

K.L. Sorensen · M.A. Hollands · A.E. Patla

## The effects of human ankle muscle vibration on posture and balance during adaptive locomotion

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**Abstract** This study investigated the contribution of ankle muscle proprioception to the control of dynamic stability and lower limb kinematics during adaptive locomotion, by using mechanical vibration to alter the muscle spindle output of individuals' stance limbs. It was hypothesised that muscle length information from the ankle of the stance limb provides information describing location as well as acceleration of the centre of mass (COM) with respect to the support foot during the swing phase of locomotion. Our prediction, based on this hypothesis was that ankle muscle vibration would cause changes to the position and acceleration of the COM and/or compensatory postural responses. Vibrators were attached to both the stance limb ankle plantarflexors (at the Achilles tendon) and the opposing dorsiflexor muscle group (over tibialis anterior). Participants were required to walk along a 9-m travel path and step over any obstacles placed in their way. There were three task conditions: (1) an obstacle (15 cm in height) was positioned at the midpoint of the walkway prior to the start of the trial, (2) the same obstacle was triggered to appear unexpectedly one step in front of the participant at the walkway midpoint and (3) the subjects' walking path remained clear. The participants' starting position was manipulated so that the first step over the obstacle (when present) was always performed with their right leg. For each obstacle condition participants experienced the following vibration conditions: no vibration, vibration of the left leg calf muscles or vibration of the anterior compartment muscles of the lower left leg. Vibration began one step before the obstacle at left leg heel contact and continued

for 1 s. Vibrating the ankle muscles of the stance limb during the step over an obstacle resulted in significant changes to COM behaviour [measured as displacement, acceleration and position with respect to the centre of pressure (COP)] in both the medial/lateral (M/L) and anterior/posterior planes. There were also significant task-specific changes in stepping behaviour associated with COM control (measured as peak M/L acceleration, M/L foot displacement and COP position under the stance foot during the step over the obstacle). The results provide strong evidence that the primary endings of ankle muscle spindles play a significant role in the control of posture and balance during the swing phase of locomotion by providing information describing the movement of the body's COM with respect to the support foot. Our results also provide supporting evidence for the proposal that there are context-dependent changes in muscle spindle sensitivity during human locomotion.

**Keywords** Proprioception · Centre of mass · Kinesthesia · Muscle spindle · Ia afferents

### Introduction

The adaptation of basic locomotor patterns in response to environmental demands is an integral part of human life. Control of posture and locomotion requires the monitoring and interpretation of visual, vestibular and proprioceptive sensory information by the central nervous system (CNS). This sensory information allows the CNS to determine the position and orientation of body segments with respect to both each other and the external environment. In adaptive locomotor tasks such as stepping over an obstacle, awareness of stance limb position and body orientation may be obtained, in part, from proprioceptive feedback.

Our present concepts regarding the influence of proprioception on the regulation of locomotor patterns stem largely from neurophysiological experimentation involving animals. These studies have provided evidence that

M.A. Hollands (✉)  
Department of Neurootology,  
Division of Neuroscience and Psychological Medicine,  
Imperial College Faculty of Medicine, Charing Cross Hospital,  
Fulham Palace Road, London W6 8RF, UK  
e-mail: markhollands@hotmail.com  
Tel.: +44-208-3835526, Fax: +44-208-3837577

K.L. Sorensen · M.A. Hollands · A.E. Patla  
Gait and Posture Laboratory, Department of Kinesiology,  
University of Waterloo, Ontario N2L 3G1, Canada

activation of large muscle afferents, arising from muscle spindles and tendon organs, are capable of shaping the activation of extensor muscles and the timing of locomotor patterns by signalling loading and extension of the leg (Conway et al. 1987; Forssberg et al. 1980; Grillner and Rossignol 1978; Hiebert and Pearson 1999; Hiebert et al. 1996).

One approach used in the investigation of the role of proprioception in human posture and movement is the mechanical vibration of muscles and tendons. Vibration techniques have provided valuable information concerning the role of proprioception in motor control. For example, during voluntary arm movements vibration of the lengthening antagonist muscle has been shown to significantly affect the accuracy of perception of limb position and movement (Bullen and Brunt 1986; Capaday and Cooke 1981; Cordo et al. 1995; Inglis et al. 1991). When applied to standing human subjects, muscle vibration induces different effects, ranging from illusions of self-motion to actual body tilt, depending on the nature of the experimental paradigm (Eklund 1972; Ivanenko et al. 2000b; Lackner and Levine 1979; Lekhel et al. 1997; Roll et al. 1989; Wierzbicka et al. 1998). Two main findings common to these studies are, firstly, that vibration evokes illusory sensations of movement in the same direction as the real movement that would normally produce a stretch of the vibrated muscle and, secondly, that the evoked kinesthetic illusion can be accompanied by a reflexive compensatory contraction of the vibrated muscle which can, in itself, result in changes to body posture and/or movement. It should be stressed, however, that the effects of vibration are heavily dependent on the functional role of the muscles at the time they are vibrated. For example, the effects of vibrating the leg muscles of standing individuals differ from the effects of vibrating the same muscles in walking or running individuals (Capaday and Stein 1986, 1987).

