

Does the application of ground force set the energetic cost of cross-country skiing?

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Bellizzi, Matthew J., Kellin A. D. King, Sara K. Cushman, and Peter G. Weyand. Does the application of ground force set the energetic cost of cross-country skiing? *J. Appl. Physiol.* 85(5): 1736–1743, 1998.—We tested whether the rate at which force is applied to the ground sets metabolic rates during classical-style roller skiing in four ways: 1) by increasing speed (from 2.5 to 4.5 m/s) during skiing with arms only, 2) by increasing speed (from 2.5 to 4.5 m/s) during skiing with legs only, 3) by changing stride rate (from 25 to 75 strides/min) at each of three speeds (3.0, 3.5, and 4.0 m/s) during skiing with legs only, and 4) by skiing with arms and legs together at three speeds (2.0–3.2 m/s, 1.5° incline). We determined net metabolic rates from rates of O_2 consumption (gross O_2 consumption – standing O_2 consumption) and rates of force application from the inverse period of pole-ground contact [$1/t_{p(arms)}$] for the arms and the inverse period of propulsion [$1/t_{p(legs)}$] for the legs. During arm-and-leg skiing at different speeds, metabolic rates changed in direct proportion to rates of force application, while the net ground force to counteract friction and gravity ($\bar{F}$) was constant. Consequently, metabolic rates were described by a simple equation ($\dot{E}_{metab} = \bar{F} \cdot 1/t_p \cdot C$, where $\dot{E}_{metab}$ is metabolic rates) with cost coefficients (C) of 8.2 and 0.16 J/N for arms and legs, respectively. Metabolic rates predicted from net ground forces and rates of force application during combined arm-and-leg skiing agreed with measured metabolic rates within $\pm 3.5\%$. We conclude that rates of ground force application to support the weight of the body and overcome friction set the energetic cost of skiing and that the rate at which muscles expend metabolic energy during weight-bearing locomotion depends on the time course of their activation.

locomotion; oxygen consumption; cost coefficient; skiing mechanics; economy

CROSS-COUNTRY SKIS allow humans to travel farther and faster than on foot. Long-distance skiers can cover 80 more miles/day than long-distance runners, and top skiers maintain paces for 6 miles that would exhaust world-class runners in only 1 mile. The metabolic power available to skiers and runners is virtually the same (29), but the energetic cost of skiing is considerably lower (22, 28). The economy of skiing confers clear performance advantages, but why skiing is less costly is not known.

The metabolic cost of terrestrial locomotion is incurred almost entirely by the active skeletal muscles (2), but how locomotor mechanics set the muscular energy expended is not fully understood. Although the

metabolic cost of muscular force and work is well known on cellular and tissue levels (10, 14, 18, 21), how this relates to the energetics and mechanics of muscle activity in vivo is unclear. Neither active muscle volumes nor shortening velocities can be readily measured, nor is it possible to measure how much of the mechanical work required for activities such as constant-speed running and skiing is performed actively by skeletal muscle. Direct (27) and indirect (5, 6, 24, 31, 32) evidence indicates that much of the work to lift and accelerate the body's center of mass and limbs during each stride is performed passively by the springlike activity of tendons and by mechanical energy transfers between body segments, rather than actively by muscle.

Regardless of how much work muscles do during locomotion, they must generate ground forces to support the weight of the body. It has been proposed that these forces and the rate at which they are applied to the ground set the metabolic rates of running animals (20). For seven animal species running and hopping at speeds from 0.25 to 10.0 m/s, Kram and Taylor (20, 32) reported that metabolic rates were directly proportional to net ground forces to support the body weight ($\bar{F}_{bw}$) and rates of muscle force generation, estimated from the inverse period of foot-ground contact ($1/t_c$; $\dot{E}_{metab} = \bar{F}_{bw} \cdot 1/t_c \cdot C$, where $\dot{E}_{metab}$ is metabolic rate and C is a proportionality constant in J/N). However, their assumption that rates of force application determine metabolic rates by setting the fiber speeds and cross-bridge cycling rates of the recruited muscle has been questioned (1). Additionally, the result of Kram and Taylor (30) has been attributed to the mutual correlation of the mechanics and energetic cost of locomotion with body mass in the species used, rather than to the causal relationship they proposed.

If the metabolic rates of active muscles are directly dependent on the rate at which they develop force, then the force hypothesis of Kram and Taylor (20) should generalize to modes of locomotion mechanically different from running, such as cross-country skiing. Unlike runners, skiers generate significant net propulsive forces to overcome the friction of the ski sliding on the snow, performing net work on the environment that must be done actively by the muscles, rather than passively by tendons and energy transfers. Skiing forces are generated in part by the arms, which differ from legs in mechanical and metabolic properties during locomotion (11). Ground forces are applied through poles and skis attached to the limbs, which could alter the mechanics and energetics of stance and swing phases. In addition, although the force hypothesis successfully accounts for 20-fold differences in meta-

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bolic rates of running and hopping animals (20, 32), it is not clear whether it can account for differences in metabolic rates as small as those during skiing at different speeds. Thus skiing provides a rigorous and independent test of the force hypothesis.

