The landing–take-off asymmetry in human running

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Summary

In the elastic-like bounce of the body at each running step the muscle–tendon units are stretched after landing and recoil before take-off. For convenience, both the velocity of the centre of mass of the body at landing and take-off, and the characteristics of the muscle–tendon units during stretching and recoil, are usually assumed to be the same. The deviation from this symmetrical model has been determined here by measuring the mechanical energy changes of the centre of mass of the body within the running step using a force platform. During the aerial phase the fall is greater than the lift, and also in the absence of an aerial phase the transduction between gravitational potential energy and kinetic energy is greater during the downward displacement than during the lift. The peak of kinetic energy in the sagittal plane is attained thanks to gravity just prior to when the body starts to decelerate downwards during the negative work phase. In contrast, a lower peak of kinetic energy is attained, during the positive work phase, due to the muscular push continuing to accelerate the body forwards after the end of the acceleration upwards. Up to a speed of 14 km h^{-1} the positive external work duration is greater than the negative external work duration, suggesting a contribution of muscle fibres to the length change of the muscle–tendon units. Above this speed, the two durations (<0.1 s) are similar, suggesting that the length change is almost totally due to stretch–recoil of the tendons with nearly isometrically contracting fibres.

Key words: locomotion, running, muscle stretch–shorten cycle.

Introduction

In running the body moves forwards through a succession of apparent bounces: kinetic energy of forward motion and gravitational potential energy of the centre of mass are absorbed and restored by the muscle–tendon units at each step (Cavagna et al., 1964). A spring-mass model was proposed to simulate the bounce of the body (Blickhan, 1989; McMahon and Cheng, 1990; Seyfarth et al., 2002). This model is largely used in the interpretation of experiments aimed to determine the changes in spring stiffness and step frequency with speed (Cavagna et al., 1988; McMahon and Cheng, 1990), with grounds of different compliance (Ferris and Farley, 1997; Ferris et al., 1999; Kerdok et al., 2002) and the effect of spring stiffness on energy expenditure (McMahon et al., 1987; Kerdok et al., 2002).

The spring-mass model assumes (i) the same characteristics of the 'spring', i.e. of the muscle–tendon units, when the spring is compressed after landing (the muscle–tendon units are stretched) as when the spring extends to take-off (the muscle–tendon units shorten), and (ii) the same height and velocity of the centre of mass at landing and take-off (Blickhan, 1989; McMahon and Cheng, 1990). As the authors proposing the model pointed out, this is a simplification because: (i) '*the leg has to be more stiff during landing than during take-off*', and (ii) '*animals in general do not have a similar take-off and landing velocity as assumed in the model. They take-off with straightened legs and land with bent legs*' (Blickhan, 1989).

The purpose of the present study was to determine if and to what extent (i) the functional characteristics of the limb in running are affected by, and adapted to, an eventual asymmetry of the movement during landing and take-off, and (ii) a possible different response of the muscle–tendon units to stretching and shortening affects the timing of negative and positive work performance during their stretch–shorten cycle in the running step.

Before describing the movement of the centre of mass during its apparent bounce at each running step it is worth noting that landing and take-off may not occur at all during trotting and low-speed running, when the vertical oscillation of the centre of mass of the body takes place entirely in contact with the ground (Cavagna et al., 1988). It is obvious that in this case the contact with the ground cannot be taken as an indication of landing and take-off when describing the bounce of the elastic system. However, in this case the vertical oscillation also takes place below and above an equilibrium position where the vertical force equals body weight. As the running speed increases and an aerial phase takes place, the contact time progressively decreases towards, but not to, the time interval during which the elastic system is loaded beyond its equilibrium position. It is therefore more appropriate to

consider 'landing' as the instant where the vertical force increases above body weight (rather than the instant where the foot contacts the ground) and 'take-off' as the instant where the vertical force drops below body weight (rather than the instant where the foot leaves the ground). In the present study the height of the centre of mass was measured both when the foot actually contacts and leaves the ground, and at its equilibrium positions during the downward and the upward displacement.

Materials and methods
Subjects and experimental procedure

The experimental procedure consisted of measuring the force exerted on the ground in the sagittal plane during running at different speeds. In this study, results are given as means ± s.d. The experiments were conducted on ten adult subjects, eight males and two females (weight 65.3±8.4 kg, height 1.8±0.1 m, age 28±9.8 years). We analyzed 359 runs ranging from 2 to 21 km h^{-1}. Informed written consent was obtained from each subject. The studies were performed according to the Declaration of Helsinki.

The subjects ran back and forth across a 4 m×0.5 m force platform sensitive to the force exerted by feet in the forward and vertical directions; lateral forces were neglected. The platform was inserted in a 50 m long corridor with its surface at the level of the floor. Two photocells fixed 1–3 m apart (according to the speed) at neck height along the side of the platform were used to determine the average running speed, $\bar{V}_f$. The characteristics of the platform have previously been described (Cavagna, 1975).

A microcomputer was used to acquire data at a sampling rate of 500 Hz per channel. Three channels were employed to acquire (i) the platform signal proportional to the force exerted in forward direction (F_f), (ii) the platform signal proportional to the force exerted in vertical direction (F_v), and (iii) the output of the photocell circuit.

