J Appl Physiol 120: 370–375, 2016.
First published November 25, 2015; doi:10.1152/japplphysiol.00546.2015.

Energetics of vertical kilometer foot races; is steeper cheaper?

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Submitted 29 June 2015; accepted in final form 22 November 2015

Giovanelli N, Ortiz AL, Henninger K, Kram R. Energetics of vertical kilometer foot races; is steeper cheaper? *J Appl Physiol* 120: 370–375, 2016. First published November 25, 2015; doi:10.1152/japplphysiol.00546.2015.—Vertical kilometer foot races consist of a 1,000-m elevation gain in <5,000 m of overall distance, and the inclines of the fastest courses are ~30°. Previous uphill locomotion studies have focused on much shallower angles. We aimed to quantify the metabolic costs of walking and running on very steep angles and to biomechanically distinguish walking from running. Fifteen runners (10 male, 5 female, 32.9 ± 7.5 yr, 1.75 ± 0.09 m, 64.3 ± 9.1 kg) walked and ran for 5 min at seven different angles (9.4, 15.8, 20.4, 24.8, 30.0, 35.0, and 39.2°) all at a fixed vertical velocity (0.35 m/s). We measured the metabolic rates and calculated the vertical costs of walking (Cw_{vert}) and running (Cr_{vert}). Using video analysis, we determined stride frequency, stride length, and duty factor (fraction of stride that each foot is in ground contact). At all angles other than 9.4°, Cw_{vert} was cheaper than Cr_{vert} (average −8.45 ± 1.05%; $P < 0.001$). Further, broad minima for both Cw_{vert} and Cr_{vert} existed between 20.4 and 35.0° (average Cw_{vert} 44.17 ± 0.41 $J \cdot kg^{-1} \cdot m^{-1}$ and average Cr_{vert} 48.46 ± 0.35 $J \cdot kg^{-1} \cdot m^{-1}$). At all angles and speeds tested, both walking and running involved having at least one foot on the ground at all times. However, in walking, stride frequency and stride length were ~28% slower and longer, respectively, than in running. In conclusion, we found that there is a range of angles for which energy expenditure is minimized. At the vertical velocity tested, on inclines steeper than 15.8°, athletes can reduce their energy expenditure by walking rather than running.

walking; running; uphill; cost of transport

IN VERTICAL KILOMETER FOOT races (VK), athletes complete a course with 1,000-m vertical elevation increase in <5,000 m of total race length (International Skyrunning Federation rules: http://www.skyrunning.com). Terrain, slope, and length vary between racecourses. To date, the world record for men in the VK is 29 min and 42 s, set on a course with a length of 1,920 m, an average inclination of 31.4° (Km Vertical de Fully, Switzerland). That equates to an average vertical velocity of ~0.56 m/s and an average velocity parallel to the ground of 1.08 m/s. A VK course with only a slight incline would require an unreasonably fast parallel velocity. For instance, a racecourse with an incline of only 1° would require the impossible running speed of 31.84 m/s to rise 1,000 m in 30 min. Conversely, a course with a gradient of 40° would require a speed of only 0.87 m/s to gain 1,000 m in 30 min. However, if the course is too steep, the rock-climbing techniques required would likely be slower than walking/running at more moderate slopes. Analysis of the best performances in different VK races suggests that there may be an optimal angle for achieving the best time (Fig. 1). Since there are no VK races with an average incline steeper than 31.4° (Km Vertical de Fully), it is unknown if the optimal gradient is actually steeper.

Another factor to consider is that in VK races, some athletes walk, some run, and some alternate gaits. It is not clear which gait or combination is optimal. On level ground or treadmills, at matched speeds slower than ~2.0 m/s, walking requires less metabolic energy than running (3, 15, 17, 25). This is generally attributed to the more effective inverted pendulum-like exchange of mechanical energy at slower walking speeds and the superior elastic energy storage and recovery of running at faster speeds (6). However, on uphill grades both of those mechanisms are disabled (8, 24). On the level (17) as well as moderate inclines and declines (18, 19), the preferred walk-run transition speed occurs near but not exactly at the metabolically optimal transition speed. As speed is increased, people typically first adopt a running gait at a speed slightly slower than the metabolic crossover point.

