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Mechanical work in terrestrial locomotion

R. BLICKHAN and ROBERT J. FULL

1. Introduction: average versus oscillatory work

The amount of metabolic energy required to travel a given distance by an animal using legged, terrestrial locomotion exceeds the costs of swimming by a factor of more than eight and of flying by more than a factor of four (1). Since terrestrial locomotion is expensive, it is reasonable to assume that the relatively high metabolic power input should generate a considerable, and therefore easily measurable, amount of mechanical power output. Surprisingly, a simple and direct link between metabolic and mechanical power during terrestrial locomotion has proved to be elusive (2). Fortunately, the challenge of investigating the link has been rewarding because these studies have and will continue to increase our knowledge of musculoskeletal function for all modes of locomotion.

During walking or running on the horizontal, a body normally returns to the same total energy level once per stride (a stride being one complete cycle of leg movements). If an animal is moving straight ahead at a constant average speed, then the average kinetic ($\bar{E}_{kin}$) and potential energy ($\bar{E}_{pot}$) remain constant from stride to stride. The *average mechanical energy* of the system, the sum of potential and kinetic energy per stride, is there-fore unchanged (assuming drag is negligible). However, by this measure, efficiency defined as mechanical power output divided by metabolic energy input, would be zero because no total mechanical work is done. When walking uphill, muscular work is necessary to increase the total potential energy from step to step and efficiency is positive (3). Yet, according to this definition, walking or running downhill decreases total potential energy and results in a negative efficiency. Obviously, a consideration of average mechanical energy alone is insufficient to explain how muscles generate movement on land.

The zero or negative work paradox can be explained partially by consider-ing fluctuations or *oscillations of mechanical energy* within each stride as opposed to average energy changes (4). During a single stride, a body's centre of mass accelerates and decelerates in at least the horizontal direction, as well

as changes potential energy by rising and falling. These changes in potential and kinetic energy increase the instantaneous mechanical energy. Transient increases in mechanical energy during a stride can be generated from muscular work and, therefore, should be considered in estimates of the mechanical power of terrestrial locomotion.

Cavagna and others (5, 6, 7) have estimated mechanical energy output from fluctuations in the energy of a human's or animal's centre of mass. By using a force platform, they determined the extent to which energy of the centre of mass changed due to the interaction with the environment (that is, due to a leg pushing against the ground and the ground exerting a force on the centre of mass). The mechanical work done by a body on the environment is termed *external work*. External work has been used with respect to the lifting and acceleration of a body's centre of mass during a stride, but more commonly refers to the lifting of weights, the pedalling of a bicycle ergometer or the work used to lift a body's centre of mass uphill.

Analysing the dynamics of the centre of mass has been invaluable in developing general models of terrestrial locomotion. However, as Winter (8) points out, the external work of the centre of mass may not represent the sum of all the energy changes in each segment of the body. He suggests that *internal work*, changes in the energy of segments relative to the centre of mass, should be summed with external work to estimate mechanical energy output. Even the general method of summing segment energies tends to underestimate energy generation and absorption at different joints (9). The calculation of *joint and muscle work or muscle power* takes into account energy generation, absorption and transfer at each joint and can provide a better estimate of muscle work (10).

In the sections that follow, we show the methods used to calculate external and internal energy oscillations as well as joint and muscle work or power. In the remaining part of the chapter, we evaluate these methods and discuss how energy exchange and transfer, elastic strain energy storage, co-contraction of antagonistic muscles and the cost of isometric and energy absorbing muscular contractions can significantly affect the link between musculoskeletal function and the mechanical energy output of terrestrial locomotion.

2. Measurement of external work

During straight ahead locomotion at constant, average speed, the fluctuations of external ground reaction forces result in instantaneous work done on the body's centre of mass (CM) and generate corresponding fluctuations of total, external mechanical energy. The external forces generated by the musculoskeletal system to accelerate and decelerate the body's CM can be measured using force platforms or force platform tracks (ref. 11; and see Chapter 3.2). The velocities and displacements of the CM can be obtained by successive

integration of the forces. These can be used in turn to calculate the changes in kinetic and potential energy of the CM.

2.1 Calculation of energy fluctuations of the CM from ground reaction force measurements

For an animal of known weight, the three components of the acceleration of the CM can be obtained by dividing the corresponding forces by the animal's mass.

The horizontal ($_1$) and lateral ($_2$) force (F) yield acceleration such that:

$$a_1 = F_1/m; \; a_2 = F_2/m \tag{1}$$

where m is mass of the animal and a is horizontal or lateral acceleration of the CM. The vertical ($_3$) component of the CM acceleration equals:

$$a_3 = (F_3 - mg)/m \tag{2}$$

where $g = 9.81 \, \mathrm{m \, s^{-2}}$. Weight can be obtained by averaging the vertical force for an integral number of strides. This calculated weight should correspond to the animal's weight determined from a scale.

The velocity fluctuations of the CM (v) are calculated by integration of each acceleration component determined from the force platform:

$$v_i(t) = \int_{t=0}^{t} a_i(t) + const_i \tag{3}$$

where i equals 1, 2, 3; t is time; and $const_i$ is the animal's average velocity in the ith direction.

The integration constants must be determined from the boundary conditions of the system. The average height of an animal's centre of mass varies little from stride to stride. Thus, the average vertical velocity ($\overline{v_3}$) after an integral number of strides is zero, a is the average lateral velocity ($\overline{v_1}$) if the animal moves in a straight line. The average horizontal speed ($\overline{v_2}$) has to be measured separately. This can be done by measuring the time that it takes an animal to cover a given distance. If the track is long enough reasonable estimates can be obtained by just measuring the time from the first step on and off the forceplate track of known length (error is about 10%; ref. 12). Speed can also be calculated from the time an animal needs to cover the distance between two photocells (13). However, errors can result in this estimate if different parts of the animal's body cross each of the two photocells. Also the distance between the photocells usually does not consist of an integral number of strides.

Changes in the kinetic energy of the CM (E_{kin}) can be calculated from the instantaneous velocities of the animal's CM:

$$E_{kin,i}(t) = \frac{m}{2} v_i(t)^2. \tag{4}$$

Changes in potential energy (E_{pot}) of the CM can be calculated from the vertical displacement (s_3), which is obtained in turn by integration of the changes of the vertical velocity of the centre of mass:

$$s_3(t) = \int_{t=0}^{t} v_3(t) + \text{const.} \tag{5}$$

The corresponding integration constant must be zero, since the average vertical displacement over an integral number of strides is unchanged. Changes in the potential energy of the animal's CM equals:

$$E_{pot}(t) = mg\, s_3(t). \tag{6}$$

The total external energy of the CM (E_{ext}) is calculated from the sum of kinetic and potential energy components:

$$E_{ext}(t) = E_{pot}(t) + \frac{m}{2}\sum_{i=1}^{3} v_i(t)^2. \tag{7}$$

Minimum estimates of mechanical work have been calculated by summing the positive increments of total external energy ($+\Delta E_{ext}$) for each stride (7, 12, 14, 15). However, see Section 5.1 for the assumptions of this calculation, since other energy components may not be accounted for by the CM approach.

