

Title	Minimum oxygen cost of human walking with geometrically similar leg movements
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Citation	Therapeutic research, 30(1): 113-124
Date of issue	2009-01-20
URL	http://hdl.handle.net/10173/741
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Text version	publisher



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Minimum Oxygen Cost of Human Walking with Geometrically Similar Leg Movements

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ABSTRACT

The mechanism by which the expenditure of oxygen to walk per unit distance at an intermediate speed is minimized, by definition *optimal walking*, was investigated to characterize optimal walking in humans with variations in individual walking speeds. Oxygen uptake and step rate (*SR*) were measured among 7 young male subjects walking at an increasing speed from 16.7 to 131.7 m min⁻¹ with 5 m min⁻¹ increments every 1 min on a level treadmill. Measurements of leg length (*L*) were also made and step length (*SL*) was calculated by dividing walking speed by *SR*. The hip joint angle (θ) was calculated as a function of both *L* and *SL* such that $\theta = 2\sin^{-1}[SL/(2L)]$ deduced from a mathematical geometrically similar model of pendulum-like legs. The minimum oxygen cost to walk per unit distance for each subject was observed over a wide range of speeds from 60 to 100 m min⁻¹. However, the oxygen cost of walking for all the subjects was minimized during a step cycle through a hip-joint angle of about 46 deg in the astride position, regardless of *L*. The stiff-legged model demonstrated that the pathway of the trunk during optimal walking with a swing leg angle of 46 deg was approximately maintained at an even level by the counteracting effects of the leg decline and the heel rise. These results suggest that the minimum oxygen cost of transport during optimal walking was achieved by the mechanism underlying the maximum interchange between the gravitational-potential and kinetic energy for the body with an even level of the trunk that reduces extra muscular work needed against internal and external resistance, as well as against gravity.

Key words : Metabolic cost, Optimal walking, Optimal speed, Step length, Step rate, Strouhal number

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INTRODUCTION

In human walking, both step length (SL) and step frequency (rate) are a major determinant of speed of transport. Walking speed, SL , and step rate (SR) are the gait characteristics that are essential for understanding walking in terms of a fundamental aspect of kinematics, biomechanics, and energetics. There have been many studies on the relationship between walking speed and the expenditure of metabolic energy in humans, as well as in animals^{1~6}). In addition, several studies have also demonstrated that the energetic costs of level walking per unit distance for humans were minimized at an intermediate speed, the optimal speed, but that a certain variation existed with respect to individual optimal walking speeds even in adults^{7~9}). Although in their papers either information about optimal speeds or how humans walk at optimal speeds was offered, the variation in individual optimal walking speeds has not been fully elucidated. In a mathematical model of the swinging leg as a physical pendulum, SL is directly proportional to the length of the walker's leg and SR is inversely proportional to the square root of the leg length (L); however, generally, taller humans walk faster than shorter ones. Due to differences in the L between individuals, only information about simple walking speeds appears to be insufficient to interpret the characteristics of optimal walking for humans of different sizes.

Therefore, the purpose of this study was to examine the relationships between SL , SR , and walking speed and to also clarify the principal mechanism that accounts for the variation in optimal walking speeds from subject to subject. We hypothesized that there would be a hidden mechanism, independent of L , by which the cost of oxygen expenditure to walk per unit distance is minimized would be related to the law of conservation of mechanical energy for the body, and that the mechanism would be common to various individual optimal walking speeds. A mathematical theory based on a walking model of a physical pendulum as a geometrically similar form^{1,7,8}) can predict the characteristics of optimal walking in humans of different sizes as a criterion for physical similarity, such as non-dimensional parameters¹⁰). In human walking, the movements of the leg resemble the movements of a pendulum, and these physical phenomena are theoretically not influenced by the length of the leg, except for a temporal dimension such as the period of leg swing oscillation. In this study, a simple mathematical model based on the geometrical similarity of movement of pendulum-like legs played a crucial role in describing and interpreting the gait characteristics of optimal walking during which humans moved with greater oxygen economy, regardless of L .

METHOD

1 Subjects

Seven healthy young male volunteers participated in this study. Descriptive data of the subjects are given in **Table 1**. All subjects were fully informed about the procedures, risks, and benefits of the study, and written informed consent was obtained from all subjects before the study. None of the subjects had a history of cardiopulmonary disease and all had normal resting electrocardiograms, blood pressure, and echocardiograms. None of the subjects were engaged in any regular physical activity or were involved in competitive sports. Each subject was given practice time to become accustomed to walking on a treadmill and to putting on ECG lines and a mask to sample expired gases on separate days about 1 week before the formal study. Each subject wore a light T-shirt, shorts, and general gym shoes. These shoes

Table 1 Physical characteristics of the subjects ($n=7$)

