# RESEARCH ARTICLE

# Energetically optimal stride frequency in running: the effects of incline and decline

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## SUMMARY

**At a given running speed, humans strongly prefer to use a stride frequency near their 'optimal' stride frequency that minimizes metabolic cost. Although there is no definitive explanation for why an optimal stride frequency exists, elastic energy usage has been implicated. Because the possibility for elastic energy storage and return may be impaired on slopes, we investigated whether and how the optimal stride frequency changes during uphill and downhill running. Presuming a smaller role of elastic energy, we hypothesized that altering stride frequency would change metabolic cost less during uphill and downhill running than during level running. To test this hypothesis, we collected force and metabolic data as nine male subjects ran at $2.8\,m\,s^{-1}$ on the level, 3 deg uphill and 3 deg downhill. Stride frequency was systematically varied above and below preferred stride frequency (PSF ±8% and ±15%). Ground reaction force data were used to calculate potential, kinetic and total mechanical energy, and to calculate the theoretical maximum possible and estimated actual elastic energy storage and return. Contrary to our hypothesis, we found that neither the overall relationship between metabolic cost and stride frequency nor the energetically optimal stride frequency changed substantially with slope. However, estimated actual elastic energy storage as a percentage of total positive power increased with increasing stride frequency on all slopes, indicating that muscle power decreases with increasing stride frequency. Combined with the increased cost of force production and internal work with increasing stride frequency, this leads to an intermediate optimal stride frequency and overall U-shaped curve.**

Key words: metabolic cost, slope, elastic energy, hill.

## INTRODUCTION

At a given speed on the level, human runners show a strong preference for a particular stride frequency, known as the preferred stride frequency (PSF). An individual's PSF is usually close to their optimal stride frequency (OSF) that minimizes metabolic cost (Hogberg, 1952; Cavanagh and Williams, 1982; Kaneko et al., 1987). The rate of metabolic energy consumption is greater at stride frequencies faster or slower than the OSF. Although many ideas have been put forth to explain why metabolic cost is minimized at the OSF, none have been conclusively proven. This paper further investigates the determinants of the OSF.

A series of studies by Cavagna and colleagues has explored some possible determinants of OSF and PSF in running. Note that the terms step and stride frequency are conceptually interchangeable in human research because in bipeds two steps are equivalent to one stride, but this issue is complicated for animals with more than two legs. Cavagna and coworkers found that running and hopping animals appear to use a step frequency slower than the symmetrically bouncing frequency that minimizes external work (Cavagna et al., 1988). By doing so, these species avoid the accompanying increase in 'internal work' due to rapid limb movements associated with faster step frequencies. Cavagna and colleagues subsequently proposed that the metabolic minimum associated with the PSF may instead be force related (Cavagna et al., 1991). They postulated that PSF is a compromise between minimizing the average force exerted by the muscles over the span of a step (which is greater at slow step frequencies) and minimizing the limb stiffness (which is greater at fast step frequencies). However, neither of these studies considered

the possibility of elastic energy storage and return, with all positive work assumed to be performed by the muscle. Using some of the same data, Cavagna and colleagues suggested that muscle activation alone is inadequate to adjust leg stiffness, which would allow for multiple resonant step frequencies (Cavagna et al., 1997). Rather, they reasoned that only the unforced resonant step frequency of ~2.7 Hz is capable of providing maximal elastic energy return and thus maximal metabolic energy savings. However, Cavagna and colleagues only studied slow running speeds of 5.3, 8 and $11\,km\,h^{-1}$ (1.5, 2.2 and $3\,m\,s^{-1}$), with much of the evidence coming from the slowest speeds (Cavagna et al., 1997). Thus, it is unclear whether these results apply to more typical running speeds.

Other researchers have speculated that minimization of mechanical work and maximization of elastic energy use play a role in determining the OSF (Taylor, 1985; Cavanagh and Kram, 1985). During bouncing gaits like running, elastic energy is stored in muscles, tendons and ligaments as the center of mass (CoM) moves downward and slows during the first half of the stance phase. These tissues subsequently release elastic energy as the body moves upward and accelerates forward during the second half of the stance phase (Alexander, 1984; Alexander, 1991). If the contribution of elastic energy to total work was maximized at the OSF, the muscles would perform less mechanical work and consume less metabolic energy than at other stride frequencies. The observation that the overall leg behaves like a simple spring at the PSF but not at slower stride frequencies supports this idea (Farley et al., 1991; Farley and Gonzalez, 1996). However, the role of elastic energy storage and return in determining the OSF is still not clearly understood. Because

running mechanics change on different slopes (Iverson and McMahon, 1992; Minetti et al., 1994; Klein et al., 1997; Swanson and Caldwell, 2000; Gottschall and Kram, 2005), comparing level, uphill and downhill running may reveal new information about the role of elastic energy in determining the OSF.

