

Continuous, bilateral Achilles' tendon vibration is not detrimental to human walk

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ABSTRACT: Sensory feedback from the moving limbs contributes to the regulation of animal and human locomotion. However, the question of the specific role of the various modalities is still open. Further, functional loss of leg afferent fibres due to peripheral neuropathy does not always lead to major alteration in the gait pattern. In order to gain further insight on proprioceptive control of human gait, we applied vibratory tendon stimulation, known to recruit spindle primary afferent fibres, to both triceps surae muscles during normal floor walk. This procedure would disturb organisation and execution of walking, especially if spindles fire continuously and subjects are blindfolded. Vibration induced significant, though minor, changes in duration and length of stance and swing phase, and on speed of walking and kinematics of lower limb segments. No effect was induced on angular displacement of the ankle joint or trunk and head kinematics. This paucity of effects was at variance with the perception of the subjects, who reported illusion of leg stiffness and gait imbalance. These findings would speak for a selective gating of Ia input during locomotion and emphasise the notion that the central nervous system can cope with an unusual continuous input along the Ia fibres from a key muscle like the soleus. © 2001 Elsevier Science Inc.

KEY WORDS: Modulation, Proprioception, Spindle Ia input, Calf muscles, Achilles' tendon vibration, Gait.

INTRODUCTION

Locomotion consists of cyclic events controlled by central pattern generating networks (CPGs) located within the spinal cord. They are under the continuous influence of descending signals and peripheral input [1,23]. Proprioceptive sensory feedback from the moving limbs has repeatedly been shown to play a significant role in the regulation of the CPG activity and in the gait adaptations to the ground. For instance, in the walking system of the cat, near the end of stance, a sensory signal switches the motor command from stance to swing [22]. In general, in many vertebrate and invertebrate motor systems, the transition from one to another phase of movement is triggered by a phasic afferent signal [32]. A possible role of muscle afferent feedback is to control the level of activity in antigravity muscles during the stance phase [33]. Positive and

negative feedback pathways from proprioceptors contribute substantially to the generation of activity in extensor muscles during stance in the cat [25]. This indicates that the sensory feedback mediated by muscle afferent fibres is closely integrated into the activity of the spinal networks generating the locomotion. However, one may note that investigations made on de-afferented cats have underlined no major alteration of the basic gait pattern [23,39].

There is evidence that a spinal stepping generator exists in humans [7,16] and there is growing support for a role of sensory feedback in normal human locomotion [14,15]. However, the question of the specific implication of the various modalities in the control of locomotion is still open. For example, damage of leg afferent fibres due to peripheral neuropathy as in diabetes does not lead to major alteration in the gait pattern [11], whilst complete loss of large afferent fibres as in ganglionopathy creates major walking problems [10]. In order to get further insight into the role of proprioceptive information on human gait control, we applied vibratory stimulation to both triceps surae muscles during normal walk. Vibration is known to adequately recruit muscle spindle group Ia afferents [6,37]. The tendon vibration reflex can be induced in the soleus muscle by the continuous vibratory stimulation [40], as evidence that muscle receptors are indeed adequately stimulated by the mechanical effects of vibration. Further, the H reflex depression, occurring both during and after vibration, indicates ongoing activation of the presynaptic inhibition onto large spindle afferent fibres. In addition, when applied at around 70 Hz, vibration can lock the firing pattern of most Ia fibres to the stimulation pattern, thereby partly occluding the spindle input during the gait cycle.

Irrespective of the induced muscle activation and reflex modulation, several investigations have established that vibration produces illusory changes in joint position [17–19] or even complex drawing illusions [38]. Oriented whole-body tilt can be induced in standing human subjects by applying vibratory stimulation [17, 30]; the vibration-induced sway is then oriented according to the muscles vibrated [29]. At the same time, subjects report a subjective feeling of whole-body displacement [36]. Vibration applied to lateral neck muscles prior to walking disrupts steering of locomotion.

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tion, possibly by producing functional loss or disorientation of internal references [5]. Dorsal neck muscle continuous vibration during human treadmill walking produces an involuntary step-like increase of velocity [27]. One can then hypothesise that this intruding procedure of vibratory stimulation shall disturb at many levels the organisation and execution of walking. All the more so if the enhanced muscle-spindle firing from *both* ankle extensors persists *tonically* during the entire gait cycles instead of being normally modulated by the natural muscle length changes. In addition, in the present experiments, subjects were blindfolded, in order to avoid the visual input, which might give a reference for path length and orientation, as well as on the reciprocal position of the body segments and of the head with respect to both space and trunk.

We decided to assess the effects of vibration by looking at both the electromyographic (EMG) and kinematics pattern during floor walking. The locomotor pattern generated by the coupling of both CPGs [43] is currently thought to respect kinematic laws based on co-variations of the elevation angle of lower limb segments in a planar constraint [4,2,21]. As a matter of fact, vibration had a minor impact on both kinematics and associated leg muscle EMG pattern, an evidence of the robustness of the locomotor plant in humans. This study was partly published as a master's thesis [12].

MATERIALS AND METHODS

Protocol

Six healthy young males (age range, 20–52 years old) volunteered for this experiment as required by the Helsinki Declaration (1964). Subjects stood on a standardised starting foot position and viewed a straight black line, which ended 3.75 m directly in front of them. This distance was chosen based on preliminary trials, because it permitted a comfortable execution of six successive steps by all subjects, and they were indeed requested to reach the final position in six steps. The subjects could freely visualise the marked trajectory up to 5 s before the task. When told to go, they walked directly for the imposed distance along the path with eyes closed, at their own preferred pace. They were instructed to walk barefoot with arms folded on the chest to allow iliac crest marker recording (see below). Note that this procedure does not modify locomotor pattern [4]. Subjects started to walk with the right leg and ended the trials with the feet together. They were first asked to repeat five times the task in control condition (C). They next performed the walking trials five times again with vibration applied to both ankles (V).

