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Mechanical power and efficiency of level walking with different stride rates

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Summary

Walking humans prefer to use the stride rate that results in the lowest rate of metabolic energy expenditure. Mechanical power requirements have been suggested to underlie the metabolic response, but mechanical power is consistently reported to be minimal at stride rates 20–30% lower than preferred. This may be due to limitations in how total mechanical power has been computed, as well as a failure to account for the efficiency with which muscular work is done. We investigated how mechanical power and efficiency depend on stride rate in walking, with both quantities computed from the work done by the hip, knee and ankle joint moments. Our hypotheses were that mechanical power and efficiency are both optimized at the preferred stride rate, which would explain why metabolic energy expenditure is minimized at this rate. Contrary to our hypotheses, mechanical power curves exhibited plateaus that spanned stride rates lower than preferred

(predicted optima: 11–12% below preferred), while net mechanical efficiency exhibited a plateau that spanned stride rates higher than preferred (predicted optimum: 8% above preferred). As expected, preferred stride rate (54.3 strides min⁻¹) was not different from the stride rate that minimized net metabolic energy expenditure (predicted optimum: 0.2% above preferred). Given that mechanical power and mechanical efficiency exhibited plateaus on opposite sides of the preferred stride rate, the preferred rate in walking likely represents a compromise between these two factors. This may also explain the relative flatness of the curve for metabolic rate in the vicinity of the preferred stride rate.

Key words: locomotion, gait, biomechanics, energetics, mechanical work.

Introduction

Normal human walking is characterized by economical patterns of movement. Not only do individuals generally choose a walking speed that requires the least energy to travel a given distance (Ralston, 1958), but over the usual range of walking speeds people also choose stride rates that minimize the rate of metabolic energy expenditure (Molen et al., 1972; Zarrugh and Radcliffe, 1978). At a constant walking speed, metabolic rate exhibits a U-shaped dependence on stride rate (Atzler and Herbst, 1927; Cotes and Meade, 1960; Holt et al., 1991; Minetti et al., 1995; Zarrugh and Radcliffe, 1978), with the minimum of the curve typically coincident with the self-selected or preferred stride rate. While the presence of an energetically optimal stride rate is well accepted, the reason that metabolic energy consumption is minimized at the preferred rate remains unclear.

Holt and coworkers (Holt et al., 1990; Holt et al., 1991) noted that the resonant frequency of a pendular model of the lower limb was not significantly different from experimentally determined preferred stride rates or energetically optimal stride rates. Yet whether these relationships are meaningful has since been challenged on both theoretical (Zatsiorsky et al., 1994) and practical (Whittlesey et al., 2000) grounds. Other researchers have suggested that minimization of mechanical power should

determine the stride rate at which metabolic energy expenditure is minimized (Cavagna and Franzetti, 1986; Minetti et al., 1995; Minetti and Saibene, 1992; Zatsiorsky et al., 1994). However, total mechanical power is usually reported to be minimized at stride rates 20–30% below the preferred rate (Cavagna and Franzetti, 1986; Minetti et al., 1995; Minetti and Saibene, 1992). Minetti et al. (Minetti et al., 1995) noted that the fraction of the total mechanical power that was associated with lifting and accelerating the body center of mass was more closely associated with the preferred stride rate, but the influence was only strong at walking speeds considerably higher than normal. Part of the discrepancy between mechanical and metabolic energy minimization may be due to shortcomings in the techniques that have been used to compute mechanical power (Minetti et al., 1995; Zatsiorsky et al., 1994). However, the difference may also be due to mechanical work not being the sole determinant of the metabolic cost of walking.

The mechanical work that muscles do in walking presumably incurs a substantial metabolic cost (Donelan et al., 2002; Grabowski and Kram, 2005; Neptune et al., 2004; Kuo, 2001), but the cost of performing work is not determined just by the changes in mechanical energy that are produced. Muscles do mechanical work with variable efficiency, which depends on both the load and speed of contraction (Barclay, 1994; Barclay

et al., 1993). Since muscle force and speed of contraction can be expected to differ when humans walk using different stride rates, the mechanical efficiency with which muscles do work in walking would be expected to vary as well. There appears to be only one report in the literature of efficiency at different stride rates for walking (Zarrugh, 1981). Power and efficiency were quantified in one subject, and gross mechanical efficiency (defined as positive mechanical power divided by gross metabolic power) was found to be maximized at the preferred stride rate. However, the method used to compute mechanical work, based on summing increments in the segment mechanical energies, resulted in a nearly constant average power across different stride rates. Thus, only the changes in gross metabolic rate were responsible for the computed efficiency response, which provided limited insight regarding variations in mechanical efficiency of the lower limb muscles.

One limitation of the existing literature is that estimates of mechanical work and power have typically been computed from increments in the body center of mass and/or segment mechanical energies (e.g. Cavagna and Franzetti, 1986; Minetti et al., 1995; Zarrugh, 1981). These techniques suffer from various uncertainties in quantifying total mechanical work. These uncertainties arise from issues such as the assumptions regarding exchanges between potential and kinetic energy, to the validity of summing the so-called external work (W_{ext}) and internal work (W_{int}) to obtain total mechanical work (van Ingen Schenau et al., 1997; Winter, 1990; Zatsiorsky, 1998). In most of the relevant literature, the term 'external work' is used to represent work associated with accelerating the whole-body center of mass, while the term 'internal work' is related to work done to accelerate the individual body segments relative to the whole-body center of mass. However, these two 'components' of the total work are not necessarily independent (Zatsiorsky et al., 1994; Kautz and Neptune, 2002), and the degree to which they overlap in walking is unknown. A better, but more complex, approach is to compute the positive and negative work done by each of the lower limb joint moments. Compared to center of mass or segmental kinetics, joint moments are more closely related to the actual muscular sources and sinks of mechanical energy in locomotion (Winter, 1990). This approach will also automatically account for any external and internal work that is done, without requiring any of the assumptions described above. An important limitation of estimating mechanical power using joint moments, which is shared with the other existing techniques, is that it is not possible to resolve cocontraction of antagonistic muscles. During walking in healthy adults, however, this is not expected to be a major concern (Nilsson et al., 1985). If mechanical work done by joint moments provides a better estimate of mechanical energy generation and absorption by muscles in human walking, it might help resolve the discrepancy between minimization of mechanical and metabolic power described earlier.