From platform records to mechanical energy changes

A custom LabVIEW (6.1) software program was used to analyze the ground reaction force records. The procedure used to derive the mechanical energy changes of the centre of mass of the body from the ground reaction forces has previously been described in detail (Cavagna, 1975). In short, only motion in a sagittal plane was considered when calculating the mechanical energy of the centre of mass. Rotational kinetic energy of the body and lateral translational energy were ignored. The time-average of the F_v record was measured after each run over an integer number of steps, encompassing those subsequently used for calculation, searching for a minimum difference with subject body weight; the ratio between this time average and the weight of the subject was 1.00±0.01 (N=359). The velocity changes of the centre of mass of the body in the vertical direction and in the forward direction were determined, by integration, from the F_v and F_f platform signals in the time interval between photocells. An integer number of running

cycles was then selected between two peaks (or valleys) of the vertical velocity changes record searching by eye for a minimum drift of both the vertical and forward records. The procedure followed to determine the instantaneous velocity in the vertical direction $V_v(t)$ and forward direction $V_f(t)$ from the corresponding velocity changes has been described (Cavagna, 1975). The instantaneous vertical velocity $V_v(t)$ was used to calculate the instantaneous kinetic energy of vertical motion $E_{kv}(t)=0.5M_bV_v(t)^2$ (where M_b is the mass of the body) and, by integration, the vertical displacement of the centre of mass, $S_v(t)$, with the corresponding gravitational potential energy change $E_p(t)=M_bgS_v(t)$ (where g is the acceleration of gravity). The kinetic energy of forward motion was calculated as $E_{kf}(t)=0.5M_bV_f(t)^2$, the total translational kinetic energy of the centre of mass in the sagittal plane as $E_k(t)=E_{kf}(t)+E_{kv}(t)$, and the translational mechanical energy of the centre of mass in the sagittal plane as $E_{cm}(t)=E_{kv}(t)+E_{kf}(t)+E_p(t)$. Since, as mentioned above, selection was initially made between peaks (or valleys) of the vertical velocity changes, the records were expanded to include the previous valley (or peak) of $E_p(t)$ until a clear picture of the step(s) was obtained (Fig. 1). The downward vertical displacement $S_{v,down}$ and the upward vertical displacement $S_{v,up}$ were calculated from the total decrement, respectively increment, of the $E_p(t)$ curve, taking place between two or more E_p peaks (or valleys), divided by the number of steps. Algorithms were made to calculate the work done during the selected steps between E_p valleys (or peaks): W_v, W_{kf} and W_{ext} were calculated from the amplitudes of valleys and peaks, and the initial and final values in the $E_p(t)$, $E_{kf}(t)$ and $E_{cm}(t)$ records. Positive values of the energy changes gave positive work, negative values gave negative work. In a perfect steady run on the level the ratio between the absolute values of positive and negative work done in an integer number of steps should be equal to one. Experimental values were as follows (N=359): W^+_v/W^-_v=0.99±0.07, W^+_{kf}/W^-_{kf}=1.03±0.18, W^+_{ext}/W^-_{ext}=1.00±0.07. All the selected steps were used for analysis.

Aerial time, brake-push durations and vertical displacement during contact

Since the mechanical energy of the centre of mass is constant when the body is airborne (air resistance is neglected), the aerial time was calculated as the time interval during which the derivative $dE_{cm}(t)/dt$=0. This time interval was measured using two reference levels set by the user above and below the section of the record where $dE_{cm}(t)/dt≈0$ [the distance between the two reference levels was the minimal distance, which included the noise of the $dE_{cm}(t)/dt$ record]. Due to the noise of the $dE_{cm}(t)/dt$ record, the aerial time was in some cases overestimated (by 6.5±7.6% in one randomly selected subject; mean ± s.d., N=28).

The brake duration, t_{brake}, i.e. the time during which external negative work is done, was calculated as the time interval during which the $dE_{cm}(t)/dt$ record was below the reference level. The push duration, t_{push}, i.e. the time during which external positive work is done, was calculated as the time

interval during which the $dE_{cm}(t)/dt$ record was above the reference level. Due to the noise of the $dE_{cm}(t)/dt$ record, t_{brake} and/or t_{push} were in some cases underestimated (5.3±6.6% for t_{brake} and 7.4±7.1 for t_{push}, N=28). Similarly, the downward and upward displacements of the centre of mass during contact, $S_{c,down}$ and $S_{c,up}$, were measured from the descending, respectively ascending portions of the $E_p(t)$ curve during the time interval where $dE_{cm}(t)/dt$ was lower, respectively greater than the two reference levels.

Vertical displacement below and above the equilibrium points

The vertical force, F_v, applied by the foot on the ground is:

$$F_v = \text{body weight} + M_b a_v, \qquad (1)$$

where a_v is the vertical acceleration of the centre of mass, i.e. the time derivative of its vertical velocity, V_v. When the vertical velocity, and $E_{kv}=0.5M_b V_v^2$, are at a maximum, the derivative is nil, a_v=0, and as a consequence F_v=body weight. The locations of the E_{kv} peaks attained during the step (Fig. 1) were therefore used to determine the instants where the vertical force equals body weight. The locations and the amplitudes of E_p simultaneous with the peaks of E_{kv} were used to determine the part of the vertical displacement taking place below the equilibrium points during the downward deceleration of the centre of mass, $S_{ce,down}$, and during the upward acceleration of the centre of mass, $S_{ce,up}$. The differences $S_{v,down}-S_{ce,down}=S_{ae,down}$ and $S_{v,up}-S_{ce,up}=S_{ae,up}$ gave the vertical displacement when the centre of mass of the body accelerates downwards and decelerates upwards, respectively (Cavagna et al., 1988).

Maximum vertical velocity and kinetic energy attained during the downward displacement and the lift

The maximal vertical velocity and the maximal kinetic energy $E_k=E_{kv}+E_{kf}$ attained by the centre of mass during the downward displacement, $V_{v,mx,down}$ and $E_{k,mx,down}$, and during the lift, $V_{v,mx,up}$ and $E_{k,mx,up}$, were determined by comparison of the peaks in E_{kv} and E_k with the simultaneous E_p curve. Since the maximal vertical velocity may increase with the amplitude of the vertical displacement, which may be different during the lift and the downward displacement (see, e.g. the E_p curves in Fig. 1), the ratio between maximal downward and upward velocities was normalized in Fig. 3 as $(V_{v,mx,down}/V_{v,mx,up})(S_{v,up}/S_{v,down})$.

