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THE APPLICATION OF GROUND FORCE EXPLAINS THE ENERGETIC COST OF RUNNING BACKWARD AND FORWARD

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Summary

We compared backward with forward running to test the idea that the application of ground force to support the weight of the body determines the energetic cost of running. We hypothesized that higher metabolic rates during backward *versus* forward running would be directly related to greater rates of ground force application and the volume of muscle activated to apply support forces to the ground. Four trained males ran backward and forward under steady-state conditions at eight treadmill speeds from 1.75 to 3.50 m s^{-1}. Rates of oxygen uptake were measured to determine metabolic rates, and inverse periods of foot–ground contact ($1/t_c$) were measured to estimate rates of ground force application. As expected, at all eight speeds, both metabolic rates and estimated rates of ground force application were greater for backward than for forward running. At the five slowest speeds, the differences in rates of ground force application were directly proportional to the differences in metabolic rates between modes (paired *t*-test, $P<0.05$), but at the three highest speeds, small but significant differences in proportionality were present in this relationship. At one of these three higher speeds (3.0 m s^{-1}), additional measurements to estimate muscle volumes were made using a non-invasive force plate/video technique. These measurements indicated that the volume of muscle active per unit of force applied to the ground was 10±3 % greater when running backward than forward at this speed. The product of rates of ground force application and estimated muscle volumes predicted a difference in metabolic rate that was indistinguishable from the difference we measured (34±6 % *versus* 35±6 %; means ± S.E.M., N=4). We conclude that metabolic rates during running are determined by rates of ground force application and the volume of muscle activated to apply support forces to the ground.

Key words: locomotion, ground force, muscle force, contact time, metabolic rate, cost coefficient, human.

Introduction

Humans have good reason for preferring to run forward rather than backward. In addition to the logistical problems of navigation and balance, running backward requires up to 30 % more metabolic energy than running forward (Flynn et al., 1994). Although the appreciably greater energetic cost of running backward is not surprising, the mechanical factors responsible are not known. These factors are difficult to assess in the absence of some larger understanding of how locomotor mechanics determine the energetic cost of transport. In running gaits, the metabolic cost is known to be incurred virtually entirely by the active skeletal muscles (Armstrong et al., 1987). However, it remains unclear how the mechanical activity of the many muscles involved determines the total amount of energy a runner expends. Here, we used the differences in the mechanics and energetics of backward and forward running (Flynn et al., 1994; Flynn and Sousas-Little, 1995) as an investigative tool to test a general hypothesis relating locomotor mechanics to the energetic cost of running.

The two most basic patterns of energy expenditure during steady-state running have been well established for decades, largely because of the ease with which metabolic rates can be determined by measuring rates of oxygen uptake under these conditions. First, for almost all runners, metabolic rates increase linearly with running speed (Zuntz, 1897; Taylor et al., 1970; Taylor, 1994) so that the energy expended to cover a fixed distance is independent of the speed of the run. Second, in covering any distance, larger runners expend less energy on a mass-specific basis than do smaller runners (Zuntz, 1897; Taylor et al., 1970; Taylor, 1994).

In contrast, the mechanical activity of the muscles determining the metabolic energy expended under these circumstances is difficult to quantify. Many attempts have been made to relate metabolic rates to the positive mechanical work performed during running (Cavagna et al., 1964; Cavagna et al., 1977; Heglund et al., 1982; Minetti et al., 1994). However, because a great deal of the work done to lift and accelerate the

body and limbs during constant-speed level running is performed passively by tendons and energy transfers (Cavagna et al., 1964; Cavagna et al., 1977; Heglund et al., 1982), these measurements overestimate the proportion of the mechanical work performed by the muscles to an unknown extent (Cavagna et al., 1964; Cavagna et al., 1977; Heglund et al., 1982, Taylor et al., 1970; Taylor, 1994; van Ingen Schenau, 1998). Thus, it is not surprising that these measurements have not provided a consistent quantitative explanation for the metabolic cost of running.

Regardless of the amount of mechanical work muscles perform during running, the metabolic rates of runners must equal the product of the volume of active muscle and the average metabolic rate per unit volume. Kram and Taylor (Kram and Taylor, 1990) suggested that these two variables could be estimated simply from the mechanics with which a runner applies force to the ground: the volume of muscle active from the net ground force applied (F_{Wb}, equal to body weight), and the average metabolic rate per unit volume from the rate of ground force application. Using the inverse period of foot–ground contact ($1/t_c$) to estimate rates of ground force application, they were able to account for the metabolic rates ($\dot{E}_{metab}$) of running and hopping animals over a 4500-fold range of body masses and a 10-fold range of speeds ($\dot{E}_{metab}=F_{Wb}\times(1/t_c)\times C$, where C is a proportionality constant in $J\,N^{-1}$]. Subsequently, the same relationship has been shown to account for the metabolic rates of humans running on their hands (Glasheen and McMahon, 1995) and cross-country skiing with either their arms or their legs (Bellizzi et al., 1998). Although differences in the posture of the limbs applying ground force can cause the value of the cost coefficient (C) to vary by more than an order of magnitude between different modes of locomotion (Bellizzi et al., 1998), a growing body of evidence suggests that metabolic rates during terrestrial locomotion are predominantly determined by the net force applied to the ground and the rate at which this force is applied.

Although the empirical relationship between the mechanics of ground force application and the metabolic rates reported during these different modes of locomotion is not disputed, the physiological basis for this relationship remains a matter of debate. Kram and Taylor (Kram and Taylor, 1990) explained the simple relationship they reported between the mechanics and energetics of running and hopping animals by reasoning that rates of ground force application determine the contractile speed, and therefore also the rates of ATP hydrolysis, of the muscle fibers recruited to apply ground force (Hill, 1950; Barany, 1967; Huxley, 1974; Taylor, 1994). However, others have pointed out that this may not be the correct explanation (Alexander, 1991; Steudel, 1990; Minetti et al., 1994). One alternative explanation (Steudel, 1990) attributes the findings of Kram and Taylor (Kram and Taylor, 1990) to the mutual scaling of locomotor mechanics and the energetic cost of running with body mass among different-sized runners, rather than the causal relationship originally proposed. Other critics (Minetti et al., 1994) have correctly pointed out that rates of ground force application do not fully account for the increases in metabolic rate with increases in running speed in humans and other bipedal runners (Roberts et al., 1998b). Thus, doubt remains regarding whether periods of ground force application are directly and causally linked to metabolic rates during running as Kram and Taylor (Kram and Taylor, 1990) suggested.

