MINIMIZATION OF THE METABOLIC energy expenditure required to perform a task has been proposed as an important goal during human locomotion (Alexander 2002) and other repetitive movement tasks (Sparrow and Newell 1998). Humans would thus be expected to prefer movement frequencies that allow the task to be accomplished with the minimal metabolic rate. Evidence supporting this proposal in locomotion derives from experiments that quantified the metabolic rate of walking at a set speed, as enforcing a step frequency higher or lower than the freely selected preferred frequency increases metabolic rate (Minetti et al. 1995; Umberger and Martin 2007; Zarrugh and Radcliffe 1978). While the mechanical demands of walking likely influence the frequency at which metabolic rate is minimized (Kuo 2001), a simple analytical method of identifying an individual’s optimal step frequency from mechanics does not currently exist.

The presence of a mechanically optimal movement frequency can be more easily investigated with a simple bouncing task. The combination of noninvasive experimental methods and system identification techniques allows identification of the neuromechanical resonant bouncing frequency for individual subjects (Bach et al. 1983; Dean and Kuo 2011). Both experiments (Takeshita et al. 2006) and model simulations (Dean and Kuo 2011) have demonstrated that appropriate choice of bouncing frequency can allow mechanical energy to be stored and returned in the Achilles tendon, enabling the plantarflexor muscles to remain close to isometric. The metabolic rate while performing positive mechanical work on the body is minimized when subjects bounce at frequencies close to this identified resonant frequency (Dean and Kuo 2011), likely because isometric muscle actions demand less metabolic energy than concentric muscle actions (Ryschon et al. 1997).

Despite the apparent metabolic benefits, humans do not appear to initially prefer bouncing at the resonant frequency. We have previously shown that varying system mechanics by adding mass or parallel stiffness predictably affects the identified resonant frequency (Raburn et al. 2011). However, in 30-s trials, subjects preferred a frequency significantly less than the resonant frequency (Raburn et al. 2011). It is possible that subjects did not initially prefer the resonant, and presumably metabolically optimal, frequency due to the unfamiliarity of the bouncing task. In contrast, walking over level ground is a more familiar task, for which humans may have learned the optimal step frequency at a given speed over the course of their development. It is also possible that the relatively short duration of our bouncing trials (30 s) was not sufficient for subjects to identify the optimal frequency.

The goal of the present project was to determine whether humans adapt their preferred bouncing frequency over time to bounce at the metabolically optimal frequency. We quantified metabolic rate while subjects bounced at their preferred frequency and at prescribed frequencies at and around the previously identified resonant frequency. We hypothesized that the metabolic rate would be minimized when subjects bounced at the resonant frequency, not when subjects were allowed to bounce at their preferred frequency. Additionally, we hypothesized that the preferred frequency would initially be lower than the resonant frequency, but would approach the resonant frequency over time as subjects adapted in response to sensory feedback.

Kristen J. Merritt, Caroline E. Raburn, and Jesse C. Dean
Division of Physical Therapy, College of Health Professions, Medical University of South Carolina, Charleston, South Carolina

Submitted 28 October 2011; accepted in final form 30 January 2012
MATERIALS AND METHODS

We quantified the rate of metabolic energy expenditure while human subjects performed a reclined bouncing task using a variety of movement frequencies, both preferred and prescribed. The characteristics of this task allowed us to determine whether subjects adapted their movement frequency toward the predetermined neuromechanical resonant frequency over time. Specifically, the simplicity of the task (1 degree of freedom, powered by 1 muscle group) has previously allowed us to identify the resonant frequency using a combination of experimental measurements and model simulations. By reclining the subjects, we decreased the force demands on the plantarflexors compared with an upright bouncing task, reducing the risk of fatigue while subjects bounced for a period of 6 min. Quantifying metabolic rate allowed us to directly address the general belief that minimizing metabolic rate is an important factor in motor control during many movement tasks involving either the lower or upper extremities.

Subjects. Twelve young, healthy subjects (10 female, 2 male; 25 ± 2 years; 65.6 ± 12.4 kg; means ± SD) participated in this study. Each of the subjects had previously (within the prior week) participated in an experiment in which the neuromechanical resonant frequency of bouncing was identified (Raburn et al. 2011). Briefly, the resonant frequency was defined as the frequency with a maximal gain between plantarflexor electromyographic activity and ground reaction force (GRF), as fit by a simple Hill-type mechanical muscle model (Dean and Kuo 2011; Raburn et al. 2011). Across the present experiment’s subjects, the identified resonant frequency was 2.64 ± 0.25 Hz (means ± SD). Written informed consent was obtained from each subject, and the protocol was approved by the Institutional Review Board at the Medical University of South Carolina.

