Somatosensory & Motor Research

http://informahealthcare.com/smr
ISSN: 0899-0220 (print), 1369-1651 (electronic)

Somatosens Mot Res, Early Online: 1–8
© 2014 Informa UK Ltd. DOI: 10.3109/08990220.2014.949007

informa healthcare

ORIGINAL ARTICLE

Impact of altered lower limb proprioception produced by tendon vibration on adaptation to split-belt treadmill walking

Charles S. Layne[1,2,3], Amber M. Chelette[1,2,3], & Amir Pourmoghaddam[2,3,4]

[1]Department of Health and Human Performance, University of Houston, Houston, Texas, USA, [2]Center for Neuromotor and Biomechanics Research, Houston, Texas, USA, [3]National Center for Human Performance, Texas Medical Center, Houston, Texas, USA, and [4]Department of Orthopedic Surgery, University of Texas Health Science Center at Houston Medical School, Orthopedic Surgery, Houston, Texas, USA

Abstract

It has been proposed that proprioceptive input is essential to the development of a locomotor body schema that is used to guide the assembly of successful walking. Proprioceptive information is used to signal the need for, and promotion of, locomotor adaptation in response to environmental or internal modifications. The purpose of this investigation was to determine if tendon vibration applied to either the hamstrings or quadriceps of participants experiencing split-belt treadmill walking modified lower limb kinematics during the early adaptation period. Modifications in the adaptive process in response to vibration would suggest that the sensory–motor system had been unsuccessful in down weighting the disruptive proprioceptive input resulting from vibration. Ten participants experienced split-belt walking, with and without vibration, while gait kinematics were obtained with a 12-camera collection system. Bilateral hip, knee, and ankle joint angles were calculated and the first five strides after the split were averaged for each subject to create joint angle waveforms for each of the assessed joints, for each experimental condition. The intralimb variables of stride length, percent stance time, and relative timing between various combinations of peak joint angles were assessed using repeated measures MANOVA. Results indicate that vibration had very little impact on the split-belt walking adaptive process, although quadriceps vibration did significantly reduce percent stance time by 1.78% relative to the no vibration condition. The data suggest that the perceptual–motor system was able to down weight the disrupted proprioceptive input such that the locomotor body schema was able to effectively manage the lower limb patterns of motion necessary to adapt to the changing belt speed. Complementary explanations for the current findings are also discussed.

Keywords

Coordination, gait kinematics, proprioception, split-belt treadmill, vibration

History

Received 14 May 2014
Revised 17 July 2014
Accepted 17 July 2014

Introduction

Walking is a goal-directed task that generally requires little conscious effort but does require precise proprioceptive information to successfully navigate the environment. To effectively locomote within an environment, it has been proposed that we rely on an internal representation of our body segments in relation to one another and the external world: a concept labeled locomotor body schema (Ivanenko et al. 2011). This schema can serve to promote both the planning and actualization of movement. Appropriate adaptation to novel external and sensory environments is a hallmark of effective locomotion with adaptation being promoted through the interaction of sensory input and a dynamic locomotor body schema.

An important input for the development and utilization of a locomotor body schema is that of proprioception which serves to provide information about the position of the body segments both in space and in relationship to one another. Based on the fact that tendon vibration preferentially activates the Ia afferents of the muscle spindle (Roll et al. 1989), it is reasonable to speculate that vibration may distort the locomotor body schema thereby leading to inefficient adaptations while walking. During static postural tasks, vibration has been shown to result in significant postural sway when applied to ankle and neck musculature. Vibration illusion is the most commonly accepted explanation for the motion that results from tendon vibration. In this phenomenon Ia spindle stimulation leads to an interpretation that the vibrated muscle is being stretched. The response to that perceived stretch is muscle contraction and the associated motion about a given joint (Albert et al. 2006). For example, Achilles tendon vibration results in backwards sway as the gastrocnemius and soleus muscles contract in response to the perceived stretch.

Correspondence: C. S. Layne, Department of Health and Human Performance, University of Houston, 3855 Holman Street, 104 Garrison, Houston, TX 77024, USA. E-mail: clayne2@uh.edu

Tendon vibration has been used to provide a potentially disruptive proprioceptive influence during both overground and treadmill locomotion with mixed results. Courtine et al. (2001) found little or no change in lower limb *kinematics* during overground locomotion in response to soleus muscle vibration, although in another study biceps femoris vibration resulted in veering off of a straight line path during overground walking in some subjects (Courtine et al. 2007). Conversely, Verschueren et al. (2002) reported changes in lower limb joint motions during overground walking in response to ankle musculature vibration and quadriceps vibration during specific points within the gait cycle. Ivanenko et al. (2000a) reported that biceps femoris vibration significantly modified the walking speed of subjects walking on a treadmill with a constant belt speed. Other investigators (Sorensen et al. 2002) have also reported context-specific changes in center of mass motion in response to vibration during an overground walking task but only when unexpected obstacles appeared in the walkway. Collectively, these findings involving the use of tendon vibration suggest that the influence of vibration is context specific and that integration of proprioception may be selectively ‘‘weighed’’ thereby increasing or decreasing its influence upon the locomotor body schema and subsequent segmental motion. Consequently, there remains an open question as to under what conditions tendon vibration may impact gait kinematics.