Here, we compared backward with forward running to test whether the relationship between rates of ground force application and metabolic rates during running is indeed a direct one as Kram and Taylor (Kram and Taylor, 1990) proposed. We expected greater rates of ground force application to directly correspond to the higher metabolic rates reported for backward *versus* forward running. We used measurements of foot–ground contact times to estimate rates of ground force application and a recently developed non-invasive technique to estimate the volume of muscle recruited to apply ground force (Roberts et al., 1998a). We anticipated that forward and backward running in the same subjects would result in different metabolic rates being incurred by the same leg extensor muscles as they supported the body's weight against gravity. A direct comparison of the metabolic energy expended by the same muscles while applying the same net ground force, but at considerably different rates, would provide a stringent test of whether the link between these variables is intrinsic, as originally proposed, or coincidental, as was later suggested (Steudel, 1990). A direct explanation for the elevated energetic cost of running in a manner that is functionally and anatomically unnatural would not only further elucidate the determinants of the energetic cost of running, but could also advance the understanding of how the mechanical activity of the musculoskeletal system determines the energetic cost of movement in general.

Materials and methods

Subjects and training

Four males, aged 20–34 years (70±6 kg, mean ± S.D.), participated in the study after providing written, informed consent. Subjects were trained to run both forward and backward on a treadmill in 20 min bouts 12–20 times over a 3- to 4-week period. Training habituated subjects to both modes of treadmill running at speeds from 1.75 to 3.5 $m\,s^{-1}$ and produced fitness levels that enabled steady-state rates of oxygen uptake to be attained at the highest speeds. Both backward and forward running values over consecutive training sessions agreed to within ±4 % prior to the start of data collection.

Experimental design

Part I

To test the hypothesis that metabolic rates during running are set by rates of ground force application, subjects ran backward and forward over the same twofold range of treadmill speeds while we measured foot–ground contact times and rates of oxygen uptake simultaneously. We hypothesized

that metabolic rates ($\dot{E}_{metab}$) during both backward and forward running would follow the equation:

$$\dot{E}_{metab} = F_{Wb} \times (1/t_c) \times C\,, \quad (1)$$

where the F_{Wb} is the average force applied to the ground during a stride (equal to the weight of the body), $1/t_c$ is the estimated rate at which this force is applied, and C is the metabolic energy expended per unit of ground force ($J\,N^{-1}$) at any rate of application.

Part II

Preliminary observations made during the training period indicated that values of the cost coefficient were likely to be nearly the same for backward and forward running at slower speeds, but different at faster ones. These observations suggested that differences in metabolic rates at these higher speeds between the two modes of running might be influenced by some factor in addition to rates of ground force application. This led us to a further test of the factor we considered most likely to introduce variability in the value of the cost coefficient (C) during backward *versus* forward running at the higher speeds examined.

Values of the cost coefficient during different modes of locomotion would be expected to vary with both the volume of muscle recruited per unit ground force and the relative shortening velocities (i.e. V/V_{max}) of the active muscles (Hill, 1950; Taylor, 1994; Bellizzi et al., 1998; Roberts et al., 1998a, Roberts et al., 1998b). We assumed that the relative shortening velocities of the active muscles during forward and backward running would be equal for several reasons. First, during both forward and backward running on a level treadmill, zero net work is performed on the environment, and the limited positive work required to lift and accelerate the center of mass in the latter portion of each stride is performed largely by the passive elastic recoil of tendons rather than by active shortening of muscle (Cavagna, et al., 1964; Cavagna et al., 1977; Biewener et al., 1998; Roberts et al., 1997). Second, direct measurements during level bipedal running in turkeys (Roberts et al., 1997), level quadrupedal running in horses (Cogger et al., 2000) and hopping in wallabies (Biewener et al., 1998) indicate that the extensor muscles exerting support forces on the ground shorten minimally over a wide range of speeds. Third, different species of runners and hoppers incur the same energetic cost of applying support forces to the ground during locomotion on level ground regardless of body mass and forward speed (Kram and Taylor, 1990). This result provides reasonable indirect evidence that the net mechanical activity of the muscles active in these animals is similar (Taylor, 1994). Although direct evidence from backward running to evaluate our assumption of equivalently slow shortening velocities in this gait is not available, the results cited above support the view that extensor muscles applying ground force generally operate at very slow shortening velocities in those modes of locomotion that do not require net work to be performed on the environment.

Given the assumption of proportionality between $1/t_c$ and the maximal rate of shortening (V_{max}) of the active muscle fibers, the metabolic cost of producing muscle force during locomotion (i.e. C) should not vary at equivalent shortening velocities (Hill, 1950; Huxley, 1974; Taylor, 1994). In accordance with these assumptions, we expected any differences in the value of C between backward and forward running to be directly related to any differences in the volume of muscle active (Vol_m) per newton of ground force (F_g) applied (Vol_m/F_g). This allowed us to express the relationship in equation 1 in terms of the volume of muscle active as:

$$\dot{E}_{metab} = Vol_m \times (1/t_c) \times k_1\,, \quad (2)$$

where k_1 is the constant relating the metabolic energy expended per unit of muscle active ($J\,g^{-1}$) at any given rate of ground force application ($1/t_c$). The value of k_1 would be expected to be the same when the shortening velocities of the active muscles are equivalent, as we assumed.

