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MECHANICAL DETERMINANTS OF THE MINIMUM ENERGY COST OF GRADIENT RUNNING IN HUMANS

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Summary

The metabolic cost and the mechanical work of running at different speeds and gradients were measured on five human subjects. The mechanical work was partitioned into the internal work (W_{int}) due to the speed changes of body segments with respect to the body centre of mass and the external work (W_{ext}) due to the position and speed changes of the body centre of mass in the environment. W_{ext} was further divided into a positive part (W_{ext}^+) and a negative part (W_{ext}^-), associated with the energy increases and decreases, respectively, over the stride period. For all constant speeds, the most economical gradient was $-10.6\pm0.5\%$ (S.D., $N=5$) with a metabolic cost of $146.8\pm3.8\,\mathrm{ml}\,O_2\,\mathrm{kg}^{-1}\,\mathrm{km}^{-1}$. At each gradient, there was a unique W_{ext}^+/W_{ext}^- ratio (which was 1 in level running), irrespective of speed, with a tendency for W_{ext}^- and W_{ext}^+ to disappear above a gradient of $+30\%$ and below a gradient of -30%, respectively. W_{int} was constant within each speed from a gradient of -15% to level running. This was the result of a nearly constant stride frequency at all negative gradients. The constancy of W_{int} within this gradient range implies that W_{int} has no role in determining the optimum gradient. The metabolic cost C was predicted from the mechanical experimental data according to the following equation:

$$C = \frac{W_{ext}^- - el^-}{\mathit{eff}^-} + \frac{W_{ext}^+ - el^+}{\mathit{eff}^+} + \frac{W_{int}}{\mathit{eff}^i} \,,$$

where eff^- (0.80), eff^+ (0.18) and eff^i (0.30) are the efficiencies of W_{ext}^-, W_{ext}^+ and W_{int}, respectively, and el^- and el^+ represent the amounts of stored and released elastic energy, which are assumed to be $55\,\mathrm{J}\,\mathrm{step}^{-1}$. The predicted C *versus* gradient curve coincides with the curve obtained from metabolic measurements. We conclude that W_{ext}^+/W_{ext}^- partitioning and the $\mathit{eff}^+/\mathit{eff}^-$ ratio, i.e. the different efficiency of the muscles during acceleration and braking, explain the metabolic optimum gradient for running of about -10%.

Introduction

In a recent paper, Minetti *et al.* (1993) examined the mechanical determinants of the metabolic cost of human walking at various gradients. The cost of walking 1 km is

minimized at a gradient of −10 % (negative values refer to downhill slopes) and increases at both more negative and more positive gradients (Margaria, 1938). This pattern appears to be the result of residual positive mechanical work during downhill walking. Unlike an ideal locomotor machine, which minimizes the oscillations of the system centre of mass (a bicycle, for example), a human walks as if on a rimless spoked wheel (McGeer, 1990) with continuous raising and lowering, and accelerations and decelerations, of the body. These deviations from movement along a straight path at a constant progression speed are responsible for the positive (raising and acceleration) and negative (lowering and deceleration) work that the muscles must perform during walking. On a bicycle, we expect to use only negative work when riding downhill, in order to brake the system; and it is possible to conceive of a way of pedalling uphill that would maintain the progression speed as constant as possible by doing positive work to account for the potential energy increase only. For walking on a level surface, the total mechanical work was expected (from physics) to be partitioned into two equal positive and negative parts. However, a motion analysis of gradient walking revealed that braking activity is negligible above a gradient of +15 %, while accelerative activity disappears below an incline of −15 %. Within this interval, both positive and negative mechanical work are required according to a sigmoidal relationship about the 0 % gradient (Minetti *et al.* 1993, see their Fig. 3). The other crucial factor required to explain the metabolic minimum gradient for walking is that our muscles use much less fuel when doing negative work (braking activity) than when doing positive work. The muscle efficiency (work done/metabolic energy spent) for negative work has been estimated to be 3–5 times higher than that for positive work (Abbot *et al.* 1952). The combination of the ratio between positive and negative work and their different efficiencies allowed us to predict the metabolic cost of walking from mechanical measurements; a good match with the metabolic measurements was found (Minetti *et al.* 1993).

In the first paper reporting the metabolic optimum walking gradient, Margaria (1938) also showed that the energetic cost of running was minimized at a gradient of approximately −10 % (see also Margaria *et al.* 1963, and see Fig. 3). Margaria's technique for calculating the efficiency of locomotion was to relate the metabolic energy consumption to an estimate of the mechanical work performed. He considered only the minimum changes in potential energy (from continuous raising or lowering of the centre of mass) occurring during the movement and provided reasonable results for walking for a gradient range (below −20 % and above +20 %) over which the mechanical work consists of only one component (either the negative or the positive component, respectively; Minetti *et al.* 1993). For running, the gradient range investigated, limited by metabolic constraints on aerobic performance, was too narrow to establish constant (asymptotic) values for the efficiency.

Davies *et al.* (1974), using similar methods to Margaria (1938), measured the energetics of running humans and estimated the mechanical work by considering only the work done to lift (or lower) the body centre of mass. Buczek and Cavanagh (1990) used a force platform installed along a 17 m downhill walkway to measure the knee and ankle joint power at a slope of about −8 %. Iversen and McMahon (1992) developed a model predicting the pattern of motion of gradient running. Apart from these papers, no other

study, to the authors' knowledge, has appeared that describes the relationship between measured mechanics and energetics of human running, particularly in relation to the optimum gradient.