Within the step $E_p \leftrightarrow E_k$ transduction

The time course of the transduction taking place within the step between gravitational potential energy E_p and kinetic energy of the centre of mass E_k can be determined from the absolute value of the changes, both positive and negative increments, of E_p, E_k and E_{cm} in short time intervals within the step cycle (Cavagna et al., 2002):

$$r(t) = 1 - |\Delta E_{cm}(t)| / [|\Delta E_p(t)| + |\Delta E_k(t)|]. \qquad (2)$$

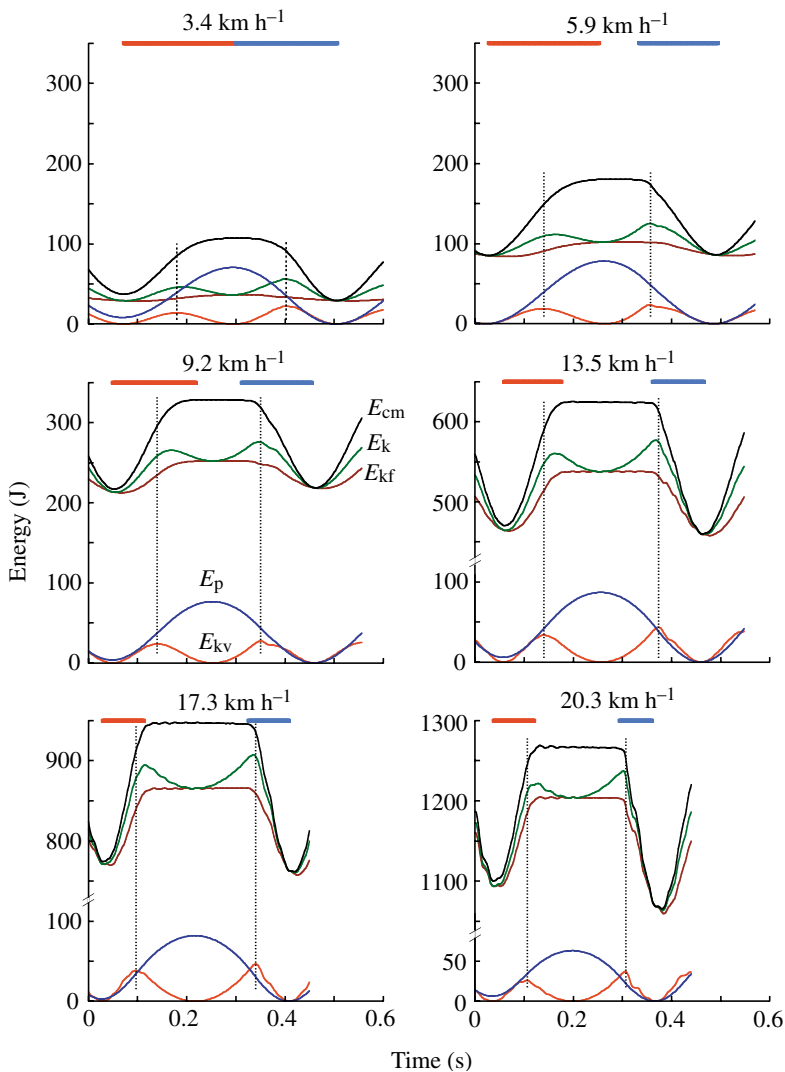The E_p–E_k transduction is complete [$r(t)$=1]

Fig. 1. Mechanical energy of the centre of mass of the body during running steps at the indicated speeds. In each panel the curves show the gravitational potential energy (E_p, blue), the kinetic energy of vertical motion (E_{kv}, red), the kinetic energy of forward motion (E_{kf}, brown), the kinetic energy of motion in the sagittal plane ($E_k=E_{kv}+E_{kf}$, green), and the total translational energy of the centre of mass in the sagittal plane ($E_{cm}=E_p+E_k$, black). The records were obtained as described in the Materials and methods from the signals of a force platform. In each panel, the zero line corresponds to the minimum attained by the E_p curve. Note that the maximum of E_k occurs in close proximity to the maximum of E_{kv} during the downward displacement, whereas it follows the maximum of E_{kv} during the lift (vertical dotted lines). The horizontal bars indicate the time of contact during the step (from minimum to minimum of E_p). The time of contact during which positive external work is done (increment of E_{cm}) is indicated in red, whereas the time of negative external work (decrement of E_{cm}) is indicated in blue. Subject: 72.5 kg mass, 1.79 m height, 23 years old.

during the aerial phase (ballistic lift and fall) when no external work is done by the muscular force. However the E_p–E_k transduction also occurs during contact, when the body is partially supported by the foot on the ground in the upper part of the trajectory of the centre of mass [$0<r(t)<1$]. The E_p–E_k transduction is nil [$r(t)=0$] in two phases of the step, α and β, where E_k increases, decreases, respectively, simultaneously with the gravitational potential energy E_p (Cavagna et al., 2002). Note that positive and negative external work is done both in the phases α and β of the step [$r(t)=0$] and in the phases of the step where a transduction occurs between E_k and E_p [$0<r(t)<1$].

In this study, $r(t)$ was calculated from the absolute value of the time derivative of E_p, E_k and E_{cm} in the time interval between two or more E_p peaks (or valleys). The cumulative value of energy recovery, $R_{int}(t)$, resulting from the instantaneous E_k–E_p transduction, was measured from the area below the $r(t)$ record divided by the step period, τ:
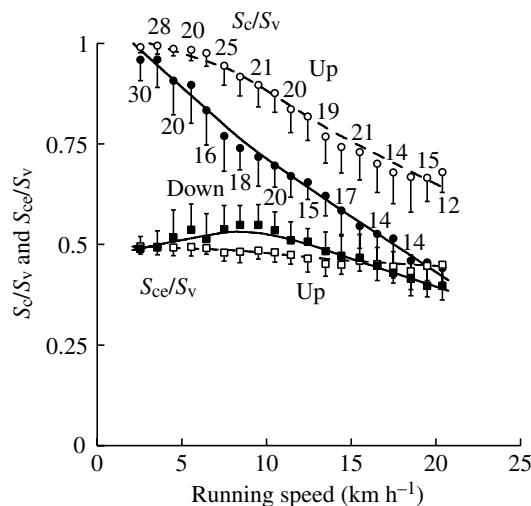