2.2 Measurement of external forces of the CM

2.2.1 Design features of force platform for mechanical work measurements

Force platforms are most often used to measure the ground reaction forces required to calculate the energetic fluctuations of the CM (see Chapter 3.2). Ground reaction forces must be measured in at least the vertical and horizontal direction. In many lower vertebrates and arthropods, the lateral force component is also essential.

If the mechanics of constant, average speed locomotion are desired, then some criteria must be set to eliminate trials in which the animal is generating net accelerations or decelerations. Typically, this is determined from the sums of positive and negative changes in velocity. Trials in which the difference of these sums is less than 15–25% have been accepted as a constant, average speed (12, 14). To judge whether animals are moving without net accelerations or decelerations, the force platform must be long enough to measure at least one complete stride with the whole animal on the platform. This requires a long force platform. To keep the resonant frequency of the force platform significantly above the highest frequencies of the investigated force signal, the platforms must be stiff and of low weight. On the other hand, the
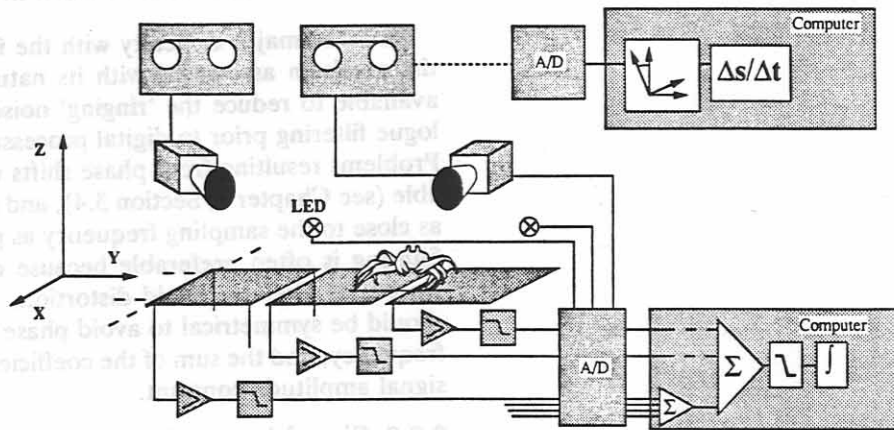
Figure 1. Experimental set-up. The signals of each force component in the corners of the platform are amplified and filtered. Subsequently these signals are digitized, summed for all corners of the platform and all platforms, filtered and integrated. Photocells can be used to provide an estimate of speed. Two high-speed cameras can collect information on the localization of body segments in three-dimensional space. After transformation of the respective coordinates, speed and angular velocities of the segments can be obtained by differentiation.

sensitivity of the plate is proportional to its compliance. Cavagna (11) and Heglund (13) solved this problem by building a track of small force platforms placed in series (*Figure 1*). The independent signals from the platforms are summed to calculate total force. The disadvantage of this design is that it becomes increasingly difficult to build and to maintain a number of platforms. By using semiconductor strain-gauges at the force-transducing support arms of the platform, stiffness of the platforms can be increased, and the number of platforms reduced (12).

2.2.2 Data processing

Data can be processed by analogue (11) or digital techniques (16). The speed and capacity of computers and their widespread use make the latter the more promising option. In digital processing, flexibility is guaranteed and the original data can be used for other analyses.

One problem that arises from the collection of force data is baseline drift. High speed taping for kinematic analysis requires bright illumination which in turn heats up the force platform components, causing drift in the voltage output of the electronic circuits. The drift in the baseline of the signal can be corrected by sampling a series of points before and after the time that the animal steps on the platform. These values can be used to provide a linear approximation of the baseline drift which can then be removed at any point in time during the recording of force (16).

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Another major difficulty with the force signals is noise due to 'ringing' of the platform associated with its natural frequency. A variety of filters are available to reduce the 'ringing' noise in the force data (9, 17). Initial analogue filtering prior to digital processing may be necessary to avoid aliasing. Problems resulting from phase shifts using analogue filters may be considerable (see Chapter 3, Section 3.4), and it is advisable to use cut-off frequencies as close to the sampling frequency as possible. For further processing, digital filtering is often preferable because original data can be passed through a variety of filters to avoid distortion. Whatever the digital filter selected, it should be symmetrical to avoid phase shifts, it should be steep at the cut-off frequency, and the sum of the coefficients should be one, in order to maintain signal amplitude constant.

2.2.3 Signal integration

The calculation of potential and kinetic energy requires integration of the force data. Each integration process suppresses the high-frequency components and thus, results in effective filtering of the velocity and displacement data. As stated by Cavagna (11), analogue integration of the force data and the calculation of the velocities can be advantageous as 'the integration process abolishes the interference caused by the vibrations of the plate'. Simple analogue circuits for integration can be built easily (see ref. 13, and ref. 17, p. 121), but there are a number of pitfalls which diminish the apparent advantage of analogue integration. In particular, the signal must be extremely stable and any offset, including errors in the subtracted weight, must be very small as they are integrated twice to determine the changes in potential energy.

Once again, digital solutions to noise reduction and integration are preferable. The simplest approach to integration is the trapezoidal rule. Here, each area between successive data points is approximated by a trapezoid:

$$\int_{t=0}^{t} f(t)\, dt = f_{sample^{-1}} \frac{1}{2} [y(0) + 2y(1) + 2y(3)$$
$$+ \dots + 2y(N-1) + y(N)] \tag{8}$$

where N is the sample size and f_{sample} is the sampling frequency. This represents a fast approach which can even be implemented with macros linked in electronic spreadsheets (12). The error from this calculation can be considerable, but is reduced by using a high sample frequency and/or by applying more elaborate integration techniques (for example, Romberg's method in ref. 18, p. 287).

2.3 Calibration and check of hardware, electronic circuits, and software

To test the operation of all circuits and software used to calculate the energy changes of the centre of mass, a sample test should be performed that

provides a direct comparison between experiment and theory. A convenient tool for this purpose is a pendulum of appropriate mass placed on the force plate (*Figure 2*; ref. 12). The forces exerted by the pendulum are generated by the swinging mass and transmitted by the string to the support of the pendulum and thus to the platform. If θ describes the angular deflection of the pendulum (length, l, and mass, m), then the force in the string (F_{string}) is the sum of the centrifugal force and the component of gravity in the direction of the string:

$$F_{string} = m\,\ddot{\theta}^2\,l + m\,g\,\cos\theta. \tag{9}$$

For the horizontal and vertical component of the ground reaction force:

$$F_1 = \sin\theta\,F_{string}; \quad F_2 = \cos\theta\,F_{string}. \tag{10}$$

For small displacements θ is a harmonic function of t:

$$\theta = \theta_0 \sin\omega t \tag{11}$$

with $\omega^2 = \dfrac{g}{l}$.