Stimulation

The triceps surae muscles were bilaterally stimulated by a vibration (70 Hz) delivered to both Achilles' tendons by two mechanical vibrators, which consisted of biaxial DC motors equipped with a small eccentric mass (Dynatronic, Valence, France). Each vibrator was cylindrical in shape, 7 cm long, with a radius of 4.5 cm, and had a weight of 150 g. Each vibration cycle delivered about 5 N peak-to-peak force, as recorded by a strain gauge, to which the vibrator was attached. Vibrators were fixed to the subject's ankles with elastic bands. Vibration began with the onset of the start signal and ended when the walking task was finished (feet together). The vibrators were fixed to the tendons both during the control trials (vibrator off) and the test trials.

Experimental Set-up and Procedure

The location of the foot placements at the target was manually measured on the floor with reference to a co-ordinate system centred on the starting spot ($x = 0$ m; $y = 0$ m). The length of the

walking path was thereafter computed. The time from the start to the end of the walk was manually measured with a chronometer. Mean velocity was calculated. The position of selected points on the right hemi-body was recorded during the first whole cycle of the right leg by means of the integrated E.L.I.T.E. system (BTS, Milano, Italy). The overall spatial accuracy of the system was enhanced by using two 100-Hz television cameras placed 1.5 m above the floor, 3.5 m apart, and 3 m from the walkway. Their optical axes intersected above the first cycle location resulting in a total length of the longitudinal field of 2 m. Eight hemispherical markers were attached to the skin overlying the following bony landmarks: the lower border of the eye-socket; the meatus of the ear; the gleno-humeral joint; the iliac crest; the greater trochanter; the knee; the lateral malleolus, and the fifth metatarso-phalangeal joint of the foot (Fig. 1). The selection of landmarks and marker placement followed standard criteria and procedures for the analysis of the orientation angles of the cranio-caudal axis of each limb segment [4].

EMG activity was recorded by means of two bipolar surface electrodes from the soleus (medially, 2 cm below the insertion of the gastrocnemii) and the tibialis anterior muscle (on the belly) of the left leg. A ground electrode was placed on the wrist. EMG signals were pre-amplified, digitised, and transmitted to the remote amplifier via an optic fibre. The signals were sampled at 500 Hz and band-pass filtered (10–200 Hz). The grand average of the rectified EMG signals was computed after transformation: the EMGs of soleus and tibialis anterior were normalised with respect to the highest value recorded, for each muscle and subject, during the gait cycle acquired under control condition. After normalisation, EMG surface was separately computed for both stance and swing phase.

Data Analysis

Kinematic sampling and EMG data recordings were synchronised at rates of 100 and 500 Hz, respectively. Two-dimension kinematics was corrected for optical distortion, calibrated, and converted to 3D co-ordinates. Data were filtered with an optimal low-pass FIR filter with automatic bandwidth selection [13].

Geometric variables. The body was modelled as an interconnected chain of rigid segments as shown in Fig. 1. The orientation of a cranio-caudal axis of each segment was defined by the 3D co-ordinates of the corresponding proximal and distal end points. Thigh, leg, and foot limb segments were analysed as shown in the figure. The main axis, G , for the lower limb was defined as the segment joining the greater trochanter to the ankle [4]. The angle of elevation (α_j) of the j^{th} segment in the sagittal plane with respect to the vertical (or gravity direction) was computed as: $\alpha_j = \arctan[(x_d - x_p)/(y_p - y_d)]$, subscripts p and d denoting proximal and distal end points of the segment, respectively, and x and y denoting the horizontal and vertical co-ordinates in the sagittal plane, respectively. Elevation angles are positive in the forward direction, i.e., in the direction of walk (counterclockwise). Ankle joint angle (γ_a) was obtained from elevation angles. The $\Delta\theta_1$ and $\Delta\theta_2$ amplitudes of the j^{th} segment angular variations were calculated as the peak-to-peak angular difference between two consecutive extremes during the gait cycle. $\Delta\theta_{tot}$ was the sum of $\Delta\theta_1$ and $\Delta\theta_2$, the complete angular excursions of the limb during the gait cycle. In addition, the angular displacement of the trunk segment and the Frankfurt plane were measured by computing their mean inclination and the oscillation around these mean positions (standard deviation) during gait (see Pozzo et al. [35] for further details).

Gait parameters. Gait cycle was identified as the interval between the zero crossings of the rate of change of the elevation