The majority of experiments employing muscle vibration techniques in man have been designed to investigate the role of proprioception in maintaining static postures or performing non-weight-bearing tasks: little is known about the contribution of proprioception to the control of human locomotion. However, Ivanenko et al. (2000a) recently published an elegant study in which they described the effects of vibrating various leg muscles on human treadmill walking characteristics. They found that vibrating the thigh muscles altered the walking speed depending on the direction of locomotion. During forward walking, vibration of the hamstring (HS) muscle resulted in an increase in the speed of walking. During backward walking, vibration of HS resulted in a reduction in walking speed whereas vibration of quadriceps resulted in a speed increase. These results led the authors to suggest that the proprioceptive input from thigh muscles may convey information about the velocity of trunk movement relative to the foot and that the changes in walking speed are compensatory adjustments in order to restore dynamic equilibrium following perception of a change in the position of the body's centre of mass (COM). There

is supporting evidence that the reflexes involved in the stabilisation of human posture are dependent upon the activity of receptors that indicate deviations of the body's COM from a neutral position within the base of support formed by the feet (see Dietz and Duysens 2000 for review). During locomotion, the COM lies outside of the base of support for the majority of each step-cycle. However the fall of the body is carefully controlled to keep the COM within the *projected* base of support under the feet (Winter 1991). This control becomes especially important during locomotion over uneven ground when the possibility of trips and falls is high. It has been demonstrated that peripheral feedback from leg muscle spindles contributes to the control of the activity of the stance limb plantarflexor muscles (Yang et al. 1991) thought to be responsible for fine-tuning both the anterior-posterior (A/P) and medial-lateral (M/L) acceleration of the body's COM during locomotion (Winter 1991). These findings suggest that the information obtained from the muscle spindles of the stance limb not only contributes to the control of lower limb kinematics but also plays a direct role in posture and balance control during locomotion.

Surprisingly, Ivanenko et al. (2000a) found vibration of the ankle muscles had little or no effect on the measured parameters. However, COM position was not measured and so the effects of vibration on balance control could only be inferred from observed changes to the measured postural parameters. Also, only analysis of body orientation and position in the A/P plane was performed and therefore investigation of the role of ankle muscles in controlling M/L COM position and acceleration was not possible. Finally, only walking on a treadmill or stepping in place was studied, neither of which accurately represent everyday walking which often requires adaptation to the basic locomotor rhythm to avoid obstacles in the travel path or reach specific goals. This is an important difference since it has been demonstrated that, in cats, Ia sensitivity and gamma dynamic drive are low during walking over level ground but can be dramatically increased during motor tasks which are either difficult or unfamiliar (Hulliger 1993; Hulliger et al. 1985, 1989; Prochazka et al. 1985). Therefore, the contributions of human ankle muscle spindle information to the control of locomotion may well increase when it is necessary to make adjustments to the basic locomotor rhythm in response to environmental demands especially if those adjustments must be made on-line in response to a changing environment.

The purpose of the present study was to investigate the contribution of proprioceptive information from the ankle muscles to the control of obstacle avoidance by perturbing, through vibration, the output of the muscle spindles of individuals' stance limbs whilst they stepped over obstacles in their travel path. The study included investigation of the relative contributions of muscle spindle information when on-line adjustment of the swing limb trajectory was required to avoid an obstacle that unexpectedly appeared in the travel path.

It was hypothesised that muscle length information from the ankle of the stance limb provides information describing location as well as acceleration of the COM with respect to the support foot during the step over an obstacle. Our prediction, based on this hypothesis was that altering ankle muscle spindle output using mechanical vibration would cause changes to the position and acceleration of the COM and/or compensatory postural responses. We also predicted that any effects of ankle muscle spindle vibration would vary with the difficulty of the locomotor task.

## Materials and methods

### Experimental set-up

The experiments were carried out in a large well-lit room along a 9-m travel path. Full-body kinematics were measured using the OPTOTRAK (Northern Digital) system. Twenty-five infra-red light-emitting diodes (IREDs) were placed bilaterally on the following anatomical landmarks of each participant: calcaneus, great toe, maleolus, patella, greater trochanter, anterior superior iliac spine, iliac crest, wrist, lateral epicondyle, acromioclavicular joint, lower ribs, xyphoid process and the ears. The IREDs were tracked using three camera arrays at a sampling rate of 60 Hz. Ground-reaction forces were collected at a sampling rate of 240 Hz, by an AMTI force platform located at the midpoint of the travel path directly in front of the obstacle.

### Protocol

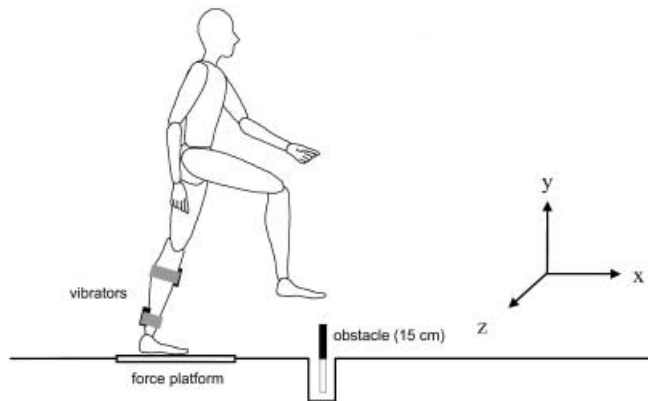
Participants were required to perform a total of 90 walking trials. For one-third of trials (30), prior to the start of the walk, an obstacle (15 cm in height) was positioned at the midpoint of the travel path. For a further one-third of trials, the same obstacle was triggered to appear one step in front of the participant. Prior to the trigger, the obstacle was hidden in a small one-inch wide slot in the floor directly in front of the force platform. The participants' starting position was manipulated so that their self-selected gait would result in the left foot landing on the force platform. The obstacle rose from this start position in the floor at a speed of 30 cm/s, when the heel of the left limb made contact with the force platform (Fig. 1). Finally, the remaining 30 control trials did not require obstacle avoidance, and the subjects' walking path remained clear. Ten trials were performed for each obstacle condition under each of the following vibration conditions: no vibration, vibration of the tibialis anterior muscle of the left leg or vibration of left leg calf muscles. All trials were randomised.