In the present study, we investigated the idea that, on the level, storage and return of elastic energy is a principal factor affecting OSF at which metabolic cost is minimized. In contrast to level running, the maximum possible storage and return of elastic energy is reduced in hill running. The difference stems from mismatches between the possibility for elastic energy storage during landing and the possibility for using that elastic energy during takeoff (Cavagna, 1977; Minetti et al., 1994; Gottschall and Kram, 2003). For example, during uphill running, the gravitational potential energy (GPE) of the CoM is greater at the end of the stance phase than at the beginning of stance because the CoM is higher. At the upper limit, elastic energy storage and return is sufficient only to bring the CoM back to its original height. During uphill running, the muscles must perform net positive work to raise the CoM to its height at toe-off and, additionally, to give it sufficient kinetic energy to raise it to its highest point during the aerial phase. Conversely, when running downhill, the CoM is lower at the end of the stance phase than at the beginning. Therefore, some energy dissipation must occur to keep speed constant, meaning more energy is available than is stored and returned. Although these patterns are a measure of maximal and not actual elastic energy storage and return, they suggest that elastic energy use is reduced uphill and downhill. Assuming elastic energy use is reduced on hills and is a major determinant of the OSF, we hypothesized that altering stride frequency by a given percentage would increase metabolic cost by a smaller amount during hill running than during level running. To test this hypothesis, we measured metabolic cost as subjects ran at a range of stride frequencies on the level, uphill and downhill.

## MATERIALS AND METHODS

Data for nine male runners between the ages of 18 and 35 are presented (age, 28.5±4.1 years; mass, 69.1±5.3 kg; leg length, 0.95±0.04 m; means ± s.d.). All subjects had recent 5 km race times below 18 min 30 s or equivalent. This restriction was imposed so that all subjects could complete the uphill running trials while consuming oxygen at submaximal rates. All subjects gave informed consent in accordance with the University of Colorado Human Research Committee.

Subjects ran at a speed of $2.8\,\mathrm{m\,s^{-1}}$ on a force treadmill on the level and tilted to 3 deg uphill and 3 deg downhill as described previously (Gottschall and Kram, 2005). The speed and treadmill slopes were chosen to make it possible for runners to use a wide range of stride frequencies on the uphill slope while maintaining submaximal rates of oxygen consumption. This constraint prevented us from studying steeper slopes or faster speeds.

During orientation sessions, each subject ran for 10 min to become comfortable with treadmill running. Each subject then practiced matching an audio metronome beat set to the PSF determined during the 10 min practice run, as well as the maximum and minimum stride frequencies used in the study. To test whether the subject had sufficient aerobic fitness to complete the protocol while remaining at a submaximal rate of oxygen consumption, each subject then ran a full trial (7 min) at his PSF on the uphill. We determined the subject's respiratory exchange ratio (RER) and metabolic rate from standard open-circuit expired gas analysis during minutes 4–6 of the trial (Brooks et al., 2004). Subjects were required to have a mean RER of ≤0.9 during this orientation trial to continue in the study.

After the orientation session, each subject completed three data collection sessions on separate days during which he ran on the level, 3 deg uphill or 3 deg downhill, in that order. The order was fixed to allow the investigators to change the slope of the treadmill, which was time consuming. This order also limited the effect of delayed onset muscle soreness from the downhill trials (Braun and Dutto, 2003). At the start of each experimental session, we measured metabolic rate per kilogram of body mass for each subject during 7 min of quiet standing ($1.79\pm0.08\,\mathrm{W\,kg^{-1}}$, mean ± s.e.m.). For the first running trial, each subject ran without any instructions so that we could determine his PSF. We determined stride frequency once per minute by measuring the time elapsed for 40 strides with a stopwatch. All subjects reached a steady stride frequency within 5 min, as defined as having a range of $<2\,\mathrm{strides\,m^{-1}}$ for a period of at least 3 min. During the last 7 min of this trial, we determined metabolic rate as well as the subject's PSF for that condition (level, uphill or downhill) by timing 40 strides once per minute and averaging these seven measurements. Subsequently, each subject completed a series of 7 min trials separated by 5 min rest periods in the following order: PSF with metronome, 108% PSF, 92% PSF, 115% PSF, 85% PSF. These values were chosen to provide a wide enough range of stride frequencies to allow for calculation of the optimum stride frequency, while remaining close enough to PSF that the subjects could match the frequency for 7 min trials. Each subject matched the metronome at his PSF to control for any increase in metabolic cost due to matching the metronome. The trials were in the expected order of rising metabolic demand (Cavanagh and Williams, 1982). We did not conduct the trials in a randomized order to avoid the possibility of metabolic rate during the subsequent trial remaining elevated from a more demanding previous trial.

