

Energy cost and muscular activity required for propulsion during walking

Jinger S. Gottschall and Rodger Kram

Department of Kinesiology and Applied Physiology, University of Colorado, Boulder, Colorado 80309

Submitted 23 July 2002; accepted in final form 23 December 2002

Gottschall, Jinger S. and Rodger Kram. Energy cost and muscular activity required for propulsion during walking. *J Appl Physiol* 94: 1766–1772, 2003. First published December 27, 2002; 10.1152/jappphysiol.00670.2002.—We reasoned that with an optimal aiding horizontal force, the reduction in metabolic rate would reflect the cost of generating propulsive forces during normal walking. Furthermore, the reductions in ankle extensor electromyographic (EMG) activity would indicate the propulsive muscle actions. We applied horizontal forces at the waist, ranging from 15% body weight aiding to 15% body weight impeding, while subjects walked at 1.25 m/s. With an aiding horizontal force of 10% body weight, 1) the net metabolic cost of walking decreased to a minimum of 53% of normal walking, 2) the mean EMG of the medial gastrocnemius (MG) during the propulsive phase decreased to 59% of the normal walking magnitude, and yet 3) the mean EMG of the soleus (Sol) did not decrease significantly. Our data indicate that generating horizontal propulsive forces constitutes nearly half of the metabolic cost of normal walking. Additionally, it appears that the MG plays an important role in forward propulsion, whereas the Sol does not.

biomechanics; locomotion; energetic cost; electromyography

WALKING IS SIMPLE TO DO BUT surprisingly difficult to understand scientifically. During walking, the need to generate various muscular forces creates a metabolic demand. We focused on two questions specific to the energetic cost and muscle activity needed for propulsion. First, what portion of the metabolic cost of walking is required for generating horizontal propulsive forces? Second, what are the individual roles of the ankle extensor muscles in producing forward propulsion?

Energetics. Past research illustrates that energy consumption during locomotion increases in proportion to external horizontal forces that impede forward motion. For instance, Donovan and Brooks (11) determined that in walking there was a positive linear relationship between a horizontal impeding force and energy expenditure. Using a wind tunnel, Pugh (25) found that energy cost for both walking or running, increased with the impeding horizontal wind force. Similarly, Bijker et al. (2), Cooke et al. (6), and Lloyd and Zacks (17) found that for running against a horizontal force applied with a harness, energy consumption increased proportion-

ally. Chang and Kram (5) utilized a similar method but also studied aiding forces to quantify the energetic demand of generating horizontal forces during normal running. They concluded that propulsive forces constitute more than one-third of the metabolic cost of running. However, there is little information regarding the energy cost of horizontal propulsion during walking.

Our first aim was to alter the horizontal forces generated during walking and to measure the corresponding changes in metabolic rate. To do so, we applied constant levels of external horizontal force at the waist. Our rationale for this part of this study was that when we provided an external horizontal aiding force, the reduction in energy consumption would reflect the metabolic cost of generating horizontal propulsive forces during normal walking. Furthermore, we determined the energetic cost of propulsion by applying an external horizontal impeding force. We hypothesized that metabolic rate would decrease with aiding forces and increase with impeding forces.

Muscle activity. In walking, the leg muscles perform a variety of functions during a stride. Throughout the second half of stance, one mechanical responsibility of the muscles is to propel the body forward. However, there is little consensus regarding the functional role of the individual ankle extensors while walking. For example, Hill (14) and Winter (31) concur that the major contributors to propulsion are the ankle extensors. In contrast, Sutherland et al. (28) surmised that the ankle extensors primarily act to restrain forward momentum. Alternatively, Hof et al. (15) and Meinders et al. (19) suggested that the primary function of the ankle extensors is to provide the energy necessary for swing initiation. Most recently, a model developed by Neptune et al. (22) concluded that the primary function of the medial gastrocnemius (MG) is to brake the trunk during midstance and that the main action of the soleus (Sol) is to aid in propulsion during the second half of stance. These studies disagree both as to which muscles are responsible for propulsion, as well as the functions of the individual ankle extensors.

Our second aim was to alter the horizontal forces generated during walking and to measure the corresponding changes in ankle extensor electromyographic (EMG) activity. Our rationale for this part of the study

Address for reprint requests and other correspondence: J. S. Gottschall, Dept. of Kinesiology and Applied Physiology, Univ. of Colorado, Campus Box 354, Boulder, CO 80309-0354 (E-mail: gottscha@ucsu.colorado.edu).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

was that by providing an external horizontal aiding force, the EMG of the specific ankle extensor muscles involved in generating horizontal forces during normal walking would decrease. We further investigated the muscular actions needed for propulsion against an external horizontal impeding force. We hypothesized that ankle extensor EMG during the propulsive phase would decrease with aiding forces and increase with impeding forces.

METHODS

Subjects. Five men and five women volunteered [age = 27.35 ± 5.08 (SD) yr, height = 1.74 ± 0.04 m, mass = 66.68 ± 9.03 kg]. All of these healthy subjects gave written informed consent that followed the guidelines of the University of Colorado Human Research Committee.

