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RESEARCH ARTICLE

Control of upright stance over inclined surfaces

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Abstract The present work investigated the control of upright posture on inclined surfaces (14°). Such conditions could, for example, change the contributions of muscle spindles resulting in alterations in postural sway. Subjects stood in quiet stance over a force platform positioned in one of three different fixed positions: horizontal (H), toes-up (ankle dorsiflexion, D) and toes-down (ankle plantar-flexion, P). The experiments were done in the presence and also in the absence of vision. The analysis of the resulting sway was based on the power spectrum of the center of pressure displacement in the anterior–posterior direction (CP_ap). Analysis of the electromyogram (EMG) of the leg muscles and evaluation of the level of presynaptic inhibition (PSI) of the soleus (SO) Ia afferents complemented the study. The results showed that the spectrum of the CP_ap changed with the inclination of the surface of support. In condition D a higher instability was found as reflected by the higher spectral amplitudes at lower frequencies (below 0.3 Hz). On the other hand, the CP_ap of subjects in condition P contained increased amplitudes at high frequencies (above 0.3 Hz) and smaller amplitudes at low frequencies. The modifications found in the CP_ap power spectra when standing over an inclined surface may indicate changes in both short-term and long-term systems of postural control. These results do not seem to be associated with changes in group Ia feedback gain since no changes in the level of PSI were found among the three standing conditions. The SO EMG increased in condition P but did not change in condition D. On the other hand, the tibialis anterior had a tendency towards increased bursting activity in condition D. Eye closure caused an increase in the power of the oscillations at all spectral frequencies in the three standing conditions (H, P or D) and also a change in the profile of the CP_ap power spectrum. This may suggest a nonlinearity in the postural control system. The control of the slow component of the postural sway was more dependent on vision when the subject was in condition D, probably in association with the biomechanical constraints of standing on a toes-up ramp. A conclusion of this work was that, depending on the postural demand (direction of the ramp of support), the ensuing proprioceptive and biomechanical changes affect differentially the fast and slow mechanisms of balance control.

Keywords Human · Posture · Motor control · Center of pressure · Quiet standing · Slope · EMG · Vision

Introduction

The central nervous system performs a complex integration of somatosensory, visual and vestibular signals in order to accomplish the control of upright stance. In spite of an evident redundancy, there is an increase in postural sway when one or more of these sensory inputs are absent, either by experimental manipulation or impairment (Diener and Dichgans 1988).

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Among the muscle afferents, the group II seems to have a major importance in the control of upright posture, as attested by the use of paradigms involving perturbations of stance (Schieppati and Nardone 1999; Nardone et al. 2000; Nardone and Schieppati 2004). However, these findings help to understand the corrective mechanisms resulting from postural perturbations but do not clarify the control mechanisms behind quiet upright stance (Marchand-Pauvert et al. 2005). A number of studies have used voluntary forward lean to investigate the effects of changes in proprioceptive input and/or imposed biomechanical constraints on postural control (Sinha and Maki 1996; Riley et al. 1997; Duarte and Zatsiorsky 2002; Marchand-Pauvert et al. 2005; Bove et al. 2006). However, in those studies the subject's primary concern would be to maintain a desired position near to the limit of the base of support, whereas on the inclined ramps of the present study the subjects have to stay in a natural upright stance, involving no special voluntary effort.

Upward or downward surfaces represent a common postural challenge in the daily activities of humans. Several authors have employed inclined surfaces to study: (1) the effects of slope on trunk kinematics during lifting a weight (Shin and Mirka 2004); (2) the postural strategies associated with walking on an inclined surface (Leroux et al. 2002); (3) the after-effects on the forward leaning of the body (on a horizontal surface) followed by a few minutes standing on a slope (Kluzik et al. 2005); (4) the action of the fusimotor system (Aniss et al. 1990).

In the present work static inclined surfaces will be used to change the proprioceptive input by exposing flexor or extensor muscle spindles to different lengths. This should result in different steady state firing rates in spindle output (Ia and II afferents), raising the question if these altered spindle discharges affect the gain of the feedback in reflex pathways involved in the control of postural sway during quiet stance. Such manipulation, besides the advantage of not involving a supra-postural task (Riley et al. 1997), provides useful information about the integration of different sensory modalities (e.g., by the study of combined effects of changes in proprioceptive and visual inputs).

To assess the quality of balance control in different static ramp inclinations the center of pressure motion in the sagittal plane (CP_ap) was evaluated. This signal, when recorded during standing on a horizontal surface, has been roughly decomposed in two components: higher frequency oscillations superimposed on low frequency oscillations (Carpenter et al. 2001). These may reflect two processes of postural control (Lestienne and Gurfinkel 1988; Zatsiorsky and Duarte 1999, 2000). However, to avoid an a priori subdivision in slow and fast components, a spectral analysis of the CP_ap was adopted in the present study.

The analysis of the measured electromyograms (EMGs) of the ankle flexors and extensors should help explaining the influence of those muscles in defining the features of the CP_ap trajectories during standing on different slopes. The H-reflex was measured in control and conditioned situations to estimate the degree of presynaptic inhibition (PSI) of the Ia terminals (Iles 1996), which has been associated with posture-related changes (Katz et al. 1988; Koceja et al. 1993; Zehr 2002). The experiments to evaluate the PSI of the Ia afferents from the soleus muscle (SO) were undertaken in order to verify if the altered afferent inflow associated with standing on a ramp could bring about changes in the gain of the short latency stretch reflex pathway.

In summary, this study analyzes some sensory and motor aspects associated with the ankle muscle action, spinal cord mechanisms involved in reflex gain modulation, and the spectral features of postural sway during quiet upright stance under challenging postural conditions.