During each trial, we determined the subject's metabolic rate and RER from standard open-circuit expired gas analysis (Physio-Dyne Inc., Quogue, NY, USA). We determined metabolic rate for minutes 4–6 of each trial to ensure that the subjects were being measured only after reaching steady state. From the mass-specific rate of oxygen consumption ($\mathrm{ml\,O_2\,kg^{-1}\,min^{-1}}$) and the mass-specific rate of carbon dioxide production ($\mathrm{ml\,CO_2\,kg^{-1}\,min^{-1}}$), we calculated the mass-specific total metabolic rate ($\mathrm{W\,kg^{-1}}$) (Brockway, 1987) and the RER. RER was required to be below 1.0 for all trials. We subtracted the standing metabolic rate from the total metabolic rate to determine the net metabolic rate ($\mathrm{W\,kg^{-1}}$). Finally, we divided the net metabolic rate by running speed to determine the mass-specific net cost of transport ($\mathrm{J\,kg^{-1}\,m^{-1}}$).

OSF was determined separately for each subject on each slope. This was done by first calculating a least-squares cubic interpolation with the absolute stride frequency as the independent variable and metabolic cost as the dependent variable. Cubic interpolation was used to allow for any asymmetric increase in cost on either side of the optimum. The optimum was then calculated by finding the zero of the derivative of the cubic for which the second derivative was positive.

We used a stopwatch to monitor stride frequency during each minute of each trial to ensure that the subject was indeed matching the metronome frequency. During minutes 3–4, we collected 30 s of ground reaction force (GRF) data at 1000 Hz (Labview 4.0, National Instruments, Austin, TX, USA) from a force treadmill (Kram et al., 1998; Gottschall and Kram, 2005). We filtered the GRF data using a low-pass bi-directional fourth-order Butterworth filter at 20 Hz. A custom-written program in Matlab (The Mathworks, Natick, MA, USA) identified heel-strike and toe-off. In order to get a more accurate measure of stride frequency than

Table 1. Mean (s.e.m.) values for net metabolic cost at a speed of 2.8 m s$^{-1}$ at each stride frequency on each slope

| Stride frequency | Downhill net metabolic cost (J kg$^{-1}$ m$^{-1}$) | Level net metabolic cost (J kg$^{-1}$ m$^{-1}$) | Uphill net metabolic cost (J kg$^{-1}$ m$^{-1}$) |
|---|---|---|---|
| 85% of PSF | 2.76 (0.11)[*,†] | 3.67 (0.04)[*,†] | 4.85 (0.10)[*,†] |
| 92% of PSF | 2.46 (0.08)[†] | 3.30 (0.05)[†] | 4.48 (0.06)[†] |
| PSF | 2.28 (0.08) | 3.17 (0.03) | 4.46 (0.08) |
| 108% of PSF | 2.45 (0.10)[†] | 3.28 (0.05)[†] | 4.65 (0.09)[*,†] |
| 115% of PSF | 2.72 (0.11)[*,†] | 3.54 (0.07)[*,†] | 4.96 (0.15)[*,†] |

$N$=9 subjects. *Cost at a given stride frequency on that slope was significantly greater than cost at preferred stride frequency (PSF) on the same slope with Sidak correction ($P$<0.0034). [†]$P$<0.05. At corresponding stride frequencies, cost on the uphill was always significantly greater than cost on the level ($P$<0.001) and the downhill ($P$<0.001). Similarly, cost on the level was always significantly greater than cost on the downhill ($P$<0.001) at a given stride frequency. Therefore no symbols are used to signify statistically significant differences across slopes. There were no significant interaction effects.

could be achieved through counting strides, we used these data to calculate stride frequency for subsequent analyses and graphs.

We calculated mechanical energy fluctuations of the CoM for each step (Cavagna, 1975) also using a Matlab program. The program integrated horizontal and vertical GRF data once to calculate instantaneous velocity in the horizontal ($\mathbf{v}_h$) and vertical ($\mathbf{v}_v$) directions. We used an integration constant of $v_t\sin\theta$ for the vertical direction and $v_t\cos\theta$ for the horizontal direction, where $v_t$ was the treadmill speed and $\theta$ was the slope of the treadmill relative to horizontal (negative for downhill). We used the Pythagorean theorem to obtain a resultant velocity, $\mathbf{v}$, and this value was used in the equation KE=$0.5m\mathbf{v}^2$ (where $m$ is body mass) to calculate total kinetic energy (KE) for each instant in each step. The vertical velocity data were then integrated again to obtain instantaneous displacement relative to touchdown using zero as the integration constant. We used these data to calculate changes in the GPE of the CoM, GPE=$mgh$ [where $m$ is body mass, $g$ is gravity (9.81 m s$^{-2}$) and $h$ is vertical displacement] over a step. Total mechanical energy of the CoM was determined by summing KE and GPE.

