EXTERNAL, INTERNAL AND TOTAL WORK IN HUMAN LOCOMOTION

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Summary

The muscle–tendon work performed during locomotion can, in principle, be measured from the mechanical energy of the centre of mass of the whole body and the kinetic energy due to the movements of the body segments relative to the centre of mass of the body. Problems arise when calculating the muscle–tendon work from increases in mechanical energy, largely in correctly attributing these increases either to energy transfer or to muscle–tendon work.

In this study, the kinetic and gravitational potential energy of the centre of mass of the whole human body was measured (using a force platform) simultaneously with calculation of the kinetic and potential energy of the body segments due to their movements relative to the body centre of mass (using cinematography) at different speeds of walking and running.

Upper and lower boundaries to the total work were determined by including or excluding possible energy transfers between the segments of each limb, between the limbs and between the centre of mass of the body and the limbs.

It appears that the muscle–tendon work of locomotion is most accurately measured when energy transfers are only included between segments of the same limb, but not among the limbs or between the limbs and the centre of mass of the whole body.

Key words: human locomotion, mechanical work, mechanical efficiency, energy transfer, external and internal work.

Introduction

Analysis of the motion of the body during locomotion is of great interest to many biological disciplines. For example, physiologists are interested in the mechanisms involved in different gaits and speeds, how the muscles function, the work done and the cost of locomotion, and physicians are interested in the description and consequences of pathological gaits. One useful approach in the study of the mechanics of locomotion is the calculation of the mechanical work performed. Although the details may vary, most studies of the mechanical energy output during locomotion use one of three techniques: measurement of the muscle power about the joints; analysis of the energy changes of a finite number of body segments from their movements relative to the ground; or analysis of the energy changes of the centre of mass of the whole body (COM_{wb}) relative to the ground and of the body segments relative to the COM_{wb}. All these methods lead to the same value for the total energy level of the body; however, the third method has several advantages which have led directly to fundamental insights into the mechanics and energetics of locomotion.

In the third method, the analysis divides naturally into two parts. The first is the analysis of movements of the COM_{wb} relative to the surroundings. In order to change the motion of the COM_{wb}, a force external to the body is required and, hence, the work associated with the mechanical energy changes of the COM_{wb} is called 'external work', W_{ext}. In contrast, the second part, the movements of the body elements relative to the COM_{wb} are to a large extent (but not exclusively) brought about by forces internal to the body and, as a consequence, the work associated with the mechanical energy changes relative to the COM_{wb} is called the 'internal work', W_{int}.

The study of W_{ext} in particular has resulted in the identification of two generally accepted fundamental mechanisms of terrestrial locomotion: the pendulum-like model of walking, associated with the maximum recovery of mechanical energy near the most economical speed; and the bouncing model of running, trotting, hopping and high-speed galloping, with its associated storage and recovery of mechanical energy by the contracting muscles and tendons (Cavagna *et al.* 1963, 1964, 1976, 1977; Alexander and Vernon, 1975; Heglund *et al.* 1982*a*). Neither of these two mechanisms is so clearly evident in any other type of analysis. In addition, force platform analysis, the technique used in determining W_{ext}, is particularly easy to implement, requires few assumptions which cause only small errors (that air resistance and skidding are negligible) and yields particularly simple to interpret, noise-free tracings (Cavagna, 1975).

The definition of W_{int} has great intuitive appeal. As W. O.

Fenn noted in 1930*a*: 'the kinetic energy turns out to be high in that limb where the work is being done. If the kinetic energy is calculated in relation to the ground, then the limb going backwards has very small kinetic energy although the actual effort on the part of the runner is as great in pushing it backwards as in pushing it forwards.' Calculation of W_{int} is more complicated than for W_{ext}; the records of the mechanical energy level of the individual body segments, obtained by cinematography, are far more complex, difficult to interpret and inherently more noisy. Furthermore, calculation of W_{int} requires assumptions about the physical properties of the body segments, as well as regarding the transfer (or lack of transfer) of energy to and from different body segments.

While it is fair to say that the external plus internal work procedure has many advantages, it is not without drawbacks. In addition to the problems associated with the measurement of W_{int} mentioned above, there has been a nagging uncertainty concerning the possible transfer of energy between the W_{int} and W_{ext} components of the total work (Fenn, 1930*a*; Cavagna, 1969; Cavagna and Kaneko, 1977; Heglund *et al.* 1982*b*; Cavagna and Franzetti, 1986; Alexander, 1989; Cavagna *et al.* 1991; Minetti *et al.* 1993). The uncertainty in the determination of total mechanical work, W_{tot}, arising from the various possibilities of energy transfer between body segments, has been demonstrated theoretically (Aleshinsky, 1986) and experimentally at one running speed on 31 subjects (Williams and Cavanagh, 1983) and on a single subject, during the swing phase, at one walking and one running speed (Caldwell and Forrester, 1992). As reviewed by Williams and Cavanagh (1983), the different computational models that have appeared in the literature yield values for the total mechanical power differing by up to 1000 % at the same running speed. These findings show the problems of defining a relationship between the positive work done by the muscles and the speed of locomotion during walking and running. In the present study, an attempt is made to determine this relationship by measuring W_{int} and W_{ext} simultaneously on several subjects at different walking and running speeds. Using this method, it is possible to investigate possible energy transfer between W_{int} and W_{ext} as well as to define the limits of the energy transfer between and within the limbs.

Materials and methods

Calculation of the mechanical energy of the body

The total energy level of the whole body ($E_{tot,wb}$), subdivided into n rigid segments of mass m, can be measured from the gravitational potential energy (E_p) and the kinetic energy (E_k) of each segment calculated at each instant relative to the surroundings:

$$E_{tot,wb} = \sum_{i=1}^{n} (m_i g h_i + \tfrac{1}{2}m_i V_i^2 + \tfrac{1}{2}m_i K_i^2 \omega_i^2), \qquad (1)$$

where h_i and V_i are the height and the linear velocity of the centre of mass of the ith segment relative to the surroundings; ω_i and K_i are the angular velocity and the radius of gyration of the ith segment around it's centre of mass; and g is the acceleration due to gravity.

From the definition of the height, H, of the centre of mass of a body of mass M:

$$H = \frac{1}{M} \sum_{i=1}^{n} m_i h_i, \qquad (2)$$

it follows that:

$$\sum_{i=1}^{n} m_i h_i g = M H g. \qquad (3)$$

This definition implies that equal and opposite vertical displacements of the body segments cancel; a point that will be discussed below.

The linear velocity of each segment of the body relative to the surroundings can be expressed as:

$$V_i = V_{cg} + V_{r,i},$$

where V_{cg} is the velocity of the COM_{wb} relative to the surroundings, and $V_{r,i}$ is the linear velocity of the centre of mass of the ith segment relative to the COM_{wb}. Thus, the translational kinetic energy of the body in equation 1 becomes:

$$\tfrac{1}{2} \sum_{i=1}^{n} m_i V_i^2 = \tfrac{1}{2} \sum_{i=1}^{n} m_i (V_{cg}^2 + V_{r,i}^2 + 2V_{cg}V_{r,i}). \qquad (4)$$

Since the sum of the linear moments of the segments relative to the COM_{wb} ($\sum m_i V_{r,i}$) is nil, equation 4 can be rewritten as:

$$\tfrac{1}{2} \sum_{i=1}^{n} m_i V_i^2 = \tfrac{1}{2}M V_{cg}^2 + \tfrac{1}{2} \sum_{i=1}^{n} m_i V_{r,i}^2, \qquad (5)$$

which is the König theorem.

It follows that the energy level of the body at each instant, including rotational kinetic energy, can also be expressed as:

$$E_{tot,wb} = M g H + \tfrac{1}{2}M V_{cg}^2 + \sum_{i=1}^{n} (\tfrac{1}{2}m_i V_{r,i}^2 + \tfrac{1}{2}m_i K_i^2 \omega_i^2). \qquad (6)$$

From equations 3 and 5, it follows that the formulations of the potential and translational kinetic energy in equations 1 and 6 are equivalent.

Measurement of W$_{ext}$

The energy/time curve of the COM_{wb} is given by the algebraic sum of the first two terms of equation 6 ($MgH + \tfrac{1}{2}MV_{cg}^2$). The sum of the increments of the resultant curve is

called external positive work, W_{ext}, because an external force is necessary to increase the mechanical energy of the COM_{wb} relative to the surroundings (Cavagna *et al.* 1963). Using the definition of work, W_{ext} is given by:

$$W_{ext} = FD\cos\varphi = F_f D_f + F_v D_v + F_1 D_1 , \qquad (7)$$

where F is the resultant of the external forces applied to the body, D is the displacement of the COM_{wb}, φ is the angle between the F and D vectors, and F_f, D_f, F_v, etc. are the projections of F and D in the forward (f), vertical (v) and lateral (l) directions, respectively. Provided that wind resistance and skidding are negligible and that the work necessary to sustain the lateral movements of the COM_{wb} is small (Cavagna *et al.* 1963), then equation 7 can be simplified to:

$$W_{ext} = Ma_f D_f + M(g + a_v)D_v , \qquad (8)$$

where a_f and a_v are the accelerations of the COM_{wb} in the forward and vertical directions, respectively.