In contrast to the likely equivalence of relative shortening velocities, the possibility that the volume of muscle recruited per unit of force applied to the ground could differ between forward and backward running is quite plausible. Although neither the time-averaged ground force exerted during each stride nor the muscle cross-sectional area per unit of muscle force should differ in these modes, the average muscle force required to apply the same net ground force could vary. Any differences in stance limb posture, and resulting differences in the muscle forces acting around individual leg joints (Flynn and Sousas-Little, 1995), during these different modes of running would alter the muscle force necessary to exert the same time-averaged force on the ground during the stride. The ratio of muscle (F_m) to ground (F_g) forces (F_m/F_g), or the mechanical advantage (Biewener, 1990) with which the muscles acting on the levers of the skeleton apply force to the ground, is a simple function of the ratio of the muscle moment

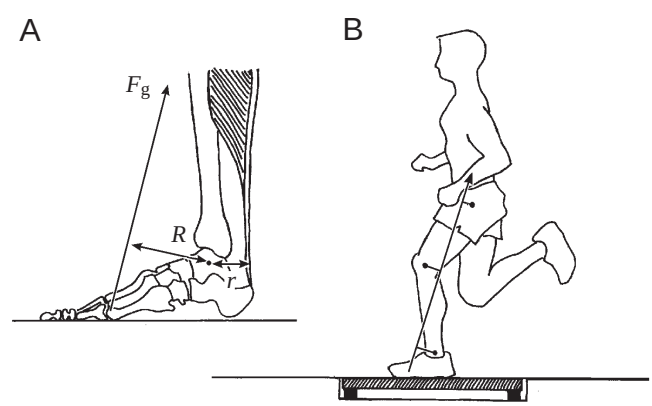

Fig. 1. Muscle forces (F_m) for the ankle, knee and hip were determined from the ratio (R/r) of the perpendicular distance of the ground force reaction vector (F_g) to the joint axis of rotation (R) to the muscle moment arm (r) as illustrated for the ankle (A) and for the ankle, knee and hip (R only, panel B). The magnitude and position of the ground reaction force vector and the muscle moment arm at each joint were used to determine the muscle forces at each joint ($F_m \times r = F_g \times R$).

Table 1. *Composite muscle characteristics*

Joint	Moment arm, r (m)	Fiber length, L (m)	Mass (g)	Area (cm^2)
Ankle	0.032	0.041	884	210
Knee	0.055	0.076	1097	134
Hip	0.057	0.117	924	76

Composite ankle, knee, and hip muscle characteristics. Mean values at the ankle, knee, and hip for muscle moment arms (r), fiber lengths (L), and muscle cross-sectional areas. Mean values (N=4) at each of these joints were determined from the individual muscles acting at the respective joints in accordance with Roberts (1998b). This technique takes into account each muscle's mass, pinnation angle and mean fiber length.

arms to the perpendicular distance between the ground force reaction vector and the joint axes of rotation (F_m/F_g, Fig. 1). Although the moment arms of the extensor muscles active at the ankle, knee and hip would not vary between forward and backward running, differences in the orientation of the ground force reaction vector could alter the perpendicular distances from the joint axes of rotation. These differences would alter the muscle forces, and therefore volumes, recruited to provide the forces necessary to counteract gravity.

In addition to potential differences in muscle forces, and therefore active cross-sectional areas, muscle volumes are also affected by the average length of the fibers active. The large differences between the lengths of the fibers in the muscles acting at the ankle, knee and hip joints (Table 1) could alter the average length of the fibers active (L_{act}) between forward and backward running if significant variation between modes existed in the relative forces generated at the three different joints.

Consequently, we concluded that our comparison of forward and backward running warranted additional measurements at a higher speed to estimate both the volume of muscle required per newton of force applied to the ground and the average length of the fibers in the active muscles (L_{act}). Accordingly, we expected the muscle volumes active during forward and backward running to follow the equation:

$$Vol_m = F_{Wb} \times (F_m/F_g) \times L_{act} \times k_2 , \qquad (3)$$

where k_2 is a constant relating muscle force to cross-sectional area. Given equivalent average shortening velocities, C in equation 1 would be expected to be equal for backward and forward running only if the volume of muscle activated to apply a unit ground force were equal for these two modes. Similarly, it would follow that any difference in the value of C under these conditions would be directly related to the difference in the volume of active muscle per unit of force applied to the ground.

By combining the relationships from equations 2 and 3, we can quantitatively express the metabolic rates during forward and backward running in terms of the product of the muscle volume active per unit ground force and the metabolic rate per unit volume as:

$$\dot{E}_{metab} = [F_{Wb} \times (F_m/F_g) \times k_2 \times L_{act}][(1/t_c) \times k_1] . \qquad (4)$$

Because the constant relating actual muscle forces to cross-sectional area during running (k_2) and the constant relating rates of muscle force application to the metabolic energy per unit of muscle force (k_1) cannot at present be estimated with reasonable confidence, we did not make specific predictions of the metabolic rates during backward and forward running from the variables measured. Rather, we predicted that any differences in metabolic rate between backward and forward running should be equal to the product of the differences in the variables measured to estimate muscle forces and rates of ground force application. Because three terms (F_{Wb}, k_1, k_2) in equation 4 are constants, and therefore would not affect these differences, we were able to predict that the differences in metabolic rates between backward and forward running would follow the equation:

$$\Delta\dot{E}_{metab} = (\Delta 1/t_c)[\Delta(F_m/F_g) \times \Delta L_{act}] , \qquad (5)$$

where Δ symbols represent the ratio of backward to forward values.

Measurements

Metabolic rate ($\dot{E}_{metab}$)

Metabolic rates were determined from rates of oxygen uptake at eight speeds ranging from 1.75 to 3.5 m s^{-1}. Runners wore a loose-fitting mask through which air was drawn at approximately 9.5 l s^{-1}. A continuous fraction of the air leaving the mask was dried, scrubbed of CO_2 using Ascarite (VWR Scientific) and analyzed for oxygen concentration (Beckman, model P3) in accordance with the method of Fedak and co-workers (Fedak et al., 1981). Runs lasted a minimum of 6 min, as determined by the time to achieve a steady-state metabolic rate (<4 % change over 4 min). At least four measurements per subject were obtained at each speed. Rates of oxygen consumption were converted to joules using an energetic equivalent of 20.1 J ml^{-1} O_2 (Blaxter, 1989). The elevations in metabolic rate incurred by running, or net metabolic rates, were determined by subtracting the rates of oxygen uptake measured during quiet standing from those measured during running. Because subject masses and the time-averaged vertical forces they applied to the ground during each stride were the same for forward and backward running, metabolic rates are reported in mass-specific units in accordance with convention for weight-bearing exercise.