During skiing the arms apply ground force throughout the period of pole-ground contact, and the inverse of this period, like that of foot-ground contact in running, was used to measure rates of arm force application. Rates of leg force application were measured from the inverse of the propulsive period during the latter portion of ski-ground contact. We hypothesized that the average cross-bridge cycling rate of the leg muscles would be set by the duration of the propulsive phase, because nearly all the muscular activity of the legs occurs during this period. During the propulsive phase the joint angles change considerably, the highest vertical forces and all the horizontal forces are exerted, and electromyogram activity of the skiing muscles is high (19). In contrast, during the glide phase at the beginning of ski-ground contact the leg is nearly straight and positioned directly beneath the body, joint rotations are small, and electromyogram activity is low.

We tested whether the rates at which net ground forces are applied, measured from the inverse periods of pole-ground contact for the arms and propulsion for the legs, set metabolic rates during classical-style cross-country skiing. A constant relationship between average force, rates of force application, and metabolic rates not only would explain how the energetics and mechanics of skiing are linked but would also indicate whether the force hypothesis may provide a general relationship between mechanical activity and the metabolic energy expended by skeletal muscle during weight-bearing locomotion.

METHODS

Experimental Design

To test the hypothesis that rates of force application set metabolic rates during skiing, we changed rates of force application in four ways during classical-style roller skiing on a treadmill while measuring O_2 uptake to determine metabolic rate. First, we had subjects ski using only their arms and changed rates of force application by increasing treadmill speed. Second, we had subjects ski using only their legs and again changed rates of force application by increasing treadmill speed. Third, at three fixed speeds we had subjects ski using only their legs and changed rates of force application by changing stride frequency over a threefold range (25–75 strides/min). Fourth, at three speeds we had subjects ski naturally with arms and legs (combined arm-and-leg skiing) and predicted the metabolic rates of the arm and leg muscles from their respective rates of ground force application to determine whether their sum matched the metabolic rates we measured during combined arm-and-leg skiing.

During roller and snow skiing the leg muscles generate the majority of their force during the propulsive period and support the body relatively passively during the glide, while the arms apply force throughout the period of pole-ground contact. In both cases the muscles do net work on the environment, in contrast to previously tested modes of locomotion (11, 20). Expecting similar relationships between metabolic rates and the application of ground force during both

types of skiing, we chose to conduct our tests using treadmill roller skiing for reasons of practicality.

Skiers isolated arm activity by standing evenly on both roller skis and poling alternately with the arms, mimicking the poling motion of the classical stride. They isolated leg activity by striding without poles, letting their arms swing naturally. The movements of the arms and legs during these activities are similar to those during combined arm-and-leg skiing, and subjects had often practiced both as technique drills.

Subjects skied with arms only at five different speeds from 2.5 to 4.5 m/s on a level treadmill (1 bout at each). We hypothesized that the relationship between rates of force application and metabolic rates would follow the equation

$$\dot{E}_{\text{metab(arms)}} = \bar{F}_{\text{arms}} \cdot 1/t_{\text{p(arms)}} \cdot C_{\text{arms}} \quad (1)$$

where $\bar{F}$ is the average ground force (N) exerted over an entire stride or poling cycle, $1/t_p$ is a measure of the rate of force application (s^{-1}), and C is a cost coefficient (J/N) that represents the metabolic energy expended to exert 1 N of ground force.

Subjects skied with legs only at the same five speeds from 2.5 to 4.5 m/s (2 bouts at each). We hypothesized that metabolic rates would be related to rates of leg force application by the equation

$$\dot{E}_{\text{metab(legs)}} = \bar{F}_{\text{legs}} \cdot 1/t_{\text{p(legs)}} \cdot C_{\text{legs}} \quad (2)$$

Subjects also skied with legs only at six different stride rates (their naturally chosen stride rate plus 3 higher and 2 lower, 1 bout at each) at each of three speeds (3.0, 3.5, and 4.0 m/s). We hypothesized for this condition that metabolic rates would again be related to rates of force application by Eq. 2.

Subjects skied naturally using arms and legs (combined arm-and-leg skiing) at 2.0, 2.6, and 3.2 m/s up a 1.5° incline while net forces, rates of force application, and metabolic rates were measured. This allowed us to determine whether metabolic rates predicted from arm-and-leg forces and rates of force application would sum to predict the measured values.

Combined arm-and-leg skiing was done up a slight incline, because skiers found this more comfortable than level skiing when using the arms and legs together. Because the propulsive force and work required to overcome friction and gravity were divided between the arms and legs and were increased only slightly by the incline, we expected arm-and-leg cost coefficients to differ from those of arms-only and legs-only skiing. Although cost coefficient values are independent of the magnitude of force generated during specific modes of locomotion (8, 11, 20), they do vary as the component of force performing net work on the environment is changed, as during uphill running (32). This is likely due to the increased energetic cost of force when muscles shorten to do more work during contraction (10, 27, 32). We therefore needed cost coefficients specific to the relative propulsive and support forces generated by the arms and legs during combined arm-and-leg skiing.