Another limitation with existing assessments of locomotor energetics has to do with the definition of efficiency. Efficiency (ϵ) in studies of human walking has commonly been defined as:

$$\epsilon = W_{\text{tot}} / E, \quad (1)$$

where W_{tot} is the total positive work (sum of W_{ext} and W_{int}) and E is metabolic energy expenditure. Aside from the uncertainties

in quantifying W_{tot} described in the preceding paragraph, this efficiency expression also ignores the negative work done in walking (i.e. work done on the body). From a thermodynamic perspective, work done on the body can be viewed as a potential source of energy, in the same sense as conversion of chemical energy (Prilutsky, 1997). A substantial amount of negative work is done on the body in walking, and recent evidence suggests that a non-trivial fraction of this energy is stored in elastic structures and released at some later point in the gait cycle (Fukunaga et al., 2001; Hof et al., 2002). Most of this research has thus far focused on energy storage and release in the triceps surae, but it appears that more proximal leg muscles also have the potential to store and release elastic energy during movement (Muraoka et al., 2001). Therefore, failure to include negative work in the definition of efficiency may yield results that do not reveal much about the energetics of the locomotor task. An alternative definition of efficiency addresses this issue (Prilutsky, 1997), and is well suited to studying terrestrial locomotion (see also Woledge, 1997). Prilutsky defined the efficiency of positive work as:

$$\epsilon = W^+ / (E + W^-), \quad (2)$$

where W^+ is the positive work done by the joint moments, W^- is the negative work done by the joint moments¹, and E is the same as defined previously. The mechanical work terms in Eqn 2, derived from joint moments, better represent the actual sites of mechanical energy generation and absorption than in Eqn 1, and the inclusion of negative work better addresses the potential for storage and release of elastic energy to affect the metabolic cost of doing work. The justification for having the W^- term appear in the denominator is that mechanical energy stored in elastic structures is energy available to do work, and our best estimate of the maximal amount of energy that could possibly be stored is the work done on the body at the joints.

The preceding arguments are not meant to imply that all of the work done on the body is stored in elastic structures and recovered later in the gait cycle, but rather that the negative work done on the body is our best estimate of the total mechanical energy input to the body. Some of this energy will be stored, with the rest being degraded as heat. The proportion of negative work that is stored and reused will partially determine the efficiency of movement, as dissipation of negative work in the form of heat and positive work done by muscles will both extract a higher metabolic cost, as reflected in a higher E term. Thus, this expression for efficiency does not directly represent the efficiency with which negative work is converted to positive work, or the conversion of chemical energy to mechanical energy. Instead, it provides an estimate of the overall efficiency of the many processes involved in producing muscular work in movements involving stretch-shortening cycles, such as walking.

At present, our understanding of why the rate of metabolic energy expenditure is minimized at the preferred stride rate in walking is incomplete. The variable requirements for muscles to generate and absorb mechanical energy with changes in stride rate seem a likely determinant of the metabolic cost, but to date

¹The W^- term is a positive quantity (i.e. the magnitude of the negative work done by the joint moments), as it represents a source of energy to the system. [For more detail, see Prilutsky (Prilutsky, 1997).]

these have not been shown to exhibit a strong correspondence with metabolic energy. Since this might be due primarily to methodological issues, one purpose of this study was to re-evaluate how walking with different stride rates at a constant speed affects the mechanical power of walking, using analyses based on the work done by the lower limb joint moments. Previous research has also not adequately characterized the manner in which efficiency varies across stride rates. Therefore, our other purpose was to evaluate how net mechanical efficiency is affected by changes in stride rate, when speed is held constant. We anticipated that mechanical power and net mechanical efficiency would exhibit U-shaped responses to changes in walking stride rate (inverted U-shaped responses for power absorption and mechanical efficiency), with optima located close to the preferred stride rate. Our specific working hypotheses were that mechanical power generation and absorption would be minimized, and net mechanical efficiency would be maximized, at the preferred rate. The bases for the hypotheses were that these are the conditions that would most directly lead to metabolic energy expenditure being minimized at the preferred stride rate. However, we also recognized that other findings could be consistent with metabolic energy being minimized at the preferred stride rate. For example, none of the variables need to be optimized right at the preferred stride rate, as long as the power variables are optimized on one side of the preferred stride rate (e.g. below preferred), while mechanical efficiency is optimized on the other side of the preferred stride rate (e.g. above preferred). Based on the existing literature (Molen et al., 1972; Zarrugh and Radcliffe, 1978), preferred and energetically optimal stride rates were not expected to be different.

Materials and methods

Six male and four female human subjects [age=26.7±3.6 years (mean ± s.d.), height=1.74±0.10 m, mass=67.9±11.9 kg] were apprised of the goals and requirements of this study, and provided informed consent in accordance with local regulations. The experimental protocol involved walking at one speed (1.3 m s⁻¹) using five different stride rates (preferred, ±10% of preferred, and ±20% of preferred), both on a motorized treadmill (for preferred stride rate determination and metabolic measurements) and overground (for kinetic and kinematic measurements). All data were collected while subjects walked with their arms folded across the chest, to minimize the influence on the experimental measures of changes in arm swing when using different stride rates. The effects of this decision

were assessed by also collecting all metabolic, kinetic and kinematic data while the subjects walked at the preferred stride rate using normal arm swing. The dependent variables based on metabolic rate and joint moments considered in this study were found to differ by no more than 6% for walking with and without arm swing. This finding, combined with a dependence of metabolic cost on stride rate that was consistent with earlier reports (see Results), indicated that the current results should generalize to walking with arm swing.

All subjects had prior experience of walking on a motorized treadmill. Nonetheless, all subjects walked for a minimum of 10 min at the experimental speed before determination of preferred stride rate, to help ensure adequate familiarization with the experimental task. No specific instructions were given to the subjects regarding how they should walk, or what stride rate they should use. Preferred stride rate was calculated from the time required to complete 50 strides (right heel strike to right heel strike), and was determined three separate times. Repeat determinations of preferred stride rate always differed by less than 1.5%, and the average of the three values was used in subsequent aspects of data collection. The temporal and frequency parameters corresponding to the five different stride rates are listed in Table 1. After preferred stride rate had been determined, subjects walked for approximately 10 more minutes on the treadmill to practice walking at the experimental stride rates. For this practice session, and all subsequent treadmill-based trials, stride rate was matched to a metronome set at the desired frequency (Laurent and Pailhous, 1986; Martin and Marsh, 1992). The actual average speed of the treadmill belt was monitored using a timing device, a photocell, and a piece of reflective tape on the belt. Measured treadmill belt speed was always within ±1% of the nominal speed of 1.3 m s⁻¹.