Rate of force generation ($1/t_c$)

Time of foot–ground contact (t_c) was measured simultaneously with metabolic rate from the vertical forces produced on a treadmill-mounted force plate (model OR6-5-1, Advanced Mechanical Technology, Newton, MA, USA; Kram and Powell, 1989). The force plate signal was amplified by a Kistler differential amplifier (model 2120), digitized by a 12-bit A/D converter (National Instruments model NB-MIO-16) and recorded at a sample frequency of 1000 Hz on a Macintosh

IIfx running custom-made software (LabView, National Instruments). Data were collected for 10 s after 3 min of running, providing a minimum of 18 steps from which a mean value of $1/t_c$ was determined. Force data were analyzed with customized LabView software (National Instruments) in which time of contact was defined as the period for which measured force was greater than 0 N. Mean noise values from all sources were less than ±6 % of peak force. The resonant frequency of the force plate was 160 Hz, as determined by rapping the force plate with a wooden block. At least four trials per subject per speed, on separate days, were averaged to obtain final values.

Active muscle volume per ground force [(F_m/F_g)×L_{act}]

We used a recently developed video/force plate technique (Roberts et al., 1998a) to estimate the active muscle volume used to generate 1 N of force against the ground during both backward and forward running. Measurements were made at 3.0 m s^{-1}, a speed at which we had measured a significantly higher value for the cost coefficient (C) for backward than for forward running. This technique uses the orientation of the ground reaction force vector relative to the ankle, knee and hip to estimate the volume of muscle active around each joint.

The technique assumes that active muscle volumes at each joint are determined by the product of muscle forces, fiber lengths (L) and a constant (specific stress; k_2):

$$Vol_{\mathrm{m}} = F_{\mathrm{m}} \times L \times k_2 . \quad (6)$$

Here, muscle force is defined as the extensor force, acting at the muscle's moment arm r between the muscle's insertion and the joint, which counteracts the torque of the ground reaction vector (Fig. 1) and prevents collapse of the joint. In addition to the support forces the extensor muscles produce to counteract gravity, this technique also takes into account the small additional extensor forces required to counteract the flexor moments produced by two-joint muscles. Flexor moments for muscles such as the gastrocnemius, that extend one joint (ankle) but flex another (knee), were added to the gravitational extensor forces required at individual joints to determine the total extensor force requirement at that joint. The addition of flexor moments increased the final F_{m} values only marginally (i.e. <10 %).

To obtain a representative average value for the total muscle volume active per newton of ground force during a stride, estimated muscle forces and effective fiber lengths at each joint (equation 3) every 10 ms during contact were summed and divided by the summed ground force. The flexor moments exerted by those extensor muscles, such as the gastrocnemius, that cross two joints were added to the extensor moments necessary to counteract gravity. This final ratio, ($F_{\mathrm{m}}/F_{\mathrm{g}}$)×$L_{\mathrm{act}}$, provided our index of the average muscle volume activated to produce a unit ground force:

$$(F_{\mathrm{m}}/F_{\mathrm{g}}) \times L_{\mathrm{act}} = \frac{L_{\mathrm{ankle}}\sum F_{\mathrm{m,ankle}} + L_{\mathrm{knee}}\sum F_{\mathrm{m,knee}} + L_{\mathrm{hip}}\sum F_{\mathrm{m,hip}}}{\sum F_{\mathrm{g}}} . \quad (7)$$

Muscle moment arm (r) and mean anatomical fiber lengths (L)

A composite muscle moment arm r and a mean fiber length L (Table 1) were determined from measurements on the individual muscles acting at each of the respective joints. These measurements were taken from four lower limbs of three cadavers selected for robustness from more than 50 limbs. The contribution of each muscle was weighted according to its potential for generating force, as determined from cross-sectional area and pinnation angle (Roberts et al., 1998a).

Determination of F_m

F_{m} was defined as the extensor force at a joint, acting at the distance r noted above, needed to counteract the torque produced by the ground force reaction vector (F_{g}) acting at a distance R (Fig. 1):

$$F_{\mathrm{m}} \times r = F_{\mathrm{g}} \times R . \quad (8)$$

The magnitude of F_{g} was determined as subjects ran forward and backward over an in-ground force plate (Kistler 9261A) located near the center of a 35 m runway. Vertical and horizontal force measurements were collected at 1000 Hz by a Macintosh computer, as described above, and filtered twice with a 60 Hz second-order Chebyshev low-pass filter, once in each direction to eliminate phase shifts. The origin of the ground force reaction vector was determined from the relative magnitude of the vertical forces at the front and rear of the plate.

The ground force moment arm (R) at each joint was determined from the distance between the force vector and the joint axis of rotation provided by simultaneous high-speed video data (NAC-200) digitized and analyzed at 100 Hz using public-domain image-analysis software (NIH Image). This represented a minimum of 24 frames per run. Joint axes of rotation were determined and marked before each session by swinging the subject's limb, palpating the joint and using anatomical landmarks for reference.

The speed of a run was determined by the time between consecutive interruptions of four photocell beams (Banner Electronic) positioned at 1 m intervals alongside the force plate and runway. Only runs for which the difference between accelerative and decelerative horizontal impulse was less than 15 % (resulting in a speed change of less than 0.03 m s^{-1}), and average speed was between 2.9 and 3.1 m s^{-1}, were analyzed. Final values for ($F_{\mathrm{m}}/F_{\mathrm{g}}$)×$L_{\mathrm{act}}$ during forward or backward running represent averages of 4–6 trials per subject.

Statistical analysis

Means values of metabolic rates, rates of ground force application and the cost coefficient and estimated muscle volumes at each speed were compared by paired t-tests (P<0.05). Values are presented as means ± S.E.M.