The procedure used to calculate W_{ext} from the vertical and forward components of the force exerted by the feet on the ground is described in detail in Cavagna (1975). In the present study, a strain-gauge platform (6 m long and 0.4 m wide), made of ten plates similar to those described by Heglund (1981), was mounted at the floor level 25 m from the end of a corridor. The plates have a natural frequency of 250 Hz and a linear response to within 1 % of the measured value for masses up to 260 kg. The differences in the electrical response to a given force applied at different points on the surface of the ten plates are less than 2.5 % for the vertical direction and 5 % for the forward direction. The 'cross-talk' between the vertical and forward axis is, at worst, 1–2.5 % of the applied force.

The plate signals were summed and the resultant values were digitised by a 12-bit A/D converter. A/D conversions were made for each frame taken by the infrared camera system, for the measurement of the movement of the limbs (see below). The time of double contact in walking was determined by using shoes with conductive soles to complete a circuit through the platform surface, as described by Cavagna *et al.* (1976). The resulting signal was recorded by the A/D converter 100 μs after the force conversion (sixth trace in Fig. 1). For running, the aerial time was measured as the zero force period on the vertical and forward force plate records.

The mechanical energy of the COM_{wb} is illustrated in Fig. 1. W_{ext} was calculated as the sum of the increments in mechanical energy over a stride. To minimize errors due to noise, the increments in mechanical energy were considered to represent positive work actually done only if the time between two successive maxima was greater than 20 ms.

The work associated with the displacement of the COM_{wb} relative to the surroundings (equation 8) can, in principle, be measured by the same cinematographic procedure used to measure the E_k changes of the limbs relative to the COM_{wb}. However, differentiation of the cinematographic position trace would increase the noise in the resulting velocity and E_k records, while integration of the force platform signals would reduce the noise in the velocity and E_k records. Furthermore,

measurement of the mechanical energy of the COM_{wb} by the force platform does not result in the errors caused by the use of the anthropometric tables (which would otherwise be necessary to assess the relative values of the different segment masses). For these reasons, the force platform was used to measure the mechanical energy of the COM_{wb}.

Measurement of W_{int} due to velocity changes relative to the COM_{wb}

The E_k/time curve of the body segments due to their velocity relative to the COM_{wb} is given by the last term in equation 6. The sum of the increments in the E_k/time curves of all the body segments (calculated from their velocities relative to the COM_{wb}) was taken as an upper limit for W_{int} necessary to accelerate the limbs relative to the COM_{wb}.

The E_k of the body segments relative to the COM_{wb} was calculated from the changes in orientation of the trunk (including the head), upper and lower arm, upper and lower leg and foot on the side of the body nearest the cameras. Segments were defined using eight infrared emitters located at the side of the neck at the height of the chin (chin–neck intersect), the glenohumeral joint, the lateral condyle of the humerus, the dorsal wrist, the great trochanter, the lateral condyle of the femur, the lateral malleolus and the fifth metatarsal phalangeal joint. Segment length was measured with a ruler after positioning the infrared emitters (Table 1). The coordinates of the infrared emitters in the forward, lateral and vertical directions were measured by means of a Selspot II system. Two infrared cameras were placed 8 m apart and 9 m to the side of the track. The combined field of the cameras encompassed about 5.5 m of the track. The camera system measured the coordinates of the infrared emitters at 250 Hz (walking) or 500 Hz (running) synchronously with the A/D converter, which recorded the force signals from the platform. The total data acquisition time was 1.9 ms per frame. Displacements in the lateral direction were ignored because their contribution to segment velocity is negligible (Williams, 1985). The angle made by each segment with the horizontal was measured in each frame and plotted as a function of time. The resulting 'displacement curves' (Fenn, 1930a) were smoothed by a least-squares method (Stavitzsky and Golay, 1964) using a 140 ms interval for walking (180 ms in four experiments at the lowest speed) and a 70–110 ms interval for running.

In the original method proposed by Fenn (1930a), and subsequently used by Cavagna and Kaneko (1977) and by Cavagna *et al.* (1991), the movements of the limbs were not measured in relation to the COM_{wb} but in relation to the shoulder joint for the upper limb and the hip joint for the lower limb. In the present study, however, as in Heglund *et al.* (1982a,b), the movements of the body segments have been measured relative to the COM_{wb}, i.e. the E_k of the limbs was measured from their linear velocities relative to the COM_{wb} and not from their velocities relative to the shoulder and hip joints.

A 'stick man' was constructed as follows. The chin–neck intersect was taken as a starting point. The position of the hip joint marker relative to the chin–neck intersect was determined
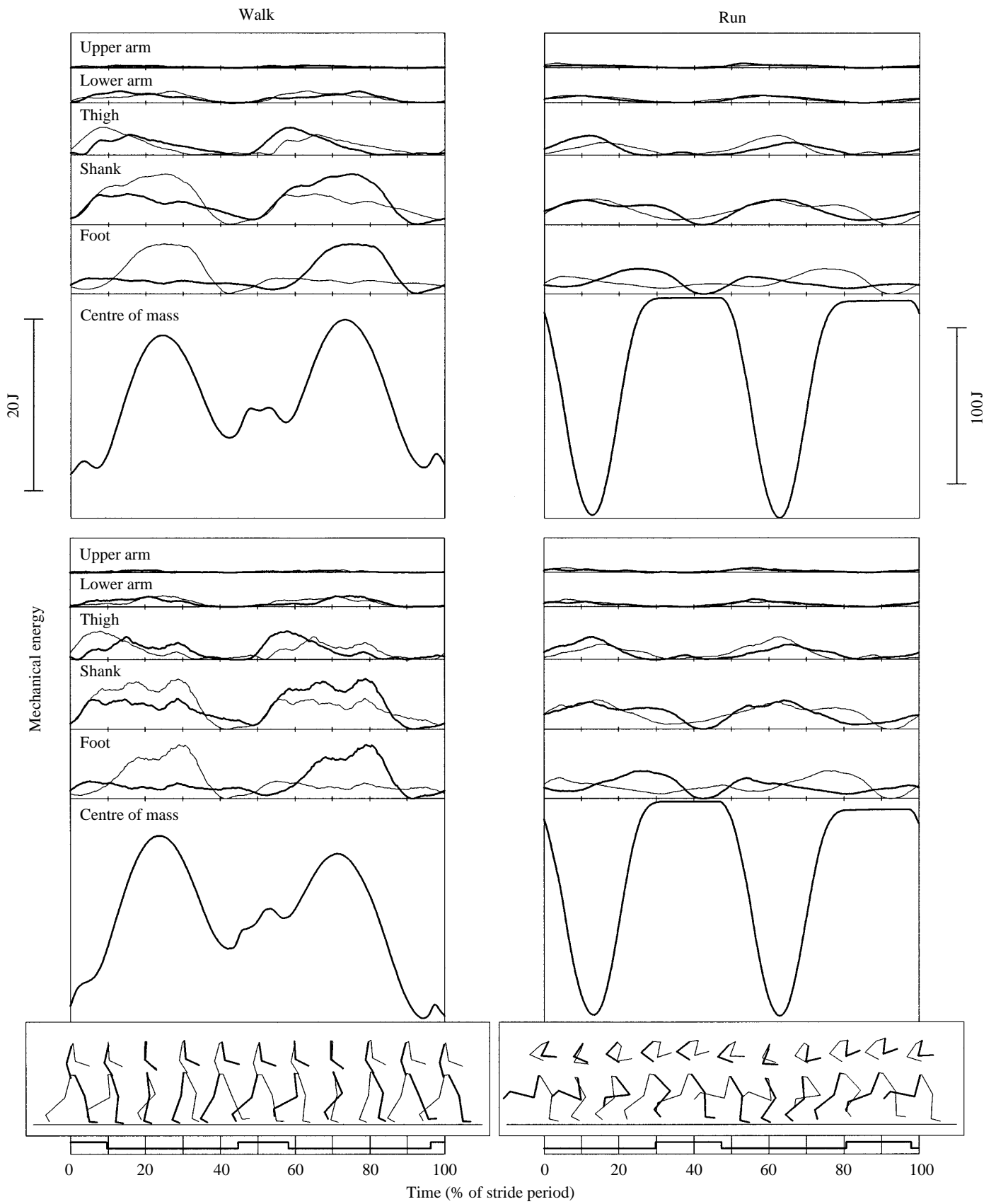
Fig. 1

Table 1. *Characteristics of the subjects*

				Distance between the anatomical landmarks defining the segments (m)							Number of trials	
Subject	Age (years)	Mass (kg)	Height (with shoes) (m)	Chin–neck intersect to hip	Shoulder to hip	Upper arm	Forearm	Thigh	Lower leg	Foot	Walk	Run
B.D.	28	78.1	1.82	0.64	0.48	0.30	0.26	0.42	0.45	0.15	24	32
C.G.	57	79.0	1.79	0.65	0.52	0.32	0.26	0.41	0.46	0.14	16	3
H.N.	38	68.5	1.78	0.68	0.54	0.30	0.25	0.38	0.43	0.14	20	19
T.J.	37	76.8	1.86	0.66	0.54	0.32	0.26	0.41	0.45	0.16	26	35
W.P.	34	82.4	1.79	0.68	0.53	0.28	0.26	0.39	0.43	0.16	20	34
Mean	39	76.7	1.81	0.66	0.52	0.30	0.26	0.40	0.44	0.15	21	25

from the distance between the two markers (measured on each subject before the experiment; Table 1) and the angle between a line connecting the two markers and the horizontal. The position of the shoulder joint relative to the hip joint was determined by the same procedure, except that the distance between the hip and shoulder markers was measured on each frame to account for the movement of the shoulder relative to the trunk (this distance was plotted as a function of time during a cycle and smoothed by the method described above, using a 220 ms interval for walking and a 130 ms interval for running). The coordinates of the elbow, wrist, knee, ankle and foot markers were then determined successively, starting from the positions of the shoulder and hip joints, using the segment lengths (Table 1) and the angles between the segment and the horizontal.

