RESEARCH ARTICLE

Preferred movement patterns during a simple bouncing task

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SUMMARY

Elastic tissues in the human body can store and return mechanical energy passively, reducing the metabolic cost of cyclical movements. However, it is not clear whether humans prefer movement patterns that optimize this storage and return. We investigated the preferred movement pattern during a bouncing task for which non-invasive techniques can identify the resonant frequency, which is the least metabolically costly. We quantified the preferred and resonant bounce frequencies for three mechanical conditions. During 'normal' trials, subjects bounced while reclined on a sled that moves along a track. During 'added mass' trials, mass was added to the sled. During 'added stiffness' trials, a spring was attached between the sled and the supporting frame, parallel to the track. Subsequently, we quantified the preferred bounce frequencies during ischemia, a technique that disrupts the available sensory feedback. Mechanical condition had a significant effect on both the preferred and resonant frequencies. Changes in preferred frequency scaled with resonant frequency, but the preferred frequency was significantly lower than the resonant frequency. These results indicate that humans adapt their preferred bouncing pattern in response to changes in mechanical condition. Humans may prefer a lower than resonant frequency because of an inability to sense metabolic cost during our relatively short trials. In contrast, during ischemia the preferred bounce frequency remained constant even when mechanical condition was varied, indicating that feedback is necessary to adapt the preferred frequency to changes in mechanics. These findings suggest that disrupted sensory feedback may prevent humans from choosing the optimal movement pattern.

Key words: ischemia, resonant frequency, sensory feedback, tendon elasticity.

INTRODUCTION

Many cyclical human movements involve the storage and return of mechanical energy by passive elastic tissues, most notably tendon. Such tasks often require a musculotendon complex to successively perform negative and positive work, allowing the tendon to provide useful mechanical energy. The mechanics of human running, hopping and bouncing are often simplified as a spring-mass system (Bach et al., 1983; Blickhan, 1989; Cavagna et al., 1964; Dean and Kuo, 2011; Farley et al., 1991; McMahon, 1985) in which the spring element partially represents passive tissue elasticity. Recent experiments that used ultrasound to quantify musculotendon length changes have suggested that walking also takes advantage of tendon elasticity, although the mechanics are more aptly described as a catapult-like action rather than an oscillating spring mass (Ishikawa et al., 2005).

Tendon elasticity has the potential to reduce the metabolic energy required to perform a task, but only for particular movement patterns. Through passive stretch and recoil, tendons can reduce the need for active muscle work by allowing muscles to produce force while remaining close to isometric (Ishikawa et al., 2005; Takeshita et al., 2006). An isometric muscle action requires less metabolic energy than a force-matched concentric muscle action (Ryschon et al., 1997), implying that tendons may reduce the metabolic cost of a task. However, this metabolic benefit will only exist for movement patterns that allow tendons to store and return mechanical energy at appropriate points in the movement cycle. Investigation of a simple movement task allows identification of the mechanically optimal movement pattern. In the present study we investigated a

bouncing task in which the subjects' feet remained in contact with the supporting surface at all times, differentiating our task from hopping. Human bouncing has a resonant frequency that can be predicted non-invasively from the relationship between muscle activity and output force (Bach et al., 1983; Dean and Kuo, 2011). Both models (Dean and Kuo, 2011) and experiments (Takeshita et al., 2006) have indicated that bouncing at the resonant frequency allows the plantarflexors to remain close to isometric. In turn, the metabolic cost is minimized at this bounce frequency, even when the positive external mechanical work is held constant across frequencies (Dean and Kuo, 2011).

Humans may prefer movement patterns that optimally store and return energy through tendon loading, thus reducing metabolic cost. Minimization of metabolic cost has often been cited as a primary goal of motor control, particularly for steady-state walking on level ground (Alexander, 2002; Zarrugh et al., 1974). However, it is not clear whether humans prefer movement patterns that minimize metabolic cost for less familiar tasks or tasks for which altered mechanics (e.g. added mass or stiffness) have changed the mechanically optimal movement pattern. The ability of humans to adapt to altered mechanics may be directly investigated in bouncing, a task which allows explicit control of system mechanics and has a clearly defined resonant frequency.

