

The landing–take-off asymmetry of human running is enhanced in old age

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SUMMARY

The landing–take-off asymmetry of running was thought to derive from, or at least to be consistent with, the physiological property of muscle to resist stretching (after landing) with a force greater than it can develop during shortening (before take-off). In old age, muscular force is reduced, but the deficit in force is less during stretching than during shortening. The greater loss in concentric *versus* eccentric strength with aging led us to hypothesize that older *versus* younger adults would increase the landing–take-off asymmetry in running. To test this hypothesis, we measured the within-step changes in mechanical energy of the centre of mass of the body in old and young subjects. The difference between the peaks in kinetic energy attained during the fall and during the lift of the centre of mass is greater in the old subjects. The difference between the time to lift and accelerate the centre of mass (positive work) and to absorb the same amount of energy during the downward displacement (negative work) is also greater in the old subjects. Both these findings imply a difference in force between stretching and shortening during the bounce, which is greater in the old subjects than in the young subjects. This is qualitatively consistent with the more asymmetric force–velocity relation found in aged muscle and supports, even if does not prove, the hypothesis that the landing–take-off asymmetry in running derives from the different response of muscle to stretching and shortening.

Key words: age, locomotion, running, muscle, force–velocity relation.

INTRODUCTION

Experiments on isolated muscle specimens (Phillips et al., 1991; Ochala et al., 2006) and *in vivo* on humans (Vandervoort et al., 1990; Porter et al., 1997; Pousson et al., 2001; Klass et al., 2005) showed that in old age muscular force is reduced less during stretching (negative work) than during shortening (positive work). The effect of this change of muscle contractile properties with age on the mechanics of locomotion is unknown.

At each running step, the muscle-tendon units are stretched after landing and shorten before take-off. The peak in kinetic energy attained before landing, to be absorbed by the muscle-tendon units during the negative work phase, is higher than the peak in kinetic energy restored before take-off during the positive work phase. On the other hand, the duration of the positive work phase is greater than the duration of the negative work phase. This landing–take-off asymmetry is consistent with an average force exerted during stretching (after landing) greater than that developed during shortening (before take-off). It has been argued that the landing–take-off asymmetry is a consequence of the force–velocity relation of muscle, and the greater the length change of muscle relative to that of tendon within the muscle-tendon units the larger the landing–take-off asymmetry (Cavagna, 2006).

We hypothesized that the increased discrepancy in old age between the greater force resisting stretching and the lower force developed during shortening, if operational during running, would increase the landing–take-off asymmetry of the apparent bounce of the body relative to that of young subjects. To test this hypothesis, we measured the mechanical energy changes of the centre of mass during the negative and positive work phases of the bounce of the body in old and young subjects running on the level at different speeds.

MATERIALS AND METHODS

Subjects and experimental procedure

The experiments were conducted on eight healthy old subjects (men, age 73.6±5.5 years, height 1.72±0.06 m, weight 71.1±9.2 kg) and eight healthy young subjects (6 men and 2 women, age 20.8±1.6 years, height 1.76±0.08 m, weight 63.4±10.0 kg) (means ± s.d.). Three subjects from each group were trained (running several kilometres at least once a week) while five were sedentary. The results reported in this study are an average of the data obtained with all subjects of each group regardless of their training. In agreement with the finding that the age-related effects on muscle-tendon units are similar in runners and non-active subjects (Karamanidis and Arampatzis, 2005), similar results were obtained here by comparing the three old trained subjects with the three male young untrained subjects (data not shown). Informed written consent was obtained from each subject. The experiments were carried out in accordance with the Declaration of Helsinki.

Subjects ran back and forth along a 50 m corridor that had built into it, at the level of the floor, a 4 m×0.5 m force platform sensitive to the force exerted by feet in the forward and vertical directions. A total of 124 runs by the elderly subjects at a speed of 3 to 13–17 km h⁻¹, and 229 runs by the young subjects at a speed of 3 to 17–21 km h⁻¹, were analyzed.

Platform records analysis

The mechanical energy of the centre of mass of the body (Fig. 1) was determined from the ground reaction forces as previously described (Cavagna, 1975). 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 only instruction given to each subject was