For small angles, equation (9) can be integrated analytically to obtain velocities, displacements, and energies; for large angular deflections numerical integration is necessary. This results in theoretical values which can be compared with experimental data. Representative experimental calibration curves for acceleration, velocity, and energy fluctuations of a pendulum are shown in *Figure 2B*. (The pendulum should show near 100% energy recovery.)

3. Measurement of internal work

Body appendages can move relative to one another in such a way that the body's CM is not affected. Nevertheless, muscle force and thus metabolic energy are necessary to power these movements. Internal work relative to the CM (19) and total work (8) have been estimated by summing the energy changes from each segment (that is, in a linked segment model) over an integral number of strides. This technique of using kinematic data or a combination of kinematic and external force data is commonly referred to as 'inverse dynamics'. Joint moments and joint reaction forces are estimated from external movements and forces. This is the reverse order of what happens in the body, since muscles actually produce the joint moments and forces which result in the movement of segments.

3.1 From kinematics to internal work

The body of an animal can be approximated by a series of linked segments. The location of the joint—or, more accurately, the instantaneous axis of rotation and the position of the CM must be determined for each body

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A

vertical

θ

m

l

mg $m\ddot{\theta}^2 l$

horizontal

B

ACCELERATION/g

0,5

0,25   horizontal

0

-0,25   vertical

-0,5

0,5   1

VELOCITY/(g l)

0,6

0,3   horizontal

0

vertical   0,5   1

-0,3

-0,6

ENERGY/(mgl)

0,15

Epot   Ekin horizontal

0,1

0,05   Ekin vertical

0

0   0,5   1
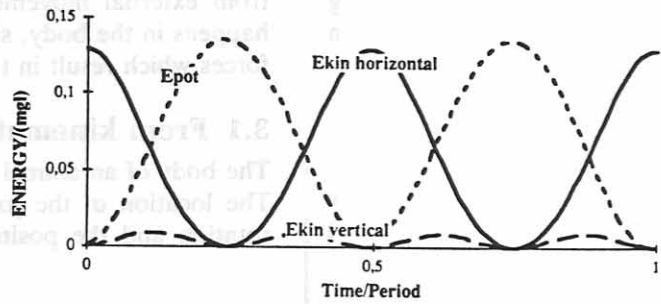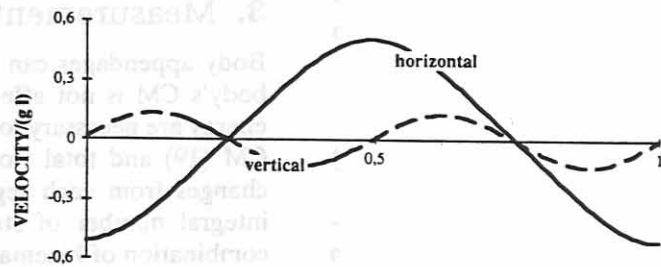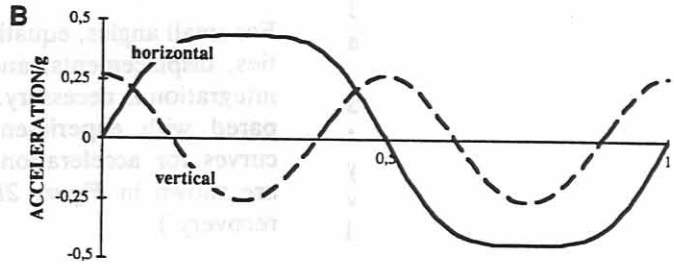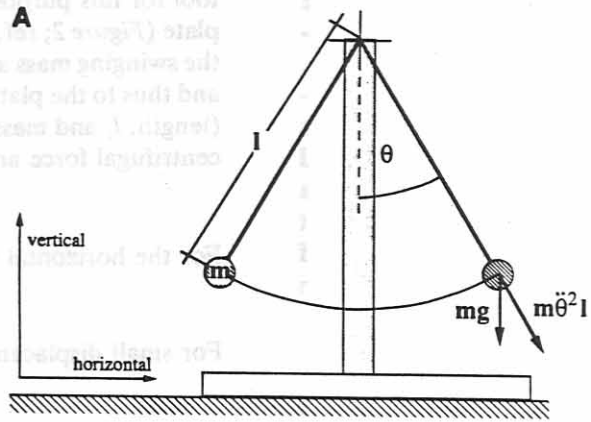
Time/Period

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Figure 2. A: Pendulum to test force plate and data processing techniques. The estimates are obtained by integration of the b asic equations of motion (see text) and can be compared with experimental results. **B:** Representative experimental calibration curves obtained from a pendulum swinging on the force plate. (Deflection: 30 degrees; results are given as dimensionless quantities).

segment relative to the segment markers used in video taping (see below). The movement of each segment can then be described by a translation of the segment's CM and a rotation around the CM (*Figure 3*). The inertia of each segment is proportional to its mass for translational displacements and to its moment of inertia for rotational movements.

Changes in potential energy ($E_{pot,k}$) can be calculated from the vertical translation or displacement ($s_{3,k}$) of the centre of gravity of each body segment (k) where:

$$E_{pot,k}(t) = m_k \, g \, s_{3,k}(t). \tag{12}$$

By differentiation of the displacements of the CM of the individual segments, changes in their velocity ($v_{i,k}$) and thus the changes in translational kinetic energy ($E_{kin,t}$) can be calculated:

$$E_{kin,t,i,k}(t) = \frac{m_k}{2} \, v_{i,k}^2(t). \tag{13}$$

By differentiating the angle of rotation (θ) with respect to time, the rotational velocity (ω) of each segment can be calculated. Provided that the three-dimensional moments of inertia (**I**) of the segment are available (see Section 3.2 below), the rotational energy of the segment ($E_{kin,r}$) can be determined:

$$E_{kin,r,i,k}(t) = \frac{1}{2} \sum_{j=1}^{3} \omega_{i,k}(t) \, I_{ij,k} \, \omega_{j,k}(t) \tag{14}$$

where $i \, (= 1, 2, 3)$ and j denotes the axes of the Cartesian coordinate system. If the rotation takes place only around the x-axis ($i = j = 1$), then the rotational energy can be written:

$$E_{kin,r,1,k}(t) = \tfrac{1}{2} \, \omega_{1,k} \, I_{11,k} \, \omega_{1,k} = \tfrac{1}{2} \, I_{11,k} \, \omega_{1,k}^2. \tag{14a}$$