Methods

Subjects

Twelve normal adults, eight males and four females, participated in this study. Their average age, height and mass were, respectively, 29.5 ± 8.3 years, 1.73 ± 0.11 m, and 74.1 ± 18.9 kg (mean ± SD). All volunteers gave their informed consent to participate in the present study according to the local ethics committee. None of the subjects had any known history of postural or neurological disorders.

Experimental procedures

Center of pressure (CP) displacement

The subjects stood barefoot in quiet stance over a force platform (AMTI, OR6-7-1000) which was inclined in three different static angles (Fig. 1a and b): (1) $\alpha = +14°$ ("toes-up"); which caused an ankle joint flexion (or dorsi-flexion), termed condition D; (2) $\alpha = -14°$ ("toes-down"); causing an ankle joint extension (or plantar-flexion), termed condition P; (3) $\alpha = 0°$; or horizontal (H) condition, parallel to the laboratory

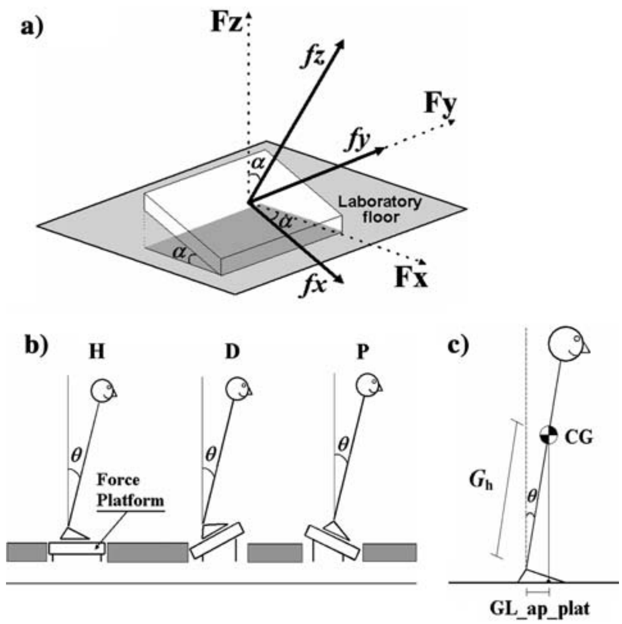

Fig. 1 **a** Reference frame for horizontal (*dashed lines*) and inclined (*thick lines*) platform positions. The angle of the platform with respect to the ground is indicated by α. **b** Subject over the force platform in different ramp inclinations. *H* horizontal (parallel to the floor; α = 0°); *D* toes-up (α = +14°); *P* toes-down (α = –14°). The subjects remained in these three positions with eyes open (*EO*) and closed (*EC*). θ is the leaning-forward angle. **c** Center of gravity (*CG*), height of the center of gravity (G_h), and projection of the CG on the platform (*GL_ap_plat*)

floor. Subjects were told to stay still with their arms comfortably hanging at their sides and their feet spaced 30 cm apart. No special instruction was given when the platform was inclined. Thus, the subjects were free to find their most comfortable orientation with respect to gravity. The volunteers performed three trials lasting 70 s, alternating two vision conditions for each ramp inclination: eyes open (EO), looking straight ahead to a target placed at a distance of 90 cm, and eyes closed (EC). The visual target was placed at the eye level for each subject. The first 10 s of the acquisition were discarded. A resting period of 30 s between trials was allowed to avoid fatigue.

When the force platform was inclined, we considered the reference frame of the force platform itself and not that associated with the gravitational vector. The CP was computed based on the axis *fz*, perpendicular to the platform, and the orthogonal axes (*fx* and *fy*) on the platform surface (thick lines in Fig. 1a). Thus, we computed the CP over the *surface of the inclined force platform* and not the projection of the CP sway on the horizontal floor (which would use the dashed reference system in Fig. 1a).

EMG signals, H-reflex and presynaptic inhibition (PSI)

The EMG signals from the soleus (SO) and tibialis anterior (TA) muscles were collected simultaneously with the signals from the force platform. The EMG signals were amplified and filtered (10 Hz to 1 kHz) by a Nihon-Kohden MEB 4200 system. Surface electrodes were placed on the SO muscle, the most proximal 4 cm beneath the inferior margin of the two heads of the gastrocnemius muscle (Burke 1997). Two other surface EMG electrodes were attached on the proximal third of the TA muscle. The surface electrode pairs were attached with an inter-electrode distance of 2 cm.

In a different day, in 6 out of the 12 subjects, the PSI upon the SO Ia afferents was evaluated through a conditioning stimulation on the peroneal nerve (1 × motor threshold) (Iles 1996). The control and test stimuli to evoke an H-reflex and/or M-wave in the SO muscle were delivered to the tibial nerve by a monopolar electrode with cathode at the popliteal fossa and anode at the patella. A bipolar electrode placed at the neck of the fibula was used to stimulate the TA muscle Ia afferents of the peroneal nerve (conditioning stimulus). The optimal inter-stimulus interval between the conditioning and the test stimuli was set for each subject (ranging from 90 to 110 ms, with steps of 10 ms) before the beginning of the experiment. Two independent stimulators of the MEB 4200 system delivered the electrical stimuli, triggered by a PC-based Data Wave signal acquisition system. The subjects remained in the upright position in a relaxed stance in each of the conditions previously described (three different ramp inclinations with eyes open and closed).

Maximal direct SO muscle response (M_{max}) was evoked by a supra maximal stimulus applied on the tibial nerve in each ramp inclination, to estimate the changes in compound action potential amplitude associated with changes in recording geometry (Simonsen et al. 1995). The same was done for the TA muscle aiming to normalize the rectified EMG values (see below).

