Published in final edited form as:
Exp Brain Res. 2014 January ; 232(1): . doi:10.1007/s00221-013-3739-2.

Reduced effects of tendon vibration with increased task demand during active, cyclical ankle movements

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Abstract

Tendon vibration can alter proprioceptive feedback, one source of sensory information which humans can use to produce accurate movements. However, the effects of tendon vibration during functional movement vary depending on the task. For example, ankle tendon vibration has considerably smaller effects during walking than standing posture. The purpose of this study was to test whether the effects of ankle tendon vibration are predictably influenced by the mechanical demands of a task, as quantified by peak velocity. Twelve participants performed symmetric, cyclical ankle plantarflexion/dorsiflexion movements while lying prone with their ankle motion unconstrained. The prescribed movement period (1s, 3s) and peak-to-peak amplitude (10°, 15°, 20°) were varied across trials; shorter movement periods or larger amplitudes increased the peak velocity. In some trials, vibration was continuously and simultaneously applied to the right ankle plantarflexor and dorsiflexor tendons, while the left ankle tendons were never vibrated. The vibration frequency (40, 80, 120, 160 Hz) was varied across trials. During trials without vibration, participants accurately matched the movement of their ankles. The application of 80 Hz vibration to the right ankle tendons significantly reduced the amplitude of right ankle movement. However, the effect of vibration was smaller during more mechanically demanding (i.e. higher peak velocity) movements. Higher vibration frequencies had larger effects on movement accuracy, possibly due to parallel increases in vibration amplitude. These results demonstrate that the effects of ankle tendon vibration are dependent on the mechanical demand of the task being performed, but cannot definitively identify the underlying physiological mechanism.

Keywords

Motor control; Movement accuracy; Proprioception; Tendon vibration

Introduction

Proprioceptive feedback provides humans with information about the mechanical state of their body and is vital for functional movement (Horak et al. 2002; Krakauer et al. 1999). Populations of muscle spindles provide feedback of muscle length and velocity, allowing the central nervous system to develop a kinematic representation of the body (see Proske and Gandevia 2012 for detailed review). Joint capsule mechanoreceptors and skin receptors can

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Conflict of Interest
The authors declare that they have no conflict of interest.

contribute to this representation by providing joint angle feedback, while Golgi tendon organs provide feedback of muscle forces and tendon stretch (Proske and Gandevia 2012).

Tendon vibration can be used to interfere with proprioceptive feedback. The application of vibration causes repetitive small length changes of the tendon, which are transmitted to the associated muscle spindles and create the perception of joint motion in which the vibrated muscle is lengthening (Goodwin et al. 1972; Gilhodes et al. 1986). The effects of tendon vibration are modulated by its frequency, and appear to be maximal around 80 Hz (Roll and Vedel 1982; Roll et al. 1989). Simultaneously vibrating antagonist muscles creates a perception of movement dependent on the difference in vibration frequency between the two muscles; matching the antagonist vibration frequency causes only minimal perceptual or motor effects at static joints (Gilhodes et al. 1986; Calvin-Figuiere et al. 1999). However, the effects of identical tendon vibration during movement are substantially larger for lengthening muscles than for shortening muscles, whether the motion is actively controlled by the lengthening or shortening muscle (Cody et al. 1990; Inglis et al. 1991).

The effects of tendon vibration have been extensively investigated for upper extremity movements, likely due to the clear importance of movement accuracy during reaching. The potential of tendon vibration to predictably alter proprioceptive feedback has motivated the use of this tool during other functional tasks. However, extending results from upper extremity experiments to lower extremity tasks may not be trivial. In comparison to the upper extremity, lower extremity joints have decreased joint position sense accuracy (Paschalis et al. 2009), which has been partially attributed to the greater abundance of muscle spindles in the arm as compared to the leg (Banks 2006). Limb crossing experiments, which investigate how posture influences the formation of internal representations of the body, have suggested that the integration of proprioceptive feedback differs between the upper and lower extremities, possibly due to differences in their typical use (van Elk et al. 2013). Additionally, performance variability is greater in the lower extremity when maintaining either a constant joint position (Kwon et al. 2011) or output force (Christou et al. 2003), which may be a result of the increased practice performing precise motor tasks with the arms.