Results

Stride length and frequency

At every speed, subjects took significantly shorter strides and had significantly higher stride frequencies during

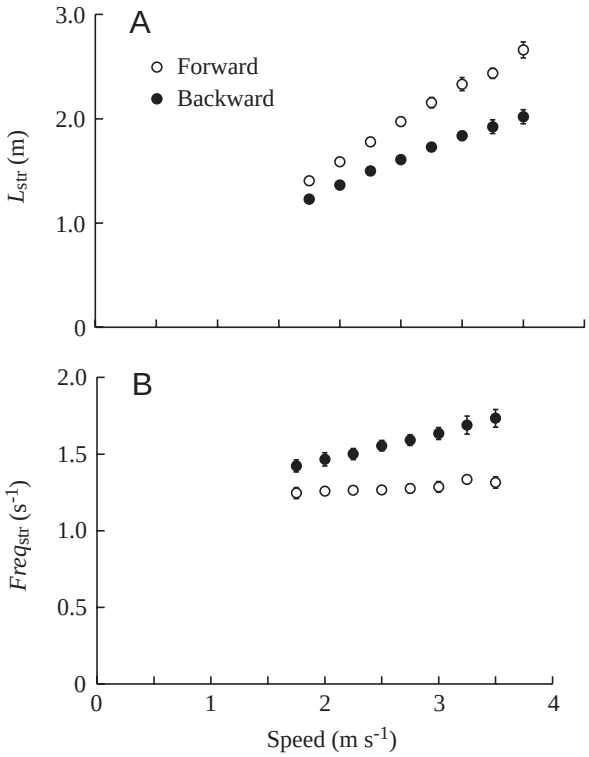

Fig. 2. Stride lengths (L_{str}, A) were shorter and stride frequencies ($Freq_{str}$, B) greater for backward than for forward running at the same speeds. Values are means ± S.E.M. (N=4).

backward than during forward running (Fig. 2). These differences were greatest at the highest speeds.

Metabolic rate ($\dot{E}_{metab}/W_b$)

Mass-specific metabolic rates (were W_b represents body weight) were significantly greater during backward than forward running at every speed, and were on average 32 % greater over the range of speeds tested (Fig. 3A). Because metabolic rates increased more rapidly with speed during backward than during forward running (P=0.001), absolute differences were greatest at the highest speeds.

Rate of force application ($1/t_c$)

Rates of force application ($1/t_c$), like metabolic rates, were significantly greater at each speed for backward running than for forward running and were on average 22 % greater over the range of speeds measured (Fig. 3B). These differences were due to the shorter periods of foot–ground contact (t_c) used during backward running at all speeds. Because rates of force generation increased more rapidly with speed during backward than during forward running (P<0.001), absolute differences in this variable were also greatest at the highest speeds.

Cost coefficient (C)

The ratio of metabolic rate to $1/t_c$, the cost coefficient C (from equation 1), was not significantly different between backward and forward running at speeds of 1.75–2.75 m s^{-1},

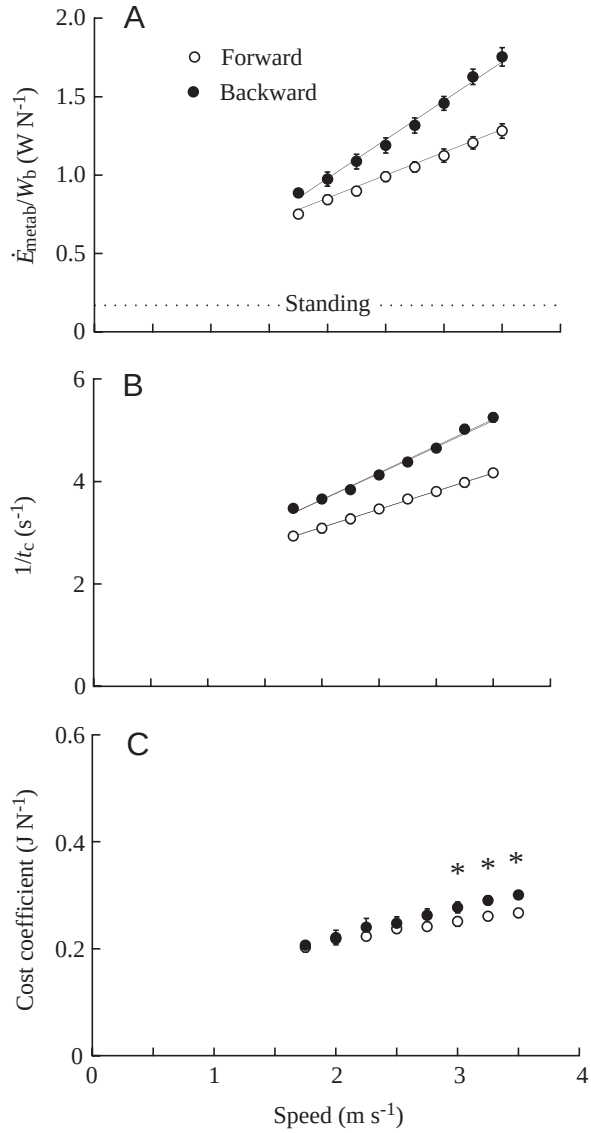

Fig. 3. Metabolic rates ($\dot{E}_{metab}/W_b$, where $\dot{E}_{metab}$ is metabolic rate and W_b is body weight; A) and ($1/t_c$, where t_c is the period of foot–ground contact; B) were greater at all speeds, and increased more rapidly with speed, during backward *versus* forward running. The ratio of metabolic rate to the rate of ground force application, the cost coefficient (C, panel C), was not different for the five slowest speeds, but was greater at the three fastest ones for backward *versus* forward running. Values are means ±S.E.M. (N=4). The equations of the least-squares regression lines are as follows: forward, $\dot{E}_{metab}/W_b$=0.23+0.30x, r^2>0.99, P<0.01; $1/t_c$=1.68+0.71x, r^2>0.99, P<0.01; backward, $\dot{E}_{metab}/W_b$=–0.03+0.50x, r^2>0.99, P<0.01; $1/t_c$=1.55+1.04x, r^2>0.99, P<0.01). In C, asterisks indicate that values are significantly different (P<0.05) between backward and forward running.