The reflex responses were elicited at every 3 s. Six trials were performed in all conditions; each of them produced five H-responses (control and conditioned). Previous to the delivery of the first conditioning stimulus of a given trial, five stimuli were applied to the tibial nerve in order to bring the H-reflex amplitude to the depression plateau, thus avoiding the effects of post-activation depression on the evaluation of the degree of PSI (Hultborn et al. 1996; Kohn et al. 1997). The corresponding first five H-responses were discarded from the analysis. The 30 control reflex responses had to have a relative amplitude of 20–30% of the respective M_{max} (Crone et al. 1990). Responses amplitudes outside this range were discarded.

Between trials, a 2 min rest period was used to avoid fatigue. The stimulus efficacy on the tibial nerve was checked at the end of each trial by applying a stimulus intensity that evoked a SO M-wave of a given amplitude (e.g., $M_{max}/3$).

In two subjects the contribution of the cutaneous afferents to the decrease of the conditioned SO H-reflex amplitude was assessed by shifting the conditioning stimulus electrode by 2–3 cm from the original position on the peroneal nerve.

Leaning-forward angle in upright stance

In a subset of nine subjects, a single trial for each ramp inclination (with eyes open and closed) was performed to estimate the mean leaning-forward angle θ (Fig. 1c) using the formula:

$$\theta = \sin^{-1}\{[\mathrm{GL\_ap\_plat}\cos(\alpha)]/G_h\};$$

where α is the platform inclination (Fig. 1a). When the platform is in the horizontal position α is zero.

In the formula above, the height of the center of gravity (G_h) was estimated by a biomechanical method which uses a balance board (Winter 1990). The results obtained from this method were very similar to the estimates based on Barin's method (Barin 1992) in which $G_h = 0.55h$, where h is the height of the subject. The projection of the center of gravity (CG) on the platform in the sagittal plane, is indicated by GL_ap_plat (drawing in Fig. 1c is for the horizontal case but applies equally to the other two conditions). It was estimated by the method of Zatsiorsky and Duarte (2000).

Signal processing and data analysis

All signals (EMGs, ground reaction forces and moments) were fed into a PC-based Data Wave data acquisition and processing system that sampled each channel at a frequency of 5 kHz.

Data files in ASCII format generated by the signal acquisition system were processed by programs written in the MATLAB (Math Works) environment. The signals from the force platform were decimated 50 times (with low-pass digital anti-aliasing filtering) resulting in signals with 6000 samples (with an effective sampling rate of 100 Hz). The same decimation (and low-pass anti-aliasing filtering) was done for the EMG signals after they were rectified, causing no loss of information.

The mean value of the rectified EMG obtained from either, the SO or the TA muscle in each condition was evaluated (for a 60 s EMG epoch). In order to normalize the EMG data, we multiplied a given mean rectified EMG value ($|\mathrm{EMG}|_M$) obtained in condition P or D from a subject, by the ratio of the averaged M_{max} evoked in condition H to the averaged M_{max} evoked in the respective condition, P or D (M_{max} factor). The M_{max} factor was evaluated from the mean of M_{max} of the subjects evoked on both muscles (and in each ramp inclination). This procedure was adopted to avoid the influence of peripheral factors, such as the displacement of the surface electrodes relative to the muscle fibres.

The power spectral density (PSD) of the CP_ap was estimated in each experimental condition. The average power spectrum obtained in each condition from all 12 subjects (each of them computed from three trials) was calculated. The mean power frequency (MPF) from the PSD was also evaluated. The average power spectra for different pairs of conditions were compared at the following frequencies: 0.05, 0.1, 0.2, 0.3, 0.4, 0.5, 1, 1.5 and 2 Hz. This frequency range was adopted because 90% of the total power of the CP signal is found below 2.0 Hz (Hayes 1982).

The power spectrum of the CP_ap signals obtained in each trial and in each condition was estimated using the Welch method with 2000 samples per periodogram, which resulted in a spectral resolution of 0.05 Hz. This also included the use of a Hann window, an overlap of 1,000 samples, and the subtraction of the best linear regression in each data window.

The envelope of the EMG (EMG rectified and then low-pass filtered to 2 Hz) was also subjected to the same power spectral analysis just described for the CP_ap.

For the estimation of the degree of PSI, the peak-to-peak amplitude of the conditioned H-reflex (H_cond) was divided by the control H-reflex (H_cont) amplitude for each condition.

Statistical analysis

The parameters that were subjected to statistical tests included: (1) the MPF and the power at the chosen frequencies of the PSD; (2) the body angle (θ) with respect to the earth-gravity; (3) the $|\mathrm{EMG}|_M$ of the SO and TA muscles; (4) the degree of PSI of the SO muscle (H_cond/H_cont).

An F test (Shumway 1982) was employed to compare the CP_ap power spectra obtained in different experimental conditions. For the remainder parameters, one-way repeated measures analysis of variance (ANOVA) was used. To assess differences between the parameters evaluated in each condition and the control condition (horizontal plane with eyes open; H–EO) a Dunnett's post hoc test was employed. A two-way ANOVA was used to check for the effect of vision in each ramp inclination (three ramp conditions vs. two vision conditions) for all parameters. For all statistical tests the significance level was set at $P < 0.05$.

Results

Body lean angle and leg muscles activity

The subjects had a small forward lean when standing quietly in all studied conditions. When standing on a horizontal surface subjects typically inclined about 4° forward (4.08° ± 1.27°) with respect to the gravitational vector. The subjects showed a mildly higher forward lean in condition D (5.03° ± 0.95°) but lower (3.45° ± 0.98°) in condition P. Although small, the differences in the body lean angle between conditions with respect to control were significant ($P < 0.05$) (Fig. 2a; Table 1). There was no significant effect of vision on the subject's leaning forward angle ($F = 0.16$; $df = 1,48$; $P = 0.69$) (Table 1).