Setup. For all trials, subject lay supine on the padded sled of a TotalGym (West Chester, PA) reclined 60° from vertical (Fig. 1). The TotalGym was instrumented with a force plate (AMTI, Watertown, MA) under the subjects’ feet to measure GRF and a position sensor consisting of a weak spring (60 N/m) in series with a load cell (Omega, Stamford, CT) to measure displacement. GRF and displacement data were sampled at 2,000 Hz. Subjects’ shoulders were in contact with padded supports rigidly attached to the sled, and they were instructed to bounce only using their ankle joints, keeping their feet in contact with the force plate. We continuously monitored knee angle throughout each trial to ensure the knees remained fully extended. Rates of oxygen consumption and carbon dioxide production were quantified using a metabolic cart (iWorx, Dover, NH).

During all bouncing trials, subjects received real-time visual feedback of their rectified, filtered movement velocity on a monitor placed directly in front of them, as described in detail previously (Raburn et al. 2011). Briefly, velocity was calculated as the time derivative of displacement (smoothed using a moving average of the previous 20 ms), rectified, and smoothed using a moving average of the previous second. This feedback established a constant mechanical demand for the task, but allowed subjects to meet this demand using a range of movement patterns. For example, subjects could bounce either with a low frequency and high amplitude, or with a high frequency and low amplitude. Subjects were instructed to match this feedback to a target level set by initially having subjects bounce with their largest comfortable range of motion at a frequency of 1 Hz, as set by a metronome. Matching the visual target would result in a constant work rate across bounce frequencies. Our previous work (Raburn et al. 2011) and preliminary experiments indicated that subjects were able to maintain this work rate for multiple bouncing trials.

Protocol. Subjects performed a series of seven 6-min trials. In one trial, subjects lay relaxed with their knees extended to quantify resting metabolic rate. In five trials, subjects bounced at a prescribed frequency as set by a metronome, which provided auditory feedback throughout these trials (at 80%, 90%, 100%, 110%, and 120% of their previously identified resonant frequency). In one trial, subjects bounced at their preferred frequency without auditory feedback, following instructions to bounce at whatever frequency was most comfortable while still matching the work rate visual target. The preferred frequency was allowed to vary during the trial. Five minutes of rest were given between trials to ensure subjects returned to their baseline steady-state metabolism. Trial order was randomized to avoid a potential systematic effect on metabolic rate. While the random trial order caused variation in the amount of experience subjects had with the bouncing task prior to performing the preferred frequency trial, all subjects had at least some experience with the task due to their participation in an earlier study (Raburn et al. 2011).

Data analysis and statistics. The rate of positive mechanical work was calculated from the GRF and displacement data, and normalized by subject mass. Net metabolic rate was calculated from oxygen consumption and carbon dioxide production data using a standard equation (Brockway 1987), subtracting out the resting metabolic rate. For each frequency condition, we tested whether steady-state metabolism had been reached by performing linear regressions of the metabolic rates measured in minutes 4, 5, and 6. For all frequency conditions, the best-fit slope was not significantly different from zero ($P > 0.32$), indicating that a steady state had been reached. Net metabolic rate was averaged over this 3-min period and was normalized by subject mass. During all trials, the respiratory exchange ratio was monitored and found to be less than 1.0, indicating that subjects were using primarily oxidative metabolism. Net efficiency was defined as the rate of positive mechanical work divided by the net metabolic rate, based on the classic definition used by Gaesser and Brooks (1975). However, it should be noted that our bouncing task differs from the cycling task of Gaesser and Brooks (1975). However, it should be noted that our bouncing task differs from the cycling task of Gaesser and Brooks (1975) in that our task involved the performance of no net work and was designed so that the amount of positive work was held constant across trials. For comparison purposes, the maximum net efficiency of the cycling task was observed to be 24.1% (Gaesser and Brooks 1975), similar to the maximum net efficiency of ∼25% while walking or running uphill (Margaria 1968; Margaria et al. 1963).

