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THE REBOUND OF THE BODY DURING UPHILL AND DOWNHILL RUNNING AT DIFFERENT SPEEDS

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Summary statement

Running on the level can be compared to a spring-mass system bouncing on the ground. This study analyses how the bouncing mechanism changes with the slope of the terrain.

Abstract

When running on the level, muscles perform as much positive as negative external work. On a slope, the external positive and negative works performed are not equal. The present study is intended to analyse how the ratio between positive and negative work modifies the bouncing mechanism of running. Our goals are (*i*) to identify the changes in motion of the centre of mass of the body associated with the slope of the terrain and the speed of progression, (*ii*) to study the effect of these changes on the storage and release of elastic energy during contact and (*iii*) to propose a model that predicts the change in the bouncing mechanism with slope and speed. Therefore, the ground reaction forces were measured on ten subjects running on an instrumented treadmill at different slopes (from -9° to +9°) and different speeds (between 2.2 and 5.6 m s^{-1}). The movements of the centre of mass of the body and its external mechanical energy were then evaluated. Our results suggest that the increase in the muscular power is contained (1) on a positive slope: by decreasing the step period and the downward movements of the body, and by increasing the duration of the push, and (2) on a negative slope: by increasing the step period and the duration of the brake, and by decreasing the upward movement of the body. Finally the spring-mass model of running was adapted to take into account the energy added or dissipated each step on a slope.

Key words: locomotion, running, bouncing mechanism, slope, external work

Introduction

When running on the level at a constant average speed, the mechanical energy of the centre of mass of the body (*COM*) oscillates throughout the step like a spring-mass system bouncing on the ground (Cavagna et al., 1976). During the rebound of the body, the muscle-tendon units (*MTU*) of the supporting lower-limb undergo a stretch-shortening cycle during which part of the mechanical energy of the *COM* is absorbed during the negative work phase to be restored during the next positive work phase (Cavagna et al., 1988).

When running on the level, the upward and downward movements of the *COM* are equal and the positive and negative work done each step to sustain its movements relative to the surroundings are equal (*i.e.* $W^{+}_{ext} = W^{-}_{ext}$). When running on a slope, muscles are compelled to produce or dissipate energy to increase or decrease the potential energy of the *COM* (DeVita et al., 2008). In this case, the spring-mass model is not suitable anymore since the ratio between positive and negative work increases or decreases with the slope of the terrain (Minetti et al., 1994). Several aspects of the mechanics of human running uphill and downhill have been studied these last decades: *e.g.* the muscular work done, the energy consumed and the muscular efficiency at different slopes (Minetti et al., 1994), the net muscular moment and power at the hip, knee and ankle during uphill running (Roberts and Belliveau, 2005), the possible elastic energy storage and recovery in the arch and Achilles' tendon while running uphill and downhill (Snyder et al., 2012).

To our knowledge, the change in the bouncing mechanism while running on a slope at different speeds has never been analysed. Indeed, this mechanism will be affected by the ratio between positive and negative work. Between 2.2 and 3.3 m s^{-1}, this ratio changes with the slope of the terrain, but not with the speed of progression (Minetti et al., 1994). However, to the best of our knowledge, this ratio has never been measured while running on a slope at higher speeds.

To analyse the bouncing mechanism, we have measured the three components of the ground reaction force (*GRF*) of ten subjects running on an inclined treadmill (from -9° and +9°, by step of 3°) at 10 different speeds (from 2.2 to 5.6 m s^{-1}). From these curves, we have analysed (*i*) the different periods of the running steps, (*ii*) the vertical movements of the *COM* and (*iii*) the energy fluctuations of the *COM* in order to understand how the bouncing mechanism of running deviates from the spring-mass model with slope and speed. We believe that three aspects of this mechanism will be affected.

First, from a mechanical point of view, a spring-mass system bouncing vertically on the ground oscillates around an equilibrium point where the vertical component of the *GRF* (F_v) is equal to body weight (*BW*) (Cavagna et al., 1988). This is true whatever the slope; indeed, when running in steady state, the average vertical velocity of the *COM* ($\overline{V_v}$) does not change from one step to the next. Consequently, the average vertical acceleration of the *COM* $\overline{a_v} = 0$ and the average force $\overline{F_v} = BW$. The step period (*T*) can thus be divided into two parts: the first during which $F_v > BW$ (t_{ce}) taking place during the contact of the foot on the ground and the second during which $F_v \leq BW$ (t_{ae}) taking place both during ground contact and aerial phase. The period t_{ce} corresponds to the half period of the oscillation of the bouncing system. During t_{ae}, the bouncing model is not valid when the body leaves the ground.

When running on a flat terrain at speeds up to ~3.1 m s^{-1}, $t_{ce} \approx t_{ae}$ (symmetric step). As speed increases above 3.1 m s^{-1}, t_{ae} becomes progressively greater than t_{ce} (asymmetric step). This asymmetry arises from the fact that, when speed increases, the average vertical acceleration during t_{ce} (*i.e.* $\overline{a_{v,ce}}$) becomes greater than the acceleration of gravity (*g*) whereas during t_{ae}, $\overline{a_{v,ae}}$ cannot exceed 1 *g*. Consequently, a longer t_{ae} is necessary to dissipate and restore the momentum lost and gained during t_{ce}. At a given speed for a given

t_{ce}, the asymmetric step requires a greater $\overline{a_{v,ce}}$, however the increase in the step period due to a longer t_{ae} results in a smaller internal power necessary to reset the limbs each step (Cavagna et al., 1988).

When running on a positive slope, muscles are performing more positive than negative work. We expect that in order to contain the increase in muscular forces during t_{ce}, the step remains symmetric above 3.1 m s^{-1} and T becomes shorter than during running on the level. On contrary when running on a negative slope, muscles are performing more negative work. Since muscles are able to develop higher forces during eccentric contractions, we expect that T is tuned to contain the internal power, rather than the force during t_{ce}. Consequently, T should become longer than during running on the level and the step should become asymmetric below 3.1 m s^{-1}.

Second, when running on a flat terrain, the momentums lost and gained over a step are equal and $\overline{V_v} = 0$. Consequently, the upwards and downwards vertical displacements of the *COM* (S^+ and S^-) are equal. On the contrary, when running on a slope, $\overline{V_v} \neq 0$ and $S^+ \neq S^-$. We expect that the dissimilarity between S^+ and S^- will be the main factor affecting the bouncing mechanism. We also expect that S^- in uphill and S^+ in downhill running will progressively disappear and with it the amount of energy that can potentially be stored in the *MTU*.

Third, on a flat terrain, the energy due to the vertical movements of the *COM* (E_v) and the energy due to its horizontal movements (E_f) are fluctuating in-phase (Cavagna et al., 1976) and the negative and positive work done are about equal: $\Delta^+ E_f \approx \Delta^- E_f$ and $\Delta^+ E_v \approx \Delta^- E_v$. However, when running on a slope $\Delta^+ E_f \approx \Delta^- E_f$, but $\Delta^+ E_v \neq \Delta^- E_v$. We expect (1) that due to this imbalance, the fluctuations of E_f and E_v are no longer in phase and (2) consequently that an energy exchange occurs between these two curves. Therefore, we have evaluated the duration of the positive and negative work phases and the energy-transduction between E_f and E_v during the period of contact t_c (Cavagna et al., 2008a).

We hypothesize that the three aspects described here above will jeopardize the bouncing mechanism of running and in turn, the possibility to store and release elastic energy into the elastic structures of the lower-limb. However, we also hypothesize that the disappearance of this mechanism is intended to restrain the increase in W^{+}_{ext} or in W^{-}_{ext} due to slope.

Finally, we propose a model that describes the vertical oscillations of the *COM* during t_{ce} while running on a slope. The aim of this model is to understand how all the lower-limb muscles are tuned to generate the basic oscillation of the bouncing system. The spring-mass system bouncing on the ground that models running on the level (Blickhan, 1989; Cavagna et al., 1988) cannot describe running on a slope since energy must be added or dissipated. Therefore, we have incorporated an actuator in the spring-mass model that will generate a force proportional to V_v and produce/absorb energy during contact.

Material and methods

Subject and experimental procedure

Ten recreational runners (3 females and 7 males) participated to the study (age: 31.8 ± 8.3 y, mass: 68.8 ± 10.2 kg, height: 1.78 ± 0.07 m, mean ± SD). Informed written consent was obtained from each subject. The studies followed the guidelines of the Declaration of Helsinki, and the procedures were approved by the Ethic Committee of the Université catholique de Louvain.

Subjects ran on an instrumented treadmill at seven different inclinations: 0°, ±3°, ±6° and ±9°. In order to neutralize the effect of learning and muscle fatigue, half of the subjects started with an inclination of 0° that was increased and the other half with an inclination of 9° that was decreased. At each slope, subjects ran at ten speeds presented in a different order (8, 10, 11, 12, 13, 14, 15, 16, 18 and 20 km h^{-1}, corresponding to 2.22, 2.78, 3.06, 3.33, 3.61, 3.89, 4.17, 4.44, 5.00 and 5.56 m s^{-1} respectively). Note that for downhill running, the speed of the belt was limited by the manufacturer to 5.0 m s^{-1}. At each slope, half the subjects started with the belt turning forwards to simulate uphill running and the other half with the belt turning backwards to simulate downhill running.

Data were recorded during a period of 3-10 s, depending of the speed and the inclination of the treadmill. Between 6 and 36 steps per trials were recorded: a total of 15 760 steps were analysed. On a +6° slope, one subject could not run at 5.6 m s^{-1} and on a +9° slope, one subject could not run at 5.0 m s^{-1} and three at 5.6 m s^{-1}.