Subject	Age (year)	Weight (kg)	Height (m)	Leg length (m)	$\dot{V}O_{2peak}$ (mL min ⁻¹ kg ⁻¹)
1	22	56	1.68	0.80	45.0
2	21	59	1.70	0.82	46.6
3	24	67	1.70	0.79	34.3
4	21	65	1.60	0.77	42.3
5	21	75	1.75	0.87	50.0
6	21	64	1.67	0.79	45.3
7	23	75	1.77	0.85	37.3
Mean	22	66	1.70	0.81	43.0
±SD	1	7	0.06	0.04	5.5

were made of soft, flexible material and a plastic sole with a heel height of 1 cm that gave a good walking grip. The weight of each subject used in computations regarding oxygen uptake (weight-specific oxygen uptake, $\dot{V}O_2$) was that of a lightly clothed subject. The L of every subject was measured from the floor to the trochanter major of the right leg in the gym shoes and it was also used to calculate gait parameters during walking. The study protocol was approved by the Institutional Human Studies Committee.

2 Experimental design

Prior to the experiments, each subject performed a 15 W min⁻¹ incremental ramp-exercise test until exhaustion on an electromagnetically-braked cycle ergometer (Corival 300, Lode, The Netherlands) to determine peak oxygen uptake ($\dot{V}O_{2peak}$)¹¹⁾. No walking-exercise test was performed to determine the $\dot{V}O_{2peak}$ because subjects on a treadmill at higher speeds are in danger of falling, especially at exhaustion.

The subjects walked on a motor-driven treadmill (AR-160 A, Minato, Osaka, Japan). After resting in a supine position for 30 min, the subjects mounted the treadmill. The speed of the treadmill was increased from 16.7 m min⁻¹ (1.0 km h⁻¹) to 131.7 m min⁻¹ (7.9 km h⁻¹) with 5 m min⁻¹ (0.3 km h⁻¹) increments every 1 min at a 0% grade. The stepwise increases in speed were controlled successively by a personal computer (PC9801RX, NEC, Tokyo, Japan).

Tests were initiated at approximately 10 : 00 a. m. for all subjects. Each subject completed 2 repetitions of the test, and each trial was performed only once a week to eliminate the influence of exercise training. Before the test, the subjects were not allowed to consume any beverages containing caffeine or alcohol after 9 : 00 p. m. the previous night and vigorous exercise was forbidden for 36h before the day of testing. The subjects ate a small breakfast at least 3h before exercising. All subjects were familiarized with the test situation in several pilot experiments. All experiments were conducted at an ambient temperature between 21 and 22°C.

3 Measurements of respiratory and gait data

During walking exercise, oxygen uptake was measured breath-by-breath using an on-line automated measurement system, as previously described¹²⁾. Ventilatory airflow was monitored using a hot-wire-type pneumotachograph (RF-2, Minato, Osaka, Japan). The composition of expired gas was continuously analyzed using a medical mass spectrometer (WSMR-1400, Westron, Chiba, Japan), which

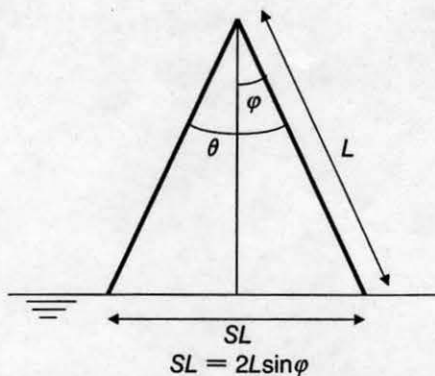


Fig. 1 Stiff-legged walk model with fixed joints of both knees and ankles in a sagittal view

This model was used to determine the characteristics of gait and to calculate both the distance and angle of the hip joint at each step. The angle (φ) was an included angle between a line connecting the hip joint with the ankle and a line drawn perpendicular to the ground. The angle of the hip joint (θ) between the legs was defined as $\theta = 2\varphi = 2\sin^{-1} [SL/(2L)]$.

was calibrated with a standard reference gas mixture before each experiment.

The number of steps in contact with the surface of the treadmill was monitored through foot contact signals generated by a pressure-sensitive mechanical switch attached to the fore-sole of the right shoe. The signals from the foot-switch were fed to a computer.

All data for respiratory and gait variables were stored on diskettes for subsequent analysis using a personal computer (PC-9821Xa13, NEC, Tokyo, Japan).

4 Data analysis

Respiratory and gait data obtained from 2 repetitions of the walking test for each subject were arranged separately with a 5-s interval time base using a Lagrange interpolation. These data were then averaged to yield a single data set for each subject. To eliminate the effects of small, if any, day-to-day variability or unexpected artifacts on the measured variables¹³, consecutive average values for all variables were calculated from the last 20 sec of averaged data obtained at each stage of incremental walking speeds¹⁴. SL was obtained by dividing walking speed by the corresponding SR . The angle of the hip joint (θ) between the legs in the sagittal view was determined on the basis of a stiff-legged walk model without the mechanism of the knee and ankle joints^{1,7,8} as schematically shown in **Fig. 1**. The hip-joint angle (the swing leg angle) was defined as $\theta = 2\varphi = 2\sin^{-1} [SL/(2L)]$, where φ is stance leg angle (the angle of leg deflection from the perpendicular to the ground). In gait analyses, the basic temporal and spatial factors were assumed to be symmetrical in each stride cycle¹⁵. It was also assumed that there was consistency between successive gait cycles during walking at each constant speed¹⁶. Least-squares fitting was also applied to the data points on $\dot{V}O_2$ and gait variables. The coefficient of variation (the ratio of its standard deviation to the mean value) for the gait variables was used to compare their variability. All values are expressed as means \pm SD.