Although the movement pattern that optimizes tendon loading may be preferred, the role of sensory feedback in identifying this pattern is unclear. Conceivably, humans could choose their preferred movement pattern without need for feedback either by following a predetermined motor plan or by minimizing the sense of effort,

defined as a cortical representation of the descending command required to accomplish a task (Burgess and Jones, 1997; McCloskey et al., 1974). Alternatively, humans may base their preference on sensory feedback including muscle length and velocity from muscle spindles, musculotendon force from Golgi tendon organs, joint position and skin pressure from cutaneous receptors (Proske and Gandevia, 2009; Windhorst, 2007), and metabolic expenditure from bloodstream chemoreceptors and peripheral metabotropic receptors (Ainslie and Duffin, 2009; Joyner, 1992; Windhorst, 2007). One method of disrupting sensory feedback commonly used in studies of human motor control is ischemic nerve blockade (Berger et al., 1984; Grey et al., 2001; Mazzaro et al., 2005; Sinkjaer et al., 2000). Applying ischemia substantially reduces sensory feedback before motor function is noticeably affected (Gottlieb et al., 1983; Magladery et al., 1950). In general, ischemia tends to first impact larger diameter afferent fibers (Magladery et al., 1950), which primarily transmit cutaneous, muscle length and muscle velocity feedback. However, there is substantial variability in diameter within afferent fiber types (Burke et al., 1983), so ischemia likely also affects the transmission of force feedback. Despite this inherent lack of precision, ischemia may be used to determine whether a general reduction in sensory feedback influences the choice of the preferred movement pattern.

We investigated the preferred movement frequency of humans performing a simple bouncing task under various conditions. The simplicity of the task allowed us to easily control system mechanics but retained the importance of tendon elasticity common to more complex movements. The response to variations in mechanics under a range of conditions revealed whether humans were able to adapt to these changes.

The purpose of these experiments was to determine whether humans choose their preferred frequency in order to match the resonant frequency, putatively minimizing metabolic cost. We hypothesized that, in response to altered mechanics, humans would adapt their preferred movement pattern to bounce at the resonant frequency. Secondarily, we hypothesized that disrupting sensory feedback with ischemia would prevent subjects from identifying the resonant frequency, thus eliminating adaptation.

MATERIALS AND METHODS

We quantified the preferred frequency and resonant frequency of a simple bouncing task. In some trials we varied the mechanical condition by either adding mass or adding external stiffness by placing a passive spring in parallel with the subject. We also disrupted sensory feedback in some trials using ischemia. The rate of positive mechanical work was controlled across frequency by providing subjects with appropriate feedback. Below we describe the experimental procedures and the simple mechanical model used to identify resonant frequency.

Setup

For all trials, subjects lay supine on the padded sled of a TotalGym (West Chester, PA, USA) instrumented with a force plate (AMTI, Watertown, MA, USA) under the subjects' feet to measure ground reaction force (GRF) and a position sensor consisting of a weak spring ($60\,\mathrm{N\,m^{-1}}$) in series with a load cell (Omega, Stamford, CT, USA) to measure displacement. Subjects were reclined 60 deg from vertical with their shoulders contacting padded supports rigidly attached to the sled (Fig. 1A). Subjects were instructed to bounce using only their ankle joints, keeping their knees fully extended. We monitored knee angle visually throughout each trial to ensure that subjects' knees were not flexing. The subjects' feet remained in contact with the force plate at all times, differentiating our task from hopping. The force plate was bolted to a custom-built aluminum frame welded to the TotalGym in order to minimize any vibration. We recorded the electromyographic (EMG) signal bilaterally from the soleus, medial gastrocnemius and lateral gastrocnemius muscles (Motion Lab Systems, Baton Rouge, LA, USA). Surface EMG electrodes were placed according to published SENIAM guidelines (Hermens et al., 1999). All data were recorded at 2000 Hz.

System mechanics were varied in some trials by adding either mass or stiffness. Mass was added to the TotalGym sled in increments of either 25 or 50% of the combined mass of the subject and the sled (11.8 kg). Stiffness was added in the form of a passive spring ($3200\,\mathrm{N\,m^{-1}}$) attached between the sled and the TotalGym frame in parallel with the sled track. When stretched, the spring exerted a force pulling the sled toward the force plate. Therefore, in both the added mass and added stiffness trials, the change in system mechanics increased the expected mean GRF during bouncing. Despite this similarity, our mechanical model (described below) predicts that adding mass would cause the preferred and resonant frequencies to decrease, whereas adding stiffness would cause the preferred and resonant frequencies to increase. The position of the spring was set so it never went slack during these trials. The stiffness value was chosen based on pilot experiments in which the spring qualitatively appeared to influence preferred bouncing frequency.