Experimental setup and data analysis

The instrumented treadmill (Fig. 1) consisted on a modified commercial treadmill (*h/p/Comos-Stellar*, Germany, belt-surface: 1.6 x 0.65 m, weight: ~240 kg) combined with four force-transducers (*Arsalis*®, Belgium), designed on the principle described by Heglund (1981). Since the whole body of the treadmill (including the motor) was mounted on the transducers, these were measuring the three components of the *GRF* exerted by the treadmill under the foot (Willems and Gosseye, 2013): F_p, the component parallel to the long axis of the tread-surface, F_n the component normal to the tread-surface and F_l the component in the lateral direction. The lowest frequency mode of vibration was > 41 Hz for F_p, 47 Hz for F_n and 27 Hz for F_l. The non-linearity was < 1% of full-scale, and the crosstalk < 1%. The fore-aft (F_f) and vertical (F_v) components of *GRF* were then computed as:

$$\begin{pmatrix} F_f & F_v \end{pmatrix} = \begin{pmatrix} \cos\theta & -\sin\theta \\ \sin\theta & \cos\theta \end{pmatrix} \begin{pmatrix} F_p \\ F_n \end{pmatrix}, \quad (1)$$

where θ is the angle between horizontal and the tread-surface. The electrical motor was instrumented with an optical angle encoder to measure the speed of the belt (V_{belt}). The average speed of the belt over a stride ($\overline{V_{belt}}$) differed by 2.8 ± 1.4% (mean ± SD) from the desired one and the instantaneous V_{belt} did not change more than 5 % of $\overline{V_{belt}}$.

The treadmill contained its own signal conditioning system: the *GRF* signals were amplified, low-pass filtered (4-pole Bessel filter with a -3dB cut-off frequency at 200 Hz) and digitized by a 16-bit analog-to-digital converter at 1000 Hz. This system was connected to a PC via Ethernet using TCP/IP (Genin et al., 2010). Acquisition and data processing were performed using a custom-build software (LABVIEW 2010-National Instruments®-USA and MATLAB 2013-MathWorks®-USA).

Division of the step

Steps were divided according to the F_v-time curves (Fig. 1): a step started and ended when F_v became greater than BW. The effective contact time (t_{ce}) was the period where $F_v \geq BW$ and the effective aerial time (t_{ae}), the period where $F_v < BW$ (Cavagna et al., 1988). The time of contact (t_c) is the period during which F_v> 10 N and the aerial phase (t_a), the period during which $F_v \leq$ 10 N. The step duration was then calculated as: $T= t_{ce} + t_{ae}$.

Measurement of the acceleration, velocity and vertical displacement of the COM

The acceleration (a), velocity (V) and displacement (S) of the *COM* and the external work done (W_{ext}) were computed from the *GRF* using a method similar to the one of Gosseye et al. (2010). Therefore, this method is only explained shortly.

These computations were done over strides (*i.e.* two steps, starting on the right foot). The fore-aft, lateral and vertical accelerations of the *COM* relative to the reference frame of the laboratory were calculated by dividing F_f, F_l and $F_v - \overline{F_v}$ by the body mass m (where $\overline{F_v}$ is the average vertical force over a stride). In theory $\overline{F_v} = BW$ (as explained in the introduction), therefore strides were analysed only if $\overline{F_v}$ was within 5% of BW.

The time-curves of the three components of a were integrated numerically to determine the fore-aft (V_f) lateral (V_l) and vertical (V_v) velocity of the *COM*, plus integration constant which was set on the assumption that the average velocity of the *COM* over a stride was equal to $\overline{V_{belt}} \cos q$ for V_f, to zero for V_l and to $\overline{V_{belt}} \sin q$ for V_v.

The vertical displacement of the *COM* (S) was then computed by time-integration of V_v. The upward and downward displacements of the *COM* were divided according to t_c (S_c^+ and S_c^-) and t_a (S_a^+ and S_a^-). The minimum vertical displacement (S_{min}) necessary to overcome the slope of the terrain each step can be computed by $S_{min} = \overline{V_f}\, T \sin q$, where $\overline{V_f}$ is the average running speed over the step and $\overline{V_f}\, T$ is the step length.

Measurement of the positive and negative external work

The external work (W_{ext}) is the work necessary to move the *COM* relative to the surroundings plus the work done on/by the environment (Willems et al., 1995). It was measured from the work done by the *GRF* (Gosseye et al., 2010).

The power spent to move the *COM* in the fore-aft ($\dot{W}_f$), lateral direction ($\dot{W}_l$) and in the vertical ($\dot{W}_v$)was computed respectively by:

$$\dot{W}_f = F_f\, V_f, \qquad \dot{W}_l = F_l\, V_l \qquad \text{and} \qquad \dot{W}_v = F_v\, V_v, \qquad (2)$$

In the fore-aft and vertical directions, the power spent by the subject on the belt or by the belt on the subject can be computed respectively by:

$$-F_f\, v \cos\theta, \qquad \text{and} \qquad -F_v\, v \sin\theta, \qquad (3)$$

where $v = V_{belt} - \overline{V_{belt}}$ represents the variation of V_{belt} around $\overline{V_{belt}}$. Since these terms represented less than 3% of W_{ext}, there were neglected in this study.

The energies (E_f, E_l and E_v) due respectively to the fore-aft, lateral and vertical movements of the *COM* were computed by:

$$E_f = \int \dot{W}_f\, dt, \qquad E_l = \int \dot{W}_l\, dt \qquad \text{and} \qquad E_v = \int \dot{W}_v\, dt, \qquad (4)$$

and the total energy of the *COM* (E_{ext}) by:

$$E_{ext} = \int \left(\dot{W}_f + \dot{W}_l + \dot{W}_v \right) dt. \qquad (5)$$

The positive and negative works over one step (W_f^+, W_l^+, W_v^+, W_{ext}^+ and W_f^-, W_l^-, W_v^-, W_{ext}^-) were computed as the sum of the positive and negative increments of the E_f, E_l, E_v and E_{ext}-curves, respectively (Fig. 2). Since W_l represents less than 1.5 % of W_{ext}, it is not presented separately in the results. The work per step was computed as the work over the stride divided by two.

Energy transduction between E_f and E_v

When running on the level, the E_f and E_v-curves are in phase (Cavagna et al., 1976). However, when running on a slope, these curves could shift one relative to the other, allowing energy transduction between E_f and E_v (Fig. 2). The amount of energy recovered (%R) over the contact phase was computed as (Cavagna et al., 2008a):

$$\%R = 100\,\frac{W_f^+ + |W_f^-| + W_v^+ + |W_v^-| + W_l^+ + |W_l^-| - \left(W_{ext}^+ + |W_{ext}^-|\right)}{W_f^+ + |W_f^-| + W_v^+ + |W_v^-| + W_l^+ + |W_l^-|}. \qquad (6)$$

Modelling the vertical movement of the body bouncing system of running

When running on the level, the vertical movement of the *COM* during t_{ce} can be compared to the movement of a spring-mass system bouncing vertically (Blickhan, 1989; Cavagna et al., 1988). In this case, the balance of force is given by:

$$F_v - BW = k\,S, \qquad (7)$$

where k is the overall stiffness generated by the lower-limb muscles. In order to describe the vertical movement of the *COM* during running on a slope, equation (7) was implemented by incorporating an actuator parallel to the spring. This actuator generates a force proportional to the magnitude of V_v:

$$F_v - BW = b + k\,S + c\,V_v, \qquad (8)$$

where b is a constant depending on the vertical velocity of the *COM* at touch down and c is the actuator coefficient. The coefficient c is positive when running uphill and negative when running downhill. In this way, the power developed by the actuator force ($c\,V_v^2$) is positive in uphill running, showing that the actuator works like a motor giving energy to the body, and negative in downhill running, showing that the actuator works like a damper absorbing energy (see insets in Fig. 7A).

At each instant i of t_{ce} (which represents the half-period of the oscillation of the system), the vertical acceleration (a_v) of the mass m was computed by:

$$a_v(i) = \frac{F_v(i) - BW}{m} = \frac{b}{m} - \frac{k}{m} S(i) + \frac{c}{m} V_v(i), \quad (9)$$

where $a_v(i)$, $V_v(i)$ and $S(i)$ were the experimental data at instant i. In this ways n equations were produced, where n is the number of samples during contact. This set of equations resulted in an over-constrained system, from which the constant (b/m), the mass-specific stiffness (k/m) and actuator coefficient (c/m) were computed by a regression analysis using singular value decomposition that minimizes the sum of squared errors.

For running on the level, we have also compared the values obtained starting from equations (7) and (8). In equation (8), c/m is close to zero and k/m differs by 1.8 ± 2.1 % (mean ± SD, n= 2440) from equation (7).

The goodness of the spring-actuator-mass model was assessed by computing (1) the variance explained by the regression model (r^2), and (2) the root mean square error (*RMSE*), which expresses the agreement between the measured and the computed values of the *GRF*.

Statistics

Data were grouped into speed-slope classes. In order to obtain one value per subject in each class, the steps of a same subject in a same class were averaged. The mean and standard deviation of the runner population were then computed in each class (grand mean). A two-way ANOVA with Bonferoni post-hoc (PASW Statistics 19, SPSS inc®, IBM company, USA) was performed in order to assess the effect and the cross-effect of speed and slope on the calculated variables (p-values were set at 0.05).

Results

Effect of slope on the ratio between positive and negative work done

The mass-specific external work done per unit distance is plotted in Fig. 3A. In the fore-aft direction, the work done to move the *COM* horizontally (W_f) increases similarly with speed at any slope (p= 0.995). Moreover, since subjects move at a constant speed, $W_f^+ = W_f^-$.

Therefore, the unbalance between W_{ext}^+ and W_{ext}^- on a slope is only due to a modification in W_v^+ and W_v^-. During uphill running, W_v^+ increases while W_v^- decreases and tends to disappear above ~4.4 m s^{-1} at +6° and above ~3.3 m s^{-1} at +9°. On a negative slope, W_v^+ tends to disappear above ~5.0 m s^{-1} at -6° and above ~4.2 m s^{-1} at -9°.

Note that the ratio W_{ext}^- / W_{ext} changes with slope (p< 0.001), but is independent of speed (p= 0.17): W_{ext}^- / W_{ext}, which equals 0.5 at 0° decreases monotonically below 0.5 on a negative slope and increases monotonically above 0.5 on a positive slope (Fig. 3B).

