MECHANICS AND ENERGETICS OF HUMAN LOCOMOTION ON SAND

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Introduction

Although it may be common knowledge that walking or running on sand requires far greater effort than on firm ground, no one seems to know exactly why. Indeed, previous studies have only measured the increase in energy expenditure in humans carrying or pushing loads on different surfaces (Heinonen et al. 1959; Strydom et al. 1966; Soule and Goldman, 1972; Haisman and Goldman, 1974; Pandolf et al. 1976) or when walking and running on a beach (Zamparo et al. 1992). Other studies have measured the change in energy cost due to different surfaces in reindeer Rangifer tarandus sibiricus (White and Yousef, 1978), goats and sheep (Dailey and Hobbs, 1989) and caribou Rangifer tarandus granti (Fancy and White, 1987).

The mechanics and energetics of locomotion have been thoroughly investigated only in the laboratory on hard, level, non-slippery surfaces, although these conditions bear little resemblance to those actually occurring in nature. It could be that the energy-saving mechanisms utilised during locomotion on a hard surface are not functional on a soft surface, or that the muscles used on a soft surface are in a condition such that they contract and do work at lower efficiency, or simply that the mechanical work required to walk or run on a soft surface is much greater since the foot does work on the substratum. The purpose of the present study was to quantify the increase in metabolic cost and the reason for that increase in humans walking and running on dry sand.

Materials and methods

Mechanical work and energy expenditure were determined on two different groups of subjects. The mechanical work done to walk and run on sand was measured on four subjects (age 39±4 years, height 1.81±0.05 m, mass 76.8±7.2 kg; mean ± s.d.) who took part in a similar study carried out on firm ground (Willems et al. 1995). The cost of locomotion was measured on 10 different subjects (age 24.1±4.1 years, height 1.79±0.06 m, mass 71.2±9 kg). Informed consent was obtained from all subjects.

Calculation of mechanical work

The muscle–tendon work performed during locomotion can be divided into two parts: the external work ($W_{ext}$), which is the positive work necessary to move the centre of mass of the whole body relative to its surroundings ($W_{com}$) plus the work done on the environment ($W_{env}$), and the internal work ($W_{int}$), which is the positive work done to move the limbs relative to the centre of mass (COM). When moving on a hard and non-slippery surface, $W_{env}$ is essentially zero because wind resistance is negligible and the foot does not slip or displace the substratum. In contrast, when moving on sand, the foot moves the sand, resulting in additional external work. The total muscle–tendon work $W_{tot}$ done while moving on sand is:

$$W_{tot} = W_{ext} + W_{int} = W_{com} + W_{env} + W_{int}.$$  (1)

Measurement of $W_{com}$

$W_{com}$ was calculated from the vertical and forward components of the force (lateral forces were ignored) exerted by the feet on the ground. This force was measured using a force platform mounted near the middle of a 40 m straight
corridor and comprising eight contiguous plates, each plate 0.6 m long and 0.4 m wide (Willems et al. 1995). A wooden trough (0.6 m long, 0.8 m wide, 0.01 m deep) was fixed on each plate, lined with a plastic sheet and filled to a depth of 0.075 m with fine (grain size <0.0005 m) and dry (density 1600 kg m\(^{-3}\)) sand. Although each plate supported 60 kg of sand, the maximum force measured was well within the linear response range of the plate. The unloaded response of the plates was a slightly damped 250 Hz, compared with a highly damped 50 Hz for the plates with sand. A 0.075 m deep sand track was built 10 m in front of and 2.5 m beyond the force platform.

Provided that no sand is thrown out of the trough, the force platform correctly measures the force exerted by the foot on the sand plus the product of the acceleration of the displaced sand times the mass of the displaced sand. This latter product was ignored in this study, which may lead to an error in the determination of the force exerted by the foot on the sand. To estimate the magnitude of this error, the following experiment was performed. A prosthetic foot instrumented with a custom-designed strain gauge force transducer was calibrated by pushing the foot onto the surface of a force plate. A wooden box containing 0.075 m of sand, as described above, was then attached to the plate, and the experiment was repeated. The foot entered the sand with the ankle in the neutral position and the leg at an angle similar to the angle of the leg at heel-strike or toe-off (approximately 30° from the vertical). The force measured by the plate was 3.1±2.1 % (mean ± s.d., N=10) greater than the force measured by the prosthetic foot. Since this error is of the same magnitude as the error due, for example, to differences in the platform’s sensitivity to forces exerted at different points on its surface, and since this error is considerably less than the variability between steps, the force measured by the force plate was considered in this study to be equal to the force exerted by the foot on the sand.