The positions of the segments on the opposite side of the body were reconstructed making the assumption that the orientation of the segments and the movements of the shoulder relative to the hip, during half a stride, were equal to those on the side closest to the cameras during the other half of the stride. The 'stick man' was then completed, starting from the chin–neck intersect, by the same procedure as described above. This method allows for the possibility that the positions of the shoulders and of the hip joints on the opposite sides of each 'stick man' could be different (e.g. right shoulder in front of

the chin and left shoulder behind it). In this way, rotation of the shoulder girdle and of the pelvis was taken into account, so that both arms and both legs were not constrained to start from the same point (rotation of the shoulder girdle and of the pelvis can be seen in the running stick man in Fig. 1). Williams (1985) showed that a procedure similar to that followed in this study [except that pelvis rotation was not taken into account: 2-D(3) in his paper] led to no significant differences in calculated power from that calculated using a more precise three-dimensional analysis of both sides of the body.

The position of the COM_{wb} was calculated from the relative positions of the body segments. The mass, the position of the centre of mass and the radius of gyration of each segment were calculated using both the anthropometric tables of Dempster and Gaughran (1967) and, for comparison, those of Braune and Fischer (1987, 1988, data first published between 1889 and 1899). The centre of mass of the trunk segment was located on a line joining the chin–neck intercept to the midpoint between the two hips. The distance from the midpoint of this line to the trunk centre of mass was assumed to be 66 % of the distance from the great trochanter to the glenohumeral joint measured on the standing subject before the experiment (Dempster and Gaughran, 1967). The coordinates of the COM_{wb} were then determined from the masses and the coordinates of the centre of mass of each of the eleven segments.

The linear velocity of the centre of mass of each segment relative to the COM_{wb} ($V_{r,i}$ in equation 6) was calculated from the slope of the curves, giving, as a function of time, the difference between the absolute coordinates of the segment and those of the COM_{wb}. The angular velocity of each segment (ω_i in equation 6) was calculated from the smoothed curves (the 'displacement curves' described above), giving, as a function of time, the angle made by the segment with the horizontal. In both cases, the velocity was computed from the average slope over intervals of 40–96 ms in walking and 28–40 ms in running (depending on the speed).

The kinetic energy of each segment, $E_{k,i}$, due to their movements relative to the COM_{wb} was then calculated as indicated in equation 6 from the sum of its translational and rotational energy (Fig. 1). W_{int} was calculated as the sum of the increments of $E_{k,i}$ during a stride. To minimize errors due to noise on the tracing (see Figs 1, 4, 7 and 8), the increments

Fig. 1. E_k changes of the limb segments due to their velocity relative to the COM_{wb} (top five traces of each panel) and the mechanical energy of the COM_{wb} (sixth trace of each panel) during one stride of walking (left) and running (right). The stick figures show the segment position every 10 % of the stride period. The 0 % and 100 % points of the stride correspond to the instant of maximum forward velocity of the COM_{wb} in walking and the instant of maximum downward velocity of the COM_{wb} in running; these points were chosen because they are clearly defined on the velocity traces of the COM_{wb} and because they correspond to about the same orientation of the limbs during walking and running. Thick lines indicate the position and E_k of the segments closest to the camera. The time of double contact (walk) and the aerial phase (run) are indicated by the upward shift in the bottom trace. The upper pair of panels are average values from seven trials on subject C.G. at 5.4 km h^{-1} (walk) and seven trials on subject W.P. at 14.7 km h^{-1} (run). The lower pair of panels show, for comparison, records from a single trial on each subject at these speeds.

of $E_{k,i}$ were considered to represent positive work done only if the time between two successive maxima was greater than 20 ms.

Measurement of W_{int} against gravity due to equal and opposite vertical movements

Equal and opposite vertical displacements of segment masses do not change the E_p of the COM_{wb}. Consequently, the work done against gravity associated with these vertical movements is measured neither as W_{ext} nor as W_{int} if only E_k is taken into account. As discussed by Cavagna and Kaneko (1977), this may underestimate the work done by the muscles against gravity.

The E_p of each segment was determined starting from the absolute value of the coordinates of the marker at the chin–neck intersect, which was subjected to a certain amount of jitter. The same jitter in the position of the COM_{wb} relative to the surroundings was irrelevant in the determination of the E_k of the segments, because each segment at each instant was referred to the COM_{wb}, irrespective of its absolute position in space. However, in the determination of the E_p of the segments, the jitter in the absolute position of the chin–neck intersect must be taken into account. For this reason, the position of the starting point for the construction of the stick figure (the chin–neck intersect) was smoothed by the method described above for the 'displacement curves', using a 220 ms interval for walking and a 130 ms interval for running.

The E_p of each segment was calculated by multiplying the absolute height of the segment's centre of mass by the segment weight. The algebraic sum of the E_p curves of all of the segments yields the E_p curve of the COM_{wb}; the sum of the increments in this curve represents the minimum work done against gravity as measured by cinematographic analysis ($W_{v,min}$). This must be equal to the sum of the increments of the E_p of the COM_{wb} (the first term of equation 6). The sum of the increments in the E_p curves of each of the segments yields the maximum work done against gravity, as measured by cinematographic analysis, $W_{v,max}$; this must be equal to or greater than the sum of the increments of the E_p of the COM_{wb}. The difference between $W_{v,max}$ and $W_{v,min}$ represents the internal positive work done against gravity in equal and opposite vertical movements. The ratio of the work done against gravity measured by the force platform to the minimum work measured by cinematographic analysis is 0.94±0.11 (mean ± S.D., N=106) in walking and 0.93±0.07 (mean ± S.D., N=123) in running. The 6–7 % difference is probably due to inaccuracies in the anatomical data used to calculate the relative mass and position of each body segments and to inherent approximations in the cinematographic analysis method.

Pendular energy transfer between E_k and E_p of the limbs

As discussed by Fenn (1930b), gravity may help the movement of the limb relative to the COM_{wb} by a pendular transfer of E_p into E_k, and vice versa. The effect of gravity on the internal work, tested by Cavagna and Kaneko (1977) on one subject at three speeds of walking and running, has been analysed in this study on five subjects for all speeds of walking and running. The E_p of each limb segment relative to the COM_{wb} was measured by plotting, as a function of time, the segment weight multiplied by the difference between the vertical coordinate of the segment and the vertical coordinate of the COM_{wb}. This E_p curve was added to the curve describing the E_k of the segment relative to the COM_{wb}. The sum of the increments in the resultant curve gives the positive work done to increase the E_{tot} of the segment relative to the COM_{wb}, assuming complete conversion between the E_k and E_p of the segment (see Fig. 3, squares). This procedure neglects the vertical acceleration of the COM_{wb} (which affects the pendular energy transfer) and the displacement of the COM_{wb} within the trunk. When the E_k and E_p of the limbs were measured relative to the trunk (instead of relative to the COM_{wb}), the E_{tot} of the limbs (E_p plus E_k) was 3.5 % greater in walking and 4.2 % greater in running.

Calculation of W_{tot}

A minimum value for W_{tot} is obtained by assuming complete energy transfer among the segments as well as between the COM_{wb} and the segments. This is done by adding the E_k/time curves of the body segments (see Figs 7 and 8, two upper panels) and the E_k plus E_p/time curve of the COM_{wb} (see Figs 7 and 8, third panel), and then by summing the increments of the resultant curve (see Figs 7 and 8, fourth panel).

A maximum value for W_{tot} is obtained by assuming no energy transfer among the segments or between the COM_{wb} and the segments. This is done by summing separately the increments in the E_k plus E_p/time curve of the COM_{wb} as well as in each of the E_k/time curves of the segments.

Subjects and experimental procedure

Experiments were carried out on five untrained male subjects (Table 1). The subjects walked or ran on an indoor track 42 m long. They were asked to follow a marker pulled by a motor at a given constant speed (1–10 km h^{-1} in walking and 7–27 km h^{-1} in running). The average velocity of the subject was measured by two photocells set 1.8–3.7 m apart for walking and 3.0–5.2 m apart for running. In most cases, trials at a given speed were repeated several times (2–9 times) in order to assess the reproducibility of the experimental results and to obtain average tracings. Tracings were averaged only if their speeds differed by less than 0.6 km h^{-1} for walking, and by less than 0.8 km h^{-1} for running. Work was calculated, as described above, from the tracings obtained during each individual run. The averaged tracings (e.g. Fig. 1, top panels) were used only for a qualitative description of the most significant features of the mechanical energy changes during the stride; they were not used to calculate the work, since this would result in reduced work values due to rounding of the energy peaks. Each subject was recorded in an average of 21 tests at five different speeds for walking and 25 tests at six different speeds for running (see Table 1). During each test,

W_{ext} and W_{int} were measured simultaneously over one complete stride.

