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The optimal locomotion on gradients: walking, running or cycling?

Accepted: 7 May 2003 / Published online: 25 July 2003
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Abstract On level ground, cycling is more economical than running, which in turn is more economical than walking in the high speed range. This paper investigates whether this ranking still holds when moving on a gradient, where the three modes are expected to be mainly facing the same burden, i.e. to counter gravity. By using data from the literature we have built a theoretical framework to predict the optimal mode as a function of the gradient. Cycling was found to be the mode of choice only below 10–15% gradient, while above it walking was the least expensive locomotion type. Seven amateur bikers were then asked to walk, run and ride on a treadmill at different gradients. The speed was set so as to maintain almost constant the metabolic demand across the different gradients. The results indicate that the “critical slope”, i.e. the one above which walking is less expensive than cycling (and running), is about 13–15%. One subject was loaded during bipedal gaits with a bicycle-equivalent mass, to simulate to cross-country cycling situation. The critical slope was close to 20%, due to the higher metabolic cost of loaded walking and running. Part of the findings can be explained by the mechanically different paradigms of the three locomotion types.

Keywords Cycling · Economy · Gradient · Running · Walking

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Introduction

It is common knowledge that bicycling (B) is the most economical human-powered locomotion on level ground. When compared to walking (W) and to running (R), the metabolic cost (C , energy per unit distance) of cycling is remarkably lower. In fact, while C_W is minimum ($2 \text{ J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$) at a speed (v) of about $1.3 \text{ m}\cdot\text{s}^{-1}$, and R is more economical ($C_R = 4 \text{ J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ for all speeds) than W when v exceeds $2.5 \text{ m}\cdot\text{s}^{-1}$, C_B is only a fraction of them (about $0.5 \text{ J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ for speeds within the walk/jogging range).

While the search for the most economical progression mode (at the highest possible speed) ranks B, then R and finally W on a level surface (and this is also true for downhill locomotion), little is known about how they compare when moving on a positive slope. Such knowledge would be relevant, not just to shed light on the mechanics and energetics of the different modes, but also in those conditions, such as cross-country bicycling, where athletes and leisure riders need to decide whether to keep on pedalling, to walk or to run, according to the change in the terrain condition and incline. In fact, if the ability to choose W or R at a given speed is expected to be supported by a well-evolved network of inputs, this would not apply to comparing them to B, a relatively new locomotion mode for humans.

It is intuitive that for shallow uphill slopes the advantage in C_B (about 18% of level C_R at a speed of $4 \text{ m}\cdot\text{s}^{-1}$) will still hold, but there could be a steeper threshold slope (or slope/speed combination) above which W and/or R are less metabolically expensive than B. Cross-country cyclists dismount their bicycle at steep inclines and keep on moving while carrying it on their shoulders, but their choice is likely to be further affected by the tyres' grip on the terrain. Thus their “critical slope” would not entirely reflect the differences in the mechanical paradigm only among W, R and B.

When walking and running on a level surface we raise/lower and accelerate/decelerate the body's centre

of mass cyclically during the stride. This is related to the positive/negative work that constitutes the so-called mechanical external work. On level ground, the amount of positive work is equal and opposite to the amount of negative work, resulting in apparently no work being done. Since muscles consume metabolic energy for both positive and negative work (positive being 5 times more expensive than negative), the only way to save energy is to reduce the vertical excursion and the acceleration of the body's centre of mass at each stride. While W and R rely on very effective strategies devoted to achieving that goal – the former by exchanging potential and kinetic energy as in a pendulum, the latter by storing/retrieving the combined potential and kinetic energy into/from tendon elastic structures as in a pogo-stick – some residual positive work in the two gaits must be performed at the expense of metabolic energy, thus leading to quite a high value of C . It is relatively intuitive, though, that the invention of bicycles greatly reduced the required metabolic energy: (1) by minimizing the vertical excursion of the body's centre of mass, most of which is suspended by the saddle, (2) by reducing the speed oscillations because of the wheels, and (3) by allowing muscles to operate in the efficient range of the contraction velocity, because of gears, despite of the high progression speed (di Prampero 2000; Minetti et al. 2001).

Such a radical difference in the mechanical paradigm among W , R , and B is going to vanish at a gradient greater than 15%, since, as suggested by Margaria (1938), the “useless” negative work of W and R have been shown (Minetti et al. 1993, 1994a) to be negligible in that condition. Certainly the three modes retain their individuality, at least as far as the internal work [the work necessary to accelerate limbs with respect to the body's centre of mass (Fenn 1930a, 1930b)] is concerned, but for all of them the most crucial burden is the work against gravity, measurable as the increase in potential energy. In addition, since for the same metabolic power the progression speed is expected to decrease at steep slopes, balance problems are going to occur and cycling effectiveness could be impaired. For the above reasons, we can hypothesize that a change in the ranking of W , R and B in terms of economy could occur at steep gradients, possibly favouring legged locomotion to cycling.

