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Mechanical energy fluctuations during hill walking: the effects of slope on inverted pendulum exchange

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Summary

Humans and other animals exchange gravitational potential energy (GPE) and kinetic energy (KE) of the center of mass during level walking. How effective is this energy exchange during downhill and uphill walking? Based on previous reports and our own reasoning, we expected that during downhill walking, the possibility for mechanical energy exchange would be enhanced and during uphill walking, the possibility for exchange would be reduced. We measured the fluctuations of the mechanical energies for five men and five women walking at 1.25 m s^{-1}. Subjects walked on the level, downhill, and uphill on a force measuring treadmill mounted at 3°, 6° and 9°. We evaluated energy exchange during the single support period based on the GPE and KE fluctuation factors of phase relationship, relative magnitude and extent of symmetry. As expected, during level walking, the GPE and KE curves were out of phase, of similar magnitude, and nearly mirror images so that the fluctuations in combined (GPE+KE) energy were attenuated. During downhill walking, the fluctuations in the combined energy of the center of mass were smaller than those on the level, i.e. mechanical energy exchange was more effective. During uphill walking, the fluctuations in the combined energy of the center of mass were larger than those on the level, i.e. mechanical energy exchange was less effective. Mechanical energy exchange occurred during downhill, level and uphill walking, but it was most effective during downhill walking.

Key words: biomechanics, locomotion, center of mass.

Introduction

Level walking is often compared mechanically to a rolling egg (Cavagna and Margaria, 1966) or an inverted pendulum (Mochon and McMahon, 1980). On a level surface, these analogies accurately describe the energy exchange mechanism utilized by humans and other animals. During the first half of the single support period, the kinetic energy (KE) of the center of mass decreases and is converted into gravitational potential energy (GPE). Conversely, during the second half of the single support period, GPE of the center of mass decreases and is converted into KE. Ideally, these opposite fluctuations of GPE and KE would result in the center of mass combined (GPE+KE) energy being constant so that the muscles need not perform any work (Cavagna et al., 1977). The purpose of our study was to investigate the effectiveness of this energy exchange during downhill and uphill walking.

Cavagna et al. evaluated the inverted pendulum mechanism during level walking, by analyzing three factors of the GPE and KE fluctuation patterns: phase relationship, relative magnitude and extent of symmetry (Cavagna et al., 1977). Three conditions must exist for ideal mechanical energy exchange. First, the GPE maximum must occur at the same time as the KE minimum and the KE maximum must occur at the same time as the GPE minimum. Second, the magnitudes of the energy fluctuations must be the same, and third, the GPE and KE fluctuations must be mirror images of each other. Our goal was to explicitly quantify how these factors are influenced by slope during hill walking.

Margaria pioneered the physiological study of slope walking (Margaria, 1938). He found that during uphill walking at a constant speed, metabolic rate increases linearly with slope. During downhill walking, the metabolic rate decreases until about –6° and then inflects and is actually greater for –9° and steeper slopes. More recently, Minetti and colleagues have further explored both the mechanical work output and metabolic cost during downhill and uphill walking at a variety of speeds. Minetti et al. (Minetti et al., 1993) reported that during downhill walking at –9°, positive work was less than 5% of the total external work, whereas during uphill walking at +9°, positive work was almost 100% of the total external work. At uphill angles above +9°, the trajectory of the center of mass increased steadily and external mechanical work was entirely positive (Minetti et al., 1993). Subsequently, Minetti and colleagues reported that mechanical energy exchange is less effective during both downhill and uphill walking (Minetti et al., 1994). However, neither of those papers nor to our knowledge any subsequent publication has provided numerical or graphical data supporting that conclusion. In fact, Minetti et al. commented that a biomechanical study is needed to appropriately characterize exactly how the inverted pendulum mechanism disappears, particularly at steep gradients (Minetti et al., 2002).

In contrast, the passive dynamic walking theory posits that bipeds can walk down slopes with perfect exchange of mechanical energy. Mochon and McMahon developed the first mathematical model of passive walking (Mochon and McMahon, 1980). McGeer extended their model and built physical machines that passively walk down gradual slopes (McGeer, 1990). These passive walkers and subsequent iterations rely on gravity to both replace energy lost at foot-ground collision and cause the swinging pendulum action of the legs (Garcia et al., 1998; Kuo, 2002). Most pertinent to the present study, passive dynamic walking models and machines demonstrate that the exchange of mechanical energy can be quite effective during downhill walking.