We determined the maximum theoretically possible elastic energy storage per step by taking the difference between the total CoM energy at the beginning of stance and the minimum energy of the CoM reached near mid-stance. The minimum energy occurred near mid-stance on all slopes. Maximum possible elastic energy return per step was defined as the difference between total energy at the end of stance and the minimum energy. We considered maximum possible elastic energy usage to be the smaller of the energy storage and energy return values. For example, if in uphill running there was a 20 J decrease in total CoM energy between touchdown and minimum energy, and then a 45 J increase in total CoM energy between minimum energy and toe-off, the maximum possible elastic energy usage would be 20 J. The body could only store 20 J of energy and therefore could only use 20 J of elastic energy. Correspondingly, if in downhill running, there was a 45 J decrease in total CoM energy between touchdown and minimal energy, and then a 20 J increase in total CoM energy between minimum energy and toe-off, the maximum possible elastic energy usage would still be 20 J. In this case the body could potentially store 45 J, but only used 20 of those 45 J to raise and accelerate the CoM. These values

were determined for each step, and then averaged to determine typical energy storage and return per step.

We used SPSS to perform a two-factor (slope, frequency), repeated measures ANOVA to analyze changes in net metabolic cost and biomechanical characteristics across slope and stride frequency with $P\leq0.05$ needed for significance. We calculated the interaction effect in order to analyze whether step frequency affected net metabolic cost similarly across slope. We used absolute measures of metabolic cost because we wanted to examine the net cost of a change in stride frequency, not the normalized cost, which would be artificially high downhill (because metabolic cost is lower) and artificially low uphill (because metabolic cost is greater). Sidak corrections were performed when doing *post hoc* analyses. Because of the stringency of the Sidak correction, in cases where more than 10 *post hoc* $t$-tests were performed, differences are also reported at the $P\leq0.05$ level. Although data were collected for 10 subjects, in the course of the statistical analysis, one subject was discovered to have much greater costs at slow stride frequencies than other subjects, with cost values nearly 3 standard deviations above the mean, and was thus labeled an outlier. Data were then recalculated for $N$=9 subjects.

## RESULTS

Runners consumed the least metabolic energy at an intermediate stride frequency on all slopes and consumed more energy at faster and slower stride frequencies (Table 1; Fig. 1A). However, contrary to our hypothesis, metabolic cost showed a similar dependence on stride frequency on all slopes, as evidenced by a non-significant interaction effect ($P$=0.33). The non-significant interaction effect shows that, when the effect of slope is accounted for and removed, varying stride frequency by a given amount leads to a similar increase in absolute metabolic cost on all slopes. By using a slow stride frequency, equal to 85% PSF, runners increased metabolic cost by 9–21% compared with the PSF, depending on the slope. By using a fast stride frequency, equal to 115% PSF, runners increased their metabolic cost by 11–19%, depending on the slope (Fig. 1B). Although the absolute change in metabolic cost with stride frequency varied among the slopes, the differences were not statistically significant (Table 1).

Table 2. Mean (s.e.m.) values for optimal stride frequency (OSF) and preferred stride frequency (PSF)

| Slope (deg) | PSF (strides s$^{-1}$) | OSF (strides s$^{-1}$) | PSF>OSF (no. of subjects) | PSF<OSF (no. of subjects) |
|---|---|---|---|---|
| −3 | 1.43 (0.03) | 1.42 (0.02) | 4 | 5 |
| 0 | 1.44 (0.02) | 1.43 (0.02) | 5 | 4 |
| 3 | 1.47 (0.02) | 1.43 (0.02) | 8 | 1 |