The aim of this study was to elucidate the effect of the locomotor paradigm of W , R and B on the progression economy at increasing gradients in order to assess the critical slope, i.e. the slope above which B is no longer more economic than W and/or R , at the same speed.

Firstly we used a simulation scheme where metabolic/mechanical data from the literature allowed us to predict the critical slope, then we measured in the laboratory C_W , C_R and C_B at different gradients and speeds to verify both the rationale and the obtained predictions.

Methods

Predictive model

For each locomotor mode we need to represent three variables: the metabolic cost ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$), as a function of the progression speed (v , $\text{m}\cdot\text{s}^{-1}$) and of the gradient (i , expressed as the ratio between the vertical and the horizontal displacement corresponding to a given slope). All the following 3D graphs were obtained by using a mathematical software package (Mathematica 3.0, Wolfram Research, USA).

For walking we used Rodolfo Margaria's data (1938) because it remains the most extensive collection of speed/gradient pairs at which the metabolic costs have been measured. To try to summarize all his data in just one equation, we inspected his graph and noticed that for each gradient a parabolic profile (cost vs. speed) should fit the data. Having done that, we observed that the three regression coefficients so obtained were a function of the gradient, and we further noticed that an exponential function would properly describe two of those relationships, while a parabolic profile was preferable for the third one. Thus, we obtained:

$$C_W = 1.866av^2 - 3.773bv + c + 4.456 \quad (1)$$

where $a = e^{4.911i}$, $b = e^{3.416i}$ and $c = 45.72i^2 + 18.90i$. Figure 1a shows Eq. 1, with the two horizontal axes representing speed and gradient (uphill and downhill).

From the same paper, we obtained the equation for the cost of running as:

$$C_R = 62.05i^2 + 17.08i + 3.806 \quad (2)$$

which is simpler than Eq. 1 because C_R is speed independent, depending just on gradient (see Fig. 1b).

For cycling we rearranged a mechanically derived equation from di Prampero (1986, 2000), as:

$$C_B = \frac{0.17(m+9)\text{Cos}[\text{ArcTan}(i)] + 0.43s_B v^2 + 39.2(m+9)\text{Sin}[\text{ArcTan}(i)]}{m} \quad (3)$$

where m is the body mass (kg), s_B is the frontal area (m^2) and 9 refers to the bicycle mass (kg). The three terms in the numerator refer to the rolling resistance, the aerodynamic drag and the potential work done to raise the rider + bicycle mass on the incline, respectively. To allow comparison with Eqs. 1 and 2 (expressed per kg of m), C_B was also expressed per kg of body mass only. By considering that air resistance will not be a burden at the slow speeds expected on slopes, and in an attempt to further simplify it, Eq. 3 can be written as:

$$C_B = (1 + m_B^{\text{fract}})\{0.17\text{Cos}[\text{ArcTan}(i)] + 39.2\text{Sin}[\text{ArcTan}(i)]\} \quad (4)$$

where m_B^{fract} is the fractional mass of the bicycle, with respect to m (0.13 in this paper). In both Eqs. 3 and 4 the importance of the potential energy term, progressively depending on gradient, and the negligence of the rolling resistance are apparent, because of a far smaller coefficient and the inverse relationship with gradient.

Figure 1c represents C_B , with null values for downhill gradients because riders can use their brakes to move downhill at a constant speed and at no metabolic cost (this is strictly true only for downhill slopes steeper than the “rolling resistance equivalent slope”, a very shallow gradient at which the negative potential energy changes balance the work necessary to overcome the rolling resistance).