The purpose of our study was to quantify the center of mass energy exchange and conservation during both downhill and uphill human walking at various slopes. We recognized that the net GPE would decrease or increase during the single support period depending on the downhill or uphill angle, respectively. In addition, because we tested constant speed walking, we reasoned that the average KE would not differ from level walking. Thus, we anticipated that the combined (GPE+KE) energy fluctuation patterns would demonstrate that energy exchange differs between downhill and uphill angles. But, we could not predict how GPE and KE would fluctuate during each single support period of downhill and uphill walking. For example, does GPE steadily decrease or increase during the single support period, or are there local minima and maxima, similar to level walking? Does KE decrease and increase with both the same magnitude and timing as level walking? Are the GPE and KE fluctuation patterns for downhill walking the inverse of the fluctuation patterns for uphill walking or are the patterns unique?

Materials and methods

Five men and five women volunteered (age=30.35±5.09 years, height=1.72±0.06 m, mass=62.56±7.59 kg, mean ± s.d.). All of these healthy, recreational athletes gave written informed consent that followed the guidelines of the University of Colorado Human Research Committee.

Subjects walked at $1.25\ m\ s^{-1}$ downhill and uphill on a custom-built treadmill secured to a force platform (ZBP – 7124-6-4000; Advanced Mechanical Technology, Inc., Watertown, MA, USA) mounted on 3°, 6° and 9° wedges (Fig. 1) in addition to walking on the level force treadmill (Gottschall and Kram, 2005; Kram et al., 1998). Due to the lengthy process of changing the slope, each subject completed experimental sessions on 4 different days. The order of the sessions was randomized for each subject. After treadmill habituation, subjects walked on the force treadmill on the level or both downhill and uphill at the determined angle, for 1 min. We collected 10 s of ground reaction force (GRF) data at 1000 Hz during each trial (LabView 4.0; National Instruments, Austin, TX, USA).

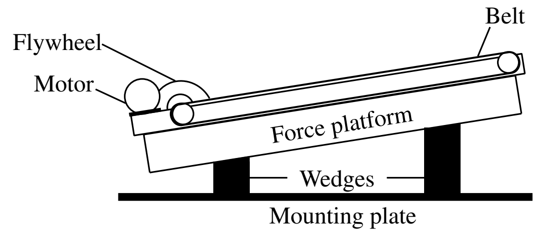

Fig. 1. Force measuring treadmill mounted at 9°.

After data collection, we filtered the GRF data, detected heel-strike and toe-off events, and calculated the mechanical energy fluctuations. The GRF data were digitally filtered using a fourth-order recursive, zero phase-shift, Butterworth low-pass filter with a cutoff frequency of 25 Hz. We detected each heelstrike by calculating the center of pressure translation; on a force treadmill, the center of pressure suddenly shifts anteriorly with each heel strike event (Davis and Cavanagh, 1993). Next, we calculated the mechanical energy fluctuations of the center of mass by integrating the GRF data. A MatLab integration program was created based on the method of Cavagna and colleagues (Cavagna, 1975; Cavagna et al., 1977) which we modified for hill walking. Our goal was to explicitly quantify how mechanical energy fluctuations are influenced by slope during hill walking. For each of these calculations we focused on the single support period, which can be modeled as an inverted pendulum. Thus, our investigation did not include calculations of the work performed during the double support period, which would require analysis of the simultaneous work of both legs on a dual belt treadmill (Donelan et al., 2002b).

In order to calculate the instantaneous energies of the center of mass, we combined the normal and parallel GRF components into a global vertical force ($F_{vertical}$) equal to ($F_{normal}\cos\theta$)+($F_{parallel}\sin\theta$). F_{normal} is the force perpendicular to the treadmill belt, $F_{parallel}$ is the force parallel to the treadmill belt, and θ is the angle of the treadmill relative to the ground. We utilized this $F_{vertical}$ to calculate the instantaneous vertical acceleration ($a_{vertical}$) equal to ($F_{vertical}$–mg)/m, where m is the subject's body mass and g is the gravitational acceleration $9.81\ m\ s^{-2}$.