Protocol. Each subject was introduced to treadmill walking, performed a standing trial, and then completed eight experimental trials. We familiarized the subjects with treadmill locomotion within 7 days of actual data collection. Next, after a 7-min standing trial, subjects walked at a speed of 1.25 m/s on a motorized treadmill. Each walking trial lasted 7 min with 3 min between each trial. The subjects walked with no applied horizontal force (0% AHF) at both the beginning and the end of the experiment. Stride frequency (strides/min) was determined during the first trial by counting strides for 30 s and multiplying by two. Subjects then matched a metronome set to that frequency for the remaining trials. We then applied horizontal forces, either aiding or impeding, equal to 5, 10, and 15% of the subject's body weight. We randomized the order of aiding and impeding forces and the order of the 5, 10, and 15% trials.

Horizontal pulling apparatus. We applied aiding and impeding forces by using a waist belt worn near the center of mass (Fig. 1). The waist belt was connected to lengths of rubber tubing that were stretched over a series of low-friction pulleys. The rubber tubing was stretched to approximately two to three times its resting length so that small changes in length would not substantially change the applied force. Thus almost constant horizontal forces were applied. The magnitude of the AHF was adjusted by altering the number of rubber tubing elements in parallel and by stretching the tubing with a hand winch. We monitored the AHF with a force transducer (Omega Engineering, Stamford, CT) in se-

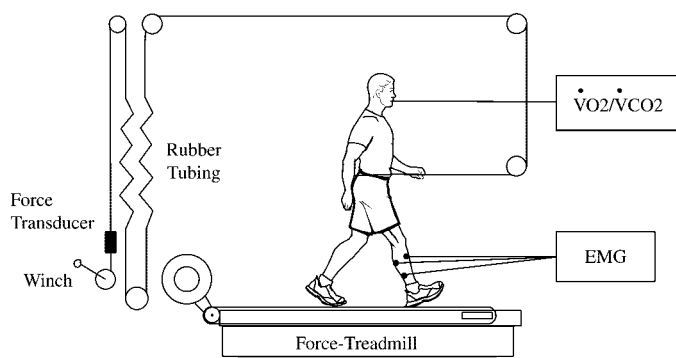


Fig. 1. Schematic of experimental setup. Rubber tubing was stretched over low-friction pulleys with a hand winch to apply a near-constant applied horizontal force to subjects walking on a force treadmill. Aiding applied horizontal force is shown. Treadmill belt and walking direction were reversed for impeding force trials. $\dot{V}O_2$, oxygen uptake; $\dot{V}CO_2$, carbon dioxide production; EMG, electromyography.

ries with the rubber tubing. Subjects were provided with a digital display of the AHF and asked to maintain the desired level of force by walking at the appropriate position on the treadmill. AHFs were maintained within $\pm 5\%$ of the desired value for each condition. The horizontal pulling apparatus was similar to the device utilized by Chang and Kram (5).

Ground reaction forces. To verify the desired effect of AHF on ground reactions forces (GRF), we utilized a treadmill mounted on a force platform (16). For each trial, we collected vertical and horizontal components of the GRF for 10 s at 1,000 Hz. The GRF data were filtered by using a fourth-order Butterworth low-pass filter with a cutoff frequency of 20 Hz. We detected each heel strike by calculating the center of pressure translation. On a force treadmill, the center of pressure suddenly shifts anteriorly with each heel strike event (9). Across all conditions of AHF, the average vertical GRF during a complete stride was equal to body weight and did not change significantly ($P = 0.78$). This indicates that our device appropriately applied only horizontal force to the subject. The horizontal GRF data were used to calculate horizontal propulsive impulses for each trial. The force treadmill cannot distinguish the individual foot horizontal GRFs during double support. Thus we could only determine the single-stance horizontal propulsive and braking impulses. During normal symmetrical walking, each foot is on the ground for 62% of the gait cycle. During the first half of that stance time (0–31%), there is a braking ground reaction force, and during the second half (31–62%) there is a propulsive ground reaction force. However, at 50% of the stride, the opposite foot is placed on the ground and for the first 12% of the gait cycle the opposite foot is in the process of toeing off (27, 29). Therefore, we calculated the single-stance impulses by integrating the positive, propulsive horizontal GRF values for 31–50% of the gait cycle and the negative, braking horizontal GRF values for 12–31% of the gait cycle for 10 complete, successive strides. These percentages were used for all subjects.

Energetic measurements. To quantify the effect of AHF on the metabolic cost of walking, we measured the rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) by using an open-circuit respirometry system (Physio-Dyne Instrument, Quogue, NY). Before beginning the experimental trials, we measured standing metabolic rate. For all trials, we allowed 3 min for the subjects to reach steady state and then calculated the average $\dot{V}O_2$ (ml O₂/s) and $\dot{V}CO_2$ (ml CO₂/s) for the subsequent 3 min. We calculated metabolic rate (W/kg) by using a standard equation (3). Lastly, we subtracted the standing value from the experimental values to derive net metabolic rate.