If the actual rotation has two components (for example, x and y; $i, j = 1, 2$), then the rotational energy becomes:

$$E_{kin,r,1,k}(t) = \tfrac{1}{2} \, [\omega_{1,k} \, I_{11,k} \, \omega_{1,k} + \omega_{1,k} \, I_{12,k} \, \omega_{2k}] \tag{14b}$$

where I_{12} denotes the element of the tensor of inertia that considers the influence of the movement around y ($j = 2$) on the first energy component ($i = 1$). If the movement is planar and the segments have a parallel plane of symmetry, equation (14) simplifies to:

$$E_{kin,r,i,k}(t) = \tfrac{1}{2} \, I_{i,k} \, \omega_{i,k}^2(t). \tag{15}$$

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Time: $t = t_o + \Delta t$ Time: $t = t_o$

SEGMENT k

Z

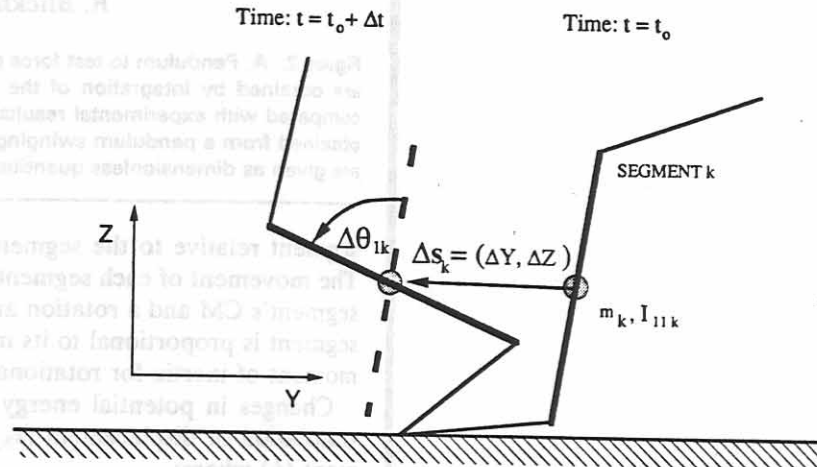$\Delta\theta_{1k}$ $\Delta s_k = (\Delta Y, \Delta Z)$

Y

m_k, I_{11k}

Figure 3. Notation for the calculation of internal energy. The leg of the animal is moving from right to left in the yz-plane. Between two frames (time interval = Δt) the CM of the kth segment (m_k = mass; I_{11} = moment of inertia for rotation around the CM in the yz-plane) is translated by Δs_k (Δy_k, Δz_k) towards the position marked by the dashed line and rotated by $\Delta\theta_{lk}$ from the dashed line to its final position. From the change in position, the velocity of translation ($v_k = \Delta s_k \, \Delta t^{-1}$) and the angular velocity ($\omega_k = \Delta\theta_{lk} \, \Delta t^{-1}$) can be determined. Velocity changes allow calculation of kinetic energy. Indices of angular changes denote the axis of rotation which is perpendicular to the instantaneous plane of movement (for example, parallel to $x = x_1$).

The mechanical energy contributed by each moving segment (E_k), then, is the sum of the respective kinetic (translational and rotational) and potential energies at each instant in time:

$$E_k(t) = E_{\text{kin},k}(t) + E_{\text{pot},k}(t). \tag{16}$$

Considering one plane (i,j) and planar symmetry of the body this yields:

$$E_k = \tfrac{1}{2} \, m_k \, (v_{i,k}^2 + v_{j,k}^2) + \tfrac{1}{2} \, I_{ii,k} \, \omega_{i,k}^2 + m_k \, g \, s_3. \tag{17}$$

The total internal energy (E_{int}) of the moving animal can be calculated by adding the contributions from every segment at each instant in time:

$$E_{\text{int}}(t) = \sum_{k=1}^{n} E_k(t). \tag{18}$$

Once again, there are numerous ways to calculate internal energy from the same data set depending on the assumptions made about the linked system (see Sections 5.1 and 5.2).

3.2 Determination of the CM and moment of inertia of body segments

Whereas the instantaneous axis of rotation can be determined from kinematic

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data, the CM and the moment of inertia must be determined for each segment independently.

The simplest approach used to determine the CM is to freeze and cut the body into segments. The CM is then determined by photographing or videotaping each segment as it is suspended from various axes. The CM is marked by the common crossing of all vertical lines drawn from the respective points of suspension. The CM of a multi-segmented system is (9):

$$s_i = \frac{1}{M} \sum_{k=1}^{n} m_k \, s_{i,k} \tag{19}$$

where s is the position of the CM of a multi-segmented body, $s_{i,k}$ is the position of the CM of a segment (k), m_k is the mass of a segment (k), n is total number of segments and M is total mass $= \Sigma_{k=1}^{n} m_k$.

A similar segmental approach can be used to determine the moment of inertia. However, it is important to note that the moment of inertia of a segment rotating in three-dimensional space can be complicated to determine. Being three-dimensional, the moment of inertia is a tensor. It is characterized by three quantities (I_{11}, I_{22}, and I_{33}), if the principal axes of the tensor are known. Otherwise, six quantities are needed for a complete description:

$$\mathbf{I} = \begin{pmatrix} I_{11} & -I_{12} & -I_{13} \\ -I_{21} & I_{22} & -I_{23} \\ -I_{31} & -I_{32} & I_{33} \end{pmatrix} \tag{20}$$

where $I_{ij} = I_{ji}$.

If the body under investigation has no symmetry and the main axis of the moment of inertia are not known, then the six independent experimental estimates are necessary to quantify this tensor using a linear system of equations and transformation of coordinates. After transformation of the coordinate system to the principal axes of the segment, the tensor contains only the three diagonal elements:

$$\mathbf{I} = \begin{pmatrix} I_{11} & 0 & 0 \\ 0 & I_{22} & 0 \\ 0 & 0 & I_{33} \end{pmatrix}. \tag{21}$$

Frequently, the segment can be approximated reasonably by a body with two perpendicular planes of symmetry with the principal axes of the tensor perpendicular to these planes (*Figure 4*).