Neurophysiological mechanisms associated with the regulation of afferent input associated with gait have been shown to be context dependent. It has been demonstrated that Ia input is often important for the control of gait, particularly in a phase-dependent manner (Sinkjaer et al. 1996; Kearney et al. 1999; Verschueren et al. 2003; Donelan and Pearson 2004). However, depending upon circumstances, other mechanisms can increase their contributions to the control of gait, including those associated with load regulation (af Klint et al. 2010b). This flexible use of afferent input during gait control serves as the neurophysiological basis of the construct of sensory input ‘‘weighting’’.

An increasingly popular technique used to investigate adaptive features of gait is split-belt treadmill walking. Split-belt walking requires that one lower limb move at a different rate to maintain a functional gait pattern that ensures dynamic equilibrium. The adaptation of kinematic parameters to split-belt walking has been reported to include an early adaptive phase consisting of changes in percent stance time and stride length and a later, continuously evolving adaptive phase, resulting in changes in double support time and step length (Dietz et al. 1994; Reisman et al. 2005). Previous authors have suggested that the ‘‘early’’ period of adaptation (i.e., the first five steps after the split) is primarily regulated by spinal mechanisms with longer term adaptation being more heavily mediated by supraspinal processes (Dietz et al. 1994; Reisman et al. 2005, 2007; Morton and Bastian 2006; Choi et al. 2009).

The adaptive kinematics during split-belt locomotion of several patient populations have been investigated (Morton and Bastian 2006; Reisman et al. 2007; Choi et al. 2009) but the possible impact of disordered proprioception as generated by tendon vibration on the ‘‘early’’ adaptive processes associated with split-belt walking has not yet been explored. The purpose of this investigation was to investigate the possibility that disordered proprioception generated by either hamstring or quadriceps tendon vibration influenced the early adaptive period when spinal processes have been suggested to dominate the adaptation process. The results are consistent with the suggestion that the perceptual–motor system has the ability to immediately and effectively ignore potentially disruptive sensory input as it adopts the lower limb kinematic patterns to successfully adapt to split-belt locomotion.

Materials and methods

Subjects

The subjects for this study were 10 healthy, young adults (mean age = 26.7, SD = 4.3, 5 females) who provided informed consent in accordance with the Committee for the Protection of Human Subjects at the University of Houston. All subjects were right footed as assessed by being asked to kick a ball that was rolled to them (Sadeghi et al. 2000).

Protocol

The basic split-belt walking protocol included walking for 1 min with the belts at the same speed, followed by 5 min of walking with the two belts at different speeds, and finally 1 min of walking with the belts returned to the same speed.

The experiment consisted of three conditions that were counterbalanced across subjects and conducted with the eyes closed: (1) walking, no vibration (W), (2) walking with hamstring vibration (WH), and (3) walking with quadriceps vibration (WQ). All subjects completed each condition a single time (i.e., trial). Vibration was initiated just prior to the start of the treadmill and remained on during the entire walking trial. Previous studies have indicated that the impact of tendon vibration is greatest on movement control when vision is removed (Ivanenko et al. 2000b; Mohapatra et al. 2012).

Procedures

Prior to conducting the experiment, each subject was trained to walk on the treadmill (both belts moving at the same self-selected comfortable walking speed) while blindfolded until the variability of their lower limb joint kinematics was determined to be within at least one standard deviation of that obtained during eyes open treadmill walking. No vibration was applied during the training required to learn to walk blindfolded on the treadmill nor were subjects being exposed to the two belts moving at different speeds (i.e., split-belt walking). No subject required more than three 20-min training sessions, conducted on separate days, to reach the accepted criterion. After the training period, participants returned to the laboratory on the next day for testing. During the testing, the initial tied-belts speed (i.e., same speed) was 20% less than the self-selected speed. When the belts split, the speed of the left belt was doubled while the speed of the right belt remained unchanged. The left belt was returned to the initial speed to complete the trial. Vibration was applied at 70 Hz (VB 115, Techno-Concept, Cerest, France) over either the tendon of the quadriceps, approximately 6 cm superior to the center of the patella, or the belly hamstring musculature, approximately 10 cm above the femoral epicondyles of the left leg. The vibrators were secured perpendicular to the direction of the fibers with a neoprene wrap.

Vibration in the 60–90 Hz frequency range are commonly used to induce movement-related effects during locomotion and posture control studies (Courtine et al. 2001; Sorensen et al. 2002; Verschueren et al. 2002; Thompson et al. 2011). The effect of vibration on the thigh musculature was evaluated because the results of previous studies utilizing muscle vibration during various forms of walking have indicated that under particular contexts thigh musculature vibration can have a large impact on gait while during other contexts thigh musculature vibration seems to have little impact (Ivanenko et al. 2000a; Courtine et al. 2001, 2007; Verschueren et al. 2002) (see Introduction). Therefore, we were interested in assessing whether thigh muscle vibration would impact the adaptation process in the context of split-belt locomotion. During the testing, the subjects were placed in a harness suspended from a beam above the treadmill. The harness provided no support but was designed to support their weight should they stumble during the trial. Although treadmill side rails were in place, no subjects used the rails during testing. To minimize participant anxiety associated with exposure to the splitting of the belt speeds while walking blindfolded, participants walked for 1 min while blindfolded without vibration prior to the beginning of the data collection session.