The activation levels of both muscles (SO and TA) in each ramp inclination (Fig. 2b and c) are indicative of the torques applied at the ankle joint. These torques keep the body in the vertical positions described by the angles presented in Fig. 2a. In the overall, the activity of the SO was more prominent in condition P ($P < 0.05$), whereas TA activity was greater in condition D but without reaching statistical significance (Table 1). The SO activity in both conditions D and H was very similar (Fig. 2b).

The increase in leaning angle in condition P upon eye closure was paralleled by an increase in SO activity (although neither reached statistical significance; Fig. 2a and b). Likewise, a decrease in forward lean angle in condition D-EC (compared to D-EO) along with an increase in TA activity was also noticed (yet, not significant; Fig. 2a and c).

In condition D, there was a slow modulation of the SO EMG along the acquisition period (Fig. 3a and c), which was absent in condition P (Fig. 3b and d) and H. For the TA muscle the picture was more complex, inasmuch as it could show bursts of activity or a nearly constant basal activity (Fig. 3a and c, respectively). Half of the subjects who participated in this study presented the former sort of basal TA EMG activity (as in Fig. 3a) in all trials of condition D. An uniform activity of TA muscle was found in the remained conditions. However, in some subjects a crosstalk from the SO muscle could not be discarded in condition P (Fig. 3b and d).

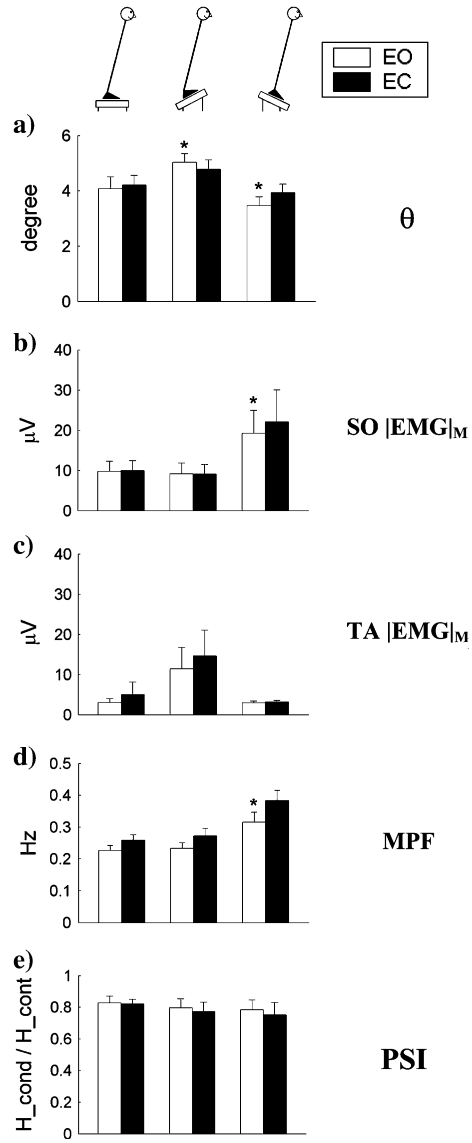

Fig. 2 **a** Leaning-forward angles (θ) in quiet stance on the three surfaces; **b** mean values of the averaged rectified SO EMG ($|EMG|_M$) from all the 12 subjects in all conditions corrected by the M_{max} factor; **c** the same as in (**b**) for the TA; **d** mean power frequencies (*MPF*) for all conditions, there was a significant effect of vision ($P < 0.05$); **e** degree of presynaptc inhibition (*PSI*) evaluated from six subjects in all conditions. *Asterisks* indicate statistical difference ($P < 0.05$) relative to control (*H-EO*). For all figures the *vertical bars* are the SEM

Spectral analysis of the CP_ap

Effect of vision

In the open eyes condition (EO) the power spectral density (PSD) showed a steady decrease starting at 0.05 Hz. In contrast, in subjects deprived of vision this decrease was less marked and the CP_ap spectrum showed higher power in frequencies starting at 0.1 Hz (Fig. 4a).

Table 1 Results of the ANOVA showing the effect of ramp inclination and vision upon the measured variables

Conditions	Independent variables				
	θ	SO	TA	MPF	PSI
H × P	*	*	n.s.	**	n.s.
H × D	**	n.s.	n.s.	n.s.	n.s.
Vision	n.s	n.s.	n.s.	*	n.s.

θ leaning forward angle, *SO* normalized EMG ($|EMG|_M$) of the soleus muscle, *TA* $|EMG|_M$ of the tibialis anterior muscle, *MPF* mean power frequency, *PSI* degree of presynaptic inhibition, *n.s.* not significant

* $P < 0.05$; ** $P < 0.01$

The PSD of the CP_ap along the frequency range was higher in the EC conditions than in the EO conditions, for all ramp inclinations, in pairwise comparison ($P < 0.05$) (except for 0.05 Hz in conditions H and P, Table 2). This means that eye closure significantly increased the power spectra in practically all the frequency range. The more gradual decrease in the PSD (as a function of frequency) in closed eyes condition was reflected on the higher MPF values: two-way ANOVA (two vision × three ramp conditions) detected a significant effect of vision ($F = 5.78$; df = 1,66; $P = 0.0190$) on MPF parameter for all ramp inclinations (Fig. 2d; Table 1). There was no different effect of vision (no interaction) for ramp conditions ($F = 0.33$; df = 2,66; $P = 0.7212$). One can notice in Fig. 4a a remarkable difference between EO and EC conditions (for all ramp inclinations) in the range of 0.1 and 0.5 Hz ($P < 0.05$). A smaller, but significant difference persisted for all frequencies up to 2 Hz ($P < 0.05$) (Table 2; Fig. 4b).

