

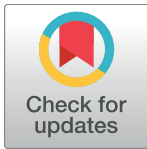
RESEARCH ARTICLE

Pendular energy transduction within the step during human walking on slopes at different speeds

Arthur H. Dewolf¹, Yuri P. Ivanenko², Francesco Lacquaniti^{2,3}, Patrick A. Willems^{1*}

1 Laboratory of Biomechanics and Physiology of Locomotion, Institute of NeuroScience, Université Catholique de Louvain, Louvain-la-Neuve, Belgium, **2** Laboratory of Neuromotor Physiology, IRCCS Santa Lucia Foundation, Rome, Italy, **3** Department of Systems Medicine and Center of Space BioMedicine, University of Rome Tor Vergata, Rome, Italy

* patrick.willems@uclouvain.be



Abstract

When ascending (descending) a slope, positive (negative) work must be performed to overcome changes in gravitational potential energy at the center of body mass (COM). This modifies the pendulum-like behavior of walking. The aim of this study is to analyze how energy exchange and mechanical work done vary within a step across slopes and speeds. Ten subjects walked on an instrumented treadmill at different slopes (from -9° to 9°), and speeds (between 0.56 and 2.22 m s^{-1}). From the ground reaction forces, we evaluated energy of the COM, recovery (i.e. the potential-kinetic energy transduction) and pendular energy savings (i.e. the theoretical reduction in work due to this recovered energy) throughout the step. When walking uphill as compared to level, pendular energy savings increase during the first part of stance (when the COM is lifted) and decrease during the second part. Conversely in downhill walking, pendular energy savings decrease during the first part of stance and increase during the second part (when the COM is lowered). In uphill and downhill walking, the main phase of external work occurs around double support. Uphill, the positive work phase is extended during the beginning of single support to raise the body. Downhill, the negative work phase starts before double support, slowing the downward velocity of the body. Changes of the pendulum-like behavior as a function of slope can be illustrated by tilting the 'classical compass model' backwards (uphill) or forwards (downhill).

OPEN ACCESS

Citation: Dewolf AH, Ivanenko YP, Lacquaniti F, Willems PA (2017) Pendular energy transduction within the step during human walking on slopes at different speeds. PLoS ONE 12(10): e0186963. <https://doi.org/10.1371/journal.pone.0186963>

Editor: Steven Allen Gard, Northwestern University, UNITED STATES

Received: August 16, 2017

Accepted: October 10, 2017

Published: October 26, 2017

Copyright: © 2017 Dewolf et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This study was funded by the Université catholique de Louvain (Belgium), the Fonds de la Recherche Scientifique (Belgium), the Italian Ministry of Health (IRCCS Ricerca corrente), Italian Space Agency (grant n. I/006/06/0) (COREA grant 2013-084-R.0), Italian Ministry of University and Research (PRIN grant 2015HFWRYY_002) and Horizon 2020 Robotics Program (ICT-23-2014 under Grant Agreement 644727-CogIMon). The

Introduction

In human walking, kinetic (E_k) and gravitational potential (E_p) energies of the center of mass of the body (COM) are largely out of phase, resulting in an exchange between these two forms of energies [1]. The present study is intended to provide a detailed description of the change in the fluctuation of the energy of the COM, by assessing the changes in pendulum-like exchange between E_k and E_p , and in the mechanical work required to sustain the motion of the COM (W_{ext}) with slope of the terrain and speed of progression during human walking.

The exchange between E_k and E_p appears after the age of one year [2, 3]. In adults, the fluctuation of the energy of the COM is known to change in various walking conditions: with

fundlers had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Abbreviations: a_x , horizontal component of the acceleration of the COM in the fore-aft direction; a_y , lateral component of the acceleration of the COM; a_z , vertical component of the acceleration of the COM; COM, center of mass of the whole body; E_{ext} , External work, work necessary to move the COM relative to the surroundings; E_{ext} , mechanical energy of the COM; E_{kf} , E_{kl} , E_{kv} , kinetic energy due to the fore-aft, lateral and vertical movements of the COM; E_k , E_p , kinetic and potential energy of the COM; $E_{k,min}$, $E_{k,max}$, local minimum and maximum of the E_k -time curve; $E_{p,min}$, $E_{p,max}$, local minimum and maximum of the E_p -time curve; E_s , pendular energy savings, i.e. amount of energy saved over a given period of time through the E_k - E_p transduction; $\dot{e}(t)$, rate of pendular energy savings; amount of energy economized through the transduction between E_p and E_k divided by the time between two samples; F_x , horizontal component of the GRF in the fore-aft direction; F_y , component of the GRF parallel to the short axis of the tread-surface; F_n , component of the GRF perpendicular to the tread-surface; F_p , component of the GRF parallel to the long axis of the tread-surface; F_v , vertical component of the GRF; g , acceleration of gravity; GRF, ground reaction force; m , body mass; R_{avg} , percentage of energy recovered during a phase of the step through the transduction between E_p and E_k ; R_{step} , percentage of energy recovered during the whole step through the transduction between E_p , E_{kv} and E_{kf} ; $r(t)$, instantaneous recovery: percentage of energy recovered between two samples through the transduction between E_p and E_k ; t , time; T1, period of the step during which E_p increases while E_k decreases, i.e. period more or less during the first part of the contact phase when the COM increases its height; T2, period of the step during which E_p and E_k are in phase, period between T1 and T3, i.e. more or less in the middle of the contact phase; T3, period of the step during which E_p decreases while E_k increases, i.e. period more or less during the second part of the contact phase when the COM loses height; T4, period of the step during which E_p and E_k are in phase, period between T3 and T1, i.e. more or less at the very end of the contact phase; θ , slope of the treadmill, i.e. angle between horizontal and the tread-surface; v_{belt} , instantaneous velocity of the belt of the treadmill; v_x , horizontal component of the velocity of the COM in the fore-aft direction; v_y , lateral component of the

walking speed [1], with the softness of the ground [4] or with the slope of the terrain [5–7]. Furthermore, African women are able to carry head-supported loads of up to 20% of their body weight for ‘free’ while enhancing the E_k - E_p transduction [8, 9].

The E_k - E_p transduction is classically evaluated over an entire step by measuring the recovery, R_{step} [1], defined as the ratio between the work theoretically saved by the pendulum-like energy exchange and the work theoretically performed assuming no energy transduction. When walking on the level ground, R_{step} varies with speed, in part because the amplitudes of the E_k -time and of the E_p -time curves change differently with speed [1].

When walking on a slope at a steady speed, the trajectory of the COM is modified since the body must gain/lose height each stride. This change in the trajectory will affect the pendulum-like exchange between E_p and E_k , since the average level of E_p changes continuously whereas the average level of E_k remains constant. Consequently, R_{step} is also altered when walking on a slope.

Minetti et al. [10], Minetti and Ardigo [11] and Gottschall and Kram [5] observed that the E_k - E_p transduction still occurs during walking even on steep positive or negative slopes. As compared to level walking, they reported that the E_k - E_p exchange is reduced when ascending. When descending, Gottschall and Kram [5] observed an increase of the energy transduction. Note that these authors estimated the pendular energy transduction after factoring out the changes in E_p due to slope, which cancels the asymmetric fluctuation of the E_p vs time curve. In two recent studies, Gomeñuka et al. [6] and Gomeñuka et al. [7] have also observed that R_{step} is reduced and that the speed at which R_{step} is maximal is higher when walking uphill. However, it remains unclear why R_{step} is reduced and why the speed at which R_{step} is maximal is increased.

The variable R_{step} is computed over the whole step and does not help understanding how the E_k - E_p transduction changes throughout the duration of a step. To our knowledge, no study has measured the time course of this transduction. For this purpose, we have calculated the ‘within-step recovery’, $r(t)$, which evaluates the E_p - E_k transduction at each instant t of the walking step [8]. In this way, it is possible to separately assess the transduction of E_p into E_k and of E_k into E_p during the different phases of the step.

Perfect energy recovery of 100% at any phase of the step cycle would indicate that the changes in potential energy mirror the changes in kinetic energy. However, this does not provide any insight into the magnitude of mechanical energy changes (in Joules). Therefore, we introduce here a new variable: the theoretical ‘pendular energy savings’ within the step (E_s), which represents the magnitude of energy exchanged, i.e. the difference between the sum of E_p and E_k assuming no transduction and the external work actually done when the E_p - E_k transduction occurs. In other words, the new parameter E_s , designed to quantify the effectiveness of the transduction between E_p and E_k in the different phases of the step, extends the information given by $r(t)$. Indeed, E_s offers the possibility to determine the periods of the step where, despite high $r(t)$, the E_p - and E_k -curves are flattened, resulting in a small amount of energy exchange.

Despite the pendulum-like exchange of energy, work must be done to sustain the movement of the COM relative to the surroundings. For example, when analyzing the energy curves of the COM, positive work must be done during two phases of the step: the first (named phase *a* by Cavagna et al [1]) occurs close to the bottom of the COM trajectory to give a push forward, and the second one (named phase *b*) occurs close to the top of the COM trajectory to complete its vertical lift. According to Kuo et al. [12] mechanical work is predominantly required to redirect the COM velocity vector during step-to-step transitions. Furthermore, the continuous changes in potential energy on slopes affect the amount and the time pattern of

velocity of the COM; v_v , vertical component of the velocity of the COM; W_{ext}^+ , W_{ext}^- , positive and negative work due to the time-changes in E_{com} ; W_f^+ , W_f^- , positive and negative work due to the time-changes in E_k ; W_k^+ , W_k^- , positive and negative work due to the time-changes in E_k ; W_i^+ , W_i^- , positive and negative work due to the time-changes in E_k ; W_{min} , minimal work done per unit distance to overcome the slope; W_p^+ , W_p^- , positive and negative work due to the time-changes in E_p ; W_v^+ , W_v^- , positive and negative work due to the time-changes in $E_p + E_{kv}$.

positive or negative work production. Therefore, the amount of positive and negative external work performed throughout the step was also measured.

The present study is intended to provide more quantitative details on the time-varying changes of the energy at COM during each step, when walking on various slopes at different speeds. This is done by including an estimate of the exchange of energy and of the amount of energy saved, at each instant of the walking step. Therefore, the following variables are assessed: (1) the 'within-step recovery', which quantify the out-of-phase fluctuation of E_p and E_k ; (2) the 'pendular energy savings', which evaluates the effectiveness of the transduction that occurs and (3) the positive and negative external work done despite energy savings. Identification of the changes of E_p - E_k transduction and external work production shed light on one potential mechanism that could minimize muscle work during slope ascent and descent.

Methods

Subject and experimental procedure

Ten healthy subjects (6 ♂ & 4 ♀, age: 22.2 ± 2.4 y, mass: 69.2 ± 14.4 kg, height: 1.75 ± 0.10 m, mean \pm SD) gave their written informed consent to participate to the experiences. The study followed the guidelines of the Declaration of Helsinki, and the procedures were approved by the Ethic Committee of the Université catholique de Louvain (Ref. number: 2015/06JUL/372).

Subjects walked on an instrumented treadmill mounted on wedges of different inclinations: 0° , 3° , 6° and 9° (corresponding to 0%, 5.2%, 10.5%, 15.8% respectively). Note that some subject did not walk at all slopes (Table 1). Each trial lasted about 45 s and data were recorded during the last 30 s. At each slope, half the subjects started with uphill walking and the other half with downhill walking. In order to neutralize the effect of learning and muscle fatigue, half of the subjects started with an inclination of 0° that was progressively increased and the other half with an inclination of 9° that was progressively decreased. Furthermore, the resting period between each trial lasted at least 3' (>15' when the slope of the treadmill had to be changed). At each slope, subjects walked at 7 speeds (from 0.56 to 2.22 m s⁻¹, i.e. 2 to 8 km h⁻¹). Some subjects started to run at the highest speed and these trials were rejected (Table 1). Between 6 and 36 strides per trials were recorded (Table 2) and a total of 8,864 strides were analyzed.

Experimental setup and data analysis

The instrumented treadmill consisted of a modified commercial treadmill (h/p/Comos-Stellar, Germany). The whole treadmill was mounted on four strain-gauge force transducers (Arsalis, Belgium) that measure the three components of the force exerted by the feet on the belt (GRF): 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 [13]. Data were sampled at a frequency of 500 Hz. From these data, the vertical (F_v) and horizontal forward (F_f) component

Table 1. Number of subjects in each slope/speed class.

	-9°	-6°	-3°	0°	3°	6°	9°
0.56 m s ⁻¹	8	8	6	10	6	8	8
0.83 m s ⁻¹	8	8	6	10	6	8	8
1.11 m s ⁻¹	8	8	6	10	6	8	8
1.39 m s ⁻¹	8	8	6	10	6	8	8
1.67 m s ⁻¹	8	8	6	10	6	8	8
1.94 m s ⁻¹	8	8	6	10	6	8	8
2.22 m s ⁻¹	5	6	5	8	5	6	5

<https://doi.org/10.1371/journal.pone.0186963.t001>

Table 2. Minimum and maximum number of steps averaged for each subject in each slope/speed class.