The minimum cost can be obtained by combining Eqs. 1, 2 and 4 as:

$$C_{\text{OPT}} = \text{Min}[C_W, C_R, C_B] \quad (5)$$

which graphically corresponds to superimposing the surfaces from Fig. 1a, b and c in a single frame of reference and taking, for each

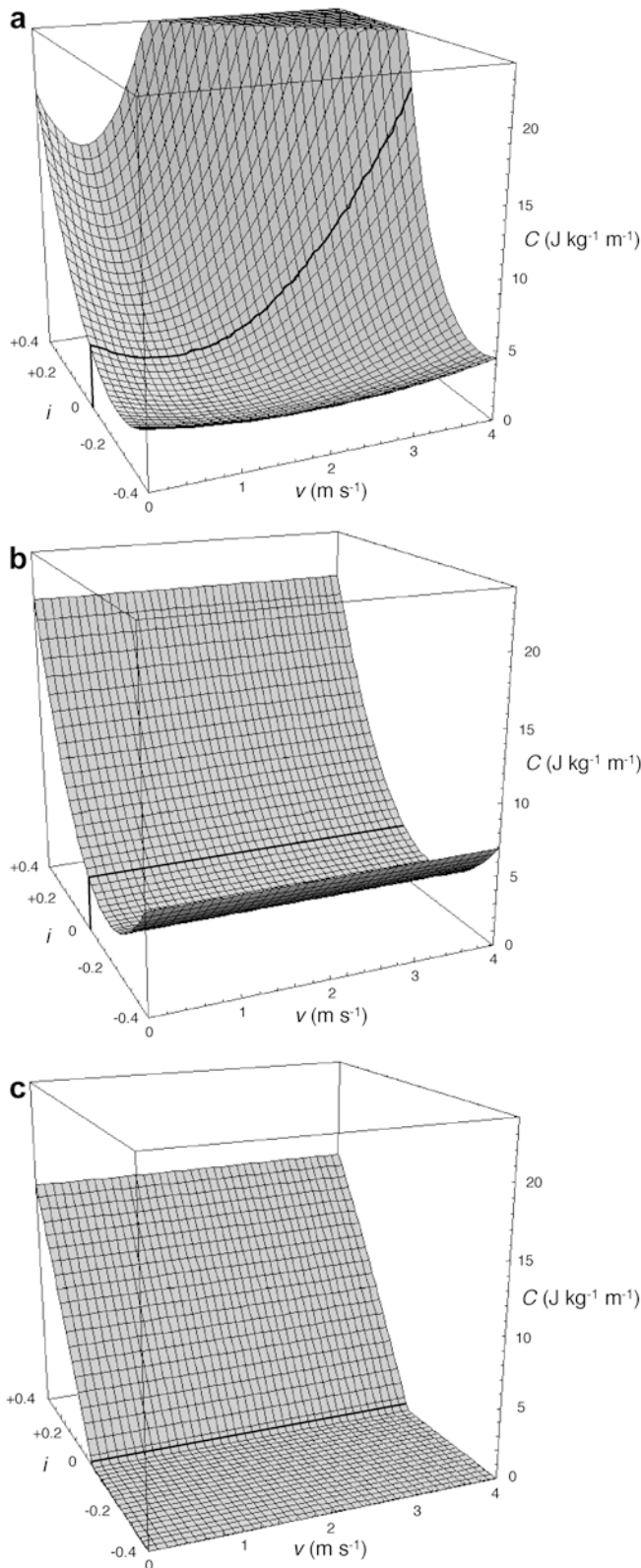


Fig. 1a–c Equations 1 (a for walking, *W*), 2 (b for running, *R*) and 3 (c for cycling, *B*) are shown. The *black curve* superimposed on the surfaces sets the relationship between metabolic cost and the progression speed at zero gradient, thus partitioning the surface into the uphill and downhill portions

speed/incline pairs (v, i), the locomotor mode with the lowest metabolic cost. Figure 2a shows an intermediate step, namely $\text{Min}[C_w, C_r]$, to display the metabolically optimum walk/run transition speed at all gradients, while Fig. 2b actually represents Eq. 5.

When representing the metabolic cost surfaces, as in the previous figures, it should be realized that only a subset of the (v, i) pairs can be regarded as metabolically feasible in the aerobic range, depending on the (available fraction of the) maximum aerobic power of the subject ($\dot{E}_{\text{MAX}}, \text{W}\cdot\text{kg}^{-1}$). Actually, only C_{OPT} values for which the metabolic work rate is less than \dot{E}_{MAX} should be meaningfully displayed.