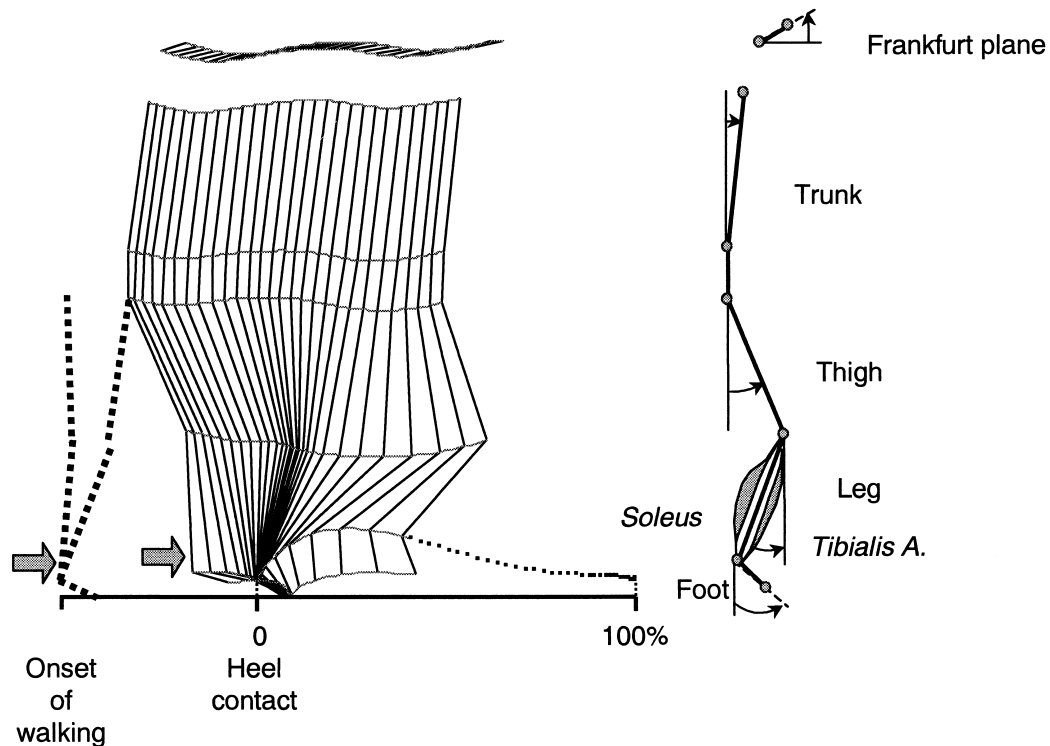


FIG. 1. Schematic illustration of the body geometry. On the right panel, the body was modelled as an interconnected chain of rigid segments identified by the markers (from top to bottom: lower border of eye-socket; meatus of the ear; the glenohumeral joint; the iliac crest; the greater trochanter; the knee; the lateral malleolus; and the fifth metatarsophalangeal). The markers identified the Frankfurt plane, trunk, pelvis, thigh, leg, and foot. On the left panel, the plotted stick diagrams (the markers placed on the right hemi-body are indicated) start before the onset of the acquired gait cycle (from 0 to 100%). The arrowheads point to the site of (bilateral) muscle vibration.

angle ($\dot{\alpha}_G$) of the limb axis G [4]. The stance and swing phases were evaluated by means of the same method. The interval between two distinct oscillation phases of the limb axis G defined the temporal parameters of gait cycle. This definition induces a stance phase duration 2–4% longer in relative percentage of the gait cycle in comparison to traditional methods. However, this procedure appeared very robust whereas criteria based on thresholds of rate of change of foot forward translation were more sensitive to measurement and biological noise. Additional parameters were: step length, S , measured as the linear translation of the greater trochanter between two identical body configurations [2], and the average speed, $vel = S/T$. In order to compare the results across subjects, a normalisation of the gait cycle duration based on 100 units was required.

Intersegmental co-ordination. The patterns of inter-segmental co-ordination of the right limb in the sagittal plane were described by the temporal co-variations of the elevation angles of the thigh, leg, and foot segments known to obey to kinematics laws [2]. The principal component analysis (PCA) was the statistical analysis employed to assess the above-mentioned patterns from the different conditions. For each set of trial data, the analysis was performed by computing the Covariance matrix D of the ensemble of time-varying elevation angles over the gait cycle after subtraction of their respective mean value. D is a real, symmetric and square (3×3) matrix that can be reduced to diagonal form with eigenvalues $\lambda_j \geq 0$ ($j = 1 \dots N$). The sum of the eigenvalues equals the sum of the variances of the original signal waveforms. The three eigenvectors u_1 – u_3 of D , rank-ordered on the basis of the corre-

sponding eigenvalues, correspond to the orthogonal directions of the maximum and minimum variance in the sample scatter. The first two eigenvectors u_1 – u_2 identify the best fitting plane of angular co-variation. The third eigenvector (u_3) is the normal to the plane whose variance tends to zero in normal gait [4]. It defines the plane orientation in the position space of the elevation angles. For each eigenvector, the parameters u_{jT} , u_{jL} , and u_{jF} correspond to the direction cosines with the positive semi-axis of the thigh, leg, and foot angular coordinates, respectively. We borrowed this procedure from Bianchi et al. [2].

Statistical Analysis

The effects of the vibration on walk were assessed by the analysis of variance (within-subjects analysis of variance [ANOVA]) and Student's paired t -test (Statistica 5.1).

RESULTS

Gait Parameters

The mean values of the general gait parameters (\pm SD) of all the subjects are displayed in Fig. 2. The average velocity of one cycle ($0.87 \pm 0.13 \text{ m}\cdot\text{s}^{-1}$ for all trial average) and of the total walk ($0.76 \pm 0.09 \text{ m}\cdot\text{s}^{-1}$ for all trial average) were similar across conditions (ANOVA, $p > 0.5$). Mean duration of both complete walk and gait cycle, obtained by averaging the means of five trials per subjects per condition, appeared to be shorter, but not significantly so (ANOVA, $p > 0.5$) for the V condition in comparison