### Vibration parameters

The vibration (amplitude 2 mm) was applied at a frequency of 90 Hz using purpose-built vibrators secured to the left leg using heavy duty duct tape. Vibration was applied at the following locations: over the muscle belly of tibialis anterior and over the Achilles tendon at the level of the ankle joint. The vibrators were checked intermittently throughout the experiment to ensure that their position was unchanged. The onset of vibration was triggered by the same force platform which triggered the appearance of the obstacle. Therefore, the vibration began one step before the obstacle and continued for 1 s.

### Participants

Five healthy adults, three male and two female, ages 23–28 years, participated in the study. The experimental protocol was approved



**Fig. 1** Schematic diagram showing the experimental paradigm. In the *triggered obstacle* condition an obstacle rose rapidly ( $30 \text{ cm s}^{-1}$ ) from below floor level to a height of 15 cm when the subject stepped on a force platform placed towards the midpoint of the travel path. In the *start obstacle* condition the obstacle was visible from the start of the trial and in the *no obstacle* condition, the obstacle remained below floor level throughout the trial. Also shown are the positions at which the mechanical vibrators were attached to the left stance leg

by the University of Waterloo Ethics Committee and informed consent was given by all participants in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. Prior to participation subjects were screened to ensure that they were sensitive to muscle vibration. This was achieved by having subjects stand with their eyes closed whilst vibration was applied bilaterally to either tibialis anterior or gastrocnemius muscles at a frequency of 90 Hz and amplitude of 2 mm. The inclusion criterion was visually observable postural sway in the posterior direction in response to bilateral calf vibration *and* anterior sway in response to bilateral tibialis anterior vibration. All subjects screened met this inclusion criterion on the first attempt.

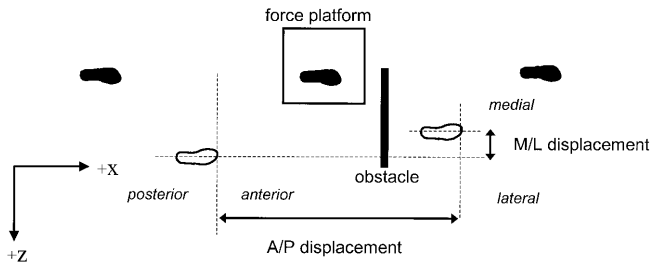
### Data analysis

The following measures were calculated at the point in time when the toe of the lead limb was directly over the obstacle (see Fig. 1): absolute COM position using a 14 linked-segment model, trunk orientation in all planes (pitch, roll and yaw), COM acceleration (derivatives were calculated using finite difference equations), and position of the COM with respect to the stance limb centre of pressure (COP) location (calculated from ground-reaction forces by the force platform), i.e. A/P COM-COP, lead limb toe elevation (vertical distance between the lead limb toe and the ground) and precision of toe elevation (log of the standard deviation calculated for each subject, obstacle and vibration level). Also peak acceleration of the COM during the swing phase was determined.

In addition the timings of step-cycle phase transitions were determined both from kinematic and force platform data (note that force plate data was only available for the left leg step prior to the obstacle). Prior to analysis, the kinematic data was smoothed using a dual-pass second-order Butterworth filter with a low-pass cut-off frequency of 6 Hz. Derivatives were calculated using finite difference equations. The times of heel contact (HC) were determined using a technique described by Hreljac and Marshall (2000). HC was defined as a local maximum in heel marker vertical acceleration determined by a zero crossing in the third derivative (jerk). Toe-off (TO) was identified as a local minimum in toe vertical displacement, determined by zero crossings in the vertical component of toe velocity. Since the zero crossings of the derivatives of the marker positions usually occurred between frames an algorithm put forth by Hreljac and Marshall (2000) was used to estimate the actual times of HC and TO.

**Table 1** Mean values of the various postural measures which showed a significant main effect due to obstacle condition. (A/P Anterior-posterior, M/L medial-lateral, COM centre of mass, COP centre of pressure)

	No obstacle			Obstacle at start			Triggered obstacle		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
A/P COM-COP (cm)	2.88	2.33	148	2.00	2.45	148	1.21	2.24	152
A/P COM displacement (cm)	64.91	8.02	146	66.89	7.11	145	70.63	7.57	149
M/L COM displacement (cm)	-0.67	1.97	146	-0.62	1.72	145	-0.17	2.02	149
Right toe A/P displacement (cm)	114.6	13.3	148	115.4	13.7	144	119.2	16.0	152
Trunk pitch (°)	6.60	3.72	148	6.97	3.73	148	7.37	4.42	152
Peak M/L COM acceleration (m/s <sup>2</sup> )	2.69	0.54	147	2.81	0.48	147	3.06	53	148

**Fig. 2** Schematic diagram showing an overhead view of the walkway and the typical footfall pattern obtained from an obstacle trial. Filled footprints correspond to the left foot and unfilled footprints to the right foot. The dotted lines illustrate the method used to calculate right foot anterior-posterior (A/P) and medial-lateral (M/L) displacement during the obstacle step. Centre of mass (COM) displacement was calculated in a similar way

The accuracy and precision of gait-event detection was evaluated through a comparison of results obtained from kinematic and force plate data. The true time of HC was defined as the time that the vertical force from the force platform rose above 10 N. Similarly, the true time of TO was defined as the time that the vertical force from the force platform fell below 10 N. The results of this analysis showed that the mean error of HC detection using kinematic data was 5.6 ms (SD=1.2 ms,  $n=10$ ) and the mean error of TO detection was 10.1 ms (SD=3.2 ms,  $n=10$ ).