Data collection

To acquire bilateral lower limb kinematics data, a 12-camera VICON motion capture system was used to collect three-dimensional positions of reflective markers placed bilaterally on the hip, knee, ankle, heel, and toe at 100 Hz (VICON, Oxford Metrics, Oxford, UK). The ground reaction forces collected from the instrumented treadmill TM-07-B (Bertec, Columbus, OH, USA) were sampled at 100 Hz and used to determine the specific gait events of heel contact and toe off. The treadmill's ground reaction forces were also used to confirm that subjects were successfully able to step on the appropriate belt, that is, left foot stepping on the left belt and right foot stepping on the right belt.

Data analysis

A custom MATLAB script (R2010b, MathWorks, Natick, MA, USA) was developed to filter the three-dimensional marker positions by the application of a Butterworth low-pass filter with the cut-off frequency of 6 Hz. Stride time was defined as the period between one heel contact to the next ipsilateral heel contact. The joint angles were calculated from the kinematics data collected by standard placement of reflective markers and utilizing biomechanical algorithms (Verschueren et al. 2002). The joint angles with positive values represented limb flexion while negative values reflected limb extension.

Previous authors have shown that intralimb parameters display immediate adaptation after the splitting of the treadmill belts. Typically, this phase of adaptation is complete within 3–15 steps after the split with these intralimb adaptations thought to be a function of feedback control dominated by spinal processes (Dietz et al. 1994; Reisman et al. 2005; Yang et al. 2005; Morton and Bastian 2006). Bastian and her colleagues have labeled the first five strides after the split as the ''early'' adaptation period (Reisman et al. 2005; Morton and Bastian 2006). Therefore, given our interest in exploring the possible role of proprioceptive feedback in the early adaptation period, we chose to focus the gait parameter analyses on the intralimb measures of stride length, percent stance time, and the relative timing between various combinations of peak joint angles (e.g., time of peak hip extension relative to time of peak knee flexion) (Reisman et al. 2005). The following measures were obtained for each of the first five strides after the splitting of the treadmill belts. Percent stance time was calculated as normalized stance time by the stride time reported in percentage. Stride length was calculated from the anterior–posterior distance the ankle marker travelled during the period of a heel contact and consecutive ipsilateral toe off event. These measures were derived for both lower limbs. To assess symmetry, ratios for stride length and percent stance time (Left/Right leg) were calculated for each subject and then used to obtain the group mean (Reisman et al. 2005). Lower limb kinematics reflecting hip, knee, and ankle motion were obtained for both limbs. Each subject's mean gait parameter measures and joint motion waveforms were obtained and used to calculate the group mean and group waveforms, for each condition. For both lower limbs, the relative timing of peak joint angles, defined as the latency between the peak angles for every combination of ankle, knee, and hip joint pairs were also determined. These data were then used to calculate group means. Peak hip and knee flexion and peak ankle extension angles were used to evaluate the temporal relationships between the various joint motions.

To determine if vibration impacted the early phase of the adaptive process during split-belt walking (i.e., the first five strides after the treadmill split), the data were assessed using a repeated measures MANOVA for each of the variables (Reisman et al. 2005). Only within leg (and ratios) were of interest for the intralimb variables as it was expected that these variables would be different between the left and right legs given the two legs were moving at different speeds. The statistical significance was set at $p < 0.05$. We used SPSS v.20 software to assess potential differences between conditions (IBM, Armonk, NY, USA).

Results

This investigation was conducted to determine if tendon vibration impacted the early phase of adaptation to split-belt locomotion when adaptive processes have been reported to be primarily mediated by feedback mechanisms under spinal control. The current data reflect that the early adaptive process is not influenced by disordered proprioception. The average self-selected speed while walking blindfolded after training was 1.015 m/s (SD = 0.051, range 0.935–1.108). Each subject's self-selected speed was reduced by 20% during the testing conditions when the two belts were tied. Table I contains the intralimb gait variable values obtained for each condition during the early adaption period. The Mauchly

Table I. Intralimb measures—group mean + 1 standard deviation—stride length, percent of stance time, relative time of peak knee flexion to hip extension, peak ankle extension to peak hip extension, and peak knee flexion to peak ankle extension. All temporal measures are expressed as a percentage of normalized stride time. The *indicates a significant difference between the Rt W and the Rt WQ percent stance time. No other comparisons resulted in significant differences. Lf and Rt represent left and right leg data, respectively. W represents no vibration, WH represents the hamstring tendon vibration condition, and WQ represents the quadriceps tendon vibration condition. Vibration was only applied to the left leg but data was collected from both legs during testing with and without left leg vibration. W, WH, and WQ represent the conditions of no vibration, hamstring vibration, and quadriceps vibration, respectively. This labeling convention reflects that ratios were computed using data from both legs.