The method used to compute the velocity, displacement and mechanical energy of the COM by integration of the force–time records of the platform (Fig. 1, lower six curves) has been described previously in detail (Cavagna, 1975; Willems et al. 1995). \(W_{\text{com}}\) was calculated as the sum of the increments in mechanical energy over one stride. To minimise errors due to noise, the increments in mechanical energy were considered to represent positive work only if the time between two successive maxima was greater than 20 ms.

**Measurement of the work done on the sand**

The work done on the sand was computed during the stance phase from the movement of the foot into the sand and the ground reaction force in the sagittal plane (lateral forces were ignored). The foot was divided into two segments at the fifth metatarsal phalangeal joint. Each segment was modelled as a rigid body and located by two infrared light-emitting diodes (LEDs) placed on the upper part of the shoe, in order to avoid their disappearance in the sand (Fig. 2 top). The lower leg was located by two additional infrared LEDs fixed on the lateral malleolus and on the head of the fibula. The coordinates of these LEDs were measured using three infrared cameras

![Fig. 1. Kinetic energy changes of an upper limb and a lower limb due to their velocity relative to the centre of mass (COM) of the body (top two curves in each part of the figure) and the mechanical energy changes of the centre of mass (bottom three curves in each part of the figure) as a function of time during one walking stride on sand at 1.25 m s\(^{-1}\) (left column) and one running stride on sand at 2.84 m s\(^{-1}\) (right column). \(E_{\text{pf}}\) is the kinetic energy due to the forward motion of the COM. \(E_{\text{p}}\) (broken line) is the potential energy of the COM. The energy due to vertical motion of the COM is the sum of the potential energy plus the kinetic energy due to the vertical velocity. \(E_{\text{com}}\) is the total energy of the COM. The stick figure shows the limb positions of one side of the body at 10% intervals of the stride. Traces are from a 41-year-old, 81 kg, 1.88 m subject.](image)

(Selspot II System) synchronised to an analog-to-digital converter which recorded the force signal from the platform. The position–time curves were smoothed by the least-squares method (Stavitsky and Golay, 1964) using a 105 ms interval for walking and a 50–55 ms interval for running. The foot was reconstructed for each frame from the LED positions and the dimensions of the rigid bodies. The position \(L\) of the force vector \(F\) along the length of the plate was also calculated each frame, from the vertical components of \(F\) measured at each end of the plate \((F_{v,1} \text{ and } F_{v,2})\) and the plate length \(L_p\):

\[
L = L_p \frac{F_{v,1}}{F_{v,1} + F_{v,2}}.
\]

The intersection between the force vector \(F\) and the sole of the shoe was taken as the application point of \(F\) under the foot (\(F\) is indicated by the arrows in the top panel of Fig. 2). This point can move from one frame to the next for two reasons: as a result of the movement of the centre of pressure along the sole of the foot, from the heel to the toe, as the subject pivots over the foot during the stance phase; or as a result of a movement of the sole of the foot into the sand. In the first case, no work is done on the sand, while work is done in the second case. In
order to calculate the work done on the sand, the position of the point of application of the force was fixed on the sole of the foot in the $i$th frame, and the displacement of the same position on the sole from the $(i-1)$th frame was used to calculate the work as follows:

$$W_{\text{sand},i} = d_{h,i}F_{h,i} + d_{v,i}F_{v,i},$$

where $d_{h,i}$ and $d_{v,i}$ are the displacement of the fixed point on the sole between the $(i-1)$th and $i$th frames in the horizontal and vertical directions, respectively, and $F_{h,i}$ and $F_{v,i}$ are the two components of the force vector $\mathbf{F}$.