Position of both feet and COM (A/P and M/L) were measured at TO and subsequent heel contact (HC) of the lead limb swing phase during the step over obstacle. This permitted calculation of the changes in M/L and A/P displacement of the feet and the COM during this step (Fig. 2).

A repeated measures ANOVA was performed on each measure. Depending on the measure, the number of levels varied; the levels are described in Results.  $P<0.05$  was considered statistically significant.

## Results

### Effects of obstacle

#### A/P COM

There was a significant main effect [ $P=0.0001$ ,  $F(2,8)=107.33$ ] of obstacle condition on mean A/P COM location with respect to COP (Table 1). The COM was significantly closer to COP (less anterior) during the triggered obstacle condition than under the no obstacle condition.

Neither A/P COM acceleration measured when the leading toe was over obstacle nor peak COM acceleration during the swing phase varied significantly with obstacle conditions.

A/P COM displacement did vary significantly with obstacle conditions [Table 1;  $P=0.0001$ ,  $F(2,8)=50.74$ ]. *Post hoc* analysis reveals that the A/P COM travelled significantly further during the course of the step when an obstacle was present than when no obstacle was present and that on average the COM travelled significantly further forward under the triggered obstacle condition than under the other conditions.

#### M/L COM

There was a significant main effect [ $P<0.05$ ,  $F(2,8)=4.5$ ] of obstacle condition on the mean M/L COM displacement (Table 1). *Post hoc* analysis reveals that the COM moved significantly less medially during the triggered obstacle condition than under the other two conditions.

There was also a significant main effect [ $P<0.05$ ,  $F(2,8)=4.8$ ] of obstacle condition on the peak M/L COM acceleration. Table 1 shows the mean peak COM acceleration for each obstacle condition. *Post hoc* analysis reveals that peak M/L COM acceleration was significantly greater whilst stepping over obstacles (both start and triggered conditions) than under the no obstacle condition and that peak acceleration was significantly greater during the triggered obstacle condition than under the start obstacle condition. There was no significant effect of obstacle condition on either the mean M/L COM location with respect to COP or the M/L COM acceleration at the point in time when the lead limb toe was over the obstacle.

### Stepping parameters

There was a significant main effect of obstacle condition [ $P<0.05$ ,  $F(2,8)=6.63$ ] on stride length (Table 1). *Post hoc* analysis revealed that the mean stride length obtained under the triggered obstacle condition was significantly longer than under the other two conditions.

Obstacle condition had no significant effect on the mean toe elevation over the obstacle. However, there was a significant main effect of obstacle condition on

the variation in toe elevation. Variability was significantly lower when the obstacle was visible from the start of the trial compared with the other two conditions (start: mean=2.4 cm; none: mean=4.0 cm; trigger: mean=4.5 cm).

### Trunk orientation

There was a significant main effect [ $P < 0.01$ ,  $F(2,8) = 6.85$ ] of obstacle condition on mean trunk pitch when the lead toe was over the obstacle (Table 1). *Post hoc* analysis revealed that the mean trunk pitch angle with respect to the vertical was significantly greater (i.e. the trunk was leaning further forward) under the triggered obstacle condition than under the no obstacle condition. Obstacle condition had no significant effect on values of trunk yaw or trunk roll.

### Success rates

Of 448 trials total, subjects hit the obstacle only 12 times to give a failure rate of 2.7%. A hit obstacle was counted if either the lead or trail limb made contact with the obstacle at any time. Of the 12 hit trials, 10 occurred during the triggered obstacle condition. The hit occurrences were distributed evenly (4 each) between the three vibration conditions.

### Summary

Manipulating obstacle characteristics had the following significant effects on postural and stepping parameters: A/P COM location with respect to COP, A/P and M/L COM displacement, peak M/L COM acceleration, stride length and trunk pitch.

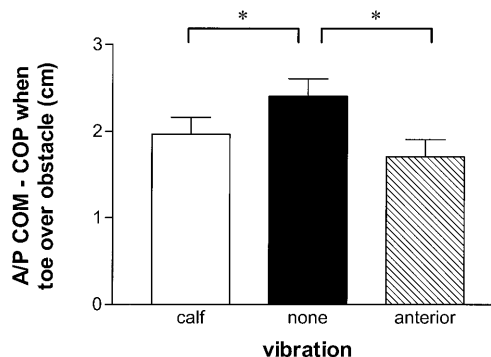
### Effects of vibration

#### A/P COM

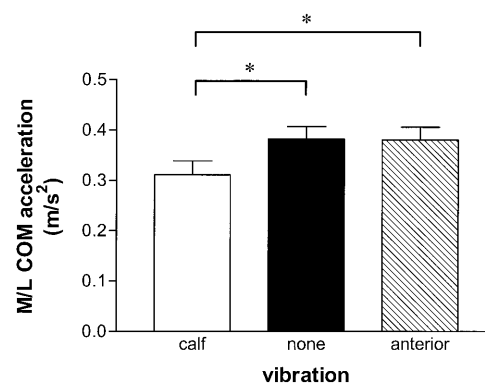
There was a significant main effect [ $P = 0.0116$ ,  $F(2,8) = 8.19$ ] of vibration on the mean COM location with respect to COP in the A/P plane when the lead limb toe was over the obstacle (Fig. 3).

*Post hoc* analysis revealed that vibrating either calf muscles or anterior compartment muscles resulted in the COM being significantly closer to the COP than under the control condition, i.e. COM is less anterior than in the control condition. There were no significant differences between mean values obtained under the two vibration conditions.