Fig. 2. Vertical displacement during contact and amplitude of oscillation of the elastic system. The fractions of the vertical displacement of the centre of mass of the body taking place during contact, S_c/S_v (filled circles: downward displacement, open circles: upward displacement), and when the vertical force is greater than body weight, S_{ce}/S_v (filled squares: downward displacement, open squares: upward displacement) are given as a function of the running speed. It can be seen that S_c/S_v decreases markedly with speed. Except at very low speeds when the aerial phase may be nil ($S_c/S_v≈1$: e.g. upper left panel in Figs 1 and 7), the downward displacement while the foot is in contact with the ground is smaller than the upward displacement during contact: the ballistic fall of the centre of mass is greater than the ballistic lift (see Fig. 7). In contrast, the amplitude of the vertical oscillation below the equilibrium point, S_{ce}/S_v, changes less with speed and approaches one half of the vertical displacement S_v both during compression (down) and recoil (up) of the spring. The vertical bars indicate the standard deviation of the mean calculated in each velocity class; the figures near the symbols indicate the number of items of the mean. Lines represent the weighted mean of all the data (Kaleidagraph 3.6.4); their only purpose is to be a guide for the eye: they do not describe the underlying physical mechanism.

$R_{int}(t)=[\int_0^\tau r(u)\mathrm{d}u]/\tau$. At the end of the step $R_{int}(\tau)=R_{int}$ (Cavagna et al., 2002).

In order to determine the asymmetry of the step cycle, it is useful to know how much of the E_k–E_p transduction occurs during the downward displacement and during the lift of the centre of mass. The derivative $\mathrm{d}E_p(t)/\mathrm{d}t$ was used to determine the amount of transduction occurring during the downward displacement, $R_{int,down}$, and during the lift of the centre of mass, $R_{int,up}$. The step asymmetry was quantified by the ratio: $R_{int,down}/R_{int}$.

Statistics

The data collected as a function of running speed were grouped into classes of 1 km h^{-1} intervals as follows: 2 to <3 km h^{-1}, 3 to <4 km h^{-1},.., 20 to <21 km h^{-1}. The data points in Fig. 2 represent the mean ± s.d. in each of the above speed intervals and the figures near the symbols give the number of items in the mean. A comparison was made to assess the difference between positive and negative external work durations as a function of speed (Fig. 6). Since each couple of means at a given running speed has the same number of items, with each item measured in the same step for each subject, a *t*-test paired two-sample for means tool (Excel 2004, version 11.2) was used to determine when the means are significantly different (Table 1).

Results

Height and velocity of the centre of mass at landing and take-off

When an aerial phase takes place during the running step, the height of the centre of mass at the instant of take-off is

Table 1. *Speeds at which t_{push} and t_{brake} are significantly different*

Speed (km h^{-1})	t_{push} vs t_{brake} P
2	2.88×10^{-11}
3	4.24×10^{-10}
4	2.03×10^{-7}
5	1.81×10^{-8}
6	4.48×10^{-8}
7	2.18×10^{-10}
8	2.60×10^{-9}
9	1.71×10^{-9}
10	6.05×10^{-8}
11	8.17×10^{-6}
12	8.63×10^{-5}
13	0.00
14	0.37
15	0.01
16	0.26
17	0.49
18	0.11
19	0.05
20	0.02

greater than its height at the instant of touch-down, indicating that the ballistic lift of the centre of mass is less than its ballistic fall. This is shown in Fig. 2: the fraction of the vertical displacement taking place when the foot is in contact with the ground S_c/S_v is greater during the lift than during the downward displacement of the centre of mass. In absolute terms, the mean values for the 313 runs with an aerial phase, are $S_{c,up}=0.077\pm0.018$ m and $S_{c,down}=0.063\pm0.017$ m ($P<0.001$).

The relative amount of the vertical displacement of the centre of mass taking place during contact changes markedly with speed, decreasing from unity at the lowest speed (when the aerial phase is nil) to ~0.6 during the lift and ~0.4 during the downward displacement at ~20 km h^{-1} (Fig. 2). In contrast, the fraction of the vertical displacement S_{ce}/S_v, from the lowest point of the trajectory to the point where the vertical force equals body weight, changes less with speed and approaches one half of S_v (Fig. 2).

Even at the equilibrium points, however, the maximal vertical velocity attained by the centre of mass during the downward displacement $V_{v,mx,down}$ is greater than that attained during the lift $V_{v,mx,up}$ (Fig. 3). This results in a maximum of kinetic energy, $E_k=E_{k,f}+E_{k,v}$, which is greater during the downward displacement than during the lift (compare the two peaks of the green line in Figs 1 and 7). However, the peak of E_k is higher during the downward displacement than during the lift not just because the maximal vertical velocity is greater during the downward displacement than during the lift. The contribution of $E_{k,v}$ to the maximum of E_k is greater during the downward displacement than during the lift also because the increment of $E_{k,v}$ adds onto the maximum of $E_{k,f}$ during the downward displacement, whereas it precedes the maximum of $E_{k,f}$ during the lift (Fig. 1; see Discussion). During the

Fig. 4. The peak in kinetic energy of the centre of mass, $E_k=E_{k,f}+E_{k,v}$, attained because of gravity in its motion forwards and downwards is greater than the peak attained because of the muscular push in its motion forwards and upwards. Note that the downward/upward asymmetry decreases with speed due to the large increase of $E_{k,f}$ relative to $E_{k,v}$ (Fig. 1). The difference between the two peaks attained by E_k at each step also remains positive at the highest running speeds (inset). Statistics as in Fig. 2.

