Adiabatic transformability hypothesis of human locomotion

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Abstract. It is hypothesized that metabolic and mechanical changes in human locomotion associated with changes in speed v are constrained by two attractive strategies: $Q_{metab} = 1$ and $\Delta Q_{metab}/\Delta v =$ a positive definite constant. $Q_{metab} = \Delta E_k \, s^{-1}/ml \, O_2 \, s^{-1}$ where $\Delta E_k \, s^{-1}$ is the summed increments and decrements per unit time in the translational and rotational kinetic energies of the body's segments and ml $O_2 s^{-1}$ is the rate at which chemical energy is dissipated. The expected constancy of $\Delta Q_{metab}/\Delta v$ was derived from an extension of Ehrenfest's adiabatic hypothesis by which transformations (increases, decreases) in locomotion v can be considered as adiabatic, even though the biological conditions are nonconservative and non-rate-limited. The expected significance of $Q_{metab} = 1$ was derived from stability considerations of the symmetry per stride of stored and dissipated energy. An experimental evaluation was provided by collecting metabolic and mechanical measures on walking (10 subjects) and running (9 subjects) at progressively greater treadmill speeds but within the aerobic limit. Results revealed that walking was restricted to $Q_{metab} \leqslant 1$, with a nonlinear trajectory in $v \times Q_{metab}$ coordinates shaped by $Q_{metab} = 1$ (primarily) and the constancy of $\Delta Q_{metab}/\Delta v$. Running satisfied $Q_{metab} > 1$, with a linear trajectory in $v \times Q_{metab}$ coordinates conforming to $\Delta Q_{metab}/\Delta v =$ a constant, with the constant predicted from invariants in the mechanical space $v \times \Delta E_k \, s^{-1}$. Results also suggested that the metabolic costs of running might be predictable from measures made in the $v \times \Delta E_k \, s^{-1}$ space.

1 Introduction

Humans locomote primarily by walking and running. The energy costs of these gaits are not identical and they vary in different ways with changes in speed. For

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example, the metabolic rate for walking – measured in milliliters of oxygen per second (ml $O_2 \, s^{-1}$) or joules per second ($J \, s^{-1}$) (given the conversion that 1 ml $O_2 = 20.1$ J) – varies curvilinearly with speed (meters per second, $m \, s^{-1}$), while the metabolic rate for running varies linearly with speed (e.g., Margaria et al. 1963; Falls and Humphrey 1976). For running, the slope of the function relating metabolic rate to speed identifies a constant amount of energy expended per unit distance travelled: the dimensions of Δ(rate of energy expenditure)/Δ(speed), with Δ signifying change, are $(J \, s^{-1})/(m \, s^{-1})$, that is, $J \, m^{-1}$. This invariant of human running has been found similarly to characterize other instances of bipedal locomotion, quadrupedal and polipedal locomotion, and to apply equally to arthropods and verterbrates, and to animals with and without limbs (e.g. Full 1989; Taylor et al. 1970; Walton et al. 1990). When expressed in mass-specific form ($J \, kg^{-1} \, m^{-1}$), the constancy is found to vary inversely with body mass (e.g., Full 1989; Taylor et al. 1970). Small animals on a per gram basis require more energy per time and per distance. A cockroach of 3 g dissipates twice as much energy to move a unit mass 1 m as does a crab or mouse of 30 g, and 9 times as much energy as a dog of 3 kg; conversely, if an arthropod, a snake, a bird, and a mammal, have similar mass, then the energy to be dissipated by each to move 1 m will be nearly identical (Full 1989).

Across variations in animal morphology, physiology, size, and taxa, the energy expended per unit distance is a constant. The constancy would seem to reflect a very general design criterion of biological movement systems rather than any specific neural or physiological mechanism. Biological movement systems constitute a class of systems for which a change in speed is a transformation that leaves invariant a particular hybrid of energy and space, namely energy dissipated per unit distance. The design criterion is a rule that prescribes a mass-specific rate of energy use (a thermodynamic quantity) for a given speed of running (a mechanical quantity). How might this rule, this invariance against speed scaling, be understood? In the present article we seek insights through

analogies with the classical physical notions of adiabatic transformation and adiabatic invariance.

1.1 Adiabatic transformability and adiabatic invariants applied to nonconservative systems

One current perspective on understanding invariant kinematic patterns of biological movements is to assume a governing physical cost function that is optimized, such as minimizing energy or minimizing jerk (Nelson 1983). With respect to understanding ratios of quantities characterizing biological movements that remain invariant over scaling, such as Δ(rate of energy expenditure)/Δ(speed), the parallel perspective would be to assume a governing physical change under which two variable quantities are related through a constant. A physical change of this kind is referred to as an adiabatic change or transformation, and the corresponding invariant is referred to as an adiabatic invariant (Arnold 1989). In the physical settings to which they typically apply, adiabatic transformations are slow (relative to the processes leading to equilibrium) and incur no transfer of energy across the system's boundaries by heating. The original adiabatic hypothesis due to Ehrenfest (Klein 1959) is that an invariant ratio exists between the time average of the kinetic energy $\langle E_k \rangle$ and the frequency of an adiabatically transformed conservative periodic system. The hypothesis is depicted by a straight line in frequency $f \times \langle E_k \rangle$ coordinates with a constant slope (the action or energy $\times$ time, J s) that intersects the origin, meaning that the mechanical action per cycle is a constant.