RESULTS

Fig. 2A shows individual changes in weight-specific oxygen uptake ($\dot{V}O_2$) during walking on the

level treadmill at an increasing speed with 5 m min^{-1} increments every minute in 7 male subjects. The $\dot{V}O_2$ during walking increased progressively with increases in speed. A least-squares fitting was applied to the data points of $\dot{V}O_2$ for each subject and a quadratic equation was held over the speeds ranging from 16.7 to 131.7 m min^{-1} indicated by the dashed lines. All the individual curves of $\dot{V}O_2$ with respect to speed fitted well with a high coefficient of determination ($0.979 < r^2 < 0.992$). **Figs. 2B** and **2C** show the corresponding changes in SL and SR , respectively, against walking speed for each subject. The SL increased almost linearly as speed increased up to 106.7 m min^{-1} and then leveled off and remained fairly constant thereafter. Similarly, the SR increased almost linearly as speed increased. Although there were some contortions in linear relationships between SL and walking speed and between SR and walking speed, the mean values of both SL and SR for the 7 subjects could be expressed as a function of forward speed ($v, \text{ m min}^{-1}$) by simple equations, which satisfied the relation $v = SL \times SR$:

$$SL \text{ (m)} = 0.075 \sqrt{v} \text{ and} \quad (1)$$

$$SR \text{ (steps min}^{-1}\text{)} = 13.3 \sqrt{v} \quad (2)$$

The results obtained by a least-squares fitting applied to the data points for each subject are summarized in **Table 2**, with high coefficients of determination ($0.950 < r^2 < 0.993$ for SL and $0.927 < r^2 < 0.993$ for SR).

Fig. 3A shows the specific-weight oxygen costs of walking to move per unit distance, provided by dividing $\dot{V}O_2$ by its corresponding speed, plotted against walking speed in each subject. The oxygen cost decreased as speed rose up to 60 m min^{-1} and then leveled off in a wide range from 60 to 100 m min^{-1} , above which it increased. The oxygen costs of walking were also plotted as a function of hip-joint angle in **Fig. 3B**. The minimum oxygen costs of walking settled down in a range of about 45 to 50 deg. **Table 3** summarizes the results of the minimum oxygen costs for optimal walking together with the other corresponding gait parameters. The coefficient of variation for the hip-joint angle was less than those for other variables, which implies that the hip-joint angle measurement is a practical predominant index of optimal walking. When the minimum expenditure of oxygen during optimal walking was associated with a hip-joint angle of 46 deg at each step, the mathematical interrelationships among gait parameters of individual optimal walking could be expressed as a function of L (m) by 3 empirical equations in combination with Eqs. (1) and (2):

$$v_{opt} = 108.4L^2 \quad (3)$$

$$SL_{opt} = 0.781L \quad (4)$$

$$SR_{opt} = 138.5L \quad (5)$$

where v_{opt} is optimal walking speed, SL_{opt} optimal SL , and SR_{opt} optimal SR . Accordingly, although there was a variation in individual L , the Strouhal number ($SR \cdot L/v$) for optimal walking was relatively constant (1.27 ± 0.03), reflected by the small coefficient of variation (0.026), which was as low as that (0.027) of the hip-joint angle (**Table 3**).

DISCUSSION

Although the minimum oxygen cost of transport per unit distance during level walking was determined in all 7 subjects, optimal walking speeds differed between them. The subjects practically achieved optimal walking during a step cycle through a swing leg angle (the hip-joint angle) of about 46 deg, despite differences in individual optimal walking speeds and L . Consequently, the gait characteristics of