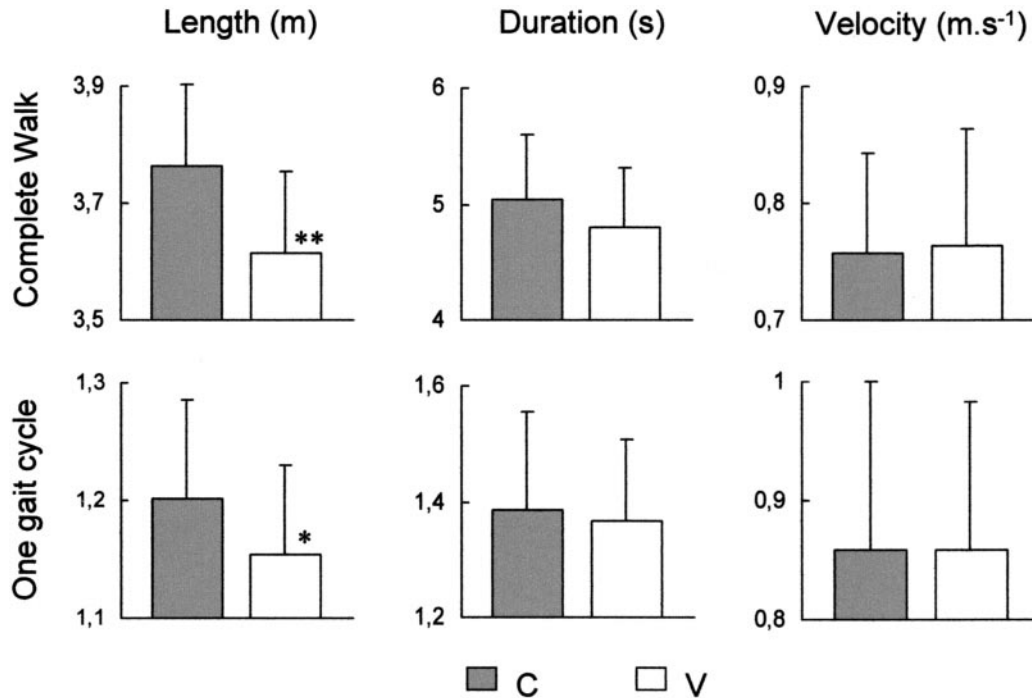


FIG. 2. Overall gait parameters. Grand averages (and their SD) of step length, walk duration, and mean velocity, calculated from all trials of all subjects under both control (C) and vibration (V) conditions. The top panels refer to the total walk, the bottom panels refer to the first whole gait cycle of the right leg. Significant differences are indicated: * $p < 0.05$; ** $p < 0.01$.

with C condition. The duration of the stance and swing phases, represented in Fig. 3, maintained the same proportion. As a consequence (and as shown in Fig. 2), a decrease in the mean length parameters was observed between C trials (120.1 ± 8 and 378.2 ± 13.9 cm for the cycle and complete walk, respectively) and V trials (115.5 ± 8 and 363.7 ± 14 cm). The vibrations induced a systematic reduction of step lengths (ANOVA, $p < 0.01$ for the total walk distance; $p < 0.05$ for the cycle length). The shortening of the step length appeared to be proportionally distributed across the entire walk, because the magnitude of the decrease of the acquired two-step cycle was about one third of the whole six-step walk.

Kinematic Parameters

Elevation angles. Changes in the geometrical configuration of the limb are described by the time course of its segment elevation angles. We considered elevation angles (α_j) in the sagittal plane only because it represents the most consistent component of the normal gait [4]. Figure 3 shows a comparison between the average time course (five trials) of the G axis and of the thigh, leg, foot elevation angles for one typical subject, following both C and V conditions during one gait cycle. This gait cycle was the first complete right leg cycle. It began with the first heel strike of the right leg.

To evaluate the effects of vibrations on the locomotor pattern, the peak-to-peak amplitude of the elevation angles were computed; these are reported for the thigh, leg, foot, and main axis G following the two conditions in the Table 1. Thigh angular variations were unchanged. Foot and leg angle amplitudes appeared weakly, yet systematically reduced with vibratory stimulation. As a consequence, because the main axis G integrates the overall variations of these elevation angles, the θ_1 , θ_2 , and global θ_{tot} amplitudes of

the former decreased significantly when vibrations were applied during the walk (paired t -test, $p < 0.05$, $p < 0.05$, $p < 0.001$, for θ_1 , θ_2 , and θ_{tot} , respectively).

This diminution of the main axis G angular amplitude was expected since this amplitude was correlated with the step length ($r = 0.75$, for θ_{tot}). Both the foot and leg elevation angles were not significantly changed by the vibration. However, the one-cycle angular excursion of the main axis G , which takes into account the above angles, was indeed significantly decreased and connected with the reduction of the stride length. One may notice that this main axis, described previously [4], appears like an appropriate tool to study the kinematic of the locomotion. In addition, Bosco and Poppele [3] have shown that the representation of cat hindfoot position-space by dorsal spino-cerebellar tract neurons could be in the polar coordinate system defined by the limb axis length and orientation, providing a physiologic validity to this tool.

Inter-segmental co-ordination. We also examined how vibratory stimulation could modify kinematic laws of inter-segmental co-ordination described previously [2]. As a matter of fact, it was found that the temporal changes of the elevation angles of the lower limb segments did not evolve independently of each others but co-varied along an attractor plane common to both stance and swing phase [2,4,21]. An illustration of this so-called co-variation plane is represented in Fig. 4, where one gait cycle is shown for one C and one V trial performed at the same velocity ($vel = 0.96 \text{ m}\cdot\text{s}^{-1}$). By plotting the elevation angles of the thigh, leg, and foot one versus the others in a 3D space, one can appreciate the regular loops thus drawn by data points during one gait cycle. The grid corresponds to the best fitting plane. In this kind of plot, time is not explicitly represented; the path progresses in the counter-