EMG measurements. To quantify the effect of AHF on muscle activity, we measured EMG signals by using a telemetered amplifier system (Noraxon, Scottsdale, AZ). Before electrode placement, we prepared the shaved skin with fine sandpaper and alcohol. We placed bipolar, silver-silver chloride surface electrodes (1-cm-diameter disks) over three muscles [MG, Sol, and anterior tibialis (AT)] of the right leg according to the recommendations by Cram and Kasman (8). Sutherland et al. (28) and Winter (31) documented that the EMG patterns of both heads of the gastrocnemius are similar in terms of the timing of activation during walking. For the MG and AT, we placed the electrodes over the approximate center of the muscle belly. For the Sol, we placed the electrodes over the distal third of the muscle lateral to the gastrocnemius. The interelectrode distance was 2 cm. The EMG amplifier had a gain of 1,700 and filtered the data with band-pass frequencies of 16–500 Hz. We verified that the cross talk between muscles was negligible with a series of

contractions suggested by Winter et al. (32). Each subject's electrodes remained in place for all trials without being removed or replaced.

After data collection at a rate of 1,000 Hz, we filtered, rectified, and averaged the EMG data. Specifically, we digitally filtered the signals with a zero-lag, second-order Butterworth filter with an effective band pass of 10–500 Hz. We full-wave rectified the signals, calculated the mean EMG (mEMG) amplitude for 31–62% of the gait cycle, and averaged 10 consecutive strides for each level of AHF. We averaged just 31–62% of the gait cycle so as to consider only the second half of the stance phase, the propulsive phase of walking. For each subject, we compared the relative muscle activity between AHF levels by using the mEMG normalized to the 0% AHF condition. To determine whether our conclusions would change if we accounted for electromechanical delay (EMD) (7, 24), we shifted the EMG values by +30 ms in time. However, unless specified, our EMG results refer to data that were not EMD adjusted.

Statistical analysis. Energetic and electromyographic data from this study were analyzed across all conditions by using a repeated-measures, seven-level design (ANOVA). We performed Tukey's honestly significant difference post hoc test to analyze the differences between each level of AHF. Significance was defined as $P \leq 0.05$.

RESULTS

Our device had the desired effects of providing much of the propulsive impulse (aiding AHF) and demanding much more propulsive impulse (impeding AHF). With an aiding force of 10% body weight, the mean horizontal propulsive impulse decreased to a minimum of 21% of the normal walking value, whereas the mean horizontal braking impulse increased to a maximum of 154% (Table 1). In contrast, with an impeding force of 15% body weight, the mean horizontal propulsive impulse increased to maximum of 192% of the normal walking value as the mean horizontal braking impulse decreased to a minimum of 10%. Figure 2 demonstrates these impulse trends graphically with the horizontal GRF vs. time plotted for one subject.

Table 1. Metabolic and impulse data for each applied horizontal force condition

Condition	$\dot{V}O_2$, ml·kg ⁻¹ min ⁻¹	$\dot{V}CO_2$, ml·kg ⁻¹ min ⁻¹	Metabolic Rate, W/kg	Propulsive Impulse, N/s	Braking Impulse, N/s
15A	5.2 ± 1.0	4.3 ± 0.9	1.8 ± 0.4	2.7 ± 0.9	20.8 ± 4.5
10A	3.9 ± 0.6	3.3 ± 0.5	1.3 ± 0.2	2.4 ± 0.8	18.9 ± 3.8
5A	4.5 ± 0.9	3.7 ± 0.8	1.5 ± 0.3	7.7 ± 1.8	13.7 ± 2.7
0	7.4 ± 0.7	6.0 ± 0.6	2.5 ± 0.2	11.5 ± 1.9	11.7 ± 1.9
5I	12.1 ± 1.0	10.6 ± 0.6	4.2 ± 0.3	16.2 ± 3.0	9.2 ± 1.5
10I	18.4 ± 0.9	15.8 ± 1.0	6.3 ± 0.3	19.7 ± 3.3	3.2 ± 1.0
15I	25.2 ± 1.1	22.5 ± 1.3	8.8 ± 0.3	22.1 ± 4.1	1.2 ± 0.7

Values are means ± SD for 10 subjects. $\dot{V}O_2$, oxygen consumption; $\dot{V}CO_2$, carbon dioxide production; 5 A, 10 A, 15 A, aiding horizontal force equal to 5, 10, and 15% of the subject's body weight, respectively; 0, no applied horizontal force; 5 I, 10 I, 15 I, impeding horizontal force equal to 5, 10, and 15% of the subject's body weight, respectively. Mean metabolic rate and braking impulse decreased with aiding forces and increased with impeding forces compared with normal walking. In contrast, propulsive impulse decreased with aiding forces and increased with impeding forces. All variables showed significant trends ($P < 0.01$).

Energetics. With an aiding horizontal force of 10% body weight, the net metabolic cost of walking decreased to a minimum of just 53% of normal walking (Table 1, Fig. 3). Thus we conservatively infer that generating horizontal propulsive forces constitutes about one-half of the net metabolic cost of normal walking. The energetic cost of generating propulsive forces in normal walking may be even greater than this estimate because our apparatus did not entirely remove the need to generate propulsive force. Furthermore, in the aiding AHF trials, greater braking impulse was generated, and that extra cost may have mitigated the true reduction in the cost of propulsion. With an aiding force of 15% body weight, metabolic rate was greater than the aiding force of 10% body weight condition, resulting in a J-shaped curve.

In contrast, net metabolic rate increased with impeding horizontal forces (Table 1, Fig. 3). With an impeding force of 15% body weight, net metabolic cost of walking increased to a maximum of 344% of normal walking. With an impeding force of 10% body weight, metabolic rate was 250% greater than normal walking. Thus impeding forces increased the net metabolic cost of walking substantially more than the aiding forces decreased metabolic cost.