Metabolic measurements

Subjects walked on the same motorized treadmill that was used for preferred stride rate determination. Rates of oxygen consumption and carbon dioxide production were recorded using an automated metabolic measurement system (TrueMax 2400, Parvo Medics, Sandy, UT, USA). Before conducting any of the stride rate trials, baseline metabolic values were quantified while subjects stood quietly on the treadmill for 5 min. Prior to the determination of baseline values, the subjects had been sitting for at least 10 min. The stride rate manipulations were presented to each subject in a random order, and rest periods were required between trials until the rate of oxygen consumption returned to within 20% of baseline values.

Table 1. Stride parameters for the five different stride rate conditions

Stride rate condition	Stride rate		Time (s)	
	Strides min ⁻¹	Hz	Stride	Stance
-20%	43.5±2.5	0.73±0.04	1.38±0.08	0.84±0.05
-10%	48.9±2.8	0.82±0.05	1.23±0.07	0.74±0.04
Preferred	54.3±3.1	0.91±0.05	1.10±0.06	0.70±0.04
+10%	59.8±3.4	1.00±0.06	1.00±0.06	0.64±0.04
+20%	65.2±3.6	1.09±0.06	0.92±0.05	0.60±0.04

Values are means ± s.d. (N=10). Stride rate condition: negative values represent stride rates lower than preferred, and positive values represent stride rates higher than preferred.

The match between subject stride rate and the beat of the metronome was monitored by one of the investigators, and verbal feedback was provided to the subjects if at any point they appeared to drift from the target stride rate. Subjects walked at each of the stride rates for 5 minutes, with rates of oxygen consumption and carbon dioxide production averaged over the final 2 min of each trial. For all subjects and all trials the respiratory exchange ratio was <1.0, indicating that energy was provided primarily by aerobic pathways.

Kinetic and kinematic measurements

Subjects walked overground along a 12 m walkway while matching their stride length to marks placed on the floor (Laurent and Pailhou, 1986; Martin and Marsh, 1992). Prior to collecting any data, subjects practiced each condition several times until they could consistently produce the proper stride length and speed while looking down at the floor as little as possible. Ground reaction forces were measured using a strain gage-based force platform (AMTI, Watertown, MA, USA) operating at 600 Hz. Kinematic data were captured using a S-VHS video camera, operating at 60 Hz, that was placed perpendicular to the plane of progression at a distance of approximately 5 m from the force platform. Reflective markers were placed over the approximate centers of rotation of the shoulder, hip, knee and ankle joints, as well as over the heel and head of the fifth metatarsal. Subject speed was monitored using a pair of photocells straddling the force platform (4 m apart), and only trials that were within $\pm 3\%$ of the target speed were considered acceptable. Synchronization of the force and video data was achieved by using the leading photocell to trigger collection of the force data, while simultaneously turning on a light that was visible in the field of view of the video camera. During data processing, stride length data were extracted from the video records using the reflective marker placed on the heel, and it was confirmed that all subjects walked with stride lengths that were within $\pm 3\%$ of the target for each condition. These measures ensured that speed and stride rates for each subject were matched for the corresponding treadmill and overground trials.

Analysis

The gross rate of metabolic energy expenditure was estimated from pulmonary gas exchange using the approach developed by Weir (Weir, 1949), and net metabolic rate (\dot{E}_{net}) was derived by subtracting the rate of energy expenditure during quiet standing. For purposes of data presentation and statistical analyses, net metabolic rate was normalized to subject body mass. The coordinates of the reflective markers were obtained from the video records using a Peak Motus motion capture system (Vicon, Centennial, CO, USA). The raw coordinate data were smoothed to reduce high frequency noise using a fourth-order, dual-pass, Butterworth digital filter (Winter, 1990). The cut-off frequencies used in the Butterworth filter (3–6 Hz) were determined for each coordinate of each marker using an objective method (Jackson, 1979). Segmental and joint angles were computed using the smoothed marker data, and angular velocities and accelerations were obtained using finite difference equations (Winter, 1990). Body segment inertial parameters were estimated using equations based on segment

lengths and body mass (de Leva, 1996). The force, segmental and inertial data were combined to calculate sagittal plane joint moments for the hip, knee and ankle, using an inverse dynamics approach (Winter, 1990). Ground reaction forces were subsequently normalized to body weight and joint moments were normalized to leg length and body weight, rendering both quantities dimensionless (Hof, 1996).

The process of determining mechanical power and efficiency involved several steps. First, at each joint, instantaneous power was computed from the product of net joint moment and joint angular velocity. Next, the positive work (W_i^+) and negative work ($-W_i^-$) performed at each joint were determined separately by numerically integrating the instantaneous positive and negative powers over the full gait cycle. The average positive joint powers (\dot{W}_i^+) and average negative joint powers ($-\dot{W}_i^-$) were computed by dividing each work expression by the cycle period, which yielded mechanical variables that were dimensionally consistent with the metabolic data (i.e. \dot{E}_{net}). The average joint powers were then summed over the hip, knee and ankle to yield the average positive power:

$$\dot{W}^+ = \sum_{i=1}^3 \dot{W}_i^+, \quad (3)$$

and the average negative power:

$$-\dot{W}^- = \sum_{i=1}^3 -\dot{W}_i^-. \quad (4)$$

Net mechanical efficiency of walking (ϵ_{net}) was calculated from \dot{W}^+ , $-\dot{W}^-$, and \dot{E}_{net} as:

$$\epsilon_{\text{net}} = 2\dot{W}^+ / (\dot{E}_{\text{net}} + 2\dot{W}^-), \quad (5)$$

where \dot{W}^+ and \dot{W}^- have been doubled to approximate the output from both legs². For purposes of data presentation and statistical analyses, mechanical powers were normalized to subject body mass. All efficiency calculations were done prior to normalization of the other variables.

Statistical analyses

The overall effects of stride rate on net metabolic rate, positive and negative mechanical power, and net mechanical efficiency were tested using one-way repeated-measures analysis of variance (ANOVA), followed by polynomial contrasts in the event of a significant *F* value (Keppel, 1991). An additional repeated-measures ANOVA was used to test for differences among the preferred stride rate, and the stride rates minimizing metabolic rate, minimizing positive mechanical power, minimizing the magnitude of negative mechanical power, and maximizing net mechanical efficiency. Pairwise comparisons were made using a false discovery rate procedure (Benjamini and Hochberg, 1995; Curran-Everett and Benos, 2004). Due to the exploratory nature of this research, statistical significance was assessed at the *P*=0.10 level (Curran-Everett and Benos, 2004), and correspondingly, 90% confidence intervals (CI) were computed for the preferred stride rate, and the optimal stride rates for metabolic rate, mechanical power,

²As with Eqn 2, the \dot{W}^- term in Eqn 5 is a positive quantity, defined such that $\dot{W}^- = |-\dot{W}^-|$.

and mechanical efficiency. SPSS version 11.5 (SPSS Inc., Chicago, IL, USA) was used for performing statistical analyses.