Effect of slope and speed on the step period

The step period (T) is given as a function of running speed in Fig. 4A. The slope has a significant effect on the step period (p <0.001): T decreases when running uphill whereas it increases when running downhill. The effect of slope on T is more marked on positive than on negative slopes, though this effect is significant at all slopes (Bonferoni post-hoc, p <0.01). The slope does not affect the effective contact time t_{ce}, except at +9° (Bonferoni post-hoc, p <0.01). Thus, the change in T is mainly due to a change in t_{ae} (p <0.001), which in turn, is largely due to a change in t_a.

When running on the level, the step is symmetric (*i.e.* $t_{ae} \approx t_{ce}$) at speeds up to ~2.8 m s^{-1} (Bonferoni post-hoc, p <0.01). These results are consistent with those reported in the literature (Cavagna et al., 1988; Schepens et al., 1998). When running uphill, $t_{ae} \approx t_{ce}$ in a larger range of speeds because the mean vertical acceleration during t_{ce} ($\overline{a_{v,ce}}$) is kept smaller than 1 g at higher speeds than on the level (Fig. 4B): up to ~3.3 m s^{-1} at +3°, to ~3.9 m s^{-1} at +6° and to 5.6 m s^{-1} at +9°. When running downhill, the difference between t_{ae} and t_{ce} tends increase because $\overline{a_{v,ce}}$ becomes >1 g at lower speeds than on the level. Consequently, the range of speeds at which $t_{ae} \approx t_{ce}$ becomes narrower, *i.e.* below ~2.2 m s^{-1} at -6° and -9°.

Effect of slope and speed on the upward and downward displacements of the COM

On the level, the upward (S^+) and downward (S^-) displacements of the *COM* over one step are equal (Fig. 5). On a slope, the difference between S^+ and S^- increases with inclination (p< 0.001).

When running uphill, S^+ increases with slope and speed. At slow speeds, the displacement upwards during the aerial phase (S_a^+) is almost nil, whatever the slope. When speed increases, S_a^+ represents a greater part of S^+. The displacement downwards (S^-) decreases when slope and speed increase: S^- disappears above 5.0 m s^{-1} at +6° and above 3.9 m s^{-1} at +9°. Note that the reduction of S^- is first due to a reduction of S_a^-. At +6° and +9°, S_a^- is almost nil at all speeds, suggesting that V_v at touchdown is close to zero.

When running downhill, the opposite phenomenon is observed: S^- increases and S^+ decreases with slope and speed. The effect slope and speed is more marked on S^- when running downhill than on S^+ when running uphill. When running downhill, S_a^- represents a significant part of S^- whereas S_a^+ is almost nil whatever the slope and the speed, indicating that V_v at take-off is close to zero.

Effect of slope and speed on the energy fluctuations of the COM

When running on a slope, muscles are compelled to modify the ratio between concentric and eccentric contraction. Consequently, the timing of negative and positive work production during t_c is modified (Fig. 6A). The time during which muscles perform negative external work (t_{brake}) is extended during downhill running (p< 0.001) while the duration of the positive work phase (t_{push}) is increased during uphill running (p< 0.001). Since at a given speed, t_c does not change significantly with slope (Fig. 6A), the modification of t_{brake} is compensated by an opposite change in t_{push}.

The relative time of occurrence of the minimum of E_f ($E_{f,min}$) changes little with slope (see arrows in Fig. 2 and Fig. 6B). On the contrary, the minimum of E_v ($E_{v,min}$) appears relatively earlier during contact in uphill running and later in downhill running. The effect of the slope on the relative time of occurrence of $E_{v,min}$ is more accentuated when speed increases. Between $E_{f,min}$ and $E_{v,min}$, the E_f and E_v-curves (grey zone in Fig. 6B) are out of phase and an energy exchange can occur from E_f to E_v when $E_{v,min}$ precedes $E_{f,min}$ and from E_v to E_f when $E_{f,min}$ precedes $E_{v,min}$. This exchange of energy allows recovering a significant amount of energy (*i.e.* %R >10%) only on steep slopes and at speeds >3.6 m s^{-1} (Fig. 6C).

Modelling running on a slope

When running on a slope, the lower-limb muscles can be modelled as a mass mounted on a spring in parallel with an actuator that generates a muscular driving force proportional to the vertical velocity of the *COM* and produces (uphill) or absorbs (downhill) energy during t_{ce}. The overall mass-specific stiffness k/m and actuator coefficient c/m generated by the lower-limb muscles (Fig. 7B) are modified both by the slope of the terrain and the speed of progression (p< 0.001). As compared to 0°, k/m decreases on a positive slope and increases on a negative slope. At a given slope, k/m increases with velocity; though the effect of speed is greater on negative than positive slopes (p< 0.001).

During level running, the complex musculoskeletal system of the lower limb behaves like a single linear spring and c/m is nil. Running uphill requires additional energy to overcome the slope. In this case, c/m is positive and increases with the mechanical demands, *i.e.* with increasing slope but also with increasing speed. On the contrary, running downhill requires dissipation of energy. Consequently, *c/m* is negative and its absolute value increases when slope becomes steeper and when speed increases. Note also that the effect of speed on *c/m* is greater on negative than on positive slopes ($p< 0.001$).

This model describes the basic vertical oscillation of the *COM* during running on a slope (Fig. 7A) without taking into account the first peak in the F_v-curve due to foot slap (Alexander et al., 1986; Schepens et al., 2000) and the vibrations of the treadmill-motor (Fig. 1); the r^2 of the least square method is always > 0.63 and the root-mean-square error (*RMSE*) ranges between 120 and 440 N (Table 1).

Discussion

This study is intended to understand how the bouncing mechanism is modified when the slope of the terrain becomes positive or negative. Our results show that the bouncing mechanism still exists on shallow slopes and progressively disappears when the slope increases. This mechanism disappears earlier on positive than on negative slopes and at high speeds than at slow speeds. In this section, we will discuss how the step period, the vertical movement of the *COM* and the energy fluctuation of the *COM* affect the bouncing mechanism of running. We will also show that these variables are tuned to contain the increase in the positive or negative muscular work and power due to slope. We finally discuss the quality and limits of the mechanical model describing the vertical movement of the *COM* during slope running.

Change in step period with slope

Minetti et al. (1994) show that on a positive slope the step period *T* decreases significantly whereas on negative slope *T* tends to increase (though this increase is not significant). Our results confirm that, at a given speed, *T* is shorter when running uphill than when running on the level. On the contrary during downhill running, our results show a significant increase in *T*, even if this change is less marked than on a positive slope. This discrepancy with the results of the team of Minetti may be explained by the fact that the number of steps analysed here (*n*= 15 760 steps) is higher than in Minetti's study (*n*= 418 steps).

In our study, we observe that t_c (Fig. 6A) and t_{ce} (Fig. 4A) at a given speed do not change significantly with slope, both in downhill and uphill running (except at +9° at the highest speeds). The change in the step period *T* is thus mainly due to a change in t_a, which in turn changes t_{ae}.

As shown by (Cavagna et al., 1991), running on a flat terrain with long effective aerial phase is a convenient strategy to decrease the average-power developed over the step, provided that muscles are able to develop enough power during the push. Our results suggest that the changes in t_{ae} are intended to contain the additional muscular power due to the slope.

When running uphill as compared to running on the level, *T* decreases because t_{ae} is reduced. Since t_{ce} is not modified by slope, the step remains symmetric (*i.e.* $t_{ce} \approx t_{ae}$) at higher speeds than on a flat terrain. These results are similar to those obtained when running on the level in hyper-gravity (Cavagna et al., 2005): at 1.3 g, the rebound remains symmetric up to 4.4 m s^{-1}.

At a given speed and for a given t_{ce}, a symmetric rebound results in a shorter step than an asymmetric rebound. As a result, the minimal height (S_{min}) that the *COM* must gain each step is smaller, the impact against the ground is reduced and the force and power during the push are decreased (Cavagna et al., 1991). However, decreasing *T* results in a greater internal power to move the limb-segments relative to the *COM*.

Snyder and Farley (2011) have observed that the optimal step period at which the oxygen consumption is minimal does not change for slopes between -3° and +3°. However, these authors show that the freely chosen T decreases slightly between 0° and 3°. This decrease in T might be a strategy to contain the mechanical power during the push.

The changes observed in uphill running are similar to those in old men running (Cavagna et al., 2008b). In older subjects, the average upward acceleration ($\overline{a_{v,ce}}$) is lower than in younger ones, leading to a symmetric rebound. According to these authors, the lower force attained during contact by the old subjects may be explained in part by the loss of muscular strength (*e.g.* Doherty, 2003). Similarly, the strategy adopted while running uphill could be due to the limits set by the muscular strength and/or power. Furthermore, in uphill running, the *GRF* vector is farther to the leg joint centres (DeVita et al., 2007). Thus, the slope of the terrain alters the muscle mechanical advantage by creating longer lever arms and leads to higher joint torques and power outputs (Roberts and Belliveau, 2005). Therefore, decreasing T might be a beneficial strategy to limit the muscular moments and to reduce the mechanical load applied to the *MTU*.

At the opposite, when running downhill, T increases as compared to running on the level because t_{ae} increases. Since t_{ce} is not modified, steps are asymmetric (*i.e.* $t_{ce} < t_{ae}$) at lower speeds than on a flat terrain. These results are similar to those obtained when running in unweighing conditions (Sainton et al., 2015): when *BW* is reduced from 40%, t_c remains unchanged while t_a is increased.

The step asymmetry has the physiological advantage to limit the internal power. However, this asymmetry requires a greater $\overline{a_{v,ce}}$ and consequently a greater power during t_{ce}. The choice of this strategy in downhill running may be due to the difference in force exerted during negative and positive work phases: during downhill running, muscles contract mainly eccentrically, allowing the development of higher forces. Moreover, in downhill running, runners land with the leg more extended (Leroux et al., 2002), resulting in reduction of the lever arms of the *GRF* about the lower-limb joints and thus of the net muscular moments.