The mean values of A/P COM acceleration (peak acceleration and acceleration measured when the leading toe was over the obstacle) did not vary significantly across vibration conditions.



**Fig. 3** Bar heights represent the mean distance in the A/P plane between COM and centre of pressure (COP) when the toe was over the obstacle for each vibration condition. Asterisks represent significant differences at the 5% level. Error bars represent the standard error of the mean



**Fig. 4** Mean M/L acceleration of the COM when the toe was over the obstacle for each vibration condition. Note that all values are positive reflecting the fact that the mean direction of M/L acceleration was lateral at this point in time, i.e. away from the left stance limb

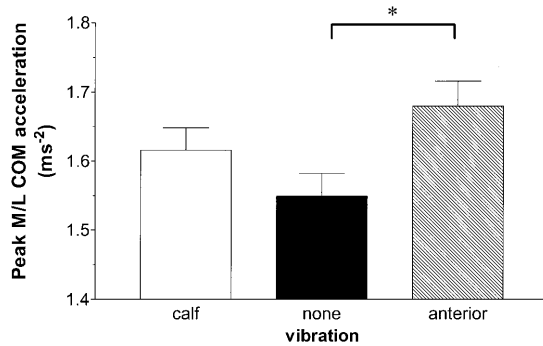
Vibration had no significant effect on the mean COM displacement in the A/P plane during the step over the obstacle.

#### M/L COM

There was a significant main effect [ $P < 0.05$ ,  $F(2,8) = 4.5$ ] of vibration on the M/L acceleration of the COM measured when the toe of the leading foot was directly over the obstacle (Fig. 4). The M/L COM acceleration in a direction *away* from the stance foot was significantly smaller during trials in which the calf muscles were vibrated than under the other conditions.

There was also a significant main effect [ $P < 0.005$ ,  $F(2,8) = 11.9$ ] of vibration on the *peak* M/L COM acceleration during the swing phase (Fig. 5). The peak M/L COM acceleration was significantly greater during trials in which the anterior compartment muscles were vibrated than during control trials (no vibration).

Muscle vibration also had a significant effect [ $P < 0.01$ ,  $F(2,8) = 8.95$ ] on the mean displacement of



**Fig. 5** Mean peak lateral acceleration of COM during the step over the obstacle for each vibration condition

COM in the M/L plane during the step over the obstacle (Fig. 6). Note that in the no vibration condition, on average, the net displacement of the COM was towards the stance foot, i.e. the COM was displaced medially (see Fig. 2).

*Post hoc* analysis reveals that the COM moved significantly less medially during steps in which the anterior muscles were vibrated than under the steps made under the other vibration conditions, i.e. vibrating anterior ankle muscles resulted in the COM being significantly more lateral at the end of the swing phase.

There was no significant effect of vibration on the mean M/L COM location with respect to COP when the lead limb toe was over the obstacle.

### Stepping parameters

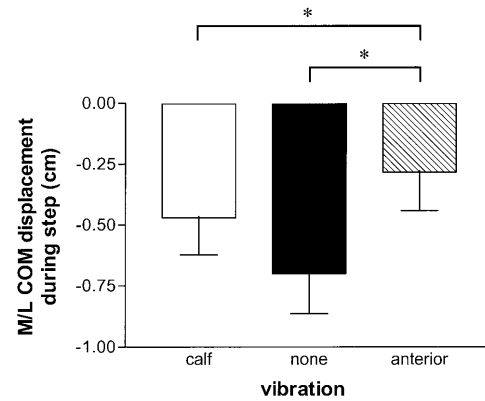
Muscle vibration had no significant main effect on the mean change in either A/P or M/L foot displacement (stride length and stride width) during the step over the obstacle. Muscle vibration had no significant main effect on either the mean toe elevation over the obstacle or the variability of toe elevation.

### Trunk orientation

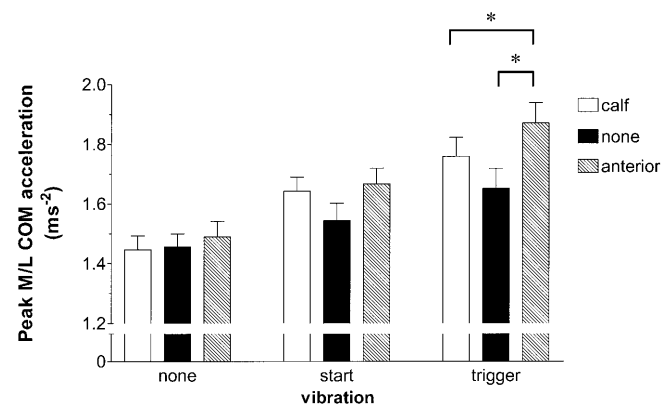
Muscle vibration had no significant effect on values of trunk pitch, yaw or roll.

### Summary

Vibrating the calf muscles resulted in significantly reduced lateral COM acceleration whereas vibrating the anterior compartment muscles resulted in significantly increased lateral COM acceleration and significantly increased lateral COM displacement. Vibration of either muscle group resulted in A/P COM being less anterior with respect to COP.