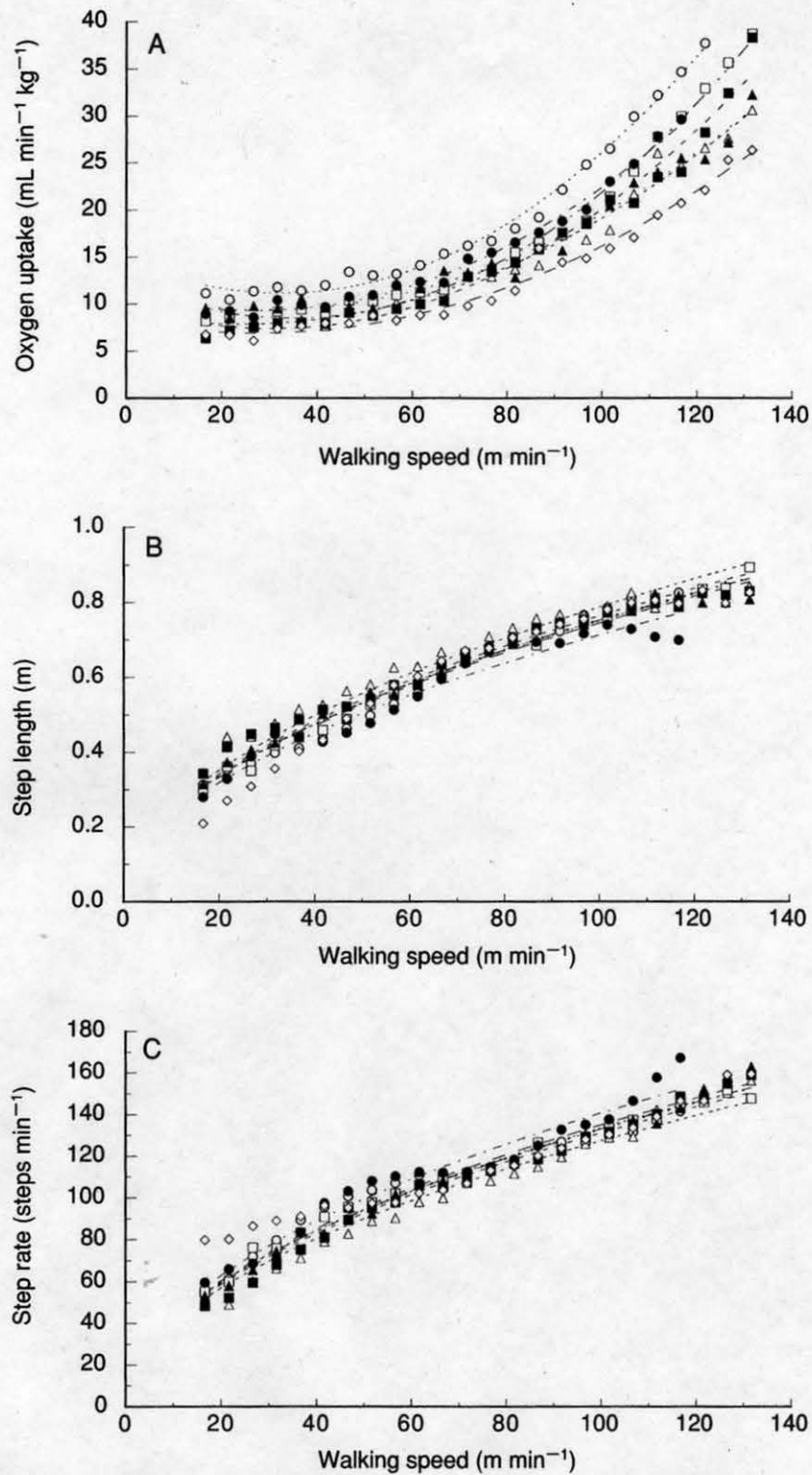


Fig. 2 Weight-specific oxygen uptake (oxygen uptake per unit of weight, A), step length (B), and step rate (C) for 7 subjects during level walking at increasing treadmill speeds
Data points for each subject are represented with different symbols.

Table 2 Relation between step length, step rate and walking speed (v) calculated by least-squares fitting ($n=7$)

Subject	Step length (m)	Coefficient of determination	Step rate (steps min^{-1})	Coefficient of determination
1	$0.075\sqrt{v}$	0.981	$13.4\sqrt{v}$	0.970
2	$0.079\sqrt{v}$	0.982	$12.7\sqrt{v}$	0.990
3	$0.075\sqrt{v}$	0.993	$13.3\sqrt{v}$	0.991
4	$0.071\sqrt{v}$	0.950	$14.1\sqrt{v}$	0.952
5	$0.075\sqrt{v}$	0.981	$13.3\sqrt{v}$	0.984
6	$0.076\sqrt{v}$	0.988	$13.1\sqrt{v}$	0.993
7	$0.075\sqrt{v}$	0.973	$13.5\sqrt{v}$	0.927
Mean \pm SD	$0.075 \pm 0.002\sqrt{v}$	0.979 ± 0.014	$13.3 \pm 0.4\sqrt{v}$	0.973 ± 0.025