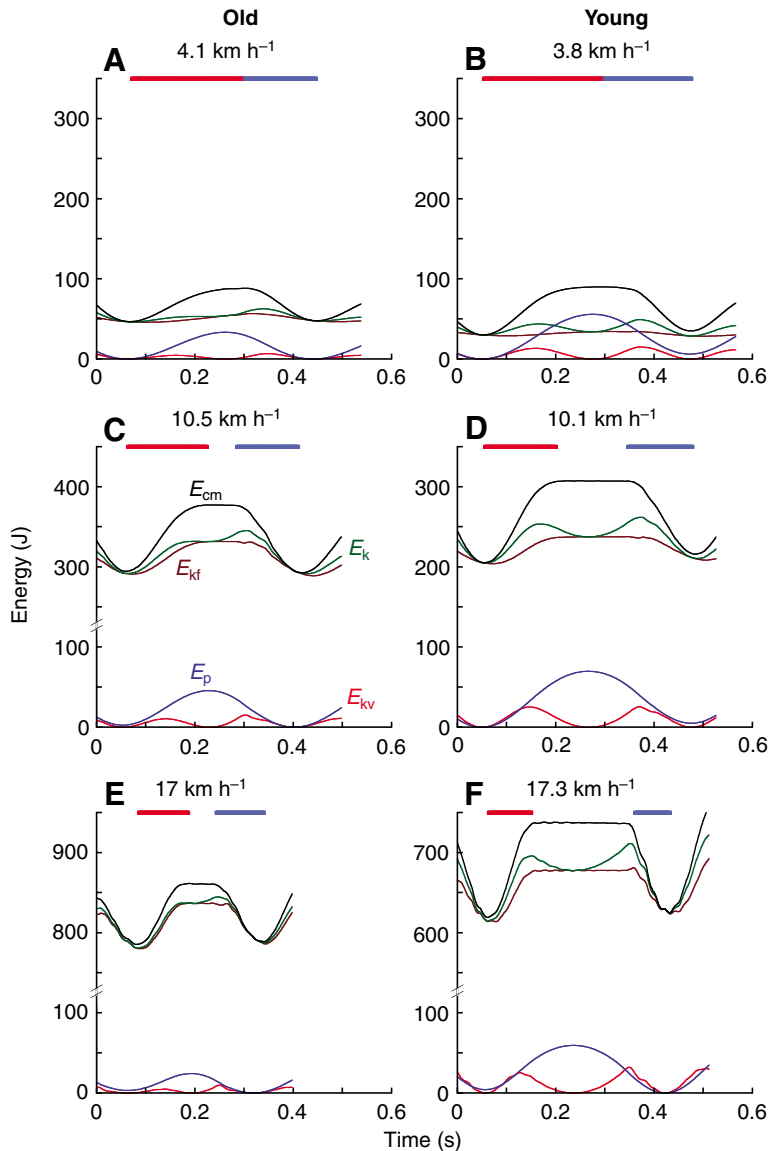


Fig. 1. Mechanical energy of the centre of mass of the body during running steps at the indicated speeds, in an old subject (A,C,E: 80 years, 73.5 kg mass, 1.71 m height, trained runner), and a young subject (B,D,F: 21 years, 58.5 kg mass, 1.79 m height, trained runner). In each panel the curves show 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 of the body in the sagittal plane ($E_{cm}=E_p+E_k$, black). The zero line corresponds to the minimum attained by the E_p curve. The horizontal bars indicate the time of contact during the step (from minimum to minimum of E_p). The time 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. The gap between red and blue bars indicates the duration of the aerial time. The records were obtained from the signals of a force platform. Note the lower vertical oscillation of the centre of mass in the old subject, indicated by a lower amplitude of the E_p and E_{kv} curves with a shorter aerial time, lower step duration and an higher step frequency.

The average vertical force measured by the force platform, $\bar{F}_{v,plate}$, in a time interval, $n_f\tau$, corresponding to an integer number, n_f , of steps periods, τ (selected between peaks or valleys of the force records), must equal the body weight measured with a balance, $\bar{F}_{v,scale}$.

$\bar{F}_{v,plate}$ was measured after each run as the area below the F_v record in the time interval $n_f\tau$ divided by $n_f\tau$. We analyzed records where $\bar{F}_{v,plate}/\bar{F}_{v,scale}=1.005\pm 0.02$ ($N=124$) for the group of old subjects and 1.002 ± 0.01 ($N=229$) for the group of young subjects.

$\bar{F}_{v,plate}$ was then subtracted from the F_v array and the result $(F_v - \bar{F}_{v,plate})/M_b$ (where M_b is the mass of the body) was integrated to obtain the record of vertical velocity changes for the time interval between photocells crossing.

One or more regular steps were subsequently chosen for analysis between two peaks or valleys of the record of V_v changes corresponding to a time interval $n_v\tau$ where n_v is an integer number of steps. The regularity of the steps was determined by the difference between positive

and negative increments in the V_v and V_f changes divided by the sum of the increments. In the old group this ratio was $3.83\pm 3.73\%$ (vertical) and $10.95\pm 9.2\%$ (forward) ($N=124$), whereas in the young group it was $3.55\pm 3.29\%$ (vertical) and $12.98\pm 11.63\%$ (forward) ($N=229$). During running on the level, the upward and downward vertical displacements of the centre of mass of the body are on average equal over n_v steps, i.e. the average V_v must be nil. On this basis, the area below the V_v changes (ΔV_v) record, corresponding to the $n_v\tau$ interval selected above, was divided by $n_v\tau$ and the result subtracted from the whole ΔV_v record between photocells crossing to obtain the instantaneous positive (upward) and negative (downward) values of V_v .

The ΔV_f record was determined by integration of the F_f/M_b array during the time interval between photocells crossing, Δt_{photo} . The area below this ΔV_f record was then divided by Δt_{photo} and the result subtracted from the same record to locate the average running speed on the tracing. The average running speed, measured as photocells distance/ Δt_{photo} , was then summed to the resulting array to obtain the instantaneous values of V_f .

The instantaneous vertical velocity $V_v(t)$ was used to calculate the instantaneous kinetic energy of vertical motion

to run normally, trying to reach and maintain a constant step-average speed over the section of the corridor where the platform was placed. The average running speed was measured by two photocells placed 1–3 m apart (depending on speed) along the side of the platform. The characteristics of the force platform were as previously described (Cavagna, 1975). The experimental procedure consisted of measuring the force exerted on the ground in the sagittal plane during running at different speeds. A microcomputer acquired data at a rate of 500 Hz per channel from (i) the platform signal proportional to the force exerted in the forward direction, (ii) the platform signal proportional to the force exerted in the vertical direction, and (iii) the signal from the photocells. Data acquisition and analysis were made *via* a dedicated DAQ board and custom LabView software (version 7.1, National Instruments, Austin, TX, USA). The platform signal from the unloaded force platform was measured immediately before each run and subtracted from the platform records of the vertical force, F_v , and fore–aft force, F_f , in order to account for a possible drift of the base line. Only the subset of the F_v and F_f records obtained between photocells crossing was used for subsequent analysis. The vertical and forward velocities (V_v and V_f , respectively) of the center of mass were obtained as follows.