It has recently been conjectured that biological movement systems (which are open, dissipative systems) might be adiabatically transformable and exhibit Ehrenfest-type relations if it can be assumed that the transformations are not severely restricted in rate and not necessarily defined by the absence of energy transfer by heating (Kugler and Turvey 1987). For the more general case it is conjectured that (i) rate limitations do not apply when the forces producing the change in the system of interest are derived from a potential within the system, and (ii) energy transfer by heating occurs but is time independent. An example is the pirouetting ice skater. By retracting the arms (through forces generated via the 'on-board' chemical potential) she increases rotational kinetic energy (in accordance with angular momentum conservation) and rotational frequency, with the increase in $\langle E_k \rangle$ proportional to the increase in f. The sliding friction between skates and ice leads to a transfer of energy by heating proportional to the distance over which the surfaces are in contact. A circular motion of skates on ice of constant circumference will result in a frequency-independent dissipation. The nonconservative version of Ehrenfest's adiabatic hypothesis is depicted by a straight line in $f \times \langle E_k \rangle$ coordinates with a constant slope $H = \Delta\langle E_k \rangle/\Delta f$ that does not intersect the origin but, rather, intersects the f axis at a positive value and the $\langle E_k \rangle$ axis at a negative value referred to as $\langle E_t \rangle$ (Fig. 1A) (Kugler and Turvey 1987; Kugler et al. 1990). As cycle f changes, at whatever rate, an amount of energy $\langle E_t \rangle$ is dissipated per cycle that is the same at

each f (e.g., Kadar et al. 1993). Where the adiabatic invariant of a one-freedom conservative oscillator is $\langle E_k \rangle/f$, that for a hypothetical one-freedom nonconservative oscillator, such as the pirouetting ice skater or a rhythmically moving limb, is $\Delta\langle E_k \rangle/\Delta f$ – that is, the rate at which $\langle E_k \rangle$ changes with changes in f is constant. Similarly, when defined only in terms of energy degradation, the invariant is $\Delta\langle E_t \rangle/\Delta f$.

The upshot is that biological locomotion could be considered adiabatically transformable if the adiabatic concept can be extended along the lines suggested by (i) and (ii) above. Under this extension, the puzzling constancy of energy dissipated per unit distance in running would be an example of an adiabatic invariant interpreted more generally. We pursue this conjecture in the experiment and analyses that follow.

1.2 A generalized quality or Q factor

In the $f \times \langle E_k \rangle$ coordinate space of Fig. 1A, the constancy of H identifies one attractive strategy for changing f. Another attractive strategy is defined by a ratio of 1 between the positive $\langle E_k \rangle$ values and the negative $\langle E_k \rangle$ intercept value, $\langle E_t \rangle$, with the intersection of the two trajectories defining the coordinates at which both strategies can be satisfied simultaneously (Kugler and Turvey 1987). The ratio of conservative, e.g., $\langle E_k \rangle$, to
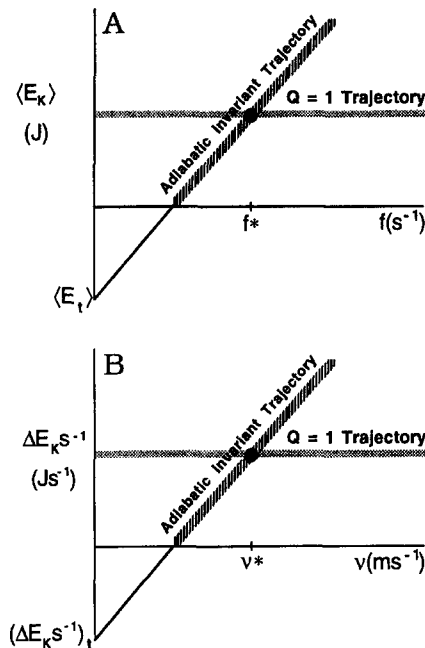

Fig. 1. A Theoretically derived relation between time averaged kinetic energy $\langle E_k \rangle$ and frequency f for a nonconservative, adiabatically transformed one-degree of freedom system: the slope represents the adiabatic invariant of action (J s). Q refers to the ratio $\langle E_k \rangle/\langle E_t \rangle$, where $\langle E_t \rangle$ is the constant energy dissipated per cycle, and f^* identifies that f equal to $2f_{intercept}$ at which the adiabatic invariant and $Q = 1$ intersect. B for a locomotory system of N-freedoms, the relevant quantities for expressing adiabatic invariance are hypothesized to be the summed changes in segmental kinetic energy $\Delta E_k s^{-1}$ and speed v. In this space, the slope represents the adiabatic invariant of $J m^{-1}$, Q refers to the ratio of $\Delta E_k s^{-1}$ to the negative intercept value indexing dissipation, and the two trajectories intersect at $v^* = 2v_{intercept}$

nonconservative, e.g., $\langle E_t \rangle$, energy forms, or energy in the external reference frame to energy in the internal reference frame, defines a (generalized) quality or Q factor. When $Q = 1$ the two energy forms balance. Prototypical oscillators – the pendulum and the mass-spring – oscillate due to their inertial and elastic forces and stop oscillating because of friction. In mechanical oscillators, a Q factor is defined roughly as the ratio of the energy stored to the average energy loss per period.