The $\dot{V}O_2$ data for standing and normal walking (Table 1) were consistent with previous studies (18, 30). For the standing trials, subjects had a $\dot{V}O_2$ of 4.92 ± 0.23 (SD) ml·kg⁻¹·min⁻¹. The metabolic rates for walking at each level of both aiding and impeding AHF differed from each other and normal walking ($P < 0.01$).

Muscle activity. With an aiding force of 10% body weight, the mEMG of the MG during the propulsive phase decreased to a minimum 59% of the normal walking magnitude (Fig. 4A). With an impeding force of 15% body weight, MG mEMG increased to a maximum of 190% of the normal walking magnitude. The MG mEMG for each condition was significantly different from normal walking except for the impeding force of 5% body weight trial.

In contrast to the MG, with aiding forces, the Sol mEMG during the propulsive phase did not differ significantly from normal walking (Fig. 4B). With an aiding force of 10% body weight, Sol mEMG only decreased by an insignificant 7% of the normal walking magnitude. However, with an impeding force of 15% body weight, Sol mEMG increased to 159% of normal walking. The mean Sol EMG for both the impeding forces of 10 and 15% body weight significantly differed from normal walking. The AT mEMG during the propulsive phase did not differ significantly from normal walking with either aiding or impeding AHF (Fig. 4C). Therefore, our MG and Sol results are not due to changes in cocontraction. Adjustment of the data for EMD made no change to any of our EMG conclusions.

DISCUSSION

Energetics. We accept our hypothesis that metabolic rate decreases with aiding forces and increases with

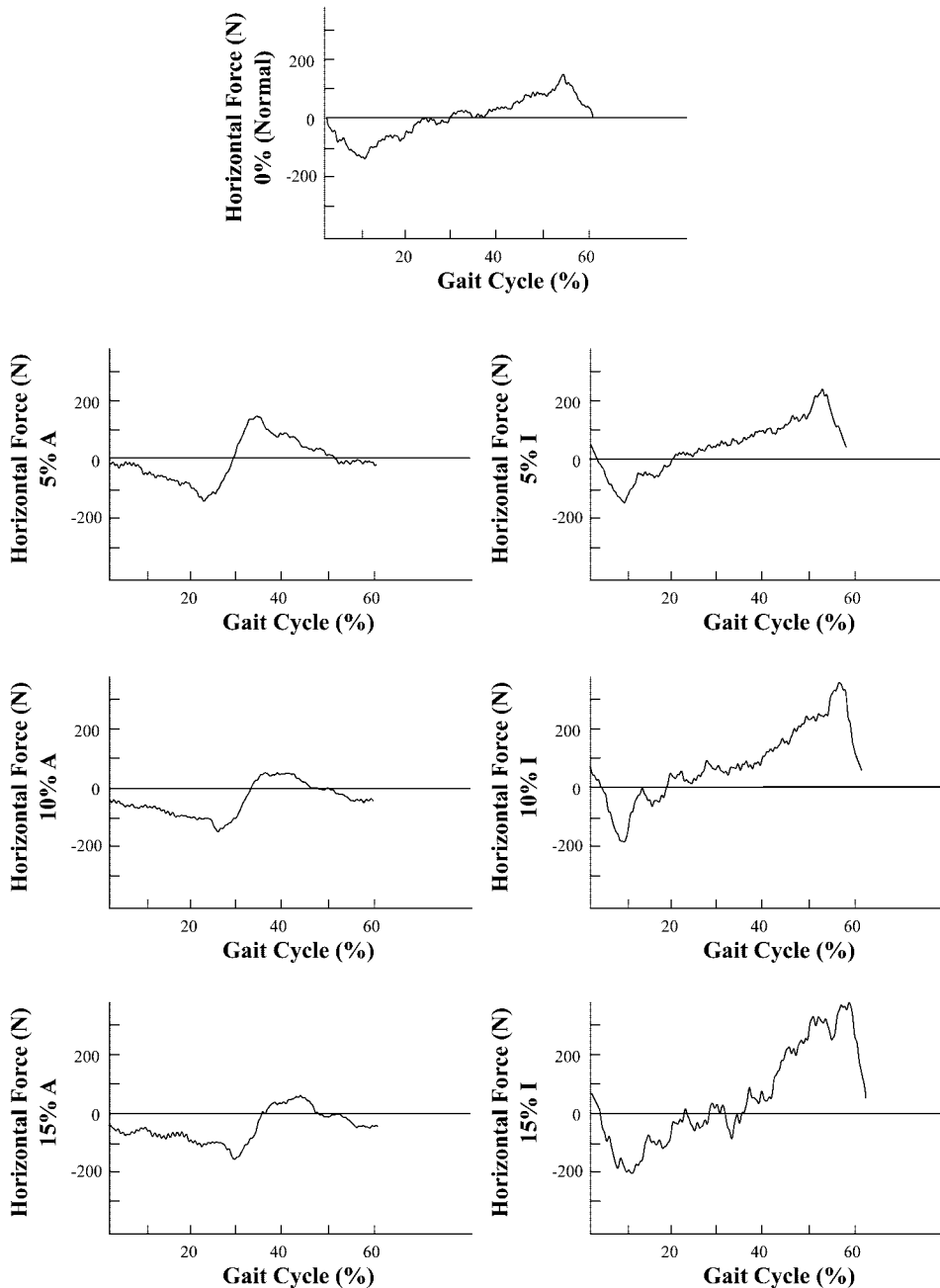


Fig. 2. Horizontal ground reaction forces vs. percentage of the gait cycle for 1 subject. A, aiding horizontal force; I, impeding horizontal force; 5, 10, and 15%, percentage of subject's body weight; 0%, no applied horizontal force (normal walking). Compared with normal walking, with aiding horizontal forces, propulsive forces were reduced, whereas braking forces were greater and began earlier. With impeding horizontal forces, propulsive forces were greater and began earlier, whereas braking forces were reduced. For experimental conditions with external applied horizontal forces, the ground reaction force offset is due to the constant applied force.