We determined these cost coefficients during arms-only and legs-only skiing with net propulsive and support forces adjusted to match those generated by the respective limbs during combined arm-and-leg skiing. Propulsive force was adjusted using a weighted bucket hanging from a rope tied around the skier's waist and passed over a pulley at the front of the treadmill. Vertical force was adjusted with a system similar to that described by He et al. (12) consisting of a lower-body harness attached via a cable and several pulleys to two long bungee cords, which could be stretched to adjust

the tension of the system. Forces, rates of force application, and metabolic rates were measured at four speeds, from 2.5 to 3.4 m/s for force-adjusted arm skiing and from 2.2 to 3.1 m/s for force-adjusted leg skiing, and cost coefficients were calculated using Eqs. 1 and 2. We hypothesized that forces and rates of force application during combined arm-and-leg skiing would predict metabolic rates according to the equation

$$\dot{E}_{\text{metab}} = \bar{F}_{\text{arms}} \cdot 1/t_{p(\text{arms})} \cdot C_{\text{arms}} + \bar{F}_{\text{legs}} \cdot 1/t_{p(\text{legs})} \cdot C_{\text{legs}} \quad (3)$$

Subjects

Eight national- and collegiate-level ski racers, 20–25 yr of age, volunteered to participate in the study and provided informed, written consent. Five were men [mass 72.4 ± 2.9 (SE) kg, height 179 ± 1 cm] and three were women (mass 59.0 ± 1.0 kg, height 161 ± 4 cm). Different subgroups for each condition were necessitated by subject availability. Within conditions all subjects completed the same number of bouts at each speed. Five men skied with legs only, four men and one woman (68.2 ± 2.4 kg) skied with arms only, and two men and three women (64.0 ± 3.4 kg) skied with combined arms and legs as well as with forces adjusted to simulate arm-and-leg forces during combined skiing. Subjects used the same pair of roller skis (model V2 900, Jenex, Amherst, NH; 1.8 kg) and one of two pairs of poles (Exel; 0.4 kg) for all tests. Subjects were habituated to treadmill roller skiing by one or more training sessions before data were collected to ensure reproducibility of mechanical and energetic measurements.

Measurements

Metabolic rate. Metabolic rates (W) were determined by measuring steady-state O_2 consumption using an open-flow system and a paramagnetic O_2 analyzer (model F-3, Beckman, Fullerton, CA), as described by Fedak et al. (9), with an energetic equivalent of 20.1 J/ml O_2 . Metabolic rates for each bout of skiing were averaged from the first steady-state 2-min period after the first 4 min of skiing. Each bout of skiing lasted 6–10 min, and skiers were allowed as much recovery as they liked between bouts (typically 1–5 min). Skiers completed an average of eight bouts per session for three to four sessions and could end the session if they felt fatigued. To obtain the net metabolic rate incurred by skiing, O_2 consumption while standing on roller skis was subtracted from that measured during skiing. Although absolute metabolic rates (W) were used in Eqs. 1–3, mass-specific metabolic rates ($\dot{E}_{\text{metab}}/M_b$, where M_b is body mass, W/kg) are reported in accordance with convention for weight-bearing exercise.

Ground force. The resultant ground forces exerted ($\bar{F}$, N) were time averaged over an entire skiing stride, which was defined as the time between the initiation of successive propulsive periods of the same limb. Forces were measured indirectly from friction and subject weight during legs-only skiing and directly from strain gauges on one ski and one pole during arms-only skiing, combined arm-and-leg skiing, force-

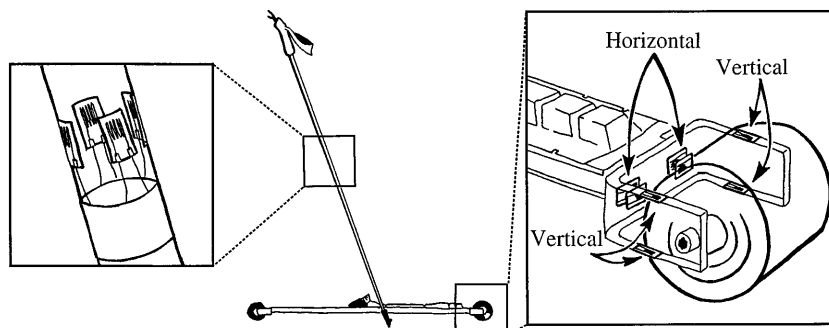
adjusted arm skiing, and force-adjusted leg skiing. Friction was measured by towing a skier on a moving treadmill belt with a line attached to a force transducer (model 9203, Kistler) or to a bucket suspended from a pulley at the front of the treadmill containing weight adjusted to counteract the force of friction exactly. Weight was added to or removed from the bucket until the skier did not drift on the moving treadmill belt for 15 s. Frictional forces were constant at speeds from 2.0 to 4.5 m/s and were $\sim 1/40$ th of the skier's body weight (0.024 N/N body wt). Measurements from the transducer and weighted bucket agreed to within 3%. Mean vertical force during legs-only skiing equaled subject weight, which was measured before each session on a platform scale (model 8412, Toledo, Toledo, OH).

Leg forces were measured from strain gauges (uniaxial 350 Ω SR-4, BLH Electronics, Canton, MA) fixed to the metal brackets holding the wheels of the roller ski (Fig. 1). Eight gauges, four each at the front and back of the ski, were positioned to measure bending induced by the vertical forces exerted on the ski. Four additional gauges were positioned to measure bending due to propulsive forces at the ratcheted back wheel of the ski. Each group of four gauges was wired to a bridge amplifier (model 2100, Vishay, Raleigh, NC) in a full-bridge configuration. Data from the amplifier were sampled at 500 Hz by LabView 4.0 software through a data-acquisition board (model NB-MIO-16H, National Instruments, Austin, TX). Gauges were calibrated before each session for vertical force by placing a known weight at different positions on the ski and for horizontal force by positioning the ski vertically and hanging known weights from the rear axle.