Condition P

At frequencies above 0.3 Hz (up to 2 Hz) the power of the CP_ap signal in condition P was higher than in H and D, whereas for smaller frequencies (lower than 0.3 Hz) the pattern was the other way around (Fig. 4a and b; Table 2). This spectral pattern was in consonance with the significantly higher MPF values in condition P ($P < 0.01$) (Fig. 2d; Table 1).

Downward platform inclination (P-EO) increased the MPF value approximately by 45% with respect to control condition (H-EO) (Fig. 2d). The combined effect of eye closure and downward inclination (P-EC) added 76% to the control MPF values. This was not an additive effect, since the increase observed with eye

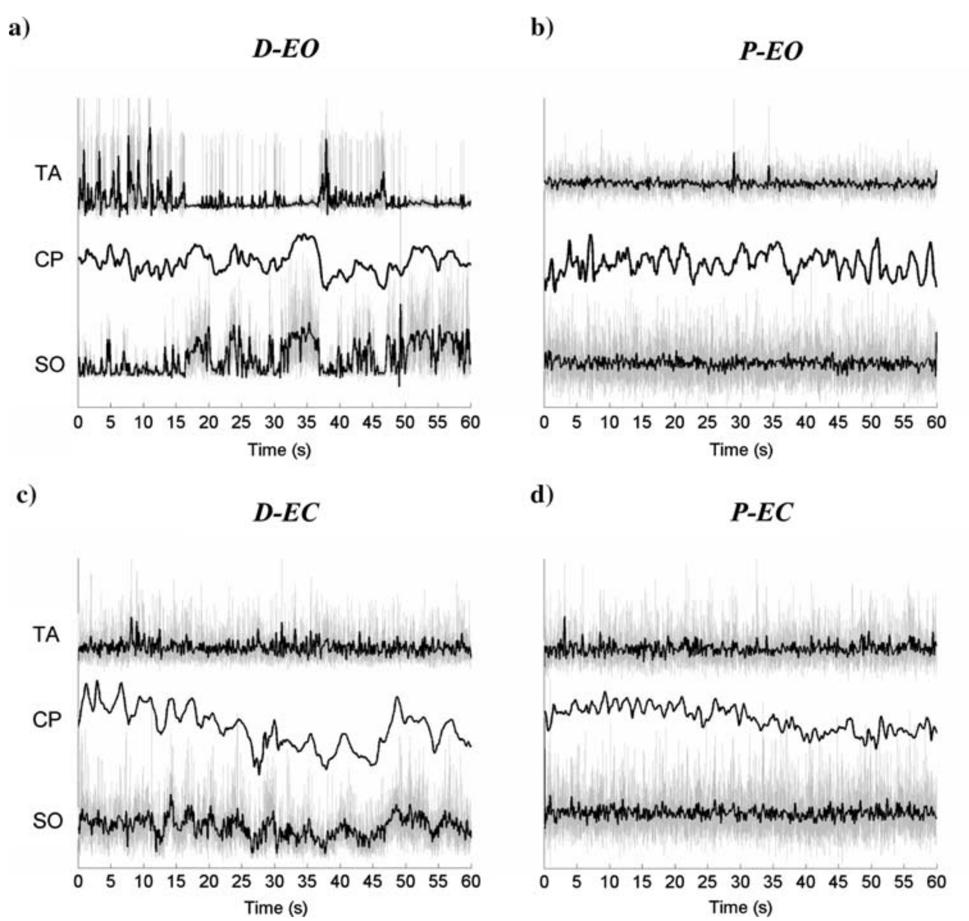

Fig. 3 Individual raw data for a qualitative analysis. In all *panels* the uppermost trace shows the rectified EMG of the TA (in *gray*) and the same signal lowpass filtered (*black*). The middle trace corresponds to the CP_ap motion (*CP*), uppward displacement means forward motion of the CP_ap. The lower trace is the SO EMG. *Panels* (**a**) and (**b**) correspond to the data obtained from one subject (in conditions D-EO and P-EO, respectively). Note the intermittent pattern of firing of the TA muscle characterized by sparse bursts in condition D-EO. *Panels* (**c**) and (**d**) correspond to data from another subject (in conditions D-EC and P-EC, respectively). Note the uniform activity registered in the SO and the increased high frequency content in the CP_ap signal in condition P (compared with condition D) irrespective of vision. Ordinates not calibrated