Change in vertical motion of the COM

When running uphill at a given speed, in order to maintain the bouncing mechanism similar to level running, the runners should increase W^{+}_{ext} to overcome the slope, without changing W^{-}_{ext} (Fig 3A). However, the runner limits W^{+}_{ext} by reducing W^{-}_{ext}. The opposite phenomenon is observed during downhill running, where W^{-}_{ext} is limited by reducing W^{+}_{ext}. Since the work done to accelerate and decelerate the *COM* forwards (W_f) does not change with slope, the change in W^{+}_{ext} and W^{-}_{ext} is due to a change in W^{+}_{v} and W^{-}_{v}, which in turn is mainly due to a modification of S^+ and S^- during the step (Fig. 5).

When running uphill, the upward displacement of the *COM* each step (S^+) increases with slope and speed because S_{min} increases. Contrarily, the downward displacement (S^-) decreases. At low speeds and on shallow slopes, S^- is still present because the muscular power at disposal during the push is great enough to increase S^+ beyond S_{min}. In this way, the presence of S^- allows the storage of elastic energy into the *MTU*, to be restored during the next positive work phase. On the contrary, at high speeds and on steep slopes, the power during the push approaches the maximal performance of the runner. Therefore, S^+ is maintained close to S_{min}; consequently, S^- and W^{-}_{v} (Fig. 3A) are almost nil and no rebound is possible.

When running downhill, S^- increases faster with slope and speed than S^+ in uphill running (Fig. 5); these changes in S^- are mainly due to a change in the downward fall of the *COM* during t_a (S^{-}_{a}). Contrariwise, the effect of slope and speed on S^+ on a negative slope is less marked than the changes in S^- on a positive slope. Consequently, when running downhill, the possibility of elastic storage increases with speed and slope. Though, as mentioned by Snyder and Farley (2011) and Snyder et al. (2012), the recoil is limited since S^+ and W^{+}_{v} are small.

Furthermore, the large S_a^- observed in downhill running results in a high V_v at touchdown, which in turn causes important *GRF*. According to Zelik and Kuo (2012), the vibrations of the soft tissues induced by the impact could reduce the muscular work done by dissipating energy.

Change in the energy fluctuations of the COM

Running is thought to employ a spring-mass mechanism where interactions between the *COM* and the ground allow storage and release of elastic energy in the *MTU*. *In vivo* measurements of muscle-tendon interaction have highlighted the importance of the stretch-recoil of tendons on the length change and power output of muscles during running (Ishikawa and Komi, 2008; Roberts et al., 2007).

On the level at low and intermediate speeds, $t_{push} > t_{brake}$ (Fig. 6A), though $W_{ext}^+ = W_{ext}^-$. This difference in time is due to the greater muscular force exerted during the eccentric phase. The fact that $t_{push} > t_{brake}$ suggests thus an important contribution of the contractile machinery to the *MTU* length change and to the work production (Cavagna, 2006). At higher speeds (*i.e.* above ~3.9 m s^{-1}), $t_{push} = t_{brake}$, which suggests that, when muscle activation is progressively augmented with increasing speed, the *MTU* length change is mainly due to tendon length change. The work contribution by the contractile machinery is thus progressively substituted by elastic storage and recovery by tendons. The ratio t_{push}/t_{brake} may therefore be an expression of the deviation of the *MTU*'s response from that of an elastic structure. On a slope, the change in the ratio between W_{ext}^+ and W_{ext}^- affects most likely the interaction between muscle and tendons during the stretch-shortening cycle (Roberts and Azizi, 2011).

When running uphill, the linear increase of W_{ext}^+ changes the partitioning of t_c into t_{push} and t_{brake} (Fig. 6A). In order to contain the average muscular power required during the push,

t_{push} increases with slope and $t_{push} > t_{brake}$. This suggests that the *MTU* length-change is mainly due to a shortening of the contractile machinery and that less elastic energy is stored - as in old men running on the level (Cavagna et al., 2008a). As proposed by Roberts and Azizi (2011), it could be that on a positive slope *MTUs* work like power amplifiers: the energy produced during the muscular contraction is stored at a low pace in the tendons to be released at a higher pace.

In downhill running when slope becomes steeper, in order to limit the power during the brake, t_{brake} increases and t_{push} becomes shorter. The higher *GRF* observed in downhill running could favour the role of tendon relative to that of muscle: muscle would perform a quasi-isometric contraction and the energy would be stored in the tendon during rapid stretch, to be dissipated later by a slower lengthening of the muscle (Roberts and Azizi, 2011).

The partition between t_{push} and t_{brake} changes because the minimum of E_v appears increasingly earlier in uphill running and increasingly later in downhill running, whereas the minimum of E_f occurs always more or less in the middle of the contact period (Fig. 6B and arrows in Fig. 2). For this reason, when slope increases a phase shift between E_f and E_v emerges and an energy transduction between these two forms of energy can occur.

When running uphill, the lower limb acts like a pole in athletics (Schade et al., 2006). During the first part of contact (*i.e.* period between the two arrows in the upper panels of Fig.2), the *COM* looses horizontal velocity, while it gains height and vertical velocity. During this phase, there is an energy transduction between E_f and E_v. The fact that E_{ext} decreases shows that the loss in E_f is greater than the gain in E_v; part of the E_{ext} lost is stored in the elastic element of the muscle-tendon unit to be released during the second part of contact to increase the kinetic and potential of the *COM*. Note that the same phenomenon was described by Mauroy et al. (2013) during the running step preceding the jump over an obstacle.

When running downhill, the energy transduction occurs during the second part of the contact, when E_v is decreasing while E_f increases. In this case, the potential energy lost is used to accelerate the *COM* forward.

In level running, the energy recovered through an exchange between E_v and E_f (equation 6) is negligible (%R< 5%), like in a spring-mass system (Cavagna et al., 1976). When running at high speed on steep slopes, the rebound of the body deviates from a spring mass system. However, the energy transduction allows recovering only a small amount of energy: at best %R≈ 20% in uphill running and %R≈ 10% in downhill running.

Model of the vertical bounce of the body

In this study, we propose a model that reproduces in first approximation, the basic oscillation of a spring-mass-actuator (see inset in Fig. 7A). The aim of this model is to understand how all the lower-limb muscles are tuned to generate an overall leg-stiffness and leg-actuation to sustain the vertical oscillation of the bouncing system.

Running on a slope is not a pure elastic phenomenon since energy must be added or released each step. Therefore, our model includes an actuator placed parallel to the spring. This actuator generates a force proportional to V_v; a linear force-velocity relation was chosen because functional tasks that involve all lower-limb joints show a quasi-linear relationship (Bobbert, 2012; Rahmani et al., 2001), rather than the classical hyperbolic relation described on isolated muscles (Hill, 1938). The coefficient *c/m* is positive during uphill running, showing that the actuator adds energy to the system, and negative during downhill running, because energy is dissipated each step. As speed and slope increase, the discrepancy between the upward and downward displacement of the *COM* increases, the rebound of the *COM* deviates from a spring-mass system and the coefficient *c/m* increases.

On a slope, *k/m* decreases when running uphill and increases when running downhill. On a positive slope, in order to maintain the step symmetric, $\overline{a_{v,ce}}$ remains ≤1 g (Fig. 4B).

This lower acceleration is most likely obtained by reducing the stiffness of the contractile elements of the *MTU* and the overall *k/m* becomes smaller than on the level (Fig. 7B).

Note also that on positive slopes, the limbs at impact are more flexed to prevent pitching backward (Birn-Jeffery and Higham, 2014; Leroux et al., 2002). On the level, runners adopting a more crouched posture, similar to *Groucho running* (McMahon et al., 1987) present lower vertical *GRF* and consequently a smaller *k/m*. In uphill running, the more flexed posture during stance could explain, at least in part, the smaller *k/m*.

On a negative slope, the step is asymmetric at most speeds and slopes because $\overline{a_{v,ce}}$ >1 *g* (Fig. 4B). When acceleration increases, muscles fibres oppose a progressively greater force to stretching and the contractile machinery becomes stiffer than the tendon. Subsequently, the overall *k/m* becomes greater than on the level. Furthermore, increasing *k/m* minimizes the lowering of the *COM* during contact (Fig. 5). This strategy might serve as an intrinsic safety mechanism to limit the risk of *MTU* damages after landing (DeVita et al., 2008).

Our simple spring-actuator-mass model predicts the vertical force-time curve, though it does not take into account the first peak in the F_v-curve, which is due to foot slap (Alexander et al., 1986; Schepens et al., 2000). In order to estimate the contribution of the foot collision on the shape of the F_v-time curve, we have used a Fourier series analysis (Clark and Weyand, 2014). This analysis decomposes the F_v-signal in low- and high-frequency components. According to these authors, the high-frequency components are mainly due to the acceleration of the lower limb during the impact phase. In our study, we observed that the variance accounted for by these high-frequency components increases at high speeds and on steep negative slopes (see Table S1 in the *SMO*). This observation supports the idea that the decrease in goodness of fit indexes (Table 1) is due to a higher contribution of the foot interaction with the ground.

These last results corroborate those of Clark and Weyand (2014) obtained in sprint running; they show that at swift speeds, the *GRF* waveform deviates from the simple spring-mass model pattern, most likely due to the greater importance of the foot-ground collision. Therefore, the authors propose a model including two masses and springs to take into account the interaction of the lower-limb segments with the ground. Our spring-actuator-mass model could thus be refined by adding a second spring-mass representing the foot and shank. Though, kinematic data of these segments are needed to feed this implemented model.

Conclusion

Cavagna et al. (1991) suggested that running with a long aerial phase limits the step-average power as long as muscles are able to develop enough power during the push and/or during the brake. Our results support this hypothesis.

When running uphill at a given speed, the average external power developed during the positive work phase seems to be the limiting factor. Actually, when slope increases, in order to keep a long aerial time t_a, the vertical velocity of the *COM* at take-off should increase because the minimal vertical displacement (S_{min}) increases. This would require a greater power during the push. As a matter of fact, this power is limited (1) by reducing t_a and thus the step period *T*, (2) by increasing the duration of the push (t_{push}) at the expenses of duration of the brake (t_{brake}) and (3) by reducing the downward displacement of the *COM*. As a result, uphill running deviates from a bouncing mechanism as speed and slope increases.