Arm forces were measured from strain gauges on the shaft of a single pole from each pair (Fig. 1). Four gauges, positioned to measure axial compression of the shaft, were wired separately to the bridge amplifier in a quarter-bridge configuration and sampled at 500 Hz. Gauges were placed 180° apart on the shaft so that length changes induced by pole bending could be canceled out. Pole strain gauges were calibrated before each session by hanging a known weight from the pole handle or by pressing the pole vertically against the calibrated roller ski. Pole and ski strain gauge voltages increased linearly with force, and the natural frequencies of pole and ski vibration (144 and 185 Hz for the respective poles and 160 Hz for the ski) did not interfere with force measurements.

Rate of force application. The period of arm force application [$t_{p(\text{arms})}$] was determined from pole force measurements. The inverse of this period [$1/t_{p(\text{arms})}$] was used as a measure of the rate of force application. Rates of leg force development were measured using the inverse of the period of propulsive leg force application [$1/t_{p(\text{legs})}$]. The propulsive period during legs-only skiing was measured from videotape recording (Sony XVC Hi-8, 30 Hz) by observing, from the position of a painted stripe, when the ratcheted rear wheel of the roller ski stopped rolling forward at the beginning of propulsive force

Fig. 1. Strain gauges were positioned on pole to measure axial compression and on ski to measure bending due to vertical and horizontal forces. Four additional gauges measuring vertical forces at front of ski were positioned symmetrically to those shown at rear. Stripe painted on ski's ratcheted rear wheel allowed propulsive period to be identified on videotape recording.



application and when the wheel lifted off the treadmill belt at the end of propulsion. Because it was necessary to measure leg forces directly during combined arm-and-leg skiing and force-adjusted leg skiing, $t_{p(\text{legs})}$ was measured under these conditions from the time of propulsive force application obtained from strain gauges on one ski. Propulsive periods measured from ski force data were 28–29% lower than those measured from videotape recording. Because this difference did not change with skiing speed, our test of a constant relationship between metabolic rates and rates of force application across speed was unaffected by measurement method. For each bout of skiing, t_p was averaged over a minimum of 25 leg strides and 15 poling cycles.

Cost coefficient. Cost coefficients (J/N) were determined from net metabolic rates, rates of force application, and time-averaged forces using Eq. 1 for arm skiing and Eq. 2 for leg skiing.

Statistics

Cost coefficients and average forces across speed and stride rate were analyzed using a one-way ANOVA ($\alpha = 0.05$). Actual and predicted metabolic rates values during combined arm-and-leg skiing were also analyzed by a one-way ANOVA ($\alpha = 0.05$). Values are means $\pm$ SE.

RESULTS

Arms-Only Skiing

Metabolic rates and rates of force application increased nearly identically as speed increased from 2.5 to 4.5 m/s during arms-only skiing (Fig. 2, A and B): net metabolic rates increased from 4.1 to 7.5 W/kg (82%), and rates of force application increased from 1.6 to 2.8 s⁻¹ (76%). The $\bar{F}$ applied during a complete poling cycle did not change with speed (22.1 ± 0.3 N, Fig. 2C) and was 1.4 times the required propulsive force (16.0 ± 0.6 N). The relationship between metabolic rate, $\bar{F}$, and rate of force application, represented by the cost coefficient C_{arms} (calculated from Eq. 1), was constant across speed at an average value of 8.2 ± 0.06 J/N (Fig. 2D).

Legs-Only Skiing

Metabolic rates and rates of force application also increased similarly with speed during legs-only skiing (Fig. 3, A and B). Metabolic rates and rates of force application were higher during legs-only skiing than during arms-only skiing: $\dot{E}_{\text{metab}}/M_b$ increased from 5.8 to 12.5 W/kg, and $1/t_{p(\text{legs})}$ increased from 4.2 to 7.8 s⁻¹. The average force applied to the ground during a complete stride was 30 times higher than during arms-only skiing and was the same at all speeds (712 ± 29 N, Fig. 3C). C_{legs} (calculated from Eq. 2) was unchanged across speed at an average value of 0.16 ± 0.004 J/N (Fig. 3D), which is 50 times lower than that for the arms.

During legs-only skiing at different stride rates, changes in metabolic rates again closely paralleled changes in rates of force application (Fig. 4, A and B). Although neither changed significantly at stride rates below the naturally chosen stride rate, both increased at higher stride rates, with metabolic rates increasing by $\geq 39\%$ at the highest stride rate at each of the three speeds. $\bar{F}$ was the same at all stride rates and speeds (712 ± 29 N, Fig. 4C). The cost coefficient was constant