	-9°	-6°	-3°	0°	3°	6°	9°
0.56 m s ⁻¹	22/36	20/40	12/24	12/36	22/32	26/34	14/36
0.83 m s ⁻¹	38/48	40/46	36/44	26/44	36/42	32/44	36/44
1.11 m s ⁻¹	42/56	46/52	46/54	42/50	44/48	42/48	42/50
1.39 m s ⁻¹	42/62	50/56	48/58	48/54	48/54	44/54	46/54
1.67 m s ⁻¹	34/60	52/60	52/64	44/60	50/58	50/58	50/60
1.94 m s ⁻¹	58/66	54/66	56/68	44/66	54/64	48/62	56/66
2.22 m s ⁻¹	50/68	48/68	42/62	60/72	60/70	60/68	52/66

<https://doi.org/10.1371/journal.pone.0186963.t002>

of the GRF were computed as:

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

where θ is the angle of the treadmill relative to level ground.

The acceleration, velocity and the displacement of the COM were determined from the GRF using the procedure described in detail in Dewolf et al. [13]. In short, the horizontal, lateral and vertical acceleration of the COM were respectively computed as $a_f = F_f/m$, $a_l = F_l/m$ and $a_v = (F_v - m g)/m$, where m is the subject’s body mass and g is acceleration due to gravity. The instantaneous velocity in the forward (v_f), lateral (v_l) and vertical (v_v) directions were obtained by integration of a_f , a_l and a_v plus an integration constant. In the fore-aft direction, this constant was chosen to make the average velocity over all the strides of the trial equal to $v_{belt} \cos\theta$ (v_{belt} is the velocity of the tread-belt measured with an optical encoder). In the two other directions, constants were chosen to make the average lateral velocity over each stride equal to zero and the average vertical velocity over each stride equal to $v_{belt} \sin\theta$. A second integration of the vertical velocity yields the vertical displacement of the COM.

Division of the step. Steps were divided according to the maximum of v_f . Steps were grouped in strides composed of a right step followed by a left step. A stride was considered to be suitable for analysis if (1) \bar{F}_v was within 5% of body weight and (2) the sum of the increments and the sum of the decrements of v_f differed less than 25%. Foot contact and toe-off were estimated from the displacement of the center of pressure on the belt [14].

Estimates of the positive and negative external work. The energy of the COM (E_{ext}) was calculated from the GRF following the methods of Gosseye et al. [15]; E_{ext} was the algebraic sum at each instant of its gravitational potential energy E_p and of its kinetic energy E_k . E_k was calculated as the sum of E_{kf} , the kinetic energy due to the forward movements of the COM, E_{kl} the kinetic energy due to its lateral movements and E_{kv} the kinetic energy due to its vertical movements.

External work is defined here as the work necessary to move the COM relative to the surroundings [16], i.e. the work needed to increase and decrease energy of the COM. Positive (W_{ext}^+) and negative (W_{ext}^-) COM work was computed by summing the increments and the absolute value of the decrements of the E_{ext} curve, respectively. Similarly, W_k^+ , W_k^- , W_p^+ and W_p^- were computed by summing respectively the increments and the absolute value of the decrements of the E_k and E_p curves (Figs 1, 2 & 3). Increments in the curves were considered to represent work only if the time between two successive extrema was greater than 20 ms. Based on the data of this study, the work done on/by the belt of the treadmill is <2% of ($W_{ext}^+ + |W_{ext}^-|$). Therefore, it was not taken into account.

0.83 m s⁻¹

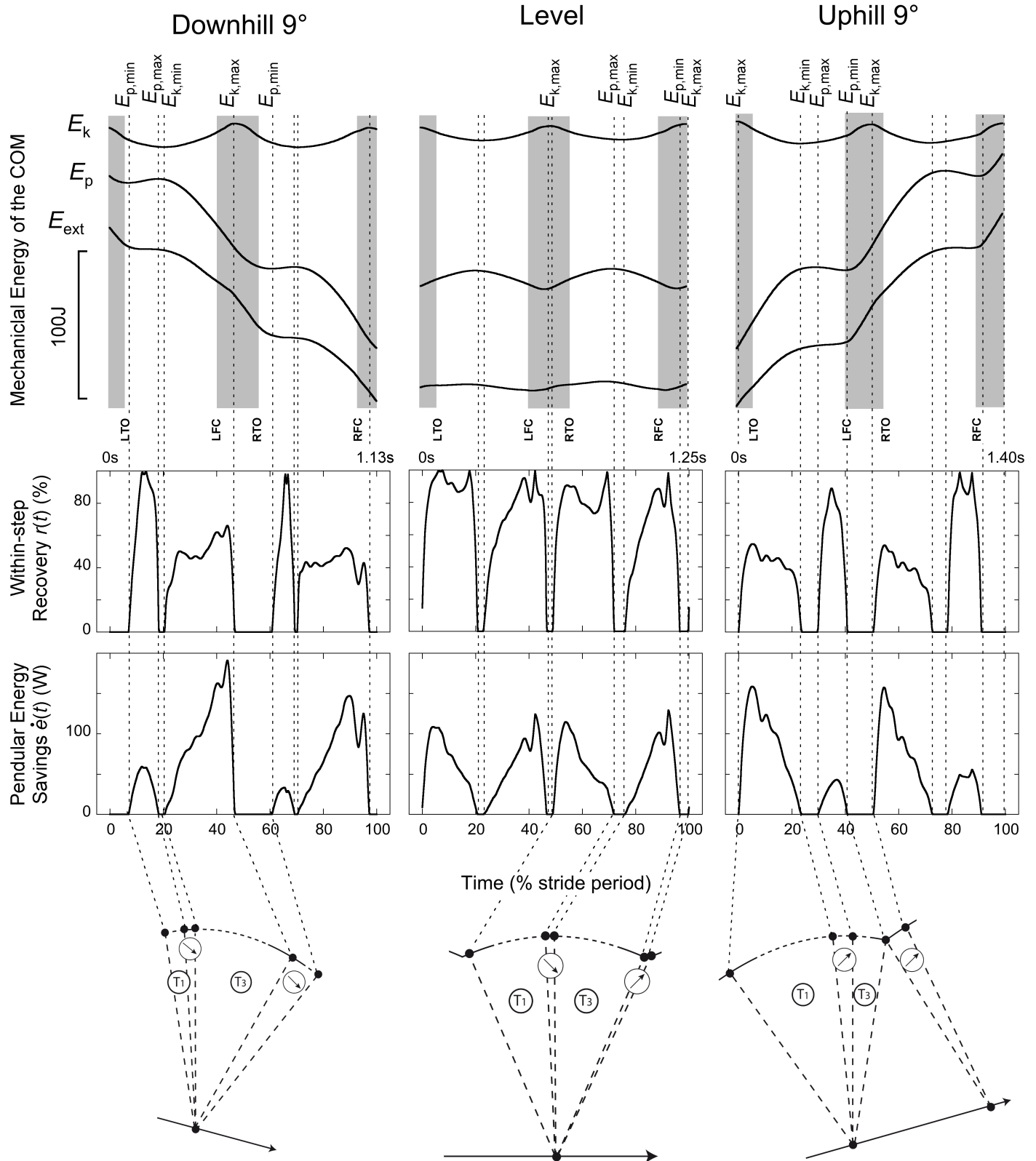


Fig 1. Typical time-traces of a subject walking at $\sim 0.83 \text{ m s}^{-1}$ (3 km h^{-1}) on a -9° slope (left column), on the level (middle column) and on a $+9^\circ$ slope (right column). Top panels: Mechanical energy-time curves of the COM during a stride. Strides are delimited by the maximal fore-aft velocity of the COM when the right foot is in front. The upper curve (E_k) refers to the kinetic energy of the COM, the middle curve (E_p) to its gravitational potential energy and the bottom curve ($E_{\text{ext}} = E_k + E_p$) to the total energy of the COM. The grey zones correspond to the double contact periods (starting at right or left foot contact -RFC or LFC- and ending at right or left toe-off -RTO or LTO). The vertical interrupted lines correspond to the extrema of the E_k and E_p curves. Note that these energy-time curves are qualitatively similar to the one obtained by Gottschall and Kram (2006). **Middle panels:** Instantaneous recovery ($r(t)$, Eq 3) at each instant t of the stride. The recovery $r(t)$ varies from 0% when the E_k and E_p curves are in phase, to 100% when the decrease of one curve equals the increase of the other. When $r(t) = 100\%$, E_{ext} is constant and no external work is done to move the COM relative to the surroundings. **Lower panels:** Rate of pendular energy savings ($\dot{e}(t)$, Eq 4) at each instant t of the stride. These curves represent the rate at which energy is economized through the transformation of kinetic into potential energy (or *vice versa*). Time is expressed as a percentage of the stride period. Tracings were recorded on a male subject (height: 1.82 m, body mass: 74.3 kg, age: 24.7 y.o.). **Lower schemas:** The schemas represent the 'compass walking' model with the approximate division of one step of the stride into the four phases T1, T2, T3 & T4 (see methods) during downhill, level and uphill walking. During T1, E_k decreases while E_p increases, during T3 E_k increases while E_p decreases. During T2 and T4, both E_k and E_p increase or decrease (arrows).

<https://doi.org/10.1371/journal.pone.0186963.g001>

Recovery over the step. To evaluate the pendulum-like energy exchange, Cavagna et al. [1] proposed to estimate the relative amount of energy recovered by the transduction between energy due to the vertical motion of the COM ($E_p + E_{kv}$) and energy due to its forward motion (E_{kf}). Here, we have also added the work due to the lateral movement of the COM. The relative amount of energy saved over a step (R_{step} in %) can then be computed as:

$$R_{\text{step}} = 100 \frac{W_f^+ + |W_f^-| + W_v^+ + |W_v^-| + W_l^+ + |W_l^-| - [W_{\text{ext}}^+ + |W_{\text{ext}}^-|]}{W_f^+ + |W_f^-| + W_v^+ + |W_v^-| + W_l^+ + |W_l^-|}, \quad (2)$$

where W_f^+ and W_f^- are the sum of respectively the increments and the absolute value of the decrements of the E_{kf} vs. time curve, W_v^+ and W_v^- the sum of respectively the increments and the absolute value of the decrements of the $E_p + E_{kv}$ vs. time curve and W_l^- and W_l^+ the sum of respectively the increments and the absolute value of the decrements of the E_{kl} vs. time curve. Of note, R_{step} has also been defined in prior literature based on E_k and E_p [17]. These authors have shown that this formulation yields similar results to those from Eq 2.

Recovery and pendular energy savings within the step. In order to identify periods within each step during which a $E_p - E_k$ transduction occurs, Cavagna et al. [8] proposed to estimate the within-step recovery at each instant t of the step ($r(t)$ in %) from the absolute value of the kinetic and potential energy changes:

$$r(t) = 100 \frac{|E_k(t) - E_k(t - \Delta t)| + |E_p(t) - E_p(t - \Delta t)| - |E_{\text{ext}}(t) - E_{\text{ext}}(t - \Delta t)|}{|E_k(t) - E_k(t - \Delta t)| + |E_p(t) - E_p(t - \Delta t)|}, \quad (3)$$

where Δt is the time between two samples.

To evaluate the theoretical amount of mechanical power saved by this recovery, we introduce a new outcome, the theoretical rate of pendular energy savings, $\dot{e}(t)$, computed as:

$$\dot{e}(t) = \frac{|E_k(t) - E_k(t - \Delta t)| + |E_p(t) - E_p(t - \Delta t)| - |E_{\text{ext}}(t) - E_{\text{ext}}(t - \Delta t)|}{\Delta t}. \quad (4)$$

Typical COM energy, $r(t)$ and $\dot{e}(t)$ curves are presented in Figs 1, 2 & 3. Two additional summary metrics were computed over four periods of the steps: (1) R_{avg} was defined as the average of $r(t)$ over each period and (2) E_s , the amount of pendular energy savings, was defined as the time-integral of $\dot{e}(t)$ over each period. Four periods (T1-T4) were defined according to the local maxima and minima of E_k and E_p : the first period T1 occurs when E_p increases while E_k decreases; a subsequent period T3 occurs when E_p decreases while E_k increases; between T1 and T3 and between T3 and T1, we define the period T2 and T4 respectively, where E_p and E_k changes are in phase.