The minimum \dot{E} associated with each (v, i) pair can be calculated as the ratio between the mechanical power ($\dot{W}_{\text{max}}, \text{W}$) necessary to just raise or lower the body's centre of mass (thus common to *W*, *R*, and *C*) and the efficiency as:

$$\dot{E}^+ = \frac{m v g \text{Sin}[\text{ArcTan}(i)]}{\text{eff}^+} \quad (6)$$

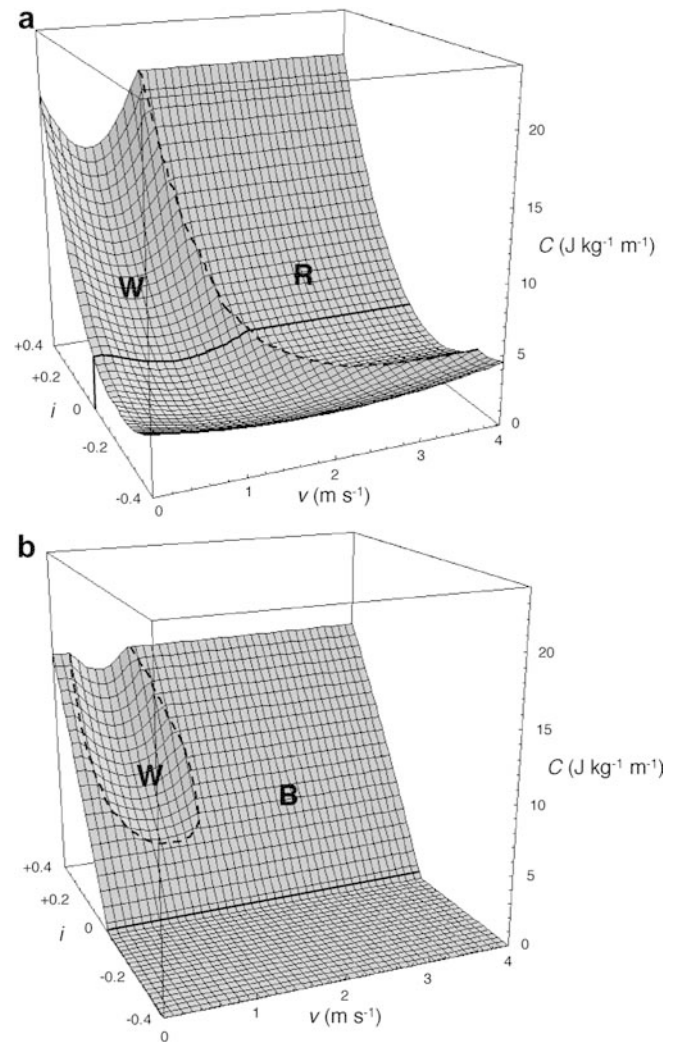


Fig. 2a, b For each (v, i) pair, surfaces represent the minimum cost of the different locomotion modes. **a** The metabolic minimum, between *W* and *R*, where the *black interrupted curve* sets the boundary between the two gaits. **b** Equation 5, namely the least expensive mode among *W*, *R* and *B* as a function of speed and gradient. Here the *loop* marked by the *black interrupted curves* contains just *W* values, while *B* is the optimal mode outside of it

and

$$\dot{E}^- = \frac{m v g \sin[\text{ArcTan}(i)]}{\text{eff}^-} \quad (7)$$

where g is acceleration due to acceleration ($9.81 \text{ m}\cdot\text{s}^{-2}$), and eff^+ and eff^- are the efficiencies of positive and negative mechanical work, respectively (0.25 and -1.25 , Margaria 1938; Abbott et al. 1952). To fulfill the “feasibility constraint”, we need to consider only C_{OPT} values whose (v, i) pair is such that $\dot{E} \leq \dot{E}_{\text{MAX}}$, where

$$\dot{E} \begin{cases} \dot{E}^+ & \text{if } i \geq 0 \\ \dot{E}^- & \text{if } i < 0 \end{cases} \quad (8)$$

In the simulation \dot{E}_{MAX} has been set to 700 W (thus corresponding to a positive mechanical power \dot{W}_{max} of 175 W) and m to 70 kg. Figure 3 shows Eq. 5 submitted to the “feasibility” constraint of Eq. 6 (no need to constrain according to Eq. 7 too, because C_{OPT} is already zero in the downhill portion of the graph since in this part C_{OPT} coincides with C_B). Graphically, it corresponds to Fig. 2b after removal of the unfeasible part of the surface.

Measurements

We measured and compared C_W , C_R and C_B at different positive slopes (range 5.0–30.0% step 2.5%) on seven amateur bikers [five males, age: 30.8 (9.1) years; body mass: 66.1 (8.6) kg; mean (SD), and two females 27–28 years; 63–64 kg].