$N$=9 subjects. Despite the appearance of an increase in PSF from level to uphill, neither OSF nor PSF changed significantly with slope ($P$=0.216). Additionally, OSF was similar to PSF on all slopes ($P$=0.113).
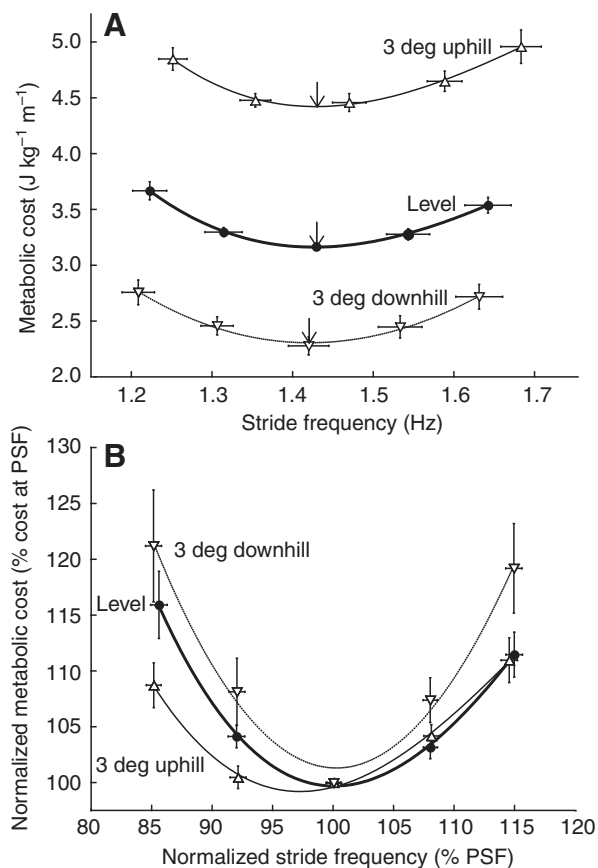
Fig. 1. (A) The relationship between stride frequency and metabolic cost did not substantially differ between downhill, level and uphill running. The points represent the mean for all nine subjects and the error bars are s.e.m. Arrows represent mean optimal stride frequencies. These were calculated by performing regression analyses for each subject and taking the mean of their optima. Metabolic cost values are given in $J\,kg^{-1}\,m^{-1}$. Regression lines are a cubic fit to the mean data, with $R^2 > 0.99$, with fits to individual subjects giving $R^2$ values of 0.93 and above. The associated regression equations for the mean data for downhill, level and uphill are $c_n = -1.639f^3 + 16.76f^2 - 37.71f + 26.75$, $c_n = -9.581f^3 + 51.18f^2 - 87.53f + 51.69$, $c_n = -12.08f^3 + 63.04f^2 - 106.2f + 62.67$, where $f$ represents frequency in Hz and $c_n$ represents net metabolic cost in $J\,kg^{-1}\,m^{-1}$. (B) Metabolic cost values are given as a percentage of cost at the preferred stride frequency (PSF). The mean cost for each condition is given in Table 1. The stride frequencies are given as a percentage of PSF. PSF values for each slope are in Table 2. Regression lines are a cubic fit to the mean data with $R^2 > 0.99$, with fits to individual subjects giving $R^2$ values of 0.93 and above. The associated equations for downhill, level and uphill running are $c_p = -1.3600 \times 10^{-4}f_p^3 - 0.1271f_p^2 - 21.39f_p + 1105$, $c_p = -8.136 \times 10^{-4}f_p^3 + 0.3095f_p^2 - 37.49f_p + 1568$, $c_p = -8.684 \times 10^{-4}f_p^3 + 0.3074f_p^2 - 35.15f_p + 1409$, where $f_p$ represents frequency in percentage of PSF and $c_p$ represents cost in percentage of cost at PSF.

It initially appeared that runners tended to prefer slightly faster stride frequencies uphill than on the level or downhill (Table 2). On the level, four subjects preferred stride frequencies that were faster than OSF, and five preferred stride frequencies that were slower than OSF (mean of $1.43 \pm 0.02\,strides\,s^{-1}$, Table 2). In contrast, on the uphill slope, eight of the nine runners preferred stride frequencies that were faster than OSF (Table 2). Downhill, five subjects preferred stride frequencies that were faster than OSF, whereas four preferred stride frequencies that were slower than OSF. However, an ANOVA of PSF and OSF across slope showed no significant differences
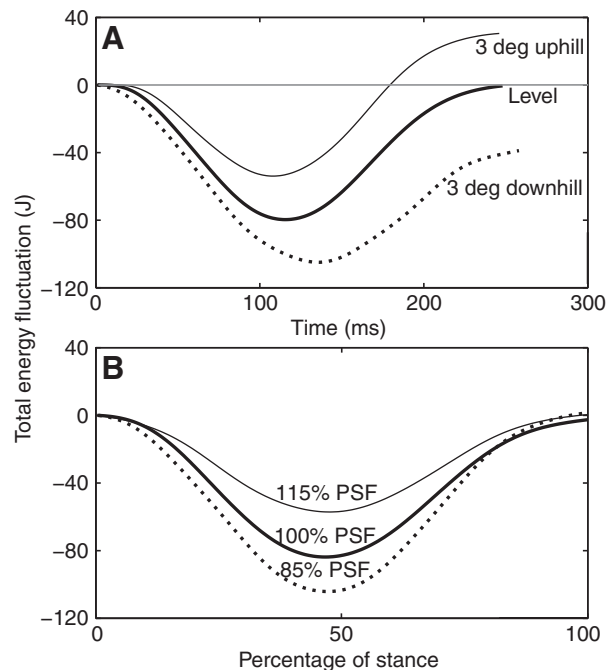


Fig. 2. (A) Fluctuations of total center of mass (CoM) mechanical energy during stance for a representative subject (mass, $m=58.5\,kg$) for 3 deg downhill, level and 3 deg uphill running at PSF. (B) Fluctuations of total CoM mechanical energy during stance for the same subject for 85, 100 and 115% PSF during level running.