When running downhill, the average external power developed during the negative work phase seems to be the limiting factor. Indeed, despite a lower vertical velocity at take-off, t_a - and thus *T* - increases with slope and speed because the ballistic fall of the *COM* increases. A longer t_a increases the external power developed during the brake because the energy to be dissipated after touchdown is greater. In spite of better muscular performance during eccentric than concentric contraction, the power during the brake is limited by (1) increasing t_{brake} at the expenses of t_{push} and (2) by reducing the upward displacement of the *COM*. Consequently, the bouncing mechanism during downhill running gradually disappear as speed and slope increases.

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List of symbol

$\overline{a_v}$	average vertical acceleration of the *COM* over a complete number of steps
$\overline{a_{v,ce}}$, $\overline{a_{v,ae}}$	average vertical acceleration of the *COM* during t_{ce} and during t_{ae}
a_v	vertical acceleration of the *COM*
b	constant depending of the initial conditions in the spring-actuator-mass model
BW	body weight
c	actuator coefficient in the spring-actuator-mass model
COM	center of mass of the whole body
E_{ext}	mechanical energy of the *COM*
E_f, E_l, E_v	energy due to the fore-aft, lateral and vertical movement of the *COM*
$E_{f,min}$, $E_{v,min}$	minimum of the E_f- and E_v-time curves
F_f, F_l, F_v	fore-aft, lateral and vertical component of the *GRF*
F_p, F_n	component of the *GRF* parallel and normal to the tread-surface
$\overline{F_v}$	average vertical *GRF* over a complete number of steps
GRF	ground reaction force
k	overall vertical stiffness of the leg-spring in the spring-actuator-mass model
L	step length
MTU	muscle-tendon unit
%R	percentage of energy recovered through the transduction between E_v and E_f
RMSE	root mean square error
S	vertical displacement of the *COM*
S^+, S^-	upward and downward displacement of the *COM* over a step
S_a^+, S_a^-	upward and downward displacement of the *COM* taking place during t_a

S_c^+, S_c^-	upward and downward displacement of the *COM* taking place during t_c
S_{min}	minimum vertical displacement necessary to overcome the slope each step
T	step period
t_c, t_a	contact time and aerial time
t_{ce}, t_{ae}	effective contact time and effective aerial time
t_{push}, t_{brake}	duration of the positive and of the negative work phase
θ	slope of the treadmill, *i.e.* angle between horizontal and the tread-surface
V_{belt}, $\overline{V}_{belt}$	instantaneous and average velocity of the belt
V_f, $\overline{V}_f$	instantaneous and average fore-aft velocity of the *COM* relative to the belt
V_l	instantaneous lateral velocity of the *COM*
V_v, $\overline{V}_v$	instantaneous and average vertical velocity of the *COM* relative to the belt
W_{ext}^+, W_{ext}^-	positive and negative external work done to sustain the mechanical energy changes of the *COM* relative to the surroundings
W_{ext}	sum of W_{ext}^+ and the absolute value of W_{ext}^-
W_f^+, W_f^-	positive and negative work done to sustain the fore-aft movement of the *COM*
W_l^+, W_l^-	positive and negative work done to sustain the lateral movement of the *COM*
W_v^+, W_v^-	positive and negative work done to sustain the vertical movement of the *COM*
$\dot{W}_f$, $\dot{W}_l$, $\dot{W}_v$	power spent to move the *COM* in the fore-aft, lateral and vertical direction

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Figures

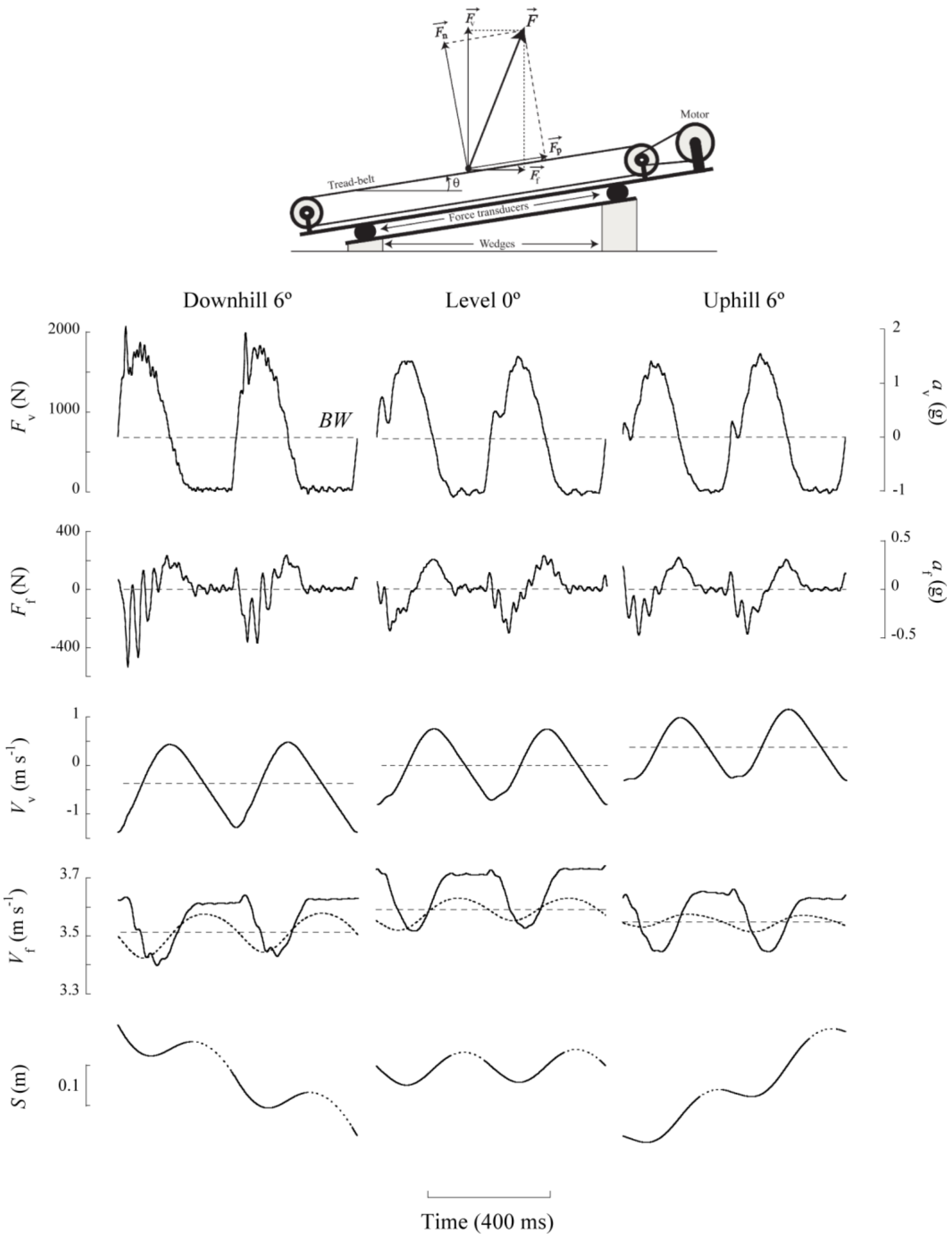


Figure 1 Schema of the instrumented treadmill (top) and typical time-traces of a subject running at ~3.6 m s^{-1} on a -6° slope (left column), on the level (middle column) and on a +6° slope (right column).

The schema at the top of the figure represents the instrumented treadmill. The whole body of the treadmill (including the motor) is mounted on four strain-gage transducers attached on wedges. F_p is the component parallel to the long axis of the tread-surface, F_n the component normal to the tread-surface and F_l the component in the lateral direction (not represented here). θ is the angle between horizontal and the tread-surface. The fore-aft (F_f) and vertical (F_v) components of *GRF* are computed using equation (1).

Traces from top to bottom. First and second row, left scale: vertical F_v and horizontal F_f components of the ground reaction force exerted by the treadmill under the foot; right scale: acceleration of the *COM*: $a_v = (F_v - BW)/m$ and $a_f = F_f / m$, where *BW* is the body weight and *m* the body mass. Third row: vertical velocity of the *COM*, V_v, relative to a referential attached to the tread-belt. The horizontal interrupted line represents the average vertical velocity of the *COM* over the stride ($\overline{V_v} = \overline{V_{belt}} \sin\theta$). Fourth row: V_f is the fore-aft velocity of the *COM*. The interrupted curve represents the instantaneous velocity of the belt in the fore-aft direction ($-V_{belt} \cos\theta$). The horizontal interrupted line represents the average fore-aft velocity of the *COM* over the stride ($\overline{V_f} = \overline{V_{belt}} \cos\theta$). Fifth row: vertical displacement of the centre of mass *S* divided into contact phase (continuous line) and aerial phase (dotted line). Tracings were recorded on a subject (height: 1.83 m, body mass: 68.4 kg, age: 24 years) running at ~3.6 m s^{-1} on the treadmill.