downward displacement, the time difference between the maximum of E_k and the maximum of $E_{k,v}$ is nil or possibly slightly negative (see vertical dotted lines in Fig. 1). During the lift, by contrast, the time difference between the maximum of
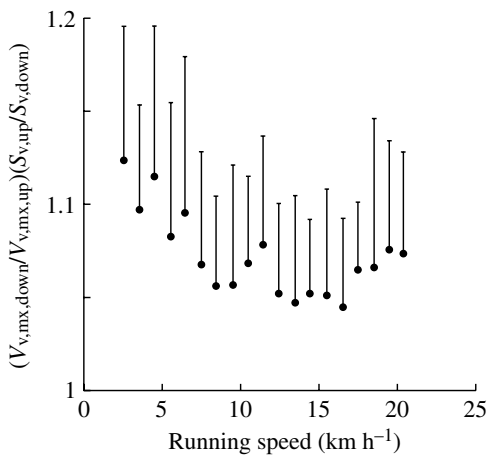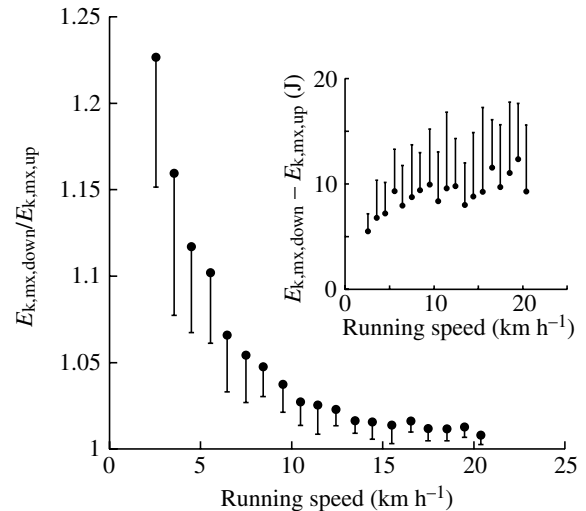

Fig. 3. The normalized ratio (see Materials and methods) between maximal downward and upward velocities attained at each step by the centre of mass of the body is plotted as a function of the running speed. The greater vertical velocity attained during the downward displacement indicates: (i) a lower vertical force exerted by the structures supporting the body at the lowest speeds when the aerial phase is nil, together with (ii) a ballistic fall greater than the ballistic lift at higher speeds (Fig. 2). Statistics as in Fig. 2.
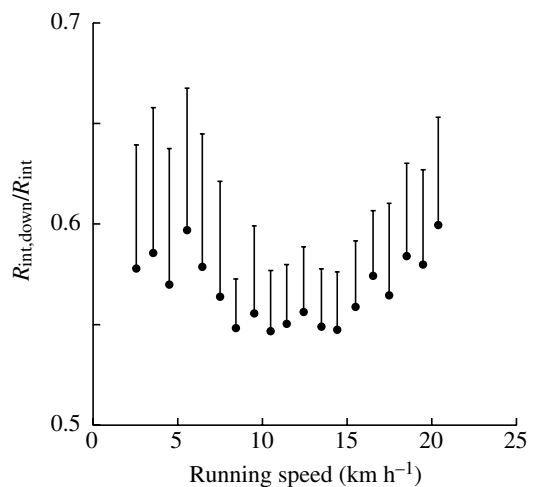

Fig. 5. The lower support of the body during the downward displacement of the centre of mass relative to upward displacement is indicated on the ordinate by a ratio $R_{int,down}/R_{int}$ greater than 0.5 at all running speeds (abscissa). Note that R_{int} is the cumulative value at the end of the step of the instantaneous E_k–E_p transduction: data show that the transduction of E_p into E_k during the downward displacement is greater than the transduction of E_k into E_p during the upward displacement [see $R_{int}(t)$ curve in Fig. 7]. Statistics as in Fig. 2.
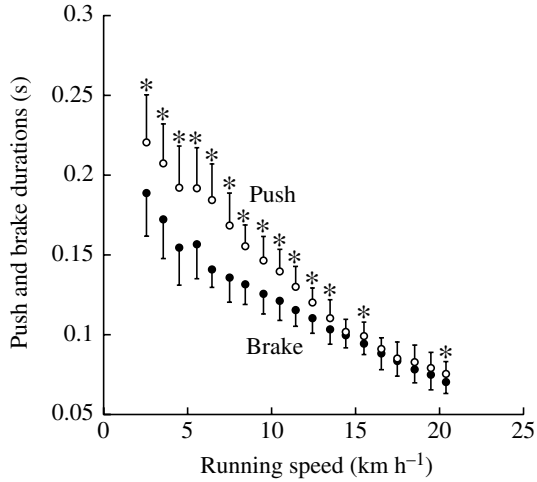
Fig. 6. Positive and negative external work durations. The times during which positive external work is done at each step during the push (open circles and red bars in Fig. 1) and negative external work is done during the brake (filled circles and blue bars in Fig. 1) are plotted as a function of the running speed. It can be seen that the duration of positive external work is clearly greater than the duration of negative external work up to a speed of 14 km h^{-1} (asterisks indicate $P<0.05$: see Table 1). This suggests that, with increasing speed, the work contribution by the contractile machinery is progressively substituted by elastic storage and recovery by tendons (see text). Statistics as in Fig. 2.
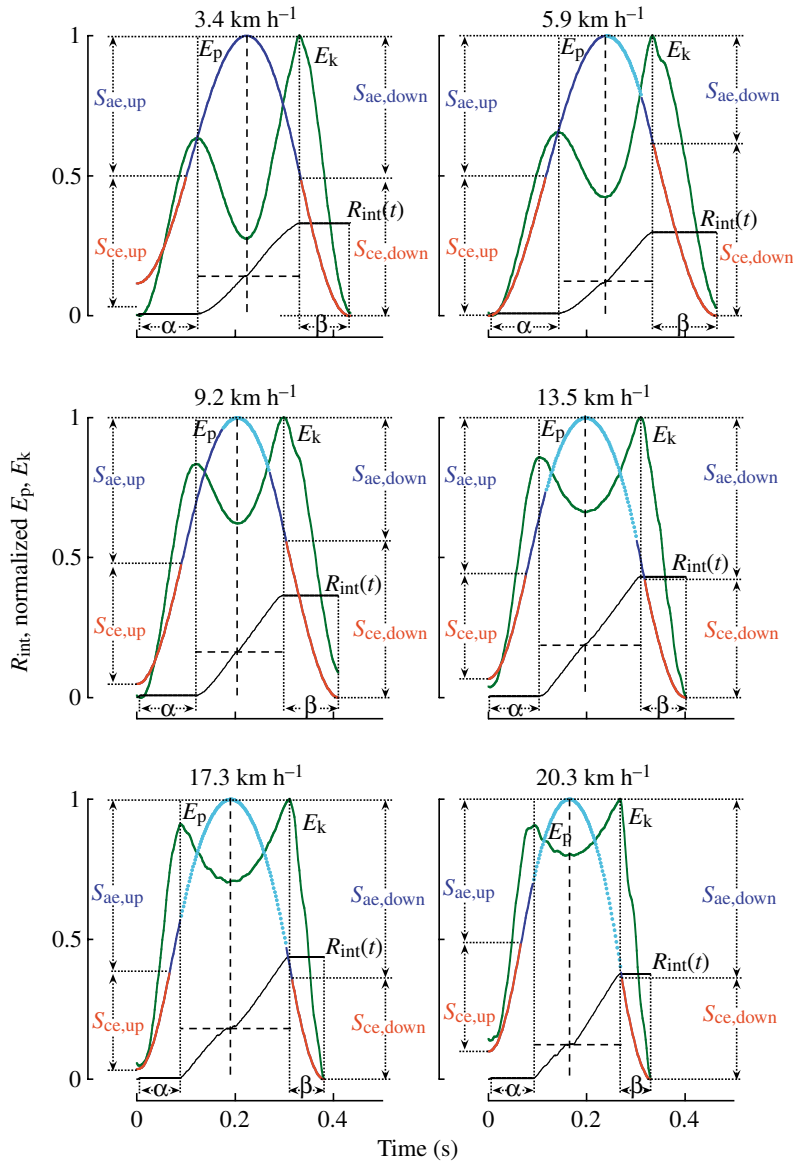