**Measurement of $W_{\text{int}}$**

The mechanical work $W_{\text{int}}$ done to accelerate the body segments relative to the COM was computed by dividing the body into 11 rigid segments: the head plus trunk, the two upper arms, the two lower arms, the two thighs, the two shanks and the two feet (Willems et al. 1995). Left segments, closest to the cameras, were defined using eight infrared LEDs located at the chin–neck intersection, the gleno-humeral joint, the lateral condyle of the femur, the lateral malleolus and the fifth metatarsal phalangeal joint. The coordinates of these LEDs were measured using the infrared camera system described above.

The position–time curves were smoothed using a least-squares method, with an interval of 125–175 ms for walking and 63–125 ms for running (Stavitsky and Golay, 1964). The angle made by each segment relative to the horizontal was then determined for each frame, and the resulting angle–time curves were smoothed using the least-squares method, with an interval of 75–85 ms for walking and 43–105 ms for running. The mass, the position of the centre of mass and the radius of gyration of each body segment were approximated using the anthropometric tables of Dempster and Gaughran (1967). The positions of the segments on the right side of the body, invisible to the cameras, were reconstructed assuming that their movements during one half of a stride were equal to those on left side during the other half of the stride. The angular velocity of each segment, and its linear velocity relative to the COM, were calculated from the position data by the method of finite difference over intervals of 25–45 ms for walking and 23–35 ms for running, depending upon the speed. The kinetic energy of each segment due to movement relative to the COM was then calculated from the sum of its translational and rotational energies (Willems et al. 1995).

The kinetic energy curves of the foot, lower leg and upper leg (=lower limb in Fig. 1, upper four curves). $W_{\text{int}}$ was calculated as the sum of the increments of the resulting kinetic energy curves during one stride. This procedure assumes complete transfer of kinetic energy between the segments of the same limb but excludes any transfer between the limbs or between the limbs and the trunk. In order to minimise errors due to noise in the energy curves, the increments in kinetic energy were considered to represent positive work only if the time between two successive maxima was greater than 20 ms.

**Procedure**

Subjects were asked to walk and run on sand at the same speeds that they had used in the previous study on firm ground (Willems et al. 1995). Trials at a given speed were repeated 2–12 times by the same subject to assess the reproducibility of the experimental results and to obtain a mean value. Measurements were made approximately every 0.15 m s$^{-1}$ between 0.5 and 2.5 m s$^{-1}$ for walking, and every 0.2 m s$^{-1}$ between 2 and 4 m s$^{-1}$ for running; only one subject walked/ran at each speed. A marker pulled along the floor next to the force platform by a motor indicated the desired speed; trials were only accepted when the speed obtained was within 0.08 m s$^{-1}$ (walking) or 0.11 m s$^{-1}$ (running) of their speed measured in
the previous study. All measurements were synchronised and taken at 200 samples s	extsuperscript{-1} when the speed of progression was less than 3.33 m s	extsuperscript{-1} and at 300 samples s	extsuperscript{-1} at higher speeds. The surface of the sand was levelled after each trial. In total, 220 walk/run trials were analysed.

The experiments were realised in two parts. \( W_{\text{int}} \) and \( W_{\text{com}} \) were measured first, with the three cameras placed approximately 4 m apart and 9 m to the side of the track to obtain a field encompassing 4.5 m of track. Afterwards, \( W_{\text{sand}} \) and \( W_{\text{com}} \) were measured, with the cameras placed 3 m from the track to reduce the field to the central plate of the platform only.

**Calculation of energy expenditure**

Each subject ran and/or walked at 1–4 predetermined speeds on a nearly round indoor track of concrete (40 m long) or of fine dry sand (45 m long, 1 m wide, 0.075 m deep). The surface of the sand was continuously raked smooth behind the subjects as they walked or ran on the track. Speed was determined by 12 evenly spaced photocells and regulated by voice commands; speed fluctuations between laps were less than 6% of the average speed. \( V_{O_2} \) and \( V_{CO_2} \) were measured using a K4 telemetric system (Cosmed, Italy; see Hausswirth et al. 1997). Each oxygen consumption experiment consisted of a rest measurement (subject standing quietly) followed by a maximum of four measurements at different walking/running speeds. The net energy cost \( (C) \) was computed from the change in \( V_{O_2} \) above the resting value only if the \( V_{O_2} \) was constant for at least 2 min and the respiratory quotient (RQ) remained less than 1.0.