The purpose of this study was to measure the metabolic cost and mechanical work of gradient running and, from the relationship between them, to try to explain the determinants of the optimum gradient.

Materials and methods

Five healthy males (25.2±6.9 years old, mass 72.8±6.3 kg, height 1.81±0.09 m; mean ± S.D.) ran on a motor-driven treadmill at different gradients (from -15% to $+15\%$ in 5% increments) at speeds of 2.20, 2.48, 2.72, 2.99 and $3.29\,\mathrm{m\,s^{-1}}$. For each condition, simultaneous mechanical and metabolic measurements were taken.

Biomechanical measurements

Each speed/gradient trial was recorded by means of an opto-electronic motion analysis system (ELITE System, B.T.S., Italy) with four cameras sampling at a rate of 100 Hz. A dedicated computer automatically recognizes for each camera the shape of reflective markers, illuminated *via* stroboscopic infrared light. Ten reflective hemispherical spots (diameter 1 cm) were placed on each side of the body in order to identify the subject's segments of interest: the head-trunk (ear lobe – iliac crest), thigh (great trochanter – knee joint), shank (knee joint – ankle malleolus), foot (heel – toe), upper arm (shoulder – elbow) and forearm (elbow – wrist). The three-dimensional positions of segment extremities were stereometrically calculated by the apparatus. Each acquisition lasted 5 s and the stride frequency was calculated by analysing the periodicity of the vertical coordinates and by counting the number of frames for a stride.

Values for segment mass, centre of mass position and radius of gyration were taken from standard tables (Dempster *et al.* 1959). Positive W_{int} was computed using the method of Cavagna and Kaneko (1977). In order to account for the kinetic energy changes of segments whose movements do not affect the position of the overall centre of mass (i.e. symmetrical limb displacements), we used König's theorem from mechanics. This theorem states that the total kinetic energy of a multi-link system can be divided into two parts: (a) the kinetic energy of the segments arising from their change of speed with respect to the overall centre of mass, and (b) the kinetic energy of the overall centre of mass. The second term is included in the W_{ext} computation, while the first is the internal work, W_{int}. Other details of the experimental design were reported by Minetti *et al.* (1993).

The three-dimensional displacement of the body centre of mass was calculated for each frame from the positions of the 12 body segments. Positive W_{ext}^{+} and negative W_{ext}^{-} were obtained by summing the increments and the decrements, respectively, of the total energy (= potential + horizontal kinetic + vertical kinetic) curve of the body centre of mass position *versus* time. Total external work (W_{ext}) was computed as the sum of W_{ext}^{+} and W_{ext}^{-}.

All the data processing and statistics were performed on an Olivetti M380 XP5

computer and an Apple Macintosh Quadra 700 computer. Low-pass filtering of the measured spatial coordinates was performed using the procedure of D'Amico and Ferrigno (1990), in which optimal filter cut-off frequencies are automatically selected. The range of cut-off frequencies was 5.0–9.0 Hz using this procedure. A custom-built program, created using LabView 2/Macintosh (National Instruments, USA), analysed the three-dimensional data and calculated the biomechanical variables for 209 strides. The procedure for data differentiation, needed to compute marker speed, was the simple dx/dt, dy/dt and dz/dt calculation on the filtered coordinates.

Metabolic measurements

Standard open-circuit respirometry was used. O_2 and CO_2 partial pressures were measured by gas analysers (OM-11 and LB-2, Beckman Inc., USA) and these values, together with a signal proportional to the displacement of a respirometer bell, were continuously fed into a MINC 11-23 computer (Digital Inc., USA) for conversion to STPD of ventilation and O_2 uptake values. Laboratory temperature was always within 21–24 °C. Data for the standing subjects were subtracted from the steady-state values, reached after about 4 min of running, to obtain the net energy expenditure for each gradient/speed trial. $\dot{V}_{O_2max}$ was assessed in a subsequent experimental session for each subject with an incremental test (Ellestad, 1980) and was used to exclude from the calculations of the average running costs the trials corresponding to an oxygen consumption higher than 90 % of $\dot{V}_{O_2max}$.

Mechanical and metabolic work values in the present paper are expressed per kilogram of body mass and per kilometre travelled. Mechanical results have been expressed in metabolic units assuming that $1 ml O_2=20.9 J$ (for a mean respiratory quotient of about 0.95).

Results

Fig. 1 shows, for each gradient, the metabolic cost associated with running at each constant speed. The optimum gradient for running, at which the metabolic cost is minimal, was estimated from the coefficients of third-order polynomial regressions for each speed, as given in Table 1. We chose a cubic polynomial in order to avoid the symmetry of descending and ascending limbs of a parabolic regression. The mean optimum gradient for all speeds was -10.63 ± 0.52 % (S.D.). The small variability in this value suggests that the optimum gradient is practically independent of speed. Owing to their small variation with speed, the external mechanical work (W_{ext}) and its constituents W_{ext}^+ and W_{ext}^- were calculated from pooled values for each gradient and are represented as single values in Figs 2 and 3, respectively. In Fig. 3, the values for walking (Minetti *et al.* 1993) have been added for comparison. Stride frequency and W_{int} are given for each speed as a function of gradient in Figs 4 and 5.