The mechanical demand of the task was set to the same level for all trials in a session (both preferred frequency trials and prescribed frequency trials) using feedback of the rectified, filtered velocity. The purpose of this feedback was to establish a constant task demand while allowing subjects to meet this demand with a range of movement patterns (i.e. either low-frequency, large-amplitude
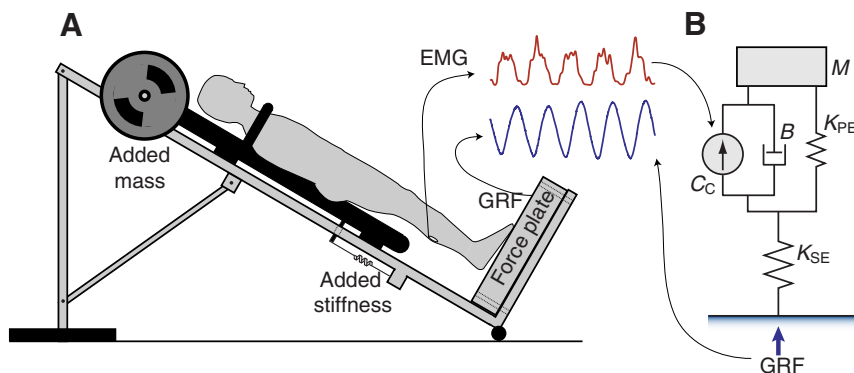

Fig. 1. A combination of experimental and modeling techniques were used to investigate a bouncing task. (A) Subjects bounced while reclined 60 deg from vertical on a TotalGym frame. This setup allowed us to add either mass or parallel stiffness to the system. (B) The electromyographic (EMG) and ground reaction force (GRF) data collected experimentally were used to perform parameter identification of a simple mechanical model. B, damping; C_C, contractile component; K_{PE}, parallel elastic component; K_{SE}, series elastic component; M, mass.

movements or high-frequency, small-amplitude movements). Velocity was calculated as the time derivative of displacement (smoothed using a moving average of the previous 20 ms). For feedback display purposes, velocity data were then rectified and smoothed (using a moving average of the previous second) so individual peaks were not visible for each bounce cycle (see Fig. 2). Subjects were visually provided with real-time feedback on a computer screen while performing the bouncing task. Subjects were instructed to match the feedback to a displayed target level, which was set prior to the recorded trials by instructing subjects to bounce with the largest comfortable range of motion at a frequency of 1 Hz, as prescribed by a metronome. By basing the feedback on a kinematic measure, we ensured that the same movement pattern (i.e. frequency and amplitude) would meet the task demands irrespective of mechanical condition. Following the target velocity behavior would keep the rate of positive mechanical work approximately constant across movement frequencies for each mechanical condition, but would allow the work rate to vary under the different mechanical conditions because of differences in the average GRF with added mass or stiffness.

Experimental protocol
Session A
Fourteen young, healthy subjects (25±2 years; 12 female, two male) participated in session A. Subjects performed a series of thirty 30 s bouncing trials. Trial order was randomized and 30 s of rest were allowed between trials. Subjects bounced under three mechanical conditions: (1) normal, (2) added mass equivalent to 50% of body and sled mass and (3) added stiffness of 3200 N m^{-1}. For each of the three mechanical conditions, subjects performed seven trials in which bouncing frequency was prescribed using a metronome set to a specific frequency (1, 1.5, 2, 2.25, 2.5, 2.75 and 3 Hz). By prescribing both processed velocity (through visual feedback) and frequency (through auditory feedback), we enforced a specific frequency–amplitude relationship in each prescribed frequency trial. Several subjects were unable to consistently match the target mechanical demand when bouncing at the slowest frequency, so all 1 Hz prescribed frequency trials were excluded from subsequent analysis. For each mechanical condition, subjects also performed three trials at their preferred frequency, for which they were instructed to bounce at whatever rate was most comfortable. For the preferred frequency trials, the processed velocity feedback was set to the same level as during the prescribed frequency trials, but frequency was not prescribed. Therefore, subjects had the freedom to bounce using any of the prescribed movement patterns if they so preferred.

Session B
Five young, healthy subjects (26±3 years; four female, one male) participated in session B, performing a series of 30 s bouncing trials. Four of these subjects had participated in session A on a previous day. Subjects bounced under three mechanical conditions: (1) normal, (2) added mass equivalent to 25% of body and sled mass and (3) added mass equivalent to 50% of body and sled mass. Initially, subjects performed nine trials with bouncing frequency prescribed by a metronome (set to 2, 2.5 and 3 Hz for each mechanical condition) in order to familiarize them with the bouncing task. For all remaining trials, subjects bounced at their preferred frequency while the available sensory feedback was varied.