**Calculation of muscular efficiency**

The efficiency of positive work production by the muscles and tendons was calculated as the ratio between the total mechanical work done and the energy expended, assuming an energetic equivalent of 20.1 J ml\textsuperscript{-1} O\textsubscript{2} consumed. This energetic equivalent was within 3% of the actual value obtained for each measurement, taking into account the measured RQ (McArdle et al. 1996).

**Statistics**

A two-way analysis of variance (ANOVA; Systat v.5.0) was performed in order to assess the effect of sand, speed and the interaction sand \( \times \) speed on the calculated variables, except for the energy cost of running, where a paired \( t \)-test (Systat v.5.0) was performed to assess the effect of sand on the energetic cost. Data were grouped into speed classes as indicated in the Figure legends.

**Results**

The mechanical energy of the COM is shown in Fig. 1 as a function of time, for one stride of walking (left panel) and one stride of running (right panel) on sand. During walking on sand, as on a hard surface, the kinetic energy due to the forward motion of the COM, \( E_{\text{kf}} \), is out of phase with the energy due to the vertical motion of the COM, the sum of \( E_{\text{p}}+E_{\text{kv}} \), with the result that the fluctuations in the energy of the COM, \( E_{\text{com}} \), are reduced due to exchanges between the kinetic and potential energy of the COM (Cavagna et al. 1976). The energy recovered (\( R \)) via this pendular transfer mechanism is calculated as follows:

\[
R = 100(W_f + W_v - W_{\text{com}})/(W_f + W_v),
\]

where \( W_f \), \( W_v \) and \( W_{\text{com}} \) are, respectively, the work done to accelerate the COM forward, to lift it against gravity and to maintain its motion in the sagittal plane. During running on sand, as on a hard surface, the curves for \( E_{\text{p}}+E_{\text{kv}} \) are in phase, with the consequence that \( W_{\text{com}} \approx W_f + W_v \).

The mass-specific work done per unit distance and \( R \) during walking and running on sand and on a hard surface are shown in Fig. 3. Sand, speed and sand \( \times \) speed had a significant effect on all variables \((P<0.001)\) except for \( R \) in running (sand \( P<0.74 \), speed \( P>0.38 \), sand \( \times \) speed \( P>0.63 \)). During low- and high-speed walking, \( W_{\text{com}} \) is similar on sand and on a hard surface. At intermediate speeds, walking on sand results in a 1.6-fold increase in \( W_{\text{com}} \). This increase is due to both a 7% reduction in \( R \) and a 1.6-fold increase in the vertical displacement of the COM (\( W_{\text{com}} \)). During running on sand compared with a hard surface, \( W_f \) and \( W_v \) both decrease significantly, with the consequence that \( W_{\text{com}} \) decreases by approximately 0.85-fold.

The mechanical work done on the sand during the stance phase of one walking step is shown as a function of time in Fig. 2. During the first part of the stance phase, work is done as the foot sinks into the sand. During this period, the energy of the COM decreases, and therefore this work (the work done on the sand during the deceleration of the COM, \( W_{\text{sand,dec}} \)) is considered to be due to passive transfer of energy from the COM to the sand. Nearly all of the muscle–tendon work done on the sand (\( W_{\text{sand,acc}} \)) is done during the second part of the stance phase, when the COM is accelerated forwards. Note that during the middle of the stance phase, despite the high forces, little work is done on the sand since there is almost no displacement of the foot. This general pattern is also true for running.

As shown in Fig. 2, the foot did not ‘bottom out’ and touch the surface of the force plate. Indeed, when the vertical forces are high (for example, during the period from 20 to 80% of the stance period), the foot rests on the surface of the sand. The maximum penetration into the sand averaged 74% (walk) or 78% (run) of the sand depth and occurred at the end of the stance phase, when the forces are reduced and directed largely horizontally.

The mass-specific work done on the sand per unit distance is shown in Fig. 4 as a function of speed. In both walking and running, \( W_{\text{sand,acc}} \) decreases with speed, because \( W_{\text{sand,acc}} \) per step is nearly constant and independent of gait \((0.41 \pm 0.07 \text{ J kg}^{-1}, \text{ mean } \pm \text{ s.d.}, \text{ } N=102, \text{ for walking and running combined})\) and step frequency increases significantly with speed \((P<0.0005)\) for both walking and running.