The metabolic cost of uphill walking and running has long been of interest to exercise physiologists (3, 14, 15, 18), but almost all studies have examined uphill walking or running on angles <9°. One highly relevant exception is the innovative study by Minetti et al. (21). They measured the metabolic cost ($J \cdot kg^{-1} \cdot m^{-1}$) of walking (Cw) and running (Cr) on a range of slopes up to 24.2°. Note, for Cw and Cr, the calculated distance is parallel to the surface or treadmill. They concluded that at a given treadmill belt speed, Cw and Cr are directly proportional to the slope above +15% (8.5°) and that Cw and Cr converge at steeper angles. Minetti et al. (21) also defined the vertical costs of walking (Cw_{vert}) and running (Cr_{vert}), as the energy expended to ascend one meter vertically. Cw_{vert} and Cr_{vert} both decreased at steeper angles reaching minimum values at slopes ranging from 20% (11.3°) to 40% (21.8°). However, we are reluctant to extrapolate from the data of Minetti et al. to the steeper slopes at which VK races are often contested. Furthermore, VK competitors often alternate between walking and running at the same speed, and Minetti et al. did not directly compare the energetics of the two gaits at matched speeds. Finally, it is not clear if the traditional biomechanical distinction between walking and running on level ground (i.e., in running, the center of mass trajectory reaches its lowest point at mid-stance and there is an aerial phase when no feet are in contact with the ground) applies on very steep slopes. Previous investigators have used the terms "Groucho running" (16) and "grounded running" (23) to describe a bouncing gait that does not involve an aerial phase.

To the best of our knowledge, there are no prior scientific studies of human walking or running at the steep angles that are encountered in the fastest VK races. Minetti et al. (20) analyzed stair running races but such "skyscraper races" are much shorter duration than VK (from 50 s to ~14 min

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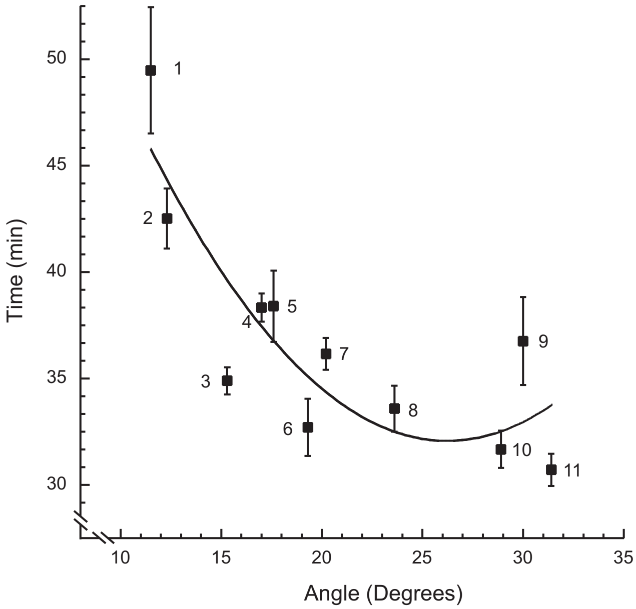

Fig. 1. The average of the 5 best performances for 10 different vertical kilometer (VK) races in the year that the each course record was set. *1*) The Rut VK (USA); *2*) Val Resia VK (I); *3*) Mont Blanc VK (F); *4*) Limone Vertical Extreme (I); *5*) Latemar VK (I); *6*) VK Lagunc (I); *7*) VK face de Bellevarde (F); *8*) Dolomites VK (I); *9*) VK Col de Lana (I); *10*) La Verticale du Grand Serre (F); and *11*) VK de Fully (CH). USA, United States of America; I, Italy; F, France; CH, Switzerland.

compared with ~30 min) and they did not measure the metabolic cost. Intriguingly, Kay's mathematical analysis of uphill mountain running races (12) concluded that if an optimum gradient for ascent exists, it is steeper than the range of gradients studied so far.