Modern tomographic methods allow a precise three-dimensional estimate of the geometry of body segments (Brüggemann, pers. comm.). Even the position of more dense skeletal structures can be determined. These techniques are expensive, but have the advantage of not requiring the sacrifice of an animal. If the density and the shape of segments of the specimens are

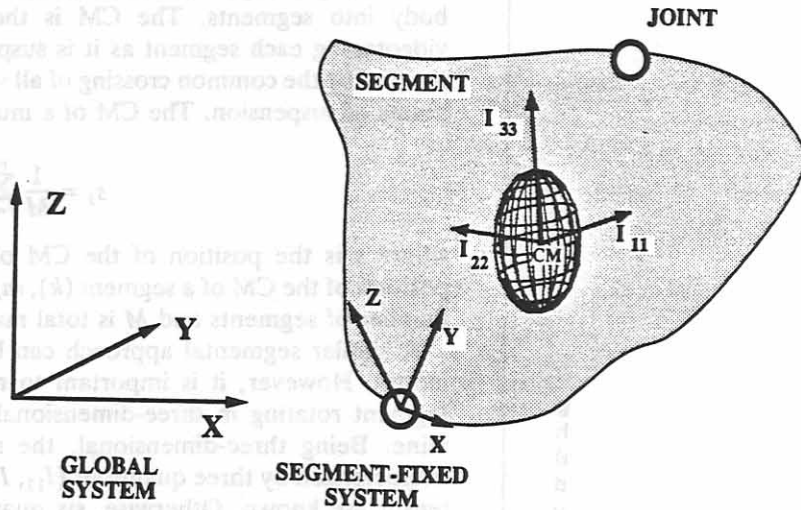Mechanical work in terrestrial locomotion

Figure 4. In a three-dimensional representation the tensor of the moment of inertia can be visualized by an ellipsoid. The lengths of the principle axes of this ellipsoid to I_{11}, I_{22}, I_{33}, respectively, and are sufficient to characterize inertia of any three dimensional body. The axes of the segment-fixed coordinate system (X,Y,Z) are frequently chosen to lie parallel to the axes of rotation defined by the construction of the joint. If the orientation of the segment-fixed system is different from the orientation of the principle axes and the segment does not rotate around one of the main axes, then the tensor must be rotated into the segment-fixed system and six quantities are necessary to describe inertia.

known, then the moment of inertia can be calculated by computing the corresponding volume (V) integrals of each of the tissues in the body segment:

$$I_{ii} = \rho_V \int (x_j^2 + x_l^2)\, dV, \; I_{ij} = \rho_V \int x_i x_j\, dV \qquad (22)$$

where $x_{i,j,l}$ are the Cartesian coordinates of points within the volume of the tissue, the origin being located at the CM of the segment. Density is represented by ρ; $m = \rho V$; $i,j,l = 1,2,3$; and $i \neq j \neq l$ for example:

$$I_{11} = \rho_V \int (x_2^2 + x_3^2)\, dV \text{ and } I_{12} = \rho_V \int x_1 x_2\, dV. \qquad (22a)$$

In many cases complicated shapes of segments can be approximated by a stack of geometrical elements (m) such as cylinders, truncated cones, etc., with known moments of inertia. The moment of inertia of the whole segment relative to rotations around the CM can be calculated by:

$$I_{ii} = \sum_m [I_{ii,m} + m_m (x_{j,m}^2 + x_{l,m}^2)] \qquad (23)$$

$$I_{ij} = \sum_m [I_{ij,m} + m_m (x_{i,m} x_{j,m})] \qquad (24)$$

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where $i,j,l = 1,2,3$ and $i \neq j \neq l$ (see equation (22)) $x_{i,m}$ is the difference in the coordinates of the CM of the total segment and the CM of elements of the stack (20).

Experimentally, the moment of inertia around any axis of rotation can be determined by letting the object oscillate as a physical pendulum:

$$I = \tau^2 \frac{m \, c \, g}{4 \, \pi^2} \qquad (25)$$

where τ is the period of the pendulum, m is the mass of the segment, and c is the distance from the axis of rotation to the CM.

Often, however, the segment of interest rotates about an axis other than its CM. The moment of inertia around this axis (I) can be calculated by applying the parallel axis theorem:

$$I = I_0 + mc^2 \qquad (26)$$

where I_0 is the moment of inertia around the CM (as determined above).

3.3 Data processing

Cinematographic techniques and kinematic analyses are described in detail elsewhere in this volume (see Chapter 3). In general, because the determination of segmental energies requires the calculation of velocities from displacement data, the application of fast and highly accurate cinematographic techniques are a necessity. The major problems encountered include digitizing error, unwanted movement of skin markers with respect to underlying skeletal structures and inadequate sampling rate.

4. Calculation of joint and muscle work and power

Muscles can both generate and absorb energy. Muscles that generate energy do positive work, whereas 'negative' work is 'done on' muscles that absorb energy. If both of these functions are important to the musculoskeletal system that is to be analysed, then in principle energy changes can be calculated from the net moments or torques (T) developed at each joint (k; see also Chapter 3; refs. 3 and 21). The rate of work done by or to muscles varies with time. Instantaneous muscle power at a joint (P_m; ref. 22) is the product of the net moment generated by the muscles at each joint (T_k) and joint angular velocity (ω_k):

$$P_m = T_k \, \omega_k \qquad (27)$$

The calculation of net joint moments requires combined ground reaction force data obtained from a force platform and kinematic data from high-speed taping (Chapter 3). Ground reaction forces, segment masses, and moments of inertia are used in a free body diagram analysis to calculate the net moment at the joint (depending on the importance of the inertial component; Chapter 3, Section 4).

Joint angular velocity at any instant is obtained directly from the kinematic analysis (Chapter 3, Section 3.5).

Total energy (E_{tot}) or work done is determined by integrating P_m over an integral number of strides for each joint:

$$E_{tot} = \sum_k \int |T_k \, \omega_k| \, dt. \tag{28}$$

In these calculations it is essential to be consistent in defining the direction of the joint moment (for example, counter-clockwise moments are positive, whereas clockwise ones are negative). To estimate the total positive and negative work done, it is important to sum both negative (energy absorbing) and positive (energy producing) areas of the P_m versus time function separately (this is the reason for the absolute value sign in equation (28), but see Section 5.2 below).

5. Evaluation of techniques used to examine the mechanical work in terrestrial locomotion

5.1 Energy exchange within segments and transfer between segments

In his initial attempts to estimate the work done during terrestrial locomotion, Fenn (4) calculated the increases in potential and kinetic energy of a body's segments. Summation of the increases in segment energy, however, can lead to an overestimate of the work done, if energy exchanges within and between segments are significant. Consider a limb that functions as an ideal pendulum. Once energy is put into the system, no additional energy input would be required to swing the limb, because all the potential energy would be exchanged with kinetic energy. Artificially high values of mechanical work (termed 'pseudo-work') would result, if the potential energy increases were simply added to kinetic energy increases.

