



# Running on a slope: A collision-based analysis to assess the optimal slope

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## ABSTRACT

When running, energy is lost during stance to redirect the center of mass of the body (COM) from downwards to upwards. The present study uses a collision-based approach to analyze how these energy losses change with slope and speed. Therefore, we evaluate separately the average collision angle, i.e. the angle of deviation from perpendicular relationship between the force and velocity vectors, during the absorptive and generative part of stance. Our results show that on the level, the collision angle of the absorptive phase is smaller than the collision angle of the generative phase, suggesting that the collision is generative to overcome energy losses by soft tissues. When running uphill, the collision becomes more and more generative as slope increases because the average upward vertical velocity of the COM becomes greater than on the level. When running downhill at a constant speed, the collision angle decreases during the generative phase and increases during the absorptive phase because the average downward vertical velocity of the COM becomes greater. As a result, the difference between the collision angles of the generative and absorptive phases observed on the level disappears on a shallow negative slope of  $\sim -6^\circ$ , where the collision becomes 'pseudo-elastic' and collisional energy losses are minimized. At this 'optimal' slope, the metabolic energy consumption is minimal. On steeper negative slopes, the collision angle during the absorptive phase becomes greater than during the generative phase and the collision is absorptive. At all slopes, the collision becomes more generative when speed increases.

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## 1. Introduction

In a well-known paper, Margaria (1968) showed that the cost per unit distance is minimal when running on a 'optimal' slope of  $-10\%$  ( $\sim -6^\circ$ ) and increases both on steeper and shallower negative slopes and on positive slopes. Previous studies have analyzed the modification of the 'elastic bounce' of the body when running on a slope (Dewolf et al., 2016; Snyder and Farley, 2011; Snyder et al., 2012). Despite the fact that the elastic mechanism has been recognized to influence significantly the metabolic energy cost of running on the level (Cavagna et al., 1964), it did not highlight factors explaining the optimal slope at which the energy expenditure is minimal.

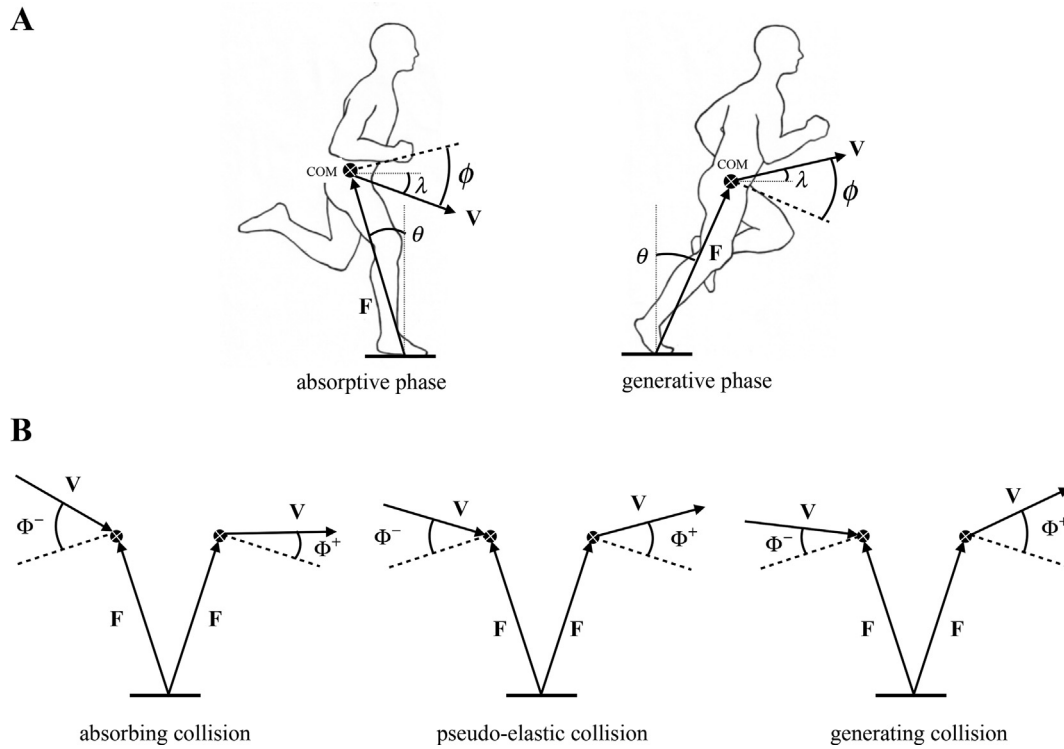
By modeling the lower-limb as an inelastic element, Ruina et al. (2005) proposed to analyze how the runners avoids or minimizes energy losses rather than to focus on the ability to conserve energy via elastic storage. According to these authors, one of the major sources of energy loss is the redirection of the motion of the center