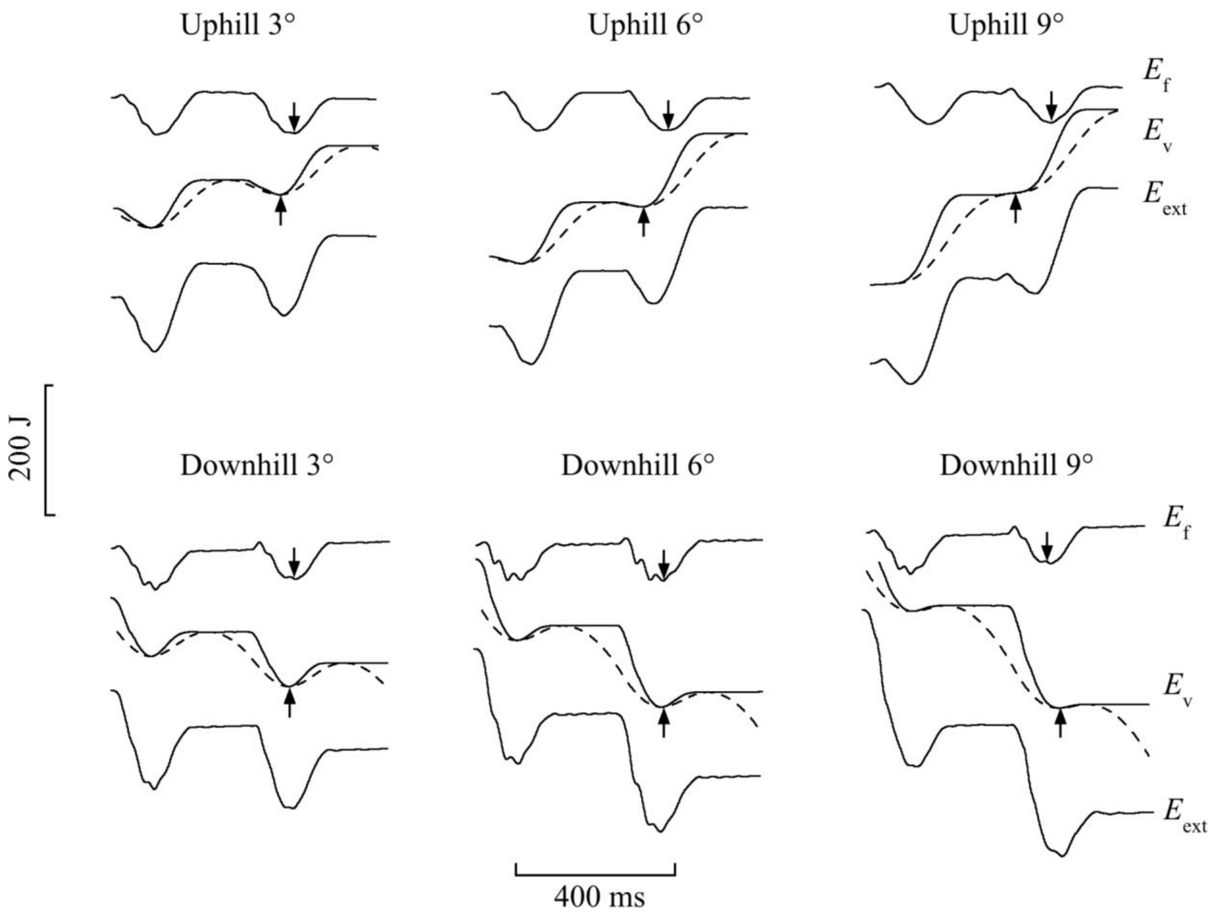
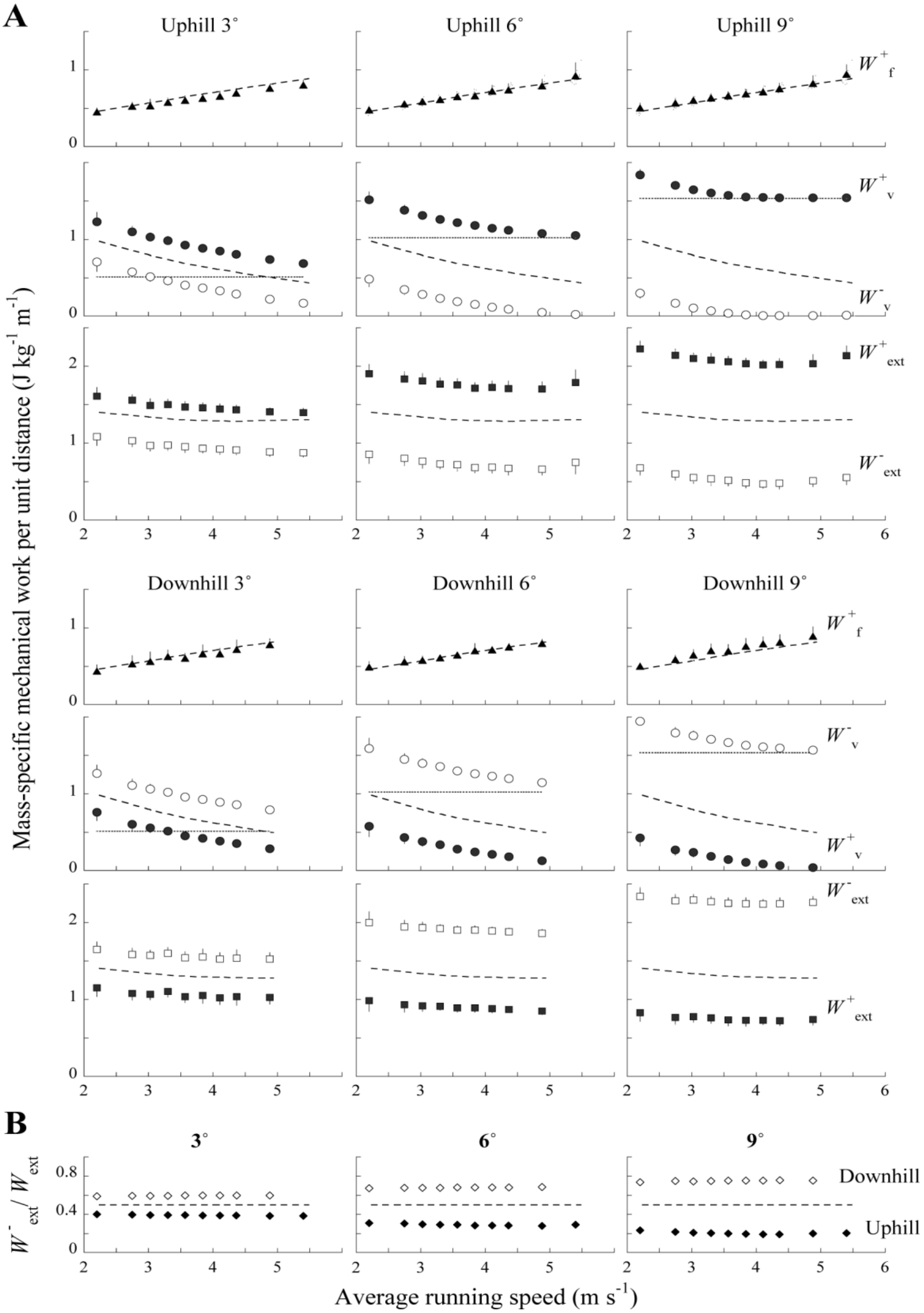


Fig. 2 Energy changes of the *COM* during a running stride

Mechanical energy-time curves of the *COM* during a stride on different slopes, while running at ~4.2 m s^{-1}. In each panel, the upper curve (E_f) refers to the kinetic energy due the forward motion of the *COM*, the middle curve (E_v) to the sum of the gravitational potential energy (interrupted line) and of the kinetic energy due the vertical motion of the *COM*, and the bottom curve ($E_{ext} = E_f + E_v$) to the total energy of the *COM*. The arrows pointing downwards indicate the minimum of E_f and the arrows pointing upwards the minimum of E_v during the contact phase of the second step. The horizontal segments of the energy-curves correspond to the aerial phase. Tracings were from the same subject than Fig. 1.



A
Uphill 3°
Uphill 6°
Uphill 9°
Downhill 3°
Downhill 6°
Downhill 9°
Mass-specific mechanical work per unit distance (J kg-1 m-1)
B
3°
6°
9°
Downhill
Uphill
W-ext / Wext
Average running speed (m s-1)

Fig. 3 Mass-specific external work per unit distance as a function of speed at each slope

A: At each slope, the mass-specific positive (closed symbols, superscript +) and negative (open symbols, superscript -) mechanical work done each step is given as a function of running speed. W_f is the work done to accelerate or to decelerate the *COM* (in this case, $W_f^+ = W_f^-$), W_v is the work to raise or lower the *COM* and W_{ext} is the muscular work actually done to sustain the movements of the *COM* relative to the surroundings. Symbols and bars represent the "grand mean" of the subjects (n=10, except for +6° at 5.6 m s^{-1} and +9° at 5.0 m s^{-1} where n= 9 and +9° at 5.6 m s^{-1} where n= 7) and the standard deviations (when the length of the bar exceeds the size of the symbol). In the middle panel, the horizontal lines represent the minimum work done to overcome the slope and the interrupted lines represent the work done during running on the level; these last lines were drawn through the experimental data (weighted mean, Kaleidagraph 4.5).

B: The bottom panel presents the ratio W_{ext}^- / W_{ext} as a function of speed. The open diamond indicates negative slopes whereas the closed diamond indicates positive slopes.