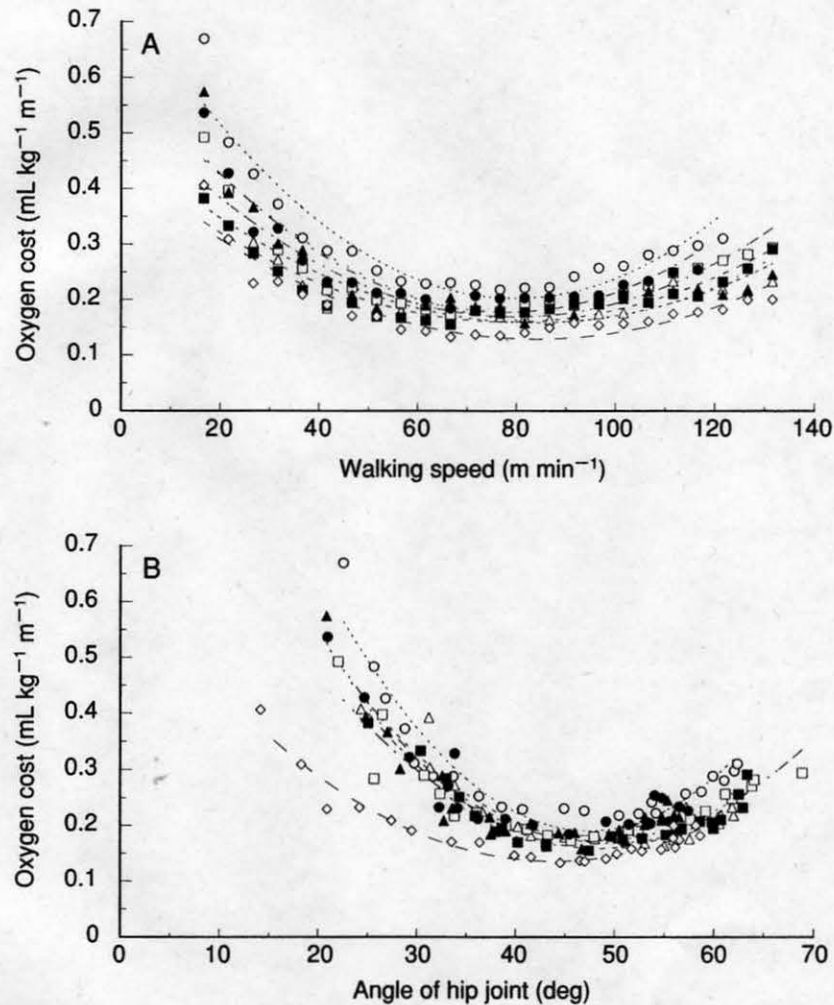


Fig. 3 Oxygen cost (weight-specific oxygen uptake divided by walking speed) for 7 subjects as a function of walking speed (A) and of hip-joint angle (B)

Data points for each subject are represented with different symbols.

Table 3 Gait variables at minimum cost of oxygen to walk per unit of distance ($n=7$)

Subject	Leg length (m)	O ₂ cost (mL m ⁻¹ kg ⁻¹)	Speed (m min ⁻¹)	Step length (m)	Step rate (steps min ⁻¹)	Hip-joint angle (deg)	Strouhal number (dimensionless)
1	0.80	0.226	71.7	0.638	112	47	1.26
2	0.82	0.182	71.7	0.669	107	48	1.23
3	0.79	0.173	66.7	0.612	109	46	1.29
4	0.77	0.184	66.7	0.595	112	45	1.29
5	0.87	0.157	81.7	0.689	119	47	1.26
6	0.79	0.155	66.7	0.635	105	47	1.24
7	0.85	0.132	66.7	0.644	104	45	1.32
Mean	0.813	0.173	70.2	0.640	110	46	1.27
±SD	0.036	0.030	5.6	0.032	5	1	0.03
CV	0.044	0.171	0.079	0.050	0.047	0.027	0.026

CV : Coefficient of variation

walking speed (v_{opt} , m min⁻¹), SL (SL_{opt} , m), and SR (SR_{opt} , steps min⁻¹) for optimal walking were represented as a function of L (m) as follows : $v_{opt}=108.4L^2$, $SL_{opt}=0.781L$, and $SR_{opt}=138.5L$, respectively. Accordingly, the Strouhal number ($SR \cdot L/v$) for optimal walking was relatively constant (1.27 ± 0.03) among the subjects.

In animals, the contraction of muscles uses both nutrients and oxygen and excretes waste products. These substances are brought to, and taken away from, the muscular tissues by the blood circulation. Our previous study quantifying the vascular branch system based on fractal geometry suggested that for any organ, a basic unit composed of a single capillary and some organ-specific cells is uniform in size and shape in mammals¹⁷⁾. Differences in body size between and within species are mainly ascribed to the accumulated number of basic units. Accordingly, mammals have the same general skeletal muscles consisting of the basic unit sarcomere with respect to the contracting mechanism, irrespective of body size^{6,18,19)}. In particular, the structure of the musculoskeletal system in humans is very uniform, and the contraction of skeletal muscles, its primary function, is independent of their size²⁰⁾ or growth process¹⁹⁾. Such a common musculoskeletal function fulfilling the ambulatory system supported by evolutionary traits in humans^{21,22)} may be designed with genetic information to bring about an optimum organ with the highest functional efficiency²³⁾. The studies of terrestrial locomotion in animals and humans by Cavagna et al.^{7,8)} demonstrated that there was an optimal walking speed for each animal of different size, and that the optimal walking was associated with the least external muscular work with which the alternate exchange between gravitational-potential energy and kinetic energy was maximal during a stride cycle. From this perspective of physiological consistency, we hypothesized that the principal mechanism by which the energetic cost of optimal walking per unit distance was minimized, irrespective of body size or especially L , would be related to the law of conservation of mechanical energy for the body and that the mechanism would be common to variations in individual optimal walking speeds. This point is discussed in the following section.