The primary purpose of this study was to quantify the metabolic costs of walking and running across a wide range of inclines up to and beyond those used in VK races. We aimed to determine if walking or running is more economical and if there are energetically optimal angles for the two gaits. Specifically, we compared walking and running at a fixed vertical velocity (0.35 m/s) at angles ranging from ~10 to ~40°. Based on the findings of Minetti et al. (21), and because the treadmill belt speeds we studied are <2.0 m/s, we hypothesized that: *1*) walking would require less metabolic energy than running. We further hypothesized that *2*) for both walking and running, there would be distinct intermediate angles (~30°) that minimize the energetic cost of ascending at a fixed vertical velocity.

Our secondary purpose was to distinguish the biomechanics of walking vs. running on steep inclines. We hypothesized that *3*) at steep angles and slow treadmill belt speeds, running would not involve an aerial phase. However, a greater stride frequency during running would distinguish it from walking.

MATERIALS AND METHODS

Subjects. Fifteen healthy, competitive mountain runners (10 males, 5 females, 32.9 ± 7.5 yr, 1.75 ± 0.09 m, 64.3 ± 9.1 kg) volunteered and provided informed consent as per the University of Colorado Institutional Review Board.

Experimental design. We modified a custom treadmill so that it was inclinable from 0 to 45° (Fig. 2). To provide adequate traction, we adhered a wide swath of skateboard grip tape (i.e., sandpaper) to the treadmill belt (Vicious Tape, Vancouver, BC, Canada). To protect the electronic motor controller, we mounted three v-belt pulleys on the treadmill drive roller, hung ropes over the pulleys and attached moderate weights to the ropes (~8 kg). We chose the minimum amount of weight such that when the subject stood on the belt with the motor turned off, the belt did not move. Providing a mechanical resistance to the motor allowed it to produce power and maintain a nearly constant treadmill belt speed.

The study consisted of three sessions. During the first session (familiarization), each athlete walked and ran for 2 to 3 min on the treadmill at 4 angles (9.4, 30.0, 35.0, and 39.2°). During the second and third visits, subjects either walked (e.g., *day 2*) or ran (e.g., *day 3*) for 5 min at seven different angles (9.4, 15.8, 20.4, 24.8, 30.0, 35.0, and 39.2°) and corresponding treadmill belt speeds (2.14, 1.29, 1.00, 0.83, 0.70, 0.61, and 0.55 m/s). Subjects had 5-min rest between trials. Half of the subjects walked on *day 2* and ran on *day 3*; the other half did the opposite. These angle and speed combinations fixed the vertical velocity at 0.35 m/s. We chose this vertical velocity knowing the VK records for men (29:42 = 0.56 m/s vertical velocity) and women (34:44 = 0.48 m/s vertical velocity) and recognizing the need for submaximal intensities so that we could record steady-state metabolic rates. Pilot testing indicated that faster vertical velocities would elicit nonoxidative metabolism. For each subject, we randomized the order of the angles used on both *days 2* and *3*.

Metabolic data. To determine the metabolic rates during walking and running, we used an open-circuit expired gas analysis system (TrueOne 2400; ParvoMedic, Sandy, UT). Subjects wore a mouthpiece and a nose clip allowing us to collect the expired air determine measure the rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$). We averaged the data of the last 2 min of each trial. We then calculated metabolic rate in W/kg using the Brockway equation (2). We only included trials with respiratory exchange ratios (RER) <1.0. We calculated the vertical costs ($J \cdot kg^{-1} \cdot m^{-1}$) of walking ($Cw_{vert}$) and running ($Cr_{vert}$) by dividing the gross metabolic power by the vertical velocity.

Biomechanical parameters. To measure stride parameters, we recorded each trial using a high-speed video camera (Casio EX-FH20) at 210 fps. We extracted contact and stride times for 10 strides using Kinovea 0.8.15 software (www.kinovea.org) and then calculated stride frequency (=1/stride time) and stride length (=velocity/stride frequency). To determine duty factor, we divided contact time for one foot by the total stride period.