The mass-specific internal work done per unit distance \((W_{\text{int}})\)
to move the body segments relative to the centre of mass increases as a function of speed in both walking and running (Fig. 6). Sand, speed and sand × speed had a significant effect on the internal work in both walking and running (P<0.0005). At low speeds of walking and running, \(W_{\text{int}}\) is similar on sand and on a hard surface. As speed increases, \(W_{\text{int}}\) becomes relatively larger on sand than on a hard surface: at the highest speeds, \(W_{\text{int}}\) is 1.25 times greater in walking and 1.4 times greater in running.

The total muscle–tendon work (\(W_{\text{tot}}\)), the net energy cost (\(C\)) per unit distance and the muscle–tendon efficiency are shown as a function of speed and gait in Fig. 7. Sand had a significant effect on the work in both walking and running (P<0.0005). Walking on sand increases \(W_{\text{tot}}\) by 2.5-fold at slow speeds, and by 1.6-fold at high speeds, compared with walking on a hard surface. Running on sand, however, increases \(W_{\text{tot}}\) by only approximately 1.15-fold at all speeds compared with running on a hard surface.
Both sand and speed had a significant effect on the cost of walking \((P<0.0005)\), although the effect of the interaction sand \times speed was not significant \((P>0.65)\). The net metabolic cost \((C)\) of walking on a hard surface takes the form of the well-known ‘U’-shaped curve as a function of speed (Margaria, 1938), with a minimum cost of 2.3 J kg\(^{-1}\) m\(^{-1}\) at the optimal speed of 1.3 m s\(^{-1}\). The curve for the cost of walking on sand has the same shape, but is shifted upwards by 2.1- to 2.7-fold, with the optimal speed being reduced to approximately 1.1 m s\(^{-1}\).

Sand had a significant effect on the energetic cost of running \((P<0.0005)\). A mean net energetic cost of 4.1 J kg\(^{-1}\) m\(^{-1}\) was found for running on a hard surface, which was independent of speed and agreed with previous studies (Margaria et al. 1963), showing that even at the highest running speeds measured (2.75 m s\(^{-1}\)) the track curvature had no effect on the energy consumption. During running on sand, \(C\) is also independent of speed, but is increased 1.6-fold relative to running on a hard surface. It is notable that, even with well-
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During high-speed walking and during running on sand, the muscle–tendon work that must be done (predominantly in walking) and a decrease in the muscle–tendon efficiency (predominantly in running).

During walking on sand, $W_{\text{int}}$ is increased by 1.25-fold as 60% of the mechanical energy of the COM can be recovered through the kinetic–potential energy exchange mechanism at the optimal speed (Fig. 3). Running is still a bouncing mechanism, since the kinetic and potential energy of the COM are in phase (Fig. 1), and the muscle–tendon efficiency remains above 0.25 (Fig. 7), i.e. above the maximum efficiency of a muscle contracting without the aid of storage and recovery of elastic energy (Cavagna and Kaneko, 1977; Willems et al. 1995). Nevertheless, the metabolic cost of moving on sand is greatly increased, by 1.6- to 2.7-fold, as a consequence of an increase in $W_{\text{tot}}$ (mainly as a result of the work done by the foot on the sand) and a decrease in muscle–tendon efficiency (Fig. 7). Zamparo et al. (1992) found essentially the same increase in metabolic rate during walking and running on a beach; they assumed that this increase when moving on sand was due to the failure of the pendular mechanism in walking and the bouncing mechanism in running, rather than to the work done on the sand and a decreased muscle–tendon efficiency, as was found here.

During walking on sand, $W_{\text{tot}}$ is increased by 1.25-fold

### Discussion

The commonly experienced increase in effort required during walking or running on a soft surface such as sand is due largely to an increase in the muscle–tendon work that must be done (predominantly in walking) and to a decrease in the muscle–tendon efficiency (predominantly in running).