Each subject walked, ran and rode (freely choosing their gear and related pedalling cadence) in different sessions on a motorized treadmill (Woodway ERGO-LG2, Germany). For each slope, speeds were chosen so as to reflect the same rate of work against gravity, i.e. the part of the total mechanical work rate that needs to be done irrespective of the gait type. This strategy, devoted to reduce the sample space to a manageable size and to keep the metabolic expenditure within a narrow range, yielded the progression speed, for a given gradient i , as

$$v = \frac{\dot{W}_{\text{max}}}{m g \sin[\text{ArcTan}(i)]} \quad (9)$$

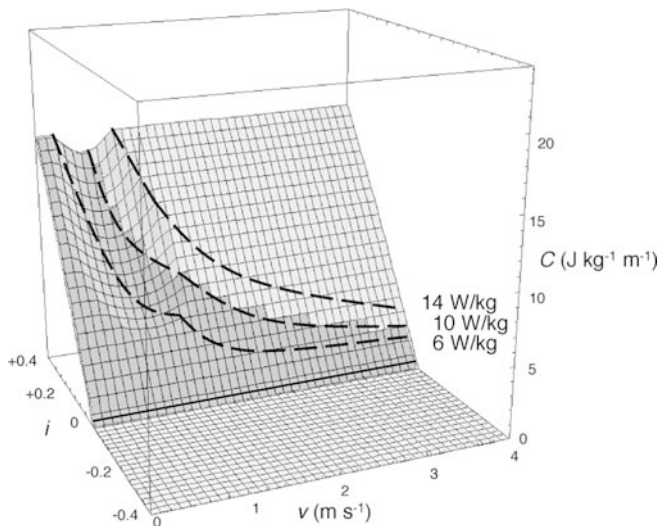


Fig. 3 The same surface of Fig. 2b is here represented, but only the metabolically feasible (v, i) zone is coloured (for a maximum aerobic power $\leq 10 \text{ W/kg}$). This surface corresponds to Eq. 5 submitted to the constraints of Eqs. 6, 7 and 8. The other two interrupted curves represent boundaries for 6 and 14 W/kg

for W and R (WP1 and RP1) and as

$$v = \frac{\dot{W}_{\text{max}}}{(m + 9) g \sin[\text{ArcTan}(i)]} \quad (10)$$

for B (BP2).

In other words, Eqs. 9 and 10 were used to select, at each gradient i for the three locomotion modes, the progression speeds that would cause muscles to deal with the same increment in potential energy per unit time (i.e. the minimum potential work rate for the gradient i). All the subjects were also asked to ride at the speed set by Eq. 9 (BP1, to compare W, R and B at the same speed), while one of them walked (WP2) and ran (RP2) with an added mass, located around the waist, corresponding to the bicycle mass.

\dot{E} (and consequently \dot{W}_{max}) was chosen for each subject so as to reflect about 85% [85.7 (5.3)%] of the predicted maximal heart rate (HR) (obtained while running on a 15% incline). \dot{E} was equal to 550 W for the two females and 700 and 850 W for three and two males, respectively.

No subject was able to adopt the three locomotion modes at all slopes (at shallow ones, the calculated W and R speeds far exceeded the achievable ones; at the steepest slopes, the speed reduction impaired B progression, for balancing problems, and sometimes also R).

Heart rate (Polar Sportester, Finland) and oxygen consumption ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$, V_{max} , SensorMedics, USA) were measured during the last minute of each 5-min trial. Net heart rate (nHR) has been calculated as the difference compared to the value recorded at rest. The metabolic cost was obtained by subtracting the basal oxygen consumption from that obtained at steady-state exercise and by dividing the result by the speed. The results were expressed firstly in $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$ by assuming 1 ml O_2 equal to 20.9 J (which is strictly true for a respiratory quotient of 0.95), then the cost was expressed per vertical metre travelled ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}_{\text{vert}}^{-1}$) by dividing it by $\sin[\text{ArcTan}(i)]$.

The statistical difference was evaluated by using a paired t -test only for the gradients where at least four subjects performed the two least expensive locomotion modes.

Results

Predictions from the comparison of literature data of energy cost, when limited to the aerobically feasible (v, i) pairs, show that B ceases to be the locomotor mode of choice at a gradient of about 10–15%, above which W is more economical both than R and B (see Fig. 3).

The average speeds, at each gradient, used in each protocol are displayed in Fig. 4, while Fig. 5 shows the comparison among experimental results. WP1, RP1 and BP1 are compared in the left-hand-side panel of Fig. 5, while WP1, RP1, BP2 and WP2, RP2, BP2 are compared in the centre and right-hand-side panels, respectively. In all comparisons it is apparent that, when choosing among the three locomotion modes, B is more economical than W and R below a given uphill slope, above which W becomes preferable. The critical slope is about 13–16% in the first two comparisons, while it is closer to about 20% for WP2, RP2 and BP2.