In the first phase, termed 'pre-ischemia', subjects bounced at their preferred frequency for nine trials, three trials for each of the mechanical conditions. We then applied bilateral ischemia to the
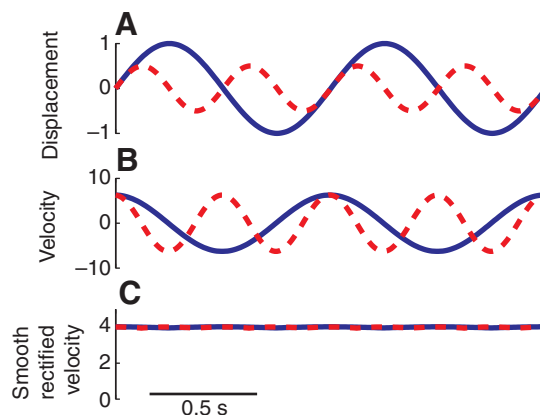

Fig. 2. During bouncing trials, subjects were provided with real-time feedback of smoothed, rectified velocity in order to set task demand. (A) Two displacement traces are illustrated. The solid line has a frequency of 1 Hz, and an amplitude arbitrarily assigned to be equal to 1. The dashed line has double the frequency (2 Hz) and half the amplitude (0.5 arbitrary units). (B) We calculate velocity as the time derivative of displacement. Note that the peak positive and negative velocity levels are identical for the two displacement traces. (C) Subjects were provided with real-time feedback of velocity, which has been rectified and smoothed over the previous second. The two traces overlap nearly identically, indicating that subjects could meet the task demand with a range of frequency values.

lower legs by inflating blood pressure cuffs around the thighs to 150 mmHg (Gottlieb et al., 1983). Once ischemia was applied, we monitored the EMG amplitude of the soleus short-latency (<60 ms) stretch reflex evoked by striking the Achilles tendon with a reflex hammer. We moved on to the next phase of the experiment, termed 'during ischemia', once the stretch reflex was substantially diminished (<20% of the pre-ischemia amplitude). This process took 16±1 min averaged across subjects, a time course similar to that reported previously (Gottlieb et al., 1983). Subjects then performed preferred frequency bouncing trials under the various mechanical conditions until they were unable to meet the task demand target level, indicating that ischemia had reduced motor function. Each of the five subjects performed from three to five ischemic bouncing trials before this occurred, including at least one trial under each mechanical condition. Finally, we slowly released the blood pressure cuffs and moved to the next phase of the experiment, termed 'post-ischemia', once the soleus stretch reflex had returned to its pre-ischemia amplitude and subjects reported normal sensation. This process took 7±1 min averaged across subjects. Subjects then repeated the nine preferred frequency bouncing trials performed prior to ischemia.

Data analysis
We calculated the rate at which positive mechanical work was performed using GRF and displacement data. The mean rate of positive work was normalized by subject mass and will be presented for the final 10 s of each 30 s trial to ensure that subjects had sufficient time to match the target behavior. We calculated the preferred bouncing frequency as the reciprocal of bounce period, the time between consecutive positive zero-crossings of the smoothed velocity (calculated as the time derivative of displacement; smoothed with a 10 Hz low-pass filter). The mean preferred frequency was calculated for each 2 s period within a 30 s trial, and for the final 10 s of each trial.

The bouncing resonant frequency was calculated using data from the series of prescribed frequency trials (1.5–3 Hz). EMG data were processed as follows: band-pass filtered at 20-1000 Hz; rectified; smoothed with a low-pass filter at 20 Hz; scaled to a percentage of the peak value across trials; and summed across all six muscles. This processing procedure was adapted from Hof and colleagues (Hof et al., 2002). At each prescribed bouncing frequency, the processed EMG signal and GRF were fit using sinusoids with variable amplitude, phase and amplitude offset. We calculated an EMG–GRF gain and phase relationship at each frequency from the amplitude and phase values (Dean and Kuo, 2011). These gain and phase values were used to determine the best-fit parameters of a simple mechanical model (Fig. 1B), as has been described in detail previously and found to accurately match experimental data (Dean and Kuo, 2011). Briefly, the model includes mass (M), a muscle with a contractile component (C_C), a damping element (B) and a parallel elastic element (K_{PE}), and a tendon represented as a series elastic element (K_{SE}). Additionally, the model includes an external elastic element (K_{EXT}), which is set to the passive spring stiffness for the added stiffness trials and set to zero for all other trials. A gain (G) from EMG to GRF is also included, as is a time delay (τ_d) for force production. The transfer function of this system in the Laplace domain, as a function of the complex argument 's', is:

$$\frac{F(S)}{E(S)} = \frac{K_{SE}Ms^2}{MBs^3 + M(K_{SE}+K_{PE})s^2 + (K_{SE}+K_{EXT})Bs + (K_{SE}K_{PE}+K_{PE}K_{EXT}+K_{SE}K_{EXT})} \cdot \frac{G}{\tau_d s + 1} . \quad (1)$$

The resonant frequency was identified as the frequency at which this model, with subject-specific parameters, had a peak gain. Examples of the experimental data and model fits are shown in Fig. 3.