Results

Altering stride rate at a constant walking speed produced noticeable changes in the joint kinematics (Fig. 1), ground reaction forces (Fig. 2) and joint kinetics (Fig. 3). At lower stride rates, subjects exhibited a greater range of motion at the hip (Fig. 1A), but the opposite was true at the knee (Fig. 1B). At the ankle (Fig. 1C), range of motion was lower at the highest stride rate. The joint angular velocities (Fig. 1D–F) were similar between stride rates at all three joints during the early to mid stance phase (0% to approximately 50% of the walking cycle). During the late stance phase and the swing phase (approximately 50% to 100% of the walking cycle), peak angular velocities were greater at higher stride rates at the hip (Fig. 1D) and the knee (Fig. 1E), but not at the ankle (Fig. 1F).

Vertical and anterior–posterior ground reaction forces exhibited a temporal response to increasing stride rate, with systematic shifts in the relative timing of all peak values, and the stance phase representing a greater proportion of the gait cycle. A deepening of the mid-stance trough for the vertical force, and decreases in peak anterior–posterior forces, were also associated with using higher stride rates. The joint moment profiles also exhibited temporal shifts, consistent with the ground reaction force data. The average magnitude of the hip

joint moment (Fig. 3A) was greater at higher stride rates, while at the ankle (Fig. 3C), the magnitude of the plantarflexion moment was greater at low stride rates. At the knee (Fig. 3B), the magnitude of the extensor moment was greater during early stance, and the magnitude of the flexor moment was lower during late stance, at low stride rates. The primary findings for the joint powers (Fig. 3D–F) were systematically higher positive power at the hip joint and negative power at the knee joint, and systematically lower positive power at the ankle joint, at higher stride rates (Table 2). Therefore, as one walks with higher stride rates, at a constant speed, there is more energy generated at the hip, more energy absorbed at the knee, and less energy generated at the ankle.

Stride rate had a significant effect on net metabolic rate (Fig. 4A), $F_{(4,36)}=25.59$, $P=0.001$, positive mechanical power (Fig. 4B), $F_{(4,36)}=11.33$, $P=0.008$, negative mechanical power (Fig. 4C), $F_{(4,36)}=8.57$, $P=0.004$, and net mechanical efficiency (Fig. 4D), $F_{(4,36)}=11.34$, $P=0.007$. A cubic trend best explained the dependence of net metabolic rate on stride rate, $F_{(1,9)}=4.45$, $P=0.064$, while the results for positive mechanical power, $F_{(1,9)}=5.66$, $P=0.041$, negative mechanical power, $F_{(1,9)}=9.22$, $P=0.014$, and net mechanical efficiency, $F_{(1,9)}=8.29$, $P=0.018$, were best fit by quadratic polynomials. The average preferred stride rate was 54.3 strides min^{-1} (s.d.=3.1, CI 52.6–56.1), while net metabolic rate was minimized at a stride rate of 54.4 strides min^{-1} (s.d.=4.2, CI 52.0–56.9). Positive mechanical

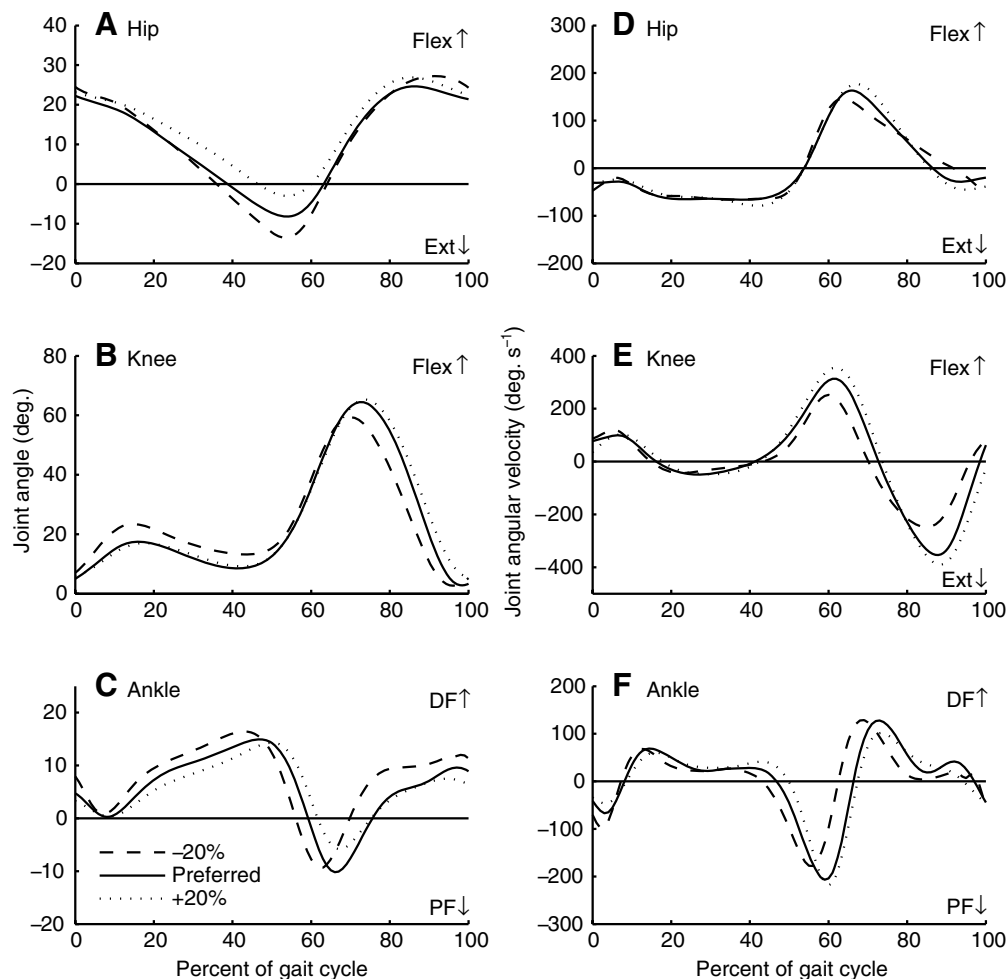


Fig. 1. Group mean sagittal plane joint angles (A–C) and angular velocities (D–F) for the hip, knee and ankle during walking with stride rates above (+20%), below (–20%), and at the preferred rate. The $\pm 10\%$ conditions have been omitted for clarity, but were generally intermediate to the preferred and $\pm 20\%$ conditions. At lower stride rates, there was a greater range of motion at the hip and a lower range of motion at the knee. The joint angular velocities were similar across stride rates for all three joints during the early to mid stance phase (0–50% of the gait cycle), but were higher for the hip and the knee during the late stance phase and the swing phase (50–100% of the gait cycle). Flex, flexion; ext, extension; DF, dorsiflexion; PF, plantarflexion.