Cavagna and others (5, 6, 7) demonstrated the importance of energy exchange and recovery during walking by calculating the energy fluctuations of the CM from ground reaction forces (that is, external work or CM approach). During walking in bipeds, quadrupeds, and even eight-legged crabs, potential and kinetic energies of the CM are out of phase by about 180 degrees much like an egg rolling end over end or an inverted pendulum (*Figure 5*; refs. 7, 14, 16). Energy lost in the kinetic form as the body slows can be recovered and used to raise the body and increase potential energy. Therefore, if the potential and kinetic energy of an animal using a pendulum-like energy exchange mechanism are summed at each instant, then the fluctuations of total, external energy (ΔE_{ext}) will be reduced. The possible degree of energy exchange or recovery can be quantified as (7):

$$\text{recovery [\%]} = 100 \, \frac{|\Delta E_{pot}| + |\Delta E_{kin}| - |\Delta E_{ext}|}{|\Delta E_{pot}| + |\Delta E_{kin}|} \tag{29}$$

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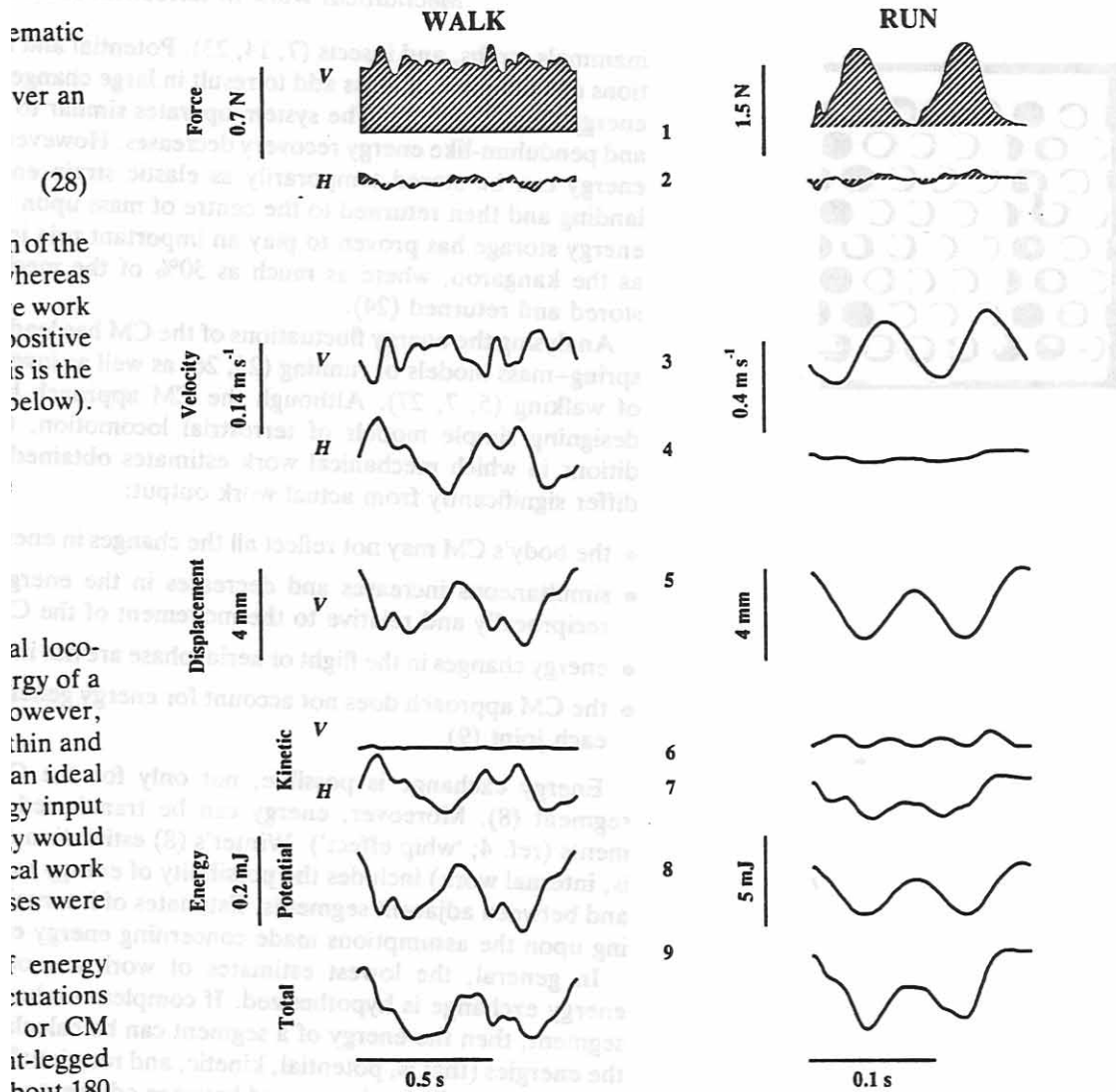dy slows
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Figure 5. Example: Fluctuations of external energy in the ghost crab. During walking potential and kinetic energies are out of phase allowing for energy exchange. During running both energies are in phase energy exchange is small but energy storage is facilitated. (Adapted from ref. 16.)

where ΔE_{pot} and ΔE_{kin} are the changes in potential and kinetic energy, respectively. Recovery would be 100% for an ideal pendulum. Surprisingly, recovery in large mammals during walking can reach 70% (7).

In contrast to walking, potential and kinetic energy fluctuations of a body's CM have been shown to be in phase during running in bipeds, quadrupedal

mammals, crabs, and insects (7, 14, 23). Potential and kinetic energy fluctuations of the centre of mass add to result in large changes in the total, external energy (Fig. 5; ref. 7). The system operates similar to a spring–mass system and pendulum-like energy recovery decreases. However, potential and kinetic energy can be stored temporarily as elastic strain energy in tendons upon landing and then returned to the centre of mass upon take-off. Elastic strain energy storage has proven to play an important role in large mammals, such as the kangaroo, where as much as 50% of the mechanical energy can be stored and returned (24).

Analysing the energy fluctuations of the CM has lead to the development of spring–mass models of running (25, 26) as well as inverted pendulum models of walking (5, 7, 27). Although the CM approach has been invaluable in designing simple models of terrestrial locomotion, there are several conditions in which mechanical work estimates obtained by this method could differ significantly from actual work output:

- the body's CM may not reflect all the changes in energy of each segment (8)
- simultaneous increases and decreases in the energy of segments moving reciprocally and relative to the movement of the CM are not measured
- energy changes in the flight or aerial phase are not included in the estimation
- the CM approach does not account for energy generation and absorption at each joint (9)

Energy exchange is possible, not only for the CM, but for each body segment (8). Moreover, energy can be transferred between adjacent segments (ref. 4; 'whip effect'). Winter's (8) estimation of total body work (that is, internal work) includes the possibility of energy exchange within segments and between adjacent segments. Estimates of internal work will vary depending upon the assumptions made concerning energy exchange.

In general, the lowest estimates of work are obtained when complete energy exchange is hypothesized. If complete exchange is assumed within a segment, then the energy of a segment can be calculated by simply summing the energies (that is, potential, kinetic, and rotational) at each instant in time. If complete exchange is assumed between adjacent segments, then the energy of the body can be calculated by summing the instantaneous segment energies as shown above. Internal work will be the greatest when no energy exchange is hypothesized (4, 28). To calculate internal work with no exchange, the absolute value of the energy changes over time is summed.