$E_{kv}(t)=0.5M_bV_v(t)^2$ and, by integration, the vertical displacement of the centre of mass, $S_v(t)$, with the corresponding gravitational potential energy $E_p(t)=M_bgS_v(t)$ (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 ΔV_v , 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).

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 n_v steps should be equal to one. Experimental values were as follows: in the old subjects group ($N=124$): $W_v^+/W_v^-=0.99\pm 0.08$, $W_{kf}^+/W_{kf}^-=1.01\pm 0.13$, $W_{ext}^+/W_{ext}^-=0.99\pm 0.07$; in the young subjects group ($N=229$): $W_v^+/W_v^-=0.99\pm 0.07$, $W_{kf}^+/W_{kf}^-=1.03\pm 0.14$, $W_{ext}^+/W_{ext}^-=1.00\pm 0.07$. These means refer to steps where $0.6 < W^+/W^- < 1.5$.

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 $dE_{cm}(t)/dt\approx 0$ (Cavagna, 2006). 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, the aerial time was in some cases overestimated (7%), and t_{brake} and/or t_{push} were in some cases underestimated (5–7%) (Cavagna, 2006). Similarly, the downward and upward displacements of the centre of mass during contact, $S_{c,down}$ and $S_{c,up}$ (Fig. 2), were measured from the descending and ascending portions, respectively, of the $E_p(t)$ curve during the time interval where $dE_{cm}(t)/dt$ was lower or greater, respectively, 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:

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

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 V_v and E_{kv} ($=0.5M_bV_v^2$) are at a maximum, the derivative is nil, $a_v=0$, and as a consequence $F_v=\text{body weight}$. 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

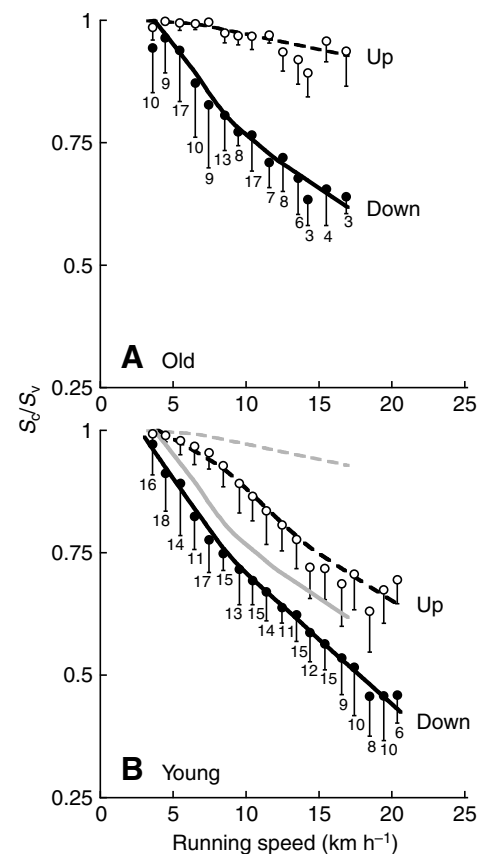


Fig. 2. Vertical displacement during contact. (A) Old subjects, (B) young subjects, with data from A (gray) superposed for comparison. The upward and downward vertical displacements of the centre of mass taking place when the foot is in contact with the ground (S_c) are divided by the total upward and downward vertical displacements (S_v) to obtain the fraction of the vertical displacement during contact (S_c/S_v). The fractions so obtained, are plotted separately during the lift ($S_{c,up}/S_{v,up}$; open circles) and during the descent ($S_{c,down}/S_{v,down}$; filled circles). The vertical bars indicate the standard deviation (s.d.) of the mean; numbers near the symbols indicate the number of items in the mean. Lines represent the weighted mean of all the data (Kaleidagraph 4.03). Their only purpose is to be a guide for the eye: they do not describe the underlying physical mechanism. Note that at very low speeds $S_c/S_v\approx 1$ because the aerial phase is often nil (e.g. Fig. 1A,B). With increasing speed an aerial phase of progressively greater extent takes place during the step and the fraction of vertical displacement during contact decreases. The decrement is less during the lift than during the descent (i.e. during the aerial phase the lift is smaller than the fall). This is particularly true in the old subjects who maintain contact with the ground for almost the whole of the lift (see also light-blue dotted lines in Fig. 3). It must be pointed out here that heel-strike and toe-off, i.e. start and end of foot contact, do not properly describe landing and take-off of the bouncing system. As described in the text, landing and take-off, in a physical sense, coincide with the instants where vertical force becomes greater than body weight (after heel-strike) and falls below body weight (before toe-off). The correct landing-take-off asymmetry of the bouncing system is described in Fig. 3.

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, $S_{ce,up}$ (Fig. 3). 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 (Fig. 3).

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 was 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):

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

The E_p-E_k transduction is complete [$r(t)=1$] 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 [$0 < r(t) < 1$]. The E_p-E_k transduction is nil [$r(t)=0$] in two phases of the step, α and β , where E_k increases or 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 [$0 < r(t) < 1$].