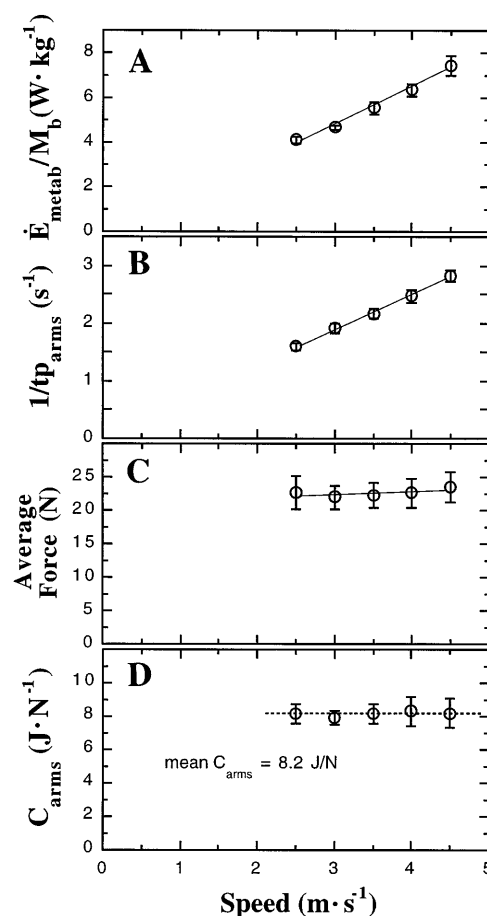


Fig. 2. Net metabolic rates ($\dot{E}_{\text{metab}}/M_b$, where $\dot{E}_{\text{metab}}$ is metabolic rates and M_b is whole body mass; A) and rates of pole force application against ground [$1/t_{p(\text{arms})}$, B] increased linearly with speed during arms-only skiing [$\dot{E}_{\text{metab}}/M_b = -0.25 + 1.68 \times \text{speed}$, $r^2 = 0.988$; $1/t_{p(\text{arms})} = 0.11 + 0.60 \times \text{speed}$, $r^2 = 0.998$], whereas average ground force exerted over poling cycle did not change (C). Consequently, metabolic rates were related to average force and rates of force application by a proportionality constant, i.e., cost coefficient (C_{arms} , from Eq. 1; D) that was the same at all speeds (8.2 ± 0.06 J/N). Values are means $\pm$ SE.

at all three speeds and across the threefold range of stride rates used (Fig. 4D) at the same average value as for leg skiing at different speeds (0.16 ± 0.002 J/N).

Force-Adjusted Arm-and-Leg Skiing

Metabolic rates and rates of force application also increased similarly with speed during arms-only and legs-only skiing, with net forces adjusted to match those generated by the arms and legs during combined arm-and-leg skiing. During force-adjusted arm skiing, metabolic rates increased by 42% (from 2.4 to 3.4 W/kg), $1/t_{p(\text{arms})}$ increased by 37% (from 1.7 to 2.4 s⁻¹) over the range of speeds, and C_{arms} was unchanged across speed at a mean value of 4.7 ± 0.15 J/N (Fig. 5, A–D). During force-adjusted leg skiing, metabolic rates increased by 49% (from 5.3 to 7.9 W/kg), $1/t_{p(\text{legs})}$ increased by 53% (from 4.9 to 7.4 s⁻¹), and C_{legs} was unchanged across speed at an average value of 0.12 ± 0.001 J/N (Fig. 5, E–H). Both cost coefficients were lower than during level arms-only and legs-only skiing,

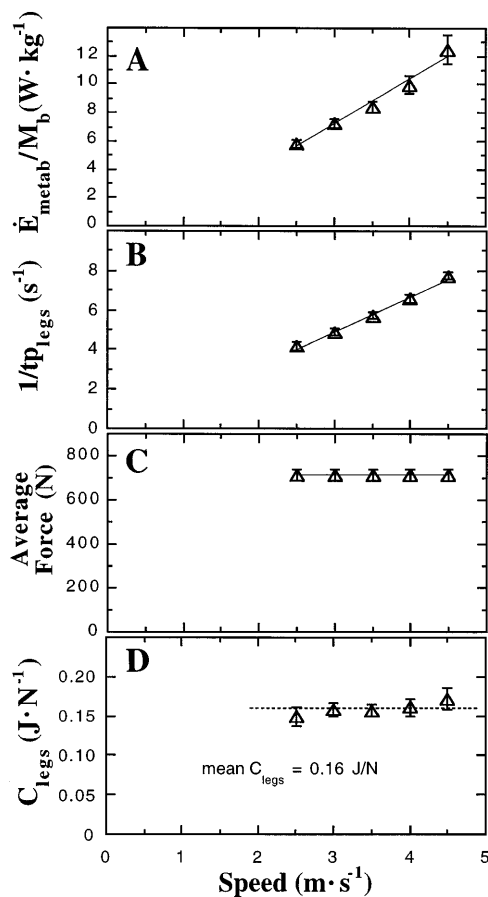


Fig. 3. Net metabolic rates (A) and rates of ground force application (B) increased linearly with speed during legs-only skiing [$\dot{E}_{\text{metab}}/M_b = -2.53 + 3.23 \times \text{speed}$, $r^2 = 0.978$; $1/t_{p(\text{legs})} = -0.39 + 1.78 \times \text{speed}$, $r^2 = 0.992$], whereas average ground force exerted during stride did not change (C). Consequently, metabolic rates were related to average force and rates of force application by a proportionality constant (C_{legs} , from Eq. 2; D) that was the same at all skiing speeds (0.16 ± 0.004 J/N).

inasmuch as the arms and legs generated different propulsive forces.

Combined Arm-and-Leg Skiing

During combined arm-and-leg skiing, the legs supplied nearly all the force needed to support the body as well as most of the required propulsive force. Mean forces exerted by the arms and the legs were constant across speed (Fig. 5, C and G) and were nearly 30-fold higher for the legs (580 ± 2 N) than for the arms (20 ± 0.2 N). At every speed the legs supplied $69 \pm 3\%$ and the arms $31 \pm 3\%$ of the propulsive force needed to overcome the drag of friction and gravity. The arms and the legs applied force more rapidly as skiing speed increased (Fig. 5, B and F), and rates of leg force application were more than twice as high as those for arms. Measured metabolic rates increased linearly across the speed range, from 7.1 to 11.9 W/kg (Fig. 6).