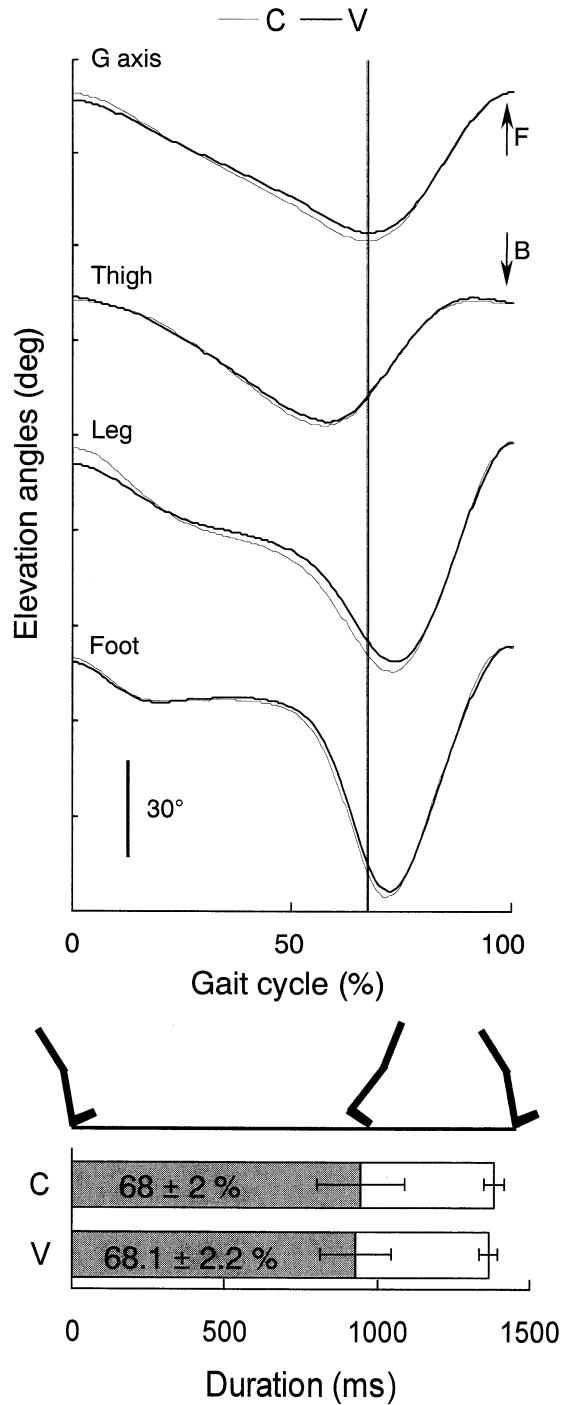


FIG. 3. Elevation angles during the gait cycle. Average of five trials for control (C; thin traces) and vibrated (V; thick traces) conditions from a typical subject. Traces from top to bottom are the elevation angles of main G axis (α_G), thigh (α_T), leg (α_L), and foot (α_F). Angle directions are indicated by the arrows (F, forward; B, backward). The stick diagram at the bottom indicates heel strikes and toe-off. Vertical thin and thick lines (almost coincident) mark the end of the stance phase for C and V conditions, respectively. Vibration induced a systematic reduction of main axis G, leg and foot elevation angles amplitudes, in particular at the end of the stance phase. The horizontal bars at the very bottom illustrate the grand averages of stance and swing phase duration. Stance phase duration as relative cycle percentage is specified in the dark stance phase bar. The duration of stance and swing phases maintained the same proportion under both control and vibration conditions.

TABLE 1

MEAN θ_1 AND θ_2 (AND THEIR SUM [θ_T] FOR THE G AXIS) AMPLITUDES (\pm SD) OF THE THIGH, LEG, FOOT, AND MAIN AXIS G OF THE RIGHT LEG DURING ONE GAIT CYCLE UNDER THE CONTROL (C) AND VIBRATION (V) CONDITIONS

Angles ($^\circ$)		C	V
Thigh	θ_1	39.4 ± 3.2	39.8 ± 3.04
	θ_2	39.8 ± 3.25	39.5 ± 2.9
Leg	θ_1	67.7 ± 4.9	66.9 ± 6.95
	θ_2	70.66 ± 3.8	70.46 ± 5.6
Foot	θ_1	75.5 ± 5.3	74.8 ± 5.9
	θ_2	79.6 ± 5.6	78.6 ± 6.3
Main G axis	θ_1	46.3 ± 3.46	$45.4 \pm 3.6^*$
	θ_2	48 ± 2.8	$46.4 \pm 3.8^*$
	θ_T	94.3 ± 6.1	$91.8 \pm 6.7^{**}$
Ankle	γ_a	24.8 ± 4	25.4 ± 3.8
Trunk inclination		5.07 ± 4.08	5.04 ± 5.4
Trunk oscillation		1.45 ± 0.64	1.42 ± 0.5
Head inclination		0.6 ± 9.5	-3.3 ± 13.6
Head oscillation		1.77 ± 0.74	2.03 ± 1.35

The main axis G peak-to-peak amplitudes appeared significantly reduced ($*p < 0.05$; $**p < 0.001$) while the vibratory stimulation was on. The peak-to-peak amplitude of the ankle joint angle (γ_a) was unchanged across conditions. The position (inclination) of the trunk and Frankfurt plane (F-P) during gait and the standard deviation around its value (oscillations) were computed separately for each trial. No differences were found in the grand averages (\pm SD) of both measurements between control and vibration conditions.

clockwise direction; heel strike and toe-off correspond to the top and bottom of the loop, respectively.

The planar regression accounts for more than 99% of the data variance over all trials for all subjects. Nevertheless, the vibration induced a significant diminution of the variance of the third component of the PCA ($0.95 \pm 0.2\%$ (C) and $0.84 \pm 0.21\%$ (V) on the average, paired *t*-test, $p < 0.05$). Therefore, the inter-segmental co-ordination emerging from coupling spinal oscillators [43] and thought to tune the efficiency of gait [2] was preserved, even enhanced, while continuous rhythmic vibratory stimulation (70 Hz) occurred at both ankle level.