Intermediate values of internal work result from assumptions of partial energy exchange. In a comparative study of terrestrial locomotion, Fedak *et al.* (19) calculated total internal energy (taken to be primarily kinetic energy) by assuming exchange within and between limb segments, but not between the limbs and body or other limbs. In other words, these workers assumed no exchange between internal work done by the limbs relative to the CM and

external work done on the CM. However, energy exchange between internal and external energy can occur during the stance phase. Consider a stick rotating around an axis through it's centre of gravity. If such a stick touches the ground, then part of its rotational energy is transferred into kinetic energy of the CM, which can be easily measured from the generated ground reaction forces. This type of interaction is used (in reverse) by gymnasts to somersault and simple summation of the positive increments of the fluctuations of internal and external energy would lead to an over-estimation of internal work. Heglund *et al.* (29) determined the maximum error due to neglected exchange during steady locomotion to be within about 30% of total mechanical energy (such as for a chipmunk and a dog). For large animals, such as a horse, values of internal work derived from partial versus complete energy exchange could differ by more than a factor of two. Williams and Cavanagh (30) found that total work done during human locomotion can vary by 75% depending on the assumptions of energy exchange.

Regardless of the assumptions made concerning energy exchange, total work can be estimated by either summing the positive increases in total energy over an integral number of strides or by summing the absolute value of the changes. The former ignores the fact that absorbing mechanical energy costs metabolic energy and gives a minimum estimate of mechanical work. The latter estimation gives equal weight to both positive and negative work. A third possibility, and perhaps the most reasonable approach used by investigators, is the weighting of negative work to be ⅓ to ⅕ the energy cost of positive work (3, 30). The decision of if or how to include negative work can alter the total work output significantly, since an equal amount of positive and negative work is done during constant, average-speed locomotion. Consequently, it is important to make clear the assumptions adopted to compute total energy changes of the animal's body.

Recognition of energy exchange within and between segments has led to a better understanding of energy conservation and an improved estimate of total work. The total work estimate for human walking can be 16–40% greater than that calculated from the CM approach, if the energy changes of each segment are included (8). Internal work can be of the same magnitude as the external energy calculated from energy changes in the CM at the highest sustainable speeds used by quadrupedal mammals (29). However, it is important to note that the simple summation of segment energies at each instant can also underestimate the generation and absorption of energy at different joints (9). Because significant amounts of energy can be generated and absorbed simultaneously at different joints, estimations of work in terrestrial locomotion may be improved by examining individual joints.

5.2 Energy production and absorption

The generation and absorption of energy at a joint can be calculated from the net joint moment and joint angular velocity (see Section 4). Instantaneous
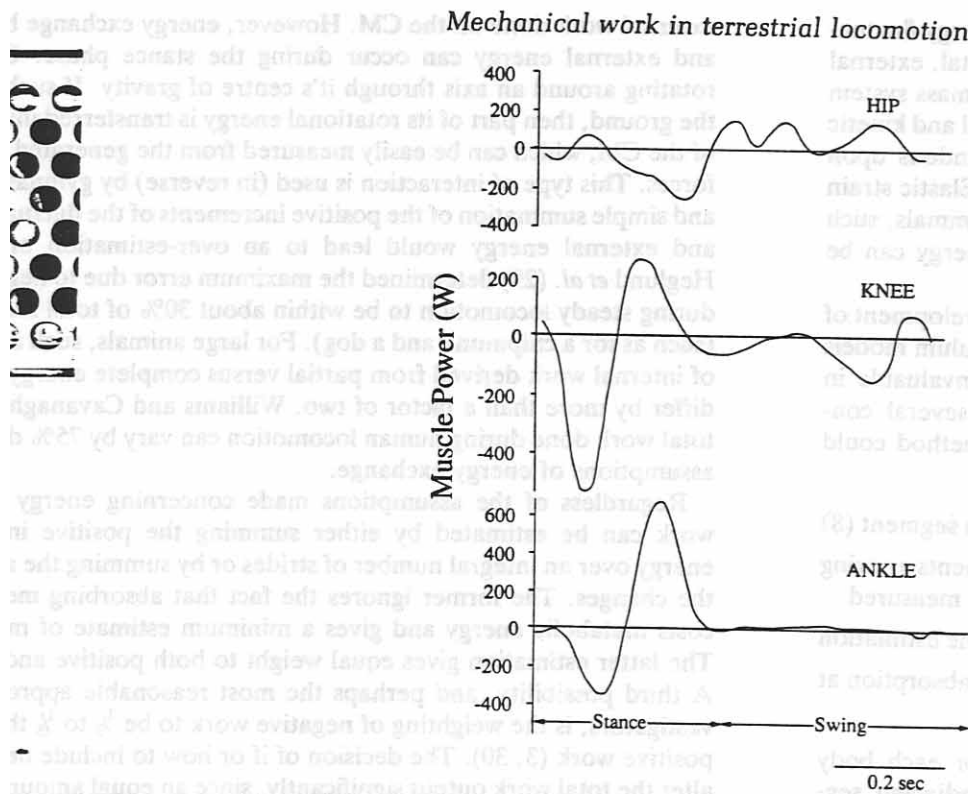
Figure 6. Summary power patterns at three joints during human jogging. (Adapted from ref. 10). Each plot shows the stance phase followed by the swing phase. The end of the stance phase is marked by the ankle's decrease of power to zero from the large maximum of power generation.

muscle power curves from a study on human jogging (*Figure 6*; ref. 10) show the advantages of using this technique. Muscle power is positive for concentric (shortening) muscle contractions in which the net moment and the joint angular velocity are of the same polarity. Energy is absorbed in eccentric (lengthening) contractions when muscle power is negative. The hip has relatively low power levels compared to the knee and ankle, probably functioning to stabilize the trunk. Surprisingly, the knee extensors do not generate energy to swing the leg (that is, no positive power). Instead, the knee absorbs energy from the swinging leg. Knee extensors absorb nearly four times as much energy as they produce. The ankle extensors clearly generate the majority of energy, producing three times as much positive work as the knee extensors.