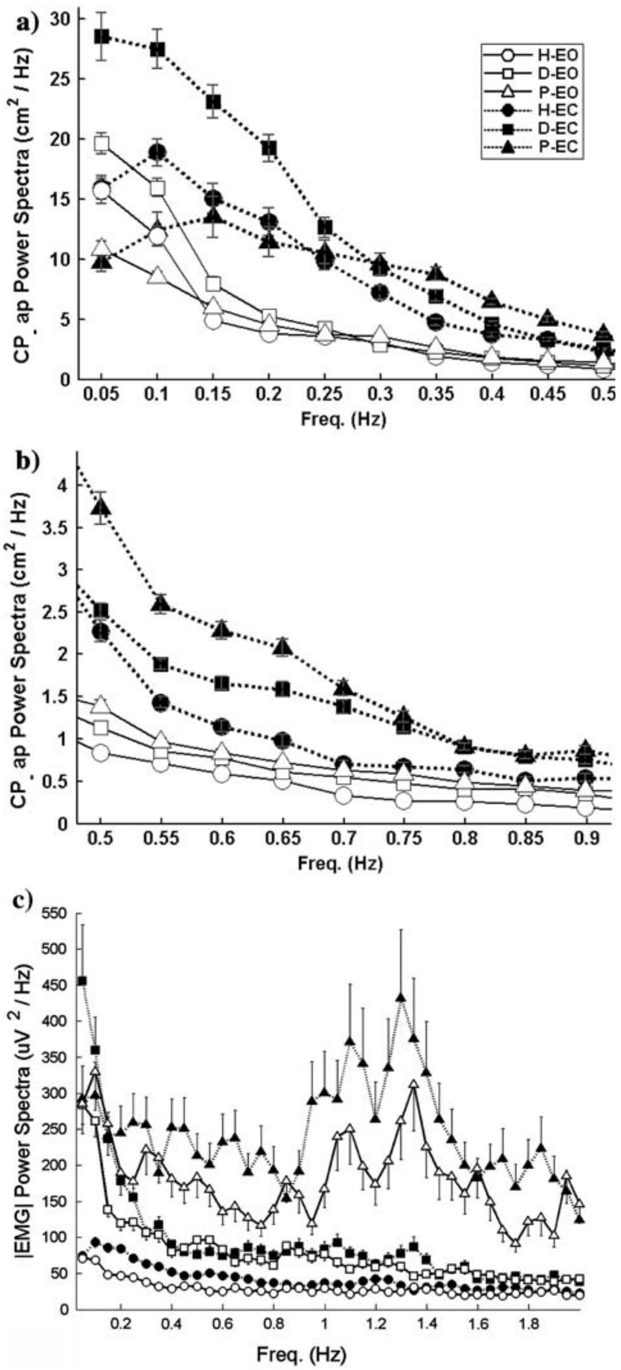

Fig. 4 Mean power spectra from 12 subjects estimated for six conditions. Spectra of the CP_ap for frequencies ranging from 0.05 to 0.5 Hz (**a**), and from 0.5 to 0.9 Hz (**b**). **c** Spectra of the SO EMG envelope. For all figures the *vertical bars* are the SEM

closure on the horizontal (H-EC compared to H-EO) was about 20% (Fig. 2d).

Condition D

The CP_ap power at low frequencies (lower than 0.3 Hz) was higher in condition D when compared to the remainder conditions (P and H), in either the presence or in the absence of vision (Fig. 4a). In condition D eye closure resulted in an increase in low frequencies, compared to the horizontal ($P < 0.05$) (last line of Table 2).

At the frequency of 0.1 Hz, for example, subjects deprived of visual input increased the power by 58% compared to the open eye condition ($P < 0.05$, Table 2; Fig. 4a). A corresponding 33% increment (not statistically significant) was observed when going from a horizontal to a toes-up ramp inclination (comparing conditions H-EO and D-EO). However, the cumulative effect of upward slope *and* lack of vision induces an increment of 130% to the power (H-EO vs. D-EC) (Fig. 4a, at 0.1 Hz), again different from an additive effect.

Qualitative analysis

Some of the general conclusions derived from the spectral analysis may be qualitatively visualized from the individual data. For example, faster components may be seen in the P condition when comparing conditions D and P directly from the raw CP_ap signals (midle trace of Fig. 3a, b or c, d).

Figure 3 also allows verifying the qualitative correlation between the EMG and the CP_ap in condition D, i.e., the slow modulation of EMG activity of the SO was correlated with the CP_ap motion. In half of the subjects the TA, in spite of its labile EMG activity, showed a negative correlation with the CP_ap (see Fig. 3a).

Spectral analysis of the SO EMG envelope

There was a significant ($P < 0.05$) increase in the power spectrum of the envelope of the SO EMG at all the frequencies tested when comparing conditions P and D with the control condition (H; Fig. 4c). In addition, in condition P there was a remarkable increase in the power at frequencies in the range from 1 to 1.6 Hz.

Presynaptic inhibition (PSI)

Each subject presented a significant PSI in all conditions tested ($P < 0.05$). In order to rule out the effect of local cutaneous afferents activated by the conditioning stimulation on the inhibition of the H-reflex, the stimulus electrode over the peroneal nerve was displaced (see ‘‘Methods’’ section). In this condition, no significant differences between control and conditioned H-reflexes were found.

Table 2 Results of the statistical *F* test for all frequencies of the average power spectrum in all conditions

Conditions	Frequencies (Hz)								
	0.05	0.1	0.2	0.3	0.4	0.5	1	1.5	2
H-**EO** × H-EC	n.s.	+	+	+	+	+	+	+	+
P-**EO** × P-EC	n.s.	+	+	+	+	+	+	+	+
D-**EO** × D-EC	+	+	+	+	+	+	+	+	+
H-EO × P-EO	–	–	n.s.	n.s.	n.s.	+	+	+	+
H-EC × P-EC	–	–	n.s.	n.s.	+	+	+	+	+
H-EO × D-EO	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	n.s.	+
H-EC × D-EC	+	+	+	n.s.	n.s.	n.s.	+	n.s.	+

n.s. not significant, *plus* (+) indicates statistical difference when the power of the chosen frequencies found in the tested condition are *greater* than those found in the control condition (H or EO, at left, in *bold*), *minus* (–) the same as (+) but when the values found in the tested conditions are *lower* than those found in the control condition

In the overall, no statistically significant differences were found in the degree of PSI in all conditions, when compared to the control (H-EO) condition. There was a small increase in the degree of PSI with eyes closed, but it did not reach statistical significance ($F = 0.40$; df = 1,30; $P = 0.53$) (Fig. 2e; Table 1).