In the lower extremity, the effects of tendon vibration have commonly been tested at the ankle during standing posture and walking. As first demonstrated by Eklund (Eklund 1972), vibration of the ankle tendons has clear effects on standing posture. Vibration of the Achilles tendons causes the body to lean backward, while vibration of the dorsiflexor tendons causes the body to lean forward (Eklund 1972; Kavounoudias et al. 1999; Ivanenko et al. 2000). This response has been attributed to increased spindle feedback from the vibrated muscle, as would be expected to normally occur due to plantarflexor stretch during an anterior lean and due to dorsiflexor stretch during a posterior lean. Humans respond to the perception of an unintended lean by swaying in the opposite direction. In comparison to standing posture, the effects of ankle tendon vibration during walking are considerably less clear. Vibration of the ankle tendons has been reported to cause both an increase (Ivanenko et al. 2000) and a decrease (Verschueren et al. 2002a) in walking speed. Similarly, the reported effects of tendon vibration on step length and step timing differ between studies (Courtine et al. 2001; Verschueren et al. 2002a). Specific to motion at the ankle joint, Achilles tendon vibration has been reported to have no effect on the range of motion during a gait cycle (Courtine et al. 2001), and to decrease dorsiflexion during swing (Verschueren et al. 2002a). While the varied results among these studies may be attributed to methodological differences, it is clear that the effects of ankle tendon vibration are less apparent during walking than during standing posture.

The reduced effects of ankle tendon vibration during walking have primarily been attributed to task-dependence of proprioceptive feedback (Ivanenko et al. 2000). During walking, proprioceptive feedback may be "gated" to prevent Ia afferent feedback from interfering with a centrally generated motor pattern (Courtine et al. 2001), an idea supported by the reduction in cerebral potentials evoked by group I afferent stimulation during walking (Dietz et al. 1985). Presynaptic inhibition of Ia feedback during walking (Courtine et al. 2007b) would reduce the ability of vibration to evoke a response. Instead, steady-state gait may be produced nearly automatically by central circuits, without relying on Ia feedback (Courtine et al. 2007a).

In addition to the task-dependence of proprioceptive feedback, the reduced effects of ankle tendon vibration during walking may be partially attributable to the mechanical demands of the task. While standing is often thought of as static, normal posture involves sagittal plane sway largely controlled by the ankle joint (Loram et al. 2005). In healthy, uninjured adults, these movements typically have a period of about 1–2 seconds, a peak-to-peak amplitude of 0.05–0.2°, and a peak angular velocity of less than 1°/s (Loram et al. 2005; Loram et al. 2007). In contrast, during walking at a typical speed, a single gait cycle has a period of approximately 0.7 seconds, peak-to-peak ankle motions of 25–30°, and peak ankle angular velocities of about 150°/s (dorsiflexion) and 250°/s (plantarflexion) (Winter 2009). Upper extremity experiments have demonstrated that the effects of vibration decrease during higher velocity movements, likely as a result of smaller differences between movement-evoked spindle activity and vibration-evoked activity (Cordo et al. 1995). Therefore, the increased mechanical demands at the ankle during walking, in the form of greatly increased velocity, could contribute to the decreased effects of tendon vibration.

The purpose of this study was to determine whether the effects of ankle tendon vibration are influenced by the mechanical demand of an ankle movement task. In contrast to previous experiments which tested the effects of tendon vibration during isolated, passive ankle motions (van Deursen et al. 1998; Verschueren et al. 2002b), we investigated active, cyclical ankle motions as a closer approximation of a functional task. Participants performed a bilateral, symmetric task in which they were instructed to move their left and right ankles through identical sinusoidal trajectories. While the task instructions remained consistent from trial to trial, the mechanical demand was varied by altering the peak-to-peak amplitude and period of the target trajectory, thereby changing the peak velocity of ankle motion. In contrast to standing and walking, our simple ankle motion minimized the additional sources of sensory feedback (e.g. cutaneous feedback from the foot, vestibular feedback) which could provide information about task performance. Therefore, the present experiments allowed us to focus on the relationship between the mechanical demand of a task and the effects of tendon vibration.

Our primary hypothesis was that the effects of tendon vibration would decrease under more mechanically demanding (i.e. higher velocity) conditions. Such a result would suggest that the mechanical demand of a task should be controlled, or at least understood, in order to use tendon vibration to quantify the role of proprioception during functional movement. Secondarily, we hypothesized that 80 Hz vibration would have the largest effect on ankle movement accuracy, as this vibration frequency most effectively activated primary muscle spindles in the isometric ankle (Roll et al. 1989).

Methods

Participants

Twelve adults participated in this experiment (11 female, 1 male; 24±1 years old; mean ±s.d.). Potential participants with self-reported current lower extremity musculoskeletal injuries, or a history of cardiac, respiratory, or neurological disease were excluded. Written informed consent was obtained prior to participation using a form approved by the Medical University of South Carolina Institutional Review Board and consistent with the Declaration of Helsinki.