impeding forces (Fig. 3). Some specific details deserve comment. First, the greater metabolic cost with an aiding force of 15% body weight, compared with 10% body weight may be due to increased muscular effort for braking (Table 1). Second, as the subjects walked with impeding forces, metabolic cost increased with a greater slope than for aiding forces. This is presumably due to differences in the energetic cost of producing concentric (propulsive) vs. eccentric (braking) forces (1, 4, 33). Compared with normal walking, with aiding AHF, subjects produced less propulsive impulse but more braking impulse (Table 1). With impeding AHF, subjects produced more propulsive impulse but less braking impulse. Overall, AHF influenced metabolic rate in the predicted directions.

Our metabolic data resemble the classic study of uphill and downhill walking by Margaria (18). Both methods elicited a J-shaped curve for $\dot{V}O_2$. However, we compare these two studies with caution because of the differences in the controlled variables. In the present study, the treadmill remained level and so the gravitational potential energy fluctuations remained the same. In contrast, during slope walking, gravitational potential energy steadily increases uphill or decreases downhill. Exchange of kinetic and gravitational potential energy is a critical aspect of walking mechanics, and the exchange process may be different between slope walking and walking with AHF.

Donelan et al. (10) developed a concept that helps explain why metabolic cost decreases with aiding

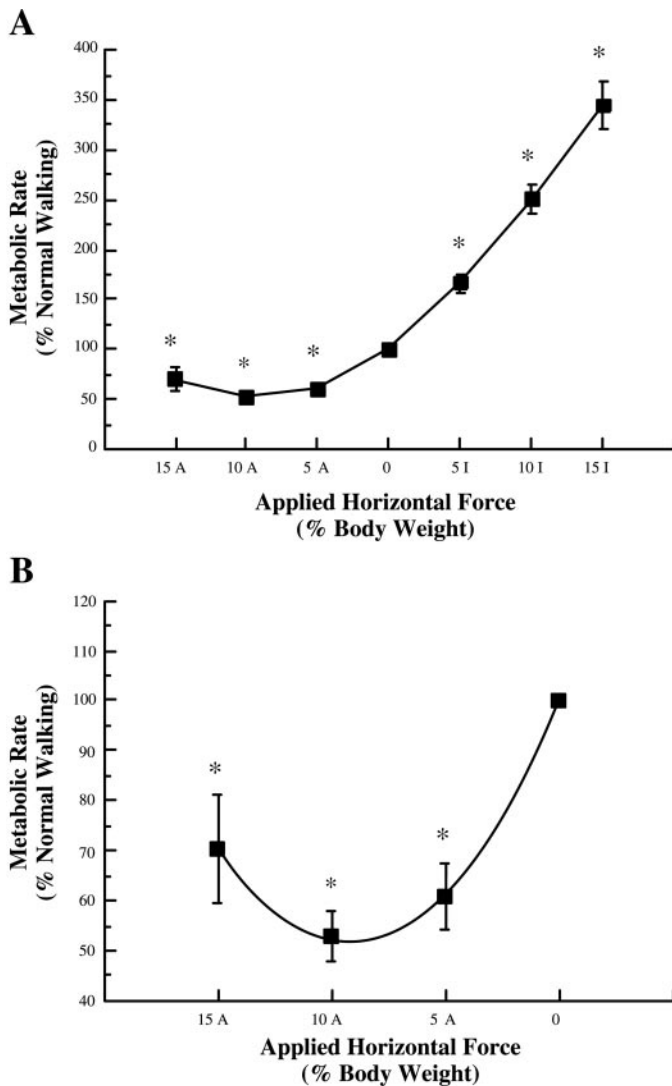


Fig. 3. A: metabolic rates relative to normal walking value vs. horizontal force. With an aiding horizontal force of 10% body weight, the net metabolic cost of walking decreased to 53% of normal walking ($P < 0.0001$). With an impeding force of 10% body weight, the net metabolic cost of walking increased to 250% of normal walking ($P < 0.0001$). Before normalization, we used a repeated-measures ANOVA to determine whether applied horizontal force had a significant effect on relative metabolic rates compared with normal walking [$F(6,9) = 418.67$, $P < 0.0001$]. B: metabolic rates relative to normal walking value vs. aiding horizontal force. Line is a second-order polynomial least squares fit ($y = 14.2x^2 - 61.1x + 117.7$, $R^2 = 0.99$). Values are means \pm SD. * $P \leq 0.05$.

forces. During the single-stance phase of walking, the center of mass motion is similar to a passive inverted pendulum. However, the double-support phase is a transition from one pendulum to another, necessitating an active redirection and restoration of the center of mass velocity, termed a step-to-step transition. This requires upward- and forward-directed forces. During the aiding force trials, our applied horizontal pulling apparatus likely provided some of this force, thereby decreasing metabolic cost.