Discussion

The experiments described herein were conducted to address the effects of static ramp inclinations and the lack of visual input on postural control dynamics. Vestibular input probably did not change when the support surface was inclined, since the average angle that each subject adopted in relation to the earth-gravity changed by a small amount (this was in fact one tenet of our experimental paradigm: alter ankle input without altering vestibular input).

Distinct spectral characteristics of the CP_ap were obtained in normal (control) and challenged postural conditions. These differences could be ascribed to alterations in the activity of sensory inputs, such as muscle and cutaneous mechanoceptors. Further potential contributing factors are the biomechanical constraints resulting from the imposed inclined surface.

The initial objective was to analyze spectral characteristics of the CP_ap signal with no a priori reference to slow and fast components. In other words, the analysis did not depart from any previously proposed theoretical framework (e.g., Bottaro et al. 2005; Zatsiorsky and Duarte 1999; Lestienne and Gurfinkel 1988). However, our results showed that the present manipulations induced differential changes at frequencies above and below about 0.3 Hz. It was inferred that these changes would reflect the action of short and long-term underlying processes of postural control. Remarkably, at 0.3 Hz there was no significant difference between ramp conditions irrespective of the presence or absence of visual input (see Table 2). Perhaps, there is an optimal efficacy of the neural feedback loops around this frequency that should be further investigated.

As pointed in Table 2, the combined effect of upward slope and lack of visual cues significantly raised the amplitude of the slow components of the postural sway (H-EC vs. D-EC), whereas the surface slope alone (with eyes open) did not cause considerable effect (H-EO vs. D-EO). Thus, the feedback loops based on the spindle afferents (and vestibular inputs) cannot cope with the demands associated with standing on an upward slope with closed eyes (condition D-EC). Therefore, the sensory reweighting did not fully compensate for the absence of vision in the upward slope, making condition D highly dependent on visual input.

The substantial stretch of the posterior leg muscles in condition D certainly caused an increase of the muscle passive stiffness. However, the following evidences suggest that subjects are unable to rely exclusively on the increased passive stiffness to achieve stability in this condition: (1) the corresponding basal activity of SO followed closely that found in the horizontal; (2) lack of vision increased the amplitude of postural sway; (3) simulation of a simple biomechanical model based on Maurer and Peterka (2005), including the representation of passive muscle stiffness, showed that increments in the passive stiffness (nominal value of 350 N m/rad) lead to a decrease in low frequency postural sway (result not shown). The model simulation results were in opposition to those obtained in our experiments. From those considerations, it follows that the increase of passive stiffness in the D condition is not the main cause of the observed changes in postural sway. The mechanisms are primarily of central origin.

Activity in the TA muscle was found chiefly in the D condition. Co-activation of triceps surae (gastrocnemius) and TA during upright stance over a horizontal plane has been reported (Sinha and Maki 1996) and could be interpreted as a specific strategy of the central nervous system. Conversely, in half of the subjects, visual inspection of the EMG signals and the CP_ap in condition D suggested an alternated activation of SO and TA, which could be interpreted as another type of postural control strategy. In addition, there was an apparent positive correlation between SO activation and CP_ap displacement (see Fig. 3a and c), as previously reported (Mezzarane and Kohn 2004), while TA presented a negative correlation (at zero delay) with CP_ap, which corroborates that SO and TA are *not* in co-contraction (Fig. 3a). One possible reason why TA activity is more prominent in the toes-up standing condition is that, from a physical point of view, this is the less stable condition for the foot with respect to a backward rotation around the calcaneus.

The analysis of the sway features in condition P pointed to a few differences from the D condition. Under the hypothesis of the existence of two processes of postural control, the spectral data suggest that long-term mechanisms acting on the control of slow postural sway (at frequencies below 0.3 Hz) would be more efficient in a toes-down condition (i.e., less sway at those frequencies).

The ankle extensor activity and the PSD of CP_ap (as well as MPF values) found during forward inclination over a level surface (Rougier 2001; Sinha and Maki 1996), resemble the current finding in condition P (in which, by the way, we found a slight backward lean). In both manipulations the main goal of the system of postural control was to preclude a potential forward fall, as indicated by the activation of the extensors and absence of activity in flexors.

The significant increase of high frequency components of the CP_ap in condition P could be ascribed to the increased SO activation leading to noise-like fluctuations in ankle joint torque (Laughton et al. 2003). This is supported by the increased power at higher frequencies (between 1 and 1.6 Hz) observed in the PSD of the SO EMG envelope (Fig. 4c). These may represent more frequent postural corrections (Maki et al. 1990), leading to a decrease in the slow postural oscillations.

Biomechanical and structural characteristics of the lower limb, such as the posterior location of the ankle joint relative to the foot, could contribute to the apparently easier equilibrium maintenance in condition P compared to conditions D and H.

Although not statistically significant, eye closure resulted in an increased forward lean in condition P that was associated with an increase in SO EMG activity (compared to eyes open condition). Similarly, in condition D-EC, as the subjects inclined less forward there was an increased TA activation (see Fig. 2a–c). Therefore, one may surmise that visual input could play a role in setting the body lean angle with respect to earth-gravity.

Our results also showed that the absence of vision affected nearly the entire range of frequencies of the spectrum and are in agreement with the findings of Duarte and Zatsiorsky (2002). It is worth noting that the profile of the CP_ap PSD is different for each ramp condition when comparing EO and EC (Fig. 4a and b), which is an indication of a nonlinear interaction between the actions of the visual and somatosensory inputs on the central nervous system (Peterka 2000; Ravaioli et al. 2005).