An oscillator has to be assembled in the sense that it has to be given an amount of energy at the outset. If it is to sustain its motions then its energy losses due to friction must be replenished (for example, by squirts from an escapement). Consequently, for a self-sustained oscillator (such as a biological rhythmic movement), $Q > 1$ means that the energy stored per cycle exceeds that lost per cycle (there is a residual from cycle to cycle) and that the sustaining energy can be injected at a minimal rate of less than once per cycle. In contrast, $Q < 1$ means that the energy stored per cycle is less than that lost and that the minimal rate of replenishment must be greater than once per cycle. When $Q = 1$, the energy stored and the energy lost per cycle are in balance; once per cycle is the minimal injection rate. Within the $f \times \langle E_k \rangle$ coordinate space of Fig. 1A, $Q = 1$ distinguishes between rhythmic movement at $Q > 1$ – dominated more by reversible exchanges (e.g., from kinetic energy to elastic strain and vice versa) than energy degradation (mechanical to thermal) – and rhythmic movement at $Q < 1$ – dominated less by reversible exchanges and more by changes in energy grade. The particular benefit of $Q \leqslant 1$ is in respect of external perturbations. When $Q \leqslant 1$, any perturbation is 'washed out' within a single cycle. The stability of $Q \leqslant 1$ amounts to keeping the responsibility for the control of the coordinates of a rhythmic motion anchored in forces generated internally (that is, muscularly) rather than in forces generated externally (that is, reactively). In contrast, when $Q > 1$ full muscular responsibility for the rhythmic motion is discharged and forces that arise reactively in the cycle are exploited. The oscillations are no longer secure against external perturbations which can play out over successive cycles. The $Q \leqslant 1$ stability oriented toward autonomy against external perturbations is no longer an option but the stability of adiabatic invariance, oriented toward limiting active muscular forces to the role of offsetting cyclic frictional losses, persists (Kugler and Turvey 1987). In view of the preceding, $Q = 1$ represents a balance between two types of demands: stability ($Q < 1$) and metabolic economy ($Q > 1$).

1.3 Method and measurement desiderata

The experimental evaluation of the adiabatic transformability hypothesis of human locomotion faces two issues, one minor and one major. The minor issue concerns the particulars of implementing changes in motion. In a recent study directed at an Ehrenfest relation in human movement, the subjects began oscillations of a single body segment at a prescribed frequency and then, over a given interval of time, altered the frequency at will and continuously, in either an increasing or decreasing direction (Kadar et al. 1993). Changes in frequency – and, therefore, the changes in the parameters responsible for frequency – occurred smoothly within a trial. A similarly continuous succession of changes would be ideal for the evaluation of the adiabatic transformability hypothesis in human locomotion. That ideal, however, must be tempered by three requirements. First, the changes should be of speed because speed rather than frequency is the relevant governing quantity for locomotion (e.g., Diedrich and Warren, 1993) – in part because of the trade-off between stride frequency and stride length. Second, each speed should persist for a time scale sufficient for stationarity in the measure of metabolic rate (usually achieved in 3–5 min in human locomotion). Third, the number of successive speeds and their magnitudes should be such that the locomotion is sustainable aerobically throughout the series of changes. In the present research we satisfy these requirements by having subjects walk or run on a treadmill that increases the speed v every 7 min by 0.28 m s^{-1} (1 km h^{-1}) to a walking limit of 2.22 m s^{-1} (8 km h^{-1}) and a running limit of 3.61 m s^{-1} (13 km h^{-1}), with metabolic measures restricted to the final 3 min of each v plateau.

The major issue to be resolved concerns the energy measure of the body's motions in walking and running. The complexity of walking and running, involving rotational and translational motions of multiple segments, suggests a measure different from $\langle E_k \rangle$ of Fig. 1A (the cycle average of rotational E_k for a single degree of freedom). The conceptual inclinations of Hill (1950) and Gray (1968) were toward the *changes* in E_k of the limbs relative to the body. ΔE_k per stride, the total change in E_k, is the amount of energy converted to E_k from other forms and the amount of E_k converted to other forms. In a biological movement system these other forms are primarily the chemical potential within muscle, the gravitational potential, and the elastic potential of muscles, tendons, and ligaments. To assemble a stride (a cycle of locomotion), converted chemical energy is stored initially in the stride as E_k. As the stride transpires, E_k is exchanged reversibly in varying degrees with gravitational and elastic forms and lost irreversibly as heat. A recent major evaluation of animal locomotion focused upon the summed segmental increments in E_k (e.g., Fedak et al. 1982), but the fact that E_k is actively and passively degenerated as well as generated argues for a measure that includes additionally the decrements in segmental E_k.

In the present analysis, therefore, it will be assumed that (a) in the shift from one speed to another, the coupled oscillators comprising the acts of walking and running (e.g., Collins and Stewart 1992) have their parameters changed together as an ensemble, (b) these parameter changes are reflected in the change of total ΔE_k per stride, and (c) the total ΔE_k per stride is given by

$$\Delta E_k = \sum_{i=1}^{S} \sum_{j=1}^{N} (|\Delta \text{Translational } E_k i, j|$$

$$+ |\Delta \text{Rotational } E_k i, j|) \qquad (1)$$

where $|\Delta E_k i, j|$ is the absolute E_k change during the jth period of time for the ith segment, N is the total number

of sample periods during one stride and S is the total number of segments. The quantity given by (1) includes all increments and decrements in E_k without respect for their origins (e.g., Pierrynowski et al. 1980). The use of (1) is not motivated by traditional concerns about quantifying true mechanical efficiency (see Kaneko 1990 for a recent review). In the present analysis, the body's segments are treated as an ensemble of systems in motion each characterized within a stride by the summed changes in the E_ks of and about their respective centers of mass. The fact that there are within and between segment transfers of E_k, and that there are other unaccounted for energy resources and metabolic costs, is immaterial to the quantification of the ensemble ΔE_k. Where these factors become important is in determining the magnitude of the relevant generalized Q factor. Given (1),

$$Q = \frac{\Delta E_k / \Delta t}{\Delta V_{O_2} / \Delta t} \qquad (2)$$

that is, Q is defined as the ratio of the total segmental E_k changes generated per unit time in executing a steady speed, to the chemical energy expended (volume V of oxygen used) per unit time in sustaining that steady speed. (For the purposes of calculation, the denominator of (2) is rendered as joules per unit time through the conversion 1 ml $O_2 = 20.1$ J.) Unlike mechanical efficiency, which cannot exceed 1, Q can take values both greater than and less than 1. The magnitude of (2) will exceed 1 as the sources of changes in segmental E_k become increasingly less metabolic; for example, elastic strain energy made available by stretched tendons and ligaments including those of the spine (Gracovetsky 1988).