Fig. 7. The four phases of the bounce of the body during the running step. Each panel illustrates the changes in gravitational potential energy, E_p, and in kinetic energy of motion in the sagittal plane, $E_k=E_{kv}+E_{kf}$, of the centre of mass of the body simultaneously with the E_p–E_k energy transduction, $R_{int}(t)$. The energy curves are normalized to oscillate between zero and one. Each panel begins and ends at the lowest value of the E_p curve. Same steps illustrated in Fig. 1. The different colors in the E_p curve distinguish the fractions of the step where the vertical force exerted on the ground is greater than body weight (red), and lower than body weight (blue), with lighter blue indicating the aerial phase (not present in the upper left panel). The four phases correspond to the vertical displacement during the upward acceleration $S_{ce,up}$ (red) and deceleration $S_{ae,up}$ (blue), and the downward acceleration $S_{ae,down}$ (blue) and deceleration $S_{ce,down}$ (red). The vertical dotted lines are drawn through the two peaks of E_k and encompass the fraction of the step where a transduction occurs between E_p and E_k as indicated by the increments of the $R_{int}(t)$ curve below and above crossing the broken lines. Note that the transduction of E_k into E_p during the lift [lower-left increment of $R_{int}(t)$] is smaller than the transduction of E_p into E_k during the downward displacement (upper-right increment). In the horizontal tracts of the $R_{int}(t)$ curve no transduction occurs between E_p and E_k and muscle–tendon units absorb simultaneously E_p and E_k (phase β) and increase simultaneously E_p and E_k (phase α). Note that whereas most of β is confined within $S_{ce,down}$, α extends beyond $S_{ce,up}$ within a large fraction of $S_{ae,up}$ due to a continuing increase of E_k.

E_k and the maximum of $E_{k,v}$ is positive (increasing with speed to 20–25 ms; data not shown).

The ratio $E_{k,mx,down}/E_{k,mx,up}$ decreases with speed, approaching asymptotically unity at high running speeds (Fig. 4) due to the large increase of $E_{k,f}$ (brown in Fig. 1) relative to $E_{k,v}$ (red in Fig. 1). The difference $E_{k,mx,down}-E_{k,mx,up}$ remains positive even at high running speeds (inset in Fig. 4).

Mechanical energy changes during the downward displacement and the lift

The transduction of gravitational potential energy of the centre of mass E_p into kinetic energy E_k during the downward displacement is greater than the transduction of E_k into E_p during the lift, as shown in Fig. 5 by a ratio $R_{int,down}/R_{int}$ greater than 0.5. This is also true at the lowest running speeds when the aerial phase is often nil, indicating that even in the absence of a ballistic fall the vertical support on the ground is less during the downward displacement than during the lift.

The total duration of positive and negative external work, including the α and β phase durations [$r(t)$=0] and the time during which external work is done in presence of a transduction between E_k and E_p [$0<r(t)<1$; see Materials and methods], is given in Fig. 6. It can be seen that at low and intermediate running speeds the time during which external positive work is done (increment of the E_{cm} curve in Fig. 1) is greater than the time during which external negative work is done (decrement of the E_{cm} curve in Fig. 1). With increasing speed the difference between the two times decreases together with their duration, and tends to become not significantly different above 14 km h^{-1} when both time values fall below 0.1 s (Fig. 6 and Table 1).

Discussion
The four phases of the bounce and the transduction of mechanical energy during the running step

The findings illustrated in Fig. 2 support the idea that the vertical oscillation of the spring mass system is centered about the equilibrium point where the vertical force equals body weight, and that 'landing' (loading of the system beyond the equilibrium point) and 'take-off' (unloading of the system from the equilibrium point) are better represented by the instants where the vertical force increases above, or falls below, body weight, respectively rather than by the instants the foot contacts and leaves the ground.

The apparent bounce of the body is therefore better described by considering the succession of its four phases above and below the equilibrium points during the downward displacement and during the lift: (i) downward acceleration, (ii) downward deceleration, (iii) upward acceleration and (iv) upward deceleration (Fig. 7).