but was slightly higher (P<0.05) for backward running at 3.0, 3.25 and 3.5 m s^{-1} (Fig. 3C). Thus, greater rates of force generation fully accounted for the higher metabolic rates of backward running at the five lowest speeds and accounted for 65–80 % of the higher metabolic rates measured at the three highest speeds. For both forward and backward running,

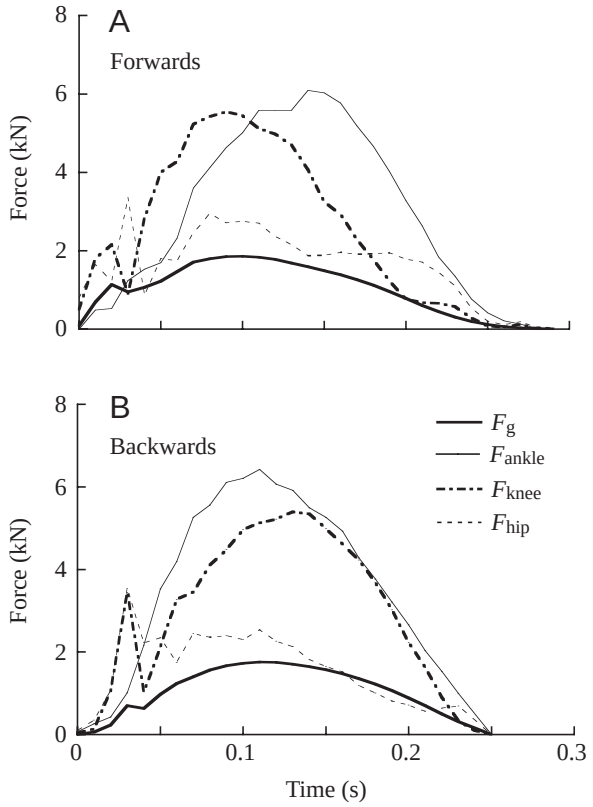

Fig. 4. Ground forces (F_g) and muscle forces at the ankle (F_{ankle}), knee (F_{knee}) and hip (F_{hip}) during the period of foot–ground contact for a single subject running forwards (A) and backwards (B) at $3.0\,m\,s^{-1}$.

the cost coefficient increased moderately (32 % and 45 %, respectively) over the twofold range of running speeds tested.

Estimated muscle volumes [(F_m/F_g)×L_{act}]

Average muscle forces per unit ground force were substantially higher (14 %) for backward than forward running, largely because the average muscle forces at the ankle were greater during backward running (Fig. 4). Because muscle fibers at the ankle are shorter than those at the knee and hip joints, the average active fiber length was slightly shorter (4 %) for backward running. The net effect of higher muscle forces being produced with slightly shorter fibers was a 10±3 % greater muscle volume being activated to produce each unit of ground force during backward *versus* forward running (Fig. 5).

Actual versus *predicted metabolic rate*

The greater metabolic rate measured during backward *versus* forward running at $3.0\,m\,s^{-1}$ (+35±6 %) was indistinguishable from the value predicted (+34±6 %) from the product of a greater rate of force generation (+22 %) and greater volume of active muscle (+10 %) (Fig. 6).

Discussion

We set out to test whether the application of ground force

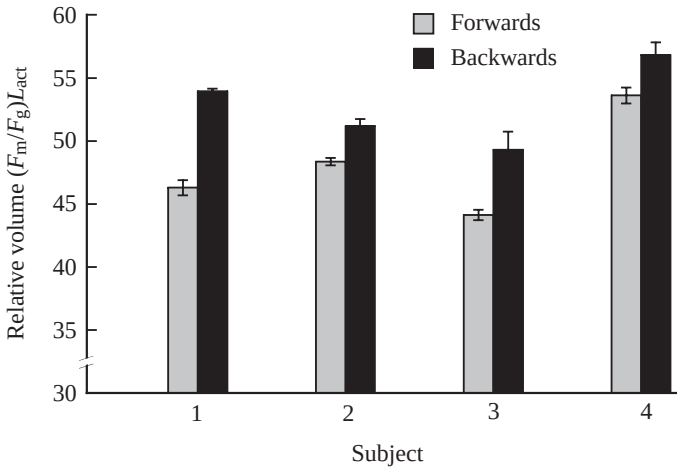

Fig. 5. Estimated muscle volumes activated per newton of ground force applied [(F_m/F_g)×L_{act}] were greater for backward running than for forward running at $3.0\,m\,s^{-1}$ for four subjects. Values are means ± S.E.M. Backward and forward values were significantly diffferent for all subjects (P<0.05). F_m, muscle force; F_g, ground force; L_{act}, mean length of fibers active.

determines the energetic cost of running by relating the higher energetic cost of backward *versus* forward running to the different mechanics of ground force application in these two modes. In accordance with our prediction, we found that the higher metabolic rates incurred during backward running were due primarily to the greater rates of ground force application used at all speeds, and at higher speeds secondarily to a slightly greater volume of muscle being activated. Although

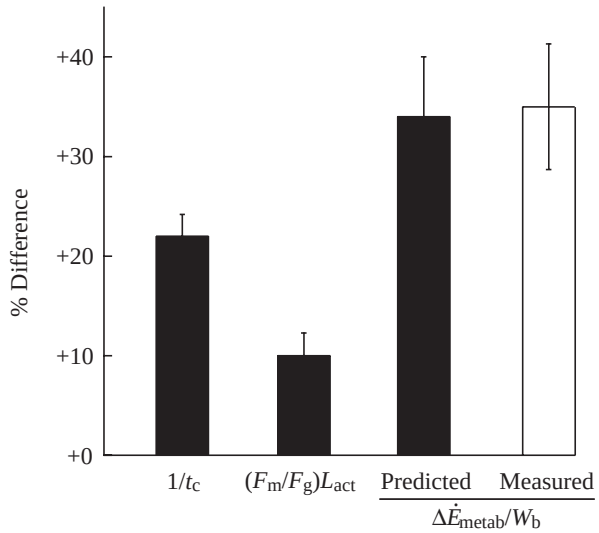

Fig. 6. The difference in mass-specific metabolic rate ($\dot{E}_{metab}/W_b$) between backward and forward running [%difference= 100(backward–forward)/backward], both measured (open column) and predicted (filled column) from the product of estimated rates of ground force application ($1/t_c$, where t_c is time of foot–ground contact) and active muscle volume (F_m/F_g)×L_{act}, where F_m is muscle force, F_g is ground force and L_{act} is the average length of active fibers). Values are means + S.E.M. (N=4). W_b, body weight.