Discussion

Metabolic cost per unit distance travelled (Fig. 1) was dependent on gradient but not on
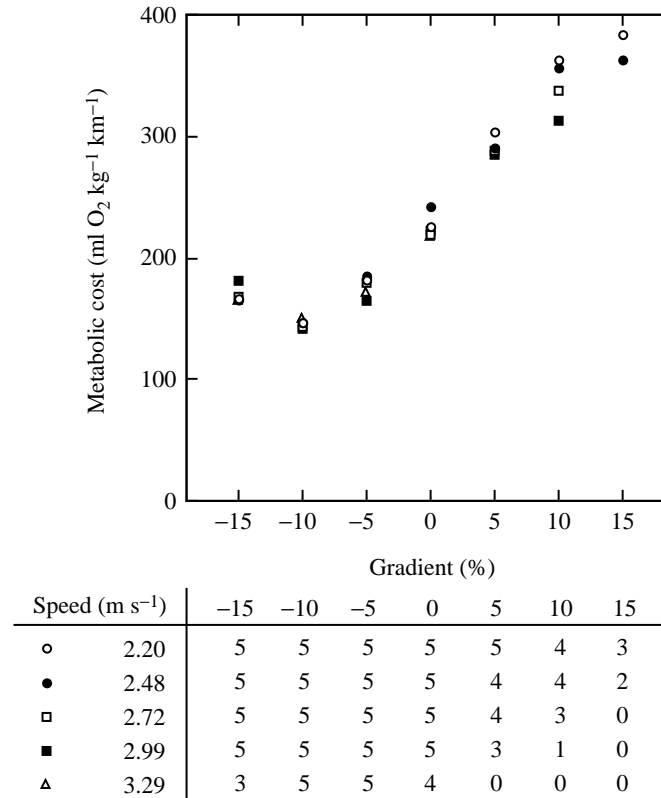
Fig. 1. The metabolic cost of running at different speeds and gradients. Each point represents the mean value for subjects capable of sustaining the exercise level at less than 90 % of their $\dot{V}_{O_2max}$ (the number of subjects for each experimental condition is shown in the table below the figure). Standard deviations have been omitted for clarity. Coefficients of variation were 3.5 % at −15 % gradient, 4.9 % at −10 %, 4.9 % at −5 %, 4.1 % at 0 %, 2.7 % at +5 %, 6.4 % at +10 % and 4.0 % at +15 %.

Table 1. *Regression coefficients for each running speed*

Speed $(m\,s^{-1})$	a	b	c	d	r^2	Optimum gradient (%)
2.20	233.870	10.843	0.389	−0.005	0.999	−10.78
2.48	237.943	12.564	0.118	−0.026	0.996	−11.27
2.72	224.785	11.918	0.183	−0.024	0.997	−10.57
2.99	223.501	12.847	0.036	−0.042	1.000	−9.82
3.29	218.102	11.009	0.290	−0.014	1.000	−10.70

The regression coefficients are for the equation $C = a + bi + ci^2 + di^3$ for each running speed, where C is the metabolic cost of running in $ml\,O_2\,kg^{-1}\,km^{-1}$ (data given in Fig. 1) and i is gradient in %.

The optimum gradient is calculated for each speed as the lowest solution of: $\dfrac{-2c \pm \sqrt{4c^2 - 12bd}}{6d}$.
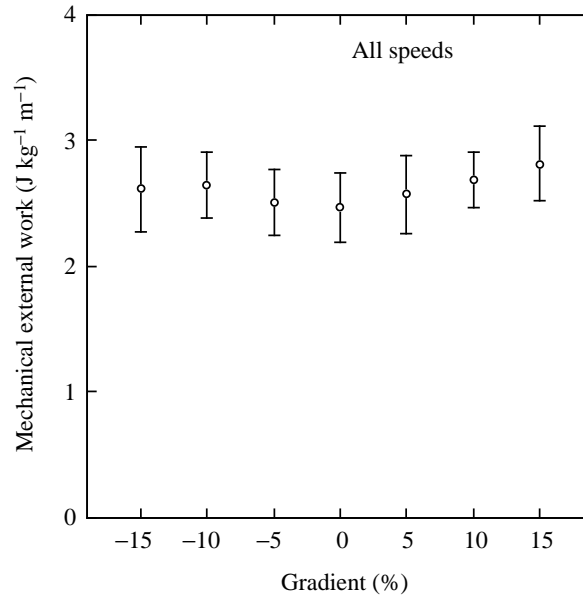
Fig. 2. External work, W_{ext} (the sum of W_{ext}^{+} and the absolute value of W_{ext}^{-}), per unit distance at different gradients. Values are the means for all subjects and all speeds ± 1 S.D.