We calculated instantaneous vertical velocity ($v_{vertical}$) by integrating the vertical acceleration ($a_{vertical}$) with respect to time and adding an integration constant. For level locomotion, the Cavagna method determines the integration constant by knowing that the average vertical velocity over a complete stride is zero. For hill walking, we calculated the integration constant by knowing that the average vertical velocity was virtually equal to the $v_{tread}\sin\theta$, where v_{tread} is the velocity of the treadmill belt.

We calculated instantaneous vertical position ($h_{vertical}$) by integrating the vertical velocity ($v_{vertical}$) with respect to time and adding an integration constant. For level locomotion, the Cavagna method determines the integration constant for this calculation by knowing that the center of mass returns to the same vertical position at the beginning of each stride. For hill locomotion, we calculated the integration constant knowing that over a complete stride the center of mass changes vertical position by an amount virtually equal to (v_{tread} sinθ)×(t_{stride}), where t_{stride} is equal to the time for one complete stride. Lastly, we calculated the instantaneous GPE, $mgh_{vertical}$.

In order to calculate the instantaneous KE fluctuations of the center of mass, we used the normal and parallel ground reaction force components (F_{normal} and $F_{parallel}$) beginning with the determination of instantaneous acceleration in each direction (a_{normal} and $a_{parallel}$) equal to (F_{normal}–mgcosθ)/m and ($F_{parallel}$sinθ)/m, respectively.

Next, we calculated the normal and parallel instantaneous velocities (v_{normal} and $v_{parallel}$) by integrating the acceleration (a_{normal} and $a_{parallel}$) with respect to time and adding an integration constant that was adjusted for hill locomotion. The integration constant was calculated by knowing that the average parallel velocity was equal to the v_{tread} and that the average v_{normal} was zero. Lastly, we combined these normal and parallel velocities (v_{normal} and $v_{parallel}$) using the Pythagorean theorem to determine v_{result} and then KE fluctuations, $0.5mv^2_{result}$.

We quantified the mechanical energy fluctuations per step, and averaged ten steps per condition for each subject. We calculated the decreases and increases in GPE, KE and combined (GPE+KE) energy. Next, we determined the positive external (+W_{ext}) and negative external (–W_{ext}) work per step from the sum of the positive and negative increments in combined (GPE+KE) energy, respectively.

We utilized these mechanical energy results to evaluate energy exchange. We calculated the phase relationship by calculating the alpha value. Alpha was equal to the product of 360° and the ratio of the difference in time between the KE maximum and GPE minimum (Δt) and the stride period (T). Given this definition, if the fluctuations were perfectly out of phase, alpha would be equal to zero degrees. We assessed the relative magnitude of the relative energy fluctuations by calculating the ratio of change (ΔKE/ΔGPE). If the fluctuations were the same magnitude, the ratio would be equal to 1. We evaluated if GPE and KE were mirror images of each other by examining the combined (GPE+KE) curves.

Finally, to compare how the mechanical energies fluctuated on the different hill angles we excluded the overall work necessary to raise or lower the center of mass. To do so, we calculated the instantaneous energies of the center of mass in the same manner as previously described. However, instead of integrating the global vertical and horizontal forces, we integrated the normal and parallel force components. Also, we calculated the integration constants as if the center of mass had no net change in height. This transformation factored out the inherent net decrease or net increase in GPE due to the hill angle. If a transformed (tGPE+KE) energy curve is flat with no fluctuations then the transformed (tW_{ext}) would be equal to zero.

These mechanical energy data were analyzed across all conditions using a repeated measures design (ANOVA). We performed Newman–Keuls *post-hoc* tests to analyze the differences between conditions and report all values as mean ± standard deviation. Significance was defined at $P<0.05$.