From the above considerations it follows that the mechanical coordinate system for expressing the hypothesized adiabatic invariance of locomotion is $v \times \Delta E_k\,\mathrm{s}^{-1}$ rather than $f \times \langle E_k \rangle$. The preceding comports with the primary intuition guiding the present research, namely that the constancy of Δ(rate of energy expenditure)/Δ(speed) in running is the essential thermodynamic form of adiabatic invariance in locomotion. Consequently, the corresponding mechanical form should be a constancy of the v rate of change of $\Delta E_k\,\mathrm{s}^{-1}$. Fig. 1B depicts the hypothesized attractive trajectories in the $v \times \Delta E_k\,\mathrm{s}^{-1}$ space. Analogous to the $f \times \langle E_k \rangle$ space of Fig. 1A, the negative intercept in Fig. 1B indexes dissipation and the $Q = 1$ trajectory is that for which $\Delta E_k\,\mathrm{s}^{-1}$ equals the intercept value. In the $f \times \langle E_k \rangle$ space of Fig. 1A, simple geometry reveals that the two attractive trajectories intersect at f^*, a value of f that is twice the f intercepted by the adiabatic invariant trajectory: $f^* = 2 f_{\text{intercept}}$ (Kugler and Turvey 1987). Similarly, in the $v \times \Delta E_k\,\mathrm{s}^{-1}$ space of Fig. 1B, the two attractive trajectories must intersect at $v^* = 2 v_{\text{intercept}}$.

1.4 The $v \times Q_{mech}$ and $v \times Q_{metab}$ coordinate spaces and predictions from adiabatic transformability

A central idea in the proposed theory of nonconservative adiabatic invariance is that the appropriate mechanical
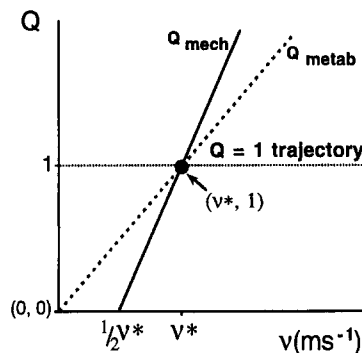

Fig. 2. The theoretical relation between $Q_{metab} = (\Delta E_k\,\mathrm{s}^{-1}/\text{metabolic rate})$ and $Q_{mech} = (\Delta E_k\,\mathrm{s}^{-1}/\text{intercept } \Delta E_k\,\mathrm{s}^{-1})$ as a function of speed v

space is informative about the system's thermodynamics (Kugler and Turvey 1987). Let Q_{mech} designate Q in the $v \times \Delta E_k\,\mathrm{s}^{-1}$ space – the ratio of $\Delta E_k\,\mathrm{s}^{-1}$ to the intercept value (Fig. 1B). A $v \times Q_{mech}$ coordinate space for running can then be defined (Fig. 2). In this space, the adiabatic invariant is given by a set of points satisfying $Q_{mech} = (2/v^*)v - 1$; it is a trajectory originating at $(v^*/2, 0)$. Let Q_{metab} designate the Q defined by (2). Then a $v \times Q_{metab}$ coordinate space can be defined. In this latter space the adiabatic invariant trajectory for walking and running can be articulated. If human location conformed to an adiabatic trajectory, then the constancies of $\Delta(\Delta E_k\,\mathrm{s}^{-1})/\Delta v$ and Δ(metabolic rate of energy expenditure)/Δv would mean that $\Delta Q_{metab}/\Delta v = $ a constant. The $\Delta Q_{metab}/\Delta v$ trajectory must originate at $(0, 0)$ because at ever-decreasing v (as running becomes walking and walking becomes standing still) the numerator $\Delta E_k\,\mathrm{s}^{-1}$ will approach 0, but the declining metabolic rate defining the denominator will remain substantial (about 90 $\mathrm{J\,s}^{-1}$ is needed for standing). Given a $(0, 0)$ origin, the invariant value of $\Delta Q_{metab}/\Delta v$ is determined by the fact that one point is common to both $v \times Q_{metab}$ and $v \times Q_{metab}$: at the coordinates $(v^*, 1)$, $Q_{metab} = Q_{mech} = 1$. Consequently,

$$Q_{metab} = (1/v^*)v \qquad (3)$$

as shown in Fig. 2. Substituting (3) into (2) yields

$$\text{metabolic rate (J s}^{-1}) = (v^*/v)(\Delta E_k\,\mathrm{s}^{-1}) \qquad (4)$$

That is, the thermodynamics of locomotion are calculable, in principle, purely from the magnitudes of mechanical energy quantities expressed in the $v \times \Delta E_k\,\mathrm{s}^{-1}$ space as long as $\Delta E_k\,\mathrm{s}^{-1}$ varies linearly, or very nearly linearly, with v (Fig. 1B).