Relationship to earlier observations

Fenn (1930*a*), Cavagna and Kaneko (1977) and Cavagna *et al.* (1991) measured W_{int} from the velocities of the segments relative to the shoulder joint for the upper limb and to the hip joint for the lower limb, rather than relative to the COM_{wb}, as was done in this study. In addition, in these studies, the foot and the shank were considered to be one rigid segment, and the relative mass, radius of gyration and position of the centre of mass of each segment were evaluated using the anthropometric tables of Braune and Fischer (1987, 1988) instead of those of Dempster and Gaughran (1967).

Values for W_{int} calculated from our experimental data but using the method of Fenn (1930*a*) are consistent with values calculated by Cavagna and Kaneko (1977). The ratios of the internal power computed using the equations given by Cavagna and Kaneko (1977, p. 473) to our values calculated using the method of Fenn (1930*a*) were 0.99±0.16 (mean ± S.D., *N*=106) for walking and 1.05±0.13 (mean ± S.D., *N*=123) for running.

The ratios between W_{int} computed from the velocities of the segments relative to the shoulder and hip joints to that computed relative to the COM_{wb} were 0.94±0.12 (mean ± S.D., *N*=106) for walking and 0.91±0.09 (mean ± S.D., *N*=123) for running. The ratios between W_{int} measured by the present method using the tables of Braune and Fischer (1987, 1988) to the internal work measured by this same method but using the tables of Dempster and Gaughran (1967) were 1.15±0.02 (mean ± S.D., *N*=106) for walking and 1.15±0.02 (mean ± S.D., *N*=123) for running. Disallowing any movements of the foot relative to the shank, and of the COM_{wb} relative to the trunk, increased W_{int} by less than 3 % in each case. In conclusion, the ratios between W_{int} measured using Fenn's method and in the present study were 1.11±0.14 (mean ± S.D., *N*=106) for walking and 1.04±0.10 (mean ± S.D., *N*=123) for running. The greater value of W_{int} obtained using Fenn's method, probably due to the use of different anthropometric tables, is partly offset by the lower values of W_{int} obtained if the movements of the limbs are measured not relative to the COM_{wb}, but relative to the hip and shoulder joints moving horizontally in the direction of the limbs.

Results

External positive work, W_{ext}

The mass-specific W_{ext} done per unit distance travelled during walking and running, to lift the COM_{wb} against gravity, W_{v}, to accelerate it forwards, W_{f}, and to maintain its movement in the sagittal plane, W_{ext}, is shown in Fig. 2A,B. The percentage recovery, a measure of the pendular transfer between E_{p} and E_{k} of the COM_{wb}, is shown in Fig. 2C. For walking, W_{ext} per unit distance is at a minimum at a speed only slightly lower than the speed where percentage recovery is at a maximum. For running, W_{ext} per unit distance decreases with speed and the percentage recovery is small at all speeds. These

results, obtained from the force platform, are consistent with those of Cavagna *et al.* (1976, see their Figs 3, 4).

Internal positive work, W_{int}

W_{int} was measured as the sum of the increments in E_{k} due to the movement of the limbs relative to the COM_{wb}, assuming no energy transfer between segments (see Materials and
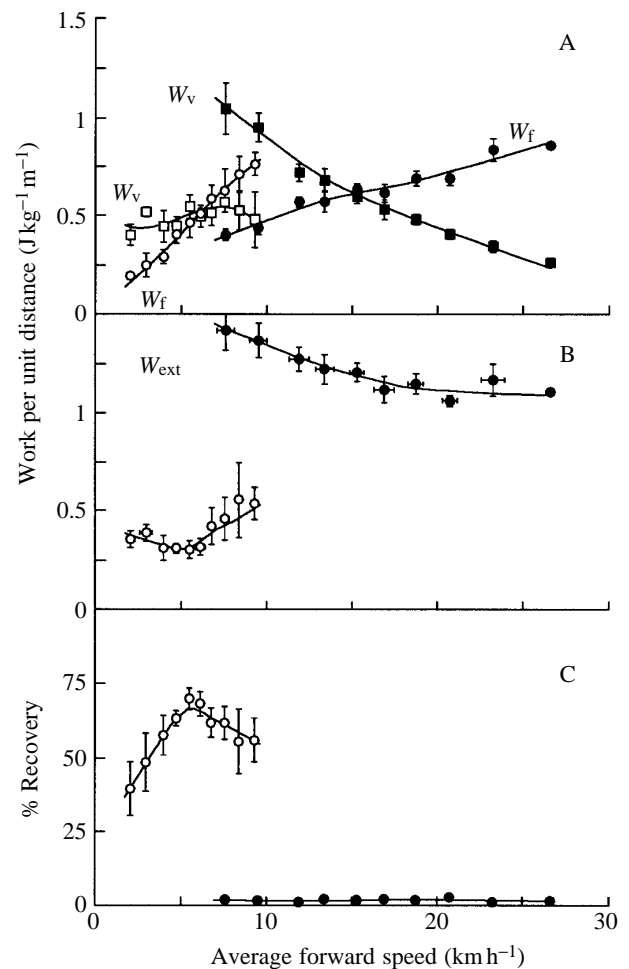
Fig. 2. Positive work associated with the mechanical energy changes of the COM_{wb} during walking (open symbols) and running (filled symbols). (A) The work done against gravity (W_{v}, squares) and to sustain the forward velocity changes of the COM_{wb} (W_{f}, circles). (B) The external work (W_{ext}) necessary to maintain the combined movements of the COM_{wb} in the sagittal plane. W_{ext} is smaller than the sum of W_{v} plus W_{f} due to the pendular transfer of E_{p} into E_{k}, and *vice versa*, which is quantified in C. % Recovery= $100[(W_{\text{f}}+W_{\text{v}}-W_{\text{ext}})/(W_{\text{f}}+W_{\text{v}})]$. Points represent mean values (±S.D.) obtained by grouping the data in the following forward velocity classes, in km h^{-1}, (*N*). Walking: 1.7–2.4 (4); 2.5–3.6 (5); 3.61–4.31 (14); 4.32–5 (8); 5.1–5.7 (13); 5.71–6.5 (8); 6.51–7.2 (17); 7.21–7.9 (9); 8–8.7 (16); 8.8–9.6 (12). Running: 6.9–8.65 (11); 8.66–10.9 (13); 11–12.6 (14); 12.61–14.4 (25); 14.5–16.2 (13); 16.21–18 (14); 18.1–20 (11); 20.1–22 (11); 22.1–25 (10); 26.6 (1). Lines represent the weighted mean of all the data, except for W_{v} in walking where the line is a third-order polynomial fit (KaleidaGraph 3.0.1).

methods) and is plotted in Fig. 3 (circles and solid lines); these results are similar to those reported by Cavagna and Kaneko (1977, see their Fig. 3).

Equal and opposite vertical movements of segment mass

Complementary symmetrical displacements of mass about the horizontal axis (e.g. lowering the arms while raising a leg, or lowering one arm while raising the other) do not result in measured work against gravity either as W_{ext}, since these movements do not result in a vertical displacement of the
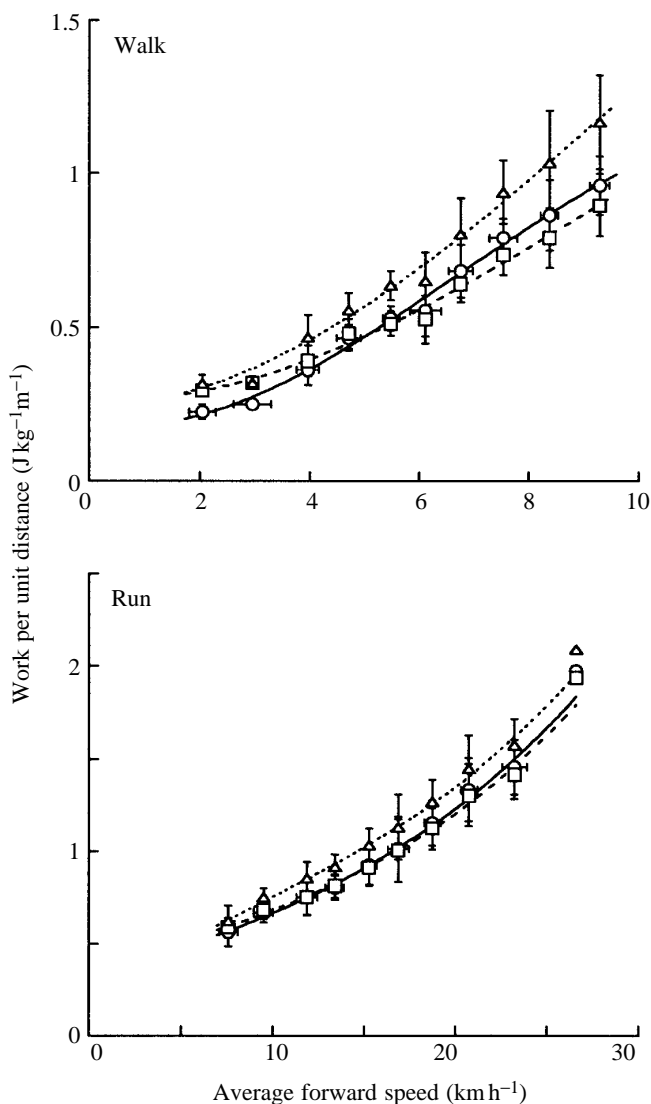
Fig. 3. Effect of gravity on W_{int} for walking and running. W_{int} due to the velocity changes of the limbs relative to the COM_{wb} (circles and solid lines) is increased by the work done against gravity in equal and opposite vertical movements to the level indicated by the triangles and the dotted line. If a pendular transfer between E_p and E_k of the limb segments is included, W_{int} changes to the level indicated by the squares and the dashed line. Lines are fitted using a third-order polynomial fit (KaleidaGraph 3.0.1). For other details, see Fig. 2.