Statistics

To determine whether subjects followed the target behavior, we quantified the rate of positive mechanical work across trials. For session A, we performed a repeated-measures two-way ANOVA to determine whether the rate of positive work was significantly influenced by bouncing frequency (six prescribed frequencies and preferred frequency) or mechanical condition (normal, added mass and added stiffness). For session B, we performed a repeated-measures two-way ANOVA to determine whether the rate of positive work was significantly different during ischemia or was significantly influenced by the mechanical condition (normal, added 25% mass and added 50% mass).

We then investigated the effects of mechanical condition and nervous system state on various aspects of bouncing performance. For session A, we performed one-way ANOVAs to determine whether mechanical condition (normal, added mass and added stiffness) had a significant effect on resonant frequency, preferred frequency or any of the best-fit mechanical model parameters. We also performed a two-way ANOVA to determine whether the preferred and resonant frequencies were significantly different from each other across mechanical conditions. For session B, we performed a series of repeated-measures one-way ANOVAs to determine whether the preferred frequency was significantly influenced by mechanical condition (normal, added 25% mass and added 50% mass) for each of the sensory feedback states (pre-ischemia, during ischemia and post-ischemia). *Post hoc* Tukey's tests were performed where appropriate. For all tests we treated $P<0.05$ as statistically significant. Data are presented as means ± s.d. unless otherwise indicated.
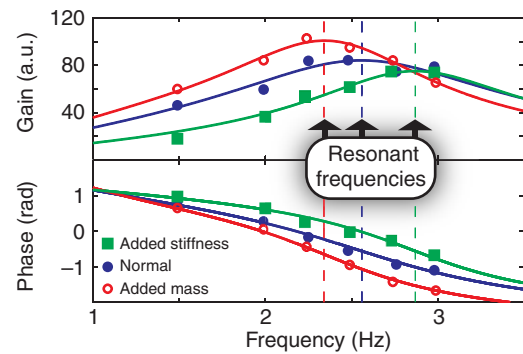

Fig. 3. The frequency-dependent relationship between EMG and GRF was affected by the addition of mass or stiffness, as illustrated for a single subject. Data points represent experimental results and solid lines represent model fits. The resonant frequency was defined as the frequency with maximal gain from EMG to GRF. Resonant frequency, which is indicated with dashed vertical lines, decreased with added mass and increased with added stiffness. The phase difference between EMG and GRF decreased at higher bounce frequencies for all mechanical conditions.

RESULTS

We found that subjects adapted their preferred movement frequency in response to altered bouncing mechanics, but consistently preferred to bounce more slowly than the resonant frequency. Disruption of sensory feedback using ischemia eliminated this adaptation. Details of our experimental findings are described below.

Subjects successfully matched the target behavior using real-time feedback of rectified, filtered velocity. In session A, the mean rate of positive mechanical work did not vary significantly between each of the prescribed frequencies (1.5–3 Hz) or the preferred frequency ($P=0.79$). However, the mean positive work rate was significantly influenced by the mechanical condition (normal, 0.29±0.07 W kg^{-1}; added mass, 0.44±0.10 W kg^{-1}; added stiffness, 0.37±0.09 W kg^{-1}; $P<0.0001$). In session B, the mean positive work rate was not significantly different during ischemia compared with before or after ischemia ($P=0.18$), but did vary significantly with mechanical condition (normal, 0.33±0.09 W kg^{-1}; added 25% mass, 0.42±0.10 W kg^{-1}; added 50% mass, 0.49±0.13 W kg^{-1}; $P<0.0001$).

The resonant frequency, as calculated with our simple mechanical model, changed when the system mechanics were altered (Fig. 3). Adding mass significantly decreased the resonant frequency whereas adding stiffness significantly increased the resonant frequency ($P<0.0001$). Although calculating resonant frequency was the primary goal of our model, the best-fit mechanical parameters are also presented (Table 1). The only mechanical parameter that was significantly influenced by mechanical condition was damping ($P=0.015$), which increased with added mass or stiffness. Of particular note, the calculated series stiffness, which represents passive tendon stiffness, remained nearly identical across mechanical conditions.