Our metabolic data for impeding forces are nearly identical to those of Donovan and Brooks (11). They

showed data for nine subjects walking at 1.25 m/s with impeding forces of ~5, 10, and 14% body weight (assuming 70 kg). Specifically, Donovan and Brooks reported values of 4.1, 6.6, and 9.1 W/kg for metabolic rate, whereas we found 4.2, 6.3, and 8.8 W/kg. In both studies, metabolic rate increased linearly with impeding horizontal force.

Generally, the metabolic rate patterns we found for walking with AHF parallel those found for running (5). Metabolic rate curvilinearly decreased with aiding forces and increased linearly with impeding forces. However, the percentage of metabolic cost required to generate horizontal propulsive forces differs considerably: 47% for walking vs. 33% for running. Our data suggest that during steady-speed walking, the metabolic costs of generating vertical and horizontal forces are similar, whereas during running, generating vertical forces is twice as expensive as horizontal (5).

The metabolic cost of supporting weight depends on how the legs are oriented during stance and the magnitudes of ground reaction forces. During the stance phase of walking, the knee typically never flexes $>20^\circ$, and the peak resultant ground reaction force is about one and one-third times body weight (28). In contrast, during the stance phase of running, the knee can flex up to 40° (20), and the resultant ground reaction force is between two and three times body weight (21). Thus, in running, the combination of increased knee flexion and increased ground reaction forces demands greater muscle forces and metabolic cost.

Muscle activity. For the MG, we accept our hypothesis that mEMG during the propulsive phase decreases with aiding forces and increases with impeding forces. Compared with normal walking (0% AHF), with an aiding force of 10% body weight, MG mEMG decreased by 41%. Although this decrease in MG mEMG with aiding forces indicates a significant role in propulsion, the MG probably plays other functional roles, perhaps accelerating the leg into swing (15). With an impeding force of 10% body weight, MG mEMG increased by 65%. This is further evidence of the propulsive role of the MG, and it indicates that overcoming impeding forces requires an increased amount of muscle recruitment.

In contrast, for the Sol, we reject our hypothesis that EMG during the propulsive phase decreases with aiding forces. Compared with normal walking (0% AHF), Sol mEMG did not significantly change with any amount of aiding force. However, with an impeding force of 10% body weight, Sol mEMG increased by 43%. The increase in Sol mEMG with impeding forces suggests that among the ankle extensors, the MG is the primary propulsor but that the Sol can serve a synergistic role when propulsive demands are great. In summary, our data indicate that the MG plays an important role in forward propulsion during normal walking, whereas the Sol does not.

There are alternative explanations for our EMG results. It may be suggested that whereas the MG can be modulated in response to changes in external loads, the Sol cannot. However, Ferris et al. (12) demon-

strated that in simulated reduced gravity walking Sol activity decreases. Therefore, Sol can be modulated, but it was not modulated in response to aiding AHF. Another possibility is that the Sol cannot be derecruited due to its contribution to knee extension (34). That is, the Sol may be important for propulsion; how-

ever, its activity may not decrease with aiding AHF because of an increased need for knee extension.

Our results agree with previous research when viewed at the level of the muscle group. Hill (14), Winter (31), and Neptune et al. (22) all concluded that the ankle extensor group contributes to forward progression. Neptune et al. and the present study specifically examined the role of the ankle extensors at the individual muscle level. Both studies demonstrate that the MG plays an important role in propulsion. However, the model of Neptune et al. indicated that the Sol provides a major amount of propulsion, whereas our experimental results show that the Sol provides a minimal amount of propulsion during normal walking. This discrepancy could be further investigated in a number of ways. First, our constant horizontal pulling force could be simulated in the Neptune et al. model. Furthermore, it may be useful to simulate a time-varying force applied at the center of mass that mimics the normal propulsive GRF during the second half of stance. It also remains to be experimentally resolved what other muscles are responsible for propulsion and what other functions the ankle extensor muscles perform.

Our apparatus was simple and our experimental design was clear, yet, there were inherent limitations to our study. Our apparatus applied constant aiding and impeding forces at the waist, as an indirect means of altering the propulsive forces generated with the lower leg. To gain insight strictly regarding propulsion would require applying the aiding forces during the second half of stance only. Our EMG technique provided reliable information regarding the timing and magnitude of muscle activation, but EMG is not a direct measure of force. Finally, our whole body metabolic measurements cannot identify which specific muscles are consuming the energy. A complete understanding of the ankle extensors' propulsive role requires investigating the muscle and tendon functions more directly (13, 26). Even with these limitations, our experimental design tested both the energetic and muscle activity hypotheses.