Setup

Participants lay prone on a padded table with six LED markers (PhaseSpace; San Leandro, CA) placed on each leg (Fig. 1), the 3-D positions of which were sampled at 120 Hz. All participants wore their own athletic shoes, which were required to not cover the ankle malleoli. Markers were placed on the lateral and medial epicondyles at the knee, on the lateral and medial malleoli at the ankle, and laterally and medially on the sole of the shoe under the ball of the foot. The axis of motion for ankle plantarflexion/dorsiflexion was defined as the line connecting the ankle malleoli markers. Plantarflexion/dorsiflexion angle was calculated based on the positions of: 1) the point midway between the epicondyle markers; 2) the point midway between the foot markers; 3) the axis of motion defined above. Ankle angular velocity was calculated by low-pass filtering the angle data at 5 Hz, and differentiating over time. Pilot experiments confirmed that this marker placement was not sensitive to ankle pronation or supination movements. By quantifying ankle motion using LED markers rather than a frame strapped to the foot (van Deursen et al. 1998; Verschueren et al. 2002), we minimized cutaneous feedback which could potentially be used to match bilateral ankle motion. While participants were not permitted to look at their legs, a monitor placed in front of the participants provided real-time visual feedback of the left ankle angle. Visual feedback of the right ankle angle was not provided in any trials.

Custom-built vibration devices were secured over both the right Achilles tendon and the right tibialis anterior tendon using elastic straps approximately 4 cm above the ankle joint. This placement was intended to alter sensory feedback from both the plantarflexors and dorsiflexors, and similar placement has been used previously during isolated ankle movements (van Deursen et al. 1998) and walking (Ivanenko et al. 2000; Verschueren et al. 2002a). By applying identical vibration to antagonist muscle groups, the effects of the vibration will predominantly influence the lengthening muscle group (Cody et al. 1990; Inglis et al. 1991). The vibration devices were constructed of small, eccentrically weighted motors attached to shaped plastic, as described previously (Celik et al. 2009). For this type of motor, the applied voltage controls the vibration frequency and amplitude, which are inherently linked. We quantified this relationship in pilot experiments by applying a range of voltages while using LED markers firmly glued to the plastic surface making contact with an individual’s tendon to measure its movement. For the present experiments, the vibration frequency was set to 40, 80, 120, or 160 Hz, with the resultant vibration peak-to-peak amplitude measured as 0.18, 0.25, 0.31, and 0.39 mm, respectively. These amplitudes fall within a range previously used to activate muscle spindles (Roll and Vedel 1982; Fallon and Macefield 2007).

Protocol

Participants performed a series of 30-second trials in which they cyclically plantarflexed and dorsiflexed their right and left ankles. In all trials, participants were instructed to perform the same movement with both of their ankles, symmetrically moving through the same range of motion and with the same period. Performing this task may be considered to be somewhat complex, as participants were required to maintain a prone position and process visual feedback of their left ankle position while matching the movement of their bilateral ankle joints, even as peripheral sensory feedback from the right ankle was manipulated.

Movement amplitude and period were varied across trials. In each trial, peak-to-peak movement amplitude was prescribed at one of three levels (10°, 15°, or 20°) using target lines displayed on the monitor. Participants were instructed to move their left ankle back and forth between these target lines, and to perform the same motion with their right ankle. The target lines were always centered around 10° of plantarflexion, so participants did not approach the limits of their range of motion for even the largest amplitude movements. Target lines always appeared identical on the screen, as the scale of the visual feedback was adjusted based on the prescribed movement amplitude. Therefore, participants were not able to determine the prescribed range of motion from the visual appearance of the screen. Movement period was prescribed at one of two levels (1s, 3s) using a metronome. Participants were instructed to move through a smooth trajectory, just reaching the target line at the time of each beep and avoiding rapid changes in direction. If participants moved their ankles through a perfectly sinusoidal trajectory, the peak angular velocity would scale proportionally with amplitude and inversely with period. With the prescribed amplitudes and periods, this would result in peak velocities ranging from approximately 10 °/s to 60 °/s across trials, falling between the peak velocities observed during standing posture and walking.

Each of the twelve participants cyclically moved their ankles for three vibration conditions. In one condition, no vibration was applied to the right ankle tendons, although the vibration devices were still secured to this leg. In a second condition, 80 Hz vibration was applied to the right plantarflexor and dorsiflexor tendons. In a third condition, an additional vibration frequency was applied to both tendons. This additional vibration frequency varied across subgroups; one subgroup (n=4) received 40 Hz vibration, another subgroup (n=4) received 120 Hz vibration, and the final subgroup (n=4) received 160 Hz vibration. For all participants, vibration was applied in two thirds of the trials. Vibration was turned on just prior to instructing participants to begin moving their ankles and turned off at completion of the trial. Therefore, vibration was applied for approximately 30 seconds during each of these trials. The vibration was always turned off for a 30 second rest period which separated all trials.