In order to evaluate the 3D-position and orientation in space of the co-variation planes, the eigenvectors of the covariance matrix were computed. The first two eigenvectors $u_1 - u_2$, orthogonal, lie on the best-fitting plane. The third eigenvector u_3 is the normal to the plane and defines its orientation. This eigenvector, and more precisely its direction cosines with the positive semi-axis of the thigh (u_{3T}), has been reported as the more sensible component of the plane, in particular with speed increment and/or phase changes between the lower limb segments [2,21,27]. These mean (\pm SD) u_1 and u_3 parameters have been obtained by averaging eigenvector co-ordinates of all the subjects computed separately for each trial. u_2 is not discussed because it can be easily derived from u_1 and u_3 . On the one hand, u_1 was unmoved by vibrations (mean u_{1i} values differed by $<0.35^\circ$ across conditions). On the other, there was a systematic change of the u_{3T} component when vibratory stimulation was applied during gait. Vibrations induced a slight (u_{3T} mean value was 0.28 ± 0.06 and 0.26 ± 0.06 for C and V conditions, respectively) yet significant (ANOVA, $p < 0.05$) position displacement of the plane in the 3D space with respect to the thigh axis. To show how the plane shifts, Fig. 4 shows the plot for both conditions with respect to the same scale and orientation (trials performed at the same velocity). One can then notice that the plane

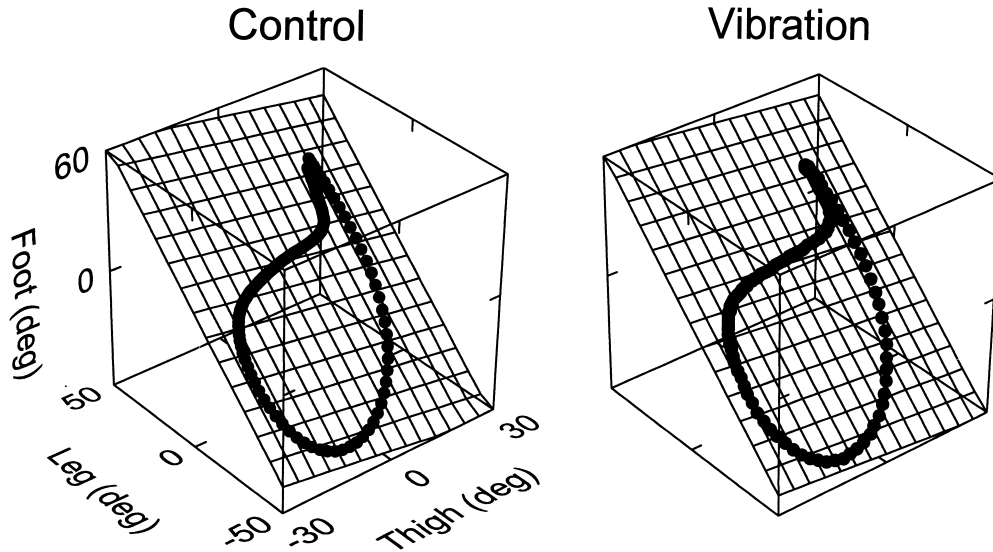


FIG. 4. Planar co-variation of elevation angles at the thigh, leg, and foot. The regular loops inside the attractor planes, obtained by plotting these angles one versus the other, concern two trials performed at the same velocity (0.96 m.s.^{-1}) under control (C; left) or vibration condition (V; right) from a typical subject. Thus expressed, the data points lie on the plane (grid) corresponding to the best fitting plane identified by u_1 – u_3 eigenvectors. The planar regression accounted for more than 99% variance for both C and V cycles. With vibration, the orientation of the plane with respect to the thigh axis shifted by 1.1° (u_{3T} decreased).

shift is connected with a change in the phase between leg and foot segments [2].

Ankle angle. The peak-to-peak amplitude of the anatomical ankle angle, identified by the markers placed on the metatarsophalangeal joint, the malleolus and the knee, during one gait cycle (see Table 1) was also computed. No significant difference was found between the C and V conditions.

Upper body. In normal gait tasks, both trunk and head are stabilized over the gait cycle [27,35]. The mean position of head and trunk during one gait cycle, and the standard deviation around head and trunk mean position were thus measured from the present data. Under control conditions, the mean head positions (Frankfurt plane) with respect to the sagittal plane were different across subjects. However, the head oscillations around this mean position was very small in every subject. The standard deviation of the angular change of the head during the cycle, for each subject and trial, was taken as a measure of this oscillation. Neither mean position nor standard deviation of the head was modified by the stimulation. The same was true for the trunk mean position in space as well as for its standard deviation. These measurements are shown in Table 1.

Soleus and Tibialis EMG Pattern

EMG patterns of the vibrated muscle and its antagonist, namely soleus (Sol) and tibialis anterior (TA) muscles, were investigated. Averages of both Sol and TA rectified EMG activity for C and V data from all trials ($n = 5$ per condition) of one typical subject are illustrated in Fig. 5 (thin and thick traces for C and V envelopes, respectively). The associated time course of the ankle joint angle is represented at the bottom. Vertical lines delimit the end of the stance phase. The overall configuration of Sol and TA envelopes is roughly unchanged during the stance phase. However, a difference between C and V TA EMGs can be systematically observed across subjects in the early swing phase, in spite of the variability of the

EMG patterns across subjects and trials, already observed in previous studies (see [39]). In order to statistically assess the EMG differences across gait phases and conditions, the area of normalized and rectified EMG activities was calculated. By looking at the EMGs histograms reported in Fig. 6, one can notice a significant (paired t -test, $p < 0.01$) vibration-induced decrease in the TA EMG activity during the swing phase of gait (77.8 ± 16.9 and 67.6 ± 15 for C and V conditions, respectively). In contrast, no difference in the TA EMG was observed between C and V in the stance phase. The soleus EMG pattern was unaffected by the vibration, either in the swing or stance phase.

DISCUSSION

Minor, though significant changes in the gait pattern were induced by bilateral continuous vibration of the extensor muscles of the leg during free, blindfolded floor walking. This was true for gait parameters like duration and length of both stance and swing phase, and for speed of walking and kinematics of lower limb segments. No effect was instead induced on angular displacement of the ankle joint, i.e., just where one would expect to see the consequences of Achilles tendon vibration. The mean angular positions of the trunk and head as well as their oscillations around their normal mean positions were not significantly affected, either, indicating that upper body balance was not affected. This paucity of effects was at variance with the subjects' perception. Indeed all our subjects reported an odd illusion of increased leg stiffness and gait imbalance: this was in keeping with known effects of vibration as applied during stance or voluntary movement, and witnesses the effectiveness of the tendon stimulation [43].