If data on energy generation and absorption at joints are combined with energy transfer analysis, an even more complete picture of energy flow can be drawn. Energy transfer, generation, and absorption at a joint can be

calculated from joint reaction forces and moments on leg segments (22, 31, 32). The power between segments acting across joints (P_b) is:

$$P_b = F_k \cdot V_k \tag{30}$$

where F_k is the reaction force vector at joint b and V_k is the velocity vector of the centre of the joint. Total power for a segment is the sum of the joint power (P_b) and the muscle power (P_m; see equation (27)); the only difference being that the muscle power is calculated using the absolute angular velocity of the segment as opposed to the joint angular velocity. *Figure 7* (from ref. 32) shows data from a power generation, absorption and exchange analysis conducted on human walking. Joint power is shown by an arrow crossing through the joint centre, whereas muscle power is represented by arrows around each joint on the side where energy is flowing. During push-off at the end of the support phase there is 533 W of power produced by the Achilles tendon. 65 W of energy is transferred to the foot (energy increase), but the majority of the energy (469 W) flows upward from the foot through the ankle joint. 108 W of energy continues upward throughout the knee joint, with little participation by knee muscles. Only 23 W of energy flows into the trunk. During weight acceptance at the beginning of ground support, 244 W flow out from the trunk and across the knee. Nearly 164 W is absorbed by the knee extensors and 33 W (that is, 145–108 W) is absorbed by the ankle dorsiflexors.
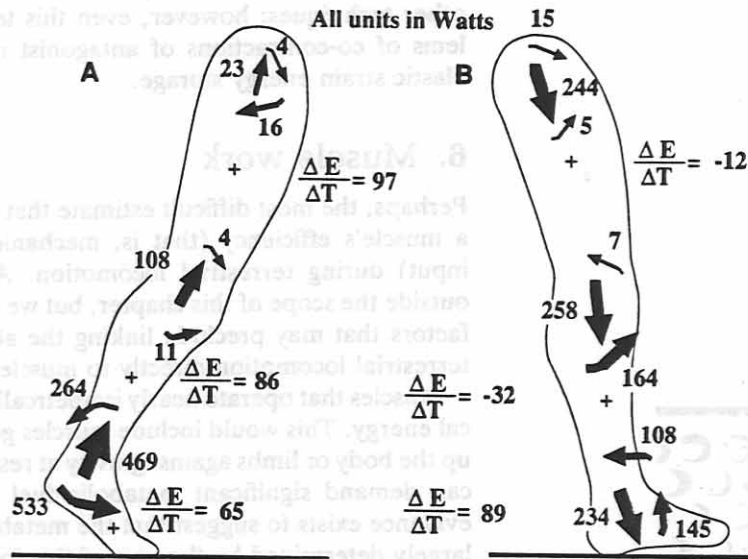

Figure 7. Mechanical power analysis of human leg during walking at (A) push-off and (B) weight acceptance. The joint power is shown by an arrow crossing through the joint centre. The muscle power is represented by arrows around each on the side where energy is flowing. Power is in watts. (adapted from ref. 32.)

Table 1. Powerflow for a single joint. For a positive (counterclockwise) angular velocity of the proximal segment 1 ($\omega_1 > 0$), the power can be transferred from segment 1 to the distal segment 2 ($\rightarrow$) via the extensor of the joint. Complete transfer (tr.) occurs if the angular velocities are similar. If $\omega_1 > \omega_2$, energy is absorbed in the extensor (abs.), the muscle contracts, i.e. power is generated (gen.). For $\omega_1 < 0$, the flow is reversed and gen. and abs. must be exchanged in this table.

Direction		$\omega_1 > \omega_2$	$\omega_1 = \omega_2$	$\omega_1 < \omega_2$
Extensor	$1 \rightarrow 2$	tr. and abs.	complete tr.	tr. and gen.
Flexor	$1 \leftarrow 2$	tr. and gen.	complete tr.	tr. and abs.

Given the absolute angular velocity of a segment and the joint moment, it is possible to describe the work relationships between two segments connected by an active muscle (21, 31). *Table 1* shows the function of muscle and the direction of power flow for a single joint muscle performing either flexion or extension. If one segment is fixed while the other is in motion, then the muscle can be either generating or absorbing energy. If $\omega_1 > \omega_2$, then the muscle is lengthening and absorbing energy while transfer is taking place. If $\omega_1 < \omega_2$, then the muscle is shortening and generating energy while transfer occurs. If $\omega_1 = \omega_2$ (that is, isometric contraction), then energy is only transferred by muscles from segment 1 to segment 2.

The determination of energy generation, absorption and transfer at the joints provides considerably more information about muscle work than most other techniques; however, even this technique cannot deal with the problems of co-contractions of antagonist muscles, isometric contractions, and elastic strain energy storage.

6. Muscle work

Perhaps, the most difficult estimate that one can attempt is a true estimate of a muscle's efficiency (that is, mechanical energy output/metabolic energy input) during terrestrial locomotion. A discussion of muscle efficiency is outside the scope of this chapter, but we will point out the several well-known factors that may preclude linking the above mechanical work estimates for terrestrial locomotion directly to muscle function.

Muscles that operate nearly isometrcally generate and absorb little mechanical energy. This would include muscles generating the force necessary to hold up the body or limbs against gravity at rest. Muscles that function isometrically can demand significant metabolic fuel consumption. In fact, considerable evidence exists to suggest that the metabolic cost of pedestrian locomotion is largely determined by the cost of this force production (2, 33).

Not only can individual muscles operate isometrically, but antagonistic muscles actively contracting against one another generate no mechanical

work and yet consume considerable metabolic energy to maintain isometric tension. In general, the effect of co-contraction is considered to be small during locomotion, but this requires further analysis. According to Alexander and Vernon (24) 15% of total concentric muscle work for a kangaroo hopping at 5.5 m/sec include work done against antagonists. The degree of co-contraction during walking in humans has been estimated to be 24% (34).

In our discussion of mechanical work, we referred to muscle force or power. To be more accurate, we were describing musculotendon force or power. Elastic strain energy storage in tendons and apodemes may significantly alter the actual work a muscle must do if the stored energy can be returned to the segments. Estimates of the energy saved by muscles due to elastic strain energy storage vary considerably. In humans mechanical power output can vary by 40% depending on the amount of elastic strain energy storage (30). Kangaroos can save as much as 59% (24). Elastic strain energy storage in small mammals may be more limited because they have relatively thicker tendons (35). The calculation of tendon strain energy is found in Chapter 3, Section 4.2.

Even if one were able to estimate isometric force production, muscle co-contraction and elastic strain energy recovery at a joint, a major difficulty may still remain. Because more than one muscle may have a similar function at a joint, individual muscle work estimates are often indeterminant (see Chapter 3, Section 4). *In vivo* recordings of muscle force, EMG quantification, and computational methods that minimize or assume equal stress or power output have all been used to address this difficulty. Further study directed toward integrating muscle function with limb performance is obviously required and will be a promising area of research in the future.

Finally, although calculation of work in terrestrial locomotion is challenging, it has led to a better understanding of musculoskeletal function generally. By continuous revision and examination of assumptions, considerable progress has been made in linking muscle function with mechanical work. For the future, we argue that one of the strongest approaches to uncover the general biomechanical rules of terrestrial locomotion is the comparative method which takes advantage of natural experiments, involving animals that possess a diversity of musculoskeletal systems and live in many different environments.

Acknowledgement

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