Each participant performed a total of 54 trials. Participants first performed a block of 18 trials, which consisted of 18 distinct trial conditions (3 vibration conditions x 3 movement amplitudes x 2 movement periods). Participants subsequently performed two additional blocks of the same 18 trial conditions. The order of the trial conditions was separately randomized within each block of trials.

Data Analysis

We analyzed the final 20 seconds of each trial, allowing participants to become accustomed to the prescribed movement amplitude and period. To ensure that participants followed the prescribed left ankle trajectory, we quantified the peak-to-peak movement amplitude, movement period, and peak dorsiflexion and plantarflexion angular velocity for each movement cycle. For all trials, we calculated the average values of each of these metrics. We also calculated the Amplitude Ratio for each trial, defined as the peak-to-peak amplitude of right ankle movement divided by the peak-to-peak amplitude of left ankle movement. An Amplitude Ratio near one would indicate that the left and right ankles were moving through approximately the same range of motion, while an Amplitude Ratio less than one would indicate that the right ankle was moving through a smaller range of motion than the left ankle.

Statistics

We performed a 4-way repeated measures ANOVA with interactions to determine if a bilateral ankle movement matching task was significantly influenced by 80 Hz tendon vibration or the parameters of the movement task. Amplitude Ratio was the dependent factor, while vibration condition (No Vibration vs. 80 Hz Vibration), prescribed peak-to-peak movement amplitude (10° vs. 15° vs. 20°), prescribed movement period (1s vs. 3s), and trial number (1 vs. 2 vs. 3) were the independent factors. Trial number was included as an independent factor to determine whether ankle matching performance changed over the course of the experiment. We also performed three additional 1-way repeated measures ANOVA to determine if vibration frequency influenced the matching task. A separate ANOVA was performed for each subgroup of participants, and data were collapsed across all prescribed movement amplitudes and periods. For these ANOVA, Amplitude Ratio was the dependent factor, while vibration condition (No Vibration vs. 80 Hz Vibration vs. 40/120/160 Hz vibration) was the independent factor. Where appropriate, we performed post-hoc Tukey-Kramer comparisons. For all tests, p values less than 0.05 were interpreted as significant.

Results

Performance of an active, cyclical ankle movement task was influenced by vibration of the plantarflexor and dorsiflexor tendons. Vibration applied at the right ankle caused a decrease in the amplitude of right ankle movement. The effects of vibration were modulated by the movement amplitude, movement period, and vibration frequency. Trial number did not significantly influence the calculated Amplitude Ratio ($p>0.05$ for main effect of trial number and all interactions involving trial number), so the three trials for each condition were combined for the analyses described below.

Participants varied their left ankle motion to match the prescribed movement amplitude and period. The ankle displacements (Fig. 2a) and velocities (Fig. 2b) were not perfectly sinusoidal, particularly for the longer period trials. However, the prescribed changes in peak-to-peak amplitude (Fig. 2c) and movement period (Fig. 2d) produced a wide range of peak angular velocities across conditions (Fig. 2e).

The application of tendon vibration at 80 Hz clearly influenced movement of the right ankle. 80 Hz vibration had a significant main effect ($p<0.0001$) on the Amplitude Ratio (Fig. 3), as the right ankle moved through a smaller range of motion when vibration was applied. Post-hoc tests revealed that the Amplitude Ratio for each movement condition with vibration was significantly ($p<0.05$) smaller than the Amplitude Ratio for each non-vibrated movement condition.

The parameters of the movement pattern (prescribed amplitude and period) modulated the effect of 80 Hz tendon vibration (Fig. 3). Across all non-vibrated movement conditions, the Amplitude Ratios were approximately 1 and were not significantly different from each other, indicating that participants were able to accurately match their bilateral movements independent of amplitude and period. However, Amplitude Ratio was influenced by both a significant main effect ($p=0.007$) of prescribed movement amplitude and a significant interaction ($p=0.0003$) between vibration condition and prescribed movement amplitude. Specifically, vibration had a larger effect during small amplitude movements, as indicated by significantly smaller Amplitude Ratios when a 10° amplitude was prescribed in comparison to a 20° amplitude. Amplitude Ratio was also influenced by a significant main effect ($p=0.0004$) of movement period and a significant interaction between vibration condition and movement period ($p<0.0001$). Specifically, vibration had a larger effect during movements with longer periods and lower peak velocities, as indicated by the significantly smaller Amplitude Ratios.