In the same line, Ivanenko et al. [28] have recently reported no major effects of triceps surae tendon vibration on treadmill locomotion without elimination of visual cues. Our data therefore partly confirm their findings, and extend the conclusions about the

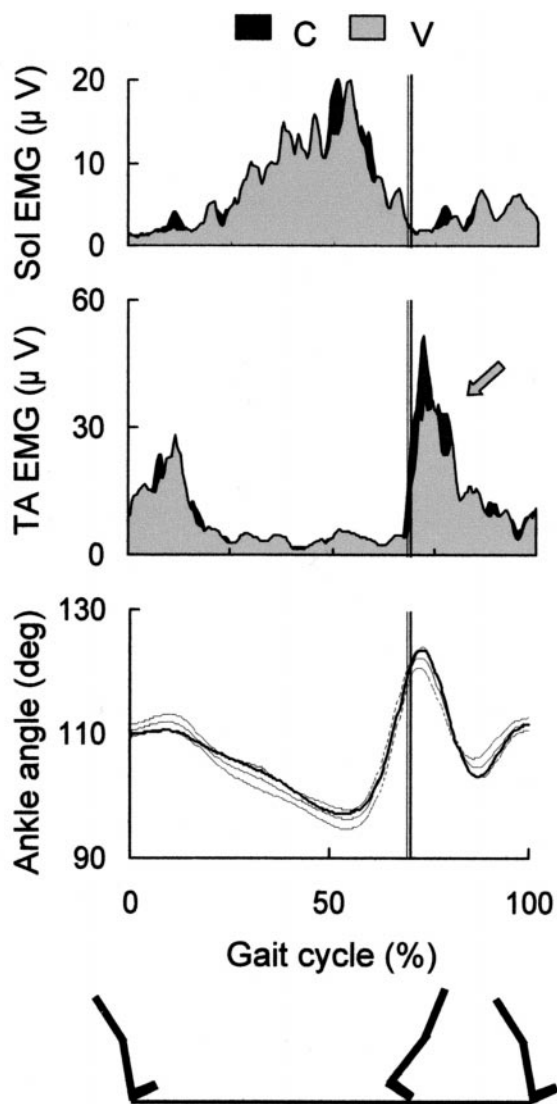


FIG. 5. Example from a typical subject of electromyographic (EMG) activity of soleus (Sol) and tibialis anterior (TA) muscles during a whole gait cycle of the right leg (average of five trials). Conventions are the same as in Fig. 3. The Sol and TA rectified and filtered EMGs are displayed at the top. The arrow indicates the decrease of the TA EMG activity during the early swing phase. The time course of the ankle joint angle (γ_a) is represented at the bottom. The thin traces correspond to the average (\pm SD) of control (C) trials ($n = 5$). The average of the vibrated (V) trials ($n = 5$, thick line) remains very close to the control trajectory.

limited effect of tendon vibration on gait to conditions of normal gait and absence of visual input.

As said above, vibration induced a consistent decrease in step length and duration. Speed was unchanged. The changes in the whole performance were mirrored by the kinematic changes observed in one complete gait cycle, and computed with reference to the analysis recently described by Bianchi et al. [2]. Computing the regression between the angles identified by the foot, leg, and thigh with respect to the vertical gave rise to a co-variation plane, with a given orientation and position in space. In our case, tendon vibration did not alter the normally high co-variation coefficient between the lower limb segments. It even produced a significant

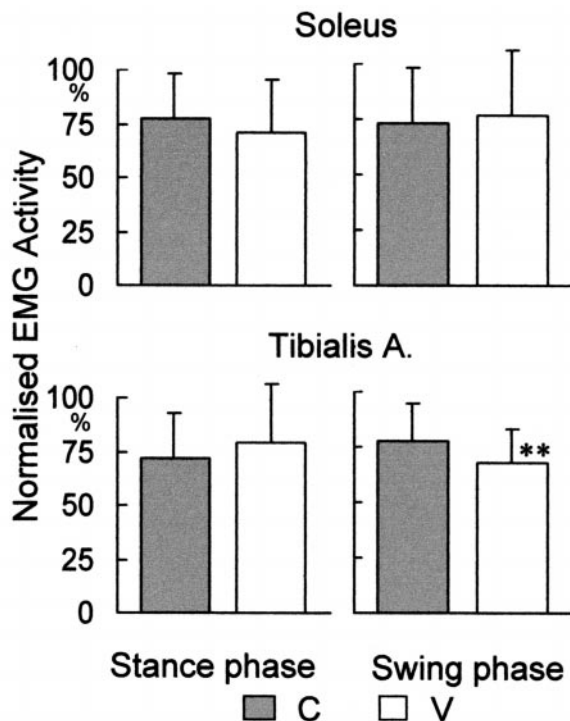


FIG. 6. Mean electromyographic (EMG) activities of soleus and tibialis anterior (TA) (all subjects collapsed). Grand average of all trials of all subjects according to conditions (EMG area is normalized). From left to right: stance and swing phases. The significant decrease of TA EMGs during the swing phase of the vibration trials is indicated (** $p < 0.01$). Abbreviations: C, control condition; V: vibration condition.

decrease of the already normally very small variance of the last component of the PCA, i.e., that connected with the inter-segmental co-ordination. A minor though significant effect in the space orientation of the co-variation plane with respect to control was also observed. The change in space orientation is explained by a decrease of the angle between the vector normal to the plane and the thigh axis (computed from u_{3T}). Bianchi et al. [2] established a negative relationship between u_{3T} and speed, possibly produced by voluntary changes in step frequency and proposed the notion that decrease of u_{3T} is associated with minimisation of energy expenditure. Therefore, in our case, where a decrease in u_{3T} was indeed observed without speed changes, vibration was obviously not impeding this process.