Proprioceptive and cutaneous input

Subjects showed different degrees of forward lean (and muscle stretch) according to the surface slope. The different leaning forward angles could indicate that subjects did not establish their set point for postural orientation based on the gravitational force vector as an absolute reference (Gurfinkel et al. 1995). Subjects very probably relied on the proprioceptive inputs arising from the leg muscles (Kluzik et al. 2005). In spite of the evidences against a significant contribution of Ia afferents to balance control in quiet upright stance (Nardone et al. 2000; Bove et al. 2006), an important role of these spindle afferents during standing on an inclined surface cannot be dismissed a priori. Indeed, the level of PSI has been shown to be greater in a neutral position of the foot as compared to either a dorsiflexed or a plantar flexed foot (Patikas et al. 2004).

The present experiments evidenced no statistically significant change in the level of PSI of the SO Ia afferent terminals across conditions, despite the change in the set point activation of the SO in condition P (i.e., increased EMG level). To compensate for this increase in the motoneuron pool excitability the stimulus to the tibial nerve was changed in the P condition to obtain a control H-reflex amplitude within 20–30% of the respective $M_{\max}$ (see ‘‘Methods’’ section). The difference between our results and those obtained in Patikas et al. (2004) is probably related to the very diffent postural conditions employed in the measurents: here the subjects were in a free standing position while in Patikas et al. (2004) the subjects were lying supine with relaxed muscles.

Viewed from a linear system standpoint, the invariance in PSI means that the correction given by the Ia-motoneuron feedback loop in response to a given perturbation will be the same irrespective of the type of slope the subjects is standing on. This result implies an absence of gain change due to modulation of the presynaptic inhibition of Ia terminals. However, oligosynaptic or polisynaptic pathways arising from peripheral afferents could have been subjected to gain changes (Iles 1996; Knikou and Conway 2001). Therefore, when our results are added to those obtained by other authors using different experiments, the general picture is that muscle spindle Ia feedback seems less important in the control of quiet upright stance in ramp conditions than feedback from other receptors.

This conclusion points to the predominant role of group II muscle afferents (and, possibly, of joint afferents) in commanding postural corrections during standing over inclined surfaces. A possible modulation of the feedback loop associated with group II afferents should not be discarded (Marchand-Pauvert et al. 2005). Indeed, there are evidences that cutaneous afferents are involved in PSI of group II terminals (Jankowska et al. 2002).

Although the effect of plantar input on postural sway in a level surface was shown to be only moderate (Meyer et al. 2004), one cannot rule out the contribution of these afferents to stance control over inclined surfaces. It could be conceivable that the imposed ramp inclination leads to a differential spatial activation of plantar afferents, which could result in specific postural responses. However, the exact contribution of plantar receptors for the balance control on inclined surfaces remains unclear and further experiments are needed to clarify their role.

As a synthesis of the discussion so far, condition P could be viewed as somewhat more stable (in terms of slow sway components) in spite of (or associated with) the increased fast components of the postural sway. One may suppose that the decrease in slow sway components would be associated with the increased gain of a medium latency stretch reflex, mediated by group II muscle afferents, compensating for the ramp inclination even in the absence of vision (compare conditions H-EC and P-EC).

Regarding condition D, the observed high amplitude in the low-frequency components of the CP_ap would be essentially associated with the corresponding biomechanical constraints. The decreased efficacy of the long-term process of postural control could justify the high sensitivity of the CP_ap (mainly at low frequencies) on the visual inputs. Therefore, in subjects deprived of vision, the balance control system could not account for the necessary fine postural adjustments based on the information inflow coming from the remaining sensory channels.

Final considerations and future directions

A number of researches have used a paradigm consisting in backward or forward voluntary inclination to investigate postural control (Riley et al. 1997; Rougier 2001; Duarte and Zatsiorsky 2002; Marchand-Pauvert et al. 2005; Bove et al. 2006). The current manipulation differs to some extent from those cited above and may provide some advantages. For instance, subjects are not performing a supra-postural task leading the body close to the stability boundary. Instead, they remain over an inclined surface without a considerable effort but still having their leg muscles differentially stretched. Therefore, there is no biomechanical-task stability trade-off that should be managed by the subjects (Riley et al. 1997), making the present approach suitable for investigating balance control in distinct motor-impaired populations (aged people, neurologic patients, etc.).

In terms of proprioceptive activation, the farthest voluntary forward lean resulted in an ankle angle of about 12° (Sinha and Maki 1986), which is smaller than the 19° observed in the present work (5° in addition to the 14° of ramp upward inclination). An increased joint angle might improve the chances of generating higher firing rates in proprioceptive muscle afferents, allowing the study of the effects of changes in these sensory inputs on balance. For instance, further studies of postural control during quiet stance on ramps of different inclinations could evaluate the influence of group II muscle afferents using the electrophysiological approaches described by Pierrot-Deseilligny (1999) and Marchand-Pauvert et al. (2005).

The present findings can also be relevant regarding the study of balance control in people wearing high-heeled shoes. Condition P is similar to that found in subjects wearing high-heeled footwear, except for the extension of toes. It could be hypothesized that women wearing high-heeled shoes would attain a more stable quiet upright stance compared to barefoot standing. This could be contrasted to the reported impairment of high heels, as compared to flat heels, on gait (Snow and Williams 1994; Kerrigan et al. 2005; Yung-Hui and Wei-Hsien 2005).

An open question yet is if standing on an inclined ramp (e.g., when waiting in a line) could result in less postural effort (e.g., overall sum of muscle activation levels or fatigue) and in a decrease of the overall energetic cost.

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