Statistical analysis. We analyzed the data using SPSS with significance set at $P \leq 0.05$. We analyzed the vertical cost of walking (Cw_{vert}), vertical cost of running (Cr_{vert}), and biomechanical parameters with a general linear model repeated measures considering two factors (slope and gait: walking vs. running). We followed up with a Bonferroni post hoc test when significant differences were detected. At 9.4° the treadmill belt speed was faster than the walk-run transition speed, thus only nine subjects were able to complete the entire 5-min

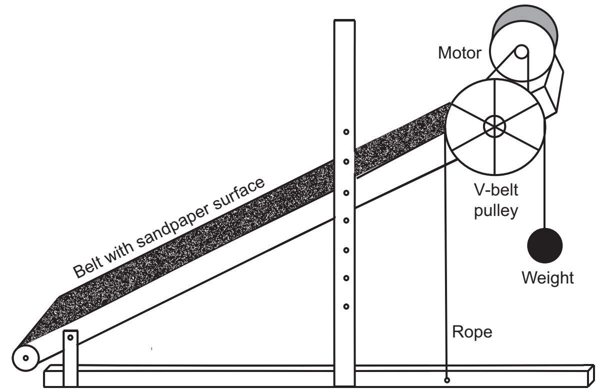

Fig. 2. Customized treadmill mounted at 30°.

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trial using a walking gait. Therefore, when making statistical comparisons of the 9.4° trials, we calculated the variables for just those nine subjects.

RESULTS

Vertical cost of walking vs. running. At 9.4°, the vertical cost of walking (Cw_{vert}) was numerically slightly greater than the vertical cost of running (Cr_{vert}) but they were not statistically different (n = 9; +1.54%; P = 0.545). However, Cw_{vert} was significantly less than Cr_{vert} at 15.8° (−6.35%; P = 0.001), 20.4° (−8.45%; P = 0.001), 24.8° (−8.73%; P = 0.001), 30.0° (−9.23%; P = 0.001), 35.0° (−8.99%; P = 0.001), and 39.2° (−8.93%; P = 0.001; Table 1).

Cw_{vert} was numerically least at 30° (43.86 ± 2.02 $J \cdot kg^{-1} \cdot m^{-1}$) but was not statistically distinguishable from 20.4° (44.23 ± 1.69 $J \cdot kg^{-1} \cdot m^{-1}$), 24.8° (44.10 ± 2.10 $J \cdot kg^{-1} \cdot m^{-1}$), or 35.0° (44.57 ± 2.14 $J \cdot kg^{-1} \cdot m^{-1}$) (Table 1 and Fig. 3). Cw_{vert} at 15.8° was less than Cw_{vert} at 9.4° (n = 9; −18.2%; P = 0.001). Furthermore, Cw_{vert} at 20.4°, 24.8, 30.0, and 35.0° was less than Cw_{vert} at 15.8° (average −5.47%; P < 0.001). Additionally, Cw_{vert} at 39.2° was significantly greater than Cw_{vert} at 20.4, 24.8, 30.0, and 35.0° (average +4.31%; P < 0.001).

Cr_{vert} was numerically least at 24.8° (48.22 ± 2.57 $J \cdot kg^{-1} \cdot m^{-1}$) but was not statistically distinguishable from at 20.4° (48.31 ± 2.54 $J \cdot kg^{-1} \cdot m^{-1}$), 30.0° (48.32 ± 3.07 $J \cdot kg^{-1} \cdot m^{-1}$), or 35.0° (48.97 ± 3.01 $J \cdot kg^{-1} \cdot m^{-1}$; Table 1 and Fig. 3). Cr_{vert} at 15.8° was less than Cr_{vert} at 9.4° (−7.88%; P = 0.001). As was true for walking, Cr_{vert} at 20.4, 24.8, 30.0, and 35.0° was less than Cr_{vert} at 15.8° (average −2.90%; P < 0.001). Finally, Cr_{vert} at 39.2° was greater than Cr_{vert} at 20.4, 24.8, 30.0, and 35.0° (average +4.42%; P < 0.001).

Biomechanical parameters. Walking stride frequency was slower than running stride frequency at every incline (average −27.99% ± 7.75%; P < 0.001; Fig. 4*A*). Thus walking stride length was longer than running stride length at every incline (Fig. 4*B*). In both walking and running, stride frequency and stride length decreased on steeper inclines at the correspondingly slower treadmill belt speeds (Fig. 4, *A* and *B*). Duty factor was >50% for both walking and running conditions at all speed/incline combinations tested, indicating nonaerial gaits. Walking duty factor was greater than the running duty factor at every incline (average 10.29 ± 5.92%; P < 0.001) except at 40°.