The frequency of the applied vibration influenced its effect on movement of the right ankle, with higher vibration frequencies having larger effects. Within each subgroup of 4 participants, we collapsed the Amplitude Ratio data across movement conditions to focus on the effect of vibration frequency. In all three subgroups, vibration condition had a significant main effect on Amplitude Ratio ($p<0.0001$). For all subgroups, applying 80 Hz vibration significantly decreased the Amplitude Ratio. In Subgroup 1, 40 Hz vibration did not significantly affect Amplitude Ratio (Fig. 4a). In Subgroup 2, 120 Hz vibration decreased Amplitude Ratio significantly more than 80 Hz vibration (Fig. 4b). Similarly, in Subgroup 3, 160 Hz vibration decreased Amplitude Ratio significantly more than 80 Hz vibration (Fig. 4c).

Discussion

Unilateral tendon vibration reduced movement accuracy during a simple task in which participants matched the symmetric, bilateral motion of their ankles. As hypothesized, the effects of vibration were decreased during faster movements, which were prescribed using either larger movement amplitudes or shorter movement periods. Unexpectedly, the effects of vibration were not maximized at 80 Hz, instead increasing with higher frequency vibration. The present results demonstrate that the effects of tendon vibration are dependent on the mechanical demand of the task being performed, but cannot directly differentiate between several possible underlying mechanisms.

Our most basic result was that vibration influenced movement accuracy during an active, cyclical ankle movement. Without vibration, participants were able to accurately match the movement of their left and right ankles for all prescribed movement parameters. However, applying 80 Hz vibration to the right ankle tendons caused participants to decrease the movement amplitude of this ankle, similar to the effect observed during active, cyclical elbow motions (Steyvers et al. 2001). This result can be explained by the different effects of tendon vibration on lengthening and shortening muscles; vibration has larger effects when applied to lengthening muscles than shortening muscles, largely independent of whether these muscles are passive or active (Cody et al. 1990; Inglis et al. 1991). While we applied identical vibration to the dorsiflexor and plantarflexor tendons, the effects of the vibration were thus likely biased toward the lengthening muscle. For example, during dorsiflexion phases of the task, the vibration-driven increases in plantarflexor spindle discharge rate would cause participants to perceive a faster dorsiflexion movement of their right ankle than was actually occurring. In order to match the movement of the non-vibrated left ankle, participants would decrease the actual motion of the vibrated right ankle. Alternatively, it is conceivable that the simultaneous vibration of antagonistic muscles reduced movement amplitude not by altering perception, but by causing muscular co-contraction. Participants may have simply maintained the descending commands to their ankle musculature, ignoring any feedback which could indicate kinematic differences between the motion of their left and right ankles. With constant descending commands, the increased stiffness and damping which can accompany co-contraction (Granata et al. 2004) would decrease the amplitude of motion at the vibrated ankle. While muscle activity was not measured in the present study, previous work has found that identical frequency antagonist tendon vibration did not cause co-contraction at either the elbow (Gilhodes et al. 1986) or wrist (Calvin-Figuiere et al. 1999). Additionally, increases in stiffness or damping caused by co-contraction would be expected to have larger effects on movements with larger amplitudes or higher velocities, directly contradicting the present observations. Therefore, we believe that the most likely explanation for the present results is an altered perception of ankle motion, matching previous results from passive, cyclical ankle motions (van Deursen et al. 1998).

The effects of 80 Hz tendon vibration decreased during faster movements, as prescribed with larger amplitudes or shorter periods. These results are consistent with the decreased effects of vibration during faster cyclical elbow motions (Steyvers et al. 2001), although this previous experiment did not control or vary movement amplitude. The decreased effects of tendon vibration at higher velocities can be attributed to the increased muscle spindle discharge frequency which normally accompanies more rapid muscle lengthening (Matthews 1963). When vibration is applied to a tendon, the overall population of muscle spindles is sensitive to a combination of both the applied vibration and the actual movement (Cordo et al. 1995; Cordo et al. 2005). With the higher spindle discharge frequencies naturally present during faster muscle lengthening, the application of tendon vibration would be expected to have a smaller net effect (Cordo et al. 1995). Therefore, the perceived change in muscle lengthening caused by tendon vibration would be smaller when the actual movement velocity was higher.