A similar trend was found in nHR measurements, with critical slopes slightly higher than illustrated above.

Discussion

The technique of superimposing in a single graph the different cost surfaces of each locomotion modes and of

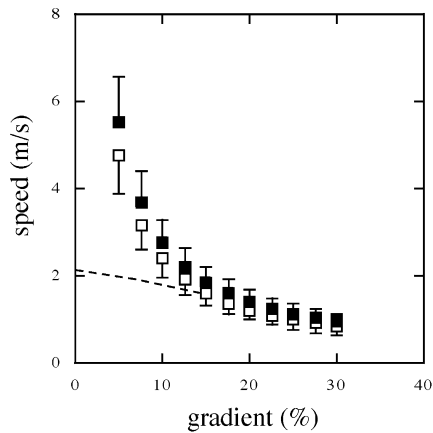
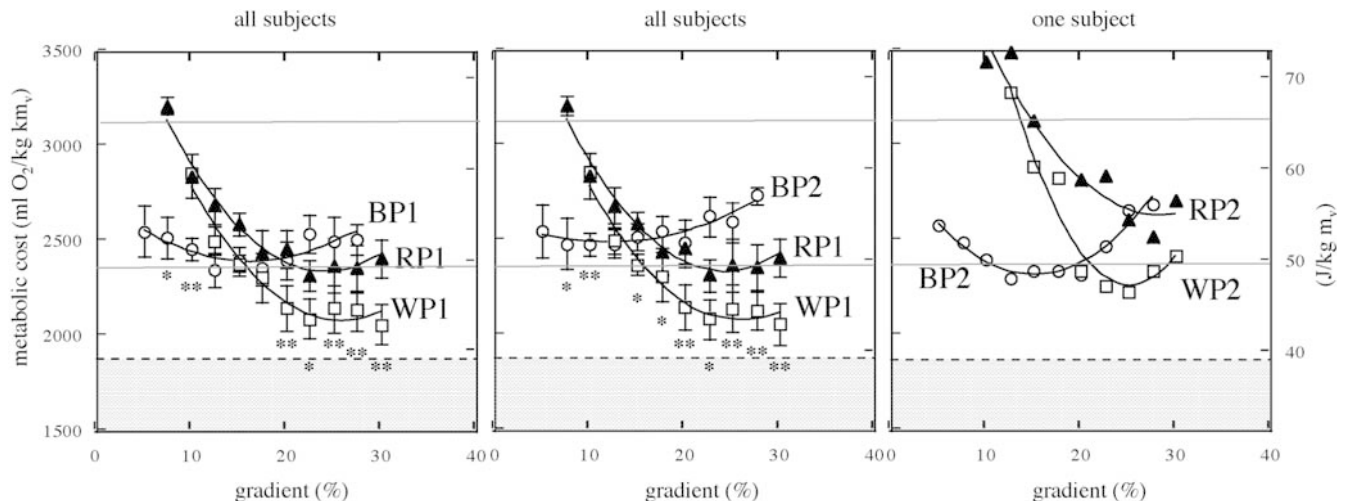


Fig. 4 Average treadmill speeds imposed at the different gradients and conditions according to the iso-mechanical power necessary to counter gravity. *Vertical bars* represent standard deviations. *Closed squares* refer to all the first protocols WP1, RP1 and BP1, while *open squares* represent the second ones, i.e. WP2, RP2 and BP2. The *dashed curve* indicates the metabolic transition speed between W and R as previously investigated (Minetti et al. 1994b)

taking the lowest value allowed us to identify the least expensive one for every (v, i) pair. As a side result of this mathematical procedure, the metabolically optimal

Fig. 5 The experimental metabolic cost, for vertical distance travelled, is plotted as a function of the gradient. The *left-hand-side panel* shows the comparison between WP1 (*open squares*), RP1 (*closed triangles*) and BP1 (*open circles*), the *middle panel* contains data regarding WP1, RP1 and BP2, while the *right panel* contains the data for WP2, RP2 and BP2 (same symbols). *Vertical bars* represent standard errors, for the sake of graphical convenience, and the *asterisks* indicate a statistical significant difference ($*p < 0.05$, $**p < 0.01$) between the two least expensive locomotion modes at the gradients where at least four subjects were able to perform them. Each data series has been fitted by a second-order polynomial curve. The *dashed horizontal line* represents the metabolic cost of pure work against gravity, i.e. the mechanical work necessary to increase the body's potential energy, assuming an efficiency for positive work equal to 0.25. That line constitutes the minimum metabolic requirement of gradient locomotion (thus no experimental point is expected to fall in the *grey area* below it). The *middle and upper horizontal lines* reflect the vertical metabolic cost for lower efficiencies of the potential work: 0.20 and 0.15, respectively



transition speed between W and R turned out to be a decreasing function of the incline, as apparent in Fig. 2a. This confirms the experimental data of a previous study about bipedal gait transition on slopes (Minetti et al. 1994b).