1.39 m s⁻¹

Downhill 9°

Level

Uphill 9°

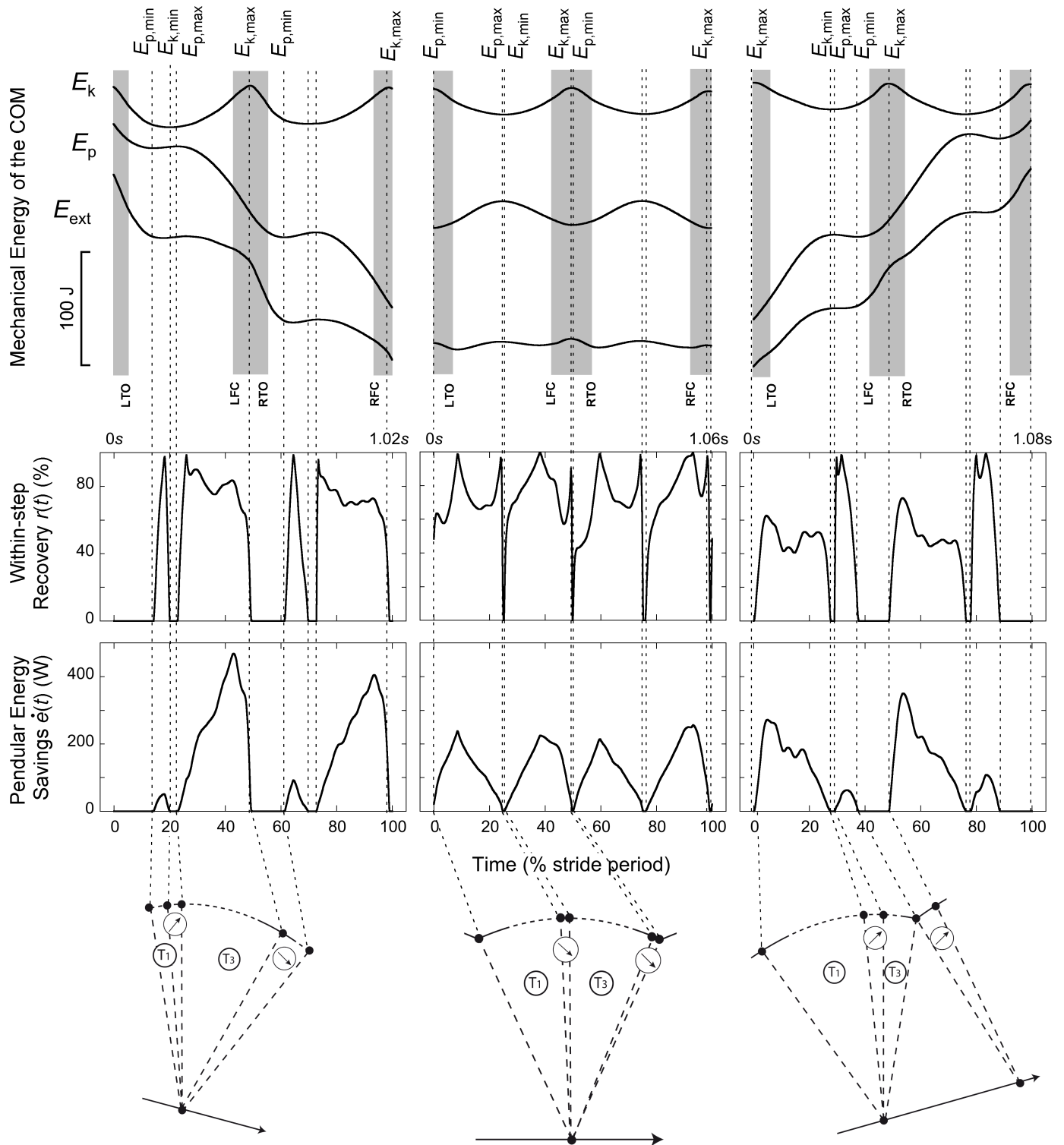


Fig 2. Typical time-traces of a subject walking at $\sim 1.39 \text{ m s}^{-1}$ (5 km h^{-1}) on a -9° slope (left column), on the level (middle column) and on a $+9^\circ$ slope (right column). Same indications as in Fig 1.

<https://doi.org/10.1371/journal.pone.0186963.g002>

Statistics

Data were grouped into speed-slope classes. Each stride was divided into a right and left step. In order to obtain one value per subject in each class, both right and left steps of a subject in a given class were averaged. The mean and standard deviation of the population were then computed in each class (grand mean). The variables were analyzed across all conditions using a repeated measures ANOVA with post-hoc Bonferroni correction to assess the difference between conditions (PASW Statistics 19, SPSS inc®, IBM company, USA). The normality of the residuals was checked visually with QQ-plots and was assumed for all variables. An α -threshold of 0.05 was used throughout to assess statistical significance.

Results

Work and recovery

External work and recovery of mechanical energy over the whole walking step (R_{step}) are presented as a function of speed when walking uphill (Fig 4) and downhill (Fig 5). W_f^+ and W_f^- increase with speed at all slopes ($F_{6,363} = 343.8, p < 0.001$). At a given speed, since the average velocity over the successive steps is constant, $W_f^+ \approx W_f^-$. However, as compared to level walking, W_f^+ and W_f^- are each slightly larger in magnitude during downhill walking and slightly smaller during uphill walking ($F_{6,363} = 30.2, p < 0.001$).

When walking on a flat terrain, $W_v^+ \approx W_v^-$ over each step. When walking on a positive slope, W_v^+ increases while W_v^- decreases as compared to level walking. On a steep positive slope, W_v^- is nil at the highest speed because the $E_p + E_{kv}$ vs. time curve increases monotonically. When walking on a negative slope, W_v^+ decreases while W_v^- increases. On a steep negative slope, W_v^+ is nil at the slowest and highest speeds because the $E_p + E_{kv}$ vs. time curve decreases monotonically.

The difference between W_v^+ and W_v^- on an incline causes an imbalance between W_{ext}^+ and W_{ext}^- . When walking uphill on a shallow slope (Fig 4), W_{ext}^- is reduced as compared to level walking. When the slope become steeper, W_{com}^- is almost nil at all speeds and the W_{com}^+ is equal to the minimum work required to overcome the slope (W_{min}). Consequently, R_{step} is reduced as compared to level walking: its maximum decreases from 68% on the level to 63% at $+3^\circ$, to 53% at $+6^\circ$ and to 45% at $+9^\circ$. Note that the speed at which R_{step} is maximal is greater than on level ground: 1.30 m s^{-1} at 0° , 1.55 m s^{-1} at $+3^\circ$, 1.65 m s^{-1} at $+6^\circ$ and 1.75 m s^{-1} at $+9^\circ$.

When walking downhill, W_{ext}^+ decreases with the slope but increases slightly with speed at each gradient. W_{ext}^+ is greater than W_{min} at all speeds (except at the lowest speed at -6° and -9°). As on a positive slope, R_{step} decreases when the negative slope increases: R_{step} decreases to 62% at -3° , to 50% at -6° and to 38% at -9° . Here also, the speed at which R_{step} is maximal is greater than on level ground: 1.53 m s^{-1} at -3° , 1.48 m s^{-1} at -6° and 1.46 m s^{-1} at -9° .

Time course of the instantaneous recovery and rate of pendular energy savings within the stride

Figs 1, 2 & 3 present typical traces of E_k , E_p , E_{ext} , $r(t)$ and $\dot{e}(t)$ during a walking stride (two steps). During T1 and T3, $r(t) > 0$ and $\dot{e}(t) > 0$ since E_k can be transformed into E_p or *vice-versa*; during T1, E_k decreases while E_p increases, whereas during T3, E_k increases while E_p

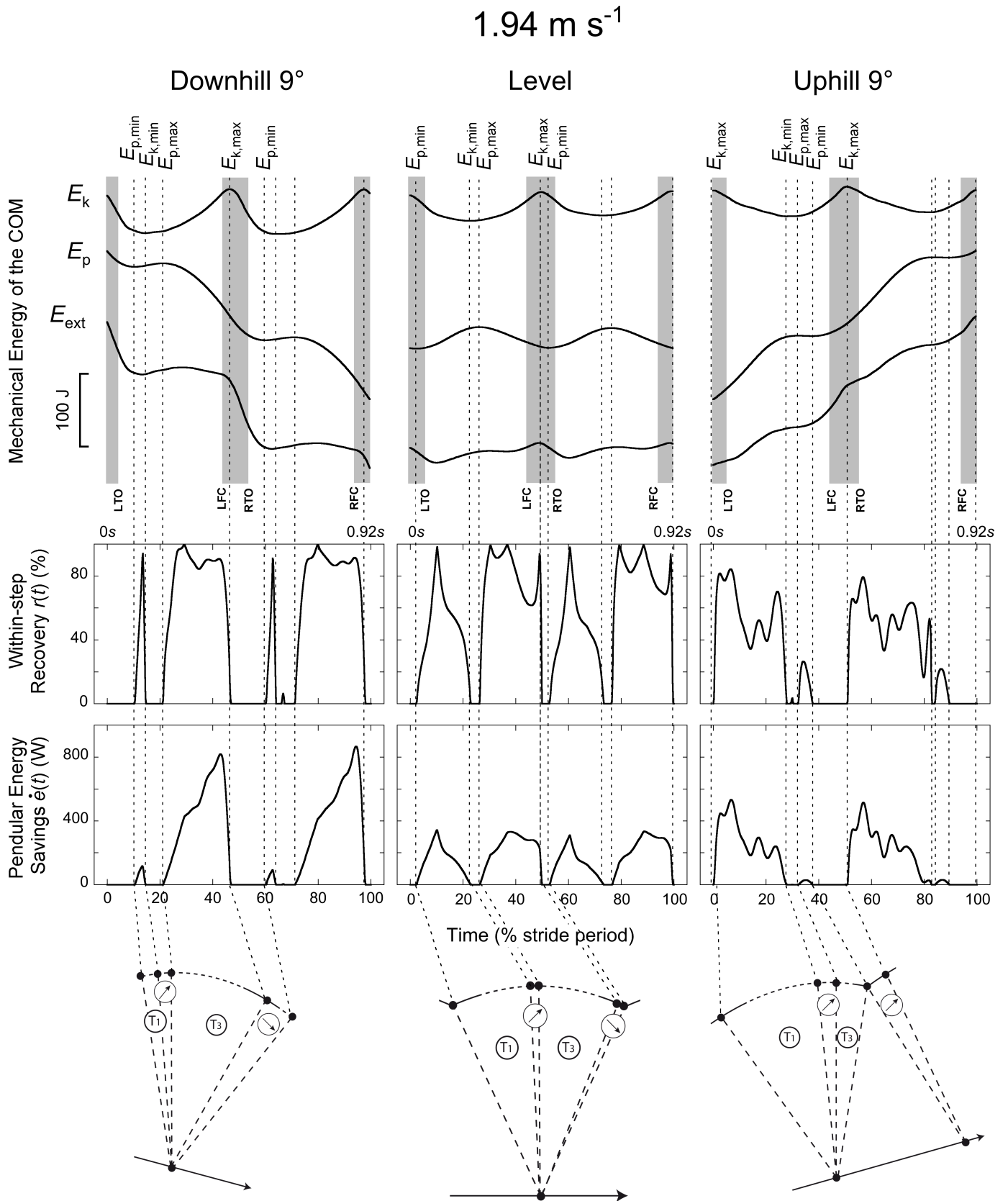


Fig 3. Typical time-traces of a subject walking at $\sim 1.94 \text{ m s}^{-1}$ (7 km h^{-1}) on a -9° slope (left column), on the level (middle column) and on a $+9^\circ$ slope (right column). Same indications as in Fig 1.

<https://doi.org/10.1371/journal.pone.0186963.g003>

decreases. During T2 and T4, E_k and E_p are both increasing or decreasing (depending on slope and speed of progression). Since these two curves are in phase, $r(t) = 0$ and $\dot{e}(t) = 0$.