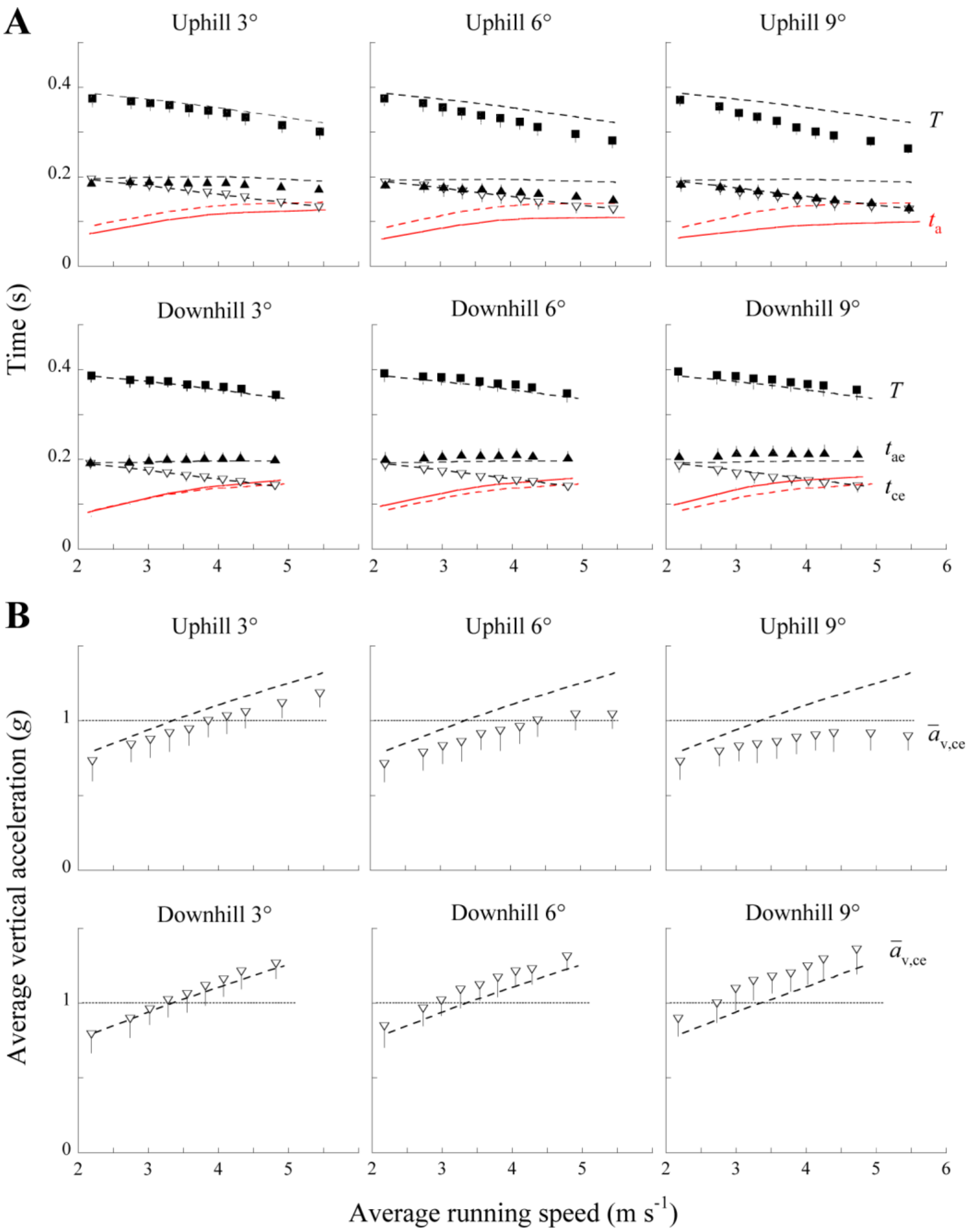


Fig. 4 Step duration and average vertical acceleration of the *COM* as a function of speed at each slope

A: At each slope, the filled squares indicate the step period (T), the open triangles the effective contact time (t_{ce}) and the closed triangles the effective aerial time (t_{ae}). The red lines represent t_a the aerial time. The interrupted lines are the results obtained on the level for T, t_{ce}, t_{ae} and t_a (weighted mean, Kaleidagraph 4.5).

B: At each slope, the open triangles indicate the average vertical acceleration of the *COM* during the effective contact time ($\overline{a_{v,ce}}$). Interrupted lines are the results obtained on the level and the horizontal dotted line represents 1 *g*.

Other indications as in Fig. 3.

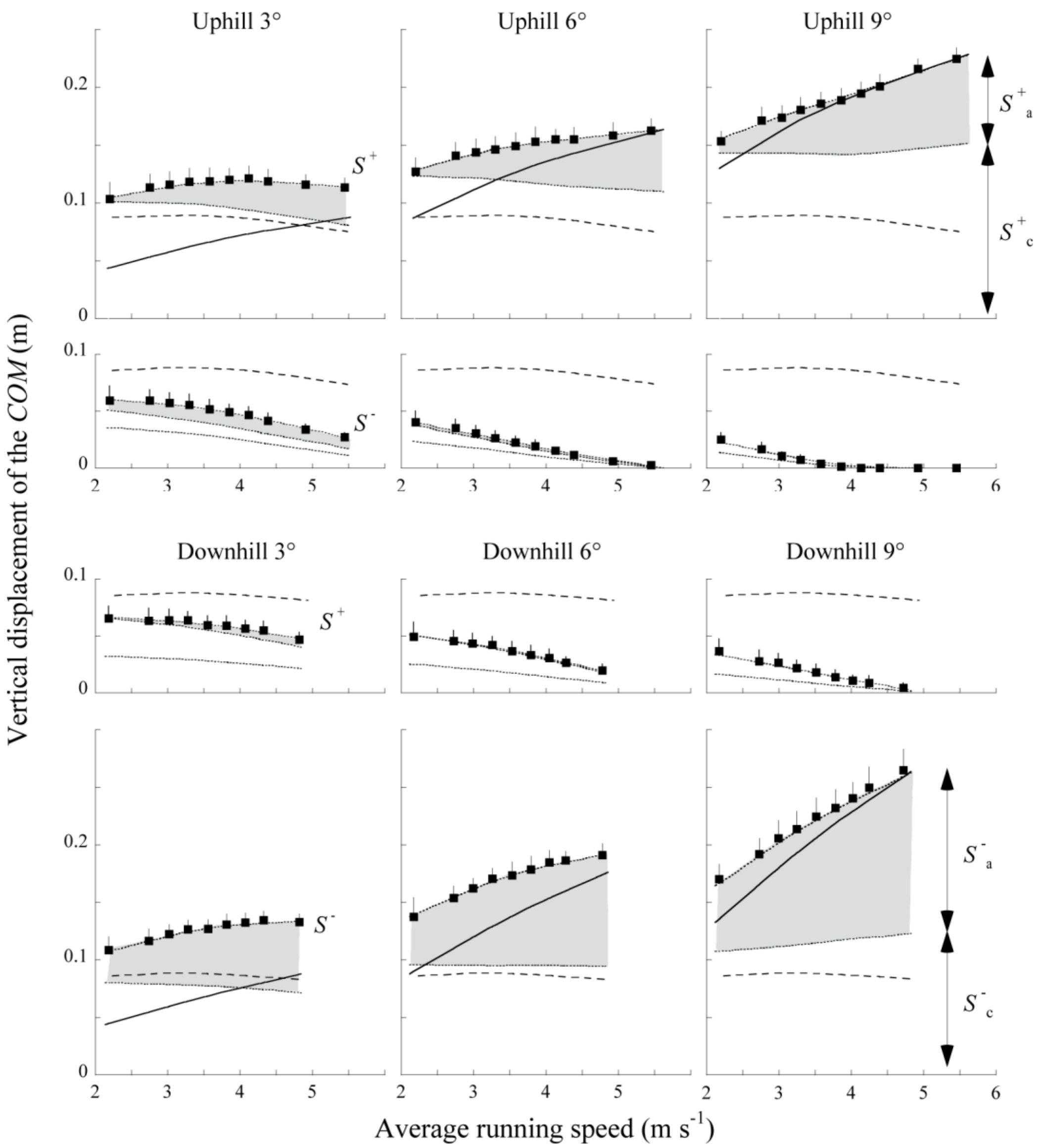


Fig. 5 Vertical displacement of the *COM* as a function of speed at each slope

At each slope, the filled squares indicate the upward (S^+, upper panel) and downward (S^-, bottom panel) vertical displacement of the *COM*. The grey zone (S_a) represents the fraction of the vertical displacement (S), taking place during the aerial phase, whereas S_c is the vertical displacement, taking place during contact. The interrupted lines indicate S during level running. The continuous line represents S_{min}, the minimum vertical displacement to overcome the slope during the step. Note that S_{min} increases with speed because the step length increases. Other indications as in Fig. 3.

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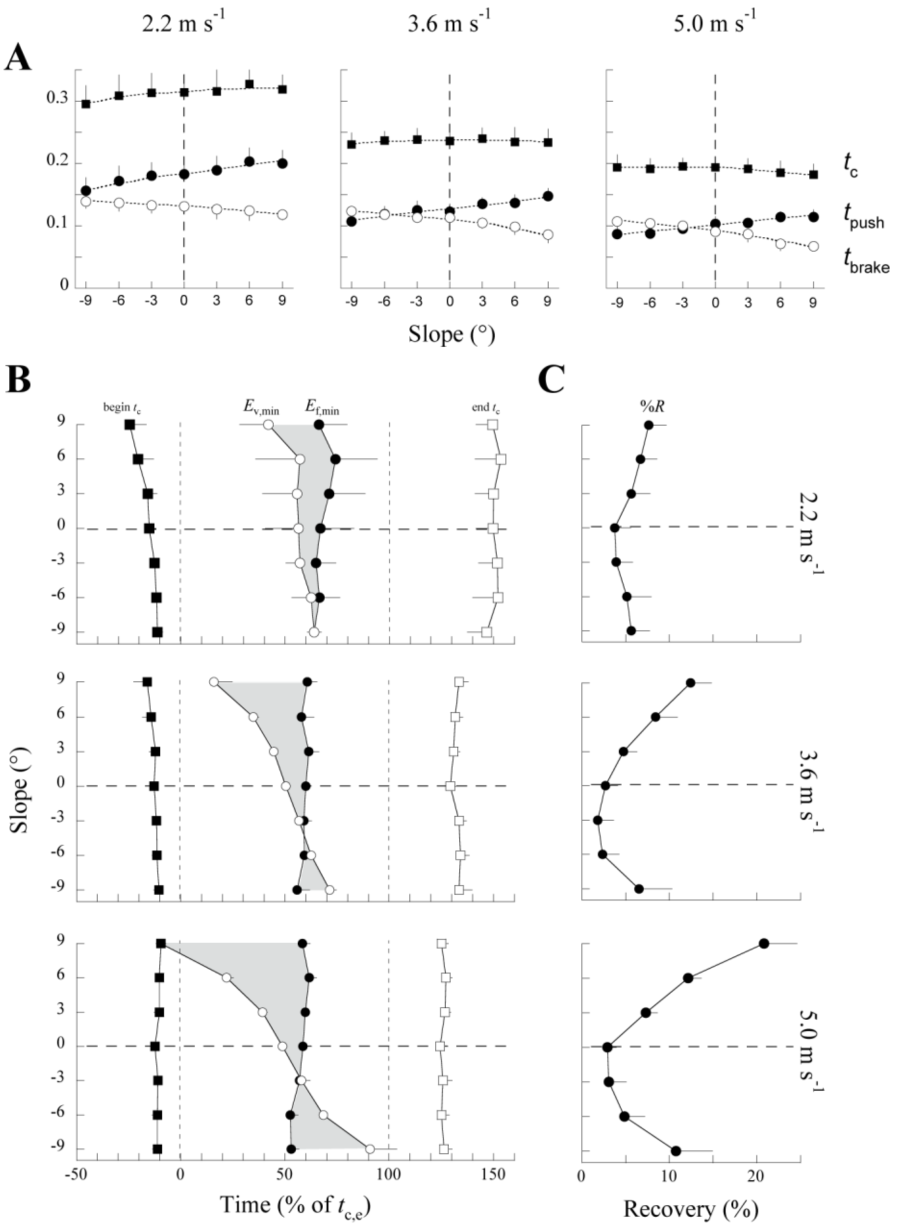

Fig. 6 Contact time & energy transduction between *E*f and *E*v during the contact phase as a function of slope at low, intermediate and fast speed

A: In each panel, the contact time (t_c, filled squares) is plotted as a function of slope and is divided into the time during which muscles perform positive external work (t_{push}, filled circles) and the time during which muscles perform negative external work (t_{brake}, open circles). The vertical interrupted lines correspond to running on the level. The dotted lines are drawn through the data (weighted mean, Kaleidagraph 4.5). Other indications as in Fig. 3.