Results

To quantify the possibility of energy exchange, we evaluated GPE and KE fluctuations during the single support period (Fig. 2). During both downhill and uphill walking at steeper hill angles, GPE local maxima and minima during the stance phase diminished. However, even during downhill and uphill walking at 9°, GPE still did not demonstrate a steady decrease or increase. The KE fluctuation patterns during both downhill and uphill walking were similar to level walking, but the magnitude

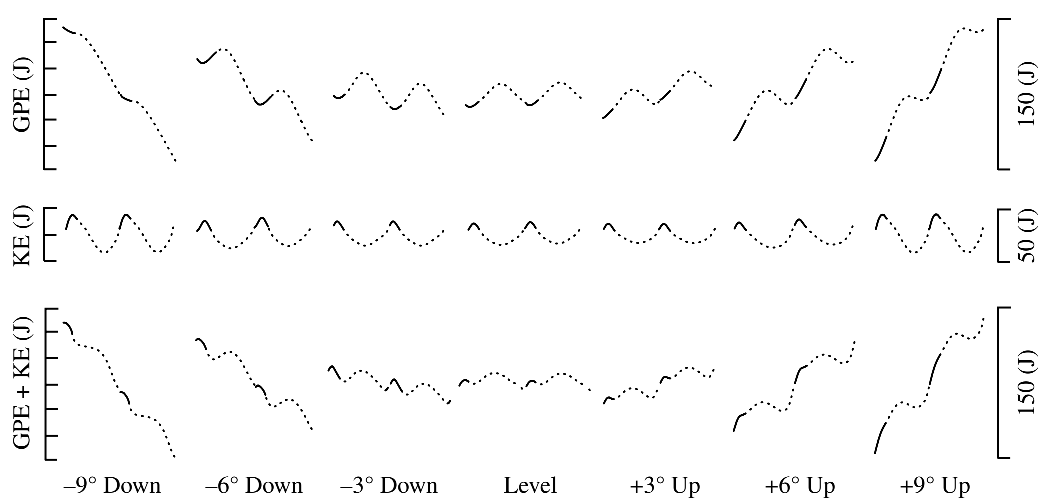

Fig. 2. Center of mass mechanical energy *versus* time for a typical subject (54 kg). Solid lines indicate double support periods and dotted lines indicate single support periods.

Table 1. *Mechanical energy exchange factors*

	α (deg.)	ΔKE/ΔGPE	$+W_{ext}$ (J kg^{-1} $step^{-1}$)	$+tW_{ext}$ (J kg^{-1} $step^{-1}$)
–9° Down	–7.33 (6.94)	1.41 (0.67)	0.15 (0.05)	0.34 (0.07)
–6° Down	2.97 (5.53)	1.27 (0.76)	0.16 (0.05)	0.36 (0.06)
–3° Down	12.91 (5.77)	1.07 (0.35)	0.24 (0.05)	0.43 (0.06)
Level	26.30 (6.77)	0.94 (0.15)	0.48 (0.06)	0.48 (0.06)
+3° Up	37.08 (10.94)	0.62 (0.07)	0.93 (0.09)	0.59 (0.07)
+6° Up	44.95 (11.68)	0.44 (0.05)	1.41 (0.14)	0.82 (0.08)
+9° Up	50.90 (12.30)	0.35 (0.03)	1.77 (0.25)	0.97 (0.09)

Work due to fluctuations in combined energy excluding the overall work necessary to lower or raise the center of mass tW_{ext}.
Values represent means (s.d.) for all 10 subjects.
All downhill and uphill running conditions differed from level walking, P<0.0001.

changes were larger during both uphill and downhill walking. As expected, during hill walking, the combined (GPE+KE) energy fluctuation patterns were dominated by changes in GPE. Yet, these patterns clearly indicate that energy was still exchanged during both downhill and uphill walking.

The three factors utilized by Cavagna et al. (Cavagna et al., 1977) to evaluate mechanical energy exchange indicated that downhill, level and uphill walking were dramatically different from each other (Tables 1, 2). During level walking, alpha was 26.30±6.77 degrees, the ratio of ΔKE and ΔGPE was 0.94±0.15, the $+W_{ext}$ value was 0.48±0.06 J kg^{-1} $step^{-1}$ and the $-W_{ext}$ value was 0.43±0.02 J kg^{-1} $step^{-1}$. During downhill walking at –9°, alpha decreased to –7.33±6.94° and during uphill walking at +9°, alpha increased to 50.91±12.32°. During –9° downhill walking, the ratio of ΔKE and ΔGPE increased to 1.41±0.67 whereas during +9° uphill walking the ratio decreased to 0.35±0.03 (all values mean ± s.d., P<0.0001).