Measure	Lf W	Lf WH	Lf WQ	Rt W	Rt WH	Rt WQ
Stride length (m)	1.33 (0.086)	1.31 (0.15)	1.33 (0.014)	0.93 (0.09)	0.91 (0.012)	0.92 (0.012)
	W	WH	WQ			
Stride length ratio	1.46 (0.12)	1.45 (0.10)	1.46 (0.13)			
	Lf W	Lf WH	Lf WQ	Rt W	Rt WH	Rt WQ*
Percent stance time	59.4 (1.3)	59.7 (2.6)	58.5 (2.2)	72.8 (2.2)	72.0 (2.2)	71.5 (1.8)
	W	WH	WQ			
Percent stance time ratio	0.82 (0.04)	0.83 (0.04)	0.82 (0.04)			
Relative angles	Peak time	Peak time	Peak time	Angle	Angle	Angle
Left leg (fast)	W	WH	WQ	W	WH	WQ
Kn flex–hip ext	22.8 (1.4)	22.5 (1.6)	22.6 (1.6)	92.4 (3.8)	92.3 (5.1)	93.5 (4.6)
Ank ext–hip ext	13.2 (2.7)	12.8 (2.0)	13.3 (2.3)	11.5 (7.6)	11.7 (8.3)	12.3 (7.2)
Kn flex–ank ext	9.6 (1.8)	9.7 (1.6)	9.3 (1.5)	80.9 (8.1)	80.7 (6.8)	81.2 (7.1)
Right leg (slow)	W	WH	WQ	W	WH	WQ
Kn flex–hip ext	21.3 (1.5)	21.9 (2.6)	21.7 (2.3)	55.5 (14.3)	57.7 (14.0)	58.4 (13.6)
Ank ext–hip ext	−37.7 (29.2)	27.9 (41.1)	24.5 (39.5)	−3.3 (12.6)	−4.3 (11.9)	−2.3 (11.8)
Kn flex–ank ext	59.0 (29.7)	49.8 (39.8)	46.3 (39.6)	58.7 (5.6)	62.0 (6.7)	61.4 (4.4)

test confirmed the assumption of sphericity for both stride length (SL) and percent stance time (ST).

Stride length was unaffected by vibration. However, vibration did impact percent stance time in the right leg ($F(2,\ 18) = 4.88$, $p = 0.02$). The *post hoc* analysis indicated that percent stance time in the WQ condition was significantly less than the W condition by 1.78% ($p = 0.012$). A similar trend emerged in the left leg with WQ percent stance time being 1.59% less than that of the W condition. The percentage differences in percent stance time between the W and WH conditions were 1.04 and 0.38% for the right and left leg, respectively. Collectively these data indicate that quadriceps tendon vibration slightly influenced percent stance time during the early adaptation period. There was no effect of hamstring vibration on percent stance time of either leg.

Figure 1(A–F) indicates that neither of the vibration conditions substantially modified the motion of any of the measured joints relative to the no vibration (W) condition. This was also supported by the fact that none of the relative time of the peak joint motion relationships were significantly modified by vibration.

Discussion

The results of this investigation demonstrate that disordered proprioceptive feedback generated by tendon vibration has very minimal impact on the early period of adaptation to split-belt walking. Research involving both healthy and patient populations can be interpreted to suggest that the adaptation experienced immediately after being exposed to split-belt walking requires very little cortex or cerebellar input, thereby suggesting spinal mechanisms are primarily responsible for this phase of adaptation (Morton and Bastian 2006; Reisman et al. 2007; Choi et al. 2009). This interpretation is consistent with the early work of Forssberg's group (Forssberg et al. 1980a,b) whose ''spinalized'' cats were able to adapt their limb motion during treadmill and split-belt walking. Similarly, human infants with undeveloped descending spinal tracts were able to produce feedback-driven adaptations to split-belt walking (Yang et al. 2005). Based on these findings, the current investigation was therefore presumably investigating the possible effects of vibration on spinally mediated processes.

The current findings are consistent with the results of other investigators who have reported that vibration has little impact on locomotion control. Courtine et al. (2001) assessed the possible impact of bilateral Achilles tendon vibration during overground locomotion and found that although stance and swing phase length and duration were slightly affected, there were no significant effects on lower limb kinematics. In a subsequent investigation, Courtine et al. (2007) found little impact resulting from lower limb musculature vibration during walking. Interestingly, in this study it was demonstrated that when vibration was applied during bipedal postural control tasks, the subjects exhibited significant postural sway, suggesting context-specific processing of proprioceptive input. On the other hand, Ivanenko et al. (2000a) did find changes in walking speed when vibration was applied to the biceps femoris during treadmill walking which is consistent with Verschueren et al. (2002) who reported small but statistically significant effects on lower limb kinematics resulting from quadriceps tendon vibration. However, Verschueren et al.'s subjects did not modify their lower limb kinematics in response to biceps femoris vibration again suggesting there is an interaction between a specific task and a specific proprioceptive input (Ivanenko et al. 2000b; Sorensen et al. 2002).