Alternatively, the reduced effects of tendon vibration during faster movements could be due to a decreased reliance of the central nervous system on peripheral feedback. It has long been suggested that producing faster movements increases the relative importance of feed-forward commands and decreases the importance or usefulness of feedback (Schmidt 2003). In the absence of vibration, participants in the present study were able to accurately move their bilateral ankles symmetrically even when the prescribed amplitudes were varied without explicit notice, indicating that some aspect of the movement must have been matched bilaterally. However, rather than solely matching proprioceptive feedback, participants may have matched their bilateral sense of effort, described by McCloskey and colleagues as the “effort of contraction rather than the actual tension produced” (McCloskey et al. 1974). Currently, it is believed that this sense of effort is derived, at least in part, from an efferent copy of the descending motor command (Proske and Gandevia 2012). During faster ankle movements, participants could potentially rely more on matching bilateral sense of effort and less on matching proprioceptive feedback. Indeed, when humans match their elbow positions while actively supporting a load through muscular contraction, the effects of tendon vibration on positioning error are reduced or even eliminated (Ansems et al. 2006). Additionally, when the position indicated by proprioceptive feedback is in conflict with the position indicated by sense of effort, stronger muscle contractions appear to increase the relative role of sense of effort (Smith et al. 2009). Therefore, increases in movement speed may result in an increased importance of sense of effort, a decreased importance of proprioceptive feedback, and consequently decreased effects of tendon vibration.

Finally, the decreased effects of tendon vibration during faster movements could be due to the increased muscle contractions required to power these movements. The relationship between a muscle’s contraction level and the effect of vibration is somewhat complex. Compared to passive muscles, weak isometric contractions have been reported to increase the response to vibration (Burke et al. 1976). However, a more extensive recent study found that weak (~5% maximum voluntary contraction; MVC) isometric contractions had mixed effects on the responsiveness of Ia afferents to tendon vibration (Fallon and Macefield 2007). Stronger muscle contractions can actually reduce the effects of tendon vibration (Goodwin et al. 1972), with contractions of around 25% MVC eliminating the effects of vibration during an elbow positioning task (Ansems et al. 2006). Therefore, the stronger muscle contractions required during our faster ankle movements may have contributed to the reduced effects of tendon vibration, possibly by increasing tendon tautness and decreasing the tendon stretch evoked mechanically by the vibration. However, the effect of muscle contraction level may be somewhat less pronounced during active, dynamic tasks. For example, during active wrist movements, altering the load (from about 6–17% MVC) did not alter the effects of tendon vibration (Cody et al. 1990). Additionally, Achilles tendon vibration still influences Ia afferent feedback during running, despite the high levels of plantarflexor muscle contraction (Cronin et al. 2011b).

The present experiments demonstrate that the psychophysical effects of ankle tendon vibration are reduced during more mechanically demanding tasks, but are unable to directly differentiate between several possible underlying mechanisms. Future experiments may be designed to distinguish between the effects of increased muscle lengthening velocity and the effects of increased descending commands. Specifically, angular velocity could be controlled by prescribing a combination of movement amplitude and period, as in the present experiments. While maintaining a constant prescribed kinematic trajectory, the required descending commands could be varied by altering the load (e.g. damping or inertia) around the ankle joint. A decreased effect of tendon vibration during higher effort movements would indicate that changes in muscle lengthening velocity are not solely responsible for the results observed in the present experiments. Similarly, varying the prescribed kinematic trajectory and load in conjunction could allow the required peak ankle torques to be held constant while angular velocity changed across trials. Under these conditions, a decreased effect of tendon vibration during faster movements would provide evidence for the importance of muscle lengthening velocity.

While the effects of vibration were influenced by its frequency, they were not maximized at 80 Hz. Vibration was more effective at 80 Hz than 40 Hz, but the effects of vibration continued to increase at higher frequencies, up to the highest tested frequency of 160 Hz. This unexpected result may be attributable to increases in vibration amplitude paralleling the increases in vibration frequency, a known limitation of the simple type of vibration device used in this study (Celik et al. 2009). Indeed, the vibration amplitude more than doubled when the vibration frequency was increased from 40 to 160 Hz (see Methods). While the effects of vibration are clearly influenced by vibration frequency (Roll and Vedel 1982; Roll et al. 1989), changes in vibration amplitude may also affect perception. When vibration frequency and amplitude are varied independently, gradual increases in vibration amplitude increase the responsiveness of individual muscle spindles (Fallon and Macefield 2007). Similarly, increasing vibration amplitude increases the psychophysical effects of tendon vibration during active movement (Cody et al. 1990). Therefore, it is possible that the increased effects of tendon vibration at 120 and 160 Hz are due to the larger vibration amplitudes during these trials, and are not directly due to increased vibration frequency.