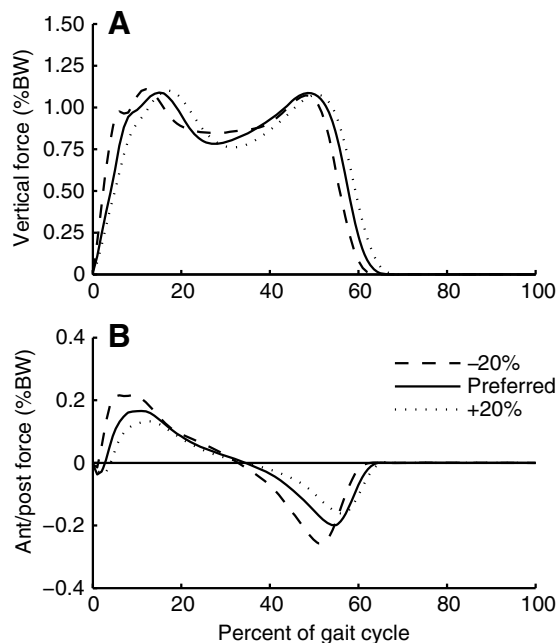


Fig. 2. Group mean vertical (A) and anterior–posterior (B) ground reaction forces (normalized to body weight, BW) during walking with stride rates above (+20%), below (–20%), and at the preferred rate. The $\pm 10\%$ conditions have been omitted for clarity, but were generally intermediate to the preferred and $\pm 20\%$ conditions. At higher stride rates there were greater fluctuations in the vertical force, reduced peak anterior–posterior forces, and the stance phase lasted a greater proportion of the gait cycle. Zero and 100% of the gait cycle correspond to right heel strike, and the end of the stance phase coincides with the forces going to zero.

power was minimized at 47.6 strides min^{-1} (s.d.=6.9, CI 43.6–51.7), whereas (the magnitude of) negative mechanical power was minimized at 48.5 strides min^{-1} (s.d.=8.0, CI 43.8–53.1). Net mechanical efficiency was maximized at 58.7 strides min^{-1} (s.d.=6.1, CI 55.2–62.2). The latter four stride rate values were determined by fitting polynomials of the order indicated above to individual subject data, computing the appropriate minimum or maximum for each subject, and then averaging across subjects.

The ANOVA that tested for differences among the preferred stride rate and the predicted optima for metabolic rate, positive power, negative power and net mechanical efficiency was significant, $F_{(4,36)}=7.27$, $P=0.006$. The multiple comparison procedure revealed that positive mechanical power, $P=0.013$, and negative mechanical power, $P=0.046$, were optimized at stride rates significantly lower than the preferred stride rate. Likewise, positive mechanical power, $P=0.014$, and negative mechanical power, $P=0.077$, were optimized at stride rates significantly lower than the metabolically optimal stride rate. The optimal stride rates for positive and negative mechanical power were not significantly different from each other, $P=0.781$. Net mechanical efficiency was optimized at a stride rate that was significantly higher than the preferred stride rate, $P=0.001$, and the stride rates that were optimal for metabolic rate, $P=0.003$, positive power, $P=0.006$, and negative power,

$P=0.018$. The preferred stride rate was not significantly different from the metabolically optimal stride rate, $P=0.874$. In summary, the trend analyses indicated that the preferred and metabolically optimal stride rates were essentially identical, while power generation and absorption were minimized at lower stride rates (11–12% lower) and efficiency was maximized at a higher stride rate (~8% higher). Observed statistical power for all tests was found to exceed 0.87.

Discussion

The results for net metabolic rate were consistent with previous reports (Atzler and Herbst, 1927; Cotes and Meade, 1960; Holt et al., 1991; Minetti et al., 1995; Molen et al., 1972; Zarrugh and Radcliffe, 1978) as there was a U-shaped response to stride rate variation at a constant speed (Fig. 4A), and the preferred stride rate did not differ from the stride rate at which energy expenditure was minimized. The results for mechanical power (Fig. 4B,C) and net mechanical efficiency (Fig. 4D), on the other hand, provided only partial support for our stated hypotheses. In the presence of altered stride rates, mechanical power and efficiency followed U-shaped (or inverted U-shaped) trends, as predicted. Contrary to our predictions, neither power nor efficiency was optimized at the preferred stride rate. The power curves exhibited plateaus that spanned stride rates lower than preferred, with the predicted optima occurring 11–12% below the preferred stride rate. In contrast, the plateau in the efficiency curve spanned stride rates higher than preferred, with the predicted optimum 8% above the preferred stride rate. The predicted optima, derived from the trend analyses, should be viewed cautiously, but the differences in the plateaus of the curves (Fig. 4B–D) represent a disassociation between performing mechanical work and the metabolic cost of the work. These data characterize a situation in which there is a narrow range of stride rates that are close to optimal for both mechanical power and efficiency. Based on these results, the preferred stride rate in walking appears to represent the best compromise between optimizing power and efficiency, at least for the one speed considered. This combination of power and efficiency should minimize the cost of doing mechanical work, which will result in the lowest rate of metabolic energy expenditure. Therefore, the major finding of this study was that during level walking near preferred speeds, the range of stride rates that is optimal for mechanical efficiency is higher than the range of stride rates that is optimal for mechanical power. This finding has direct implications for our understanding of the determinants of the metabolic cost of walking.