COM_{wb}, or as W_{int} as defined here, since we take only the E_k changes of the body segments into account. In order to include the work due to such movements relative to the COM_{wb}, W_{int} done against gravity in equal and opposite vertical movements was measured (as described in Materials and methods) and added to W_{int} as shown in Fig. 3 (triangles and dotted lines). Equal and opposite vertical movements increase W_{int} by as much as 35 % at low walking speeds and 12 % for running.

As discussed by Fenn (1930b) and tested by Cavagna and Kaneko (1977), the E_k of a body segment may be sufficient to lift the limb about its joint in a pendular motion, so that no muscular work is required to sustain these vertical movements. To test this prediction, the E_p and E_k of the limb segments (relative to the COM_{wb}) were added (as described in Materials and methods) and the increments of the resulting curve were summed to give the positive work necessary to increase the E_{tot} of the segment relative to the COM_{wb} (squares and dashed lines in Fig. 3).

At the lowest walking speed, there is not sufficient E_k to lift the body segment passively against gravity; vertical movements of the limbs will increase the muscle–tendon work (Fig. 3, dashed lines). However, as walking speed increases, the E_k of the segments also increases. At walking speeds above approximately $5\,\mathrm{km\,h^{-1}}$, the positive work necessary to increase the E_{tot} of the limbs is smaller than that necessary to increase the E_k alone, i.e. the work required to accelerate the limbs relative to the COM_{wb} is slightly reduced by gravity.

At all running speeds, the E_{tot} changes of the segments are similar to those of the E_k alone (Fig. 3). Thus, work associated with E_p changes due to limb movements relative to the COM_{wb} can be neglected. It is, therefore, possible that, during running, part of the work done against gravity due to the vertical movements of the limbs, measured as W_{ext}, is in fact already measured as W_{int} (Fenn, 1930b). These errors, giving overestimates for W_{ext} for running and high walking speeds and underestimates for low walking speeds, have been neglected in the present study as in the earlier work of Cavagna and Kaneko (1977).

Effect of inertia on the movements of the limbs relative to the COM_{wb}

If the COM_{wb} decelerates forwards, the limbs tend to maintain their forward velocity by inertia and, therefore, to accelerate forwards relative to the COM_{wb}. Consequently, in this case, the increase in E_k of the limbs is not due to positive work done by the muscles. This example shows that, while the body is in contact with the ground, external forces may change the movement of the limbs relative to the COM_{wb}, and such movement, therefore, cannot be attributed solely to internal forces.

According to the fundamental law of relative dynamics:

$$ma_r = F_e + F_s + F_c, \qquad (9)$$

where m is the mass of the segment, a_r is the acceleration of the segment relative to the COM_{wb}, F_e is the effective force
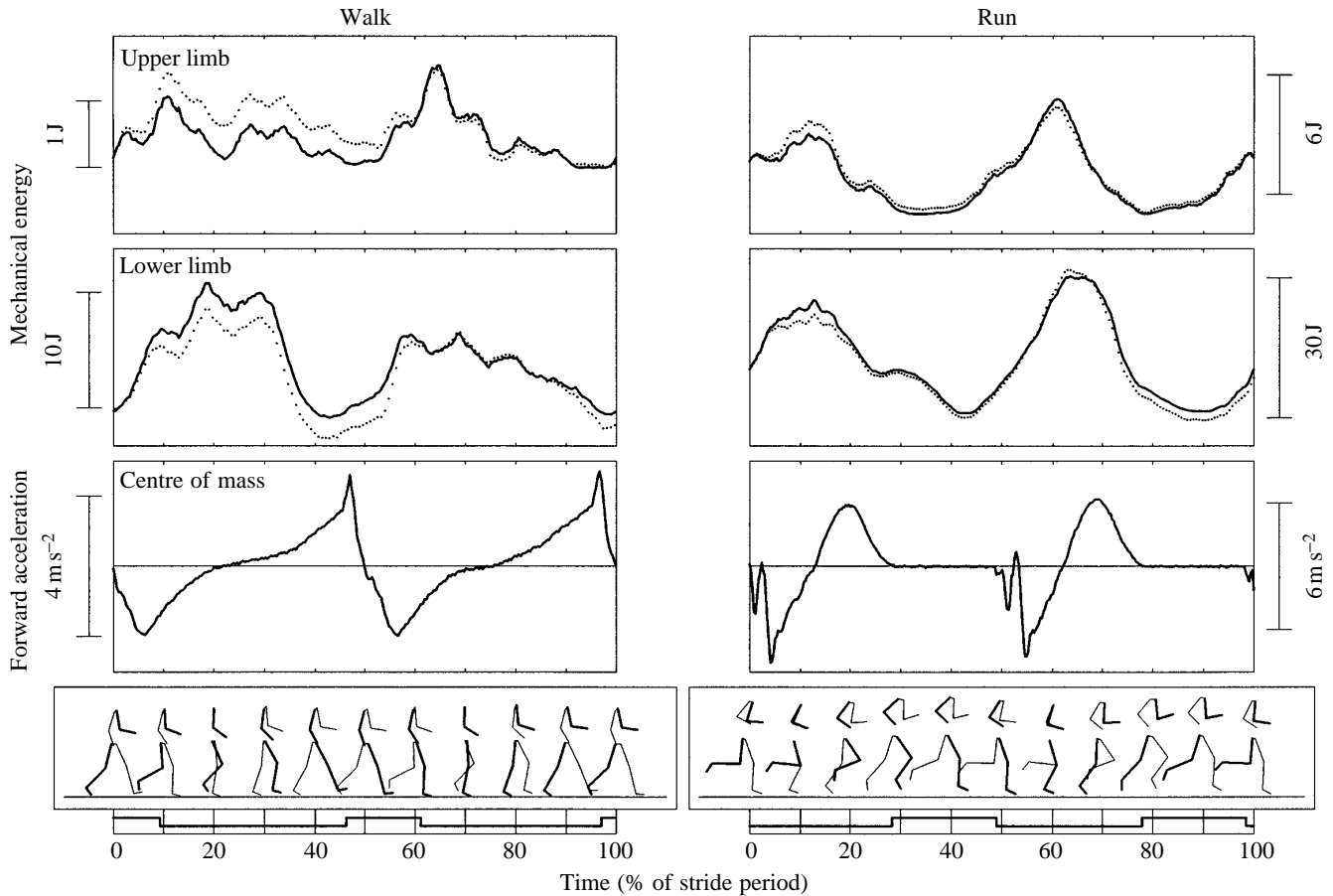
Fig. 4. The effect of inertia on the mechanical energy of the upper and lower limbs during walking at 5.6 km h^{-1} (left, subject C.G.) and running at 13.9 km h^{-1} (right, subject T.J.). The mechanical energy of the limbs closest to the camera (thick lines on the 'stick man'), calculated from the forward velocity of the limb segments relative to the COM_{wb} (solid lines, top two panels), is compared with the mechanical energy calculated using equation 10 (dotted lines), which takes into account forward accelerations of the limb segments, due to their inertia, arising from accelerations of the COM_{wb}. For simplicity, results from the two segments of the upper limb were summed (top panels), as were results for the three segments of the lower limb (second panels). The forward accelerations of the COM_{wb} are shown in the third panel. Note, for example, that the positive work required to accelerate the lower limb forwards (increments of the energy curves) is reduced by inertia during the forward deceleration of the COM_{wb} and the work required to accelerate the upper limb backwards is simultaneously increased. For further details, see Fig. 1.

exerted on the segment, F_s is the apparent force due to the acceleration of the COM_{wb} relative to the surroundings ($F_s = -ma_s$, where a_s is the acceleration of the COM_{wb}) and F_c is the complementary force of Coriolis. The work in a relative movement is the sum of the work done by the effective force F_e plus the work done by the apparent force F_s; the work done by the Coriolis force F_c is nil (Finzi, 1959).