Table 1. *The vertical cost of walking and running as a function of the slope angle*

Angle, °	Treadmill Belt Speed, m/s	Walk, $J \cdot kg^{-1} \cdot m^{-1}$	Run, $J \cdot kg^{-1} \cdot m^{-1}$	Difference, %	P
9.4	2.14	55.67 ± 3.80	54.83 ± 2.29	1.53	0.545
15.8	1.29	46.73 ± 2.19	49.90 ± 2.37	−6.35	0.001
20.4	1.00	44.23 ± 1.69	48.31 ± 2.54	−8.45	0.001
24.8	0.83	44.01 ± 2.10	48.22 ± 2.57	−8.73	0.001
30.0	0.70	43.86 ± 2.02	48.32 ± 3.07	−9.23	0.001
35.0	0.61	44.57 ± 2.14	48.97 ± 3.01	−8.99	0.001
39.2	0.55	46.07 ± 2.49	50.59 ± 3.70	−8.93	0.001

Vertical cost of walking and running (means ± SD, in $J \cdot kg^{-1} \cdot m^{-1}$) as a function of the slope angle (°) and treadmill belt speed (m/s). Vertical velocity was fixed at 0.35 m/s. At 9.4°, only 9 subjects were able to walk at the required speed (2.14 m/s). For all other angles, n = 15.

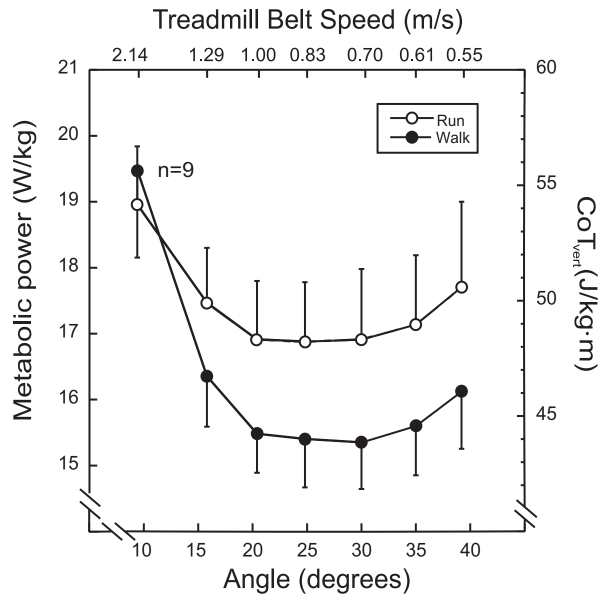

Fig. 3. Metabolic power (W/kg) and vertical cost of transport (CoT_{vert}, $J \cdot kg^{-1} \cdot m^{-1}$) of walking (●) and running (○) plotted as a function of angle (degrees) and treadmill speed (m/s) for 15 subjects. At 9.4° only 9 subjects were able to walk at the required speed (2.14 m/s). Except for 9.4°, walking was less metabolically expensive than running. See text for more details.

DISCUSSION

Our major findings are *1*) across the range of angles and speeds tested, which fixed the vertical velocity, walking is less expensive than running, *2*) there is a broad range of angles for which the vertical costs of walking and running are minimized, and *3*) at the angle/speed combinations we studied, in both walking and running, at least one foot is always in contact with the ground.