differences in limb and body posture, stride lengths and frequencies and the reversed direction of angular excursions at the hip during backward running could have affected energetic cost in many ways, we were able to quantitatively account for the higher metabolic demands of running in this unconventional manner from the mechanics of ground force application as hypothesized (equation 5). This explanation for the elevated energetic cost of running in a manner that is both physiologically and anatomically unnatural provides additional evidence that the energetic cost of running is determined by the rates of ground force application and the volume of muscle recruited to support the body's weight. In addition to advancing the general understanding of the function of the musculoskeletal system during dynamic exercise, our results further illustrate the utility of foot–ground contact times for monitoring both the metabolic cost (Hoyt et al., 1994) and the mechanics of running (http://www.nbcolympics.com, see Michael Johnson 'Wired Athlete').

General implications for the force hypothesis

Our analysis indicating that the higher energetic cost of running backwards can be explained by the mechanics of ground force application makes a unique contribution to the growing body of experimental evidence (Kram and Taylor, 1990; Glasheen and McMahon, 1995; Bellizzi et al., 1998; Roberts et al., 1998a; Roberts et al., 1998b) supporting a basic relationship between the metabolic rates of the muscles active during locomotion and the duration of their activation periods. Previously, foot–ground contact times have been shown to predict the metabolic rates of different-sized quadrupedal runners with a high degree of accuracy (Kram and Taylor, 1990) and those of different-sized bipedal runners with reasonable accuracy (Roberts et al., 1998b). The present design allowed us to evaluate this relationship more directly by assessing differences in metabolic rates while the same runners applied the same net ground force with the same muscles, but at rates that differed considerably between these two modes. At five of the eight speeds examined, equivalent values of the cost coefficient supported our hypothesis that the higher metabolic rates incurred during backward running result largely from greater rates of force application against the ground. These results strongly suggest that the relationship between the shorter foot–ground contact periods of smaller runners and their higher mass-specific metabolic rates is causal, rather than coincidental, in nature (Steudel, 1990). Obviously, the mass of our runners did not differ between backward and forward running. Yet, when our 70 kg subjects ran backwards and applied ground force at the more rapid rates of a smaller bipedal runner, their mass-specific metabolic rates increased in direct proportion to their greater rates of ground force application. These results provide additional evidence that metabolic rates during running are closely linked to rates of ground force application rather than to the size of the runner or the running speed at which specific rates of ground force application are utilized.

At the three highest speeds examined, the differences in rates of ground force application were not as large as the differences in metabolic rates between modes, indicating that these rate differences do not entirely account for the elevated cost of higher-speed backward running. For one of these three speeds, at which we also estimated active muscle volumes, the 10 % greater muscle volume estimated to be activated during backward *versus* forward running predicted the remainder of the measured cost difference in close accordance with our hypothesis (equation 5). Although this non-invasive technique did not provide the absolute cross-sectional area of muscle activated per unit of ground force, nor were we able to determine how well the fiber lengths in the muscles of our subjects matched those measured in the cadaver specimens, these technical limitations matter little for the present comparison. We recognized that any error resulting from these uncertainties would affect our volume estimates in a given subject equally during backward and forward running and would, therefore, not affect our estimates of differences between these modes. The consistency with which small differences between subjects and between modes were detected (Fig. 5) indicates that this technique served our experimental purposes well. The quantitative agreement of the measured difference in metabolic rates between modes with the product of our estimated active volumes and rates of ground force application (Fig. 6 and equation 5) supports our belief that there is a direct relationship between the volume of muscle active and the metabolic cost of applying ground force (C) at any given rate.

This design also provided a unique test by comparing a mode of running that is natural with respect to limb design and function with one that is not. During backward running, the muscles, tendons and bones involved in support experienced stresses mechanically distinct from those shaping both the structural and functional properties of these tissues. During backward running, ground force was applied more rapidly and with a differing limb orientation that altered the relative distribution of force among the different joints. Despite these deviations from the mechanics of normal running, the relationship between rates of ground force application and metabolic rates was the same at five speeds, and similar at all eight speeds, between these two modes. These results support our premise of a basic relationship between the rates at which muscles apply ground force and the rates at which they hydrolyze ATP regardless of whether the mechanical activity in question falls within or outside the customary functional range of the tissues involved.

Does the application of ground force explain the increases in metabolic rate with increases in running speed?

While differences in rates of ground force application were closely linked to the differences measured in metabolic rates during backward *versus* forward running at the eight speeds examined, the increases in the value of the cost coefficient with increases in running speed in both modes indicate that some portion of the increase in metabolic rate that occurs with increasing running speed is not explained by the rate at which

human runners apply force to the ground. Over the twofold range of speeds tested, the cost coefficient increased by 45 and 32 % during backward and forward running, respectively. Although similar increases have been noted previously for humans and other bipedal runners (Roberts et al., 1998b), and interpreted as an indication that rates of ground force application are not a primary determinant of metabolic rates (Minetti et al., 1994), this is not necessarily the case. Our results here, as well as other recent results (Bellizzi et al., 1998; Roberts et al., 1998a), indicate that the absolute value of the cost coefficient is directly affected by the volume of muscle activated to apply support forces to the ground. Thus, the possibility exists that bipeds recruit progressively larger volumes of muscle to apply ground force at higher running speeds while the relationship between the metabolic rate per unit of active muscle and $1/t_c$ is unchanged. Although the correct explanation is not known at present, some indirect evidence is available to support the latter hypothesis.