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

Statistics

The data collected as a function of running speed were grouped into classes of 1 km h^{-1} intervals as follows: 3 to $<4 \text{ km h}^{-1}$, 4 to $<5 \text{ km h}^{-1}$..., 20 to $<21 \text{ km h}^{-1}$. The data points in Figs 2 and 4 represent the mean \pm s.d. in each of the above speed intervals and the figures near the symbols in Fig. 2 give the number of items in the mean. A paired samples t -test was used to determine when the means, within a subject group with the same number of items at a given speed interval, are significantly different (Table 1). When comparing the means of different variables between the two subject groups having different numbers of items, an independent-samples t -test was used (Table 2). The t -tests were performed using SPSS for Windows version 11.0.1 (SPSS, Chicago, IL, USA).

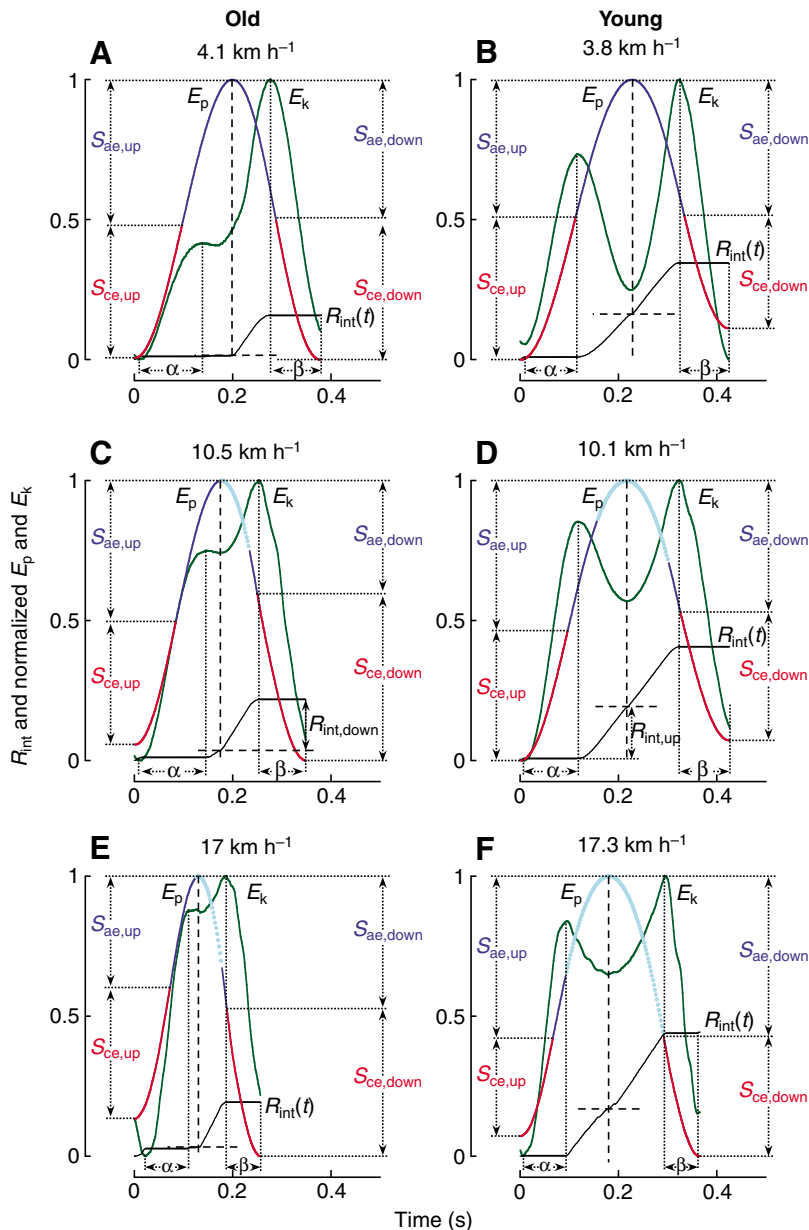


Fig. 3. The four phases of the bounce of the body. Same subjects and speeds as in Fig. 1. In (A–F) the trend of the E_p-E_k transduction, $R_{int}(t)$ (black), is illustrated with the simultaneous changes in gravitational potential energy, E_p , and kinetic energy, $E_k = E_{kv} + E_{kf}$ (green), normalized to oscillate between zero and one. The 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). The continuous E_p line indicates the contact phase whereas the dotted E_p line (light-blue) indicates the aerial phase (not present in A and B). 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 the E_p-E_k transduction occurs, as indicated by the increment of the $R_{int}(t)$ curve. Note that, particularly in the old subject, the transduction of E_k into E_p during the lift (increment $R_{int,up}$ of $R_{int}(t)$, below crossing of the interrupted lines) is smaller than the transduction of E_p into E_k during the downward displacement (increment $R_{int,down}$ of $R_{int}(t)$, above crossing of the interrupted lines). This asymmetry is accompanied by a ballistic lift (almost nil in the old subject) smaller than the ballistic fall. In the horizontal tracts of the $R_{int}(t)$ curve no transduction occurs between E_p and E_k and muscle-tendon units absorb E_p and E_k simultaneously (phase β), and increase E_p and E_k simultaneously (phase α). Whereas most of β is confined within $S_{ce,down}$, α usually extends beyond $S_{ce,up}$ within a large fraction of $S_{ae,up}$ due to a continuing increase of E_k . Also this asymmetry is larger in the old subject. In summary, the following features of the landing–take-off asymmetry of the bounce of the body are shown: (i) a peak of E_k greater during the fall than during the lift, (ii) a transduction of E_p into E_k during the fall greater than the transduction of E_k into E_p during the lift (i.e. $R_{int,down} > R_{int,up}$), and (iii) a simultaneous decrement of E_k and E_p after landing shorter than the simultaneous increment of E_k and E_p before and after take-off (i.e. $\beta < \alpha$). All these deviations from an elastic bounce are larger in the old subject.