($P=0.216$, 0.113 and 0.647 for slope, stride frequency and interaction, respectively). A power analysis revealed that as few as four or as many as 10 additional subjects could lead to statistical significance for the main effects (Table 2).

**DISCUSSION**

We found that changes in stride frequency affected metabolic cost similarly during level, uphill and downhill running. We therefore reject our hypothesis that deviating from OSF would cost less when running uphill and downhill. Our hypothesis was based on the idea that runners consume the least metabolic energy at the OSF during level running predominantly because of optimal elastic energy usage. Because elastic energy usage was thought to be 'much less' important in hill running than in level running (Minetti et al., 1994; Gottschall and Kram, 2003), we predicted a smaller metabolic penalty for deviating from OSF in hill running. However, this was not the case.

We analyzed the total CoM energy fluctuations during stance to verify that 3 deg did impair maximum possible elastic energy usage. In both uphill and downhill running, the asymmetrical energy fluctuations of the CoM showed that the maximum possible elastic energy usage was reduced by 21% from level running (Figs 2–3; Table 3). In level running, the CoM fluctuations were symmetrical (Fig. 3). Thus, ideally, all of the CoM energy stored elastically in the first half of stance could be used to lift and accelerate the CoM in the second half of stance with no muscle work. In uphill running, CoM energy decreased less in the first half of stance than it increased in the second half of stance (Fig. 2A). Therefore, less CoM energy could be stored elastically during landing than was needed to increase the CoM energy during takeoff ($P<0.001$), and muscles must have performed net positive work (Fig. 3). Conversely, in downhill
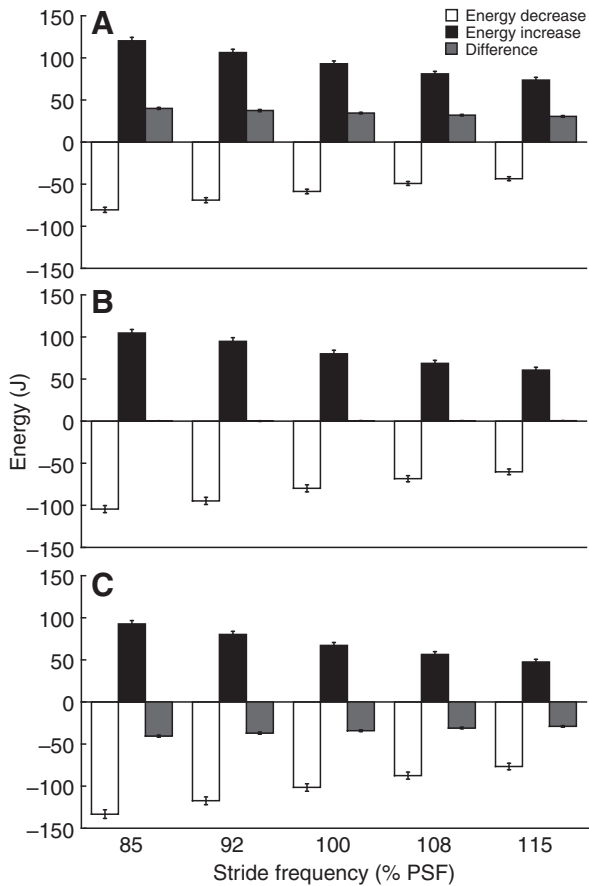
Fig. 3. The total mechanical energy of the CoM decrease during the first half of stance, the energy increase during the second half of stance, and the difference between the two for all stride frequencies while running uphill (A), on the level (B) and downhill (C). Differences were found between all stride frequencies and all slopes for maximum possible elastic energy stored, returned and used ($P<0.001$). Values are means ± s.e.m. for 9 subjects.

running, the body must dissipate mechanical energy (Fig. 3). Though opposite in direction, the energy difference between storage and return was similar in magnitude in uphill and downhill running. For instance, at PSF, the average subject produced 34.5±2.7 J step$^{-1}$ in uphill running and dissipated 34.1±4.4 J step$^{-1}$ in downhill running. However, the larger forces in downhill running increased KE and GPE fluctuations (Fig. 2A), leading to a greater possibility for elastic energy storage during downhill than during uphill running (Table 3).

Regardless of slope, CoM energy fluctuated more during stance at slower stride frequencies than at faster ones (Fig. 2B). Consequently, more energy per step was theoretically available for elastic usage at slower stride frequencies than at faster ones

($P<0.001$). However, because more mechanical work per step was necessary to lift and accelerate the CoM, it was probably not advantageous to use a slower stride frequency.

We found no difference in the relationship between stride frequency and metabolic cost across slope, although maximum possible energy usage was significantly reduced on the slopes studied. However, although maximum possible elastic energy usage was reduced by over 20%, it was not negligible for any slope. We therefore estimated the actual elastic energy storage uphill, downhill and on the level, to see whether it revealed a different pattern that might influence the OSF.