Fig. 4A shows the effects of both the leg deflection and planter flexion of the foot on the vertical

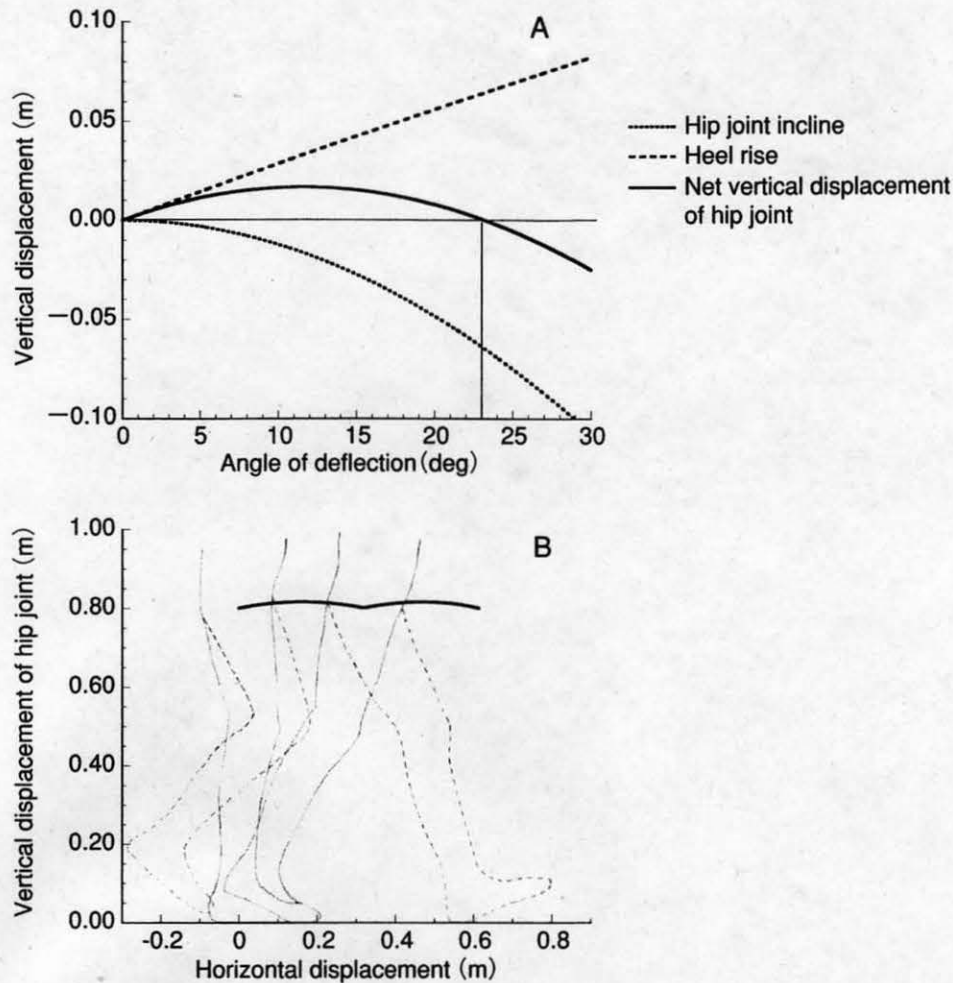


Fig. 4 Vertical displacement of the hip joint downwards due to the step effect and upwards due to plantar flexion of the foot (A). The pathway of the hip joint in the plane of progression (B)

A : The displacements were calculated with a leg length of 0.80 m and effective length of the foot between the ankle joint and the ball of the foot as 0.165 m in plantar flexion. B : The trajectory was derived from the relationship between the vertical and horizontal displacements during 1 step with a 23.0 deg leg deflection from the perpendicular to the ground and with 23.0 deg foot plantar flexion from the ground, using the results from Fig. 4A.