When walking on a positive or negative slope, the duration of the different phases changes as compared to level walking (Figs 1, 2 & 3). When walking on a flat terrain, the duration of T1

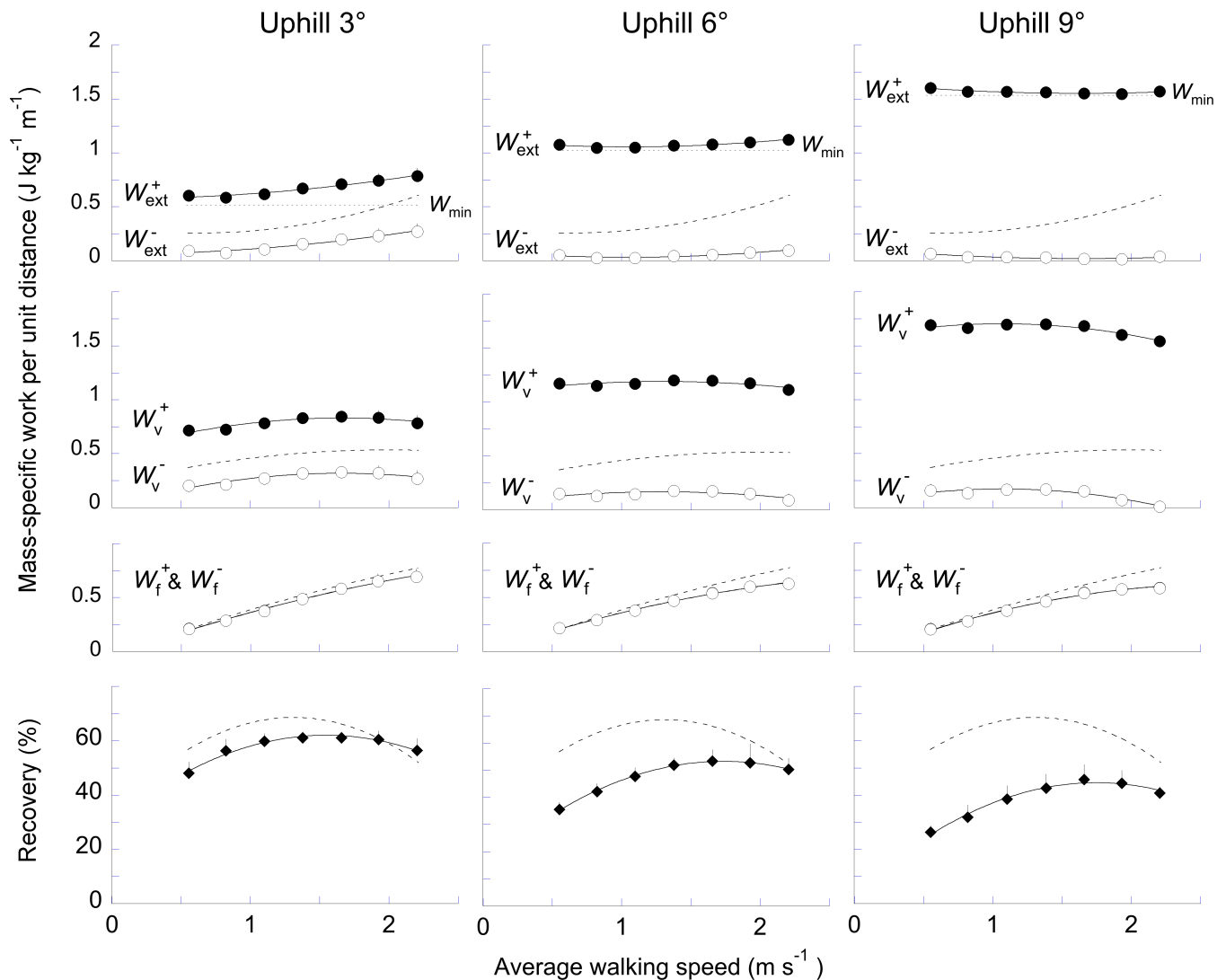


Fig 4. Mass-normalized work per unit distance and recovery over the step as a function of speed and slope while walking uphill. Three top rows: For each slope, the mass-normalized positive (closed symbols, superscript +) and negative (open symbols, superscript -) mechanical work done per unit distance is given as a function of walking speed. **Top row:** W_{ext}^+ and W_{ext}^- are the positive and negative external work estimated to move the COM through its observed trajectory, relative to the surroundings. The horizontal dotted line (W_{min}) represents the minimal work necessary to overcome the change in gravitational potential energy. **Second row:** W_v^+ and W_v^- are the positive and negative work due to the changes in $E_p + E_{kv}$ vs. time curve. **Third row:** W_f^+ and W_f^- are the positive and negative work due to the changes in E_k vs. time curve (since the average speed is constant, $W_f^+ = W_f^-$). Because W_f^+ and W_f^- represents less than 1.5% of W_{ext}^+ and W_{ext}^- , it is not presented in this figure. **Bottom row:** The bottom panels present the recovery calculated over the whole step (R_{step} , Eq 2) as a function of speed. In each panel, symbols and bars represent the "grand mean" of the subjects (see Methods and Table 1) and the standard deviations (when the length of the bar exceeds the size of the symbol). The continuous lines were drawn through the experimental data (polynomial function, Kaleidagraph 4.5). The dashed lines represent the work done or the recovery during walking on the level; these lines were also drawn through the experimental data (polynomial function, Kaleidagraph 4.5).

<https://doi.org/10.1371/journal.pone.0186963.g004>

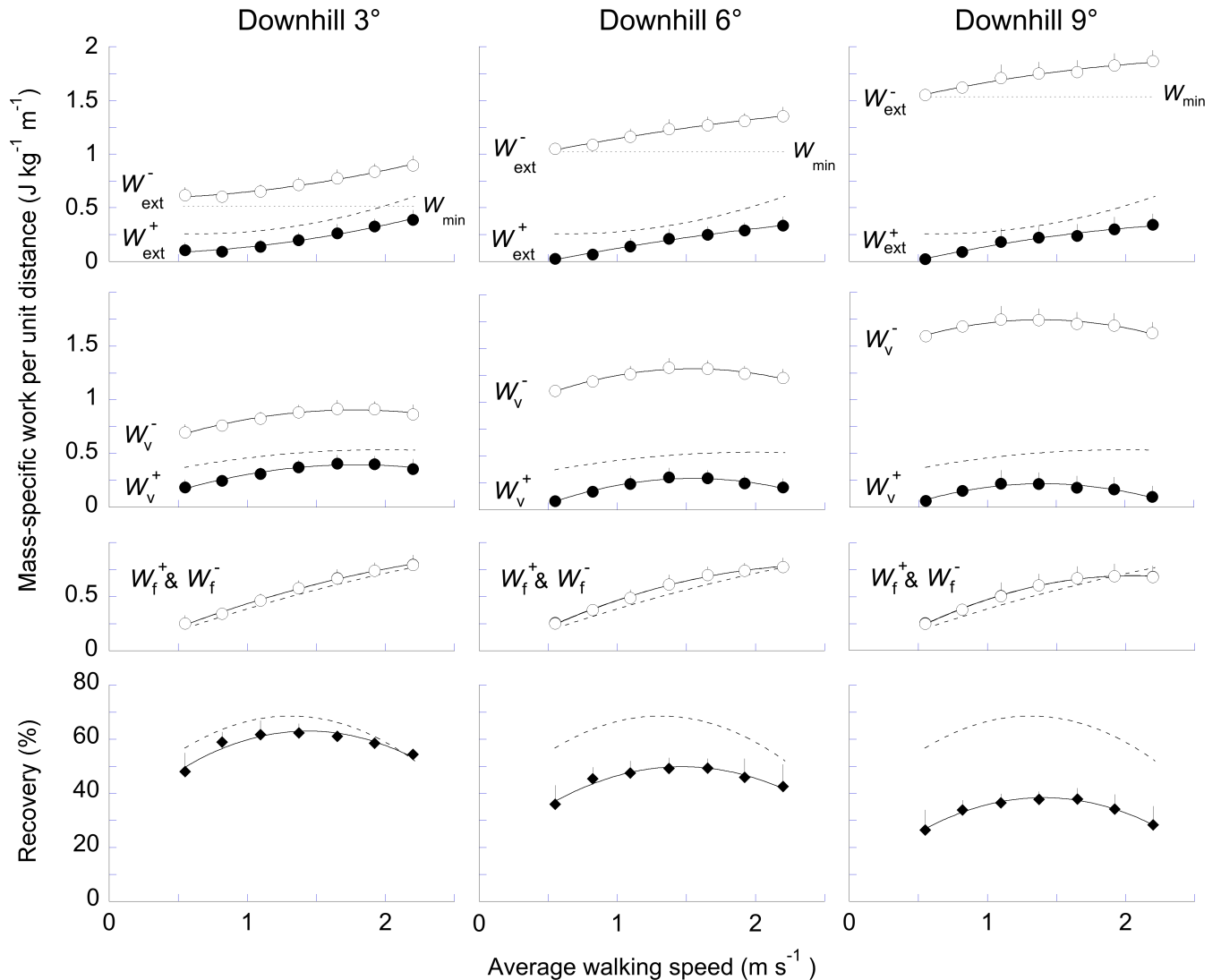


Fig 5. Mass-specific work per unit distance and recovery over the step as a function of speed and slope while walking downhill. Same indications as in Fig 4.

<https://doi.org/10.1371/journal.pone.0186963.g005>

and T3 are about equal at all speeds (Fig 6, $t = -1.39, p = 0.166$). On a positive slope, T3 becomes relatively shorter while T1 becomes relatively longer than at 0° slope. On a negative slope, T1 becomes shorter while T3 becomes longer. Both effects are more pronounced when walking at high speeds. At all speeds and slopes, T2 does not exceed $\sim 10\%$ of the step period. On the contrary, T4 increases with slope and speed: at the highest speed, T4 represents $\sim 30\%$ of the step on a positive slope, while it represents $\sim 20\%$ on a negative slope. When walking uphill both the E_k and E_p curves increase during T4 (since $E_{p,\min}$ precedes $E_{k,\max}$), while when walking downhill both curves decrease (since $E_{p,\min}$ follows $E_{k,\max}$).

Instantaneous recovery and pendular energy savings

During T1, W_p^+ and W_k^- tend to increase from -9° to $+9^\circ$, while during T3, W_p^- and W_k^+ tend to decrease (Fig 7). These changes are more important at high speeds than at low speeds. The effect of slope seems more marked on W_p^+ and W_p^- , whereas the influence of speed is more

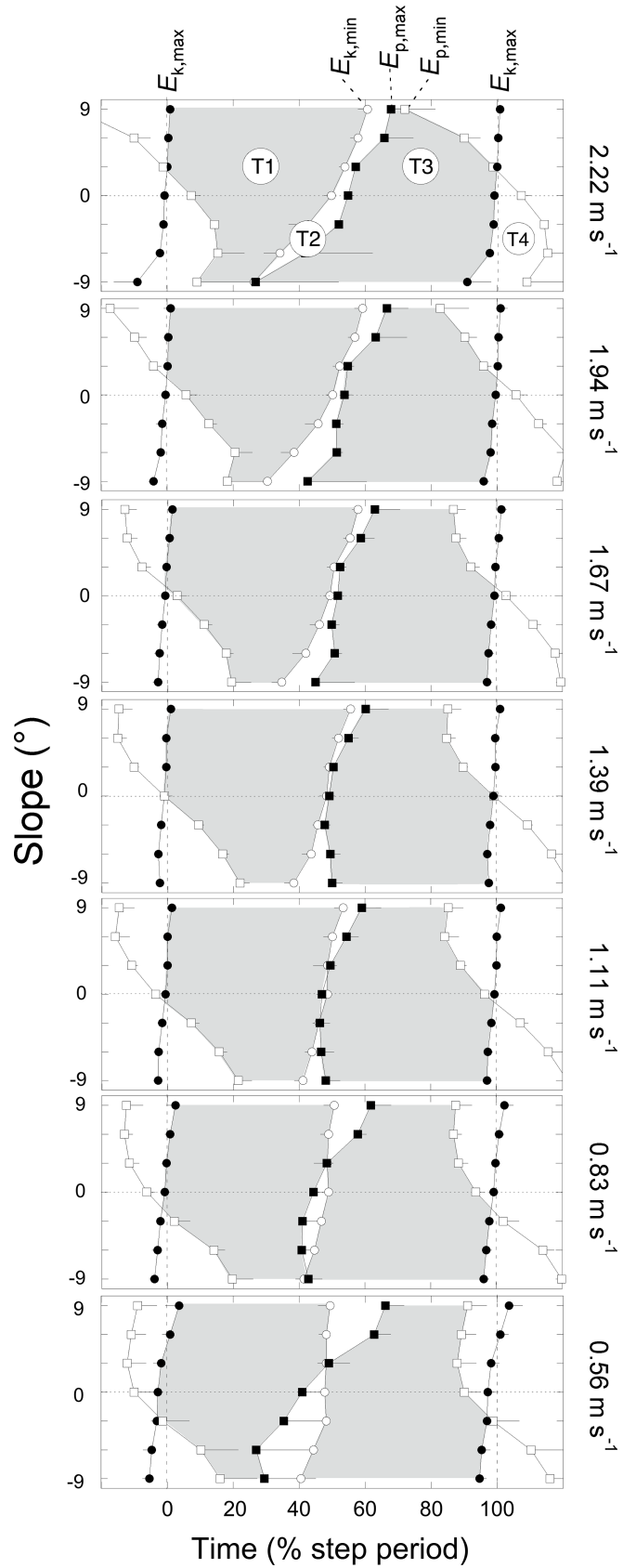


Fig 6. Duration of the four phases of the step as a function of slope at each speed. In each panel, the time is expressed as a percentage of the step duration: 0% and 100% (vertical interrupted lines) correspond to the moments at which the fore-aft velocity of the COM is maximal. The closed circles correspond to the instant of $E_{k,max}$, the open circles to $E_{k,min}$, the closed squares to $E_{p,max}$, and the open squares to $E_{p,min}$. The grey zones correspond to the phases during which E_k can be transformed into E_p (T1) and *vice versa* (T3). The white zones correspond to the phases where the curves are in phase. Symbols and bars represent the "grand mean" of all subjects (Table 1) at a given speed and slope and the standard deviations (when the length of the bar exceeds the size of the symbol).