Four specific hypotheses based on the assumption that human locomotion is adiabatically transformable can now be identified with the aid of the coordinate spaces developed above. Unless stated otherwise, Q in the following is Q_{metab} defined by (2).

Hypothesis 1. The boundary between walking and running occurs at $Q = 1$, with ordinary walking constrained to $Q \leqslant 1$. Examination of the mechanical energy changes during locomotion of mammals indicate two distinct mechanisms of alternately storing and recovering energy,

one corresponding to walking and one corresponding to running (Cavagna et al. 1977; Alexander 1992). The walking mechanism is analogous to a pendulum, exchanging E_k and gravitational E_p (potential energy) within each stride. The running mechanism is analogous to a bouncing ball, where current motions of the limbs exploit energy stored elastically in previous motions. The pendulum nature of walking means that ΔE_k is largely a matter of interconversion of E_k and E_p within segments and the passive transmission of E_k across adjacent segments. Consequently, in walking, a measure of passive energy exchanges per stride should approximate ΔE_k. A ratio of this measure with metabolic cost should, like (2), be less than or equal to 1. The total energy transfer within and between segments, ΔE_{TWB}, is given by the difference between

$$\sum_{i=1}^{S} \sum_{j=1}^{N} (|\Delta \text{Translational } E_k i,j|$$

$$+ |\Delta \text{Rotational } E_k i,j| + |\Delta E_p i,j|) \quad (5)$$

and

$$\sum_{j=1}^{N} \left| \sum_{i=1}^{S} (\Delta E i,j) \right| \quad (6)$$

where (5) is the total energy assuming no exchanges within or between segments and (6) assumes both (Pierrynowski et al. 1980). When (6) is subtracted from (5) the residual is the intra- and inter-segmental passive energy exchange per stride (for reservations, see Chapman et al. 1987). Restating the requirement from above: For walking, $(\Delta E_{TWB} s^{-1}/ml O_2 s^{-1}/ml O_2 s^{-1}) \leqslant 1$, with $ml O_2 s^{-1}$ converted to $J s^{-1}$ for the purposes of calculation.

In running, gravitational E_p and translational E_k are in phase and, therefore, cannot be exchanged, but energy can be stored elastically in mid step. An overall smaller contribution of ΔE_{TWB} to ΔE_k is to be expected, accompanied, however, by an augmentation in a low-cost mechanism of energy storage (stretched tendons and ligaments and stretched contracted muscle) with increasing v. Whereas walking is achieved largely by reversibly exchanging E_k and E_p, with E_k generated from muscular work, running is achieved by complementing the metabolically based E_k with an elastic recoil. Thus, in running ΔE_k can exceed the energy injected metabolically into the locomotory pattern because a resource not directly dependent on the metabolic cost of moving body segments has been added.

Hypothesis 2. In accordance with (3), Q versus v should be positively linear with slope $1/v^*$, intersecting the line $Q = 1$ at v^* and intersecting the Q axis at 0. Can v^* be anticipated? Given hypothesis 1, it should be that value of v at which both walking (oriented toward $Q = 1$) and running (oriented toward $\Delta Q/\Delta v =$ a positive definite constant) occur, that is, the point at which walking becomes running and vice versa. On the basis of research directed at the v of spontaneous transition from walking to running (e.g., Beuter and Lalonde, 1989; Diedrich and Warren, 1995) we suspect that v^* must be about 2 m s^{-1}. If so, then $\Delta Q/\Delta v \cong 0.5$.

Hypothesis 3. Walking Q should be nonlinearly dependent on walking v, reflecting the competition between the contrasting strategies of $Q = 1$ and the nonconservative adiabatic invariant. That is, hypothesis 2 should hold only approximately. For $Q \leqslant 1$, Q will be deflected from the $(1/v^*)$ slope by the attractiveness of $Q = 1$.

Hypothesis 4. The metabolic rate $(J s^{-1})$ for running at each v should satisfy (4). To date, efforts to link the thermodynamic variable of metabolic cost with a mechanical quantifier of locomotion have met with little success (e.g., Martin et al. 1993).

2 Method

2.1 Subjects

Ten unpaid student volunteers, 9 women and 1 man, from the Boston University community participated in the walking condition. The mean age, height, and weight of the walkers were 25.6 ± 6.08 years, 1.66 ± 0.10 m, and 595 ± 142.7 N, respectively. Nine additional student volunteers, 7 women and 2 men, from the same community participated in the running condition of the experiment. The mean age, height and weight of the runners were 27.2 ± 4.49 years, 1.71 ± 0.04 m, and 617.1 ± 72.9 N, respectively. All 19 subjects had previous experience with walking or running on a treadmill.

2.2 Apparatus and measurements

An open circuit spirometry technique was used to assess metabolic cost. Expired gases were collected continuously through a tube equipped with a non-rebreathing valve and were analyzed every 30 s using a metabolic cart (Sensormedics MMC Horizon, Sensormedics, Yorba Linda, Calif.). Metabolic energy cost $(\dot{V}_{O_2})$ in $ml O_2 s^{-1}$ was determined by measurement of steady-state oxygen consumption.

To calculate ΔE_k according to (1), data were collected using the Peak Performance Motion Analysis System (Peak Performance Technologies, Englewood, Colo.). Retroreflective markers 2.5 cm in diameter were placed on the anatomical landmarks of the fifth metatarsal head, the lateral malleolus of the ankle, the lateral condyle of the knee, the greater trochanter, the acromion process of the shoulder, and the head. Leg length was defined as the distance from the greater trochanter to the floor, thigh length from the greater trochanter to the lateral condyle of the knee, shank length from the lateral condyle of the knee to the lateral malleolus, and foot length from the lateral malleolus to the fifth metatarsal head.