Bouncing frequency was defined as the reciprocal of bounce period, the time between consecutive zero crossings of movement velocity. We calculated the average bouncing frequency for 5-s periods throughout each trial, and for the final 3 min of each trial. For the purpose of statistical comparisons, bouncing frequency was expressed as a percentage of the identified resonant frequency. These values were also converted back to more familiar units (Hz) when the data were plotted. The time course of the change in preferred frequency was quantified by fitting the average group data with a standard equation for a decaying first-order exponential with a constant offset:

$$f(t) = f_{ss}(1 - Ae^{-ct})$$

In this equation, $f(t)$ represents the bouncing frequency at a given point in time, $f_{ss}$ represents the steady-state bouncing frequency, $t$
represents time, and \( \tau_c \) represents the adaptation time constant. The \( A \) term accounts for the initial non-zero offset of the bouncing frequency.

Three repeated measures one-way ANOVA were performed to determine if the frequency condition significantly affected metabolic rate, rate of positive mechanical work, or net efficiency. A repeated measures one-way ANOVA was performed to determine if the frequency condition (5 prescribed frequency trials and 1 preferred frequency trial) significantly affected the actual bouncing frequency during the final 3 min of each trial. An additional repeated measures one-way ANOVA was performed to determine if the preferred frequency changed over the course of the 6-min trial. Post hoc Tukey tests were performed when significant main effects of the ANOVA were found. For all tests, we treated \( P < 0.05 \) as statistically significant.

RESULTS

We found that the metabolic rate was not minimized during the preferred frequency trial, but was lowest when subjects bounced at prescribed frequencies near resonance. The preferred bouncing frequency changed over the course of the 6-min trial, gradually approaching the calculated neuromechanical resonant frequency.

Allowing subjects to bounce at their preferred frequency did not optimize metabolic energy expenditure. The average net metabolic rate varied significantly across frequency conditions (\( P = 0.0055 \)), with a minimum value close to the resonant frequency (Fig. 2A). The average net metabolic rates were \( 1.05 \pm 0.35, 0.98 \pm 0.51, 0.81 \pm 0.34, 0.73 \pm 0.31, 0.97 \pm 0.41, \) and \( 1.00 \pm 0.40 \) W/kg (means \( \pm SD \)) for the 80%, 90%, 100%, 110%, 120%, and preferred frequency trials, respectively. None of the subjects exhibited a minimum metabolic rate during the preferred frequency trial; for all subjects, metabolic rate was minimized during a prescribed frequency trial at either 90%, 100%, or 110% of the calculated resonant frequency. While we prescribed a constant rate of positive mechanical work, there was a significant (\( P = 0.041 \)) main effect of bouncing frequency, as subjects performed slightly more positive work during prescribed bouncing at the resonant frequency (Fig. 2B). Net efficiency also was significantly (\( P = 0.0016 \)) influenced by the frequency condition (Fig. 2C). The net efficiency exceeded 25%, the expected value of performing positive muscular work, when subjects bounced near the resonant frequency but not when they bounced at their preferred frequency. Efficiency was highest when subjects bounced at the resonant frequency (\( 40.3 \pm 17.6\% \)) and 110% of the resonant frequency (\( 40.8 \pm 13.2\% \)).

Bouncing frequency scaled with the prescribed metronome frequency, but subjects did not exactly follow the specified behavior. On average, the actual bouncing frequency was higher than prescribed for the low-frequency trials (80% and 90% resonant frequency) and lower than prescribed for the highest-frequency trial (120% resonant frequency), in both cases becoming closer to the resonant frequency (Fig. 3A). Averaged over the final 3 min of each trial, the actual bouncing frequency was significantly (\( P < 0.0001 \)) influenced by the prescribed frequency condition (Fig. 3B).

The preferred bouncing frequency changed significantly (\( P < 0.0001 \)) over the course of the 6-min trial. The average preferred frequency was initially \( \sim 80\% \) of the resonant frequency, but gradually became faster throughout the trial (Fig. 3A). Averaged over the final 3 min, the preferred frequency (\( 2.49 \pm 0.50 \) Hz) was not significantly different from the bouncing frequency when resonance was prescribed (\( 2.66 \pm 0.11 \) Hz) (Fig. 3B). However, the preferred frequency was more variable between subjects than any of the prescribed bouncing frequencies, as evidenced by the magnitude of the standard deviation error bars (Fig. 3B). The change in preferred frequency over time was well fit (\( R^2 = 0.97 \)) by a decaying exponential with a time constant of 136 s (Fig. 4). The preferred frequency was significantly (\( P < 0.05 \)) less than the resonant frequency for the first 110 s of bouncing.

