded sway as a percentage of the sway during the voluntary simulation of an unstable posture. *A*, each pair of columns shows sway before (□) and after (▨) anaesthesia of the feet and ankles. Sway was least for standing with eyes open when all sensory modalities – 'Eyes, ears and legs' – were available. Sway was greatest for balancing the equivalent body with eyes shut when the only sensory information came from the legs. Before anaesthesia (Legs, □) sensory input could have come from receptors in the feet and ankles, but after anaesthesia the sensory input was restricted to proprioceptors in the leg muscles (Legs, ▨). *B*, the overlapping pairs of columns show the effects of splinting the body (□, segmented body; ▨, splinted body) when standing with eyes open (Eyes, ears and legs) and with eyes shut (Ears and legs). In each case there was a significant increase in sway when movement was restricted to the ankles. Sway is also restricted to the ankles when balancing the equivalent body. The filled columns show the sway when balancing the equivalent body so that vestibular inputs (Ears) are removed. For both the eyes-open and eyes-shut conditions, sway was unchanged by removing vestibular inputs (compare ▨ and ■). Thus, the data in *A* suggest that removal of modulated vestibular inputs increases body sway, but the data in *B* indicate that such increases in sway can be wholly attributed to splinting.

There were no significant statistical interactions between visual inputs, somatosensory inputs and whether the task was standing or balancing the equivalent body.

Experiment 2: effects of the segmented body

When subjects balanced their equivalent mechanical bodies, the r.m.s. estimate of sway in the sagittal plane was 38% greater than when they stood freely and balanced their own bodies ($P < 0{\cdot}001$, three-way ANOVA). Two explanations for this instability are apparent: (i) vestibular inputs to the postural control system provide stability and in this situation they are absent; and (ii) the segmented nature of the body assists stability and in this situation the equivalent body is not segmented. When subjects stood with their eyes open and were splinted to limit sway to the ankles and prevent movement of body segments, sway was 52% greater than when they stood freely with the eyes open ($P < 0{\cdot}05$, 2-way ANOVA followed by Student–Newman–Keuls test for multiple comparisons; Fig. 3*B*, compare segmented (open columns) with splinted (shaded columns)). Similarly, when the eyes were shut, sway was 35% greater than when subjects were standing freely ($P < 0{\cdot}05$, 2-way ANOVA with Student–Newman–Keuls test). For both the eyes-open and eyes-shut situations, there was no significant difference in sway between standing while splinted and balancing the equivalent mechanical body (Fig. 3*B*, compare splinted (shaded columns) with equivalent body (filled columns)).

DISCUSSION

Subjects did not find it difficult to support the equivalent body (sway-related vestibular inputs excluded), even when they closed their eyes, and when the feet were anaesthetized. They could do it without training and when distracted or engaged in conversation, suggesting that the task did not require a complex volitional modulation of muscle activity. In an earlier study we used very small unperceived postural disturbances to show that a reflex response based on sensory information from the legs was sufficient to support a subject's body during standing, or to support the equivalent body (Fitzpatrick *et al.* 1992*b*). The present study demonstrates that this response almost certainly originates from receptors in the leg muscles. Ankle stiffness was measured in one subject by using similar imperceptible postural disturbances when the feet and ankles were anaesthetized and the subject supported the equivalent body. The ankle stiffness in this situation was greater than the measured 'load stiffness' of the equivalent body (and the subject's own body). Therefore, an involuntary response based on sensory input from the leg muscles was sufficient to provide stability despite the perturbation.

In standing humans, postural sway is traditionally considered to require a co-ordinated response from vestibular, visual and stretch reflexes. The present study demonstrates that normal subjects can stand in a stable manner when receptors in the leg muscles are the only source of information about postural sway. Under such conditions of sensory restriction studied here, sway was less than one-tenth of the sway during the simulated unstable posture when subjects swayed voluntarily. This simulated condition can be taken to approximate cases of clinical instability because there is approximately a 10-fold increase in sway in patients with cerebellar disease or neuropathies (Dichgans & Mauritz, 1983; Horak, Nashner & Diener, 1990).