To estimate actual elastic energy storage, we used the methods of Alexander (Alexander, 1977) and Ker and colleagues (Ker et al., 1987). Alexander estimated that the Achilles' tendon stores 42 J of elastic energy at a speed of 3.9 m s$^{-1}$ on the level (Alexander, 1977). Ker and colleagues estimated that the arch of the foot stores 17 J of elastic energy at a speed of 4.5 m s$^{-1}$, with a peak GRF of 1.9 kN (Ker et al., 1987). At 2.8 m s$^{-1}$, we found mean peak GRFs of 1.50–1.66 kN for stride frequencies of 115–85% PSF on the level. Assuming similar stiffness and tendon moment arm values to Alexander and Ker et al., we can estimate energy storage using:

$$E = \tfrac{1}{2}k\mathbf{x}^2 = -\tfrac{1}{2}\mathbf{F}\mathbf{x} = -\tfrac{1}{2}\mathbf{F}(-\mathbf{F}/k) = \mathbf{F}^2/2k,\qquad(1)$$

where $\mathbf{x}$ is the tendon length and $k$ is the tendon stiffness, and the ratio:

$$\frac{E'}{E} = \frac{\mathbf{F'}^2/2k}{\mathbf{F}^2/2k} = \left(\frac{\mathbf{F'}}{\mathbf{F}}\right)^2,\qquad(2)$$

where $\mathbf{F}$ is the force in the tendon or arch, calculated from the GRF using the appropriate moment arms, and the prime designations refer to our calculations (e.g. $E'$, $\mathbf{F'}$) while the unmarked variables refer to those of Ker et al. and Alexander (Ker et al., 1987; Alexander, 1977).

Using this method, we found elastic energy storage estimates for running on the level of 27–33 J step$^{-1}$ (Achilles'), 11–13 J step$^{-1}$ (arch) and 37–46 J step$^{-1}$ (total) for stride frequencies of 115–85% PSF. The peak GRFs decreased for uphill running to 1.47–1.57 kN ($P=0.021$). This led to smaller uphill elastic return estimates of 26–29 J step$^{-1}$ (Achilles'), 10–12 J step$^{-1}$ (arch) and 36–41 J step$^{-1}$ (total) for stride frequencies of 115–85% PSF, a decrease of about 4–13% (mean 8%) from the level ($P=0.020$). Downhill did not differ significantly from level in either peak force ($P=0.172$) or energy storage ($P=0.195$). On all slopes, though the estimated amount of elastic energy storage tended to decrease with stride frequency, this pattern was not significant ($P=0.270$).

The advantage of elastic energy usage is how much muscle work it can replace. We therefore used the estimated elastic energy usage and the total CoM energy increase in the second half of stance (Fig. 3) to calculate the percentage of the total positive power that was due to the elastic element as opposed to muscle. To calculate power, we

Table 3. Mean (s.e.m.) values for maximum possible elastic energy usage for each condition

| Slope (deg) | 85% of PSF | 92% of PSF | PSF | 108% of PSF | 115% of PSF |
|---|---|---|---|---|---|
| −3 | 92.7 (4.0) | 80.3 (3.6) | 67.3 (3.5) | 56.5 (3.4) | 47.6 (3.1) |
| 0 | 103.4 (4.1) | 93.7 (4.2) | 79.0 (4.1) | 67.6 (3.6) | 59.6 (3.3) |
| 3 | 80.5 (3.0) | 68.9 (3.0) | 58.6 (2.7) | 49.1 (2.4) | 43.4 (2.4) |

$N=9$ subjects. Maximum possible elastic energy usage (in J step$^{-1}$) was defined to be the minimum of either the energy decrease during the first half of stance or the energy increase during the second half of stance. There was a significant decrease in maximum possible elastic energy going from level to uphill or downhill ($P<0.001$). There was also a significant decrease in maximum possible elastic energy usage with an increase in stride frequency ($P<0.001$).
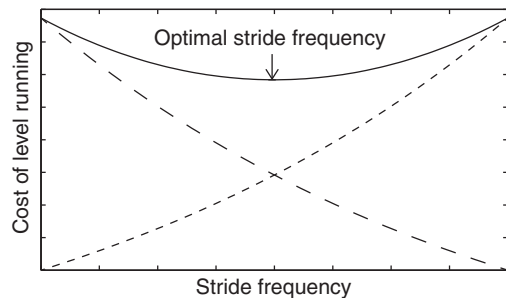
Fig. 4. Proposed relationship for factors affecting the metabolic cost of running. The total cost of running at a given stride frequency (solid line) may be a combination of the cost of muscle work/power (long-dash line) and the cost of internal work and force production (short-dash line). The optimal stride frequency (arrow) occurs at a frequency where the sum of these costs is minimized.