The participants were filmed at 60 Hz (Panasonic Model WV-D5100, Panasonic, Secaucus, N.J.) in the sagittal plane as they walked on a treadmill (Quinton Model Q65, Quinton Instrument, Seattle, Wash.). The video camera was leveled in the frontal and sagittal planes and was placed 7.4 m from the subject. Actual treadmill speed was measured using a hand-held wheel tachometer (Shimpo Model DT-107, Shimpo America,

Lincolnwood, Ill.) accurate to $+ 0.001\, \mathrm{h\, h^{-1}}$ placed directly on the treadmill belt. A stride was defined as heel strike to heel strike of the ipsilateral leg. Stride f was obtained using a stopwatch and recording the time for 20 strides. Mean stride f was calculated as strides $\mathrm{s^{-1}}$.

The videotaped kinematic data were digitized and filtered (fourth-order Butterworth, cutoff frequency 5 Hz) using the automatic module of the Peak Performance 2D System. ΔE_k was determined using a seven-segment model: the head, neck and trunk (HNT), two thighs, two shanks and two feet (Winter 1979). Anthropometric data (Dempster 1955) and position data from a right sagittal view were used. Bilateral lower extremity symmetry was assumed during treadmill walking to allow the segmental energy calculations for the opposite leg. In summing segmental energies, values for the opposite leg were offset by π rad or one step.

Translational and rotational ΔE_k were calculated separately for each segment in each frame over a single stride. At any instant in time, translational E_k for the ith segment was calculated as translational $E_{\mathrm{k}i} = 1/2\,(m_i v_i^2)$ where m_i is the mass of the ith segment (kg) and v_i is the linear velocity of the ith segment $(\mathrm{m\,s^{-1}})$. Rotational E_k for the ith segment was computed as rotational $E_{\mathrm{k}i} = 1/2(I_i \omega_i^2)$, where I_i is the moment of inertia of the ith segment $(\mathrm{kg\,m^2})$ and ω_i is the rotational velocity of the ith segment $(\mathrm{rad\,s^{-1}})$. Total body ΔE_k for each stride was calculated by (1), and the average over strides at a given velocity was the estimate used in the analyses. The error of the calculated total ΔE_k was estimated to be 3.4% based on errors in computing the segmental inertias from anthropometric tables [these errors were determined through analysis of variance and multiple regressions involving known segmental inertias from Dempster (1955)].

2.3 Procedure

When the subject was walking, treadmill v was increased by $0.28\,\mathrm{m\,s^{-1}}$ $(1\,\mathrm{km\,h^{-1}})$ from $0.56\,\mathrm{m\,s^{-1}}$ $(2\,\mathrm{km\,h^{-1}})$ to $2.22\,\mathrm{m\,s^{-1}}$ $(8\,\mathrm{km\,h^{-1}})$, and when the subject was running it was increased by $0.28\,\mathrm{m\,s^{-1}}$ from $1.67\,\mathrm{m\,s^{-1}}$ $(6\,\mathrm{km\,h^{-1}})$ to $3.61\,\mathrm{m\,s^{-1}}$ $(13\,\mathrm{km\,h^{-1}})$. A subject walked or ran on a given treadmill v for 7 min. The metabolic cost was the mean reading over the final 3 min. This steady-state oxygen consumption $(\dot{V}_{\mathrm{O}_2})$ in $\mathrm{ml\,O_2\,s^{-1}}$ was converted to $\mathrm{J\,s^{-1}}$ $(1\,\mathrm{ml\,O_2} = 20.1\,\mathrm{J})$. Also over the final 3 min of each treadmill v the walker or runner was videotaped and his or her mean step f was calculated.

3 Results and discussion

For the analyses that follow we adopt the convention of using the prefix 'internal' for metabolic quantities and the prefix 'external' for the mechanical quantities. The evaluation of hypotheses 1–4 is prefaced by an analysis of external and internal power $(\mathrm{J\,s^{-1}})$ and external and internal energy per unit distance $(\mathrm{J\,m^{-1}})$.

3.1 Analysis in $v \times Js^{-1}$ coordinates

The mean internal power and the mean external power at each treadmill velocity were calculated by averaging across the 10 walking subjects and the 9 running subjects. The walking and running external power $(\mathrm{J\,s^{-1}})$ were obtained by dividing the mean ΔE_k computed by (1) for a given treadmill v by the mean step cycle duration (s). For the seven walking speeds the ΔE_k values averaged across the 10 subjects were 85.4, 131.2, 170.1, 234.7, 291.5, 369.4, and 432.1 J, respectively. The standard deviation of ΔE_k was the measure of the step-cycle-to-step-cycle variation in ΔE_k at a given speed. For the seven walking speeds these standard deviations averaged across the 10 subjects were 17.3, 16.1, 14.9, 13.9, 18.6, 21.7, and 22.7 J, respectively. For the eight running speeds the subjects' averages of ΔE_k and its standard deviation were 340.2 ± 49.7, 424.2 ± 40.9, 509.9 ± 39.4, 604.3 ± 41.44, 708.33 ± 44.9, 816.7 ± 70.3, 941.3 ± 77.0, 1034.7 ± 68.9. It may be concluded that the mean estimates of ΔE_k used in calculating walking and running external power were reliable.