**Fig. 6** Mean M/L displacement of the COM during the step over the obstacle (right toe-off to right heel contact) for each obstacle condition. Note that all values are negative reflecting the fact that the average direction of displacement was medial, i.e. towards the left stance limb



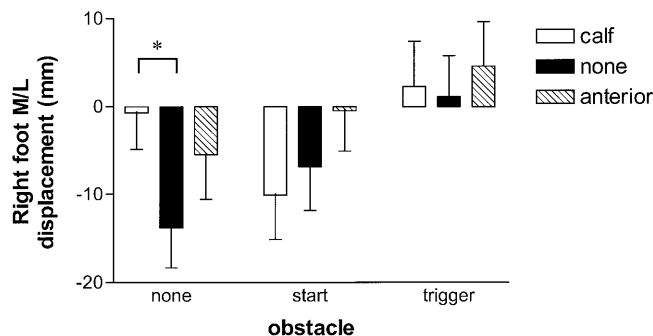
**Fig. 7** Mean peak M/L acceleration of COM during the step over the obstacle for each vibration and obstacle condition. All values are positive reflecting acceleration away from the left stance limb

### Combined effects of obstacle and vibration

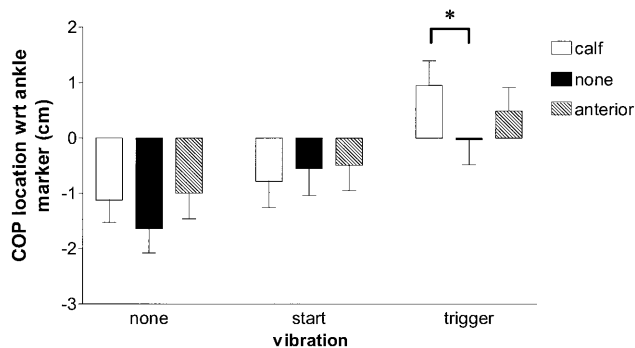
There was a significant interaction effect [ $P < 0.005$ ,  $F(4,16) = 6.28$ ] between obstacle and vibration conditions on the peak M/L COM acceleration during the step over the obstacle (Fig. 7).

*Post hoc* analysis revealed that in the triggered obstacle condition the peak acceleration was greater during anterior compartment muscle vibration than under control conditions (no vibration). Vibration had no significant effect on this parameter when there was no obstacle or when the obstacle was visible from the start of the walk. Therefore, the effect of muscle vibration on peak M/L COM acceleration varied with the locomotor task requirements.

There was also a significant interaction effect [ $P < 0.01$ ,  $F(4,16) = 4.95$ ] between obstacle and vibration conditions on the mean M/L foot displacement (change in M/L foot separation) during the step over the obstacle (Fig. 8).



**Fig. 8** Mean M/L displacement of the right foot during the step over the obstacle for each vibration and obstacle condition. Negative mean values correspond to net medial foot displacement (towards left stance foot) and positive values to net lateral foot displacement (away from left limb)



**Fig. 9** Mean location of the COP with respect to (*wrt*) the stance foot ankle marker. Positive values correspond to conditions in which, on average, COP is anterior (further forward) to the ankle marker and negative values to conditions in which the COP is posterior to the ankle marker

*Post hoc* analysis revealed that, in the no obstacle condition, the leading foot landed significantly further laterally (with respect to its position at the start of swing) during calf muscle vibration than under the control condition (no vibration).

Finally, there was a significant interaction effect [ $P < 0.05$ ,  $F(4,16) = 3.30$ ] between obstacle and vibration conditions on the mean A/P COP position relative to the stance foot (ankle marker) when the lead limb toe was over the obstacle (Fig. 9).

*Post hoc* analysis revealed that in the triggered obstacle condition the mean A/P distance between COP and ankle marker was significantly reduced during calf muscle vibration as compared with the control condition (no vibration). Vibration had no effect on this measure during the no obstacle and start obstacle conditions. Therefore, the effect of muscle vibration on A/P COP position with respect to the ankle was context-dependent.

## Summary

Vibration of anterior compartment muscles resulted in significantly increased peak lateral COM acceleration

and reduced distance between A/P COM and COP only during the triggered obstacle condition. Vibration of calf muscles resulted in significantly increased lateral foot displacement only during the no obstacle condition.

## Discussion

Ankle muscle proprioception contributes to control of adaptive locomotion

This study was designed to investigate the contribution of ankle muscle proprioception to the control of posture and balance during adaptive locomotion. It is the first study to accurately describe the effects of muscle vibration on behaviour of walking subjects' COM. It was hypothesised that muscle length information from the ankle of the stance limb provides information describing location as well as acceleration of the COM with respect to the support foot during a step over an obstacle. Our prediction, based on this hypothesis was that altering ankle muscle spindle output using mechanical vibration would cause changes to the position and acceleration of the COM and/or compensatory postural responses. Our results clearly demonstrate that vibrating the ankle muscles of the stance limb during the step over an obstacle results in changes to both COM behaviour in the M/L and A/P planes and stepping behaviour associated with COM control.

Yang et al. (1991) demonstrated that the application of small rapid stretches to the calf muscles, contributed 30% to 60% of the activation of the soleus muscle during the early part of the stance phase. Since the majority of the variance in the EMG response could be accounted for by a mathematical model based solely on velocity of the perturbation, the authors suggested that a velocity-sensitive element contributes substantially to the activation of the soleus muscle during locomotion. In our experiment vibration of the calf muscles (which has been shown in cats to alter velocity-sensitive spindle output in a similar manner to real stretches; Hiebert et al. 1996) resulted in a smaller difference between stance foot A/P COM and COP. It is possible that this resulted directly from a spinally mediated reflex increase in plantarflexor activity (due to their perceived stretch) which, in turn, resulted in the COP being more anterior and therefore closer to the COM. Indeed our results show that in the triggered obstacle condition, vibrating the calf muscles resulted in the COP being more anterior with respect to the stance foot ankle marker when the lead limb toe was over the obstacle.