Mean forces and rates of force application during combined arm-and-leg skiing were used with the cost coefficients from force-adjusted arm and force-adjusted leg skiing to predict metabolic rates of the arms and legs during combined arm-and-leg skiing (according to Eqs. 1 and 2). Predicted metabolic rate values were

2–2.4 times higher for legs than for arms (Fig. 6). Predicted metabolic rate values of the arms and legs were summed to predict the total metabolic rate during combined arm-and-leg skiing (Eq. 3). Predicted and measured metabolic rates agreed closely at all speeds (Fig. 6): 7.1 ± 0.4 vs. 7.4 ± 0.3 , 9.4 ± 0.3 vs. 9.3 ± 0.5 , and 11.9 ± 0.5 vs. 12.0 ± 0.5 W/kg at 2.0, 2.6, and 3.2 m/s, respectively.

DISCUSSION

We set out to determine whether the rate at which net force is applied to the ground sets metabolic rates during cross-country skiing. Regardless of whether our subjects skied with arms, legs, arms and legs together, or at nearly one-half of or twice their natural stride frequency, we found that metabolic rate values were a constant function of net ground force and rates of force application at different skiing speeds. The tight relationship between these variables, despite large structural and functional differences in the limbs used, dramatic alterations of natural skiing mechanics, and complex-

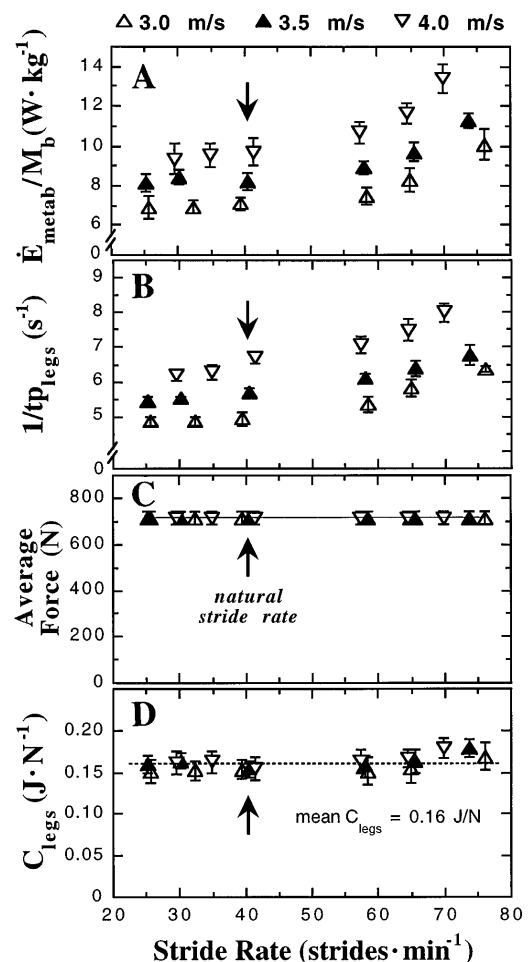


Fig. 4. Net metabolic rates (A) and rates of ground force application (B) increased at rates above but did not change at rates below naturally chosen stride rate. Average ground force exerted was the same at different stride rates (C). Consequently, metabolic rates were related to average force and rates of force application by a proportionality constant (D) that was unchanged over the 3-fold range of stride rates at each of 3 different speeds (3.0, 3.5, and 4.0 m/s; 0.16 ± 0.002 J/N). Arrows, naturally chosen stride rates.

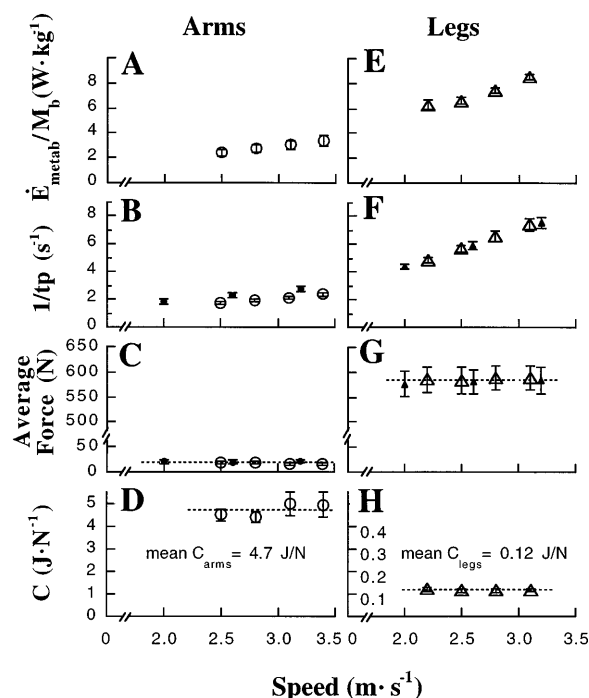


Fig. 5. Average forces exerted by arms and legs (C and G) during arms-only and legs-only skiing (open symbols) were adjusted to match those generated by respective limbs during combined arm-and-leg skiing (filled symbols). These forces were constant across speed and were 26 times greater for legs than for arms (580 ± 2 vs. 20 ± 0.2 N). Net metabolic rates (A and E) and rates of force application (B and F, open symbols) increased linearly with speed during force-adjusted arm-and-leg skiing. Consequently, force-adjusted arm-and-leg cost coefficients (from Eqs. 1 and 2, D and H) were constant across speed and were 40 times higher for arms than for legs (4.7 ± 0.15 vs. 0.12 ± 0.001 J/N). Rates of arm-and-leg force application during combined arm-and-leg skiing (B and F, filled symbols) increased with speed and were similar to those during force-adjusted arm-and-leg skiing.