Long-term effects of vibration did not appear to influence matching performance. Under certain conditions, brief periods of tendon vibration can have relatively long lasting effects on perception (Rogers et al. 1985; Wierzbicka et al. 1998). However, matching performance was not influenced by trial number in the present experiments, indicating that the effects of tendon vibration did not gradually accumulate over the course of the experiment. It is possible that the early bouts of tendon vibration caused a relatively rapid change in the responsiveness of muscle spindles, which was then maintained throughout the experiment. However, participants were able to accurately match their bilateral ankle movements (Amplitude Ratio ~ 1) in all trials without vibration, and were just as accurate at the end of the experiment as at the beginning. It is possible that identical vibration of antagonist muscles does not produce substantial long-term effects, as has been observed previously under isometric conditions (Gilhodes et al. 1992). Alternatively, the proprioceptive feedback produced during active, cyclical ankle movements may have been sufficient to reset the perception of movement and prevent any lasting effects of vibration.

The application of tendon vibration during active cyclical movements may have the potential to improve our understanding of novel aspects of functional human motor control. It is currently well understood that proprioception influences walking behavior by contributing to ongoing muscle activity, responses to mechanical perturbations, and phase transition timing (Cronin et al. 2011a). It has recently been suggested that proprioception may also contribute to the identification of the preferred movement pattern (Dean 2013), based on the results of experiments using simple ankle movements (Raburn et al. 2011; Merritt et al. 2011). Ankle tendon vibration could be used during such tasks to experimentally test whether proprioceptive feedback influences the choice of the preferred movement pattern, or whether the atypical preferred movement patterns in clinical populations can be partially attributed to altered proprioception.

Conclusions

Tendon vibration can be used to disrupt proprioceptive feedback during isolated active, cyclical ankle movements. The effect of vibration decreases during more mechanically demanding movements with increased peak velocities, although the mechanism underlying this change is not entirely clear. Future work could potentially use tendon vibration to test whether humans use proprioceptive feedback in the identification of the preferred movement pattern, and whether disrupted feedback predictably changes these patterns of movement.

Acknowledgments

This study was partially funded by a grant from the Department of Veterans Affairs, number 1IK2RX000750.

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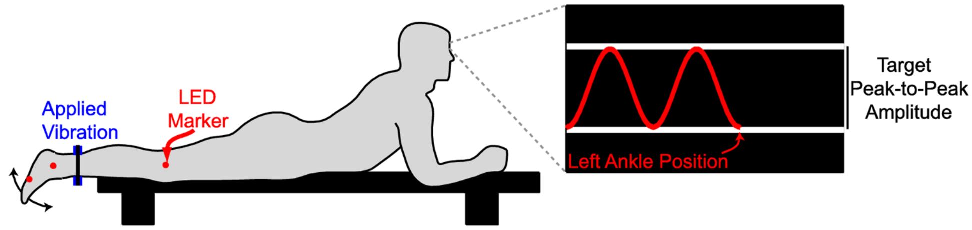

Fig. 1.
Participants matched the motion of their left and right ankles while lying prone on a padded table. Active LED markers on the legs were used to calculate ankle angle in near real-time. Visual feedback of the left ankle position was provided, along with target lines to set the movement amplitude. In some trials, vibration was applied to the right ankle plantarflexor and dorsiflexor tendons.

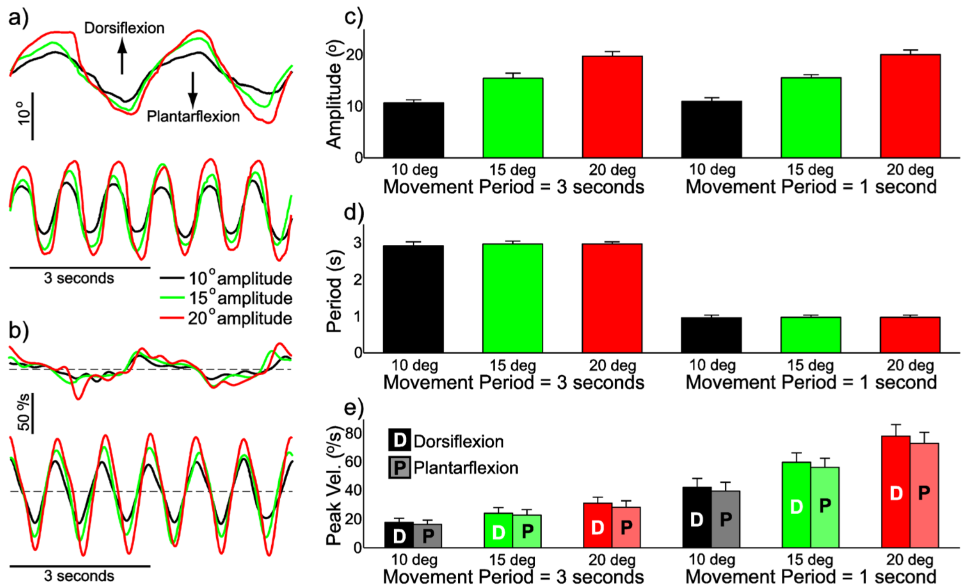

Fig. 2.