speed, except for at the steepest positive inclines ($+10$, $+15\%$), where the metabolic cost per unit distance travelled was lower at higher speeds. At the highest speed and the steepest inclined gradient, the metabolic demand probably exceeded the subjects' aerobic capacities. Thus, for these measurements, the rate of oxygen consumption probably underestimated the total metabolic energy required. For downhill gradients, the variability due to speed was low and the minimum cost can be estimated (from the regressions in Table 1) to be $146.8\pm3.8\,\mathrm{ml\,O_2\,kg^{-1}\,km^{-1}}$. The curve for the relationship between external mechanical work (W_{ext}) and gradient is flatter for running than for walking (Fig. 2; Minetti *et al.* 1993) and the partitioning of W_{ext} into W_{ext}^{+} and W_{ext}^{-} (represented as W_{ext}^{-}/W_{ext} in Fig. 3) follows a linear trend with gradient. This suggests that, during running, W_{ext}^{+} and W_{ext}^{-} become negligible below a gradient of about -30% and above a gradient of $+30\%$, respectively. In order to validate this prediction, we asked two subjects to run for a few seconds at gradients below -15% and above $+15\%$. W_{ext}^{+} and W_{ext}^{-} values from these experiments (filled triangles in Fig. 3) confirm our prediction. However, since prolonged running at these extreme gradients (particularly for uphill gradients) is beyond the aerobic capacity of most human subjects, extension of the curve to gradients of $\pm30\%$ is of interest only from a biomechanical point of view.

Before directly comparing the mechanical and metabolic results, we must also consider the mechanical internal work, W_{int}, an important component of the total mechanical work. As shown in Fig. 5, W_{int} remained nearly constant at all downhill gradients, but increased with positive gradients. These changes in W_{int} parallel the measured changes in stride
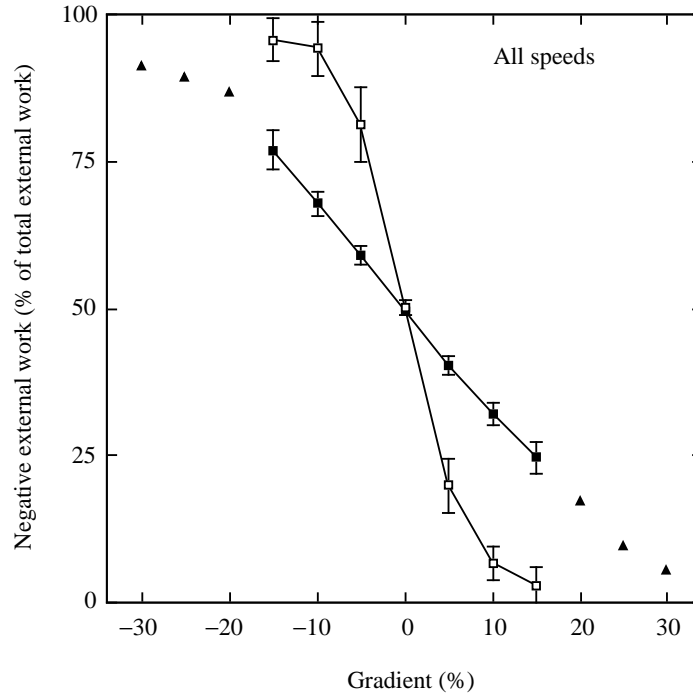
Fig. 3. Negative external work (as a percentage of W_{ext}) as a function of gradient; running data (filled squares) and walking values (open squares, Minetti *et al.* 1993) are both shown. Values are means ±1 s.D. for all subjects and all speeds. The filled triangles represent results from further experiments in which two subjects ran at even higher gradients. Each of these points is the mean of two values.

frequency (Fig. 4). The lack of change in W_{int} at negative gradients suggests that W_{int} has little influence on the optimal gradient. In addition, W_{int} is, by definition, formed from equal positive and negative components at all gradients (Minetti *et al.* 1993). The lesser dependence of W_{int} on speed during running than during walking (Minetti and Saibene, 1992) is due to the flight time, which allows the limbs to move more slowly with respect to the progression speed during the swing phase in running.

Fig. 6A represents the first attempt to predict the metabolic cost of running C from the measured mechanical data (see the legend for details) using the following equation:

$$C = \frac{W_{ext}^-}{eff^-} + \frac{W_{ext}^+}{eff^+} + \frac{W_{int}}{eff^i} \,, \tag{1}$$

where eff^- (0.80), eff^+ (0.18) and eff^i (0.30) are the efficiencies of W_{ext}^-, W_{ext}^+ and W_{int}, respectively. Each term of the equation is represented (in metabolic units) in Fig. 6. The choice of values for eff^- and eff^+ follows the results obtained for gradient walking (Minetti *et al.* 1993), while the higher eff^i value reflects (a) the partially ballistic
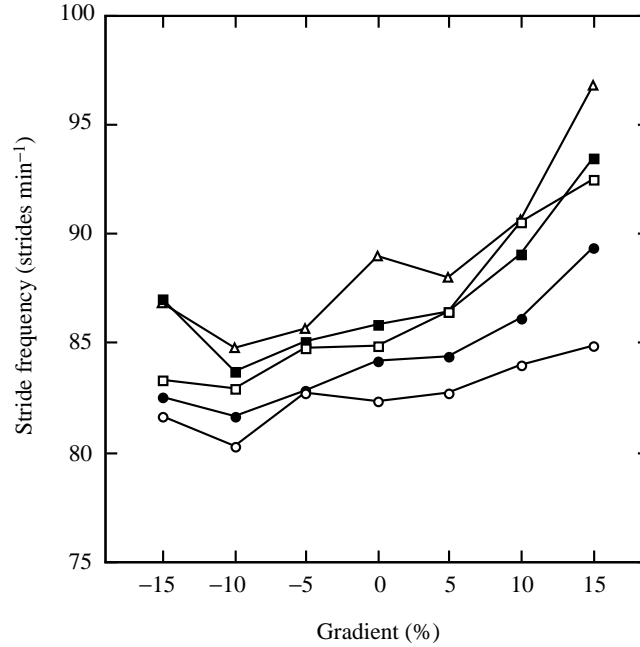
Fig. 4. Stride frequency at different speeds as a function of gradient. Values are means for all subjects. Symbols are as in Fig. 1. Standard deviations have been omitted for clarity.