The lack of an effect of vibration in the current study may also reflect a methodological consideration. In the investigations conducted by Sorensen et al. (2002) and Verschueren et al. (2002), the vibration was initiated at the beginning of a particular pass down a walkway and then turned off at the end of that trial. In contrast, the current procedures involved continuous vibration from the beginning of the trial which

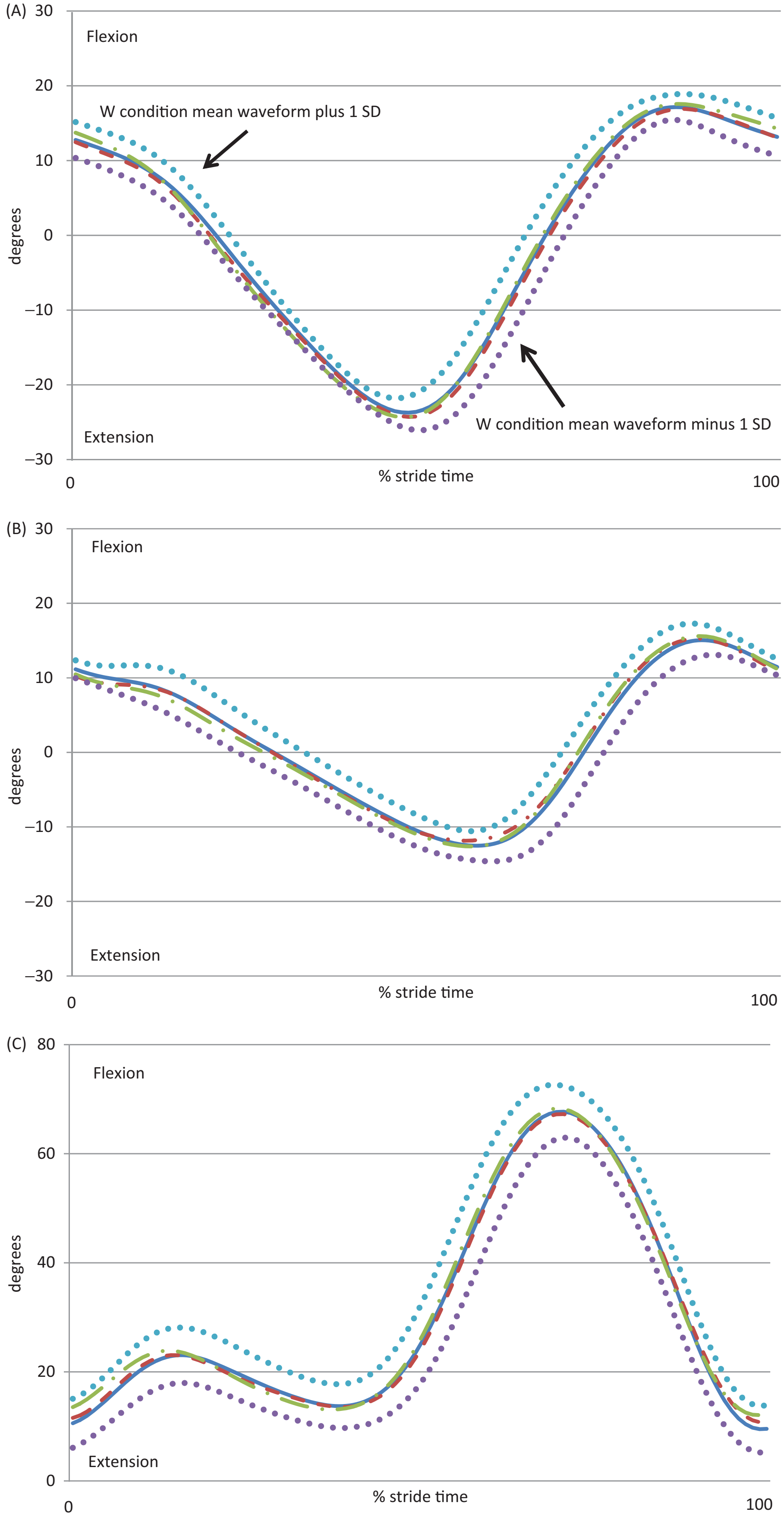

Figure 1. (A–F) Group mean waveforms (±1 standard deviation) obtained during the early adaptation period of split-belt locomotion for the left hip, knee, and ankle (A, C, and E, respectively) and the right hip, knee, and ankle (B, D, and F, respectively), with and without vibration. The solid lines represent W condition (no vibration), the shorter dashes represent the WH condition (hamstring tendon vibration), and the longer dashes represent the WQ condition (quadriceps tendon vibration). The lines composed of small dots represent ± 1 standard deviation of the W condition. This is explicitly identified in graph A but applies to all the graphs. The data are normalized from heel strike to that same lower limb's next heel strike.