The possibility that variability in active muscle volumes may account for speed-induced increases in the cost coefficient in accordance with equation 5 is consistent with a number of observations. For those modes of locomotion for which the cost coefficient is relatively constant across speed, the support mechanics affecting the volume of muscle recruited are apparently constant as well. Specifically, the horizontal distance moved by the body during the contact period, or contact length, does not vary with speed in those modes of locomotion for which the cost coefficient is relatively constant. These include quadrupedal running, human hand-running and roller-skiing with either the arms or the legs only (Kram and Taylor, 1990; Glasheen and McMahon, 1995; Bellizzi et al., 1998). In contrast, for those modes of locomotion for which the cost coefficient increases with increasing speed, such as bipedal running, stance lengths increase in a parallel fashion (Minetti et al., 1994; Roberts et al., 1998b). Our results for both backward and forward running conform to this general pattern. Over the twofold range of speeds tested, contact lengths and cost coefficients increased progressively with speed for both forward and backward running. These speed-induced increases in the cost coefficient were slightly greater for backward than for forward running, while step length increases were slightly smaller for reasons that are not clear at present.

Do the vertical oscillations of the body affect the metabolic cost of running?

Our findings also indicate that vertical work is not an important determinant of the metabolic cost of running despite the widespread belief to the contrary. The view that greater vertical excursions of the body, and therefore greater amounts of vertical work, increase the metabolic cost of running has been expressed by many (Williams and Cavanagh, 1987; Kaneko, 1990; Willems et al., 1995). On a per kilometer basis, our subjects expended one-third more metabolic energy to run backwards than forwards, although the vertical excursions of their center of mass were, on average 16 % less while running backwards (59.4 *versus* 68.5 m km^{-1} for backward and forward running, respectively). Thus, metabolic cost was appreciably greater in the mode in which less vertical work was performed. Similarly at odds with the belief that the vertical work of running incurs an appreciable energetic cost are results indicating that deliberately reducing the vertical oscillations that occur naturally by 'Groucho running' elevates, rather than reduces, the metabolic cost of running (McMahon et al., 1987). These and other results suggest that the mechanics runners select naturally allows the vertical work involved in this gait to be performed primarily passively by tendons that do not use metabolic energy, rather than actively by muscles that do (Cavagna et al., 1964; Cavagna et al., 1977; Roberts et al., 1997). During both Groucho and backward running, vertical oscillations are reduced in comparison with conventional forward running, but these reductions coincide with alterations in support mechanics that have an adverse effect on the metabolic energy expended to apply force to the ground. Thus, rather than increasing the muscular work and the metabolic energy required for running, the vertical oscillations characteristic of running gaits likely allow for support mechanics that minimize both the muscle forces required and the metabolic energy expended to generate these forces.

The energetic cost of ground force application increases as the net work required during locomotion increases

Here, as in previous tests of the force hypothesis, we have assumed the average relative shortening velocities of the active muscles to be roughly proportional to the net work performed on the environment during each stride (Kram and Taylor, 1990; Taylor, 1994; Bellizzi et al., 1998; Roberts et al., 1998b). In modes of locomotion that do not require net work, the limited direct evidence available supports this assumption, indicating that muscles shorten little while active across a range of speeds (Biewener et al., 1998; Roberts et al., 1997; Cogger et al., 2000). In contrast, by physical necessity, all the net work performed in modes of locomotion requiring net work must be performed by skeletal muscles that shorten while producing force. Thus, logic and both general (Biewener et al., 1998; Cogger et al., 2000) and specific (Roberts et al., 1997) evidence suggest that the assumption of equivalent average shortening velocities made here and in previous tests of the force hypothesis should not be applied when comparing modes of locomotion with different requirements for the amount of net work performed on the environment with each stride.

Two groups of authors have noted that when net work requirements are introduced, either by running uphill (Minetti et al., 1994) or by running in sand (Lejeune et al., 1998), values of the cost coefficient are considerably greater than those during level running on a firm surface. These elevations resulted from greater metabolic rates being incurred with similar contact times at similar running speeds while subjects ran uphill or in sand. These authors correctly note that the increased requirement for net mechanical work under these circumstances elevates the energetic cost of running and of applying force to the running surface. We believe that the mechanistic explanation for these increases in the metabolic

cost incurred per newton of force applied to the ground (Taylor, 1994; Minetti and Alexander, 1997) is likely provided by the classic muscle properties initially established for isolated preparations (Hill, 1950). Because the metabolic cost of generating muscular force in isolated muscle increases with increased shortening (Hill, 1950), values of the cost coefficient would be expected to increase as the requirements for net mechanical work and muscle shortening increase (Taylor, 1994). Two factors seem likely to contribute to this. First, the volume of muscle active to support the body's weight during the period of foot–ground contact would likely increase because the force provided per unit of active muscle decreases as the distance shortened during the activation period increases (Hill, 1950). Second, the metabolic rate per unit of active muscle would also likely increase progressively with the distance shortened during the activation period (Hill, 1950).

Concluding remarks

The close agreement between the increases in metabolic cost we measured and those we predicted from the different mechanics of ground force application when humans run in a manner that is both functionally and anatomically unnatural supports the belief that the energetic cost of running is set by the application of ground force to support the body's weight. In this respect, our results provide further evidence that the energetic cost of running is incurred in discrete pulses during the periods of foot–ground contact when force is applied, and that the movements occurring during the aerial phase of the stride incur negligible metabolic cost (Kram and Taylor, 1990; Taylor, 1994; Glasheen and McMahon, 1995; Bellizzi et al., 1998). We further infer that the metabolic cost of accelerating the body and limbs during constant-speed locomotion is also quite small because the large majority of this mechanical work is performed passively by tendons and energy transfers between body segments rather than actively by skeletal muscle (Cavagna et al., 1964; Cavagna et al., 1977; Heglund et al., 1982; Roberts et al., 1997). Our results also support our premise that the mechanical activity of the musculoskeletal system incurring a metabolic cost during dynamic exercise can be assessed non-invasively from the mechanical interaction between an animal and the environment. Our success in linking metabolic cost to whole-body mechanics suggests that this approach has potential to further advance the understanding of the relationship between the mechanical activity of the musculoskeletal system and the energetic cost of movement in general.

Finally, we conclude that metabolic rates during running are determined by the time course of muscular activation and the volume of muscle recruited to apply support forces against the ground.

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