B: The abscissa represents the relative time expressed as a % of t_{ce} and the ordinate represents the different slopes studied. Filled and open squares correspond respectively to the touchdown and take-off. The vertical interrupted lines represent the beginning and the end of t_{ce}. Note that the period between touchdown and the beginning of t_{ce} and the period between the end of t_{ce} and take-off change little with slope. Both the E_f and the E_v-curves decrease during the first part of contact, and increase during the second part (Fig. 2). The open and closed symbols represent respectively the time at which the E_v and the E_f-curves reach a minimum ($E_{v,min}$ and $E_{f,min}$). The grey zone illustrates the period during which an energy transduction between E_v and E_f is possible because one curve still decreases while the other already increases. Note that the instant of $E_{f,min}$ changes little with slope. As compared to level running, $E_{v,min}$ appears earlier in the stride on positive slopes and later on negative slopes.

C: The amount of energy recovered during the phase encompassed between the two minima of E_f and E_v, computed by equation (6) is presented at each slope for the three speeds.

In each panel, the horizontal interrupted lines correspond to running on the level. Other indications as in Fig. 3.

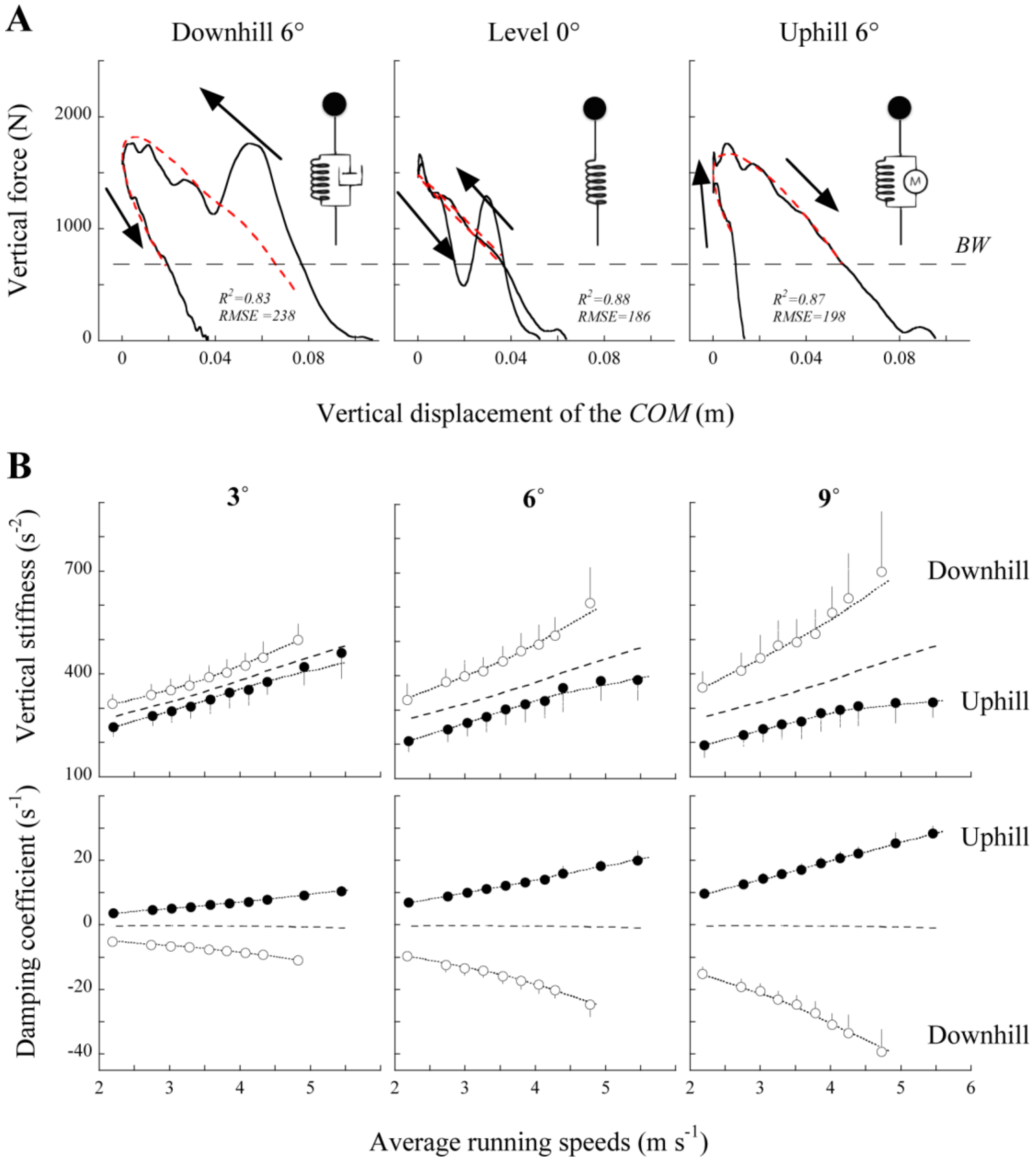

Fig. 7 Mechanical model of running on a slope

A: Typical trace of the vertical force F_v during the contact period (t_c) plotted as a function of vertical displacement S during running at ~3.6 m s^{-1}. The left panel corresponds to running at -6°, the middle panel to 0° and the right panel to +6°. The arrow pointed upwards indicates the downward movement of the *COM* taking place during the first part of t_c and the arrow pointed downwards indicates the upward movement of the *COM* taking place during the second part of t_c. The interrupted line corresponds to $F_v = BW$. The red dotted line corresponds to the predicted value of F_v computed by equation (9) during t_{ce} using the values of *b*, *k* and *c* obtained by the regression analysis. Tracings are from a male subject (height: 1.83 m, body mass: 70.0 kg, age: 31 years). The coefficient of determination, the root-mean-square error are indicated on each traces. The inset in each panel illustrates the model used in downhill (a spring in parallel with a damper), level (a single spring) and uphill (a spring in parallel with a motor) running.

B: The upper row presents the mass-specific vertical stiffness *k/m* as a function of speed and the lower row the mass-specific coefficient *c/m* of the actuator. The left column corresponds to a slope of 3° (open circles for downhill running and filled circles for uphill running), the middle column to a slope of 6° and the left column to 9°. Interrupted lines correspond to level running. The dotted lines are drawn through the data (weighted mean, Kaleidagraph 4.5). Other indications as in Fig. 3.

Table. 1 Coefficient of determination and root-mean-square error of the model

Slope (°)	Speed (m s^{-1})									
	2.2	2.8	3.1	3.3	3.6	3.9	4.2	4.4	5.0	5.6
9	0.80±0.04 217±45	0.80±0.04 232±52	0.78±0.04 246±51	0.77±0.05 250±55	0.76±0.05 254±54	0.75±0.05 259±49	0.74±0.07 269±53	0.72±0.05 280±46	0.70±0.04 280±52	0.66±0.06 307±37
6	0.86±0.03 182±35	0.87±0.03 188±42	0.87±0.03 194±43	0.86±0.03 206±43	0.85±0.02 210±43	0.84±0.03 226±48	0.83±0.04 234±48	0.82±0.04 242±51	0.77±0.03 276±50	0.75±0.05 295±54
3	0.93±0.01 139±29	0.92±0.01 146±31	0.92±0.02 155±33	0.91±0.02 167±35	0.90±0.02 178±28	0.89±0.02 189±33	0.87±0.02 209±29	0.86±0.03 216±33	0.82±0.06 258±43	0.75±0.1 312±52
0	0.94±0.02 120±29	0.92±0.03 153±37	0.90±0.05 175±48	0.87±0.04 200±37	0.86±0.06 210±39	0.84±0.05 238±49	0.80±0.07 264±51	0.78±0.07 291±55	0.72±0.1 347±71	0.68±0.1 400±89
-3	0.93±0.05 125±40	0.93±0.02 142±28	0.92±0.02 153±33	0.91±0.02 170±33	0.90±0.03 188±44	0.88±0.04 203±34	0.86±0.04 230±49	0.84±0.04 251±48	0.77±0.07 308±66	
-6	0.81±0.2 207±98	0.86±0.07 207±60	0.86±0.04 211±43	0.84±0.04 234±51	0.83±0.04 248±55	0.82±0.05 269±66	0.8±0.04 289±60	0.77±0.04 311±60	0.72±0.06 369±64	
-9	0.77±0.1 248±63	0.75±0.1 292±62	0.76±0.09 297±64	0.73±0.08 330±84	0.71±0.11 339±88	0.70±0.08 357±75	0.70±0.06 372±73	0.68±0.06 392±82	0.63±0.1 444±91	

The mass-specific stiffness (*k/m*) and damping/motor coefficient (*c/m*) during t_{ce} were evaluated using a least square method.
In each class, the first line corresponds to the coefficient of determination r^2 of the least square method and the second line to the *Root Mean Square Error* (expressed in Newton).
Each class are the 'grand mean' (see methods) ± Standard Deviation. In each class, *n*=10 except for (+6°; 5.6 m s^{-1}) and (+9°; 5.0 m s^{-1}) where *n*= 9 and for (+9°; 5.6 m s^{-1}) where *n*= 7.