Overall, we infer that the 47% reduction in metabolic rate, when an external horizontal aiding force is applied, reflects the cost of generating horizontal propulsive forces during normal walking. The 60% reduction in MG activity reflects its important role in generating

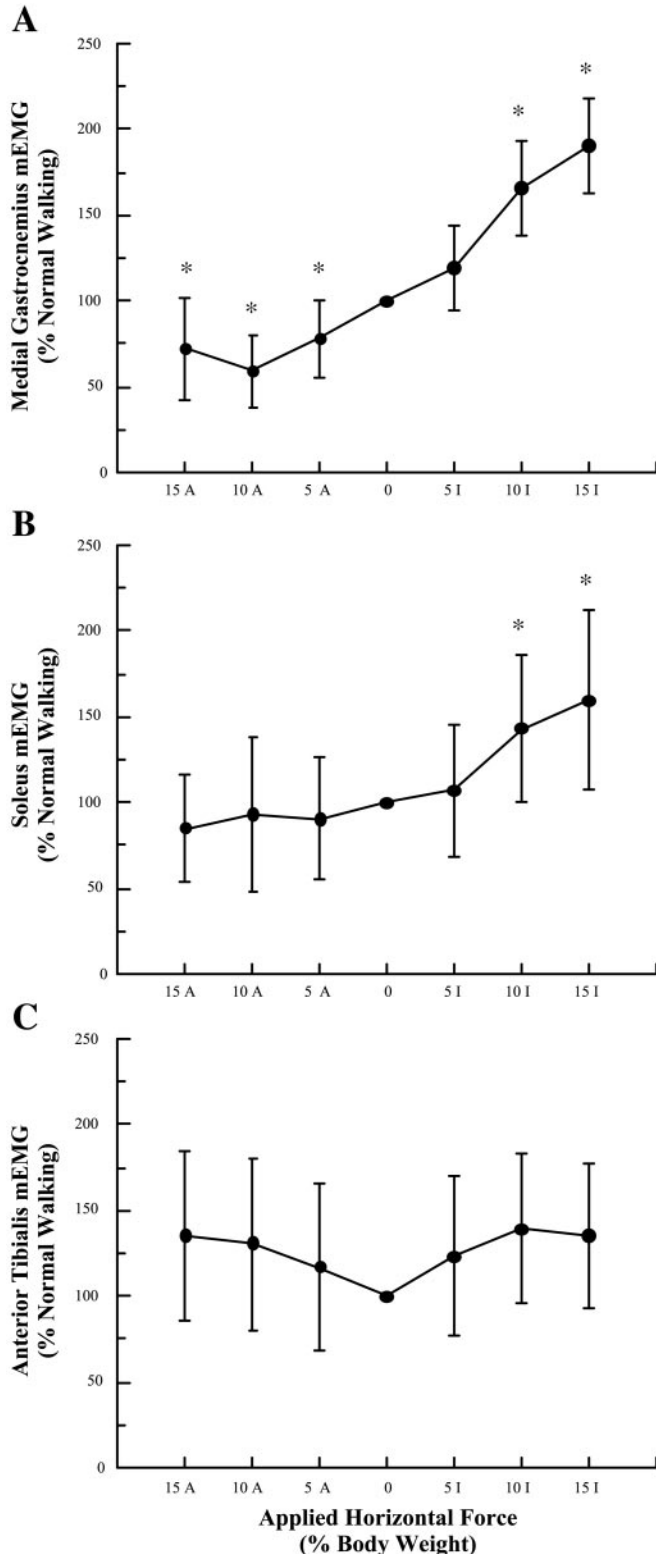


Fig. 4. Mean muscle EMG (mEMG) during the propulsive phase relative to normal walking value vs. applied horizontal force. Before normalization, we used a repeated-measures ANOVA to determine whether applied horizontal force had a significant effect on muscle activity compared with normal walking. *A*: with an aiding horizontal force of 10% body weight, medial gastrocnemius mEMG decreased to 59% of normal walking. With an impeding force of 10% body weight, medial gastrocnemius mEMG increased to 166% of normal walking [$F(6,9) = 34.28, P < 0.0001$]. *B*: soleus mEMG was not significantly different from normal walking for any level of aiding force. With an impeding force of 10% body weight, soleus mEMG increased to 143% of normal walking [$F(6,9) = 4.49, P < 0.05$]. *C*: anterior tibialis mEMG was not significantly different from normal walking for any level of aiding or impeding force [$F(6,9) = 3.62$]. Values are means \pm SD. * $P \leq 0.05$.

forward propulsion, whereas the insignificant reduction in Sol activity indicates that it performs functions other than propulsion.

We thank Chet Moritz for invaluable assistance in writing the analysis program for the detection of heel strikes. We also thank past and present members of the University of California at Berkeley and University of Colorado Locomotion Laboratory for insightful comments and suggestions.

This work was supported by National Institute of Arthritis and Musculoskeletal and Skin Diseases Grant AR-44688.