After sensory information from the feet and ankles has been excluded, it can be assumed that the only remaining source of information from the legs is from proprioceptors in the leg muscles that operate at the ankles. Our current experiments were designed to test the hypothesis that proprioceptors in the leg muscles provide a sensory input that is sufficient for stable standing. Group I or group II muscle spindle afferents, and group Ib afferents from Golgi tendon organs are the probable sources of this proprioceptive information. However, it was not the purpose of our experiments to identify the proprioceptors responsible and, indeed, our results cast no light on the identity of the intramuscular receptors nor of the neural pathways involved.

When one is standing, mechanoreceptors throughout the body are a potential source of information about sway. The 'equivalent task' used in this study would exclude this proprioceptive input, in addition to vestibular inputs, because the body remains stationary. The ankles are the only joints where movement occurs so that sensory information must originate in the legs. One could consider that a possible source of input when balancing the equivalent body could have been from cutaneous receptors on the back from the support of the body. However, because of the large surface area of the back that was in contact with the support and the long lever arm of the upright support when compared with the size and length of the feet, there would be minimal pressure changes on the back arising from the small sway seen here.

When subjects supported their equivalent bodies, sway was greater than when they supported their own bodies. This finding might suggest that the availability of vestibular inputs reduces sway. However, sway increased by a similar amount when subjects were splinted while standing, a situation in which vestibular inputs were available. This indicates that the lack of segmental movements, rather than the lack of vestibular inputs, was the cause of the increased sway when balancing the equivalent body. Therefore, there is nothing in this experiment to indicate that vestibular inputs related to sway play a part in the control of normal standing. It remains conceivable, however, that vestibular-based facilitatory signals that are not directly related to sway may assist in maintaining upright posture, possibly by signalling the position of the vertical. In contrast to vestibular inputs, the availability of visual information about sway does assist stability if sway occurs only at the ankles, and indicates that responses to visual inputs can modulate activity of the leg muscles to control sway.

It could be expected that having a segmented (rather than a rigid) body might increase body sway because of uncontrolled movements of the upper segments and the greater complexity of the control task. However, this study shows that the opposite is the case: the segmented body confers stability. This finding implies that balancing the 'equivalent body' is a more difficult task than standing normally. Movement at the ankles is not the only determinant of stability, and movements seen at the hips and vertebrae (Day *et al.* 1993) probably play a role in controlling postural sway. Loads with a large inertia are difficult to control, and the segmented body would mean that the inertial component of the load seen by the leg muscles was reduced. With appropriate levels of stiffness and damping of the upper segments, total sway could be reduced by corrections at upper segments. On the sensory side of the control process, detection of sway and activation of postural reflexes may be improved if movements of upper segments occur simultaneously with rotation of the ankles.

Ischaemia of the feet does not affect the amount of sway, or the reflex responses in the leg muscles, evoked by a rapid perturbation of standing subjects (Diener *et al.* 1984). However, there is electrophysiological evidence that receptors in the skin and small muscles of the feet can modulate the activity of the leg muscles (Aniss, Diener, Hore, Burke & Gandevia, 1990). After anaesthetizing the feet by immersion in iced water, Magnussen *et al.* (1990) measured a 35% increase in the velocity of the movement of the 'centre of foot pressure', but in the present study, sway increased by only 17%. The difference is likely to reflect the different measurements. The 'centre of foot pressure' reflects the forces of muscle activity as well as the passive reaction forces produced by body sway, and differentiating the signal to obtain velocity will further increase the average value.

When standing normally with the eyes open (the most stable situation), sway was 40% of that when only input from the leg muscles was available (the least stable situation). Most of this improved performance can be explained by the effects of visual stabilization and of having available segmental movements of the body. A large increase in the r.m.s. estimate of sway with eye closure would constitute a numerical equivalent of the Romberg's sign used by clinicians. Even in the absence of input from the vestibular organs and from receptors in the feet and ankles, the normal subjects documented here would not exhibit a Romberg's sign because the increase in sway with eye closure (44%) was similar to the increase during normal standing (58%) which is virtually undetectable, and insignificant, clinically.

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