<https://doi.org/10.1371/journal.pone.0186963.g006>

discernable on W_k^+ and W_k^- , as one would expect. Due to the change in the magnitude of the E_p and the E_k curves, the average recovery (R_{avg}) during each period changes with slope and speed (Fig 8).

Uphill walking. During T1, when walking uphill at low speeds, R_{avg} decreases with slope. Indeed, W_k^- is close to zero at all slopes (Fig 7), thus there is only a small amount of kinetic energy change to be transformed into potential energy change and $W_{ext}^+ \approx W_p^+$. Since W_p^+ increases with slope, R_{avg} decreases (Eq 3). As speed increases, W_k^- becomes greater; there is thus more and more kinetic energy change that can be transformed into potential energy and R_{avg} increases with slope. Since the duration of T1 tends to lengthen on steeper inclines, E_s during T1 increases with slope (Fig 9), even when R_{avg} decreases.

During T3, when walking uphill at speeds $< 1.39 \text{ m s}^{-1}$, R_{avg} is rather constant at all slopes (Fig 8) because W_p^- is about equal to W_k^+ (Fig 7). Consequently, the E_{ext} curve is almost flat (Fig 1), $r(t)$ reaches a peak close to 100% and R_{avg} is close to 50%. However, E_s is reduced as compared to level walking (Fig 9) because: (1) even if the E_k and E_p curves are out of phase, these curves change little (i.e. W_p^- and W_k^+ are small), which limits the amount of energy that can be exchanged, and (2) the time during which this exchange can occur is reduced as compared to level walking. At speeds $> 1.39 \text{ m s}^{-1}$, R_{avg} decreases (Fig 8) because the E_p curve is increasing quasi monotonically (Fig 3). Consequently, W_p^- tends to zero when slope increases (Fig 7) and the amount of potential energy that can be transformed into kinetic energy becomes smaller and smaller. Furthermore, the duration of T3 is shorter as slope increases. As a consequence, E_s becomes smaller on steeper slopes (Fig 9).

Downhill walking. When walking downhill, R_{avg} over T1 decreases from 0° to -9° and from 0.83 to 2.22 m s^{-1} (Fig 8). Furthermore, when negative slope increases, W_k^- and W_p^+ tend to zero (Fig 7) and the duration of T1 decreases (Fig 6). Therefore, E_s during T1 diminishes with slope down to zero at -9° (Fig 9).

During T3, below 1 m s^{-1} , R_{avg} decreases from 60% at 0° to $< 40\%$ at -9° (Fig 8) because W_k^+ is much smaller than W_p^- (Fig 7). Consequently, W_p^- cannot be transformed in W_k^+ and R_{avg} is low. Above 1 m s^{-1} , more and more potential energy can be transformed into kinetic energy (Fig 7) and R_{avg} increases mostly with speed (Fig 8): from $\sim 65\%$ at 1.11 m s^{-1} to $\sim 80\%$ at 2.22 m s^{-1} . Furthermore, the duration of T3 becomes also longer when the negative slope increases (Fig 6). For these two reasons, E_s is greater on steeper than on shallow declines and at high than at low speeds (Fig 9).

External work within the step

Despite the fact that energy is saved during T1 and T3 through E_p - E_k transduction, positive or negative work is still performed by biological tissues (i.e. muscles, tendons, ligaments, soft tissues) during each walking step (Fig 10). When walking uphill, the principal positive external work phase occurs during T4 and the following T1; this work increases with slope and speed of progression. On a shallow positive slope when walking faster than 1.5 m s^{-1} , a small amount

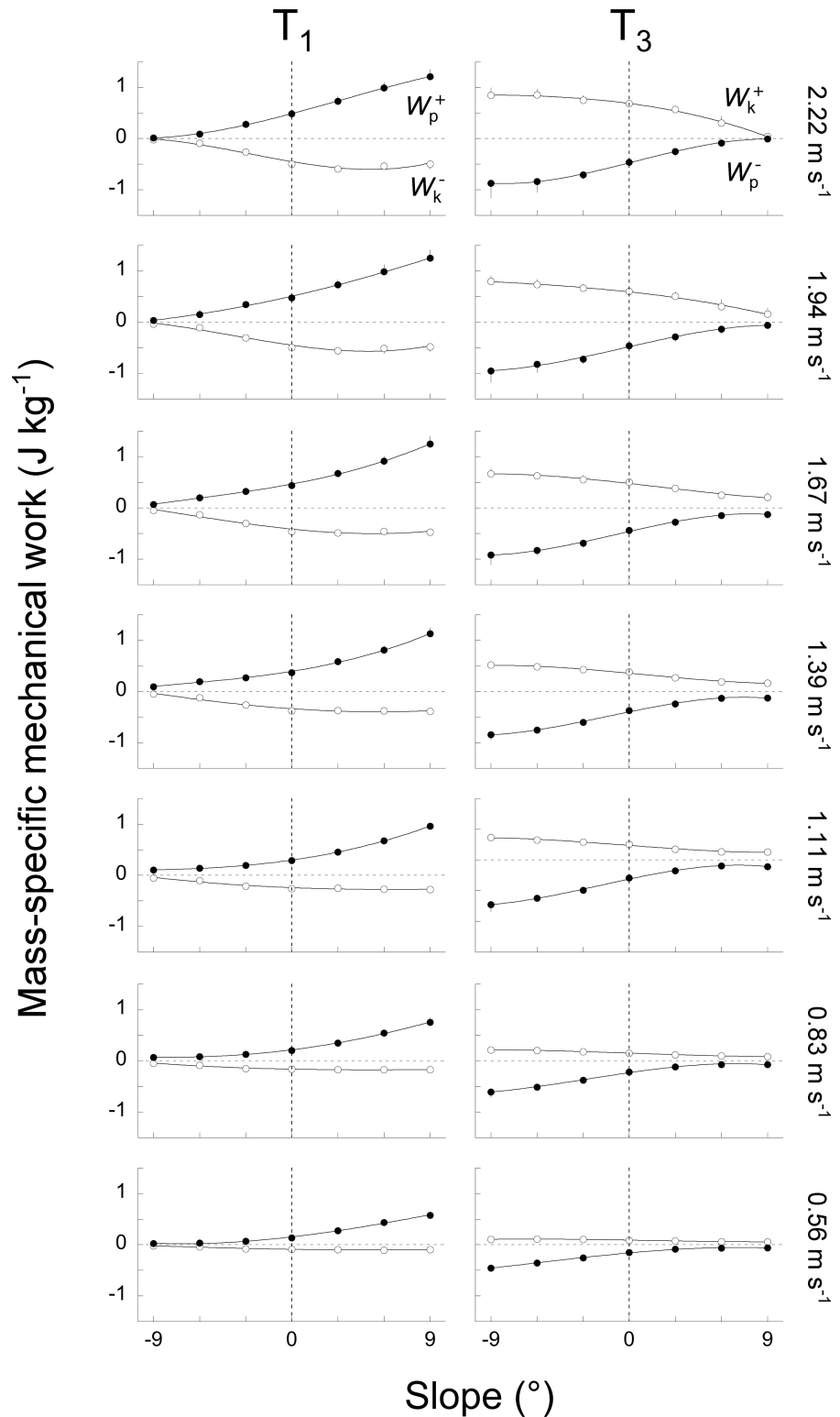


Fig 7. Change in the kinetic and potential energy during the periods T1 and T3 as a function of slope at each speed. At each speed, the left panel presents the increments of the E_p curve (W_p^+ , closed circles) and the decrements of the E_k curve (W_k^- , open circles) during the period T1 whereas the right panel presents the decrements of the E_p curve (W_p^- , closed circles) and the increments of the E_k curve (W_k^+ , open circles) over the period T3. Other indications as in Fig 4.

<https://doi.org/10.1371/journal.pone.0186963.g007>

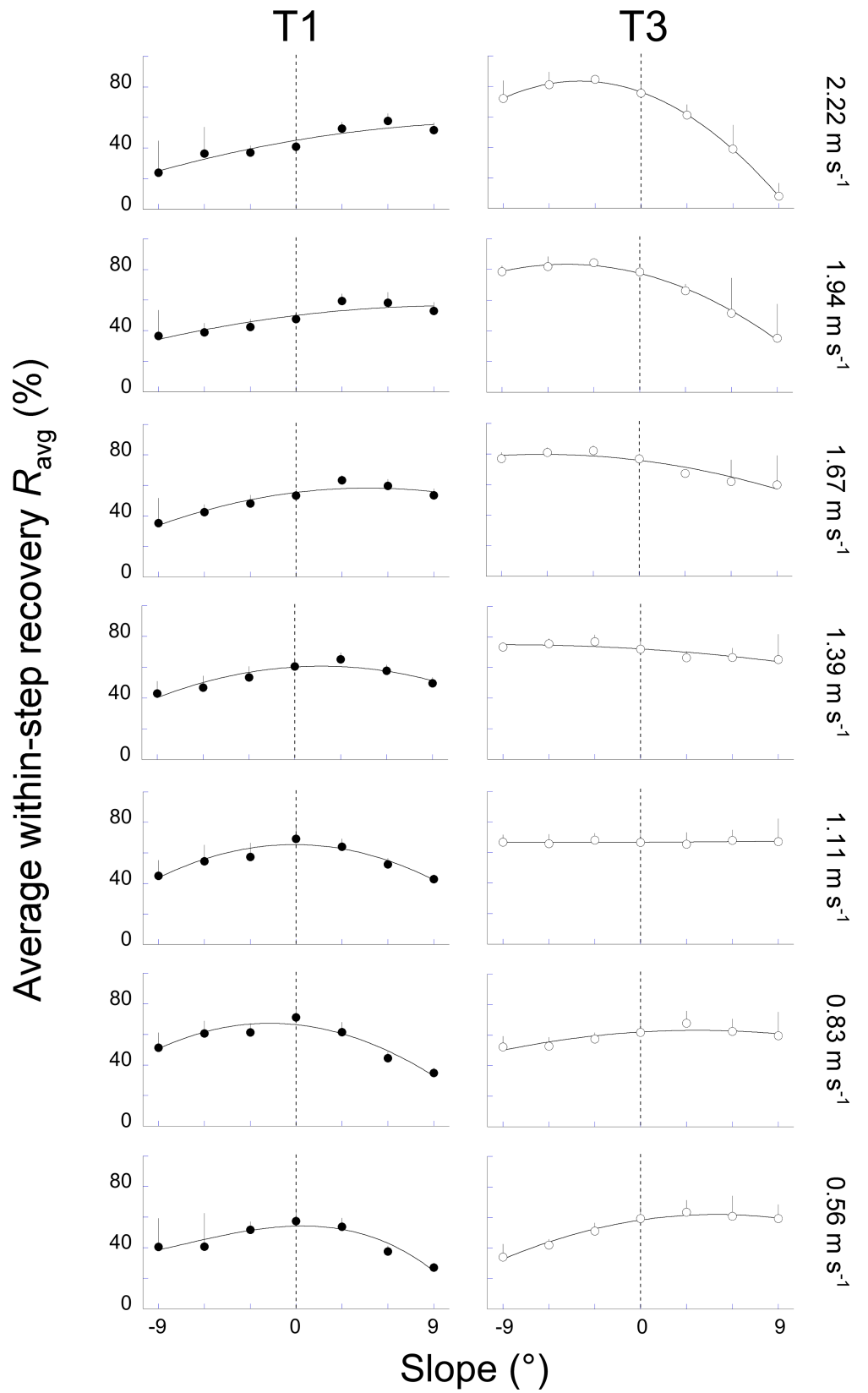


Fig 8. Average of the instantaneous recovery (R_{avg}) over the periods T1 and T3 as a function of slope at each speed. At each speed, the left panel (closed circles) presents R_{avg} (see Methods) over the period T1 whereas the right panel (open circles) presents R_{avg} over the period T3. Other indications as in Fig 4.

<https://doi.org/10.1371/journal.pone.0186963.g008>

of negative external work is also done during T1. This negative work increases with speed and decreases with slope.