The center of mass GPE fluctuation patterns were asymmetrical during each single support period for both downhill and uphill walking (Fig. 2, top row of traces). On the level, the increases and decreases of the GPE during the stance phase were nearly equal in magnitude, ±0.43 J kg^{-1} $step^{-1}$. But at steep angles, during the single support period the center of mass GPE predominately decreased during downhill walking and predominately increased during uphill walking. During downhill walking at the –9°, –6° and –3° angles, the center of mass GPE increased 86%, 60% and 54% *less* than it decreased (all values P<0.0001). Conversely, during uphill walking at the +3°, +6° and +9° angles, the center of mass GPE increased 63%, 79% and 81% *more* than it decreased (all values different from level values, P<0.0001).

Table 2. *Kinematic factors*

	Stride frequency (Hz)	Contact time (s)	Swing time (s)
–9° Down	0.61 (0.03)	0.62 (0.03)	0.39 (0.02)
–6° Down	0.62 (0.03)	0.64 (0.03)	0.39 (0.02)
–3° Down	0.64 (0.03)	0.66 (0.03)	0.40 (0.02)
Level	0.66 (0.03)	0.68 (0.03)	0.41 (0.02)
3° Up	0.68 (0.04)	0.70 (0.04)	0.42 (0.02)
6° Up	0.69 (0.04)	0.71 (0.04)	0.43 (0.04)
9° Up	0.71 (0.04)	0.72 (0.04)	0.44 (0.04)

Values represent means (s.d.) for all 10 subjects.

These GPE fluctuations during downhill and uphill walking were a result of the inherent net increases and decreases in the center of mass position during the single support period due to the hill angle. For comparison, the center of mass position during level walking ascended, on average, 4.4 cm during the first half of the stance phase and descended, on average, an equal 4.4 cm during the second half of the stance phase. During downhill walking at –9°, the subjects' center of mass height during the stance phase ascended by less than 1.5 cm and descended by 8.7 cm. During uphill walking at +9°, the subjects' center of mass height during the stance phase ascended by 9.2 cm and descended by only 1.8 cm (all values different from level values, P<0.0001).

The center of mass KE fluctuation patterns during the stance phase of both downhill and uphill walking were similar to level walking in terms of the symmetrical decrease and increase (Fig. 2, middle row of traces). However, the magnitude of these fluctuations increased as the angle of the hill increased. On the level, the decreases and increases of KE during the stance phase were an equal and symmetrical ±0.38 J kg^{-1} $step^{-1}$. For downhill walking at angles of –9°, –6° and –3°, the center of mass KE fluctuated 47%, 32% and 16% *more* than level walking (all values different from level values, P<0.01). Similarly, during uphill walking at +3°, +6° and +9° angles, the center of mass KE fluctuated 5%, 23% and 29% *more* than level walking (all values different from level, P<0.05).

These KE fluctuations during downhill and uphill walking reflect the velocity fluctuations during each single support period. For comparison, the center of mass velocity during level walking decelerated and accelerated by 0.09 m s^{-1} during the stance phase. During downhill and uphill walking at 9°, the subject's center of mass velocity during the stance phase decelerated and accelerated by 0.18 m s^{-1} and 0.11 m s^{-1}, respectively.

After factoring out the inherent net decrease or increase in combined (GPE+KE) energy due to the hill angle, the transformed energy fluctuations demonstrated that mechanical