Our results support the hypothesis that at a fixed vertical velocity of 0.35 m/s, walking would be less expensive than running at steep inclines, although at 9.4° there was not a significant difference between gaits. Explaining the energetic difference between walking and running is not straightforward. We know that the inverted pendulum and spring mechanisms that conserve mechanical energy during level walking and running, respectively, are disabled during uphill locomotion (8, 24), but it is not yet possible to quantify those effects. Minetti et al. (18) showed that during uphill locomotion the "internal work" for reciprocating the limbs is actually greater in walking than in running despite the slower stride frequencies in walking. Kram and Taylor (13) established that metabolic rate is inversely proportional to contact time during level running. At the inclines and speeds in the present study, the contact times for running averaged 34.4 ± 3.2% less than for walking and that may at least partially explain the metabolic cost difference between the two gaits. Furthermore, because of how the legs are positioned differently in the two gaits, the mechanical advantages of the extensor muscles at the knee are larger in level walking vs. running (1). Smaller muscle forces require a smaller active muscle volume which is energetically cheaper. However, we are not aware of any mechanical advantage measurements for steep uphill locomotion.

At 9.4°, the treadmill belt speed (2.14 m/s) was much faster than during the other trials and is nearly equal to the sponta-

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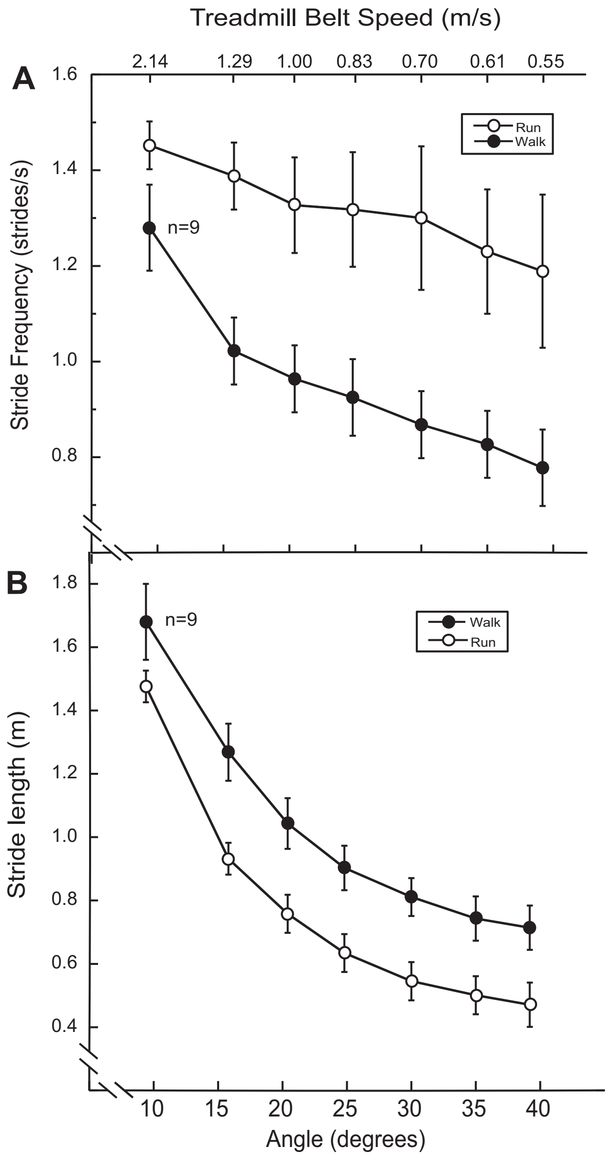

Fig. 4. Stride frequency (strides/s, 4A) and stride length (m, 4B) for walking (●) and running (○) as a function of angle (degrees) and treadmill speed (m/s) for 15 subjects. At 9.4° only 9 subjects were able to walk at the required speed (2.14 m/s).

neous walk-run transition speed on level ground, ~2 m/s (3, 11, 15). Previous studies (4, 10, 11) have demonstrated that the preferred transition speed is slower on moderate inclines and that humans generally choose the gait that minimizes their metabolic cost (17). In the present study, at 9.4° and 2.14 m/s, all of the subjects informally expressed that they would prefer to run. At 15.8° and 1.29 m/s, walking was significantly cheaper but most of the subjects expressed that they would prefer to run. Between 20.4° and 1.00 m/s and 30.0° and 0.70 m/s subjects mentioned that walking felt better. However, if there were no constraints, they thought that they would prefer to alternate between the two gaits every 1 or 2 min. At 35.0° and 0.61 m/s and 39.2° and only 0.55 m/s, gait preference was ambiguous. Subjects expressed that they did not strongly prefer walking (the less expensive gait) because they felt running involved less musculoskeletal "stress" and also balance was more challenging when walking. A future study focused on gait preference, metabolic cost, and perceived effort during both walking and running on steep inclines is needed to better understand this topic.