Assuming that the muscular force is the only effective force accelerating the ith segment during the ground contact phase, the muscular work is:

$$W_i = (m_i a_{r,i} - F_{s,i})d_{r,i} = m_i(a_{r,i} + a_s)d_{r,i}, \qquad (10)$$

where $d_{r,i}$ is the displacement of the segment relative to the COM_{wb}. This means, for example, that a forward acceleration ($+a_s$) of the COM_{wb} must be added to the forward acceleration of the segment ($+a_{r,i}$) relative to the COM_{wb} and the resulting

W_{int} done by the muscles will be increased. When all of the body segments are taken into account, equation 10 becomes:

$$W = \sum_{i=1}^{n} W_i = \sum_{i=1}^{n} m_i a_{r,i} d_{r,i} + a_s \sum_{i=1}^{n} m_i d_{r,i}. \qquad (11)$$

Thus, the overall effect of inertia on W_{int} is nil because:

$$\sum_{i=1}^{n} m_i d_{r,i} = 0. \qquad (12)$$

However, the effect of inertia on the muscular work done in accelerating individual body segments relative to the COM_{wb} may not be nil. This effect was tested by comparing W_{int} calculated using equation 10 with W_{int} calculated as the sum
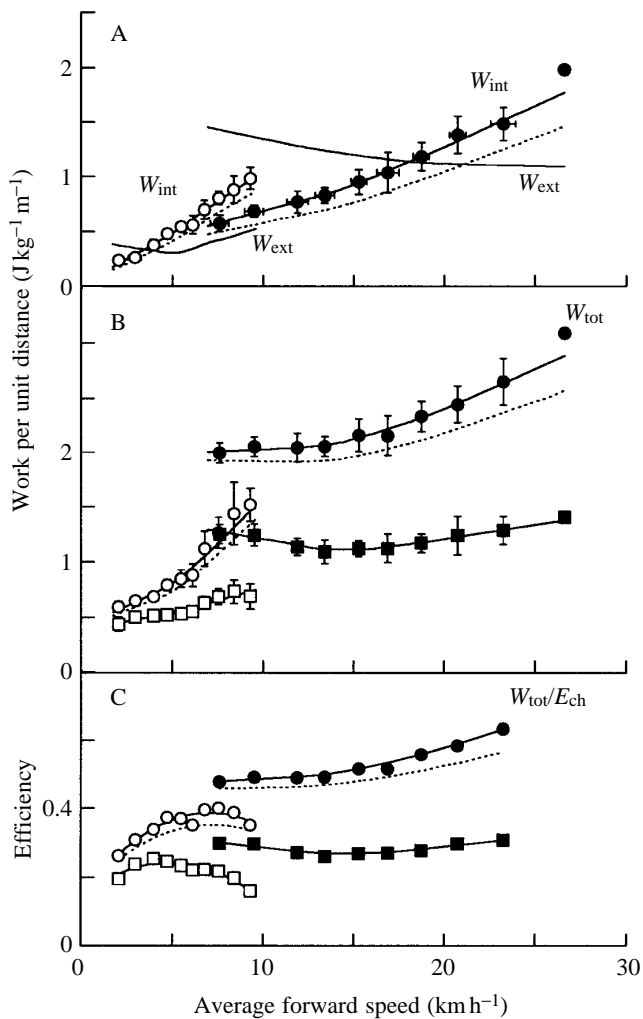
Fig. 5. (A) Positive work associated with the mechanical energy changes of the COM_{wb} (W_{ext}, from Fig. 2) and with the E_k changes due to the movement of all the body segments relative to the COM_{wb} (W_{int}). The dotted line represents W_{int} calculated by assuming transfer of energy between the segments of each limb (see text). (B) W_{tot} calculated assuming either no transfer (circles) or complete transfer (squares) of mechanical energy among the body segments as well as between the segments and the COM_{wb}. The circles are the sum of the W_{ext} and W_{int} curves in A. The dotted line is the sum of W_{ext} and the dotted line in A. (C) The minimum and maximum values of muscular efficiency (W_{tot} divided by net energy expenditure, E_{ch}) calculated using values of W_{tot} from B. E_{ch} is computed from total oxygen consumption minus standing oxygen consumption (same data as used by Cavagna and Kaneko, 1977). Lines represent the weighted mean of all the data except for the efficiency during walking, where the lines are a second-order polynomial fit (KaleidaGraph 3.0.1). For further details, see Fig. 2.

of the increments in E_k of the limbs relative to the COM_{wb} (see Fig. 4). The term $a_{r,i}$ in equation 10 was calculated from the slope of the limb segment velocity curves; the term a_s was calculated from the force plate records for both vertical and forward directions. The value for $a_{r,i}$ was confirmed by comparing the work measured from the acceleration of the segments ($m_i a_{r,i} d_{r,i}$) with the work measured from the sum of

their E_k increments: for walking, the ratio of these two values was 0.99±0.02 (mean ± S.D., $N=106$); for running the ratio was 1.00±0.01 (mean ± S.D., $N=123$). The corresponding ratios for W_{int} measured on each limb from equation 10 to W_{int} measured as the sum of the increments of the E_k of the limb relative to the COM_{wb} were 0.97±0.03 (mean ± S.D., $N=106$) for walking and 1.03±0.03 (mean ± S.D., $N=123$) for running.

An example of the effect of inertia in modifying the mechanical energy curves of the upper and lower limbs due to their forward movements relative to the COM_{wb}, as a result of an acceleration forwards, is illustrated in Fig. 4 for both walking and running.

Total work, W_{tot}

In this study, simultaneous measurement of W_{ext} and W_{int} makes it possible to add, at each instant, the mechanical energy of the COM_{wb} (E_p plus E_k) to that of each body segment (E_k only, calculated from the velocity of that segment relative to the COM_{wb}) to assess the $E_{tot,wb}$ level of the body (equation 6). As described in Materials and methods, the sum of the positive increments of the resulting curve gives a hypothetical minimum value for W_{tot} (Fig. 5B, squares). The maximum W_{tot} (Fig. 5B, circles) is calculated as:

$$W_{tot,max} = |W_{ext}| + |W_{int}|, \qquad (13)$$

i.e. the sum of the positive increments of the mechanical energy of the COM_{wb} plus the positive increments of each of the E_k curves of the separate body segments.

Energy transfer between segments

The hypothetical minimum values for W_{tot} (Fig. 5B, squares) are for the case where there is complete energy transfer between body segments, whereas the maximum values (Fig. 5B, circles) correspond to the case where there is no energy transfer between segments. The relative effects of different energy transfers on W_{tot} are shown in Fig. 6 as a function of speed. The upper lines in Fig. 6 (circles) show that including energy transfer between the segments within each limb in our calculation reduces W_{tot} by no more than 10%. Assuming energy transfer between all the segments within each limb and across the trunk (squares) results in a reduction of W_{tot} by no more than 20%. A more drastic reduction of W_{tot}, by about 50%, is observed when energy transfer between the E_k of the body segments (due to their movement relative to the COM_{wb}) and the mechanical energy of the COM_{wb} is also included (triangles).

All the curves in Fig. 6 show that there is a greater reduction in W_{tot}, due to the possible energy transfers, at higher speeds. This is particularly true during walking for the hypothetical exchange between the E_k of the limbs relative to the COM_{wb} and the mechanical energy of the COM_{wb}. The reason for this is shown in Fig. 7, which illustrates the effects of the speed of walking on the trends and the amplitudes of the mechanical energy changes of the COM_{wb} and of the limbs (for clarity, the energies of the segments of each limb have been added). The
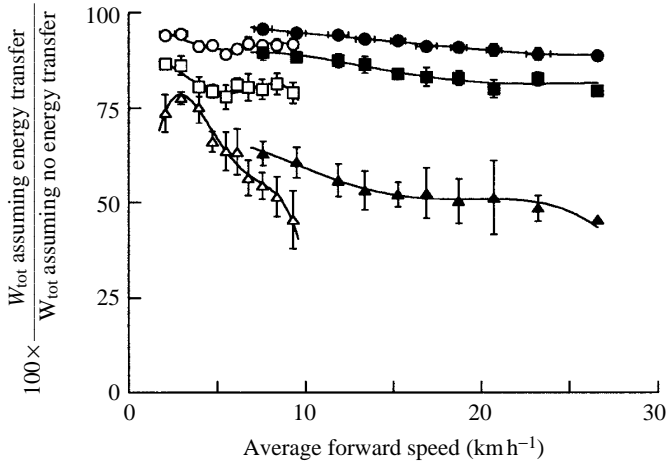
Fig. 6. W_{tot} during walking (open symbols) and running (filled symbols), calculated using different assumptions of energy transfer, expressed as a percentage of the maximum calculated value for W_{tot} (Fig. 5B, circles). Energy transfer between limb segments results in a $\leqslant 10\%$ decrease in W_{tot} (circles). W_{tot} is reduced by $\leqslant 20\%$ when energy transfer of the limb segments across the trunk is also included (squares). Finally, including energy transfer between the COM_{wb} and the body segments results in a larger reduction in W_{tot} (up to approximately 50%; triangles). Lines were fitted using fourth-order polynomial regressions (KaleidaGraph 3.0.1). For other details, see Fig. 2.

mechanical energy changes of the COM_{wb} and of the limbs are approximately in phase at the lowest speed, whereas an E_k minimum for the limbs is attained almost in phase with a mechanical energy maximum for the COM_{wb} at the highest speed. These out-of-phase energy changes cancel, thus explaining the reduction in W_{tot} with speed seen in Fig. 6.