DISCUSSION

We investigated a simple, one degree-of-freedom bouncing task to determine whether humans prefer the metabolically optimal movement frequency. As hypothesized, the net efficiency of bouncing was maximized during prescribed frequency trials near resonance, not during the preferred frequency trial. Also supporting our hypothesis, the preferred frequency was initially lower than the neuromechanical resonant frequency, but gradually approached resonance over time. As predicted from the system mechanics, bouncing frequency influenced task performance. Supporting earlier results

![Fig. 2](http://jn.physiology.org/)

**Fig. 2.** Metabolic and mechanical measures varied with frequency condition. A: net metabolic rate was significantly (\( P = 0.0055 \)) influenced by frequency. B: rate of positive mechanical work varied significantly (\( P = 0.041 \)) with frequency. C: net efficiency varied significantly (\( P = 0.0016 \)) with frequency. The expected efficiency value of performing positive muscular work (25%) is indicated by a dashed line. For all panels, results of post hoc tests are indicated symbolically (a, significantly different from 80% trial; b, significantly different from preferred trial; c, significantly different from 25% efficiency). Data are plotted as means \( \pm SD \).
data are plotted both as a percentage of the resonant frequency (right axis) and post hoc tests indicated that the preferred frequency was significantly (P < 0.0001) main effect on actual bouncing frequency. Data are plotted as means ± SD. Post hoc test significance is indicated symbolically (d, significantly different from 100% trial; e, significantly different from 110% trial; f, significantly different from 120% trial). For both A and B, data are plotted on the right axes as a percentage of the identified resonant frequency. On the left axes, these values are converted back into the more familiar units of Hz using the group average resonant frequency. (Dean and Kuo 2011), metabolic rate was minimized and net efficiency was maximized near the resonant frequency. In contrast, allowing subjects to bounce with their preferred movement pattern did not minimize metabolic rate. Across trials, the maximum net efficiency was 41%, higher than expected from muscles performing positive work and similar to the previously reported value during upright bouncing of 45% (Dean and Kuo 2011). Such high net efficiency values during cyclical tasks have long been attributed to the storage and return of mechanical energy by passive elastic elements (Thys et al. 1975), allowing muscles to act nearly isometrically without producing substantial costly mechanical work (Ryschon et al. 1997). This proposal is supported by recent work that used experiments (Takeishi et al. 2006) or model simulations (Dean and Kuo 2011) to investigate muscle behavior during a bouncing task similar to that tested in the present study.

The preferred bouncing frequency changed over time, indicating that the preferred movement pattern was not chosen through a feed-forward process but was instead dependent on feedback. Initially, subjects preferred a bouncing frequency lower than the resonant frequency, as previously reported during shorter 30-s trials (Raburn et al. 2011). But rather than maintaining this motor plan over time, subjects gradually increased their preferred frequency to approach resonance. In contrast, Snaterse and colleagues (2011) reported that the preferred step frequency during walking is chosen based primarily on a preprogrammed motor plan. This apparent contradiction may be due to differences in practice or familiarity with the movement task (Thoroughman and Shadmehr 1999). Walking at a range of speeds is a familiar task, which would be conducive to the development of a motor plan allowing rapid choice of the optimal step frequency at a given speed. A reclined bouncing task is less familiar and may thus be less likely to be associated with a preprogrammed movement pattern. Future research could test this explanation by allowing subjects to practice the bouncing task under various conditions, and determine whether they develop a motor plan that allows them to immediately identify and prefer the metabolically optimal movement pattern. Alternatively, our subjects may have been able to adapt over time based on the relative simplicity of the task. In contrast to walking, bouncing involves only one degree of freedom and can be powered by a single muscle group. This may reduce the complexity of the feedback upon which adaptation is based.

The preferred frequency gradually increased over a period of minutes, suggesting a relatively slow mechanism underlying the adaptation process. The adaptation time course (calculated τc = 136 s) is limited by two factors: 1) the speed with which the sensory feedback driving adaptation becomes available; and 2) the rate at which the brain can optimize the movement pattern by evaluating this sensory feedback, a process that has been termed reward prediction (Izawa and Shadmehr 2011). Proprioceptive feedback from peripheral sensors (e.g., muscle spindles) representing the body’s mechanical state is sensed by the cortex in a matter of milliseconds (Starr et al. 1981), potentially contributing to the rapid adaptation to altered bouncing mechanics (Raburn et al. 2011). In comparison, metabolic cost feedback has a relatively long time course, with metabotropic group IV peripheral afferents displaying firing latencies of 5–30 s after the start of a contraction.
Hayes 2002), and central bloodstream receptors having a reported time constant of ~100 s to sense carbon dioxide concentration (Ainslie and Duffin 2009). Regardless of the feedback used to drive adaptation, identification of the resonant bouncing frequency from this feedback may require substantial additional time, particularly if humans must first develop an internal model of system dynamics as suggested by optimal control theory (Todorov 2004).