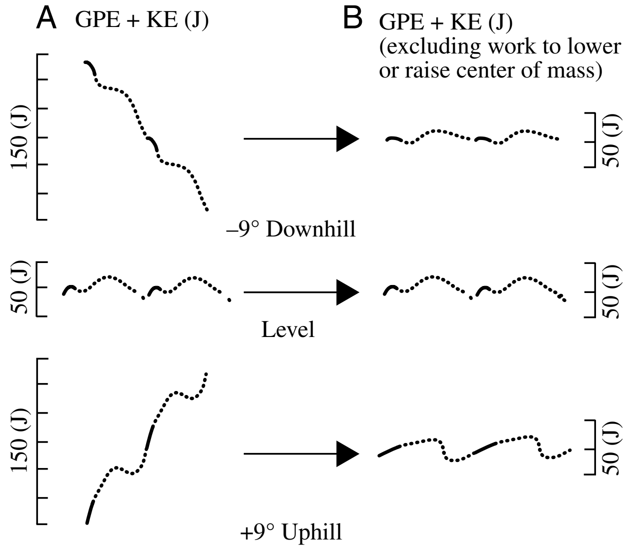

Fig. 3. (A) Combined gravitational potential energy and kinetic energy (GPE+KE) curves at –9°, level and +9°. (B) Transformed (tGPE+KE) energy curves at –9°, level and +9° excluding the overall work necessary to lower or raise the center of mass.

energy is exchanged most effectively during moderate slope downhill walking and least effectively during uphill walking (Fig. 2, bottom row of traces and Fig. 3). During level walking, the center of mass combined energy fluctuated by an average of ±0.32 J kg^{-1} $step^{-1}$. At downhill angles of –9°, –6° and –3°, the center of mass transformed energy fluctuations (tGPE+KE) were 12%, 33% and 41% smaller, respectively (all values $P<0.05$). At uphill angles of +3°, +6° and +9°, the center of mass transformed energy fluctuations (tGPE+KE) were 19%, 41% and 51% larger, respectively (all values $P<0.01$). The transformed combined (tGPE+KE) energy curves indicated that the $+tW_{ext}$ and $-tW_{ext}$ values were 0.36±0.06 J kg^{-1} $step^{-1}$ and –0.38±0.07 J kg^{-1} $step^{-1}$ during downhill walking at –9° and 0.97±0.08 J kg^{-1} $step^{-1}$ and –1.03±0.12 J kg^{-1} $step^{-1}$ during uphill walking at +9° ($P<0.0001$).

Discussion

Mechanical energy is exchanged and conserved during the single support period of level and both downhill and uphill walking. During downhill walking, to maintain a constant average speed, energy must be dissipated to resist gravity. This occurs at and immediately after heelstrike, and both GPE and KE of the center of mass decrease. During uphill walking, energy must be generated to overcome gravity. This occurs prior to toe-off, and both GPE and KE increase. But, for both downhill and uphill walking, during the remainder of the step, KE fluctuations are mitigated by opposite GPE fluctuations and GPE fluctuations are mitigated by opposite KE fluctuations, indicating mechanical energy exchange.

Ideal mechanical energy exchange during the single support period is indicated by an alpha value equal to zero, the ratio of KE and GPE magnitude fluctuations equal to 1, and the sum of positive and negative external work equal to zero (Table 1). First, compared with level walking, the alpha value decreased during downhill walking and increased during uphill walking. The GPE and KE fluctuations were nearly out of phase during downhill walking at an angle of –6°. Second, as the downhill and uphill angles increased from level walking, the ΔKE/ΔGPE ratio increased or decreased away from 1, respectively. This ratio demonstrated that the relative magnitude of the energy fluctuations was closest to 1 during downhill walking at –3°. Third, compared with level walking, at steeper downhill angles, the positive external work was substantially less, as indicated by the smaller fluctuations in the combined energy curve. By contrast, at steeper uphill angles the positive external work was substantially greater as indicated by the larger fluctuations in the combined energy curve. After factoring out the inherent net decrease or increase in combined (GPE+KE) energy due to the hill angle, the transformed energy fluctuations demonstrated that mechanical energy is exchanged most effectively during moderate slope downhill walking and least effectively during uphill walking. This indicates that the work due to fluctuations in GPE+KE, excluding the overall work necessary to lower or raise the center of mass, was minimized during downhill walking at –6° and –9°. Thus, our data show that humans walking downhill are quite similar to passive dynamic walking robots (McGeer, 1990).