ity of coordinating four limbs to apply ground force, leads us to conclude that the application of ground force does set metabolic rates during skiing. In addition to furthering the understanding of the energetics and mechanics of locomotion, this relationship is of potential applied value for field measurements of skiers'

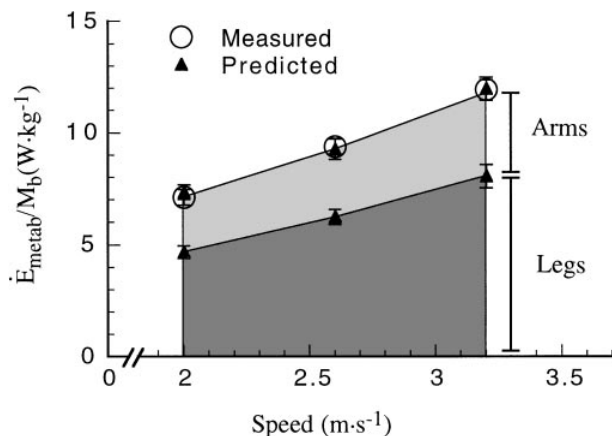


Fig. 6. Metabolic rates predicted for combined arm-and-leg skiing (from Eq. 3) matched those measured at 2.0, 2.6, and 3.2 $\text{m}\cdot\text{s}^{-1}$ to within 3.5, 1.1, and 0.4%, respectively (measured = $-0.99 + 4.03 \times \text{speed}$, $r^2 = 0.999$).

metabolic rates. Although propulsive forces during roller skiing and snow skiing differ because of effects of wind resistance and the friction between the ski and skiing surface, our results show that metabolic rate values depend on the application of ground force regardless of the amount of force required. Similar to foot-ground contact monitors used during walking and running (17), portable systems that measure forces and propulsive periods from the skis and poles (25) could be used to estimate metabolic rates during skiing when collection of expired gases is impractical.

How General Is the Force Hypothesis?

Our experiments have extended support for the force hypothesis beyond running and to a mode of locomotion that requires net work on the environment. Although running limbs store energy in a springlike fashion that allows most of the mechanical work to be performed passively (5, 11, 27), skiing requires net work for propulsion that must be performed actively by muscles. Although the metabolic cost of force increases with the work done during contraction (10, 14, 18), our results indicate that the metabolic rates of muscles that do net work on the environment depend on periods of force application and not simply the amount of mechanical work they do. When our subjects increased stride rate at the same skiing speed, the net work performed was unchanged but metabolic rates increased in direct proportion to rates of force application (Fig. 4). The time course of muscular activation appears to tightly regulate rates of cross-bridge cycling and ATP hydrolysis in the recruited fibers whether muscles do net work or simply generate force during locomotion. These results provide further support for the hypothesis (20) that muscles use fibers with faster cross-bridge cycling rates to generate force over shorter periods of time.

The dependence of metabolic rates on the period of ground force application indicates that the muscles expend virtually all their metabolic energy while applying ground force and that mechanical activity occurring outside these periods, such as the swinging of limbs, incurs virtually no metabolic cost. The results of legs-only skiing at different stride rates demonstrate the independence of limb swinging from metabolic rates. Limbs were swung one-half as often at the lowest stride rate as at the naturally chosen one, but rates of force application and metabolic rates did not change. In addition, the application of ground force fully accounted for the metabolic cost of combined arm-and-leg skiing, in which all four limbs were weighted by poles or skis and were coordinated to apply force sequentially. This suggests that, even for an acquired and complex mode of locomotion, the mechanical work necessary to swing the limbs can be performed for negligible metabolic cost, likely by passive mechanisms of energy storage and transfer (27, 33).

The independence of metabolic rate from the duration of the glide during skiing at different stride rates (Fig. 4) also supports our assumption that the time of leg muscle activation could be estimated from the time of propulsion. At the lowest stride rates the glide period was up to 66% longer than at the naturally chosen

stride rate, but neither propulsive periods nor metabolic rates differed. Over the entire range of stride rates, metabolic rate values were directly proportional to $1/t_{p(\text{legs})}$ but showed no consistent relationship to glide duration.

The success of the force hypothesis in accounting for small changes in metabolic rates under a number of conditions suggests that the relationship between the time during which muscles develop force and the metabolic energy they expend is basic to weight-bearing locomotion. Rates of ground force application fully accounted for metabolic rate values that were only twice the basal value during force-adjusted arm skiing and four times the basal value during arms-only skiing and force-adjusted leg skiing. Similar results have been reported for humans running on their hands at different speeds and on their hands or feet with different loads (8, 11). Collectively, these results support a relationship between rates of force application and E_{metab} that is causal (20), rather than coincidental, as has been suggested (30). The proportion of metabolic rates not accounted for by rates of force application during human running at different speeds (23) we believe is due to speed-related differences in other factors that can affect the cost of applying ground force, rather than to an uncoupling of this basic relationship.