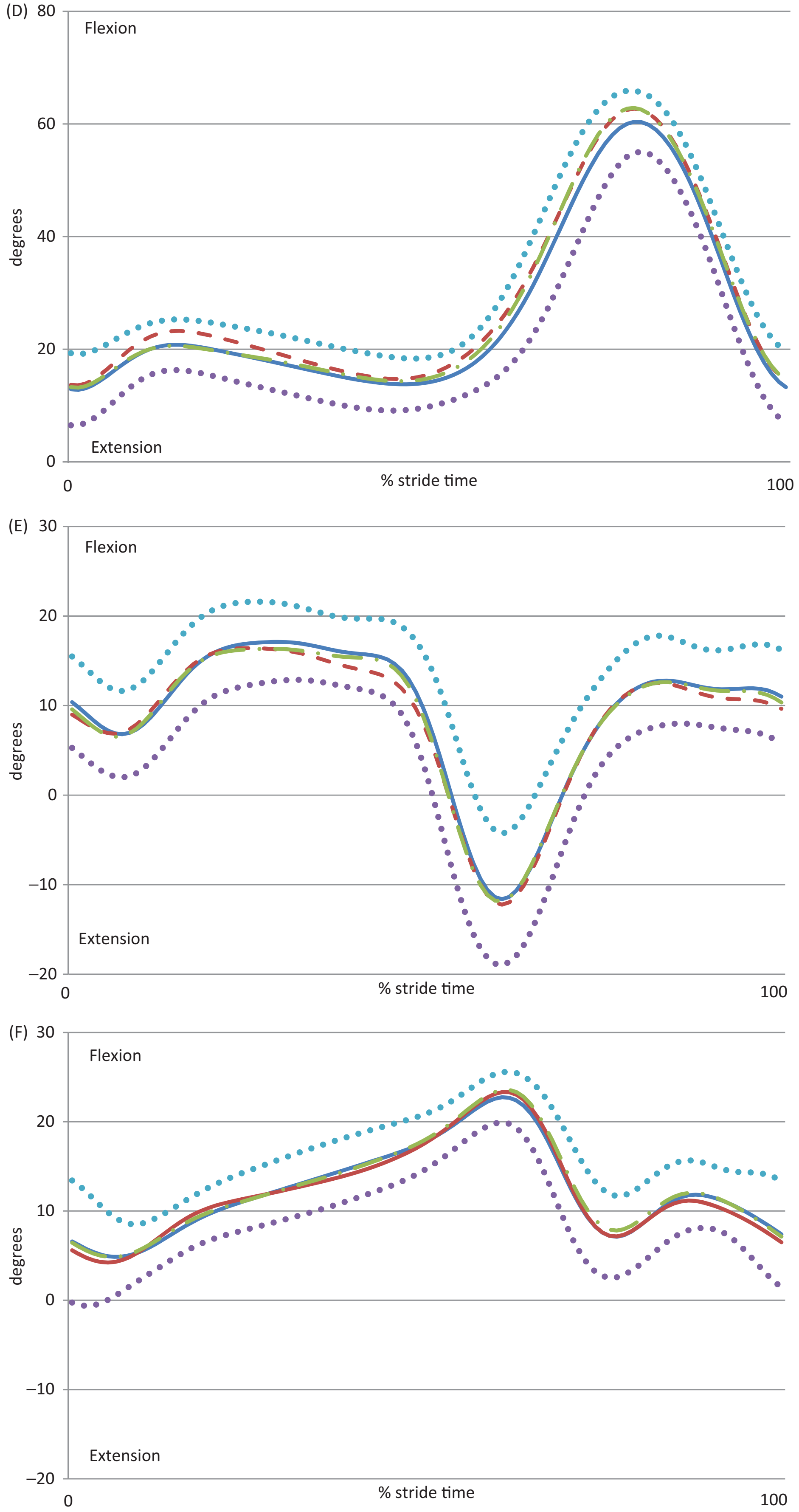

Figure 1. Continued.

included 1 min of tied-belt walking prior to the belts splitting. This is similar to Ivanenko et al.'s (2000a) subjects whose gait kinematics displayed little response to vibration while receiving continuous vibration during a treadmill walking task. Therefore, it is possible the current subjects had adapted to any potentially significant impact of vibration prior to the belts splitting. This explanation, while plausible, by itself does not account for the current findings. Similar to other protocols (Sorensen et al. 2002; Verschueren et al. 2002), Courtine et al.'s (2001, 2007) subjects only received vibration at the beginning of each pass down a walkway and their gait kinematics were unaffected by vibration pointing towards the effect of vibration being heavily context conditioned.