Participants altered their left ankle motion across trials. a) Angular displacement was varied during both 3-second period (top row) and 1-second period (bottom row) movements, as illustrated for a single participant. b) Angular velocity scaled with angular displacement for both 3-second period (top row) and 1-second period (bottom row) movements, as illustrated for the same participant. Horizontal dashed lines represent a velocity of zero. c) Peak-to-peak amplitude varied as prescribed. d) Movement period also varied as prescribed. e) Peak dorsiflexion and plantarflexion velocities were influenced by both movement amplitude and period. For panels c)-e), bars represent means across all participants and vibration conditions, and error bars represent standard deviations.

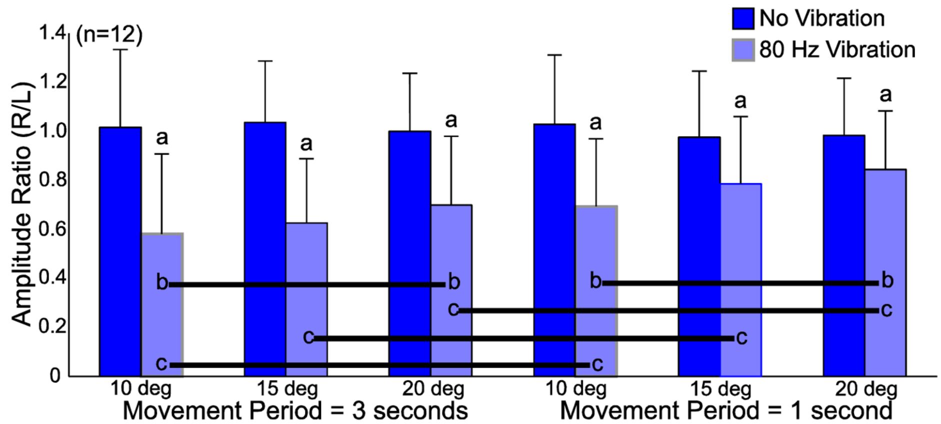

Fig. 3.

The ratio between right ankle movement amplitude and left ankle movement amplitude was influenced by the application of 80 Hz vibration and by parameters of the prescribed movement pattern. Error bars represent standard deviation, and the results of post-hoc tests ($p<0.05$) are indicated by lower case letters (a, b, or c) as described below. (a) The Amplitude Ratio during each vibration condition was significantly smaller than the Amplitude Ratio during each non-vibration condition. (b) Within the vibration trials, the Amplitude Ratio was significantly smaller for prescribed amplitudes of 10° than for prescribed amplitudes of 20°. (c) Within the vibration trials, the Amplitude Ratio was significantly smaller for periods of 3 seconds than for periods of 1 second.

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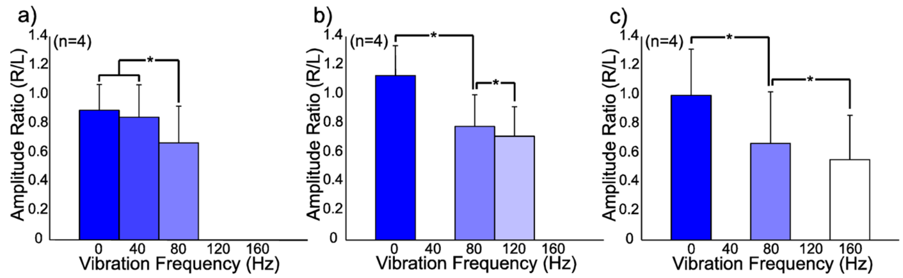

Fig. 4.
Vibration frequency influenced Amplitude Ratio. a) 40 Hz vibration did not affect Amplitude Ratio, while 80 Hz vibration caused a significant decrease in Amplitude Ratio. b) 120 Hz vibration decreased Amplitude Ratio significantly more than 80 Hz vibration. c) 160 Hz vibration also decreased Amplitude Ratio significantly more than 80 Hz vibration. For all panels, error bars represent standard deviation, and post hoc significance ($p<0.05$) is indicated by asterisks (*).