The mechanical work done by muscles in walking, reflected by our average mechanical power expression, is believed to extract a significant metabolic cost (Donelan et al., 2002; Grabowski and Kram, 2005; Neptune et al., 2004; Kuo, 2001). However, the cost of doing mechanical work in walking cannot be understood only in terms of the amount of mechanical energy that is generated (or absorbed). Previous researchers have sought an association between the preferred stride rate, and the stride rate at which mechanical work or power is minimized (Cavagna and Franzetti, 1986; Minetti et al., 1995; Minetti and Saibene, 1992). Yet, mechanical work or power has always been found to be minimized at stride rates lower than those selected by the subjects, which was also true in our study. This

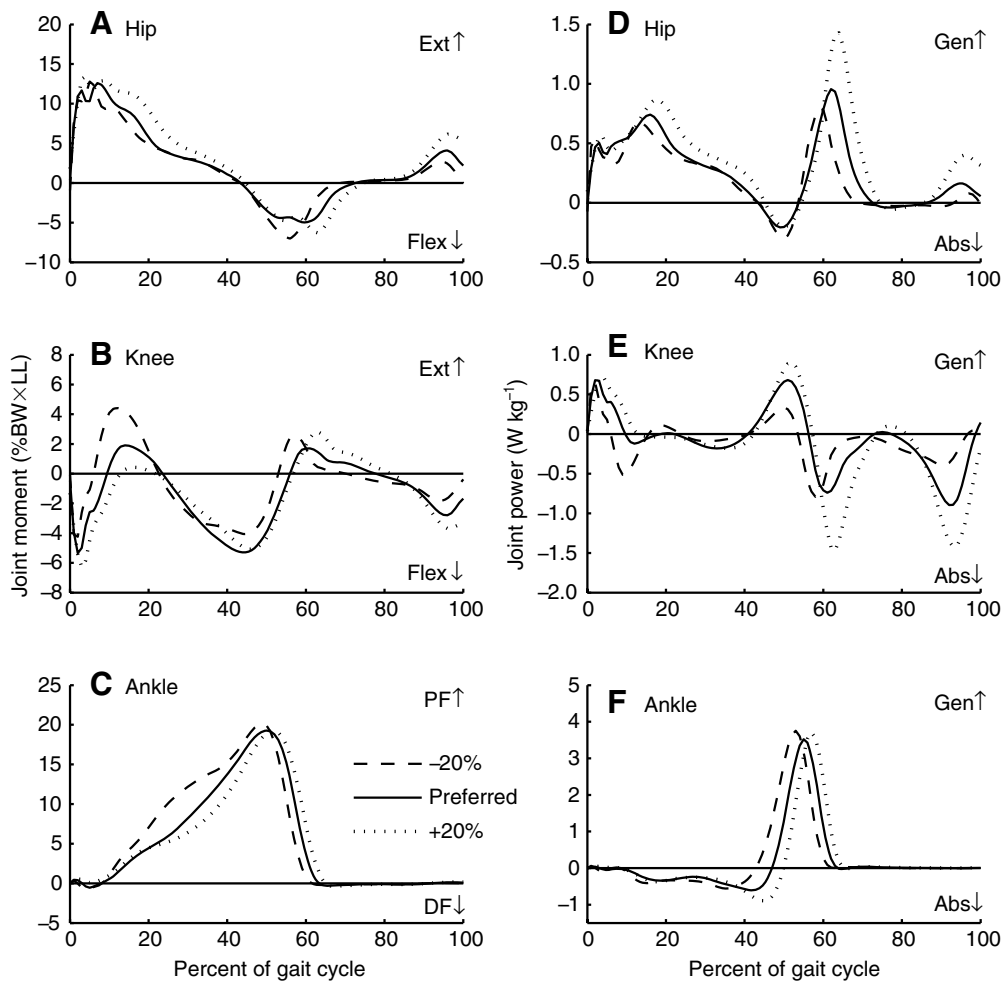


Fig. 3. Group mean sagittal plane net joint moments (A–C) and powers (D–F) for the hip, knee and ankle during walking with stride rates above (+20%), below (–20%), and at the preferred rate. The $\pm 10\%$ conditions have been omitted for clarity, but were generally intermediate to the preferred and $\pm 20\%$ conditions. Moments have been normalized to body weight (BW) and leg length (LL), and powers have been normalized to body mass. At higher stride rates there were larger moments and more power produced at the hip joint, and smaller moments and less power produced at the ankle joint. The knee joint was the major site of energy absorption, with more absorption occurring at higher stride rates. Flex, flexion; ext, extension; Gen, generation; Abs, absorption; PF, plantarflexion; DF, dorsiflexion.

discrepancy can presumably be accounted for by the present results for net mechanical efficiency. Compared to walking at the preferred stride rate, walking at stride rates 10–20% lower than preferred resulted in little change in mechanical power demand (Fig. 4B), but net mechanical efficiency (Fig. 4D) was considerably lower (29% lower at the lowest stride rate). Conversely, walking at stride rates 10–20% higher than preferred resulted in little change in net mechanical efficiency (Fig. 4D), but mechanical power output (Fig. 4B) was elevated (19% higher at the highest stride rate). Therefore, moderate deviations from the preferred stride rate will incur a disproportionate penalty in either power or efficiency, depending on the direction of the deviation. One must be careful about extrapolating beyond the bounds of the data set, but the regression lines in Fig. 4B,D suggest that if one were to stray from the preferred stride rate by more than 20% in either direction there would be both an increase in power requirements and a decrease in efficiency. This would help explain the relative flatness of the metabolic power curve (Fig. 4A) near the preferred stride rate, and the gradual increase in the steepness of this curve, as stride rate is increased or decreased further from the preferred stride rate.

We hypothesized that power and efficiency would both be optimized at the preferred (and metabolically optimal) stride rate, but this hypothesis was not supported by our results. Based

on polynomial trend analyses, mechanical power was predicted to be optimized at roughly 10 strides min^{-1} below the preferred stride rate, while net mechanical efficiency was predicted to be optimized at roughly 10 strides min^{-1} above the preferred rate. The magnitudes of the confidence intervals around these predicted optima (Fig. 4) suggest a fair degree of uncertainty in the exact values of the optima, which is likely tied to the relative flatness of the power, efficiency and metabolic responses in the vicinity of the respective optima. Despite the uncertainty in the exact values of the optima, there was no overlap between the confidence intervals for mechanical power and net mechanical efficiency, indicating that mechanical power is optimized at a lower stride rate than efficiency. Furthermore, there was only limited overlap between the confidence interval for the metabolically optimal stride rate and the confidence intervals for mechanical power and net efficiency (overlap ranged from 0.0–1.7 strides min^{-1}). Thus, it is unlikely that metabolic cost, mechanical power and net efficiency are all optimized at the preferred stride rate, or any other single stride rate. One might ask why mechanical power and efficiency would be optimized at different stride rates, rather than at the same stride rate. Walking would probably be less costly if power and efficiency were both optimized at the preferred stride rate, but this would be true only at that one stride rate. At other stride rates, walking would be more costly, which would make the system less