RESULTS

The apparent landing-take-off asymmetry

Fig. 2 shows the fractions of the vertical displacement of the centre of mass taking place when the foot is in contact with the ground, plotted separately during the lift ($S_{c,up}/S_{v,up}$, open circles) and during the descent ($S_{c,down}/S_{v,down}$, filled circles).

When the aerial phase is nil, at the lowest running speeds (e.g. Fig. 1A,B), the whole vertical displacement takes place with the foot in contact with the ground and $S_c/S_v=1$. With increasing speed, an aerial phase of progressively greater extent takes place during the step. It follows that the fraction of the vertical displacement in contact with the ground decreases. The decrement is less during the lift than during the fall, i.e. $S_{c,up}/S_{v,up}$ is greater than $S_{c,down}/S_{v,down}$ (Fig. 2). In other words, the height of the centre of mass at the instant of take-off is greater than its height at the instant of touchdown: i.e. the ballistic lift is smaller than the ballistic fall (light-blue segments of E_p in Fig. 3) (Cavagna, 2006).

This landing-take-off asymmetry is present in both subject groups, but is larger in the old subjects than in the young subjects, mainly due to a smaller reduction with speed of $S_{c,up}/S_{v,up}$: a larger fraction of the lift of the centre of mass takes place in contact with the ground in the old subjects.

The effective landing-take-off asymmetry

The landing-take-off asymmetry described above bears no relation to loading and unloading of the spring-mass system during the bounce of the centre of mass at each running step (Cavagna, 2006). Indeed, as mentioned above, landing and take-off may not occur at all during low-speed running. It is obvious that, in this extreme case, the time of contact gives no information on the loading of the elastic system. Even in the presence of an aerial phase, the time of contact exceeds the time during which the spring-mass system is loaded beyond its equilibrium position, where the vertical force equals body weight (Blickhan, 1989).

It is therefore more appropriate to consider 'effective landing' as the instant where the vertical force increases above body weight (rather than the instant where the foot contacts the ground) and 'effective take-off' as the instant where the vertical force drops below body weight (rather than the instant where the foot leaves

the ground). Loading of the elastic system with a force greater than body weight (downward deceleration and upward acceleration) takes place during the lower part (S_{ce}) of the vertical oscillation of the centre of mass, and unloading (upward deceleration and downward acceleration) during its upper part (S_{ae}) (Cavagna et al., 1988).

The changes in gravitational potential energy, E_p , translational kinetic energy, $E_k=E_{kf}+E_{kv}$, and their transduction $R_{int}(t)$ are therefore depicted in Fig. 3 during loading (red) and unloading (blue) of the system relative to its equilibrium position, regardless of the contact time and the aerial phase. These records have been analyzed in detail (Cavagna, 2006) and are only briefly described here to assess the different landing-take-off asymmetry in old and young subjects.

During the downward acceleration ($S_{ae,down}$, Fig. 3, blue), the support of the body on the ground is low with the consequence that a large transduction of E_p into E_k occurs both in the presence and the absence of an aerial phase. The amount of this transduction is given by the increment $R_{int,down}$ of the $R_{int}(t)$ curve. As a consequence of this transduction, the kinetic energy E_k attains its highest peak in the running step, just prior to the effective landing (start of downward deceleration).

During the downward deceleration ($S_{ce,down}$, Fig. 3, red), negative external work is done to decrease E_p and E_k simultaneously, as indicated by the horizontal tract of the $R_{int}(t)$ curve showing that no transduction occurs between E_p and E_k : this is the β fraction of the step.

During the upward acceleration ($S_{ce,up}$, Fig. 3, red), positive external work is done to increase E_p and E_k simultaneously, as indicated by the lower horizontal tract of the $R_{int}(t)$ curve showing that no transduction occurs between E_p and E_k : this is the α fraction of the step. At the end of the α fraction the kinetic energy E_k attains its maximum during the lift, which is lower than that attained during the fall. The difference between the two E_k peaks is on average greater in the old subject. Note that whereas β is almost totally contained within $S_{ce,down}$, α continues after the end of $S_{ce,up}$, within the upward deceleration of the centre of mass ($S_{ae,up}$, Fig. 3, blue). In other words, the muscular push is still lifting and accelerating the body forwards even though the vertical force has dropped below body weight. The intrusion of α into $S_{ae,up}$ is larger in the old subject.

During the upward deceleration ($S_{ae,up}$, Fig. 3, blue), the transduction of E_k into E_p given by the increment $R_{int,up}$ of the $R_{int}(t)$ curve is confined to the last part of the lift because, as described above, E_p and E_k increase simultaneously for an appreciable part of $S_{ae,up}$. Indeed, the transduction of E_k into E_p is almost nil in the oldest subject of Fig. 3. In particular, the ratio $R_{int,down}/R_{int,up}$ is much larger in the old subject.

The different features of the rebound of the body described above translate into different durations of positive and negative work (red/blue bars in Fig. 1). These are plotted in Fig. 4 as a function of speed. It can be seen that, in both old and young subjects, the duration of positive work t_{push} is greater than the duration of negative work t_{brake} up to $\sim 13 \text{ km h}^{-1}$. At higher speeds, both durations fall below 0.1 s and become similar. In the common speed range, the ratio t_{push}/t_{brake} is greater in the old subjects than in the young subjects (Table 2).