During walking on sand, it was not possible to maintain steady-state running on sand at speeds higher than only 2.75 m s$^{-1}$.
relative to walking on a hard surface, but this increase is only found at high speeds (Fig. 6). Since step frequency is unchanged by the surface (Fig. 5), this increase must be related to the awkward limb movements caused by the foot moving in the sand. At all walking speeds, the work done on the body, $W_{\text{com}}+W_{\text{int}}$, is increased on sand compared with walking on a hard surface by an average of only 1.2-fold. By far the greatest part of the increase in $W_{\text{tot}}$ is accounted for by the work done on the sand, $W_{\text{sand,acc}}$ (Figs 2, 4). When walking on a hard surface, $W_{\text{tot}}$ is equal to $W_{\text{com}}+W_{\text{int}}$, since the work done on the environment is essentially zero (wind resistance is negligible and the foot does not slip or move the substratum). In contrast, during walking on sand, the foot moves the sand, resulting in $W_{\text{sand,acc}}$. This work done on the substratum is actually greater than $W_{\text{com}}+W_{\text{int}}$ at slow speeds, decreasing at higher speeds (Figs 3, 4, 6).

The situation during running on sand is somewhat different. Since the sand acts like a damper, the accelerations during the contact phase are reduced, with the consequence that the kinetic energy variations and the vertical motion of the COM are also reduced, leading to a 0.85-fold decrease in $W_{\text{com}}$ (Fig. 3). However, since the vertical take-off velocity is lower, the period and distance travelled during the aerial phase are shorter, resulting in a slight increase (less than 1.15-fold) in the step frequency (Fig. 5). This increase, coupled with the awkward limb movements, explains the 1.4-fold increase in $W_{\text{int}}$ on sand relative to running on a hard surface. Overall, the work done on the body, $W_{\text{com}}+W_{\text{int}}$, is roughly the same on sand or a hard surface, and the mean 1.15-fold increase in $W_{\text{tot}}$ is therefore almost entirely due to $W_{\text{sand,acc}}$. Note that running on sand is completely different from running on a tuned track; whereas sand is a damper, absorbing energy only, a tuned track is a lightly damped spring, returning most of the energy absorbed (McMahon and Greene, 1979).

The second major factor contributing to the increase in the cost of locomotion on sand is a relative decrease in the efficiency of the muscles plus tendons (Fig. 7). At slow walking speeds, the increase in $W_{\text{tot}}$ when going from a hard surface to sand results in a proportional increase in $C$ (Fig. 7) and, therefore, efficiency remains unchanged at approximately 0.20. However, at high walking speeds, the increase in $W_{\text{tot}}$ is less than the increase in $C$ and, consequently, efficiency decreases from 0.36 on a hard surface to 0.25 on sand. During running on sand, the increase in $W_{\text{tot}}$ is only approximately one-quarter of the increase in $C$ at all speeds and, consequently, efficiency is decreased relative to running on a hard surface from 0.45 to 0.30.

The relative increase in the cost of locomotion on sand can be explained on the following basis. During locomotion on a hard surface, little work is done on the environment and, consequently, all the positive work done on the body by the muscles and tendons in one phase of a step must be absorbed by the muscles and tendons in a subsequent phase. Part of this absorbed energy can be used for positive work production during the following step, increasing the overall efficiency above 0.25, which is considered to be the maximum efficiency for the conversion of chemical energy into mechanical work by the muscles (Dickinson, 1929). However, during locomotion on a yielding surface such as sand, significant work is done on the environment, which represents energy lost from the body. This energy must be replaced at each step by the muscles, at an overall muscle–tendon efficiency considerably less than the overall efficiency obtained on a hard surface (Fig. 7) and certainly somewhat less than the maximum value of 0.25.

The relative increase in the cost of locomotion on sand can be explained quantitatively by dividing the positive work into two types: work that is done solely from the conversion of chemical energy into mechanical work, and work that is done with the aid of energy absorbed in an earlier phase of the step. The first type of work is equal to the total work done on the sand, $W_{\text{sand,dec}}+W_{\text{sand,acc}}$ (Fig. 2); the second type of work is $W_{\text{tot}}-W_{\text{sand,dec}}-W_{\text{sand,acc}}$. We will assume that the efficiency of the first type of work is 0.2, somewhat less than the maximum value of 0.25 since the efficiency is lower than the peak value at higher and lower speeds of contraction, and we will assume that the efficiency of the second type of work is the same as the efficiency of moving on firm ground at the same speed, $\text{Eff}_{\text{hard}}$ (broken lines in Fig. 7). The predicted cost per unit distance ($C_{\text{pred}}$) for walking and running on sand can then be calculated from the mechanical work as follows:

$$C_{\text{pred}} = \frac{W_{\text{tot}} - W_{\text{sand,dec}} - W_{\text{sand,acc}}}{\text{Eff}_{\text{hard}}} + \frac{W_{\text{sand,dec}} + W_{\text{sand,acc}}}{0.2}.$$  (5)

The curve of $C_{\text{pred}}$ versus speed calculated using equation 5 is shown in Fig. 7 and is in quite close agreement with the experimentally measured $C$.