At the highest walking speed, 3 walking subjects had to run. The internal and external power measures of these trials were excluded from the average. The mean walking and mean running internal power as a function of v reproduced the standard observation (e.g., Margaria et al. 1963; Falls and Humphrey 1976): a curvilinear relation for walking $(\mathrm{J\,s^{-1}} = 162v^2 - 222v + 237,\ r^2 = 1)$ and a linear relation for running $(\mathrm{J\,s^{-1}} = 179v + 150, r^2 = 1)$ (Fig. 3A). The slope of the latter function identifies the theoretically important constancy of metabolic $\mathrm{J\,m^{-1}}$. The constancy of $\mathrm{J\,m^{-1}}$ was evident in the running of all 9 subjects as summarized in Table 1.

The external power of both gaits was nonlinearly dependent on v (for walking, $\mathrm{J\,s^{-1}} = 129v^2 - 59v + 59$, $r^2 = 1$; for running, $\mathrm{J\,s^{-1}} = 74v^2 + 155v - 47$, $r^2 = 1$). The nonlinearity of the function for running was small, however. Linear regression of running external $\mathrm{J\,s^{-1}}$ on v yielded $r^2 = 0.99$ for the means over subjects. For subjects 1–9 taken individually the r^2 were 0.98, 0.96, 0.99, 0.99, 0.99, 0.99, 0.99, 0.97, and 0.99, respectively. Clearly, the v rate of change of $\Delta E_\mathrm{k}\,\mathrm{s^{-1}}$ was nearly invariant.

Table 1. Individual linear regressions of metabolic rate $(\mathrm{J\,s^{-1}})$ on $v\,(\mathrm{m\,s^{-1}})$ for running

Subject	Slope	Intercept	r^2
1	180.12	168.50	0.99
2	161.98	184.21	0.98
3	100.87	261.87	0.96
4	272.65	62.09	0.99
5	221.11	53.98	0.98
6	116.83	243.62	0.99
7	290.13	51.37	0.99
8	86.72	321.07	0.92
9	172.50	13.95	0.99

Note: for subject 6 an outlier at the lowest v was excluded from the regression

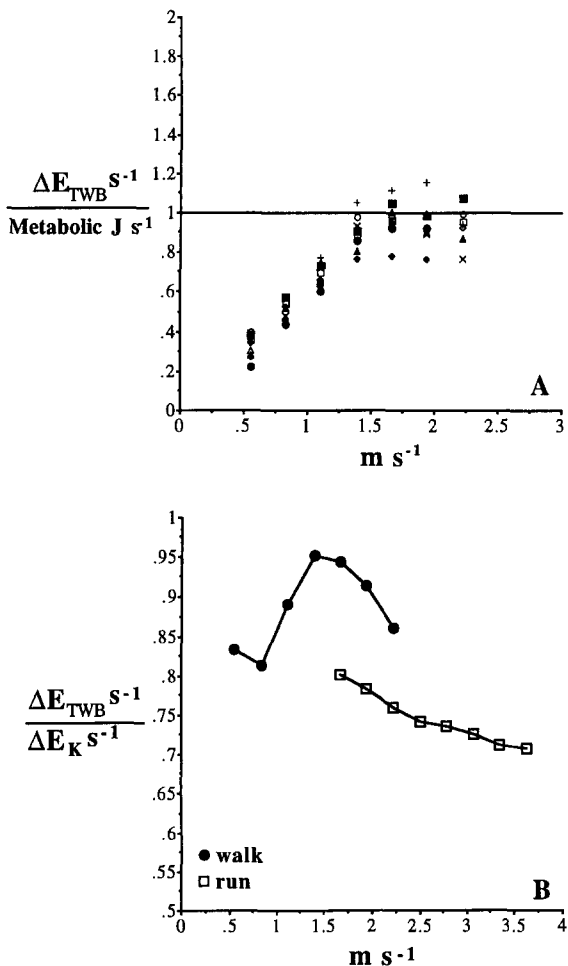Fig. 5. **A** Within- and between-segment energy transfer $\Delta E_{TWB}\,s^{-1}$ relative to metabolic cost for the individual subjects in the walking condition. **B** Mean $\Delta E_{TWB}\,s^{-1}$ relative to the mean summed changes in kinetic energy as a function of gait and speed

body segments and the irreversible energy changes associated with the degradation of 'on-board' potentials (chemical fuel).

Further understanding of walking and its contrast with running is achieved by computing $\Delta E_{TWB}\,s^{-1}/\Delta E_k\,s^{-1}$. As Fig. 5B reveals, $\Delta E_{TWB}\,s^{-1}/\Delta E_k\,s^{-1}$ is maximal at the preferred walking pace, is greater for walking than for running, and decreases in running with increases in speed. A possible reason for the minimal internal $J\,m^{-1}$ in walking in the vicinity of 1.3–1.4 m s^{-1} (Fig. 3B) is that at this speed the mechanical motions are most conservative: proximity to true pendulum motion dictates the metabolic minimum. With respect to running, the proportion of ΔE_k due to the passive exchanges captured by ΔE_{TWB} is much reduced, as expected. As noted above, gravitational E_p and translational E_k cannot exchange in running. Comparison of Fig. 5B with Fig. 4 implies that the $Q > 1$ character of running must be due to E_k reversibly exchanging with another energy form, namely that associated with the elasticity of tissue, E_e.