Calf muscle vibration also produced significant changes in M/L COM behaviour. Calf muscle vibration resulted in significantly smaller lateral COM acceleration when the leading toe was over the obstacle, i.e. the acceleration of the COM away from the stance limb was reduced. It is possible that this resulted from compensation for an erroneous interpretation by the CNS that the COM was more lateral than it should be. This conclusion

is supported by the finding that vibration of the calf muscles resulted in participants increasing their step width at heel contact (in the no obstacle condition). This would have had the effect of placing the leading foot in a more lateral position with respect to COM. Since the difference between COP and COM during swing dictates COM acceleration in the M/L plane (McKinnon and Winter 1993; Winter 1995), adopting this strategy would increase medial COM acceleration during the *subsequent* swing phase to compensate for the CNS interpretation that the COM was more lateral than it ought to be. This interpretation by the CNS would result from vibration-induced changes to the output of inverter muscle spindles which would normally only occur in response to inverter muscles being stretched. Although none of the posterior compartment muscles act as evertors, foot eversion is the main action of adjacent lateral compartment muscles (fibularis longus and fibularis brevis). Therefore it is possible that the lateral compartment muscles are also affected by vibrating at the Achilles tendon and it is changes in muscle spindle activity in these muscle groups that are responsible for the resulting changes in M/L COM behaviour.

Anterior compartment muscle vibration also had a significant effect on the position and acceleration of the COM in the both the A/P and M/L planes. Since the tibialis anterior muscle attaches distally to the medial and inferior surfaces of the medial cuneiform bone and the base of the first metatarsal it both dorsiflexes and inverts the foot. Therefore one would expect perceived lengthening of this muscle due to mechanical vibration to be interpreted by the CNS as foot plantarflexion and eversion. The correct compensatory response therefore would be to invert and dorsiflex the foot. Stance limb foot inversion and dorsiflexion would caused the body (and therefore the COM) to move to a position more lateral and more anterior (further forward) with respect to the stance foot. As predicted, anterior muscle vibration resulted in the COM moving more laterally during the step over the obstacle, i.e. the body was pushed further away from the stance limb. This is attributable to a greater peak COM M/L acceleration in the lateral direction during the swing phase. Surprisingly, vibration of the anterior compartment muscles also resulted in the location of the A/P COM being *less* anterior with respect to the COP of the stance foot. This unexpected result can also be explained by the putative effects of vibration on lateral compartment muscles. The lateral compartment muscles have a weak plantarflexor action on the foot in addition to their main role as evertors whereas the anterior compartment muscles are primarily dorsiflexors and weak invertors. Therefore, anterior vibration may well produce conflicting information from different muscles describing the orientation of the foot with respect to the leg. It is possible that when faced with this conflict the CNS relies on other sensory modalities (such as vision or vestibular input) to determine an appropriate response. The fact that there were no significant changes to COP position with respect to the ankle marker in response to

anterior muscle vibration suggests that the changes to COM position are due to a body postural response rather than a segmental reflex resulting in increased plantarflexion.

#### The relationship between COM/COP position and COM acceleration

Previously it has been demonstrated that during normal straight path walking there is a significant relationship between COM-COP (COM position with respect to the COP) and COM acceleration in both the frontal and sagittal planes (McKinnon and Winter 1993; Winter 1995). The body acts as an inverted pendulum and the distance of the COM from the base of support determines the rate at which the body falls under the influence of gravity (Winter 1995). In the present study we observed vibration-induced changes to COM-COP that were not accompanied by corresponding changes to COM acceleration and vice versa. It should be noted, however, that during walking foot placement is the primary determinant of COP position. Although COP position within the stance foot is likely to change in response to contraction of ankle muscles, the resulting change in COM-COP is unlikely to be large enough to make a significant change to COM acceleration. Our results clearly show that there were significant changes in COM-COP in response to posterior and anterior ankle muscle vibration and attributable to a significant posterior shift in COP location due to ankle plantarflexion. Although this vibration-induced change in ankle rotation was large enough to cause detectable changes in COP location it was not large enough to produce significant changes to COM behaviour.

The fact that we *did* observe vibration-induced changes in M/L COM acceleration without changes in COM-COP suggests that stance ankle muscle inversion/eversion does not result in significant changes to M/L COP location. While the relationship between COP-COM and COM acceleration is significant during walking, it is not perfect due to the nature of the body segment movements. This lack of perfect inverted pendulum during locomotion may result in observed changes in COM acceleration but may not be reflected in the COP-COM measure.

#### Nature of afferent information

Neurophysiological studies indicate that out of the three types of proprioceptor found in skeletal muscle (primary and secondary muscle spindle endings and Golgi tendon organs) by far the most sensitive to vibration are the primary endings, the activity of which is mainly related to velocity of changes in muscle length (Burke et al. 1976; Goodwin et al. 1972; Roll and Vedel 1982; Roll et al. 1989). Secondary-ending (type II afferents) and Golgi tendon organs are generally much less sensitive than primary endings and respond only to low frequency



(<60 Hz) and large amplitude vibration (Burke et al. 1976; Roll and Vedel 1982; Roll et al. 1989). Indeed, it has been demonstrated that vibration of iliopsoas and extensor digitorum longus muscles of the cat during locomotion produced similar effects to those produced by muscle stretch or by electrical stimulation of the Ia afferents (Hiebert et al. 1996). However, it should be noted that during locomotion there are phasic changes in sensitivity of the stretch reflex pathway in the plantarflexor muscles (Capaday and Stein 1986; Schneider et al. 2000). The amplitude of the H-reflex increases during the stance phase in a ramp-like fashion in parallel with soleus EMG and is strongly suppressed or completely inhibited during swing. In late stance the amplitude of the evoked H-reflex is in fact substantially larger than that evoked using the same stimulus during quiet standing (Schneider et al. 2000). Our vibration stimuli were administered at the onset of the stance phase and lasted for at least 1 s. Therefore, the muscle spindles were being stimulated over a time when they were at their most sensitive. Therefore, it is reasonable to conclude that in the present experiment the main effect of vibration (at a frequency of 90 Hz and amplitude of 2 mm) was to change the activity of Ia afferents.