While there is some heterogeneity in the equations used in the comparison (C_W and C_R are regressions on experimental data and C_B is a mechanical model equation converted into metabolic cost according to constant $\text{eff}^+ = 0.25$), the final graph (Fig. 3) provides preliminary indications about the critical gradient. When all three modes of locomotion are compared, only W and B survive the competition for the most economical progression type on the incline (see Fig. 2b). The prediction of B being preferable to W at low-middle steepness is generally confirmed by the experimental data (Fig. 5).

The cost units for the experimental data are expressed “per vertical kilometer or metre”, in analogy to other previous papers (Minetti 1995; Minetti et al 2002). This was done to allow better comparisons between locomotion modes but also to identify their dependence on constraints other than the need to counter gravity (which is obviously the common feature of them all). If a hypothetical mode of progression requires metabolic energy just to counter gravity, the vertical cost is expected to be gradient independent (and equal to g/eff^+ , the horizontal dashed line in Fig. 5), unless two or more reciprocally increasing and decreasing components of the metabolic cost cancel out in the sum.

While the data shown in Fig. 5 refer to three different comparisons, the results are substantially similar. The vertical cost of B is almost constant in the left and middle panel (only three out of nine comparisons were statistically different). When the choice is between W and R only, R is not preferable, with the exception of the shallowest investigated gradient for walking, where the two costs are quite similar. This is expected because at steep slopes the chosen speed is low and typical for a walking gait (at which running is much more expensive

than walking). At low gradients the speed increases to values close to or above the speed at which running becomes more economical than walking (see Fig. 4), thus favouring running.

When all the three locomotion modes are compared, the critical slope does not seem to be affected by the difference between the first two protocols. Both the “iso vertical mechanical power” and the “iso progression speed” showed that above 13–16% slope W is more economic than B. The choice of investigating the speeds corresponding to a given level of the maximum aerobic power certainly influenced the value of the critical slope. While different speeds could not have changed the results obtained for R (because of the speed-independency of running), the shape of the curves for W and possibly for B would have been affected. Such metabolic power was chosen according to the demand often found in mountain bike competitions (Impellizzeri 2002). As already stated, only one metabolic level was investigated to keep the sample size of experiments within a manageable limit. However, since the theoretical approach shows similar qualitative results when other metabolic levels are considered (see Fig. 3), we expect that the take-home message would still hold in other conditions, with a shift of the critical slope towards slightly higher values for increased metabolic power imposed.

In the simulation regarding cross-country cycling (right-hand panel in Fig. 5), where the subject was loaded with a bicycle-equivalent mass during W and R at the same speeds, the critical slope moved to about 20%. This seems to be caused by an increase in the vertical cost of W (and of R), at their minimum values, of about 10%. Such an increase, expected on the basis of the literature on loaded locomotion (Ardigò et al. 1997), ruled out R even more than in the other simulations and moved the intersection between B and W to the right of the graph.

The mechanical interpretation of the illustrated results is partially supported by previously obtained knowledge on gradient locomotion.

W and R are known to require at gradients steeper than +15% only the positive external work corresponding to the increase in potential energy at each stride (Minetti et al. 1993, 1994a). There is no surprise, then, that their vertical cost decreases at increasing gradient and that they get closer to the line of “pure potential work”. The only other component of the total mechanical work, namely the “internal” work necessary to accelerate limbs with respect to the body’s centre of mass, would account for the unexplained difference. In the “cross-country cycling” simulation, the increased discrepancy between the vertical cost of W and R and the line of “pure potential work” could be explained by an additional metabolic cost of producing a greater vertical force, required because of the added mass, which does not necessarily generate any extra mechanical work. The issue of simultaneously taking into account the costs of producing force and of

generating work during locomotion has been recently addressed by Alexander (2002).