When walking downhill, the main negative external work phase occurs during T3 and the following T4. This negative work increases when negative slope increases. When speed increases, the negative work decreases during T3, while it increases during T4. On a shallow negative slope when walking faster than 1.2 m s^{-1} , positive external work is also done during T1, this work increases with speed and decreases with slope.

Because T2 occurs around $E_{p,max}$ and $E_{k,min}$, the changes in amplitude of the E_p and E_k curves are small (Figs 1, 2 & 3). Furthermore, due to the short duration of T2 (Fig 6), the magnitude of COM work done during T2 is negligible (Fig 10).

Discussion

In walking, the trajectory of the body tends to minimize the muscular work by limiting the absorption and production of E_p and E_k occurring each step [18]. The present study is intended to analyze the interaction between the forward and vertical motion of the COM by assessing the changes in pendulum-like exchange between E_k and E_p with the slope of the terrain and the speed of progression. Therefore, we employed estimates of the 'instantaneous' recovery and of the rate of pendular energy savings, within each step. During phases of perfect E_p - E_k exchange (i.e. when $r(t) = 100\%$), no muscle work is theoretically required to move the COM along its trajectory. However, a high $r(t)$ does not imply a great amount of mechanical energy exchanged. Therefore, we introduce a new variable to measure the effectiveness of the E_p - E_k transduction: the pendular energy savings E_s . Furthermore, a high rate of energy savings does not imply *per se* a low amount of external work done (Figs 9 & 10). Therefore, we also evaluated the mechanical work required to sustain the motion of the COM throughout the step.

Effect of slope and speed on the external work and recovery over the whole step

To allow comparison with earlier studies, the recovery over the whole step (R_{step}) is computed here from the work associated with the horizontal (W_f) and vertical (W_v) movements of the COM. When walking on level ground, Cavagna et al. [1] showed that in walking the recovery of mechanical energy is maximal (i.e. about 65%) at $4\text{--}5 \text{ km h}^{-1}$. Our data are consistent with these results but also with others (e.g. [1, 2, 6]): R_{step} reaches a maximum of $\sim 65\%$ around 1.39 m s^{-1} . At that speed, the peak-to-peak amplitudes of E_p and of E_k are about the same (Fig 7) and the phase shift between $E_{p,min}$ and $E_{k,max}$ is about zero (Fig 6). At low speeds, the magnitude of E_p is greater than that of E_k and $E_{p,min}$ precedes $E_{k,max}$ yielding R_{step} values $< 60\%$. At high speeds, the amplitude of E_p is smaller than that of E_k and $E_{p,min}$ follows $E_{k,max}$ yielding R_{step} values $< 50\%$.

When walking on any slope at a steady speed, $W_f^+ \approx W_f^-$ since the average acceleration of the COM in the fore-aft direction is nil over a complete step. However, at a given speed the magnitude of the E_{kf} curve varies across slopes. When walking downhill, W_f^+ and W_f^- increases slightly (Fig 5). This observation is in agreement with previous studies showing that the peak of the horizontal component of the GRF is greater after foot contact when walking on negative slopes [19–21]. Conversely, W_f^+ and W_f^- are smaller when walking uphill, especially at high

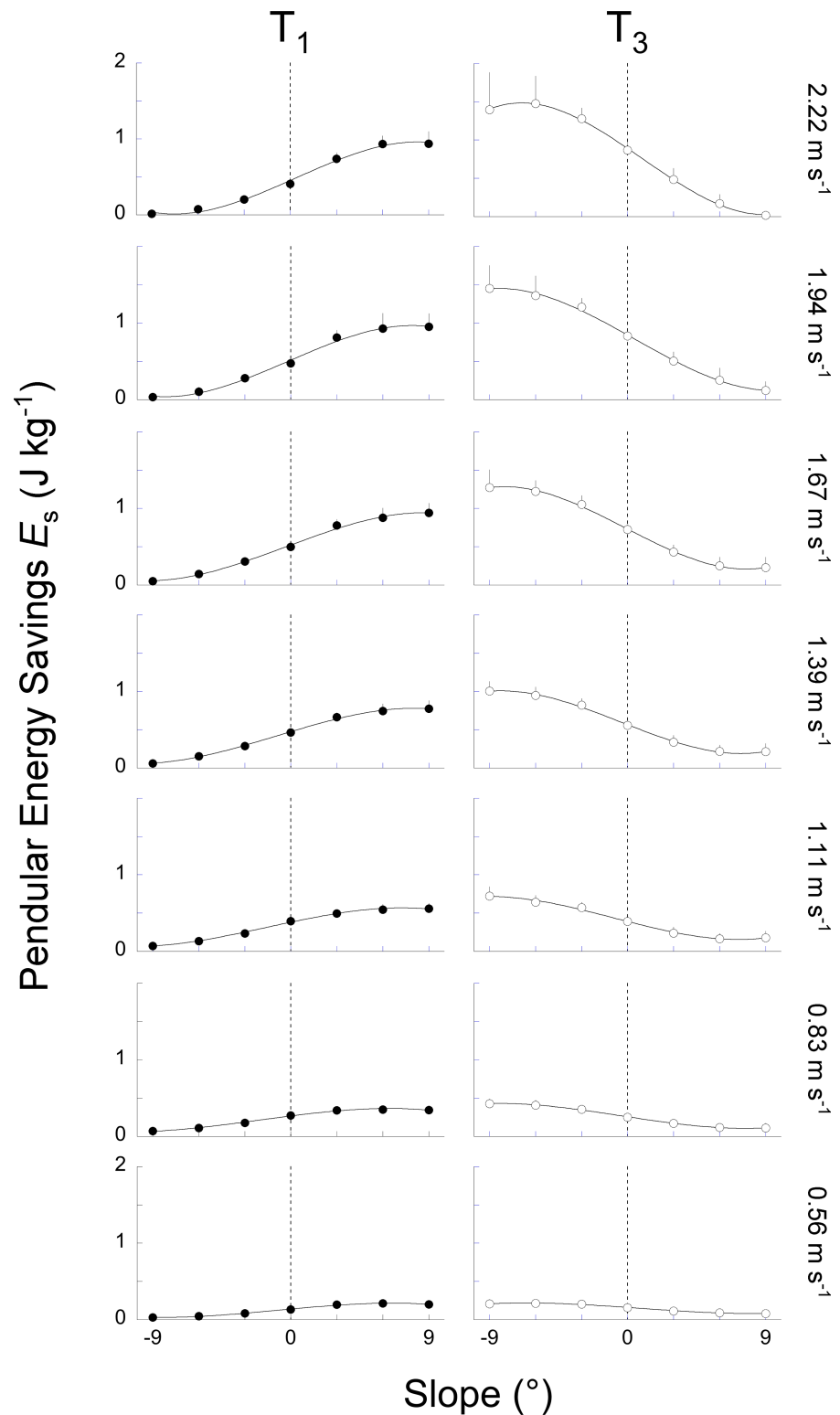


Fig 9. Pendular energy savings (E_s) over the periods T1 and T3 as a function of slope at each speed. At each speed, the left panel (closed circles) presents E_s (see Methods) over the period T1 whereas the right panel (open circles) presents E_s over the period T3. Other indications as in Fig 4.

<https://doi.org/10.1371/journal.pone.0186963.g009>

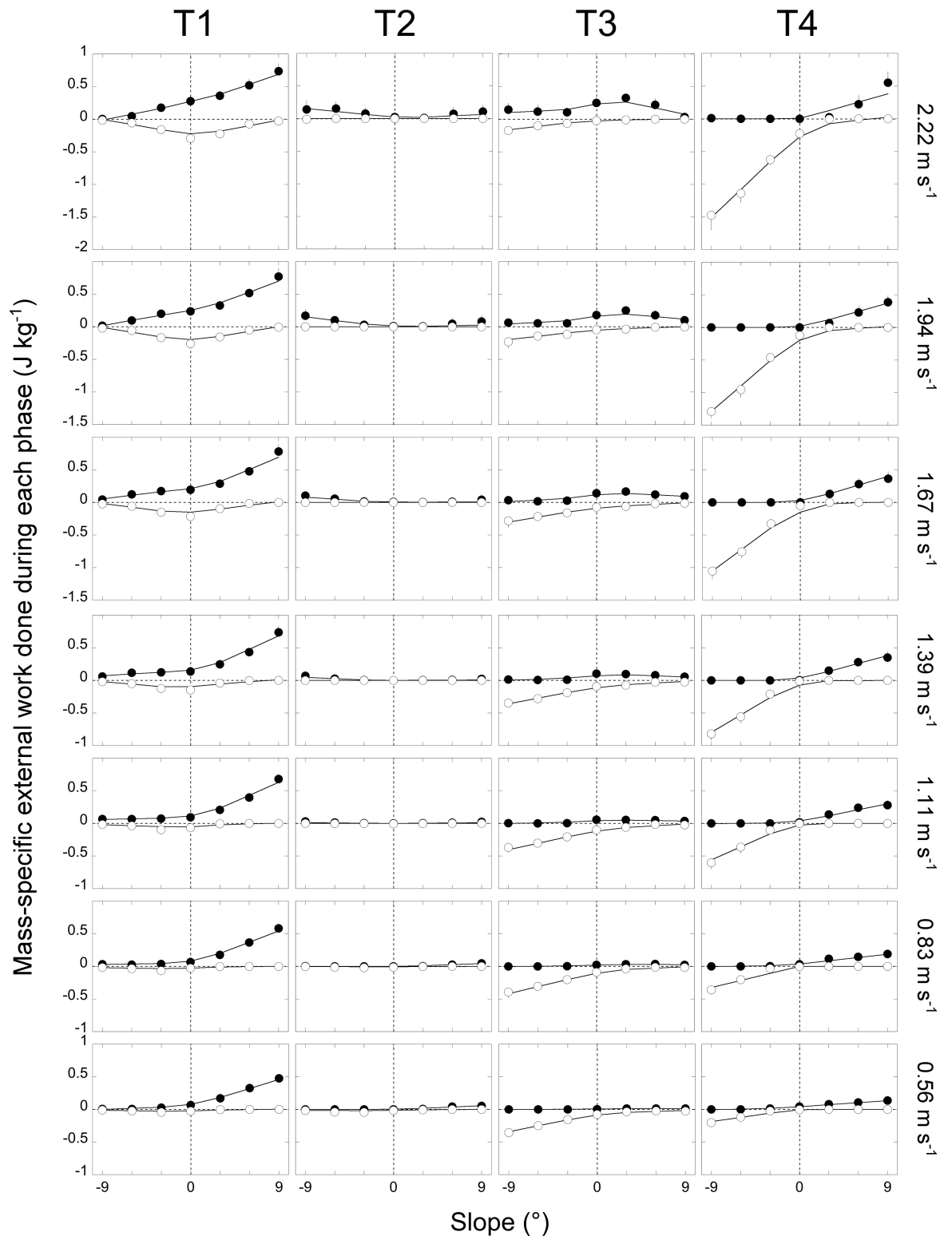


Fig 10. External work done during the four phases of the step as a function of slope at each speed. At each speed, the mass-normalized external work is presented during the four phases of the step as a function of the slope. In each panel, the closed and open circles correspond respectively to the positive and negative external work done during that phase. Other indications as in Fig 4.

<https://doi.org/10.1371/journal.pone.0186963.g010>

speeds (Fig 4). These observations are in accordance with previous results reporting a smaller posterior shear GRF [20, 21]. The change in W_f with slope could be due to a modification of the distance between the COM and the front foot at foot contact [22].

When walking uphill, the increase in W_{ext}^+ to ascend the slope is accompanied by a decrease in W_{ext}^- (Fig 4). Conversely, when walking downhill, the increase in W_{ext}^- is accompanied by a reduction of W_{ext}^+ . These results are in agreement with those of Minetti et al. [23]. The opposite change in the magnitude of W_{ext}^+ and W_{ext}^- jeopardizes the E_k - E_p transduction. When walking uphill, R_{step} is reduced, as compared to level. Our results corroborate those of Gomeñuka et al. [6] and of Gomeñuka et al. [7] obtained at speeds between 0.3 and 1.4 m s⁻¹. When walking downhill, R_{step} is also reduced. Our results differ instead from those of Gottschall and Kram [5], who observed an increase in R_{step} after factoring out the changes in E_p due to slope. The reduction in R_{step} observed here fails to explain the reduction of the metabolic cost on gentle negative slope [24].

Furthermore, both on a positive and negative slope, R_{step} reaches a maximum at a higher speed than on level walking (Figs 4 & 5). One reason could be the following: on a slope, the changes in the E_p curve increase mainly with slope while the E_k curve increases with speed. Consequently, when slope increases, the possibility of maximal exchange between E_p and E_k occurs at a higher speed.