What Sets the Cost of Applying Ground Force?

The cost coefficient represents the amount of metabolic energy that the muscles expend to apply 1 N of force against the ground at any given rate of force application. The value of the cost coefficient depends on the volume of muscle needed to generate force and the energy expended per unit volume, both of which can vary considerably during different activities. The cost of applying ground force was >50 times higher during arms-only than legs-only skiing, likely because arms exert force on the ground with poorer leverage. Although the legs apply force on the ground directly beneath them, the arms exert force through the poles at a large distance from the elbow and shoulder and likely require more muscle to generate 1 N of ground force (3). The shoulder joint also rotates through greater excursions than do the leg joints, implying that arm muscles shorten more during propulsion. This would further increase the volume of active muscle and the energy expended per unit volume (10, 14, 18, 27).

The energetic cost of ground force application varied between conditions but was constant across speed under four independent conditions (arms-only, legs-only, force-adjusted arm, and force-adjusted leg skiing). Because changes in the muscle volume per unit ground force or the relative shortening velocity would affect the energetic cost of force, this result strongly implies that neither variable changed with speed. Also constant across speed were the distances through which propulsive force was applied (1.59 ± 0.01 m for arms and 0.60 ± 0.01 m for legs) and the net efficiencies with which the arm and leg muscles did work to overcome friction (14.4 and 9.6%, respectively). Although muscular activity likely varied with skiing mode, it appears that the musculoskeletal system meets the mechanical

requirements of increasing skiing speed through equivalent muscular activity simply by modulating the recruited muscle to perform the same task more rapidly.

From the Cost of Applying Ground Force to the Cost of Locomotion

Differences in net ground forces, rates of force application, and the metabolic cost of force explain the relative economy and preferential use of different modes of locomotion. Level arms-only skiing requires 40% less energy than legs-only skiing, because the body's weight is supported relatively passively by straight legs and the arms generate propulsive forces that are very low, only 1/40th of body weight. In addition, the poles allow the arms to apply force slowly: propulsive periods were 2.6 times longer for arms than for legs. Low forces and long periods of force application likely explain why ski racers propel themselves over flat terrain almost exclusively using double poling, an arms-only skiing technique in which both arms pole simultaneously, and also why double poling is the most economical of the classical skiing techniques on level ground (15, 28).

The increased propulsive force required during inclined skiing alters the relative economy of arm-and-leg skiing and changes skiers' limb preferences accordingly. Because the arms supply force primarily for propulsion, the total force they generate increases dramatically on an incline when they are required to lift the body against gravity in addition to overcoming friction. Even a slight incline (1.5°) increased the total arm force to 2.5 times that during level skiing. In contrast, leg force requirements are changed little by steeper inclines, because the additional propulsive force required is a small fraction of the forces generated to support the weight of the body. Because an incline increases force requirements much more for the arms than for the legs, the arms incur greater additional cost when a skier is skiing uphill. Consequently, arm skiing is no more economical than combined arm-and-leg skiing on an incline (16), and three subjects that we tested on an inclined treadmill (1.5°) expended the same amount of energy skiing with arms only, legs only, or arms and legs together. Although the mode of inclined skiing did not affect economy, we found that skiers generated 69% of the propulsive force with the legs and 31% with the arms at all speeds when instructed to ski naturally. They also reported that combined arm-and-leg skiing was more comfortable than using either pair of limbs separately on this incline. The distribution of propulsive force between arms and legs appears to be tightly regulated by some factor other than economy, perhaps the minimization of tissue-specific metabolic rates for greater comfort and endurance.

Finally, our results explain why it is more economical to ski than to run. Because skis allow the foot to slide over the ground, skiers can glide forward while supporting themselves passively on a relatively straight leg. Effectively standing at rest during the glide phase, they generate much of the required support force for minimal metabolic cost. Because gliding dramatically reduces the cost of support, the energetic cost of applying ground force during leg skiing ($C_{\text{legs}} = 0.16$ J/N) is only

one-half that during running ($C_{\text{run}} = 0.30 \text{ J/N}$) (26). The lower cost of ground force and slightly faster rates of force application during skiing quantitatively explain why legs-only skiing is 30–50% more economical than running over the range of speeds we tested. In practice, the cost of skiing can be reduced further by providing propulsive force with the arms, because the poles allow long periods of arm force application. Skiers can cover >250 miles in a day and can race hilly 6-mile courses at paces <4 min/mile, largely because skis lower the cost of supporting the body against gravity and poles economize propulsion.

Conclusion

The constant relationships between net ground force, rates of force application, and metabolic rates under numerous skiing conditions lead us to conclude that the energetic cost of cross-country skiing is set by the generation of force to support the weight of the body and overcome friction. Our results provide further evidence that the generation of net support and propulsive forces sets the metabolic cost of locomotion in general and also explain how the simple devices humans have used for centuries lower this cost. Skis reduce the cost of transport by allowing skiers to support their weight relatively passively during a fraction of each stride. By providing all the support force passively, bicycles lower transport costs further still (7), because the only muscular requirement is to generate the low pedal forces necessary for propulsion.

Finally, we conclude that metabolic rates during weight-bearing locomotion depend on the magnitude of the force applied to the ground and the time course of muscular activation.

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