The records in Figs 1, 3 and 4 show that the landing-take-off asymmetry is greater in the old than in the young subjects. The results supporting this conclusion are summarized in Table 2 where a comparison is made between old subjects, young subjects and the symmetric rebound of an elastic system.

Table 1. Speeds at which the pairs of variables listed are significantly different within each age group

Speed (km h ⁻¹)	Old	Young
	t_{push} vs t_{brake}	t_{push} vs t_{brake}
3	3.29×10^{-5}	6.78×10^{-5}
4	1.37×10^{-4}	1.99×10^{-7}
5	3.58×10^{-7}	8.95×10^{-6}
6	1.01×10^{-6}	1.76×10^{-5}
7	5.55×10^{-5}	5.96×10^{-11}
8	2.78×10^{-7}	8.04×10^{-8}
9	2.87×10^{-4}	1.12×10^{-4}
10	8.68×10^{-7}	3.17×10^{-7}
11	5.80×10^{-4}	7.31×10^{-5}
12	1.72×10^{-3}	2.67×10^{-4}
13	0.06	0.01
14	0.24	0.61
15	0.10	0.45
16	0.04	0.46

Significance levels (P) from paired-samples t -tests are given below each pair of variables.

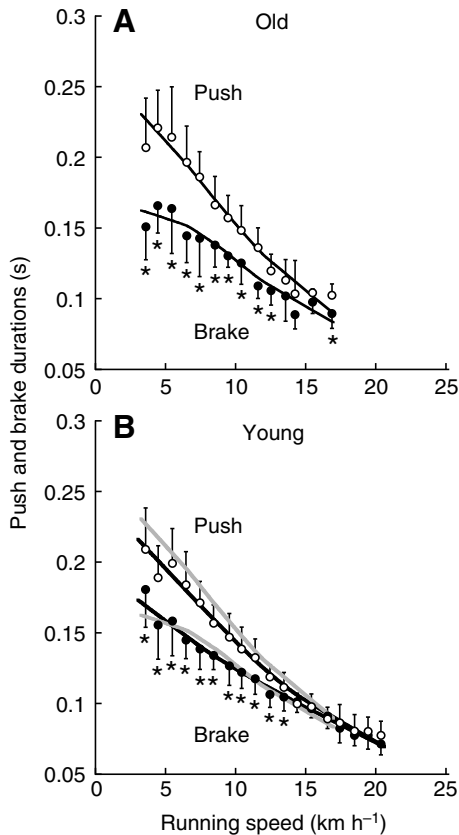


Fig. 4. Positive and negative external work durations. (A) Old subjects, (B) young subjects, with the data from A (gray) superposed for comparison. The time during which positive external work is done at each step during the push (open circles and red horizontal bars in Fig. 1), and negative external work is done during the brake (filled circles and blue horizontal 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 greater than the duration of negative external work up to a speed of ~ 13 km h $^{-1}$ (Table 1) indicating an average force during the brake greater than during the push, which is qualitatively consistent with the force–velocity relation of muscle. This suggests that work done by muscle within the muscle-tendon units at low speeds is progressively substituted, with increasing speed, with elastic energy storage and recovery by tendons (see text). On average, the ratio $t_{\text{push}}/t_{\text{brake}}$ is greater in the old subjects indicating a less elastic behavior (Table 2). Asterisks denote statistically significant difference ($P < 0.05$). Other indications as in Fig. 2.

DISCUSSION

The physiological meaning of $R_{\text{int,down}}/R_{\text{int,up}}$ being greater in the elderly

$R_{\text{int}}(t)$ is the cumulative value of energy recovery resulting from the instantaneous transduction $r(t)$ between gravitational potential energy E_p and translational kinetic energy $E_k = E_{k_f} + E_{k_v}$ during the step cycle (Cavagna, 2006). In running, the kinetic energy of forward motion E_{k_f} increases and decreases essentially in phase with the potential energy E_p (Cavagna et al., 1964), with the consequence that the $E_{k_f} - E_p$ transduction is negligible. It follows that in running the $E_k - E_p$ transduction takes place essentially between gravitational potential energy E_p and kinetic energy of vertical motion E_{k_v} . This transduction is obviously complete during the aerial phase when the support of the body on the ground is nil [$r(t) = 1$], but it also occurs during contact when the body is only partially supported by the foot on the ground in the upper part of the trajectory of the

Table 2. Comparison of the landing–take-off asymmetry between old subjects, young subjects and a symmetric elastic bounce

	Old	Young	Elastic
$R_{\text{int,down}}/R_{\text{int,up}}$	2.13 ± 1.30	1.26 ± 0.32	1
$E_{k,\text{mx,down}} - E_{k,\text{mx,up}}$ (J)	$10.03 \pm 6.25^*$	7.52 ± 5.42	0
α/β	1.24 ± 0.18	1.06 ± 0.10	1
$t_{\text{push}}/t_{\text{brake}}$	1.25 ± 0.16	1.15 ± 0.13	1

Values are means \pm s.d. [$P < 0.001$, $N = 124$ ($*N = 122$) for old and $N = 195$ for young].

Speed range: 3–17 km h $^{-1}$. For an explanation of symbols, please see the List of symbols and abbreviations.

centre of mass [$0 < r(t) < 1$] [see the increment of the $R_{\text{int}}(t)$ curve in Fig. 3A,B where the aerial phase is nil].