The downward acceleration occurs during the $S_{ae,down}$ fraction of the step, between the maximum of E_p and the maximum of E_{kv} (downward displacement with a vertical force exerted on the ground less than body weight; blue section of the E_p curve in Fig. 7 with lighter blue indicating the aerial phase). The E_p into $E_k=E_{kv}+E_{kf}$ transduction takes place entirely during this phase and is indicated by the increment of the $R_{int}(t)$ curve after the maximum of E_p. Note that a large E_p into E_k transduction also occurs in the absence of an aerial phase (upper left panel in Figs 1 and 7). The kinetic energy of the centre of mass E_k attains its maximum value in the running step in close proximity to the end of this phase, due to the increment of $E_{k,v}$ caused by gravity (Fig. 1).

The downward deceleration occurs during the $S_{ce,down}$ fraction of the step, between the maximum of E_{kv} and the minimum of E_p (downward displacement with a vertical force exerted on the ground greater than body weight, red section of the E_p curve in Fig. 7). In this phase, translational kinetic energy E_k and gravitational potential energy E_p are simultaneously absorbed by the muscle–tendon units. The E_p–E_k transduction is nil during this phase, as indicated by the upper horizontal tract of the $R_{int}(t)$ curve, which corresponds to the β fraction of the step. Note that the maximum of kinetic energy E_k in the running step, attained during the negative work phase, is consistent with a high velocity of stretching of the muscle–tendon units and, according to the force–velocity relation, with a high force exerted by the forcibly stretched muscle.

The upward acceleration occurs during the $S_{ce,up}$ fraction of the step, comprised between the minimum of E_p and the maximum of E_{kv} (lift with a vertical force exerted on the ground greater than body weight). In this phase of the step muscle–tendon units deliver both E_k and E_p. The E_p–E_k transduction is nil during most of this phase, as shown by the lower horizontal tract of the $R_{int}(t)$ curve, corresponding to the initial part of the α fraction of the step, when E_k and E_p simultaneously increase (except for a small time interval during which E_p begins to increase while E_{kf} is still decreasing).

The upward deceleration occurs during the $S_{ae,up}$ fraction of the step, between the maximum of E_{kv} and the maximum of E_p (lift with a vertical force exerted on the ground less than body weight). During this phase E_{kv} decreases, but E_{kf} continues to increase: the leg is still exerting a propulsive force to accelerate the body forwards even though the vertical force has dropped below body weight. The increment in E_{kf} exceeds the decrement of E_{kv} with the result that E_k increases, but to a peak lower than during the downward displacement due to the opposite changes of E_{kf} and E_{kv}. As a consequence of the push of the foot that is about to leave the ground, E_k increases simultaneously with E_p, i.e. the α fraction of the step [lower horizontal tract of the $R_{int}(t)$ curve] extends into this phase whereas the transduction of E_k into E_p is limited to the last part of it [increment of the $R_{int}(t)$ curve taking place before the maximum of E_p is attained]. It follows that the transduction of E_k into E_p during the lift is smaller than the transduction of E_p into E_k during the downward displacement: the increment of the $R_{int}(t)$ curve during the downward displacement is larger than during the lift, i.e. $R_{int,down}/R_{int}>0.5$ (Fig. 5). In the presence of an aerial phase the ballistic fall is larger than the ballistic lift (dotted E_p line in Fig. 7). The protracted execution of positive external work during the lift results in a blunt attainment of a plateau by E_{cm} (black line in Fig. 1), which

contrasts with its sharper decrease at the end of the plateau. These findings are the mechanical counterpart of the observation that in running the lower limb is more extended at take-off than at landing [see e.g. the photographs of Muybridge (Muybridge, 1955)].

Muscle–tendon unit response during stretching and shortening

The finding that at low and intermediate running speeds the time required for external positive work production is greater than the time required for external negative work production (Fig. 6) suggests that the muscle–tendon units act differently during shortening (positive work) and during stretching (negative work). Above 14 km h^{-1}, however, the difference between the two time values tends to be not significantly different (Table 1) suggesting that the muscle–tendon units act as a spring with similar characteristics during compression and recoil, as assumed in the spring-mass model of running. A possible explanation of this finding is given below.

During running at a constant step-average speed, the momentum (force × time) lost at each step in the forward direction during the brake equals the momentum gained during the push. The force responsible for the change in momentum is mainly the muscular force (neglecting the negative work done by frictional forces outside muscle–tendon units). It follows that the shorter duration of the momentum lost during the brake implies an average force exerted by the muscle–tendon units during stretching (the brake) greater than during shortening (the push). This is in qualitative agreement with what is expected from the force–velocity relation of muscle for an equal number of active fibres.

According to the force–velocity relation of muscle, however, the difference in force between stretching and shortening, and as a consequence the difference in time for the same change in momentum, should increase with the velocity of the length change. This contrasts with the present findings, which indicate that the difference between push and brake times decreases with running speed, i.e. with the velocity of the length change.

The force–velocity relation of muscle applies to ramp stretches and releases, when the sliding velocity of the actin filament relative to the myosin filament influences cross-bridge attachment and detachment (Huxley, 1957). Is it reasonable to infer, from the results described in Fig. 6, that the amount of lengthening and shortening of muscle fibres (sliding of filaments) decreases progressively with running speed, and with it the impact of the force–velocity relation on the timing of positive and negative external work production?

Lengthening imposed to muscle–tendon units is shared between muscle fibres and the tendon in series with them. It has been suggested that the energy expenditure during running is due to the cost of generating force in quasi isometric contracting fibres, not due to the work done by them (Kram and Taylor, 1990; Alexander and Ker, 1990). Experiments on turkeys (Roberts et al., 1997) and kangaroos (Biewener et al., 1998) have shown that the length change of the muscle–tendon units bending and extending the ankle, while the foot is on the ground in a running step on the level, is mostly due to tendon

stretching and recoil, with a small change in the length of muscle fibres. On the other hand a contribution of the contractile machinery to the mechanical work done is suggested at low running speeds in humans by a greater energy expenditure when the mechanical work is made greater by decreasing the step frequency below the freely chosen step frequency (Cavagna et al., 1997). The present results suggest that both views, i.e. tendon *vs* muscle contribution to mechanical work, may possibly apply to human running, depending on the speed of the run.