When walking on the level, the speed at which the metabolic costs is minimal (i.e. the optimal metabolic speed) corresponds approximately to the speed at which R_{step} is maximal [6] and W_{ext} is minimal [1, 17]. Therefore, the optimal metabolic speed is often explained by a minimal external work, which in turn is linked to an optimal recovery. When walking on a slope, the optimal metabolic speed decreases from -9° to +9° [6, 25]. On the contrary, both in uphill and downhill walking, R_{step} reaches a maximum at higher speeds than on the level (Figs 4 & 5) and W_{ext} does not present anymore a minimum. Therefore, the relation between optimal metabolic speed, minimum external work and maximum recovery seems to cease, undermining the usefulness of the pendular transduction analysis to predict metabolic energy expenditure.

While R_{step} characterizes energy exchange in walking, it cannot be used to identify functionally distinct gaits; for example, many different types of animal gait exhibit the same recovery [26, 27]. In humans, gaits with orthopedic pathologies [28] or hemi-paretic walking [29] did not highlight the expected reduction in R_{step} . This lack in sensitivity could be due to the fact that R_{step} is measured over the whole walking step and does not give information about the time-course of the energy transduction within the step.

The compass gait model during walking on a slope

At first approximation, the trajectory of the COM during walking on the level can be described by a 'compass gait' model (e.g. [30–33]). In this case, the arc of the 'compass gait' model is more or less symmetric with respect to the vertical (see schemas in Figs 1, 2 & 3). Here we adapt this 'compass gait' model to illustrate how and why the E_k - E_p transduction is reduced when walking on a slope at different speeds.

On a positive slope, the changes in the pendulum-like energy exchange can be illustrated by tilting the arc of the compass backwards (Figs 1, 2 & 3). As a consequence, the lower-limb reaches its vertical position later during the contact phase. As speed and slope increase the duration of T1 becomes longer and T3 becomes shorter than at 0° slope (Fig 6). Furthermore, when the arc is inclined to the back, its end portion is oriented more horizontally while its first portion is more vertical. Consequently, when the positive slope becomes steeper, the vertical movement of the COM increases during T1 and decreases during T3 (Fig 7). This means that

most of the energy recovery during the step occurs during the phase T1, where W_k^- is transformed in W_p^+ to raise the COM. As speed and slope increase, both W_k^- and W_p^+ increase, which enhances the possibility of energy transformation. Consequently, E_s increases with speed and slope during T1; however, the recovery is not faultless and positive work is still performed to elevate the COM (Fig 10). During T3, as speed and slope increases, E_s trends toward zero because W_p^- and W_k^+ become smaller and smaller and the duration of this phase shortens, due to the tilt of the compass.

On a negative slope, the changes in the pendulum-like energy exchange can be illustrated by tilting the arc of the compass forwards (Figs 1, 2 & 3). Consequently, the lower-limb reaches its vertical position earlier during the contact phase, as also shown by Gottschall and Kram [5], so that the duration of T1 becomes shorter and the duration of T3 longer. Furthermore, when the arc is declined to the front, its first portion is oriented more horizontally while its last portion is more vertical. This means that most of the energy transformation is done during T3, when the COM falls and accelerates forward. Since W_k^+ increases with speed and W_p^- with slope (Fig 7), E_s during T3 is greater when walking on a steep terrain at high velocity (Fig 9). During T1, E_s is limited and trends toward zero as speed and slope increase, since the duration of this phase as well as the magnitude of W_p^+ and of W_k^- diminish, due to the tilt of the compass.

Our results suggest that at each slope the arc of the compass and consequently the position of the COM relative to the foot at mid-stance are tilted relative to level walking (Figs 1, 2, 3 & 6). These observations are in accordance with the gait kinematics data of Lay et al. [20] and McIntosh et al. [21].

Effect of slope and speed on the external work during the phases of the step

During T2 and T4, the E_k and E_p curves are in phase and thus no E_k - E_p exchange is possible. The phase T2 occurs during single-contact around $E_{p,max}$ and $E_{k,min}$. At all speed and slopes, the duration of T2 is short or even nil sometimes [8]. Consequently, the external work is close or equal to zero. The phase T4 occurs around $E_{p,min}$ and $E_{k,max}$. When walking on a flat terrain, T4 happens during the double contact phase, as the leading leg performs negative work while the trailing leg generates positive work [34–37]. At low speeds, net positive external work is done during T4 to accelerate and redirect the COM upward [38], whereas at high speeds, net negative work is done to decelerate and lower the COM. Although brief, T4 is crucial because the action of the muscle-tendon units during the double-support phase establishes the initial conditions for the subsequent single support phase [39]. Using a simple relationship between muscular work and energy consumption, Yeom and Park [40], Kuo et al. [41] and Ruina et al. [42] have suggested that the most economical way of walking on the level would be to compensate the collision loss after foot contact in the leading limb by push off work of the trailing limb around the double support phase and to perform limited (or zero) additional work during the single support phase.

In uphill walking, the duration of T4 is extended because $E_{p,min}$ appears increasingly earlier in the step as slope increases (Fig 6). Functionally, a longer T4 indicates that the COM is still rising when its forward velocity starts to increase (Figs 1, 2 & 3). Walking uphill on steeper slopes involves a greater W_{ext}^+ during double support and this positive work is done both by the leading and the trailing legs [43, 44]. Our results show that, a significant part of the positive external work performed during the step is generated during T4 and T1 and that this work increases when speed increases (Fig 10). These results are in accordance with those of Gottschall and Kram [45]. According to Oh et al. [46], from a purely mechanical perspective,

the external work would be minimal if the positive work done during the double support phase was equal to the potential energy necessary to overcome the slope and was followed by a single support phase during which the COM vaults passively over a stiff limb. However, generating a large magnitude of work over a short time duration may be metabolically expensive for muscles [45] and most likely exceed a maximum suitable push-off limit [46]. Instead, to prevent pitching backward when moving on an incline, the hip and knee flexion increases at foot contact [47, 48] and mechanical work is performed to raise the COM of the body during T1 when extending the knee and hip [21]. During T1, up to 60% of the increase in E_p comes from the decrease in E_k . Additional positive muscle work is also performed during this period, incurring a metabolic energy cost [49].

In downhill walking, the duration of T4 is extended because $E_{p,\min}$ appears later and later in the step as slope increases (Fig 6). Functionally, a longer T4 indicates that the COM is still lowering when its forward velocity starts to decrease. Walking downhill on steeper slopes and at higher speeds involves greater negative external work during double support (Fig 10) and this work is mainly done by the leading leg but also by the trailing leg [43, 44]. Similar to uphill walking, the external work performed during downhill walking is predicted to be minimal if the negative work done during the double contact was equal to the decrease in potential energy due to the slope and if no additional work was done during the single support phase [46]. Our results show that, at low walking speed, R_{avg} is small during T3 suggesting that negative muscle-tendon work is performed to control the velocity of the COM during the descent (Fig 10) and to restrain the body from falling [50]. As speed increases, R_{avg} during T3 increases up to ~80% so that most of the kinetic energy required to move the COM forward comes from transduction of potential energy [31, 41, 51]. Consequently, the negative work performed during T3 tends to zero and the major part of the energy dissipation occurs during T4. These results are in agreement with those of Gottschall and Kram [45] and Lay et al. [52] and suggest that the major contribution of biological tissues to absorb energy occurs around the step-to-step transition.

Limitations of the study

The pendular transduction analysis performed in this study could not shed any light on the relation between mechanical external work and metabolic energy expenditure (for a discussion of this issue, see [5, 6, 23, 25]). However, external work does not represent the total work done, which also includes (among others) the internal work done to move limbs relative to the COM [16, 23, 53–55] and the work done by the trailing limb against the leading limb during double support [35, 56]. Unfortunately, the method used here does not allow measuring individual limbs *GRF*. Therefore, we cannot take into account the simultaneous mechanical work performed by each limb during the step-to-step transition [35]. Furthermore, metabolic cost is a function of work but also of other factors like force and rate of force production [57], whether work is from muscle, tendon or soft tissue [58, 59], which muscles are active and what part of the force-length and force-velocity curves a muscle is on.

Conclusion and perspectives

The present study characterizes the within-step recovery $r(t)$ and a new outcome metric, the theoretical pendular energy savings E_s , to analyze human walking biomechanics. These continuous within-step estimates offer the possibility to determine the phase of the step during which motion of the COM exhibits pendulum-like energy transduction. Our study shows that during uphill walking, the pendular energy savings are larger during the first part of stance phase (T1), when kinetic energy is transformed into potential energy. On the contrary, during

downhill walking, the pendular energy savings are larger during the second part of stance (T3), when potential energy is transformed into kinetic energy. Both in uphill and downhill walking, the main phase of external work production/absorption occurs around the double support phase. The changes observed in the pendulum-like energy exchange with slope and speed can be illustrated by tilting the 'classical compass model' backwards (uphill) or forwards (downhill). Future research should link this tilting behavior with the changes in the kinematics of the limb-segments and should correlate the modifications of the mechanical demand with the changes in the muscular activity.

Supporting information

S1 Dataset. All_Data_Dewolf. Data of all subjects in each condition. (XLSX)

Acknowledgments

The authors want to thank Prof. K. Zelik for his skillful help in carrying out the experiments and for his helpful and constructive advice during the preparation of this manuscript.

Author Contributions

Conceptualization: Patrick A. Willems.

Data curation: Patrick A. Willems.

Formal analysis: Arthur H. Dewolf, Yuri P. Ivanenko, Patrick A. Willems.

Funding acquisition: Francesco Lacquaniti, Patrick A. Willems.

Investigation: Arthur H. Dewolf, Yuri P. Ivanenko, Francesco Lacquaniti, Patrick A. Willems.

Methodology: Arthur H. Dewolf, Yuri P. Ivanenko, Francesco Lacquaniti, Patrick A. Willems.

Project administration: Francesco Lacquaniti, Patrick A. Willems.

Resources: Francesco Lacquaniti, Patrick A. Willems.

Software: Arthur H. Dewolf, Patrick A. Willems.

Supervision: Yuri P. Ivanenko, Francesco Lacquaniti, Patrick A. Willems.

Validation: Patrick A. Willems.

Visualization: Yuri P. Ivanenko, Francesco Lacquaniti, Patrick A. Willems.

Writing – original draft: Arthur H. Dewolf.

Writing – review & editing: Arthur H. Dewolf, Yuri P. Ivanenko, Francesco Lacquaniti, Patrick A. Willems.

References

1. Cavagna GA, Thys H, Zamboni A. The sources of external work in level walking and running. *Journal of Physiology*. 1976; 262(3):639–57. PMID: [1011078](https://pubmed.ncbi.nlm.nih.gov/1011078/)
2. Cavagna GA, Franzetti P, Fuchimoto T. The mechanics of walking in children. *The Journal of Physiology*. 1983; 343(1):323–39. <https://doi.org/10.1113/jphysiol.1983.sp014895>
3. Ivanenko YP, Dominici N, Cappellini G, Dan B, Cheron G, Lacquaniti F. Development of pendulum mechanism and kinematic coordination from the first unsupported steps in toddlers. *Journal of Experimental Biology*. 2004; 207(21):3797–810. <https://doi.org/10.1242/jeb.01214> PMID: [15371487](https://pubmed.ncbi.nlm.nih.gov/15371487/)