The preferred frequency was also influenced by system mechanics, with the changes qualitatively similar to those in resonant frequency. Over the course of the 30 s trials, preferred frequency gradually increased before appearing to reach a plateau (Fig. 4A). Throughout the duration of the trials, added mass decreased the preferred frequency whereas added stiffness increased the preferred frequency. Averaged over the final 10 s of each trial, the main effect of mechanical condition on preferred frequency was significant ($P=0.0029$; Fig. 4B). However, for all mechanical

Table 1. Best-fit parameters for our simple mechanical model using experimental data from the normal, added mass and added stiffness trials of session A (means ± s.d.)

Parameter	Normal	Added mass	Added stiffness
Resonant frequency (Hz)	2.64±0.23	2.33±0.16[#]	3.02±0.27*
Total mass (kg)	75.2±10.9	110.5±17.6	75.2±10.9
Series stiffness (N m^{-1})	26900±3800	26700±5400	26600±4200
Damping (N s m^{-1})	2730±810	3580±660*	3720±1320*
Parallel stiffness (N m^{-1})	13200±4600	7800±9100	13200±13800
External stiffness (N m^{-1})	0	0	3200

Resonant frequency was significantly influenced by mechanical condition (#, significantly lower than normal; *, significantly higher than normal; $P<0.05$). The only mechanical model parameter significantly affected by changes in mechanical condition was damping, which increased with both added mass and stiffness. The best-fit parallel stiffness value was quite variable across subjects, particularly with altered mechanics. In part, this is due to a best-fit value of zero in some subjects, essentially reducing the model to one without parallel stiffness [as used by Bach et al. (Bach et al., 1983)]. Statistical tests were not performed on total mass or external stiffness, which changed by definition.

conditions, the preferred frequency was significantly lower than the calculated resonant frequency ($P=0.0001$; Fig. 4B).

Peripheral ischemia of the lower legs eliminated subjects' ability to adapt their preferred frequency to altered mechanics (Fig. 5). Prior to ischemia being applied, the addition of mass (25 and 50% body mass) significantly affected the preferred frequency ($P=0.0001$). Similarly, once subjects had recovered from ischemia, adding mass had a significant effect on the preferred frequency ($P=0.003$). However, during ischemia the addition of mass had no effect on the preferred frequency ($P=0.69$).

DISCUSSION

Investigation of a simple bouncing task revealed that humans adapted their preferred movement pattern to altered system mechanics, but only when sensory feedback was intact. The resonant bouncing frequency was influenced by altered mechanics, whether in the form of added mass or added stiffness. Although subjects scaled their preferred frequency with the resonant frequency, the preferred frequency was consistently lower than the resonant frequency, contradicting our hypothesis. This result may be combined with the earlier finding that the metabolic cost of bouncing is minimized at the resonant frequency (Dean and Kuo, 2011) to suggest that humans

do not immediately choose the movement pattern with the lowest metabolic cost when faced with unfamiliar tasks. Future research should directly test this suggestion. Ischemia eliminated the adaptation to altered mechanics, consistent with our hypothesis that sensory feedback is required for this adaptation to occur.

The calculated resonant frequency, at which tendon elasticity was optimally harnessed, was predictably influenced by adding mass or stiffness. Adding mass decreased the resonant frequency and adding stiffness increased the resonant frequency, similar to previously reported results for pendular arm swing (Hatsopoulos and Warren, 1996). Qualitatively, the changes in resonant frequency match our expectations for a simple spring-mass system. Any quantitative differences between simple spring-mass behavior and our experimental results may be explained by the damping included in our model. The calculated damping increased for both added mass and added stiffness, potentially because of increased muscle viscosity resulting from the higher forces required to power the movement, as reported for a reduced animal preparation (Cecchi et al., 1997).

The preferred bouncing frequency also varied with altered mechanics, scaling with the resonant frequency. The effects of system mechanics were evident throughout the trials, with the
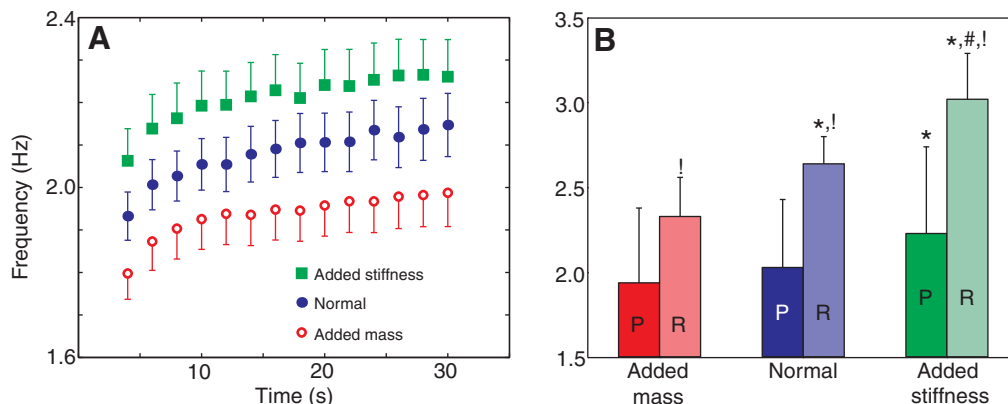