Over the range of slopes we studied, the center of mass GPE does not exclusively decrease or increase during downhill or uphill walking, respectively. Before this study, we could calculate the net change in center of mass height per step required to descend or ascend a hill. However, we could not predict the specific fluctuation patterns or magnitudes. During level walking, the center of mass height rises and falls with equal magnitude. In addition, the peak height occurs at midstance. Compared with level walking, during downhill walking, as the angle of the hill increases, the rise in the center of mass height is less, and the maximum occurs before midstance. By contrast, compared with level walking, during uphill walking, the fall in the center of mass height is less, and the minimum occurs after midstance. During downhill and uphill walking, the timing of the GPE fluctuations changes because of the necessity to decrease or increase the center of mass height. Based on these results, neither downhill nor uphill walking conform to the definition of walking established by McMahon and colleagues (McMahon et al., 1987). They proposed that walking be defined as a gait in which the center of mass is at the highest point during midstance. But, we still consider the gait utilized by our subjects to be a walk owing to the lack of an aerial phase and because mechanical energy patterns were more similar to an inverted pendulum than a spring–mass system.

The center of mass KE fluctuations during both downhill and uphill walking are larger in magnitude than during level walking. During level walking, the parallel braking and propulsive impulses are essentially equal but opposite and the subjects maintain a constant average velocity without large fluctuations. Because generating propulsive impulse is expensive (Gottschall and Kram, 2003), we expected that during downhill walking the braking impulse would not change and the propulsive impulse exerted by the person would decrease since a component of gravity was acting to provide propulsion. We also expected that during uphill walking the braking impulse exerted by the person would decrease since a component of gravity was acting to provide braking while the propulsive impulse would not change. In short, we presumed that propulsive impulse production and effort would be minimized. Contrary to this intuition, during downhill walking, the parallel braking impulse increases disproportionately to the downhill angle and thus the parallel propulsive impulse does not decrease as much as expected. This unnecessary increase in braking impulse caused an increase in the velocity and KE fluctuations. Similarly, during uphill walking, the braking impulse does not decrease as much as expected and so the parallel propulsive impulse increases disproportionately to the uphill angle. This seemingly needless increase in propulsive impulse caused increases in velocity fluctuations and increased ΔKE magnitude. Presently, we do not have an explanation for why propulsive impulse production and effort was not minimized. It may be the result of aligning the ground reaction force vectors with the leg joint centers so as to minimize joint torques and hence muscle forces (Alexander, 1991; Chang et al., 2000; Full et al., 1991).

Our data illustrate that humans exchange mechanical energy most effectively during moderate downhill walking. Margaria showed that walking is least metabolically expensive at a downhill angle between –6° and –9° (Margaria, 1938; Margaria, 1976). At steeper downhill angles, metabolic cost inflects and increases. In terms of mechanical energy exchange, the alpha and the transformed external work values indicate that mechanical energy exchange is greatest at a downhill angle of –6° and –9° corresponding to the metabolic minimum. By contrast, metabolic cost is greater during uphill walking. Margaria showed that the relationship between uphill angle and metabolic cost is linear and proportional. The phase relationship, relative magnitude, and extent of symmetry values indicate that energy exchange is progressively less effective at steeper uphill angles. However, there is still some mechanical energy exchange during uphill walking even at +9°.

Future studies of hill walking should employ the individual limbs method of calculating step-to-step transition work (Donelan et al., 2002a; Donelan et al., 2002b) in addition to discerning muscular contributions. Because we only had a single belt force-treadmill we could not discern the forces exerted by the individual legs and thus could not calculate work during the double support period using the individual limbs work method. Given the insight into level walking mechanics and energetics provided by that method, the next logical study should incorporate a dual-belt force-treadmill. Finally, our study only resolved the overall motions of the center of mass and not the contributions of individual muscles. Neptune et al. completed detailed musculoskeletal simulations of human walking and indicated that even during the single support period, muscles perform substantial amounts of mechanical work (Neptune et al., 2004).

Overall, our findings demonstrate that substantial mechanical energy exchange occurs during hill walking. During the single support period, GPE and KE of the center of mass are converted between each other, resulting in energy savings. The magnitude of mechanical energy exchange probably influences the rate of metabolic energy consumption during hill walking. At moderately steeper downhill angles, mechanical energy exchange is greater, and a metabolic minimum is reached. During uphill walking, substantial positive work must be performed, mechanical energy exchange is less, and metabolic rate is correspondingly greater.

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