During running, therefore, R_{int} gives a quantitative measure of the ‘lack of support’ of the body on the ground over the whole step cycle, including both the aerial phase and the ground contact phase. R_{int} would attain unity in a hypothetical ‘step’ made up completely of an aerial phase.

In the elderly, $R_{\text{int,old}} = 0.28 \pm 0.05$, which is about 70% of the value attained by the young subjects: $R_{\text{int,young}} = 0.38 \pm 0.06$ ($P = 3.66 \times 10^{-44}$). This gives a measure of the greater support on the ground during the step in the old subjects relative to the young subjects. A lower flight time in the elderly has already been reported during running at ~ 10 km h $^{-1}$ (Karamanidis and Arampatzis, 2005).

The $E_k - E_p$ transduction has a different meaning during the descent $R_{\text{int,down}}$ and during the lift $R_{\text{int,up}}$ of the centre of mass (Fig. 3).

$R_{\text{int,down}}$, i.e. the E_p into E_k transduction during the fall, can be viewed as a mechanism exploiting gravity to passively increase the vertical downward velocity and, as a consequence, the kinetic energy. $R_{\text{int,down}}$ precedes the negative work phase of the step. This has two physiological effects. (i) It provides mechanical energy to be stored within the muscle-tendon units during the subsequent brake, but (ii) it requires a force to decelerate the body downwards which, in the old subjects, may be insufficient and/or may decrease the safety of their muscular–skeletal system (Karamanidis and Arampatzis, 2005). A large value of $R_{\text{int,down}}$ relies on an adequate muscular force to be exerted during subsequent stretching. In the elderly, $R_{\text{int,down,old}} = 0.18 \pm 0.02$, which is about 85% of the value attained by the young subjects: $R_{\text{int,down,young}} = 0.21 \pm 0.03$ ($P = 3.97 \times 10^{-25}$).

$R_{\text{int,up}}$, i.e. the E_k into E_p transduction during the lift, follows the positive work phase of the step and is greater the greater the push-average power developed before take-off. In fact, the greater the push, the greater the increment in kinetic energy of vertical motion and therefore its subsequent decrement when the centre of mass is lifted during the phase of partial support and the aerial phase. The push-average power depends in turn on the capability to (i) recover elastically the mechanical energy stored during the preceding negative work phase, and (ii) add work done during shortening by the contractile component. A large $R_{\text{int,up}}$ therefore relies on an adequate muscular force to be exerted during shortening by the muscle-tendon units. In the elderly, $R_{\text{int,up,old}} = 0.10 \pm 0.04$, which is about 60% of the value attained by the young subjects: $R_{\text{int,up,young}} = 0.17 \pm 0.04$ ($P = 1.34 \times 10^{-45}$).

Since $R_{\text{int,down}}$ is 15% less in the elderly than in the young subjects whereas $R_{\text{int,up}}$ is 40% less, the ratio $R_{\text{int,down}}/R_{\text{int,up}}$ is appreciably greater in the old subjects than in the young subjects (Table 2). As mentioned above, a large $R_{\text{int,down}}$ requires a large force to be exerted during the following negative work phase (stretching), whereas a large $R_{\text{int,up}}$ requires a large force to be exerted during the preceding

positive work phase (shortening). The finding that $R_{\text{int,down}}$ is less affected by age than $R_{\text{int,up}}$ suggests that the deficit in force during stretching is less than the deficit in force during shortening, which is a characteristic of aged muscle (Vandervoort et al., 1990; Porter et al., 1997; Pousson et al., 2001; Klass et al., 2005). The relatively greater $R_{\text{int,down}}$ and lower $R_{\text{int,up}}$ in the elderly translate into a larger difference between peaks in kinetic energy attained during the fall $E_{k,\text{mx,down}}$ and during the lift $E_{k,\text{mx,up}}$ (Table 2).

The physiological meaning of $t_{\text{push}}/t_{\text{brake}}$ being greater in the elderly

Fig. 4 and Table 1 show that the positive work duration t_{push} is greater than the negative work duration t_{brake} up to $\sim 13 \text{ km h}^{-1}$. This is true in both subject groups, but the ratio $t_{\text{push}}/t_{\text{brake}}$ is on average greater in the old subjects than in the young subjects (Table 2).

During running on the level at a constant step-average speed, the momentum lost during negative work, $\bar{F}_{\text{brake}}t_{\text{brake}}$, equals the momentum gained during positive work, $\bar{F}_{\text{push}}t_{\text{push}}$. When $t_{\text{push}} > t_{\text{brake}}$ (Fig. 4) then $\bar{F}_{\text{push}} < \bar{F}_{\text{brake}}$, i.e. the average force during positive work is less than the average force during negative work, as expected from the force–velocity relation of muscle (Cavagna, 2006).

The present findings show that $t_{\text{push}}/t_{\text{brake}}$ is on average greater in the old subjects (Table 2), i.e. that $\bar{F}_{\text{push}}/\bar{F}_{\text{brake}}$ is less in the old subjects than in the young subjects. This indicates a lower force during shortening relative to stretching in old age, which is qualitatively consistent with the more asymmetric force–velocity relation of aged muscle (Vandervoort et al., 1990; Porter et al., 1997; Pousson et al., 2001; Klass et al., 2005).

At running speeds greater than about 14 km h^{-1} , negative and positive work durations fall below 0.1 s and approach each other, seen more clearly in the young than in the old subjects. An explanation for this finding has previously been proposed (Cavagna, 2006) and is briefly given below.