An E_k minimum for the limbs almost in phase with a mechanical energy maximum for the COM_{wb} also occurs during running (Fig. 8). However, the phase relationship between the mechanical energy changes of the limbs and of the COM_{wb} is less affected by speed during running than during walking; the relative amplitudes become more similar at high speeds due to a relative increase in the E_k changes of the limbs. This explains why, during running, the lower and middle curves in Fig. 6 diverge with speed less than during walking.

As mentioned above, both during high-speed walking and during running, the E_k minimum for the limbs occurs near the mechanical energy maximum for the COM_{wb}. At this point in the step, the limbs reverse their movement relative to the COM_{wb} and, therefore, possess the lowest E_k due to their motion relative to the COM_{wb}. This phase of the step occurs when the COM_{wb} is at its lowest point during walking and at its highest point during running (the aerial phase). This reflects the fundamental difference between walking and running: the
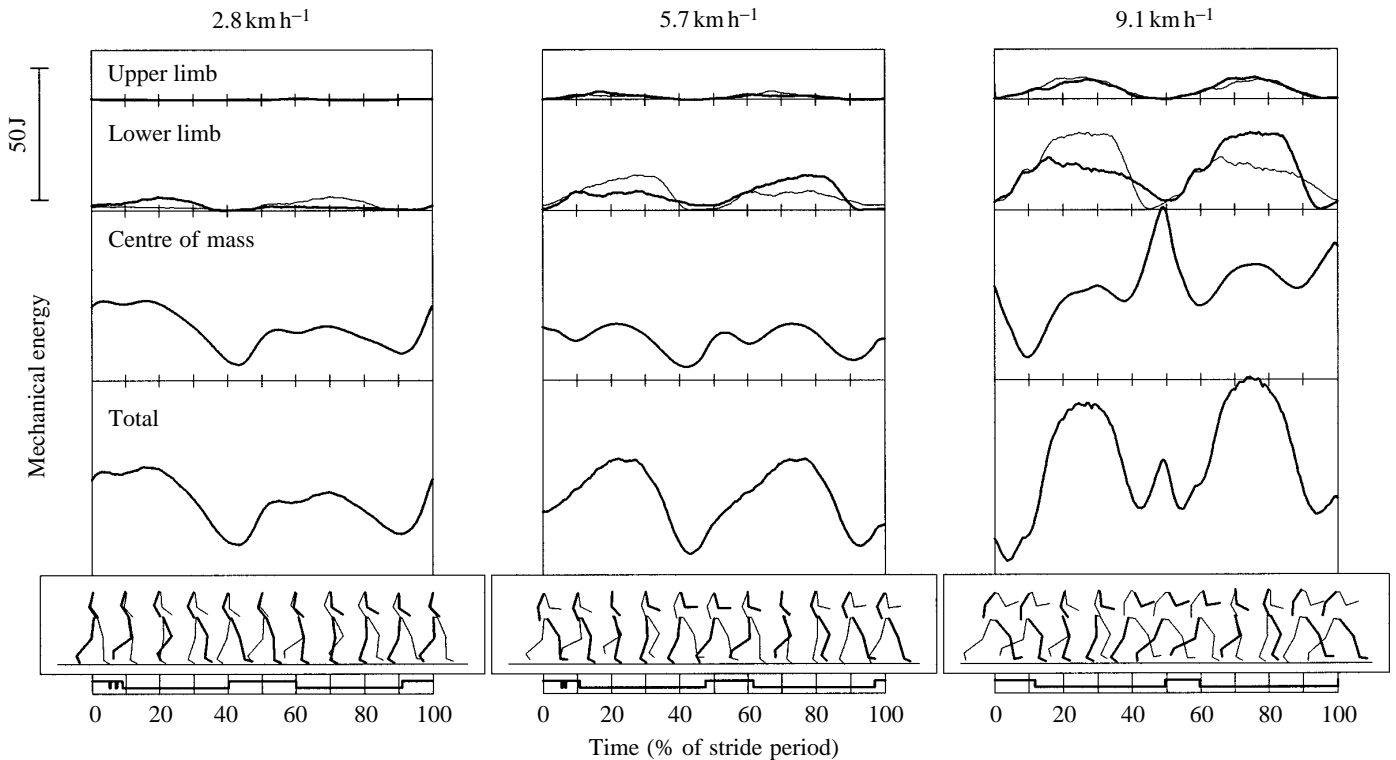

Fig. 7. Effect of walking speed on the mechanical energy level of the body. The two upper panels at each speed indicate the E_k changes of the upper and lower limbs, due to their movement relative to the COM_{wb}, calculated by adding the E_k curves of the segments of each limb. The third panel indicates the mechanical energy of the COM_{wb} (E_k plus E_p). The fourth panel indicates the E_{tot} of the body, calculated by summing the curves in the three upper panels; the sum of the increments in this curve represents the minimum value of W_{tot}, as shown in Fig. 5B (squares). Individual traces of subject B.D. Other details are as in Fig. 1.

E_p and E_k changes of the COM_{wb} are 180° out of phase during walking and in phase during running (Cavagna *et al.* 1963, 1964). Despite the opposite mechanisms for walking and running, comparison of Figs 7 and 8 shows that the movements of the limbs relative to the COM_{wb} are similar in both cases.

Efficiency of positive work production

In Fig. 5, the minimum and maximum possible values of the efficiency of positive work production during level walking and running were calculated as:

$$\text{Efficiency} = W^+/E_{ch}$$
$$= (W_{ch}^+ + W_{el}^+)/(E_{ch}^+ + E_{ch}^- + E_{ch,isom} + E_{ch,frict}), (14)$$

where W^+ is the minimum or the maximum value of W_{tot} (Fig. 5B); E_{ch} is the net energy expenditure calculated from the oxygen consumption; W_{ch}^+ is the mechanical work deriving from the transformation of chemical energy; W_{el}^+ is the mechanical work deriving from the elastic potential energy stored in the muscles and tendons; E_{ch}^+ is the chemical energy used during positive work to increase the mechanical energy of the body; E_{ch}^- is the chemical energy spent during negative work done by the muscles in absorbing E_k and E_p released during another phase of the step; $E_{ch,isom}$ is the chemical energy spent during isometric contractions; and $E_{ch,frict}$ is the chemical energy spent to overcome internal friction and to sustain antagonistic muscular contractions (one muscle doing positive work while another does negative work) and other activities not directly related with the performance of positive work (e.g. respiration).

Efficiency reaches a maximum at intermediate speeds for walking (as expected from the force–velocity relationship of muscle), but not for running, where values are higher than for walking and higher than the maximum efficiency of the conversion of chemical energy into positive work by muscle $W_{ch}^+/E_{ch}^+ \leqslant 0.25$ (Dickinson, 1929). In this study, positive work done by the muscles and tendons was measured from the increments of E_{tot} of the limbs and the COM_{wb}. E_{tot}, in turn, was measured from the E_k and E_p of the body segments and/or of the body as a whole, taking care to include possible energy transfers between the segments (so that the positive work done was not measured twice). No attempt was made to measure the elastic potential energy stored and recovered in the muscles and tendons, W_{el}^+. If this storage and release of mechanical energy does occur, the efficiency of positive work production would be increased above the predicted value of 0.25 attained by the unstretched contractile component of skeletal muscles. In addition, no attempt was made to determine the proportion of the total metabolic energy expenditure associated with E_{ch}^-, $E_{ch,isom}$ and $E_{ch,frict}$. These would tend to decrease the calculated values of efficiency below 0.25. Our finding, that the efficiency of positive work is greater than 0.25, particularly during running, suggests that the gain due to the elastic storage and recovery of mechanical energy (W_{el}^+) more than compensates for the possible losses (E_{ch}^-, $E_{ch,isom}$ and $E_{ch,frict}$).
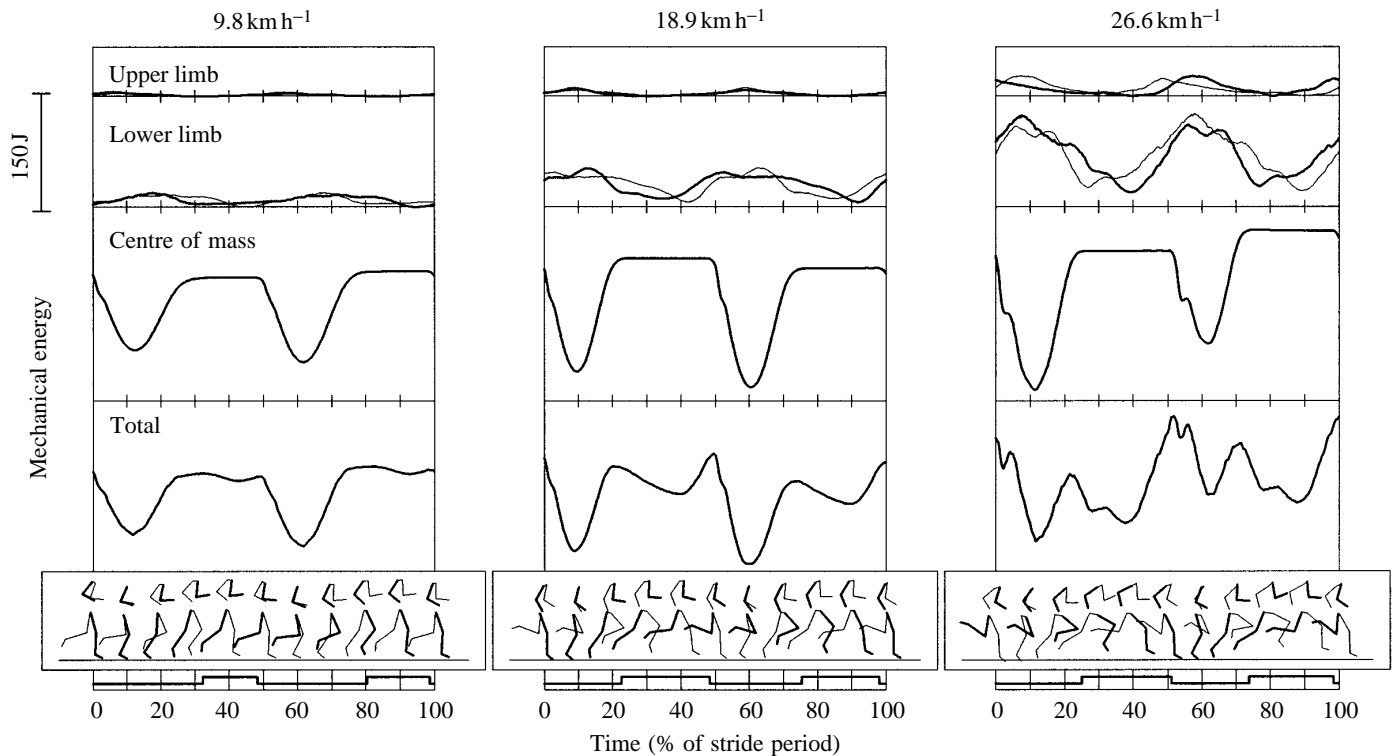