characteristics of the swing phase, and (b) overestimation of the mechanical work of the limbs due to splitting of the total work into internal and external components (Alexander, 1989). As stated above, whatever the value chosen for $eff^{\,i}$, the shape of the curve would be the same.

There is an obvious discrepancy between the predicted and the measured metabolic values (open and filled squares, respectively, in Fig. 6A). This is the result of applying values for muscle efficiencies to the total mechanical work, i.e. including that done by non-muscular tissues. The high running efficiencies reported previously (40–80 %, Cavagna and Kaneko, 1977) arose because of an overestimation of the mechanical work attributable to muscle activity, i.e. elastic storage and release of energy was neglected. Those efficiencies referred to the ability of the whole locomotor system (bones, joints, tendons and muscles) to maintain the high energy levels required for motion. The present paper deals with the determinants of the measured metabolic minimum, and this can be estimated only by subtracting the work stored and recovered from elastic tissues from the total work. The structures that store elastic energy are the muscle tendons (mainly the Achilles tendon) and ligaments in the arch of the foot, and these are not metabolically active. With this in mind, we can extend equation 1 to give:

$$C = \frac{W_{\text{ext}}^{-} - el^{-}}{eff^{-}} + \frac{W_{\text{ext}}^{+} - el^{+}}{eff^{+}} + \frac{W_{\text{int}}}{eff^{i}} \,, \qquad (2)$$
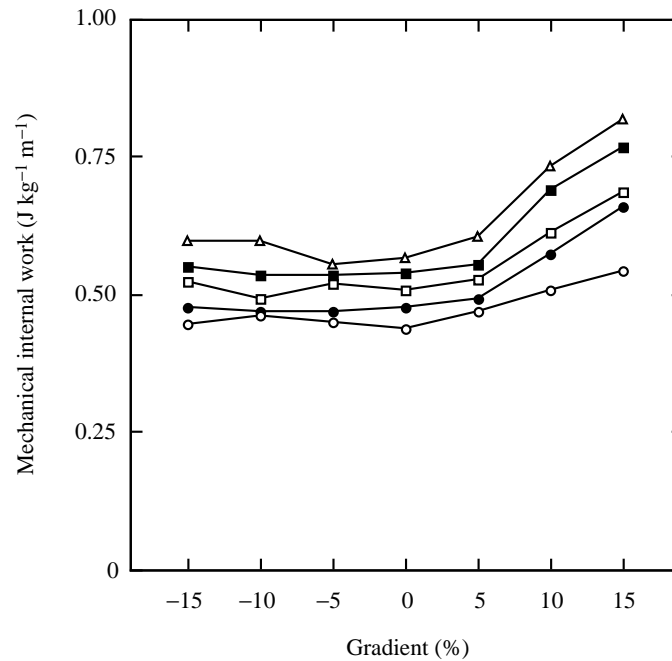
Fig. 5. Internal work per unit distance travelled at different speeds as a function of the gradient. Values are means for all subjects. Symbols are as in Fig. 1. Standard deviations have been omitted for clarity.

where el^- and el^+ represent the amounts of stored and released elastic energy, respectively. Equation 2 was used to calculate the values shown in Fig. 6B with the following rationale (see also Table 2). At each gradient, we can assume a constant maximum amount of elastic energy per step that can be stored and later released by the springs (tendons and ligaments). During this process, we have to consider (a) that the elastic energy stored must be less than the measured W_{ext}^-, (b) that the elastic energy released must be less than the elastic energy stored and less than the measured W_{ext}^+, and (c) that the elastic energy released must be smaller than the elastic energy stored because of energy dissipation within the springs (95 % in this case, a value compatible with the literature; Ker, 1981).

This algorithmic framework was created on a spreadsheet (Excel 4, Microsoft Corp., USA, see Table 2 for details); we used average values for metabolic cost, stride frequency, W_{ext}^+, W_{ext}^- and W_{int} as input values. We were encouraged to do this simulation by the constant shape and/or amplitude of our measurements (see Figs 1–5). We obtained, by trial and error, the best correspondence with the experimental metabolic results when el^- was equal to about 55 J step^{-1} (open and filled squares are almost coincident in the graph, the discrepancy at a gradient of +15 % being largely due to metabolic constraints at high gradients).