Table 2. Average mechanical power over the full gait cycle

Power (W kg ⁻¹)	-20%	-10%	Preferred	+10%	+20%
Summed					
Positive	0.67±0.08	0.66±0.07	0.72±0.13	0.75±0.11	0.85±0.13
Negative	0.37±0.12	0.36±0.05	0.37±0.06	0.44±0.07	0.51±0.09
Hip					
Positive	0.23±0.07	0.24±0.06	0.28±0.07	0.33±0.09	0.39±0.09
Negative	0.04±0.03	0.04±0.03	0.03±0.03	0.04±0.04	0.03±0.03
Knee					
Positive	0.07±0.04	0.08±0.03	0.12±0.06	0.13±0.06	0.15±0.07
Negative	0.18±0.06	0.18±0.03	0.20±0.06	0.24±0.03	0.31±0.07
Ankle					
Positive	0.37±0.09	0.34±0.06	0.32±0.08	0.29±0.07	0.30±0.09
Negative	0.15±0.05	0.13±0.04	0.14±0.04	0.16±0.04	0.17±0.05

Values for positive and negative power are means \pm s.d. ($N=10$). Preferred is the preferred stride rate condition; negative values represent stride rates lower than preferred, and positive values represent stride rates higher than preferred. For negative powers the magnitudes are shown. Data are presented for a single limb. The first two rows (Summed) are positive and negative powers summed over the hip, knee and ankle joints, and were the quantities used in computing net mechanical efficiency.

flexible. Stated differently, the U-shaped metabolic cost–stride rate relationship would be narrower, and deviations from the metabolically optimal stride rate would result in greater penalties in terms of energy cost. The discrepancy in optimal stride rate for power and efficiency results in a broader range of stride rates with relatively low cost, at the expense of having a single stride rate with an even lower cost. If this is true, it would help further explain the flatness of the metabolic–stride rate response in the vicinity of the preferred stride rate.

The analyses in this study focused on factors that influence the cost of performing mechanical work, but there are other factors that may also influence the cost of locomotion. One contemporary perspective on locomotor energetics is that the total metabolic cost of locomotion is largely explained by the combined costs of generating muscular force and doing mechanical work (Kram, 2000). In this paradigm, the cost of generating force is determined by the amount of force that muscles must generate, and the rate at which these forces must be produced. One might expect muscular force and rate of force development to vary with stride rate, but at present these data do not exist in the literature. We can speculate on the average rate of force development, based on the changes that occurred in stance time across the different stride rates (Table 1). Going from the lowest stride rate to the highest, stance time decreased by about 30%. This would appear to be a non-trivial difference, but it is actually rather small compared to the differences in stance time that are observed when comparing across different speeds and/or species (Kram, 2000). In addition to our current uncertainty about how muscular force and rate of force development vary with stride rate, the proportion of the total metabolic cost of walking that is attributable to the cost of generating force is also unknown. One recent study indicated that the cost of generating force accounted for most of the metabolic cost of human walking (Griffin et al., 2003); however, subsequent research from the same laboratory placed the cost of generating force at less than one third of the net cost of walking (Grabowski et al., 2005). If the cost of generating force does represent a substantial fraction of the cost of walking,

then it must also be minimized within the general vicinity of the preferred stride rate. Otherwise, net metabolic power would not exhibit a minimum at the preferred stride rate. Given these uncertainties, there is a need for additional research focused on determining how muscular force requirements, the rate of force development, and the metabolic cost of generating force vary with stride rate and speed during walking in humans.

The basic data from which the mechanical power and net mechanical efficiency variables were computed were generally in good agreement with data from the existing literature. The patterns and magnitudes for the ground reaction forces, joint moments and joint powers were generally consistent with earlier data from Winter (Eng and Winter, 1995; Winter, 1990). The only noticeable difference was a lower peak knee extensor moment during the stance phase in the present data set, although our data were still well within the reported standard deviation envelope for this variable. Mechanical energy generation exceeded absorption (Table 2), as had been reported previously (Eng and Winter, 1995). This can be explained by mechanical energy being dissipated *via* non-muscular mechanisms, such as deforming the foot and shoe during ground contact (Webb et al., 1988). Thus, the joint moments must do more positive work than negative work during each stride. The results for metabolic energy expenditure were also in good agreement with data from the literature (Holt et al., 1991; Minetti et al., 1995; Zarrugh and Radcliffe, 1978), once account is taken of the conversion from rate of oxygen consumption to energy expenditure (Weir, 1949), and subtraction of the baseline metabolic rate (Minetti et al., 1995). Mechanical power was computed in a different manner in this study than in other related research (Cavagna and Franzetti, 1986; Minetti et al., 1995; Minetti and Saibene, 1992); thus, it was interesting to note that the stride rate at which mechanical power was minimized in our study was lower than the preferred rate, just as was reported in these earlier studies. However, power generation and absorption were minimized at a stride rate considerably closer to the preferred rate (11–12% below) than

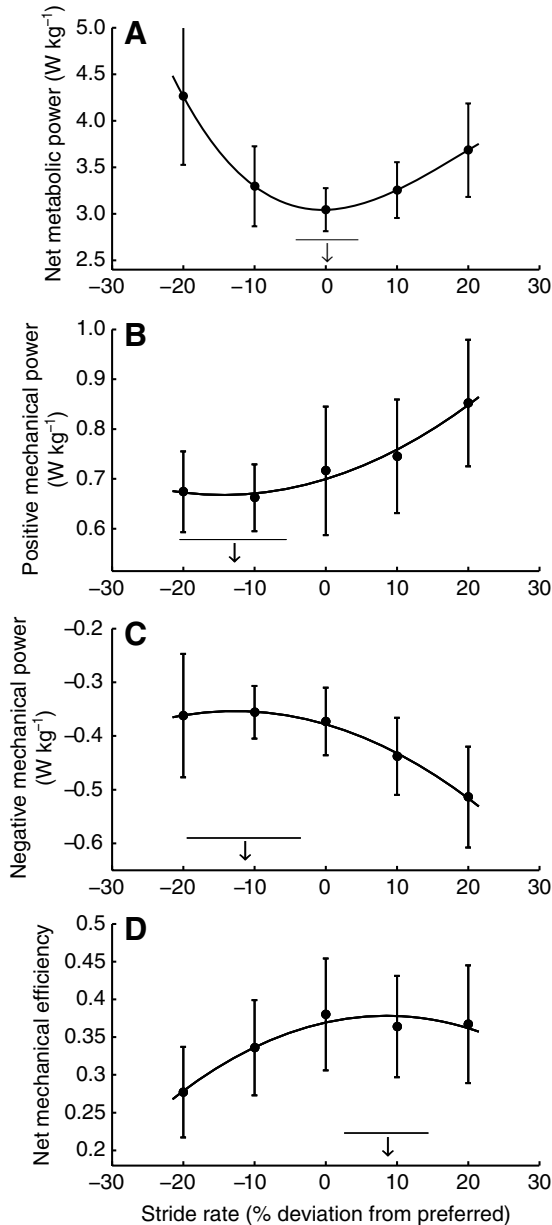


Fig. 4. Net rate of metabolic energy expenditure (A), average positive (B) and negative (C) mechanical power (summed over the hip, knee and ankle joints) and net mechanical efficiency (D) during walking with the preferred stride rate (0), and with stride rates above (+) and below (-) the preferred rate. Metabolic and mechanical powers have been normalized to body mass. Values are means \pm 1 s.d. and the vertical arrows indicate the location of the predicted minimum or maximum for each variable. The horizontal bars are the confidence interval for the predicted minimum or maximum. Net metabolic power was minimized near the preferred stride rate, while mechanical power exhibited a plateau that spanned stride rates lower than preferred, and mechanical efficiency exhibited a plateau that spanned stride rates higher than preferred.