At each running step the muscle-tendon units are subjected to a stretch–shorten cycle as the body bounces off the ground. Muscle-tendon units are composed of two structures in series having a very different response to stretch and recoil. While tendons have a similar stretch–shorten relation due to their small hysteresis (Ker, 1981; Alexander, 2002), muscle exerts a larger force during stretching than during shortening, depending on its force–velocity relation. This fact results in a different response of the muscle-tendon units to a stretch–shortening cycle depending on the relative length change of muscle and tendon during the cycle (Cavagna, 2006).

The lengthening of muscle relative to the lengthening of tendon depends on the stiffness of muscle relative to that of tendon; the stiffness of muscle, in turn, depends on its activation, i.e. on the force exerted by its contractile component. If the muscle is relaxed, i.e. the force is nil, the whole of the lengthening will be taken up by muscle. If the force is low, as at low speeds of locomotion [e.g. fig. 3 of Biewener (Biewener, 1998)], an appreciable fraction of the length change will be taken up by muscle. In this case, the average force developed during stretching is expected to exceed that developed during shortening according to the force–velocity relation of muscle, and the characteristics of the bounce would deviate from those of an elastic body. If, on the other hand, the force is high, as at high speeds of locomotion [e.g. fig. 3 of Biewener (Biewener, 1998)] and the muscle is kept isometric, as some studies suggest for running (Kram and Taylor, 1990; Roberts et al., 1997; Biewener et al., 1998), most of the length change will be taken up by tendons and the characteristics of the bounce will approach that of an elastic body.

These observations are in agreement with the finding that at low and intermediate running speeds the positive work duration is greater than negative work duration (Fig. 4), indicating that the average force during positive work is less than the average force during negative work as expected from the force–velocity relation of muscle. At speeds greater than 14 km h^{-1} , $t_{\text{push}} \approx t_{\text{brake}}$, indicating that $\bar{F}_{\text{push}} \approx \bar{F}_{\text{brake}}$, as expected from an elastic system. This suggests that when the duration of the rebound, $t_{\text{push}} + t_{\text{brake}}$, falls below 0.2 s (Fig. 4) the length change of the muscle-tendon units is taken up almost completely by tendons and other undamped elastic elements, with muscle in a quasi-isometric contraction. Fig. 4 shows that this apparent elastic behavior at high speeds is more evident in the young subjects than in the elderly.

In conclusion, a muscular force greater during stretching than during shortening with a large energy loss during the stretch–shorten cycle, which are both consequences of the force–velocity relation of muscle, may explain, at least qualitatively, the ensemble of the deviations from the elastic model during the bounce of the body (Table 2). Assuming that the old subjects we tested exhibit the modification of the force–velocity relation characteristic of their age, the larger deviation from the elastic model found in the old subjects may be due to: (i) the greater difference in force between stretching and shortening described in the aged muscle, and (ii) the lower force developed by their muscles, implying a relatively larger length change of muscle relative to tendons within the muscle–tendon units.

LIST OF SYMBOLS AND ABBREVIATIONS

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
$E_{k,\text{mx,down}}$	kinetic energy peak attained during the descent of the centre of mass
$E_{k,\text{mx,up}}$	kinetic energy peak attained during the lift of the centre of mass
E_{kf}	kinetic energy of forward motion of the centre of mass
E_{kv}	kinetic energy of vertical motion of the centre of mass
E_p	gravitational potential energy of the centre of mass
\bar{F}_{brake}	average force during negative external work
F_f	fore-aft force
\bar{F}_{push}	average force during positive external work
F_v	vertical force
g	acceleration of gravity
M_b	body mass
$r(t)$	instantaneous recovery of mechanical energy calculated from the absolute value of the changes, both increments and decrements, in E_p , E_k and E_{cm} during each time interval in the step period (Eqn 2)
R_{int}	cumulative energy recovery attained at the end of the step due to $E_k - E_p$ transduction
$R_{\text{int,down}}$	fraction of R_{int} attained during the downward displacement of the centre of mass
$R_{\text{int,up}}$	fraction of R_{int} attained during the lift of the centre of mass
$S_{\text{ae,up}}$	upward displacement of the centre of mass taking place during its upward deceleration
$S_{\text{ae,down}}$	downward displacement of the centre of mass taking place during its downward acceleration
$S_{\text{c,down}}$	downward displacement of the centre of mass during contact
$S_{\text{c,up}}$	upward displacement of the centre of mass during contact
$S_{\text{ce,down}}$	downward displacement of the centre of mass from the equilibrium position where $F_v = M_b g$ to the lowest point of its trajectory
$S_{\text{ce,up}}$	upward displacement of the centre of mass from the lowest point of its trajectory to the equilibrium position where $F_v = M_b g$
$S_{\text{v,down}}$	downward displacement of the centre of mass

$S_{v,up}$	upward displacement of the centre of mass
t_{brake}	duration of negative external work production
t_{push}	duration of positive external work production
V_f	forward velocity
V_v	vertical velocity
W_{ext}^+	positive work done at each step to increase the mechanical energy of the centre of mass: W_{ext}^+ is the sum of the positive increments of E_{cm} during the period τ
W_{kf}^+	positive work done at each step to increase the forward speed of the centre of mass: W_{kf}^+ is the sum of the positive increments of E_{kf} during the period τ
W_v^+	positive work done at each step to sustain the gravitational potential energy changes of the centre of mass: W_v^+ is the sum of the positive increments of E_p during the period τ
α, β	step phases during which E_p and E_k increase (α) or decrease (β) simultaneously
Δt_{photo}	time interval between photocells crossing
τ	step period, i.e. period of repeating change in forward and vertical velocity of the centre of mass

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