Our predicted value for the degree of elastic energy storage in tendons and ligaments is
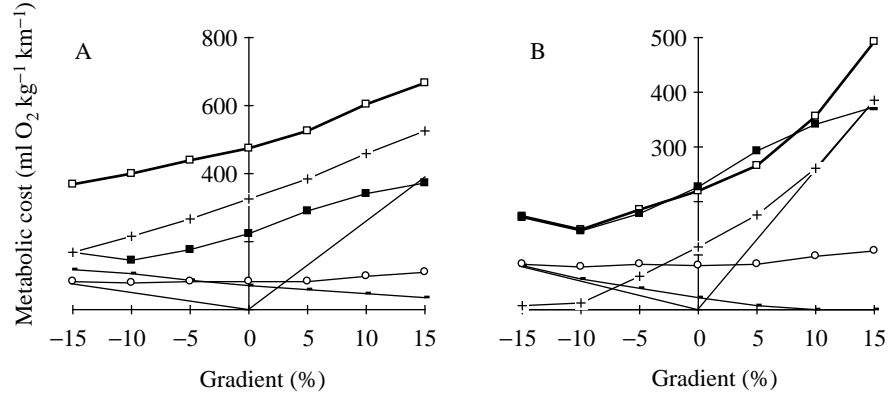
Fig. 6. Mechanical explanation of the minimum energy expenditure in downhill running. In A and B, the predicted metabolic equivalents of W^+_{ext} (+ symbols), W^-_{ext} (− symbols), W_{int} (open circles) and total mechanical work (open squares) are shown. Filled squares are values for the measured metabolic cost of running (obtained by pooling all values for all speeds). Lines starting from the origin represent the metabolic equivalent of the positive and negative minimum external work (Minetti *et al.* 1993) according to the following equations:

$$W^-_{ext,min} = \begin{cases} -g \times i & i < 0 \\ 0 & i \geq 0 \end{cases} \quad \text{and} \quad W^+_{ext,min} = \begin{cases} 0 & i < 0 \\ g \times i & i \geq 0 \end{cases},$$

where g is the acceleration due to gravity and i is gradient (in the equations, $W^-_{ext,min}$ and $W^+_{ext,min}$ are in $J\,kg^{-1}\,m^{-1}$). (A) Metabolic equivalent of the mechanical work calculated using the efficiency coefficients from Table 2 and not including any elastic storage or release of energy (see equation 1). (B) Metabolic equivalent of the mechanical work calculated including the energy saving due to elastic storage and release at each step (equation 2 and the algorithm illustrated in spreadsheet format in Table 2).

in agreement with values from the literature. Alexander and his co-workers (Alexander, 1988; Ker *et al.* 1987) estimated that the amount of elastic energy stored during a running step was 35 J for the Achilles tendon and 17 J for the arch of the foot (a total of 52 J for an average body mass of 70 kg). However, we are aware of the problems inherent in assuming constant efficiencies (of positive and negative work) for all experimental situations. Running at different gradients could require different postures and, consequently, inefficient muscle usage (i.e. operating in disadvantageous parts of the power/velocity curve or with lower 'transmission' efficiency or effectiveness; Lafortune and Cavanagh, 1983). It has been suggested (Alexander, 1991) that the coupling between muscles and tendons may reduce the importance of such disadvantages.

The efficiency values used in the present paper are in agreement with values from the literature (Aura and Komi, 1986*a,b*, Minetti *et al.* 1993). Even taking into account that the efficiency of muscular contraction in running could be different from that during walking because of the higher shortening and lengthening speeds involved, it is also important to remember (Minetti *et al.* 1993) that the shape of the predicted metabolic curve will not change while the *eff*⁻/*eff*⁺ ratio is kept constant (at about 5; as reported by Abbot *et al.*

Table 2. *Algorithmic framework used to convert mechanical measurements into metabolic equivalents*

	A	B	C	D	E	F	G	H	I	J	K	L	M
1	Elastic energy-saving simulation							eff^+	0.18	el^-	0.076	55.6	J step⁻¹
2						eff^i 0.30		eff^-	0.80	el^+/el^-	0.95		
3													
4													
5	Gradient	C		W^-_{ext}	W^+_{ext}	Storable	Stored and	W_{int}	W^-_{net}	W^+_{net}	W_{int}		Predicted
6	(%)	(ml O₂ kg⁻¹ km⁻¹)	(Stride km⁻¹)	(as C)	(as C)	(as C)	released (as C)	(as C)	(as C)	(as C)	(as C)		C (as C)
7	−15	169.2	516.8	94.8	30.2	39.3	30.2	25.0	80.8	8.4	83.3		172.5
8	−10	146.1	506.9	84.4	38.8	38.5	38.5	23.6	57.3	12.2	78.7		148.2
9	−5	176.4	516.5	70.4	48.4	39.3	39.3	24.8	38.9	61.7	82.7		183.3
10	0	225.7	522.8	57.0	58.6	39.7	39.7	24.2	21.6	115.8	80.7		218.1
11	5	291.5	525.0	46.0	69.2	39.9	39.9	25.2	7.6	173.9	84.0		265.5
12	10	342.1	540.1	37.8	82.6	37.8	37.8	29.2	0.0	259.4	97.3		356.7
13	15	373.7	560.4	26.8	94.8	26.8	26.8	32.8	0.0	385.2	109.3		494.6