In B the mechanical interpretation of the results is more difficult. While the metabolic costs of W and R obtained in this study closely resemble previous findings (Margaria 1938; Margaria et al. 1963; Minetti 1995; Minetti et al. 1993, 1994a, 2002), no paper has published the measured cost of cycling as a function of the gradient, thus no check can be done. The quasi-constancy of the vertical cost of B suggests that most of the work is done against gravity, but the distance from the line of “pure potential power” is quite remarkable and the curvi-linearity is reflecting other determinants of the cost. The other components of the total mechanical work in cycling, namely the air drag, the rolling resistance and the internal work, are not thought to fully account for the high metabolic cost. The first is nil on the treadmill, the second is expected to be very low, though the rolling resistance of rubber tyres on a rubber surface is certainly much higher than normal. Regarding internal work, whose existence in cycling is still a matter of debate in the scientific community, its influence is thought to be small (Minetti et al. 2001) because of the rather low pedalling frequency (despite of the use of gears). Only other two potential reasons can be claimed to explain the relatively high vertical cost of gradient cycling: (1) a lower transmission efficiency than W and R, as caused, for instance, by an impaired push on the pedals on steep gradients, and/or (2) a notable increase in co-contractions of postural muscles, necessary to stabilize and control the bicycle while riding on a narrow and short treadmill at slow speeds. To account for the first effect, more definitive opinions in the literature are needed about the mechanical internal work, while the balance is an additional burden (to a lesser extent, though) on inclined firm ground as well. These aspects related to the high vertical cost of gradient B will remain unaddressed until other studies measure the steady-state metabolic demand of cycling at constant speeds on uniformly steep roads.

While waiting for a future check, Fig. 5 seems to suggest that a smaller vertical cost of B (within a reasonable range) should not drastically change the conclusions obtained from the present data.

We conclude that the critical slope, i.e. the slope above which B is more metabolically expensive than W and R, is partially explainable on the basis of the different mechanics of the three progression modes considered. Being supported by the predictions made available by comparing literature data and model equations, the critical slope was found to be close to 13–16% and to 20%, depending on the loading of a bicycle-equivalent added mass when using bipedal gaits on the slope.

Acknowledgements Dr Pietro Mariano Casali is kindly thanked, for having enthusiastically supported the study. We declare that the experiments comply with the current Italian laws.

References

- Abbott BC, Bigland B, Ritchie JM (1952) The physiological cost of negative work. *J Physiol (Lond)* 117:380–390
- Alexander RMcN (2002) Work or force minimization as a criterion for the evolution of locomotion. *World Congress of Biomechanics*, Calgary
- Ardigò LP, Minetti AE, Saibene F (1997) The mechanics and energetics of loaded locomotion. Abstract XXXIII, Congress IUPS, St. Petersburg, P042.07
- di Prampero PE (1986) The energy cost of human locomotion on land and in water. *Int J Sports Med* 7:55–72
- di Prampero PE (2000) Cycling on earth, in space, on the moon. *Eur J Appl Physiol* 82:345–360
- Fenn WO (1930a) Frictional and kinetic factors in the work of sprint running. *Am J Physiol* 92:583–611
- Fenn WO (1930b) Work against gravity and work due to velocity changes in running. *Am J Physiol* 93:433–462
- Impellizzeri F, Sassi A, Rodriguez-Alonso M, Mogno P, Marcora S (2002) Exercise intensity during off-road cycling competitions. *Med Sci Sports Exerc* 34:1808–1813
- Margaria R (1938) Sulla fisiologia e specialmente sul consumo energetico della marcia e della corsa a varia velocità ed inclinazione del terreno. *Atti Accad Nazional Lincei* 7:299–368
- Margaria R, Cerretelli P, Aghemo P, Sassi G (1963) Energy cost of running. *J Appl Physiol* 18:367–370
- Minetti AE (1995) Optimum gradient of mountain paths. *J Appl Physiol* 79:1698–1703
- Minetti AE, Ardigò LP, Saibene F (1993) Mechanical determinants of gradient walking energetics in man. *J Physiol (Lond)* 471:725–735
- Minetti AE, Ardigò LP, Saibene F (1994a) Mechanical determinants of the minimum energy cost of gradient running in humans. *J Exp Biol* 195:211–225
- Minetti AE, Ardigò LP, Saibene F (1994b) The transition between walking and running in humans: metabolic and mechanical aspects at different gradients. *Acta Physiol Scand* 150:315–323
- Minetti AE, Pinkerton J, Zamparo P (2001) From bipedalism to bicyclism: evolution in energetics and biomechanics of historic bicycles. *Proc R Soc Lond B* 268:1351–1360
- Minetti AE, Moia C, Roi GS, Susta D, Ferretti G (2002) Energy cost of walking and running at extreme uphill and downhill slopes. *J Appl Physiol* 93:1039–1046