multiplied the estimated energy usage per step and the total positive energy change per step by step frequency (steps s$^{-1}$). On the level, the positive power from elastic energy usage increased with stride frequency from 85% PSF to 115% PSF (41, 48, 54, 58, 62%). There was a significant decrease ($P$<0.001) in the positive power from elastic energy usage from level to uphill running across stride frequency (34, 38, 42, 45, 49%). There was a significant increase ($P$<0.001) in the positive power from elastic energy usage from level to downhill running across stride frequency (51, 58, 67, 73, 81%). Lastly, there was a similar pattern ($P$=0.019) of increased power from elastic energy ($P$=0.009) as stride frequency increased on all slopes.

Therefore, although the percentage of power from elastic usage decreased from level to uphill running, this power increased when going from level to downhill running. Further, we can infer that, as the percentage of positive power from elastic energy return increases with increasing stride frequency, the percentage of positive power that must be produced by the muscles decreases with increasing stride frequency. Because both the maximum power produced and the percentage power produced by the muscle decrease with increasing stride frequency, the absolute muscle power must decrease with increasing stride frequency. This suggests that, for stride frequencies slower than OSF, the increase in metabolic cost with decreasing stride frequency could be due to the increased need for muscle work at these stride frequencies.

Many factors could explain why metabolic cost increases for step frequencies faster than OSF. One possibility is that the 'internal work' of swinging the limbs relative to the body's CoM increases with stride frequency. While we did not measure internal work, we can estimate it using Minetti's (Minetti, 1998) model based on duty factor, speed and stride frequency. We calculate that mechanical internal work increased by a mean of 0.07 J kg$^{-1}$ m$^{-1}$ from PSF to 115% PSF on the level. The change in metabolic cost from PSF to 115% PSF was 0.37 J kg$^{-1}$ m$^{-1}$. The ratio of the change in mechanical work to the change in metabolic work gives a delta efficiency value of 20%, close to the 25% efficiency expected for positive muscle work. Thus, internal work could explain the changes seen for stride frequencies faster than OSF. Uphill and downhill running had similar efficiency values of 17.5 and 15%, though the model was created with level data. Minetti showed that both stride frequency and internal work increase in uphill running (Minetti et al., 1994). However, Minetti also showed that internal work increases with stride frequency on the level (Minetti, 1998). Thus, it is unclear

how much of the increase in internal work in uphill running is due to slope as opposed to stride frequency.

Another factor that could affect the stride frequency–velocity relationship is the increased cost of muscular force when it is produced over a shorter period of time (Kram and Taylor, 1990). This would lead to greater metabolic cost at faster stride frequencies. Because of this physiological property, the metabolic cost of generating muscle force likely has a similar dependence on foot–ground contact time regardless of slope. We found that contact time decreased (17, 20 and 21% for running downhill, on the level and uphill, respectively) as step frequency increased from 85% to 115% PSF, but varied little across slope (<3%). This similarity would lead to comparable cost of force generation $vs$ stride frequency curves, with this cost increasing with stride frequency for each slope.

The U-shape of the step frequency $vs$ metabolic cost curve could result from the increase in muscle mechanical power with decreasing step frequency, and the increase in the cost of force production and internal work with increasing step frequency (Fig. 4). In this scenario, at stride frequencies slower than OSF, the metabolic cost of producing power with the muscles increases. At stride frequencies faster than OSF, the metabolic cost associated with producing force over a shorter period of time and with moving the limbs more quickly increases. Thus, OSF may occur at an intermediate stride frequency where the sum of these costs is minimized.

Moreover, these stride frequency–cost relationships could explain why we do not see a change in OSF when going from level to uphill running. We know that the cost of muscle work increases with slope across all stride frequencies. Additionally, Roberts and Belliveau (Roberts and Belliveau, 2005) showed that much higher forces must be produced by the hip extensors in uphill running than in level running, increasing the cost of force production across stride frequency. If both the muscle work $vs$ cost curve and the force production $vs$ cost curve translate upward, their sum is translated upward, leading to an increased cost of running, but a similar OSF.

Overall, we found that neither the pattern of stride frequency $vs$ metabolic cost nor OSF significantly change with slope. The general pattern of estimated elastic energy storage and return with increasing stride frequency stays consistent, and indicates that more muscle work must be done at slow stride frequencies than at fast ones. This relationship in combination with an increased cost of producing force and performing internal work with increasing stride frequency could explain the presence of an OSF at an intermediate value.

## LIST OF ABBREVIATIONS

| | |
|---|---|
| CoM | center of mass |
| GPE | gravitational potential energy |
| GRF | ground reaction force |
| KE | kinetic energy |
| OSF | optimal stride frequency |
| PSF | preferred stride frequency |
| RER | respiratory exchange ratio |

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