Contextual conditioning of responses to vibration may occur as a result of the process of sensory weighting. It has often been proposed that a process by which unreliable sensory input can effectively be ignored is a gating mechanism where sensory inputs are ''weighed'' for their relative values and either effectively utilized or discarded during a particular activity (Horak et al. 1994; Allison et al. 2006; Isableu et al. 2010; Dettmer et al. 2013). This mechanism facilitates an effective down weighting of the distorted Ia input generated as a result of tendon vibration so as not to negatively influence the adaptive process necessary to respond to the changing of the belt speeds during split-belt walking. If, as has been suggested, both percent stance time and stride length adaptations to split-belt locomotion are primarily the result of spinal mechanisms and vibration input is down weighted such that it has little impact on the adaptation process, this suggests that some neurophysiological mechanisms responsible for the process of sensory reweighting may be mediated in the spinal cord.

It has been shown that ankle muscle stretching during gait causes stretch reflexes that are modulated throughout the gait cycle and influence lower limb kinematics (Sinkjaer et al. 1996; Kearney et al. 1999; Donelan and Pearson 2004). These rapid corrective reflexes are influenced by Ia, II, and Ib afferent inputs and illustrate that sensory inputs of multiple origins can play a role in modulating neuromuscular responses (af Klint et al. 2010b). Although it is a common assumption that vibration will preferentially modify Ia input and potentially disrupt ongoing gait control (Ivanenko et al. 2000b; Verschueren et al. 2003), several investigators have shown that other afferent neurophysiological mechanisms can exert significant influence on gait patterns, depending upon the task-related context. For example, load receptor feedback has been demonstrated to play a significant role in the modulation of both neuromuscular activity and gait parameters (Grey et al. 2007; af Klint et al. 2010a,b). Additionally, mechanisms such a pre-synaptic inhibition, alterations in central motoneuron drive and fusimotor drive can serve to negate any disruptive effects of Ia input stemming from vibration (Cronin et al. 2009). These neurophysiological mechanisms can effectively function as the processes utilized to down weight disordered sensory feedback.

The accumulating evidence of context-specific processing of proprioceptive inputs resulting in a range of responses to vibration during various gait tasks is consistent with the proposition that there is a dynamic locomotor body schema that can be used for planning and generating gait (Ivanenko et al. 2011). Of interest is the fact that percent stance time of the right leg was decreased during quadriceps tendon vibration relative to walking without vibration even though it was the left leg that received vibration. This may indicate that the response to vibration, at least within the current context, is influenced by sensory input integrated into a locomotor body schema that can be used to regulate behavior in segments not directly receiving the stimulus.

To further investigate the possible influence of vibration of the adaptive processes associated with split-belt treadmill locomotion several additional questions should be explored. It has been suggested by af Klint et al. (2010b) that extended unloading during treadmill walking could result in central nervous system (CNS) adaptation of altered loading feedback and therefore might have been responsible for the lack of change in the unloading response observed by Grey et al. (2001). A similar phenomenon could have occurred in the current protocol in that the CNS may have adapted to the modified input associated with sustained vibration, thereby contributing to the null findings. It is unknown if vibration would affect the adaptive process if it were initially applied simultaneously with the splitting of the two treadmill belts. Additionally, it is possible that vibration would have more influence if it is applied to the slow leg (right leg in the current protocol). Yang et al. (2005) reported that infants exposed to split-belt walking displayed greater adaptations in gait cycle duration in the slow leg than those of the fast leg. This is because the overall gait pattern during split-belt walking is more similar to the speed of the fast leg when the two belts are tied and thus necessitating the slow leg modify its temporal features to a greater degree than the fast leg. Therefore, it is possible that vibration could exert greater influence on the adaptive processes of the slow leg as it experiences greater adaptation than the fast leg.

Acknowledgements

The authors would like to thank Dr Daniel O'Connor for advisement during data analysis, Stacy Nguy for assistance with data collection, and Sara Lalani for assistance with data processing.

Declaration of interest

The authors report no conflicts of interest.

References

af Klint R, Cronin NJ, Ishikawa M, Sinkjaer T, Grey MJ. 2010a. Afferent contribution to locomotor muscle activity during unconstrained overground human walking: An analysis of triceps surae muscle fascicles. J Neurophysiol 103:1262–1274.

af Klint R, Mazzaro N, Nielsen JB, Sinkjaer T, Grey MJ. 2010b. Load rather than length sensitive feedback contributes to soleus muscle activity during human treadmill walking. J Neurophysiol 103: 2747–2756.

Albert F, Bergenheim M, Ribot-Ciscar E, Roll JP. 2006. The Ia afferent feedback of a given movement evokes the illusion of the same movement when returned to the subject via muscle tendon vibration. Exp Brain Res 172:163–174.

Allison LK, Kiemel T, Jeka JJ. 2006. Multisensory reweighting of vision and touch is intact in healthy and fall-prone older adults. Exp Brain Res 175:342–352.

Choi JT, Vining EP, Reisman DS, Bastian AJ. 2009. Walking flexibility after hemispherectomy: Split-belt treadmill adaptation and feedback control. Brain 132(3):722–733.

Courtine G, Pozzo T, Lucas B, Schieppati M. 2001. Continuous, bilateral Achilles' tendon vibration is not detrimental to human walk. Brain Res Bull 55(1):107–115.