4. Lejeune TM, Willems PA, Heglund NC. Mechanics and energetics of human locomotion on sand. *Journal of Experimental Biology*. 1998; 201(13):2071–80.
5. Gottschall JS, Kram R. Mechanical energy fluctuations during hill walking: The effects of slope on inverted pendulum exchange. *Journal of Experimental Biology*. 2006; 209(24):4895–900. <https://doi.org/10.1242/jeb.02584> PMID: 17142678
6. Gomeñuka NA, Bona RL, da Rosa RG, Peyré-Tartaruga LA. Adaptations to changing speed, load, and gradient in human walking: Cost of transport, optimal speed, and pendulum. *Scandinavian Journal of Medicine and Science in Sports*. 2014; 24(3). <https://doi.org/10.1111/sms.12129> PMID: 24102934
7. Gomeñuka NA, Bona RL, da Rosa RG, Peyré-Tartaruga LA. The pendular mechanism does not determine the optimal speed of loaded walking on gradients. *Human Movement Science*. 2016; 47:175–85. <https://doi.org/10.1016/j.humov.2016.03.008> PMID: 27017543
8. Cavagna GA, Willems PA, Legramandi MA, Heglund NC. Pendular energy transduction within the step in human walking. *Journal of Experimental Biology*. 2002; 205(21):3413–22.
9. Heglund NC, Willems PA, Penta M, Cavagna GA. Energy-saving gait mechanics with head-supported loads. *Nature*. 1995; 375(6526):52–4. <https://doi.org/10.1038/375052a0> PMID: 7723841
10. Minetti AE, Ardigo LP, Saibene F. The transition between walking and running in humans: metabolic and mechanical aspects at different gradients. *Acta Physiologica Scandinavica*. 1994; 150(3):315–23. <https://doi.org/10.1111/j.1748-1716.1994.tb09692.x> PMID: 8010138
11. Minetti AE, Ardigo LP. The transmission efficiency of backward walking at different gradients. *Pflügers Archiv European Journal of Physiology*. 2001; 442(4):542–6. <https://doi.org/10.1007/s004240100570> PMID: 11510887
12. Kuo AD, Donelan JM, Ruina A. Energetic consequences of walking like an inverted pendulum: Step-to-step transitions. *Exercise and Sport Sciences Reviews*. 2005; 33(2):88–97. <https://doi.org/10.1097/00003677-200504000-00006> PMID: 15821430
13. Dewolf AH, Peñailillo LE, Willems PA. The rebound of the body during uphill and downhill running at different speeds. *Journal of Experimental Biology*. 2016; 219(15):2276–88. <https://doi.org/10.1242/jeb.142976> PMID: 27207641
14. Meurisse GM, Dierick F, Schepens B, Bastien GJ. Determination of the vertical ground reaction forces acting upon individual limbs during healthy and clinical gait. *Gait and Posture*. 2016; 43:245–50. <https://doi.org/10.1016/j.gaitpost.2015.10.005> PMID: 26549482
15. Gosseye TP, Willems PA, Heglund NC. Biomechanical analysis of running in weightlessness on a treadmill equipped with a subject loading system. *European Journal of Applied Physiology*. 2010; 110(4):709–28. <https://doi.org/10.1007/s00421-010-1549-9> PMID: 20582597
16. Willems PA, Cavagna GA, Heglund NC. External, internal and total work in human locomotion. *Journal of Experimental Biology*. 1995; 198:Pt 2/.
17. Schepens B, Bastien GJ, Heglund NC, Willems PA. Mechanical work and muscular efficiency in walking children. *Journal of Experimental Biology*. 2004; 207(4):587–96. <https://doi.org/10.1242/jeb.00793>
18. Biewener AA. Patterns of mechanical energy change in tetrapod gait: Pendula, springs and work. *Journal of Experimental Zoology Part A: Comparative Experimental Biology*. 2006; 305(11):899–911. <https://doi.org/10.1002/jez.a.334> PMID: 17029267
19. Redfern MS, DiPasquale J. Biomechanics of descending ramps. *Gait and Posture*. 1997; 6(2):119–25. [https://doi.org/10.1016/S0966-6362\(97\)01117-X](https://doi.org/10.1016/S0966-6362(97)01117-X)
20. Lay AN, Hass CJ, Gregor RJ. The effects of sloped surfaces on locomotion: A kinematic and kinetic analysis. *Journal of Biomechanics*. 2006; 39(9):1621–8. <https://doi.org/10.1016/j.jbiomech.2005.05.005> PMID: 15990102
21. McIntosh AS, Beatty KT, Dwan LN, Vickers DR. Gait dynamics on an inclined walkway. *Journal of Biomechanics*. 2006; 39(13):2491–502. <https://doi.org/10.1016/j.jbiomech.2005.07.025> PMID: 16169000
22. Silverman AK, Wilken JM, Sinitski EH, Neptune RR. Whole-body angular momentum in incline and decline walking. *Journal of Biomechanics*. 2012; 45(6):965–71. <https://doi.org/10.1016/j.jbiomech.2012.01.012> PMID: 22325978
23. Minetti AE, Ardigo LP, Saibene F. Mechanical determinants of gradient walking energetics in man. *The Journal of Physiology*. 1993; 472(1):725–35. <https://doi.org/10.1113/jphysiol.1993.sp019969>
24. Margaria R. Positive and negative work performances and their efficiencies in human locomotion. *Internationale Zeitschrift für Angewandte Physiologie Einschließlich Arbeitsphysiologie*. 1968; 25(4):339–51. <https://doi.org/10.1007/BF00699624>
25. Ardigo LP, Saibene F, Minetti AE. The optimal locomotion on gradients: Walking, running or cycling? *European Journal of Applied Physiology*. 2003; 90(3–4):365–71. <https://doi.org/10.1007/s00421-003-0882-7> PMID: 12898263

26. Bertram JEA, Hasaneini SJ. Neglected losses and key costs: Tracking the energetics of walking and running. *Journal of Experimental Biology*. 2013; 216(6):933–8. <https://doi.org/10.1242/jeb.078543> PMID: 23447662
27. Lee DV, Comanescu TN, Butcher MT, Bertram JEA. A comparative collision-based analysis of human gait. *Proceedings of the Royal Society B: Biological Sciences*. 2013; 280(1771). <https://doi.org/10.1098/rspb.2013.1779> PMID: 24089334
28. Detrembleur C, van den Hecke A, Dierick F. Motion of the body centre of gravity as a summary indicator of the mechanics of human pathological gait. *Gait & posture*. 2000; 12(3):243–50.
29. Detrembleur C, Dierick F, Stoquart G, Chantraine F, Lejeune T. Energy cost, mechanical work, and efficiency of hemiparetic walking. *Gait and Posture*. 2003; 18(2):47–55. [https://doi.org/10.1016/S0966-6362\(02\)00193-5](https://doi.org/10.1016/S0966-6362(02)00193-5) PMID: 14654207
30. Saunders JB, Inman VT, Eberhart HD. The major determinants in normal and pathological gait. *The Journal of bone and joint surgery American volume*. 1953; 35 A(3):543–58. PMID: 13069544
31. McGeer T. Passive Dynamic Walking. *The International Journal of Robotics Research*. 1990; 9(2):62–82. <https://doi.org/10.1177/027836499000900206>
32. Alexander RM. Tendon elasticity and positional control. *Behavioral and Brain Sciences*. 1995; 18(4):745. <https://doi.org/10.1017/S0140525X00040711>
33. Usherwood JR, Szymanek KL, Daley MA. Compass gait mechanics account for top walking speeds in ducks and humans. *Journal of Experimental Biology*. 2008; 211(23):3744–9. <https://doi.org/10.1242/jeb.023416> PMID: 19011215
34. Alexander RM. Optimum walking techniques for quadrupeds and bipeds. *Journal of Zoology*. 1980; 192(1):97–117. <https://doi.org/10.1111/j.1469-7998.1980.tb04222.x>
35. Donelan JM, Kram R, Kuo AD. Simultaneous positive and negative external mechanical work in human walking. *Journal of Biomechanics*. 2002; 35(1):117–24. [https://doi.org/10.1016/S0021-9290\(01\)00169-5](https://doi.org/10.1016/S0021-9290(01)00169-5) PMID: 11747890
36. Bastien GJ, Willems PA, Schepens B, Heglund NC. Effect of load and speed on the energetic cost of human walking. *European Journal of Applied Physiology*. 2005; 94(1–2):76–83. <https://doi.org/10.1007/s00421-004-1286-z> PMID: 15650888
37. Adamczyk PG, Kuo AD. Redirection of center-of-mass velocity during the step-to-step transition of human walking. *Journal of Experimental Biology*. 2009; 212(16):2668–78. <https://doi.org/10.1242/jeb.027581> PMID: 19648412
38. Cavagna GA, Margaria R. Mechanics of walking. *Journal of applied physiology*. 1966; 21(1):271–8. PMID: 5903923
39. Mochon S, McMahon TA. Ballistic walking. *Journal of Biomechanics*. 1980; 13(1):49–57. [https://doi.org/10.1016/0021-9290\(80\)90007-X](https://doi.org/10.1016/0021-9290(80)90007-X) PMID: 7354094
40. Yeom J, Park S. A gravitational impulse model predicts collision impulse and mechanical work during a step-to-step transition. *Journal of Biomechanics*. 2011; 44(1):59–67. <https://doi.org/10.1016/j.jbiomech.2010.08.024> PMID: 20971468
41. Kuo AD. Energetics of actively powered locomotion using the simplest walking model. *Journal of Biomechanical Engineering*. 2002; 124(1):113–20. <https://doi.org/10.1115/1.1427703> PMID: 11871597
42. Ruina A, Bertram JEA, Srinivasan M. A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *Journal of Theoretical Biology*. 2005; 237(2):170–92. <https://doi.org/10.1016/j.jtbi.2005.04.004> PMID: 15961114
43. Franz JR, Lyddon NE, Kram R. Mechanical work performed by the individual legs during uphill and downhill walking. *Journal of Biomechanics*. 2012; 45(2):257–62. <https://doi.org/10.1016/j.jbiomech.2011.10.034> PMID: 22099148
44. Jeffers JR, Auyang AG, Grabowski AM. The correlation between metabolic and individual leg mechanical power during walking at different slopes and velocities. *Journal of Biomechanics*. 2015; 48(11):2919–24. <https://doi.org/10.1016/j.jbiomech.2015.04.023> PMID: 25959113
45. Gottschall JS, Kram R. Energy cost and muscular activity required for propulsion during walking. *Journal of Applied Physiology*. 2003; 94(5):1766–72. <https://doi.org/10.1152/japplphysiol.00670.2002> PMID: 12506042
46. Oh K, Ryu JK, Park S. A modeling study of mechanical energetic optimality in incline walking. *Journal of Mechanical Science and Technology*. 2014; 28(4):1393–401. <https://doi.org/10.1007/s12206-014-0126-2>
47. Birn-Jeffery AV, Higham TE. The scaling of uphill and downhill locomotion in legged animals. *Integrative and Comparative Biology*. 2014; 54(6):1159–72. <https://doi.org/10.1093/icb/ucu015> PMID: 24733147

48. Leroux A, Fung J, Barbeau H. Postural adaptation to walking on inclined surfaces: I. Normal strategies. *Gait and Posture*. 2002; 15(1):64–74. [https://doi.org/10.1016/S0966-6362\(01\)00181-3](https://doi.org/10.1016/S0966-6362(01)00181-3) PMID: 11809582
49. Neptune RR, Zajac FE, Kautz SA. Muscle mechanical work requirements during normal walking: The energetic cost of raising the body's center-of-mass is significant. *Journal of Biomechanics*. 2004; 37(6):817–25. <https://doi.org/10.1016/j.jbiomech.2003.11.001> PMID: 15111069
50. Honeine JL, Schieppati M, Gagey O, Do MC. The Functional Role of the Triceps Surae Muscle during Human Locomotion. *PLoS ONE*. 2013; 8(1). <https://doi.org/10.1371/journal.pone.0052943> PMID: 23341916
51. Garcia M, Chatterjee A, Ruina A, Coleman M. The simplest walking model: Stability, complexity, and scaling. *Journal of Biomechanical Engineering*. 1998; 120(2):281–6. PMID: 10412391
52. Lay AN, Hass CJ, Richard Nichols T, Gregor RJ. The effects of sloped surfaces on locomotion: An electromyographic analysis. *Journal of Biomechanics*. 2007; 40(6):1276–85. <https://doi.org/10.1016/j.jbiomech.2006.05.023> PMID: 16872616
53. Zelik KE, Adamczyk PG. A unified perspective on ankle push-off in human walking. *Journal of Experimental Biology*. 2016; 219(23):3676–83. <https://doi.org/10.1242/jeb.140376> PMID: 27903626
54. Minetti AE, Capelli C, Zamparo P, Prampero PE, Saibene F. Effects of stride frequency on mechanical power and energy expenditure of walking. *Medicine and Science in Sports and Exercise*. 1995; 27(8):1194–202. PMID: 7476065
55. Fenn WO. WORK AGAINST GRAVITY AND WORK DUE TO VELOCITY CHANGES IN RUNNING. *American Journal of Physiology—Legacy Content*. 1930; 93(2):433.
56. Bastien GJ, Heglund NC, Schepens B. The double contact phase in walking children. *Journal of Experimental Biology*. 2003; 206(17):2967–78. <https://doi.org/10.1242/jeb.00494>
57. Griffin TM, Roberts TJ, Kram R. Metabolic cost of generating muscular force in human walking: Insights from load-carrying and speed experiments. *Journal of Applied Physiology*. 2003; 95(1):172–83. <https://doi.org/10.1152/jappphysiol.00944.2002> PMID: 12794096
58. Zelik KE, Kuo AD. Human walking isn't all hard work: Evidence of soft tissue contributions to energy dissipation and return. *Journal of Experimental Biology*. 2010; 213(24):4257–64. <https://doi.org/10.1242/jeb.044297> PMID: 21113007
59. Fu XY, Zelik KE, Board WJ, Browning RC, Kuo AD. Soft tissue deformations contribute to the mechanics of walking in obese adults. *Medicine and Science in Sports and Exercise*. 2015; 47(7):1435–43. <https://doi.org/10.1249/MSS.0000000000000554> PMID: 25380475