displacement of the hip joint. In a walking model without the mechanism of the knee and ankle joints, the vertical displacement of the hip joint from the neutral standing position was decreased with an increase in angle of the inclined leg, represented by the shorter dotted line. In contrast, the vertical displacement of the heel from the ground was increased with the plantar flexion of the foot, represented by the longer dotted line. As a result, the net vertical displacement of the hip joint (the trunk or the body's center of mass), which was brought about by the sum of the opposite effects of the leg inclining and the heel rising, was convex upward, exhibited a zenith, and then returned to the initial neutral position through the maximum leg deflection angle of 23.0 deg, namely a hip-joint angle (the swing leg angle) of 46.0 deg. Fig. 4B shows the relationship between the vertical and horizontal displacements of the hip joint using the results of Fig. 4A, together with a drawing of leg movements. The downward arc

of the hip joint was counteracted by the upward arc of the ankle due to foot planter flexion, so that the vertical position of the hip joint (the trunk) could be approximately maintained at an even level. Such a counteracting effect of the harmonious lower-extremity system could sustain the pathway of the trunk forward at an approximately horizontal level during walking, resulting in a greater economy of metabolic energy due to the conservation of mechanical energy, including gravitational-potential energy and kinetic energy. This hypothesis is consistent with the results of studies by Cavagna et al.^{7,8)} demonstrating that the total work to move a given distance was minimal under the conditions that the exchange between the gravitational-potential energy and the kinetic energy for the center of mass of the body was maximal. However, the energy for the body during walking is most likely to be lost due to internal resistance of the body joints and of moving tissues, as well as external resistance including the drag in air and friction between the soles of the feet and the ground. Since part of the potential and kinetic energy is inevitably lost due to both resistance and friction, even though the legs and arms swing with gravitation, in order to keep these energies interchangeable and in balance, extra energy must be supplied by muscular work^{7,8)}.

To verify that the presented model for analysis of human walking was useful to characterize optimum walking with the minimum expenditure of oxygen to move per unit of distance, we applied this model to the data from the literature^{2,3,7)}. When kinematical information of both SL and L was provided with the optimal walking speed, the angle of the hip joint, as shown in **Fig. 1**, was given by $\theta = 2\sin^{-1}(SL/(2L))$: 1) $\theta_{opt} = 44.5^\circ = 2\sin^{-1}(0.694/(2 \times 0.916))$ at the optimal speed of 80.7 m min^{-1} (Ref. 3); 2) $\theta_{opt} = 45.1^\circ = 2\sin^{-1}(0.683/(2 \times 0.890))$ at the optimal speed of 67.5 m min^{-1} in calculations where a L of 0.890 m was used, although the mean L was 1.09 m measured as the floor-to-iliac crest length in their study²⁾; 3) $\theta_{opt} = 47.2^\circ = 2\sin^{-1}(0.80/(2 \times 1.00))$ at the optimal speed of 76.7 m min^{-1} (Ref. 7). These estimates of hip-joint angle are very close to 46 deg and support our assertion that optimal walking for humans is achieved during leg swing oscillation at the hip-joint angle of 46 deg , regardless of L , although there is quite a wide variation among humans with respect to their optimal walking speeds.

Our analysis was based on the geometrically similar walking model of pendulum-like legs in this study. The geometric similarity, especially the static similarity, generally requires similar geometric forms of human body segments between one and another¹⁰⁾. In contrast to the static similarity, the dynamic similarity between 2 systems (e. g. 2 humans have the same shape but differ in size) is relevant to the dynamic behaviour of their motions. When 2 geometrically similar shape systems, but of different sizes, satisfy the dynamic similarity in kinetics, they give equal Strouhal number values ($SR \cdot L/v$), such as non-dimensional parameters²⁴⁾. Here v , L , and SR indicate forward speed, leg length, and step rate, respectively, of optimal walking in particular. In this study, the mean value of the Strouhal number was 1.27 and its coefficient of variation was 0.026 (**Table 3**). Because the Strouhal number for optimal walking is mathematically equivalent to $1/(2\sin\varphi)$ in the present model, optimal walking may exist under special conditions that satisfy simultaneously the static and dynamic similarity.

Recently, the assessment of locomotor responses to different gravity environments, such as on other planets than the earth, has created considerable scientific interest^{25,26)}. Information on physical activity or cardiovascular dynamics under different gravity conditions will be necessary for humans to live safely on other planets or on space stations for short or long periods of time. In addition, clinical

interest may help develop a new technology of gravitational-mediated medicine, including orthopedic treatments and rehabilitation training, or circulatory treatment for cardiovascular diseases. However, currently we are interested in the economy of human walking in the earth's environment, including gravity and atmospheric pressure, because it is important that hidden principles of biological design could be discovered in the structure and function of organs and organism systems that evolved under certain conditions^{23,27}). If humans live on other planets with different gravities for a long period, the muscle and skeleton masses and the distribution of blood for the body will change from those before moving to the other planet due to gravity changes²⁸). Because of such an adaptive change to different gravity forces, it is no longer desirable for us to estimate the optimal walking on other planets using the optimal solution for locomotion on the earth.

Limitations

Since we assumed the present model of stiff-legs swing to be that the knee and ankle joint mechanisms were not operating, the accuracy of this model remains incomplete to determine precisely the individuality in walking due to some differences in musculoskeletal configurations or articular flexibility. Further studies are necessary to analyze the motion of walking from not only the sagittal view, but also the frontal view, using a more realistic walking model with a mechanism of multiple joints.