#### Context-dependent effects of muscle vibration

It is well established that the characteristics of ankle muscle spinal reflexes are strongly dependent on the motor task (Capaday and Stein 1986, 1987; Edamura et al. 1991; Llewellyn et al. 1990; Morin et al. 1982). For example, at similar levels of EMG activity, the amplitude of the soleus H-reflex is much greater during standing than during the early part of the stance phase of walking (Capaday and Stein 1986; Morin et al. 1982). Also, it has been clearly demonstrated in cats that Ia sensitivity and gamma dynamic drive are low during walking over level ground but can be dramatically increased during motor tasks which are either difficult or unfamiliar (Hulliger 1993; Hulliger et al. 1985, 1989; Prochazka et al. 1985). Therefore, the contributions of ankle muscle spindle information to the control of locomotion in man may well increase when it is necessary to make adjustments to the basic locomotor rhythm in response to environmental demands especially if those adjustments must be made on-line in response to a changing environment. One objective of this study was to determine if the effects of ankle muscle vibration vary with the difficulty of the locomotor task. Therefore, in addition to trials in which participants were required to step over an obstacle that they could see from the start of the walk, we included trials in which on-line adjustment of the swing limb trajectory was required to avoid an obstacle that unexpectedly appeared in the travel path. We also included control trials in which no obstacle appeared. We predicted that any effects of ankle muscle spindle vibration would be greatest during on-line adjustment of locomotion (in which the threat to stability is greatest).

We found a significant interaction effect between obstacle and vibration conditions in the peak lateral acceleration of the COM during the step over the obstacle. The only significant vibration effect was during trials in which the anterior compartment muscles were vibrated whilst participants stepped over an obstacle that unexpectedly appeared one step in advance. Vibration had no significant effect when there was no obstacle or when the obstacle was visible from the start of the walk. We found another interaction effect between obstacle and vibration conditions in the mean location of the COP with respect to the stance foot ankle marker. Again, vibration of the anterior compartment muscles did have an effect, but only during the triggered obstacle condition. Although, it is hard to explain the functional significance of the finding that only vibration of anterior compartment muscles had an effect on these measures in the triggered obstacle condition, one possibility is that reducing lateral and anterior COM acceleration (as would be predicted by calf muscle vibration) would compromise the successful completion of the adaptive step. Therefore, these responses may be selectively gated out by the CNS when the perceived threat of instability is greatest.

Because of our experimental design, during both the triggered and no obstacle conditions the participants were unaware of whether they would be faced with an obstacle until the last possible moment (onset of the stance phase of the support foot). However, the subjects knew the exact location of the hidden obstacle and how high it would be were it to appear (same height as in start condition). The subjects could theoretically make the same stepping movement at the obstacle irrespective of the obstacle condition and successfully complete the task. The fact that there was no significant difference in the mean toe elevation between obstacle conditions supports this theory. However, there *were* significant effects of obstacle condition on posture (mean A/P COM location with respect to COP, mean change in both A/P and M/L COM location, mean stride length and mean trunk pitch) which clearly demonstrates that participants were making on-line postural adjustments in response to obstacle appearance.

These results lend strong support to the notion that the contributions of ankle muscle spindle information to the control of locomotion increase when it is necessary to make adjustments to the basic locomotor rhythm in response to environmental demands, i.e. there is context-dependent variability in the role of human ankle muscle spindles.

Surprisingly, there was also a significant interaction effect between obstacle and vibration conditions in the change in step width during the swing phase of the obstacle step, i.e. change in the M/L displacement of the right foot between TO and subsequent heel contact. *Post hoc* analysis revealed that the only significant vibration effect was in the no obstacle condition whereby calf muscle vibration resulted in a significantly greater mean step width than the control condition (no vibra-

tion). This selective effect could have resulted from the sensitivity of ankle muscle spindles during the no obstacle condition being greater than during the two obstacle conditions. However, it is not clear why this would occur. It is, therefore, hard to explain the observed significant effect in the no obstacle condition in terms of increased difficulty. Nevertheless, the finding that there were significant effects of vibration on stepping behaviour in one obstacle condition but not in others lends further support to the notion that there are significant context-dependent differences in the effects of vibration on the stepping parameters of locomotion.

### The way forward

Although our methodology did not allow determination of which muscles were being activated in response to vibration we can state confidently that vibration of the ankle muscles evokes significant changes in both COM location and acceleration and stepping behaviour implicated in its control. The non-reciprocal effect of vibration in the A/P plane on COM and stepping behaviour may be a result of non-postural responses to muscle vibration, such as changes to ankle joint muscle stiffness. Nevertheless, the fact that there is reciprocal direction-specific effect of vibration in the M/L plane (posterior muscle vibration reduces lateral COM acceleration whereas anterior muscle vibration increases peak lateral COM acceleration) lends strong support to the notion that information obtained from the proprioceptors of the stance limb plays a direct role in posture and balance control during locomotion. In order to fully understand the complex effects of ankle muscle vibration on adaptive locomotion as observed in the present study, there is a clear need for further studies including determining through electromyography the specific muscles that are activated by muscle vibration.

### Conclusions

The results of our experiment provide strong evidence that the primary endings of ankle muscle spindles play a significant role in the control of posture and balance during the swing phase of locomotion by providing information describing the movement of the body's COM with respect to the support foot. Our results also provide supporting evidence for the proposal that there are task-dependent changes in muscle spindle sensitivity during human locomotion.

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