We reject our second hypothesis. Rather than there being a distinct optimum, we found that there is a range of angles for which Cw_{vert} and Cr_{vert} are minimized. For both walking and running, the minimum values were reached between 20.4 and 35.0°. A second order polynomial regression suggests that the minimum values for Cw_{vert} and Cr_{vert} would be attained at 28.4° (R^2 = 0.64) and 27.0° (R^2 = 0.33), respectively. At angles shallower than 20°, both Cw_{vert} and Cr_{vert} are significantly greater. This could be due in part to the greater metabolic power required to support body weight at faster treadmill belt speeds (9). Furthermore, at our extreme angle of 39.2°, there was an increase in Cw_{vert} and Cr_{vert}, which we believe is caused by the difficulty of maintaining balance at such steep angles. Part of the balance challenge was due to the fact that at 39.2°, the treadmill belt speed was only 0.55 m/s and involved exaggerated contact times (0.924 ± 0.09 s for walking and 0.588 ± 0.11 s for running). In a pilot study, two subjects tried to walk and run with the treadmill inclined to 45° and the Cw_{vert} and Cr_{vert} both increased dramatically compared with ~40°. Balance was quite difficult for those pilot subjects and they frequently grabbed the handrails. Moreover, at that extreme slope, both subjects reported discomfort in their calves and feet because of excessive stretch. For that reason, we "only" studied up to 39.2° in the actual experiment. For Cw and Cr at angles between 10° and 24.8°, our results are congruent with the fifth order polynomial regression formula given by Minetti et al. (21). However, extrapolating beyond 24.8° that formula leads to large overestimates of the Cw and Cr (Fig. 5).

A recent article from our laboratory, Hoogkamer et al. (9), proposed a new explanation for the metabolic cost of running

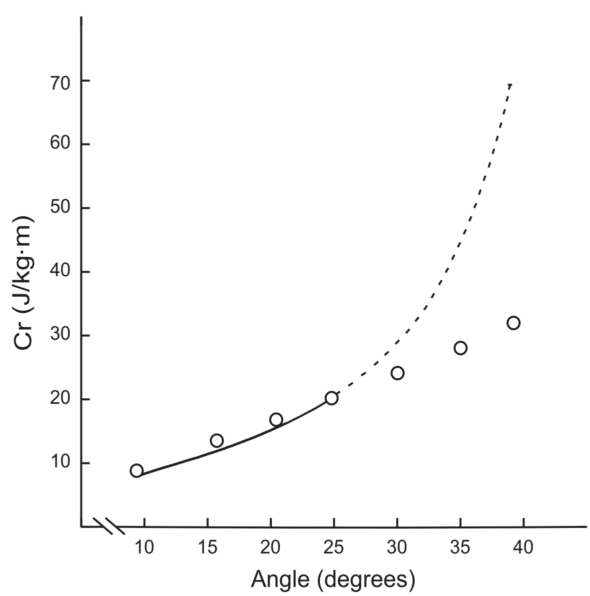

Fig. 5. Mean cost of running (Cr, in J·kg^{-1}·m^{-1}) measured in the present study (○) and computed with the formula of Minetti et al. (21) (black line). The dashed line extrapolates to angles steeper than 24.2° (45%). The relationship between Cr and the slope for our data is described by the formula Cr = 0.7686*(angle in degrees) + 1.3614 (R^2 = 0.97).