Fig. 4. Both the preferred and resonant bouncing frequencies were significantly affected by mechanical condition. (A) The group mean preferred frequency is plotted for 2 s periods over the duration of the 30 s trial. The first 2 s are ignored. Throughout the trial, subjects preferred a higher frequency with added stiffness and a lower frequency with added mass. The preferred frequency appeared to reach a plateau after approximately 15 s. To avoid overlap, data are plotted as means ± s.e.m. (B) The preferred frequency (P) over the final 10 s of the bouncing trials was significantly affected by mechanical condition. The calculated resonant frequency (R) was also significantly influenced by the mechanical condition, while the preferred frequency was significantly lower than the resonant frequency. Data are plotted as means ± s.d. Significant results of Tukey's *post hoc* tests ($P<0.05$) are indicated symbolically: *, significantly greater than the comparable added mass frequency; #, significantly greater than the comparable normal frequency; !, significantly greater than the preferred frequency for the matched mechanical condition.
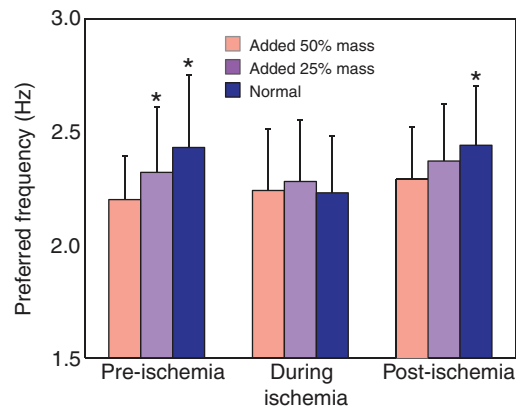
Fig. 5. Disrupting sensory feedback with ischemia limited subjects' ability to adapt to added mass. Pre-ischemia and post-ischemia, mechanical condition had a significant effect on the preferred frequency. During ischemia, added mass did not significantly affect the preferred frequency. Data are plotted as means ± s.d. Significant results of Tukey's *post hoc* tests ($P<0.05$) are indicated symbolically: *, significantly greater than the added 50% mass frequency for the matched nervous system state.

preferred frequency appearing to reach a plateau by the end of the 30 s period (see Fig. 4A). Our bouncing results can be compared with earlier studies of hopping, in which adding mass decreased the preferred frequency (Austin et al., 2002) but adding external stiffness did not significantly increase the preferred frequency (Ferris et al., 2006). These hopping experiments differed from the present experiments in several ways, most notably in that they included a clear aerial phase in which the feet were not in contact with the support surface. The hopping experiments also did not quantify resonant frequency and did not control the mechanical demands of the task, allowing both movement frequency and amplitude (hopping height) to vary freely. By providing real-time velocity feedback and a prescribed target level, we ensured that task demand remained constant across bouncing frequency.

Although both the preferred and resonant bouncing frequencies were similarly affected by altered mechanics, the preferred frequency was consistently lower than the resonant frequency. This finding contradicts our hypothesis that subjects prefer to bounce at the resonant frequency, at which elastic energy return would be optimized and metabolic cost would likely be minimized (Dean and Kuo, 2011). This result also conflicts with the reported match between resonant and preferred frequency for pendular arm swing (Hatsopolous and Warren, 1996), and the finding that the preferred step frequency minimizes metabolic cost during walking on level ground (Zarrugh et al., 1974). It is possible that subjects chose a non-optimal movement pattern because of the unfamiliarity of our bouncing task. Although subjects scaled their preferred frequency with the resonant frequency, they may not have had sufficient time to sense metabolic cost and adapt their preferred movement pattern in response. Sensing changes in carbon dioxide concentration using central bloodstream chemoreceptors has been reported to take a matter of minutes (Ainslie and Duffin, 2009), substantially longer than our 30 s trials.