Evaluation of hypothesis 2. A value of $1/v^*$ for $\Delta Q/\Delta v$ was

predicted by (3) with a best guess for v^* of approximately 2 m s^{-1}. The best guess was substantiated. For the mean running data, v^* computed as the intercept with v of the linear regression in $v \times \Delta E_k\,s^{-1}$ coordinates (Fig. 1B) was 1.96 m s^{-1}. For runners 1–9, v^* was found by linear regression to be 2.07, 2.14, 1.82, 2.18, 1.98, 2.06, 2.34, 1.02, and 2.04 m s^{-1}, respectively. Excluding subject 8, the mean v^* of 2.07 m s^{-1} agrees closely with the 2.05 m s^{-1} transition speed reported by Beuter and Lalonde (1989) and the value of 2.07 m s^{-1} found by Hreljac (1993) and Diedrich and Warren (1995). As Fig. 4 suggests, the linear regression of all mean Q on all v revealed a close fit to the predicted adiabatic trajectory: $Q = 0.45v + 0.21$, r^2 (15) $= 0.97$, $p < 0.0001$. The preceding empirical linear trajectory intercepts the line $Q = 1$ at $v = 1.76$ m s^{-1}. For the mean running data along, $Q = 0.47v + 0.15$, $r^2 = 1.0$, $p < 0.0001$, with $Q = 1$ intercepted at 1.81 m s^{-1}. The tendency for running Q to increase linearly with v at a rate approximating 0.5 was characteristic of most of the running subjects. The individual linear regressions are given in Table 2.

Evaluation of hypothesis 4. According to (4), the metabolic rate is equal to $(v^*/v)\,(\Delta E_k\,s^{-1})$. Table 3 reports internal $J\,s^{-1}$ at each running v and the corresponding $(v^*/v)\,(\Delta E_k\,s^{-1})$ for the average data. Inspection of Table 3 reveals the predictive success. The r^2 was 1 and the mean difference between actual and predicted was 27 $J\,s^{-1}$ (or 1.34 ml $O_2\,s^{-1}$). For runners 1–9, the r^2 values of the linear regressions of actual metabolic rate on $(v^*/v)\,(\Delta E_k\,s^{-1})$ were 0.93, 0.86, 0.83, 0.98, 0.97, 0.90, 0.98, 0.72, and 0.98, respectively, and the mean differences between metabolic metabolic rate and $(v^*/v)\,(\Delta E_k\,s^{-1})$ were 24.67, 50.38, 87.13, $-$187.7, 7.2, $-$240.92, $-$69.1, 211.2, and 202.15 $J\,s^{-1}$, respectively. In brief, for 5 of the 9 runners, $(v^*/v)\,(\Delta E_k\,s^{-1})$ provided values closely similar

Table 2. Linear regression of Q on v for running

Subject	Slope	Intercept	r^2
1	0.45	0.04	0.96
2	0.45	$-$0.04	0.93
3	0.47	$-$0.03	0.96
4	0.53	0.11	0.98
5	0.38	0.32	0.96
6	0.71	0.00	0.95
7	0.44	0.06	0.98
8	0.50	0.26	0.97
9	0.52	0.48	0.98

Table 3. Evaluation of (4) of mean running data

v (m s^{-1})	$(v^*/v)\,(\Delta E_k\,s^{-1})$	Metabolic rate (J s^{-1})
1.66	489.95	444.19
1.94	547.49	503.64
2.22	581.34	551.92
2.50	624.47	596.19
2.78	669.23	645.73
3.06	718.21	696.53
3.33	776.42	750.50
3.61	794.06	796.88

to the actual metabolic rate. Quantities derived from the mechanics of running appear to be reasonably predictive of the directly measured constant rate of metabolism.

4 Concluding remarks

The primary motivation for the present research was the independence of metabolic cost and speed observed widely in animal locomotion (eg., Full 1989). From considerations that suggest a generalization of the notions of adiabatic transformability and adiabatic invariance to biological movement systems (Kugler and Turvey, 1987), it was hypothesized that (a) the aforementioned independence is an expression of an essential design feature of an adiabatically transformable open system, and (b) Figs. 1B and 2, based on adiabatic invariance, describe the strategies for human locomotion. An experimental evaluation was provided by collecting mechanical and metabolic measures on walking and running at progressively greater speeds. The results suggest that Figs. 1B and 2 do provide a meaningful description of human locomotion. With Q defined as Q_{metab}, the coupled oscillations of walking appear to be assembled in the domain $Q \leqslant 1$, shaped by both $Q = 1$ and the constancy of $\Delta Q/\Delta v$ but primarily by the former. The coupled oscillations of running appear to be assembled in the domain $Q > 1$ and shaped almost entirely by the constancy of $\Delta Q/\Delta v$. In accordance with expectations from the hypothesis of adiabatic transformability in dissipative systems, the metabolic costs of running were predictable from measures made strictly on the mechanics of locomotion.

Despite the positive outcomes there are reasons for being circumspect. Crucial to the fit of theory and data are (1) and (2). These quantities are speculative given the absence of any consensus about the proper measures of locomotion's mechanics and energetics (e.g., Williams 1985; Chapman et al. 1987; Kaneko 1990) Also of importance to the fit of theory and data is the computation of (1) via the seven-segment model (Winter 1979). One major reason for questioning its appropriateness is the model's neglect of spinal contributions (Gracovetsky 1988). Finally, with respect to the proposed extension of adiabatic transformability and invariance to changes in biological movement systems, it remains the case that these concepts have been rigorously developed only for hamiltonian (conservative) systems and even in that domain their application beyond systems of one-freedom to systems of N-freedoms poses significant challenges (e.g., Reinhardt and Dana, 1987).

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