Cell(s)	Content	Comments
K1	Maximum assumed elastic storage per stride	In ml O₂ kg⁻¹ stride⁻¹
K2	Ratio between energy in and energy out in the elastic structures, the tendon hysteresis coefficient	Almost all of the elastic energy stored during negative work is successively released during positive work (95 %)
F7:F13	=IF[(D7-$K$1*C7)>=0;$K$1*C7;D7]	No more than the measured negative work can be stored as elastic energy
G7:G13	=IF[(E7-F7)>=0;F7;E7]	No more than the storable negative elastic work or than the measured positive can be released
I7:I13	=(D7-G7)/$I$2 (− symbols in Fig. 6)	Metabolic equivalent of net negative external work
J7:J13	=(E7-G7*$K$2)/$I$1 (+ symbols in Fig. 6)	Metabolic equivalent of net positive external work (the elastic energy subtracted is decreased according to the tendon hysteresis coefficient K2)
K7:K13	=H7/$G$1 (open circles in Fig. 6)	The metabolic equivalent of the mechanical internal work is calculated using a separate efficiency value (see text)
M7:M13	=I7+J7+K7 (open squares in Fig. 6)	The predicted overall metabolic cost of gradient running is obtained by summing the metabolic equivalents of negative and positive external work and the internal work

The framework is in Microsoft Excel, border outline: solid, measured data; light, computed variables; dotted, assumed variables; double-line, our estimate.
The hypothesis is that the storable elastic energy (per km) is determined by the product of a fixed amount of energy (per stride) and of the number of strides (per km). Such a quantity has to be subtracted from the measured negative and positive external work before the metabolic cost can be predicted from mechanical data.
The spreadsheet capabilities are used to meet two important requirements: (1) no more than the measured negative work can be stored as elastic energy (this can occur at high inclines), and (2) no more than the measured positive work can be seen as elastic energy released (which can occur at steep declines).
All the work and energy values are expressed in ml O₂ km⁻¹ kg⁻¹ (1 ml O₂=20.9J).
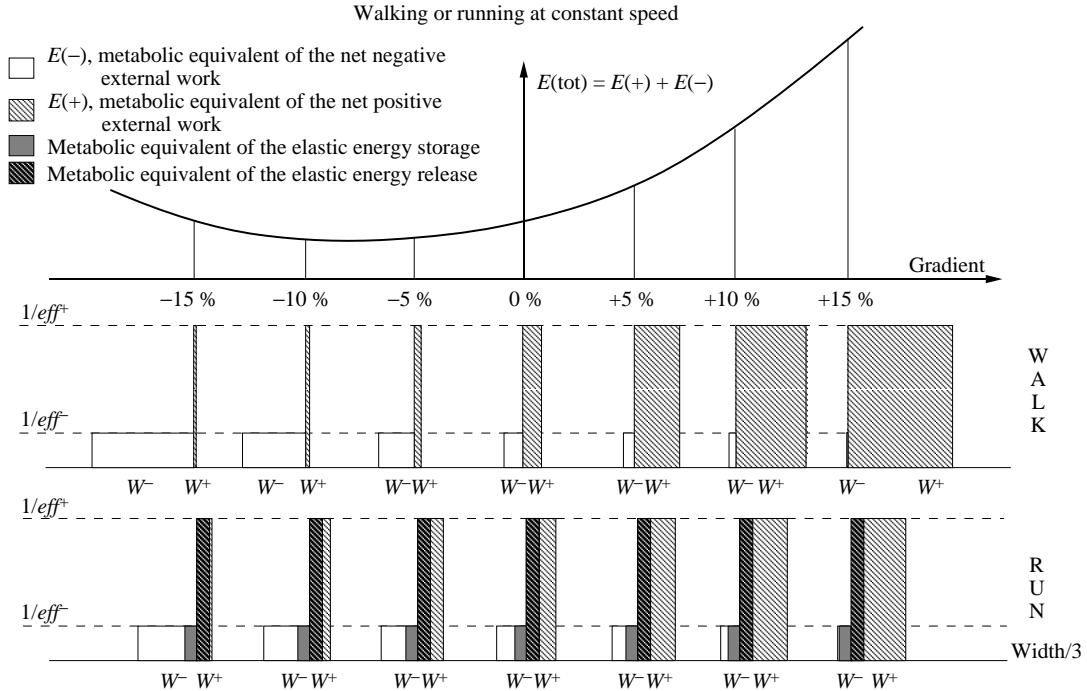
Fig. 7. Graphical summary of the mechanical explanation of both gradient walking and gradient running (the upper part of this figure is taken from a previous paper on gradient walking, Minetti *et al.* 1993). This plot shows that the optimum gradient for walking (about $-10\,\%$) is determined by the presence of W_{ext}^{+} in downhill gradients (width of the light cross-hatched histograms) and by the remarkable difference between the efficiencies of the positive and negative mechanical work (histogram heights). In this representation, the histogram area corresponds to the metabolic equivalent of positive or negative external work, and their sum is a prediction of the overall metabolic cost of walking at each gradient. The lower bank of histograms, related to the optimum gradient for running, shows how this gait is similar to walking with respect to the division between negative and positive work, provided that the mechanical measurements have been corrected for the storage and release of elastic energy (i.e. when the stippled and dark cross-hatched histograms are removed, the proportions between the left-most and right-most histograms, at each gradient, are similar to those in the walking ones).

1952). In addition, Hof (1990) found a broad plateau in the efficiency *versus* speed curve of calf muscles such that there was no great change in efficiency (within 90–100 %) over a fivefold range of contraction speed that included both walking and running.