in these other studies (20–30% below). Much of this discrepancy is presumably due to differences in how mechanical work and power were computed.

While any study has strengths and weaknesses, there are

some issues with the current investigation that are worthy of further comment. Mechanical powers were computed from net joint moments calculated using a two-dimensional model. The use of a planar model could potentially exclude sources of mechanical work done outside of the sagittal plane. However, the mechanical work done by most of the joint moments in the frontal and transverse planes during walking is either small in magnitude, mostly passive in nature, or both (Eng and Winter, 1995). The one case for which this is not true is work done by the hip abduction moment, which accounts for about 25% of the mechanical work at the hip joint. Subjectively, the balance requirements in the frontal plane seemed greater when subjects used lower stride rates and longer strides. Thus, one might expect more mechanical work to be done at the hip when walking at low stride rates. If mechanical power was disproportionately elevated at low stride rates, it would shift the predicted optimum closer to the preferred stride rate (Fig. 4B). Using data reported in Eng and Winter (Eng and Winter, 1995), we estimated that the mechanical work done by the hip abduction moment would need to increase threefold from the preferred to the lowest stride rate for positive mechanical power to be minimized at the preferred stride rate. Such a large change in hip abduction work seems unlikely, given the changes observed in the sagittal plane (Table 2).

Another factor worth further consideration was the expression for net mechanical efficiency that was used. Our definition of efficiency was based on Prilutsky (Prilutsky, 1997), and is related to the positive work done by muscles, relative to the total energy available (both metabolic energy and mechanical energy that might be stored in muscle–tendon springs). This definition of efficiency is well suited for studying terrestrial locomotor performance, and should not be confused with another expression for the efficiency of positive work (sum of external and internal power, divided by the rate of metabolic energy expenditure), which has recently been criticized in the literature (van Ingen Schenau et al., 1997; Zatsiorsky, 1998). The peak value of 0.38 we obtained for net mechanical efficiency was higher than has been reported for isovelocity shortening in isolated mammalian muscle [approximately 0.30 (Barclay et al., 1993)]. However, our findings are consistent with the higher efficiencies obtained using cyclic contraction protocols, which more closely mimic the shortening and lengthening patterns of muscles *in vivo* (Barclay, 1994). For comparative purposes, we also calculated locomotor mechanical efficiency using gross metabolic rate, which yielded a value of 0.28 at the preferred stride rate. This value is in good agreement with the original application of this approach by Prilutsky (Prilutsky, 1997).

We further evaluated the influence of having the magnitude of the negative mechanical power appear in the denominator of the efficiency expression (Eqn 5) by computing an additional efficiency expression that did not include the negative power (i.e. $\epsilon = 2\dot{W}^+/\dot{E}_{net}$). The primary effect of ignoring the negative power was to increase the magnitude of the computed efficiency, with a larger difference at higher cadences (Fig. 5). The general shape of the response to variations in stride rate did not differ between the two efficiency expressions in a manner that would have fundamentally changed the conclusions of this study. The efficiency expression that did not include the

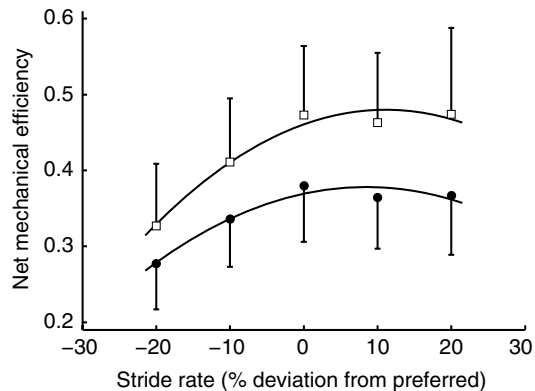


Fig. 5. Net mechanical efficiency computed two different ways for walking with the preferred stride rate (0), and with stride rates above (+) and below (-) the preferred rate. Efficiency was computed either including (closed circles) or excluding (open squares) the magnitude of the negative power in the denominator of the efficiency expression (see text for details). When negative power was ignored, the computed efficiency was higher, with the effect being greater at higher stride rates. The overall dependence of mechanical efficiency on stride rate was similar for both expressions.

negative work is consistent with the more commonly used definition, but still does not provide a direct comparison with other studies, as mechanical power was obtained from the joint moments, rather than from changes in mechanical energy of the center of mass and/or body segments. More research is clearly needed to evaluate the merits of the different ways of computing mechanical work and efficiency in locomotion.

Conclusion

The present results offer a reasonable explanation for the dependence of metabolic energy expenditure on stride rate as subjects walk at a fixed speed. Our data suggest that the increase in net metabolic rate with moderate increases in stride rate is due mainly to an increase in the amount of mechanical work that the lower limb muscles must do, while the increase in net metabolic rate with moderate decreases in stride rate is due to a decrease in the mechanical efficiency of performing muscular work. For larger deviations from the energetically optimal (and preferred) stride rate, there is expected to be both an increase in the amount of work done, and a decrease in the efficiency of performing work, resulting in relatively larger increases in net metabolic cost. We conclude that the preferred stride rate in walking represents the best compromise between minimizing the amount of mechanical work done by muscles, and maximizing the efficiency with which that work is done. In other words, walking at the preferred stride rate appears to minimize the cost of doing mechanical work. While the current research should be expanded to determine how well these results generalize to other walking speeds, it seems that fundamental advances in our understanding of the cost of locomotion are likely to require other methods. Especially promising are new *in vivo* techniques that are presently limited to use in non-human animal studies (Marsh et al., 2004) and computer simulation models capable of predicting muscle metabolic energy expenditure (Umberger et al., 2003).

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