Ischemia eliminated the effect of added mass on preferred bouncing frequency, suggesting that sensory feedback is required for short-term adaptation to changes in system mechanics. During ischemia, the preferred frequency no longer scaled with the resonant frequency. Sense of effort, which would not be affected by ischemia, thus appears to be insufficient to identify the preferred bouncing frequency. This contrasts with the primary role of sense of effort during bilateral isometric (Simon and Ferris, 2008) and dynamic (Simon et al., 2009) force matching tasks. Although our results suggest the importance of peripheral feedback, ischemia does not permit discrimination between different types of feedback. Ischemia also has a gradual effect on motor function, although our subjects were able to voluntarily meet the target task demand for several trials once the stretch reflex had been substantially decreased. Future research should investigate the roles of specific sources of feedback using techniques that will minimally disrupt motor function: vibration may be used to eliminate or alter feedback primarily from muscle spindles through Group Ia fibers (Cordo et al., 1995; Roll and Vedel, 1982; Roll and Vedel, 1989); tizanidine may be used to eliminate feedback from muscle spindles through Group II fibers (Grey et al., 2001); local anesthetic may be used to reduce cutaneous sensation (Meyer et al., 2004); and fentanyl may be used to disrupt peripheral metabotropic feedback from Group III or IV fibers (Amann et al., 2009).

The decrease in plantarflexor stretch reflexes caused by ischemia may have directly affected muscle activity during our bouncing task, but probably did not cause the observed elimination of short-term adaptation. In hopping, the plantarflexors exhibit a burst of muscle activity at a post-landing time consistent with a short-latency stretch reflex (Funase et al., 2001; Zuur et al., 2010). Subjects performing our bouncing task were in contact with the support surface at all times, so the lack of a landing event would likely reduce the elicited stretch response. Also, the stretch reflex is time-locked to mechanical events during a movement cycle (i.e. rapid muscle stretch), so the elicited muscle activity would be expected to encourage bouncing at a particular frequency independent of added mass or stiffness. Therefore, it is unlikely that disruption of sensory feedback eliminated the adaptation to altered mechanics as a result of spinal reflex changes. Instead, we suggest that short-term adaptation is lost because ischemia reduces the available sensory information that subjects use to choose their preferred frequency.

Despite the limitations of ischemia as a neurophysiological technique, it has previously been used to investigate the effects of feedback during more complex tasks, including locomotion. These studies have largely focused on the role of sensory feedback in the response to perturbations during gait (Berger et al., 1984; Grey et al., 2001; Mazzaro et al., 2005; Sinkjaer et al., 2000). In contrast, our focus was on the role of feedback in choosing the steady-state preferred movement pattern. Our results suggest that sensory feedback is necessary for humans to adapt to altered mechanical demands, scaling their preferred frequency with the mechanically optimal frequency. Therefore, sensory feedback may be required during locomotion for appropriate storage and return of mechanical energy in the elastic tendon. During human running, the gastrocnemius remains close to isometric for much of stance while the Achilles tendon stores and returns mechanical energy (Lichtwark et al., 2007). Our results suggest that intact sensory feedback may be required to identify this mechanically advantageous movement pattern. Similarly, recent work suggests that humans prefer walking patterns in which the plantarflexors do not contract concentrically throughout stance, but rather either slightly lengthen or remain nearly isometric (Ishikawa et al., 2005), which could be sensed using feedback from muscle spindles. When the mechanical demands of gait are altered by having subjects walk uphill or downhill, the medial gastrocnemius activation pattern changes in such a way that the muscle remains close to isometric (Lichtwark and Wilson, 2006), thereby continuing to effectively store and return elastic tendon energy. This change may be the result of adaptation dependent on sensory feedback, as found for our simpler bouncing task.

Our findings may have implications for clinical populations with limited functional mobility. Sensory feedback can be disrupted through many pathological mechanisms, from peripheral neuropathy often associated with diabetes (Zochodne et al., 2008) to a reduced ability to integrate and interpret sensory information following a cortical or subcortical stroke (Schabrun and Hillier, 2009). Disrupted feedback could prevent identification of appropriate movement patterns, thus precluding optimal storage and return of mechanical energy in the tendon during either bouncing or a more complex task such as running or walking. Future research should investigate whether reduced sensory accuracy limits the ability of patients to identify the optimal movement pattern, thus contributing to the increased metabolic cost of locomotion that can restrict mobility (Macko et al., 1997).

LIST OF SYMBOLS AND ABBREVIATIONS

B	damping
C_C	contractile component
EMG	electromyographic
G	gain
GRF	ground reaction force
K_{EXT}	external elastic component
K_{PE}	parallel elastic component
K_{SE}	series elastic component
M	mass
τ_d	time delay

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