The predicted overall efficiency of walking and running on sand is the ratio of $W_{\text{tot}}$ to $C_{\text{pred}}$ (Fig. 7); this ratio is also in close agreement with the experimental data.

The determination of the energetic cost of running in sand allows a simple test of the hypothesis of Taylor (1985) and Kram and Taylor (1990) that the metabolic cost of running is determined by the mean force generated (assumed to be the subject’s weight) and the time course of force generation, irrespective of the work performed. The mean vertical force during running on sand is the body weight, and the time course of force generation is slightly longer than when running on a firm surface which, according to their hypothesis, should result in an unchanged or reduced metabolic cost. Instead, we have found that the cost increases significantly. In fact, as shown in equation 5 and Fig. 7, the increase in cost can be explained simply by the increase in work.

**List of symbols**

- $C$ net metabolic energy cost
- COM centre of mass of the body
- $C_{\text{pred}}$ predicted net metabolic cost
$d_{h,i}$ \quad \text{horizontal displacement of a fixed point on the sole of the foot between frames $i-1$ and $i$}

$d_{v,i}$ \quad \text{vertical displacement of a fixed point on the sole of the foot between frames $i-1$ and $i$}

$E_{\text{com}}$ \quad \text{total energy of the COM.}

$E_{\text{eff,hard}}$ \quad \text{muscle–tendon efficiency during locomotion on a hard surface}

$E_{\text{kf}}$ \quad \text{kinetic energy due to the forward motion of the COM}

$E_{\text{kv}}$ \quad \text{kinetic energy due to the vertical motion of the COM}

$E_{p}$ \quad \text{gravitational potential energy of the COM}

$F$ \quad \text{ground reaction force vector}

$F_{h,i}$ \quad \text{horizontal component of the force vector $\mathbf{F}$ in frame $i$}

$F_{v,i}$ \quad \text{vertical component of the force vector $\mathbf{F}$ in frame $i$}

$F_{v,1}$ \quad \text{vertical component of $\mathbf{F}$ measured at end 1 of the force plate}

$F_{v,2}$ \quad \text{vertical component of $\mathbf{F}$ measured at end 2 of the force plate}

$L$ \quad \text{position of the force vector $\mathbf{F}$ along the length of the force plate}

$L_{p}$ \quad \text{length of the force plate}

$R$ \quad \text{energy recovered by pendular transfer between the kinetic and potential energy of the COM}

$R_{Q}$ \quad \text{respiratory quotient, $V_{CO_2}/V_{O_2}$}

$V_{CO_2}$ \quad \text{rate of carbon dioxide production}

$V_{O_2}$ \quad \text{rate of oxygen consumption}

$W_{\text{com}}$ \quad \text{positive muscle–tendon work required to move the COM relative to the surroundings}

$W_{\text{env}}$ \quad \text{positive muscle–tendon work done on the environment, such as work against wind resistance or against the substratum}

$W_{\text{ext}}$ \quad \text{positive muscle–tendon work to move the COM relative to the surroundings plus the work done on the surroundings ($=W_{\text{com}}+W_{\text{env}}$)}

$W_{\text{f}}$ \quad \text{mechanical work done to accelerate the COM forwards}

$W_{\text{int}}$ \quad \text{mechanical work–tendon work done to accelerate the body segments relative to the COM}

$W_{\text{sand,acc}}$ \quad \text{mechanical work done on the sand while the centre of mass is accelerating, assumed to be equal to the muscle–tendon work done on the sand}

$W_{\text{sand,dec}}$ \quad \text{mechanical work done on the sand while the centre of mass is decelerating}

$W_{\text{tot}}$ \quad \text{total positive muscle–tendon work performed during locomotion ($=W_{\text{ext}}+W_{\text{int}}+W_{\text{sand,acc}}$)}

$W_{v}$ \quad \text{mechanical work done to lift the COM against gravity}

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