While we prescribed a constant work rate across frequency, subjects performed significantly more positive work when bouncing at the resonant frequency. Also, prescribed frequencies either higher or lower than the resonant frequency tended to drift toward resonance over time. Both of these deviations from the prescribed behavior may be due to the relatively small amount of effort required to bounce at resonance, and may be indirect indicators of subjects’ gradually developing preference for the resonant frequency. It is possible that in a longer trial, the preferred frequency would have reached a stable plateau around resonance.

Metabolic rate was not minimized during the preferred frequency trial, even though the preferred frequency approached resonance over time. This may be partially explained by the slow time course of measuring metabolic energy expenditure; the metabolic rate measured during the last 3 min of the trial was likely affected by the subject’s behavior earlier in the trial. Additionally, the preferred frequency was quite variable (see Fig. 3B), indicating that some individual subjects preferred frequencies substantially slower or faster than resonance, which would be expected to increase metabolic rate.

Our finding that the initial preferred movement pattern is not always the most economical is not altogether unique, as described for several previous studies below. Most similar to our bouncing task, increasing the frequency of hopping above the preferred rate decreased metabolic rate (Grabowski and Herr 2009). However, hop height was not controlled, so this result may have been partially due to a decrease in positive mechanical work at higher bounce frequencies. Model simulations have indicated that humans do not optimize energy expenditure when hopping (Bobbert and Richard Casius 2011), but metabolic rate was not measured experimentally and subjects bounced for only 10 s, which may be insufficient time to choose an economical movement pattern. During cycling, humans prefer pedaling cadences higher than those which minimize metabolic rate (Marsh and Martin 1997). The lack of a mechanical resonant frequency during cycling could preclude the use of proprioceptive feedback to identify the optimal movement pattern, which we previously suggested to be important (Raburn et al. 2011). It has also been reported that humans do not minimize the energetic cost of reaching during upper extremity motions in a force field (Kistemaker et al. 2010), although this study did not directly measure metabolic rate.

Even during walking, metabolic rate is not always minimized. For example, humans do not minimize metabolic rate when walking down moderate slopes (Hunter et al. 2010). This finding has been used to suggest a trade-off between metabolic rate and stability. An alternative explanation is suggested by the results of Snaterse and colleagues (2011), as their subjects preferred to maintain a preprogrammed speed-step frequency relationship rather than minimize metabolic rate. However, this seems unlikely to explain the downhill walking results, in which subjects varied their preferred speed-step frequency relationship with changes in slope (Hunter et al. 2010). In contrast to each of the studies described above, our methods allowed the a priori identification of the resonant frequency and subsequent comparison with the preferred frequency. Our results suggest that while humans may not initially prefer to bounce at the resonant frequency, they can learn to prefer this pattern over a matter of minutes. However, this may only be true for relatively simple movement tasks with an easily identifiable resonant frequency.

The results of this study may have implications for clinical populations. We found that humans do not initially prefer the bouncing frequency with a minimal metabolic rate but rather adapt their movement pattern over time, requiring the use of feedback. Many clinical populations exhibit a reduced ability to sense or interpret sensory feedback, potentially preventing identification of the metabolically optimal movement pattern. For example, patients who have experienced a stroke commonly display impaired proprioception (Connell et al. 2008) and decreased sensitivity to central measures of blood flow and potentially blood chemistry (Doux and Yun 2006; Eames et al. 2002). These deficits may partially contribute to the finding that following a stroke, functionally limited patients tend to prefer a gait speed that is slower than the metabolically optimal speed (Reisman et al. 2009). It is not currently clear whether such patients similarly prefer nonoptimal step frequencies for given walking speeds. Our finding that prescribing the resonant bouncing frequency reduces the metabolic rate suggests that auditory feedback may have metabolic benefits during gait, beyond the known improvements in speed and symmetry (Prassas et al. 1997; Thaut et al. 1997). By understanding how humans adapt their preferred movement patterns to take advantage of their body’s mechanics, we may be able to improve functional mobility in clinical populations.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J. C. Dean conceived the research; K. J. Merritt, C. E. Raburn, and J. C. Dean designed the experiment, performed the experiment, analyzed the data, and wrote and edited the manuscript.

REFERENCES