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up relatively shallow inclines <9°. In that model, the cost of running (Cr) is determined by three factors: the cost of perpendicular bouncing, the cost of parallel braking and propulsion, and the cost of lifting the center of mass. They assumed a constant efficiency for performing the center of mass lifting work, their results supported that assumption, and they derived a value of ~29% efficiency. In the present study, the vertical work rate was held constant between the different inclines and thus with the same efficiency the vertical cost would be the same between running conditions. In the Hoogkamer et al. study, as the incline approached 9°, the cost of parallel braking and propulsion approached zero. At the even steeper angles used in the present study, the cost of parallel braking and propulsion (the "wasted impulse") presumably is nil. Finally, Hoogkamer et al. reasoned that the cost of perpendicular bouncing would not change over the moderate inclines they studied. At the steeper inclines used in the present study, just based on trigonometry, the perpendicular forces would be less than during level running (e.g., ~13% reduced on a 30° incline, cosine = 0.866). However, the running speeds on the inclines studied here were much slower than typical level running speeds and involved prolonged contact times. Prolonged contact times presumably would allow recruitment of slower (and more economical) muscle fibers to generate the perpendicular forces, but long contact times impair the spring-like bouncing motion and therefore might be less economical (5). Overall, from the Hoogkamer et al. (9) perspective, the broad plateau of Cr_{vert} observed for running at angles from 20.4 to 35.0° probably results from counteracting savings vs. costs for perpendicular bouncing at the different speed and angle combinations. A similar model for uphill walking has not yet been put forth.

As we hypothesized, there was no aerial phase in steep uphill running, i.e., the duty factor (average 62.7 ± 0.80%) was >50% at every incline tested. This suggests that other parameters should be considered to distinguish between walking and running uphill. McMahon et al. (16) defined "Groucho running" as a nonaerial gait that still involved a bouncing center of mass trajectory, i.e., the center of mass was lowest at mid-stance. Rubenson et al. (23) used the term "grounded running" for the same phenomenon in running birds. Because our subjects were running uphill, the center of mass-based definition probably does not apply (8). Nonetheless, when we asked our subjects to either "walk" or "run," they all subjects immediately and intuitively distinguished the two gaits. Previous studies reported that when treadmill speed is fixed, on steeper inclines, stride length and aerial time decrease and stride frequency increases (7, 22). We observed decreases in both stride frequency and stride length at steeper angles (Figs. 4 and 5) because treadmill speed was slower at the steeper angles we tested. Thus, with our experimental design, we could not determine how speed and incline independently affect stride frequency and stride length.

Limitations and future research. One limitation of our study is that it was conducted on a treadmill whereas VK races are performed on uneven terrain (ski slopes, trails) with the presence of stones, stairs, gravel, etc. Voloshina and Ferris (26) report that the energy expenditure of running on an uneven terrain treadmill was only 5% higher than on a smooth treadmill. However, Zamparo et al. (27) showed that running on a sandy terrain requires 20% more energy than on firm terrain. Thus the cost of transport during a real VK race is surely somewhat greater than what we measured on our treadmill. Another limitation was that our treadmill did not permit the use of poles. The VK world record as well as most of the fastest performances outdoors were achieved using poles.

Future studies should compare uphill walking and running with and without poles to determine if using poles is advantageous. Further studies involving different combinations of vertical velocity, treadmill speed, and angle are also needed. Finally, a more thorough biomechanical comparison of walking vs. running is in order since on steep inclines the defining characteristic(s) of these two gaits are not yet clear.

In conclusion, we studied the cost of walking and running at angles substantially steeper than any previous study. We found that for both walking and running there is a range of angles (20.4-35.0°) for which energy expenditure is minimized. Our data suggest that, to achieve the best results, VK races should be contested within this range of angles. Although other factors may be important, on very steep slopes, athletes can reduce their energy expenditure by walking rather than running.

ACKNOWLEDGMENTS

We thank Dr. Wouter Hoogkamer for valuable suggestions and all of participants for time and effort.

GRANTS

We are grateful to the University of Colorado Boulder Undergraduate Research Science Training (BURST) and Undergraduate Research Opportunity Program (UROP) for supporting A. Ortiz.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: N.G., A.L.R.O., and R.K. conception and design of research; N.G., A.L.R.O., and K.H. performed experiments; N.G. and R.K. analyzed data; N.G., A.L.R.O., and R.K. interpreted results of experiments; N.G and A.L.R.O. prepared figures; N.G., A.L.R.O., and R.K. drafted manuscript; N.G., A.L.R.O., K.H., and R.K. edited and revised manuscript; N.G., A.L.R.O., K.H., and R.K. approved final version of manuscript.

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