Courtine G, De Nunzio AM, Schmid M, Beretta MV, Schieppati M. 2007. Stance- and locomotion-dependent processing of vibration-induced proprioceptive inflow from multiple muscles in humans. J Neurophysiol 97(1):772–779.

Cronin NJ, Ishikawa M, Grey MJ, af Klint R, Komi PV, Avela J, Sinkjaer T, Voigt M. 2009. Mechanical and neural stretch responses of the human soleus muscle at different walking speeds. J Physiol 587: 3375–3382.

Dettmer M, Pourmoghaddam A, O'Connor DP, Layne CS. 2013. Interaction of support surface stability and Achilles tendon vibration during a postural adaptation task. Hum Mov Sci 32:214–227.

Dietz V, Zijlstra W, Duysens J. 1994. Human neuronal interlimb coordination during split-belt locomotion. Exp Brain Res 101(3):513–520.

Donelan JM, Pearson KG. 2004. Contribution of sensory feedback to ongoing ankle extensor activity during the stance phase walking. Can J Physiol Pharmacol 82:589–598.

Forssberg H, Grillner S, Halbertsma J. 1980a. The locomotion of the low spinal cat. I. Coordination within a hindlimb. Acta Physiol Scand 108(3):269–281.

Forssberg H, Grillner S, Halbertsma J, Rossignol S. 1980b. The locomotion of the low spinal cat. II. Interlimb coordination. Acta Physiol Scand 108(3):283–295.

Grey MJ, Ladouceur M, Andersen JB, Nielsen JB, Sinkjaer T. 2001. Group II muscle afferents probably contribute to the medium latency soleus stretch reflex during walking in humans. J Physiol 534: 925–933.

Grey MJ, Nielsen JB, Mazzaro N, Sinkjaer T. 2007. Positive force feedback in human walking. J Physiol 581:99–105.

Horak FB, Shupert CL, Dietz V, Horstmann G. 1994. Vestibular and somatosensory contributions to responses to head and body displacement in stance. Exp Brain Res 100:93–106.

Isableu B, Ohlmann T, Cremieux J, Vuillerme N, Amblard B, Gresty MA. 2010. Individual differences in the ability to identify, select and use appropriate frames of reference for perceptuo-motor control. Neuroscience 169:1199–1215.

Ivanenko YP, Grasso R, Lacquaniti F. 2000a. Influence of leg muscle vibration on human walking. J Neurophysiol 84:1737–1747.

Ivanenko YP, Solopova IA, Levik YS. 2000b. The direction of postural instability affects postural reactions to ankle muscle vibration in humans. Neurosci Lett 292:103–106.

Ivanenko YP, Dominici N, Daprati E, Nico D, Cappellini G, Lacquaniti F. 2011. Locomotor body scheme. Hum Mov Sci 30: 341–351.

Kearney RE, Lortie M, Stein RB. 1999. Modulation of stretch reflexes during imposed walking movements of the human ankle. J Neurophysiol 81(6):2893–2902.

Mohapatra S, Krishnan V, Aruin AS. 2012. Postural control in response to an external perturbation: Effect of altered proprioceptive information. Exp Brain Res 217(2):197–208.

Morton SM, Bastian AJ. 2006. Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. J Neurosci 26(36):9107–9116.

Reisman DS, Block HJ, Bastian AJ. 2005. Interlimb coordination during locomotion: What can be adapted and stored? J Neurophysiol 94(4):2403–2415.

Reisman DS, Wityk R, Silver K, Bastian AJ. 2007. Locomotor adaptation on a split-belt treadmill can improve walking symmetry post-stroke. Brain 130(7):1861–1872.

Roll JP, Vedel JP, Ribot E. 1989. Alteration of proprioceptive messages induced by tendon vibration in man: A microneurographic study. Exp Brain Res 76(1):213–222.

Sadeghi H, Allard P, Prince F, Labelle H. 2000. Symmetry and limb dominance in able-bodied gait: A review. Gait Posture 12:34–45.

Sinkjaer T, Anderson JB, Larsen B. 1996. Soleus stretch reflex modulation during gait in humans. J Neurphysiol 76(2):1112–1120.

Sorensen KL, Hollands MA, Patla E. 2002. The effects of human ankle muscle vibration on posture and balance during adaptive locomotion. Exp Brain Res 143(1):24–34.

Thompson C, Bélanger M, Fung J. 2011. Effects of plantar cutaneo-muscular and tendon vibration on posture and balance during quiet and perturbed stance. Hum Mov Sci 30(2):153–171.

Verschueren SM, Swinnen SP, Desloovere K, Duysens J. 2002. Effects of tendon vibration on the spatiotemporal characteristics of human locomotion. Exp Brain Res 143(2):231–239.

Verschueren SM, Swinnen SP, Desloovere K, Duysens J. 2003. Vibration-induced changes in EMG during human locomotion. J Neurophysiol 89:1299–1307.

Yang JF, Lamont EV, Pang MY. 2005. Split-belt treadmill stepping in infants suggests autonomous pattern generators for the left and right leg in humans. J Neurosci 25(29):6869–6876.