REFERENCES

1. **Abbott BC, Bigland B, and Richie JM.** The physiological cost of negative work. *J Physiol* 117: 380–390, 1952.
2. **Bijker KE, De Groot G, and Hollander AP.** Delta efficiencies of running and cycling. *Med Sci Sports Exerc* 33: 1546–1551, 2001.
3. **Brockway JM.** Derivation of formulae used to calculate energy expenditure in man. *Hum Nutr Clin Nutr* 41: 463–471, 1987.
4. **Cavanagh PR and Kram R.** Mechanical and muscular factors affecting the efficiency of human movement. *Med Sci Sports Exerc* 17: 326–331, 1985.
5. **Chang YH and Kram R.** Metabolic cost of generating horizontal forces during human running. *J Appl Physiol* 86: 1657–1662, 1999.
6. **Cooke CB, McDonagh MJ, Nevill AM, and Davies CT.** Effects of load on oxygen intake in trained boys and men during treadmill running. *J Appl Physiol* 71: 1237–1244, 1991.
7. **Corcos DM, Gottlieb GL, Latash ML, and Agarwal GC.** Electromechanical delay—an experimental artifact. *J Electromyogr Kinesiol* 2: 59–68, 1992.
8. **Cram JR and Kasman GS.** Electrode placements. In: *Introduction to Surface Electromyography*, edited by Cram JR, Kasman GS, and Holz J. Gaithersburg, MD: Aspen, 1998, p. 371–375.
9. **Davis BL and Cavanagh PR.** Decomposition of superimposed ground reaction forces into left and right force profiles. *J Biomech* 26: 593–597, 1993.
10. **Donelan JM, Kram R, and Kuo AD.** Simultaneous positive and negative external mechanical work in human walking. *J Biomech* 35: 117–124, 2002.
11. **Donovan CM and Brooks GA.** Muscular efficiency during steady-rate exercise. II. Effects of walking speed and work rate. *J Appl Physiol* 43: 431–439, 1977.
12. **Ferris DP, Aagaard P, Simonsen EB, Farley CT, and Dyhre-Poulsen P.** Soleus H-reflex gain in humans walking and running under simulated gravity. *J Physiol* 530: 167–180, 2001.
13. **Fukunaga T, Kubo K, Kawakami Y, Fukashiro S, Kanehisa H, and Maganaris CN.** In vivo behaviour of human muscle tendon during walking. *Proc R Soc Lond B Biol Sci* 268: 229–233, 2001.
14. **Hill AV.** The mechanics of active muscle. *Proc R Soc Lond B Biol Sci* 141: 104–117, 1953.
15. **Hof AL, Nauta J, van der Knaap ER, Schallig MAA, and Struwe DP.** Calf muscle work and segment energy changes in human treadmill walking. *J Electromyogr Kinesiol* 2: 203–216, 1993.
16. **Kram R, Griffin TM, Donelan JM, and Chang YH.** Force treadmill for measuring vertical and horizontal ground reaction forces. *J Appl Physiol* 85: 764–769, 1998.
17. **Lloyd BB and Zacks RM.** The mechanical efficiency of treadmill running against a horizontal impeding force. *J Physiol* 223: 355–363, 1972.
18. **Margaria R.** *Biomechanics and Energetics of Muscular Exercise*. Oxford, UK: Clarendon, 1976.
19. **Meinders M, Gitter A, and Czerniecki JM.** The role of ankle plantar flexor muscle work during walking. *Scand J Rehabil Med* 30: 39–46, 1998.
20. **Miller DI.** Ground reaction forces in distance running. In: *Biomechanics of Distance Running*, edited by Cavanagh PR. Champaign, IL: Human Kinetics, 1990, p. 203–224.
21. **Millron MJ and Cavanagh PR.** Sagittal plane kinematics of the lower extremity during distance running. In: *Biomechanics of Distance Running*, edited by Cavanagh PR. Champaign, IL: Human Kinetics, 1990, p. 65–99.
22. **Neptune RR, Kautz SA, and Zajac FE.** Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking. *J Biomech* 34: 1387–1398, 2001.
23. **Nilsson J and Thorstensson A.** Ground reaction forces at different speeds of human walking and running. *Acta Physiol Scand* 136: 217–227, 1989.
24. **Prilutsky BI and Gregor RJ.** Swing and support related muscle actions differentially trigger human walk-run and run-walk transitions. *J Exp Biol* 204: 2277–2287, 2001.
25. **Pugh LGCE.** The influence of wind resistance in running and walking and the mechanical efficiency of work against horizontal or vertical forces. *J Physiol* 213: 255–276, 1971.
26. **Roberts TJ, Marsh RL, Weyand PG, and Taylor CR.** Muscular force in running turkeys: the economy of minimizing work. *Science* 275: 1113–1115, 1997.
27. **Sutherland DH and Cooper L.** The events of gait. *Bull Prosthet Res* 10: 281–282, 1981.
28. **Sutherland DH, Cooper L, and Daniel D.** The role of the ankle plantar flexors in normal walking. *J Bone Joint Surg Am* 62: 354–363, 1980.
29. **Sutherland DH, Kaufman KR, and Moitza JR.** Kinematics of normal walking. In: *Human Walking*, edited by Rose J and Gamble JG. Baltimore, MD: Williams & Wilkins, 1994, p. 23–44.
30. **Waters RL and Mulroy S.** The energy expenditure of normal and pathologic gait. *Gait Posture* 9: 207–231, 1999.
31. **Winter DA.** Energy generation and absorption at the ankle and knee during fast, natural, slow cadences. *Clin Orthop* 175: 147–154, 1983.
32. **Winter DA, Fuglevand AJ, and Archer SE.** Crosstalk in surface electromyography: theoretical and practical estimates. *J Electromyogr Kinesiol* 4: 15–26, 1994.
33. **Wolledge RC, Curtin NA, and Homsher E.** *Energetic Aspects of Muscle Contraction*. London: Academic, 1985.
34. **Zajac FE and Gordon ME.** Determining muscle's force and action in multi-articular movement. *Exerc Sport Sci Rev* 17: 187–230, 1989.