Fig. 8. Effect of running speed on the mechanical energy level of the body. Individual traces of subject T.J. Other details are as in Fig. 7.

Discussion

This study was designed to obtain a reasonable value for both muscle–tendon work and efficiency during level walking and running, and to evaluate approximations made in previous studies, which often assume that $W_{tot}=|W_{ext}|+|W_{int}|$.

Since no major assumptions are made in the measurement of W_{ext}, possible ambiguities in our calculation of W_{tot} arise only in the degree of assumed energy transfer between body segments, in their motion relative to the COM_{wb}, and between the body segments and the COM_{wb}. Such energy transfers can be considered by simply including a decrease in energy from a possible donor to cancel out a simultaneous increase in energy for a possible recipient; by selecting these donors and recipients, the consequences of different possible energy transfers can be investigated. However, indiscriminate use of this technique, without regard to the feasibility of the suggested transfer sites, can result in erroneous values of W_{tot}.

Fig. 6 (circles) shows that including a complete transfer of E_k between adjacent segments of each limb may decrease W_{tot} by up to 10 %; such transfers are likely to occur. A further energy transfer across the trunk, between the segments of different limbs, would reduce W_{tot} by up to an additional 10 % (Fig. 6, squares). In this case, however, as discussed by Fenn (1930*a*, pp. 608–609), a maximum of only 10 % of the E_k of a limb may be passed to another limb through the trunk, and the actual energy transfer is likely to be much closer to zero. Therefore, it would appear that the transfer of energy between limb segments could reduce W_{tot} by up to a maximum value of approximately 10 %.

A much larger reduction of W_{tot} (Fig. 6, triangles) can be obtained, particularly at high walking speeds and for running, by adding the E_k/time curves of the body segments to the mechanical energy/time curve of the COM_{wb}. This summation implies that some of the E_k of the COM_{wb} may appear as E_k in the limbs (and *vice versa*). However, this hypothesised transfer is unlikely to occur for the following reasons.

The magnitude of a change in E_k depends both on the change in velocity and on the absolute value of the velocity. However, as shown above (equation 10), the work necessary to accelerate the limbs relative to the COM_{wb} is affected only by the change in velocity of the COM_{wb}, i.e. by its acceleration (a_s in equation 10), and not by its absolute velocity. For this reason, it is necessary to compare the acceleration of the COM_{wb} with that of the segments relative to the COM_{wb} when considering energy transfers between the two, regardless of the absolute velocity of the COM_{wb} and, hence, its E_k change. For example, a $0.5\,\mathrm{m\,s^{-1}}$ increase in velocity results in a more than 20-fold greater increase in E_k when the initial velocity is $5\,\mathrm{m\,s^{-1}}$ than when it is $0\,\mathrm{m\,s^{-1}}$. If, for a hypothetical running step, the decrease in E_k of the COM_{wb}, due to deceleration upon landing, were matched with an equal increase in energy of the limbs relative to the COM_{wb}, the sum of the two would be zero, suggesting a complete transfer of energy from the COM_{wb} to the segments. However, since the starting velocity of the COM_{wb} is

approximately equal to the running speed (e.g. $5\,\mathrm{m\,s^{-1}}$), while the starting relative velocity of the limbs is zero, the deceleration of the COM_{wb} must have been much less than the acceleration of the limbs in order to yield the same E_k change. Consequently, the energy transferred can equal only that fraction of the total increase in E_k of the limbs that can be attributed to an increase in velocity equal to the decrease in velocity of the COM_{wb}; any further increase in E_k of the limbs must have resulted from muscle–tendon work. Our data show that, in some phases of the stride (Fig. 4), when the absolute values of the velocities are taken into account, the transfers of energy by this mechanism increase the work required to accelerate the limbs by 19±7.5 % (mean ± S.D., $N=106$) for walking and 16±6.9 % (mean ± S.D., $N=123$) for running and decrease the work required to accelerate the limbs by 22±5.6 % for walking and 16±6.6 % for running. However, as shown above (see Results), the increase in work during acceleration of some segments equals the decrease in work during acceleration of other segments, resulting in no net change in W_{int} over a complete stride.

As a result of these considerations, the algebraic sum of the mechanical energy of the COM_{wb} plus the E_k of the segments due to their movements relative to the COM_{wb} (equation 6) does not appear to be a proper measure of the positive work done by the muscles and tendons. This algebraic sum includes energy transfers that are not likely to occur.

It is clear from this study that W_{int}, as defined here, is affected by external forces. The two effects considered are (i) equal and opposite vertical movements against gravity (Fig. 3), and (ii) the effect of the velocity changes of the COM_{wb} (Fig. 4). A possible third effect would be deformation of the body due to the impact with the ground, shown during running by the abrupt flexion of the lower limb which takes place at the moment of contact. This flexion is due to an external force and must not be included as W_{int} required to accelerate the limb upwards relative to the COM_{wb}. The mechanical energy change due to this third effect was measured in this study and found to be negligible.

In conclusion, it appears that W_{ext} is correctly measured and that W_{int} is most accurately measured as the E_k changes of the segments, including energy transfer only between segments of the same limb (Fig. 5, dotted line). The most accurate estimate of W_{tot} is the sum of $|W_{ext}|$ plus $|W_{int}|$. Consequently, conclusions on muscular efficiency reached previously (Cavagna and Kaneko, 1977), and on the choice of the optimum step frequency in walking (Cavagna and Franzetti, 1986; Minetti and Saibene, 1992) and running (Cavagna *et al.* 1991), based upon values of W_{tot} calculated in line with the above recommendations, remain substantially correct.

List of abbreviations

a_f forward acceleration of COM_{wb}

a_r acceleration of a segment relative to COM_{wb}

a_s acceleration of COM_{wb}

a_v	vertical acceleration of COM_{wb}
COM_{wb}	centre of mass of the whole body
D	displacement of COM_{wb}
d_r	displacement of a segment relative to COM_{wb}
E_{ch}^+	chemical energy used during positive work to increase mechanical energy
E_{ch}^-	chemical energy spent during negative work
E_{ch}	net energy expenditure calculated from the oxygen consumption
$E_{ch,frict}$	chemical energy spent to overcome internal friction, antagonistic muscular contractions, and other activities not directly related with the performance of positive work
$E_{ch,isom}$	chemical energy spent during isometric contractions
E_k	kinetic energy
E_p	gravitational potential energy
$E_{tot,wb}$	total mechanical energy level of whole body
F	resultant of external forces
F_c	complementary force of Coriolis
F_e	effective force exerted on a segment
F_s	apparent force due to the acceleration of the COM_{wb} relative to the surroundings
g	acceleration due to gravity
H	height of COM_{wb}
h	height of body segment
K	radius of gyration of body segment
m	mass of a body segment
M	whole body mass
φ	angle between force and displacement vectors
V	velocity of centre of mass of body segment relative to the surroundings
V_{cg}	velocity of COM_{wb}
V_r	linear velocity of segment centre of mass relative to COM_{wb}
ω	angular velocity
W_{ch}^+	mechanical work deriving from the transformation of chemical energy
W_{el}^+	mechanical work deriving from the elastic potential energy
W_{ext}	positive work required to maintain the motion of COM_{wb}
W_f	work to accelerate the COM_{wb} in the forward direction
W_{int}	positive work required to accelerate the body segments relative to COM_{wb}
W_{tot}	positive muscle–tendon work to maintain locomotion
W_v	work done against gravity

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