Another point of interest in Fig. 6B is the tendency of the corrected values for the W_{ext}^{-} and W_{ext}^{+} curves to approach the lines representing the minimum work expected for downhill and uphill gradients (left and right lines starting from the origin, respectively). It is also of note that the corrected values for W_{ext}^{-} and W_{ext}^{+} tend to vanish outside the gradient range of ±15 %, in agreement with the results of gradient walking (Minetti *et al.* 1993).
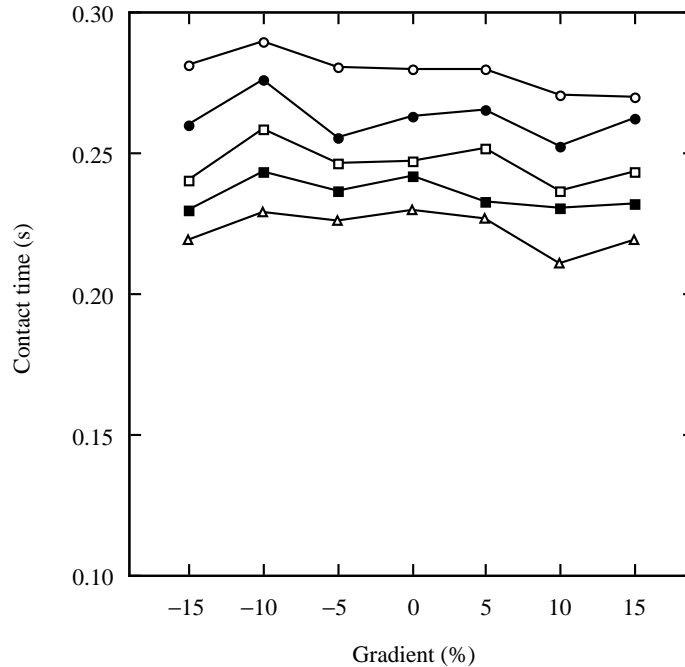
Fig. 8. Contact time during a stride at different speeds as a function of gradient (average of all subjects, symbols as in Fig. 1). Standard deviations have been omitted for clarity.

We summarise the present results in Fig. 7, together with values for gradient walking (from Fig. 1 in Minetti *et al.* 1993), to illustrate the similarity between the two gaits. The apparent differences reside in the W_{ext}^-/W_{ext}^+ ratio (see Fig. 3), which results in an absence of an optimum gradient from the predicted metabolic values (see Fig. 6A). When the effects of elastic storage and release have been removed, the metabolic equivalents of W_{ext}^- and W_{ext}^+ in running (light grey and white areas, respectively) and their ratios are rather similar to those for walking, and the minimum cost is found at the same optimum gradient.

Kram and Taylor (1990) and Alexander (1991, 1992) have pointed out that the mechanical work cannot be used *per se* to calculate the total metabolic cost of walking and running since muscles use extra fuel when they exert force without producing mechanical work, for example during isometric contractions. In particular, Kram and Taylor (1990) suggested that, during level running, a crucial variable needed to predict the metabolic cost is the time of contact between the feet and the ground. A longer contact time implies lower average values for the vertical ground reaction force during the stance period and thus a lower cost. Fig. 8 shows the foot contact time, taken from motion analysis data (note that the use of vertical thresholds to assess the foot contact time from spatial coordinates may lead to some inaccuracies). It is intriguing that the time of contact tends to be highest at the optimum gradient (and, interestingly, that the stride frequency shows a corresponding minimum at -10% at all speeds, see Fig. 4). The flatness of the

contact time *versus* gradient curves and the success obtained in this study and that of Minetti *et al.* (1993) in matching mechanical work to metabolic cost, without taking contact time into account, support the hypothesis that in human gradient walking and running the mechanical work is the major determinant of the metabolic cost. In addition, the flatness of the curves in Fig. 8 corresponds with the constancy of the peak values of the normal-to-treadmill reaction force in the gradient range -20 to 0%, found by Iversen and McMahon (1992) using a treadmill-mounted dynamometric platform. The approach proposed by Kram and Taylor (1990) for level running appears not to apply to gradient running. Their hypothesis also implies that, within each gradient, for a speed increase by a factor k the contact time should be scaled by $1/k$ in order to keep the metabolic cost constant (combine their equations 1 and 2). In our experiments, with a speed range scope of 1.495, we obtained a value for k of 1.251 ± 0.025 (s.d.), indicating that the average vertical force *per se* cannot explain the metabolic requirements of gradient running. However, since there is no doubt about the potential metabolic contribution of isometric muscular contractions (and co-contractions), it is possible that in certain locomotory situations the combination of the cost of generating work and the cost of exerting force must be considered.

In conclusion, the mechanics of uphill and downhill running elucidate the relationship between the constraints associated with the human locomotor machinery (i.e. the excess power required for acceleration and braking inherent in a legged animal) and the metabolic requirements. The overall metabolic trend and the minimum cost of gradient running at a gradient of about -10% depend on the differences between the ideal energetic requirements (W_{min} lines in Fig. 6B), due to potential energy changes alone, and the actual requirements, reduced by the metabolically inexpensive storage and release of elastic energy by tendons and ligaments. This difference originates from the combination of acceleration (W_{ext}^{+}) and braking (W_{ext}^{-}) effects on the body centre of mass and the different efficiencies associated with the different work they perform, as also happens in gradient walking (Minetti *et al.* 1993).

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