CONCLUSIONS

The minimum oxygen cost to walk per unit distance was achieved during the swing of 2 legs between which the hip-joint angle was about 46 deg, regardless of L . The stiff-legged model demonstrated that the pathway of the trunk during optimal walking was approximately maintained at a horizontal level by the counteracting effects of leg decline and heel rise. The minimization of vertical displacement of the trunk resulted in optimal walking with the lowest rate of oxygen expenditure at which extra muscular work would be needed against the internal and external resistance, as well as against gravitation, which was most probably minimized by the maximum interchange between the gravitational-potential and kinetic energy.

REFERENCES

- 1) Cotes JE, Meade F. The energy expenditure and mechanical energy demand in walking. *Ergonomics* 1957;1:97-119.
- 2) Van Der Walt WH, Wyndham CH. An equation for prediction of energy expenditure of walking and running. *J Appl Physiol* 1973;34:559-63.
- 3) Zarrugh MY, Todd FN, Ralston HJ. Optimization of energy expenditure during level walking. *Eur J Appl Physiol Occup Physiol* 1974;33:293-306.
- 4) Zarrugh MY, Radcliffe CW. Predicting metabolic cost of level walking. *Eur J Appl Physiol Occup Physiol* 1978;38:215-23.
- 5) Hoyt DF, Taylor CR. Gait and the energetics of locomotion in horses. *Nature* 1981;292:239-40.
- 6) Schmidt-Nielsen K. *Scaling : Why is animal size so important?* New York : Cambridge University Press ; 1984.
- 7) Cavagna GA, Thys H, Zamboni A. The sources of external work in level walking and running. *J Physiol* 1976;262:639-57.
- 8) Cavagna GA, Heglund NC, Taylor CR. Mechanical work in terrestrial locomotion : two basic mechanisms for minimizing energy expenditure. *Am J Physiol* 1977;233:R243-61.
- 9) Takahashi T, Okada A, Tamura T, Miyamoto Y. Cardiorespiratory responses to walking and running at an incremental speed of treadmill. *Adv Exp Med Biol* 2001;499:363-8.

- 10) Duncan WJ. *Physical Similarity and Dimensional Analysis*. London : Edward Arnold & Co. ; 1953.
- 11) Takahashi T, Miyamoto Y. Influence of light physical activity on cardiac responses during recovery from exercise in humans. *Eur J Appl Physiol* 1998;77:305-11.
- 12) Takahashi T, Okada A, Saitoh T, Hayano J, Miyamoto Y. Difference in human cardiovascular response between upright and supine recovery from upright cycle exercise. *Eur J Appl Physiol* 2000;81:233-9.
- 13) Durnin JVGA, Namyslowski L. Individual variations in the energy expenditure of standardized activities. *J Physiol* 1958;143:573-8.
- 14) Takano N. Effects of pedal rate on respiratory responses to incremental bicycle work. *J Physiol* 1988;396:389-97.
- 15) Milner M, Quanbury AO. Facets of control in human walking. *Nature* 1970;227:734-5.
- 16) Hirokawa S, Matsumara K. Gait analysis using a measuring walkway for temporal and distance factors. *Med Biol Eng Comp* 1987;25:577-82.
- 17) Kamiya A, Takahashi T. Quantitative assessments of morphological and functional properties of biological trees based on their fractal nature. *J Appl Physiol* 2007;102:2315-23.
- 18) Hill AV. The dimensions of animals and their muscular dynamics. *Sci Progr* 1950;38:209-30.
- 19) Close RI. Dynamic properties of mammalian skeletal muscles. *Physiol Rev* 1972;52:129-97.
- 20) Fung YC. *Biomechanics : Mechanical Properties of Living Tissues*. New York : Springer-Verlag ; 1993.
- 21) McHenry HM, Corruccini RS. Fossil hominid femora and the evolution of walking. *Nature* 1976;259:657-8.
- 22) Bramble DM, Lieberman DE. Endurance running and the evolution of Homo. *Nature* 2004;432:345-52.
- 23) Weibel ER. *Symmorphosis : On Form and Function in Shaping Life*. Cambridge : Harvard University Press ; 2000.
- 24) Alexander RM. Optimization and gaits in the locomotion of vertebrates. *Physiol Rev* 1989;69:1199-227.
- 25) Cavagna GA, Willems PA, Heglund NC. Walking on Mars. *Nature* 1998;393:636.
- 26) Minetti AE. Walking on other planets. *Nature* 2001;409:467-9.
- 27) Baba K, Kawamura T, Shibata M, Sohirad M, Kamiya A. Capillary-tissue arrangement in the skeletal muscle optimized for oxygen transport in all mammals. *Microvasc Res* 1995;49:163-79.
- 28) Blomqvist CG, Stone HL. Cardiovascular adjustments to gravitational stress. In : Shepherd JT, Abboud FM, editors. *Handbook of Physiology. The Cardiovascular System*. Bethesda : American Physiological Society ; 1983. section 2, vol III, part 2, chapter 28, p.1025-63.

<Received on November 13, 2008>