The lengthening of the fibres relative to lengthening of the tendons depends on the stiffness of muscle relative to that of tendon; the stiffness of the muscle in turn depends on its activation. In the relaxed muscle, most of the lengthening imposed on the muscle–tendon units is taken by the muscle fibres. In fact only few cross-bridges resist filament sliding in a relaxed muscle fibre (Hill, 1968), with the consequence that during a stretch filaments will oppose a force much smaller than when the muscle is activated and will transmit this smaller force to the tendon in series with them. As a consequence the tendons will not lengthen appreciably during stretching a relaxed muscle. At low running speeds muscle activation is likely to be moderate with the result that some of the length change of the muscle–tendon units is sustained by muscle fibres. In this case the force exerted during stretching is expected to be greater than during shortening according to the force–velocity relation of muscle, and as a consequence the time of positive work is expected to be greater than the time of negative work, as explained above. When muscle activation is progressively increased with speed, muscle fibres oppose a progressively greater force to stretching and a progressively greater fraction of the lengthening imposed to the muscle–tendon units must be absorbed by tendons. At speeds greater than ~14 km h^{-1} muscle activation may be increased to such an extent that muscle fibres are held almost isometric, so that the length change is taken almost completely by tendons. In this case the muscle–tendon units would operate as a simple spring with similar characteristics during stretching and recoil, as assumed in the spring-mass model. Obviously a work input by the contractile machinery must always be added to account for the losses due to tendon hysteresis which, however, is small (Ker et al., 1987; McMahon, 1987; Alexander, 2002). In other words, the decrease with speed of the difference between positive and negative external work durations (Fig. 6) suggest a decrease in muscle length change relative to tendon length change within the muscle–tendon units.

This interpretation is consistent with (i) the increase in peak muscle stress with speed towards the peak stress developed in the isometric contraction found in the limb muscles of the horse (Biewener, 1998) and (ii) the *in vivo* measurements of muscle fibre length in running turkeys [Roberts et al. (Roberts et al., 1997), their fig. 3], showing that the contribution of muscle work to the total work production by the muscle–tendon units is greater at low speeds than at high speeds.

In conclusion, the landing–take-off asymmetry consists of the vertical support of the body being greater during the lift

than during the downward displacement of the centre of mass. Gravity is exploited during the downward displacement to increase the downward velocity of the centre of mass, thus attaining the maximum of kinetic energy in the running step. This provides a high velocity of stretching to the muscle–tendon units during the negative work phase, followed by a more prolonged push during the lift. A fast stretch, during which the maximal force is quickly attained, followed by a slower shortening, was the strategy used in isolated muscle experiments to get the maximal efficiency of positive work production in ramp stretch–shorten cycles (Heglund and Cavagna, 1987). This is similar to what naturally happens during running at low and intermediate running speeds. With increasing speed, the work done by the contractile component decreases progressively for two reasons: (i) the relatively larger length change taken up by tendons during the stretch (as described above), and (ii) the decrease in force with the velocity of shortening (as described by the force–velocity relation). It follows that the mechanical energy released during shortening at high speeds [the 'irreducible work' (Hill, 1970)] is in practice only that previously stored by the elastic elements, due to their negligible damping. The role of the contractile machinery at high speeds is to provide a force large enough to exploit a large fraction of the force–length relation of the elastic elements for the storage of mechanical energy.

List of symbols

a_v	vertical acceleration of the centre of mass
E_{cm}	mechanical energy of the centre of mass
E_k	kinetic energy of the centre of mass in the sagittal plane
$E_{k,mx,down}$	maximum kinetic energy of the centre of mass in the sagittal plane during the downward displacement
$E_{k,mx,up}$	maximum kinetic energy of the centre of mass in the sagittal plane during the lift
E_{kf}	kinetic energy of forward motion
E_{kv}	kinetic energy of vertical motion
E_p	gravitational potential energy
F_f	force exerted on the force platform in forward direction
F_v	force exerted on the force platform in vertical direction
g	acceleration of gravity
M_b	body mass
R_{int}	cumulative energy recovery attained at the end of the step due to the E_k–E_p transition
$R_{int,down}$	fraction of R_{int} taking place during the downward displacement of the centre of mass
$R_{int,up}$	fraction of R_{int} taking place during the lift of the centre of mass
$S_{ae,up}$	vertical displacement of the centre of mass taking place during its upward deceleration
$S_{ae,down}$	vertical displacement of the centre of mass taking place during its downward acceleration
$S_{c,down}$	downward displacement of the centre of mass during contact
$S_{c,up}$	upward displacement of the centre of mass during contact
$S_{ce,down}$	downward displacement of the centre of mass from the equilibrium position where $F_v=M_b g$ to the lowest point of its trajectory
$S_{ce,up}$	upward displacement of the centre of mass from the lowest point of its trajectory to the equilibrium position where $F_v=M_b g$
$S_{v,down}$	downward vertical displacement of the centre of mass
$S_{v,up}$	upward vertical displacement of the centre of mass
t	time
t_{brake}	duration of negative external work production
t_{push}	duration of positive external work production
V_f	forward velocity of the centre of mass
$\bar{V}_f$	average running speed
V_v	vertical velocity of the centre of mass
$V_{v,mx,down}$	maximal vertical velocity of the centre of mass during the downward displacement
$V_{v,mx,up}$	maximal vertical velocity of the centre of mass during the lift
W_v, W_{kf} and W_{ext}	work done during the selected steps between E_p valleys (or peaks) calculated from the increments of the $E_p(t)$, $E_{kf}(t)$ and $E_{cm}(t)$ records
α,β	step phases during which E_p and E_k increase (α) or decrease (β) simultaneously
τ	period of repeating change in the motion of the centre of mass

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