The absence of overriding effects of continuous vibration on gait can be discussed along several lines.

1. One might assume that the CPG gates any unwanted, or unforeseen proprioceptive input. This is likely to occur under conditions, like ours, where: (a) The locomotion was executed on a flat and solid surface, well known to the subjects. (b) Our subjects were motivated to walk from the start to the end of the planned trajectory, without paying attention to the perceptive effects of vibration. (c) The subjects had practiced the locomotion task prior to vibration (the five vibrated trials always followed the control trials, in order to get rid of any vibration after-effects on the control trials). These conditions might have minimized the effects of visual input suppression, which would otherwise have presumably worsened the effect of the vibration.

2. Our perturbation was continuous in nature, and was applied bilaterally. On the one hand this would have challenged the central nervous system (CNS) with a large mass of unwanted information. On the other, one might envisage that the afferent input from the vibration would not have been sufficient to decrease or attenuate the normally occurring phase and side modulation of the soleus proprioceptive input during the locomotion [37]. In fact, the CNS is likely to extract the necessary information from a small amplitude modulation even when this modulation is superimposed on a strong background firing. In addition, it is highly likely that the CNS might have obtained from other sources (e.g., the non-vibrated muscles) the necessary information for timing of activity and amplitude of burst activity of the soleus and tibialis anterior muscles.
3. The absence of major effects is also not surprising in the light of recent findings by Gurfinkel et al. [24], who showed that, in resting and suspended leg, continuous vibration applied to one of a few leg muscles, soleus included, induced locomotor-like patterns of EMG activity and joint angular changes. Their findings are indeed strong evidence in favour of the hypothesis that vibration-induced spindle firing has access to the CPG and can efficiently drive its alternating activity. In this light, the vibration input from leg muscles should not necessarily be seen as a disrupting perturbation.
4. Vibration is the adequate stimulus for activating the primary spindle endings, connected to the large Ia afferent fibres, but not the secondary endings, connected to the smaller diameter group II fibres [37]. Therefore, even in the case that the gait-related Ia barrage would be completely occluded, the length-modulated activity from the secondary spindle endings would be basically unaffected by the vibration. As a matter of fact, there is increasing evidence that the input from the group II spindle afferent fibres plays a major role in both upright stance and gait control [31,41,44]. The former authors have shown that group I input may not be necessary for the control of body sway, the latter authors have suggested that the group II input, but not group I, might be a good candidate in the regulation of the antigravity muscle activity during the stance phase of walking.
5. There are several indications in the literature that the soleus reflex activity in response to a synchronized Ia volley on its nerve (as tested by the H reflex in humans) is depressed during gait compared to resting conditions [8,42]. This selective gating of the autogenetic excitatory input has been recently analysed in detail in the cat, during fictive locomotion [20]. The above findings would contribute to explain why major alteration in the amplitude and pattern of Ia input was not, in our hands, detrimental to the gait pattern including the duration of the stance and swing phase. Ivanenko et al. [26] have reported that reduction in the support stability during stance diminished significantly the effect of Achilles' tendon vibration, and concluded that responses to muscle vibration depend on the support properties. They suggested that support insecurity could reset the system for equilibrium control and change the way it integrates the proprioceptive information.

The above considerations seem to be supported and extended by the analysis of the EMG recordings. As a matter of fact, in spite of the known effects of high frequency tendon vibration on EMG, recording from the soleus muscle has shown in our hands no major alterations in the normal gait-related EMG activity pattern. The duration and amplitude of the soleus EMG burst during the stance phase, as well as during the swing phase, was unchanged, despite the presumed perturbation or offset in the natural gait-related modulation of the pattern of spindle firing produced by the vibration. In particular, there was no evidence of extra activity in this

muscle, possibly related to the tonic vibration reflex. Obviously, the CPG was delivering the adequate command to the soleus pool, enough for the planned trajectory and speed of gait, in spite of any excitatory input from the periphery. Whether this would be connected to a presynaptic gating of the Ia input or to a 'wise' diminution in the strength of the command issued by the CPG to take into account the ongoing excitatory peripheral input, cannot be assessed on the basis of the present findings.

The tibialis anterior EMG activity was, however, diminished to a significant extent, but only during the swing phase of gait. This depression in activity might be the expression of the reciprocal inhibition from soleus Ia tonic (vibration-induced) input to its antagonistic motor pool. A phase-related gating of the reciprocal inhibitory effect would therefore occur during gait, and possibly be connected with the operation of the CPG. This swing-selective inhibition would possibly prevent depression of the tibialis motor pool to occur during the stance phase, when the tibialis muscle would contribute to foot fixation [9]. It would allow the inhibition to operate whenever the role of tibialis muscle activity would be less crucial for the gait progression. Such simple explanation, however, seems not to be supported by recent experiments that directly addressed this issue of the reciprocal effect in human gait [34]. In fact, a decrease in the efficacy of the reciprocal inhibition was indeed shown to take place during the swing phase. The origin of this depression in the tibialis activity would therefore to be searched in a re-programming of the command to the tibialis muscle. The soleus vibration would be interpreted by the CNS in terms of soleus lengthening [36]; in turn, the CPG might take this lengthening to mean foot dorsiflexion. To avoid 'excessive' foot dorsiflexion during the swing phase of gait, therefore, a decreased tibialis activity would be required.

To conclude, the present findings strengthen the notion of a selective, possibly pre-synaptic gating of the Ia input during locomotion. They also emphasise the notion that the CNS can adequately cope with an unusual, continuous input along the Ia fibres from a key muscle like the soleus.

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