of mass of the body (COM), from downward to upward during stance. This down-to-up redirection is actively mediated by the legs and can, at first approximation, be considered as a collision with the ground. While a wheel prevents collision by maintaining a perpendicular relationship between the force and the velocity vector of its center of mass, a collision occurs if this relationship is not perpendicular; the angle of deviation from orthogonal relationship between the force vector ( $\mathbf{F}$ ) and the velocity vector ( $\mathbf{V}$ ) of the COM is called the collision angle  $\phi$  (Fig. 1A).

Running results in a collision because  $\mathbf{F}$  deviates from the vertical axis and  $\mathbf{V}$  deviates from the horizontal axis in an opposite sense during stance (Fig. 1A). Based on a point mass collision model (described in details in the Methods section), Ruina et al. (2005) have shown that the collisional energy loss is minimized if the collision angle of the absorptive phase mirrors the subsequent collision angle of the generative phase. In this case, the collision is called a 'pseudo-elastic' collision and is energetically better than other ways of using legs.

Only few studies have performed collision-based analysis on human gaits (Gutmann et al., 2013; Lee et al., 2013), but neither of these two considers the difference between landing and takeoff.

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**Fig. 1.** Illustration of the collision model. **A:** The angle  $\theta$  is the angle between  $\mathbf{F}$  and the vertical,  $\lambda$  is the angle between  $\mathbf{V}$  and the horizontal during the absorptive (left) and generative (right) phases of the stance. The collision angle  $\phi$  represents the deviation from an orthogonal relationship of  $\mathbf{F}$  and  $\mathbf{V}$ . **B:** When the average collision angle during the absorptive phase ( $\Phi^-$ ) is greater than the average collision angle during the generative phase ( $\Phi^+$ ), the collision is absorptive (left). When  $\Phi^- < \Phi^+$ , the collision is generative (right) and when  $\Phi^- = \Phi^+$ , the collision is 'pseudo-elastic' (middle).

The present study evaluates if and how the collision deviates from a 'pseudo-elastic' model when running on a slope at different speeds. We separately assess the COM dynamics during the generative and absorptive part of stance. Because the down-to-up redirection of the COM is a key factor influencing the cost of running, we hypothesize that, at all speeds, the coordination strategies employed during this redirection will be close to a 'pseudo-elastic' collision around the 'optimal' slope of  $\sim -6^\circ$ .

## 2. Methods

### 2.1. The point-mass collision model

Ruina et al. (2005) proposed a point-mass collision model to evaluate the costs associated with the down-to-up redirection of the COM during stance. In this model, the runner is a point-mass (located at its COM) and the lower-limbs are assimilated to mass-less sticks that transmit forces along their axis. Three angles are defined (Fig. 1A):  $\theta$  is the angle between ground-interaction force  $\mathbf{F}$  and the vertical,  $\lambda$  is the angle between the velocity vector  $\mathbf{V}$  of the COM and the horizontal and  $\phi$  the angle between  $\mathbf{V}$  and a line orthogonal to  $\mathbf{F}$ . Because the motion of the COM is a more forwards than up-downwards, the collision angles  $\phi$  are shallow and one can use small angle approximation:  $\cos \phi \approx 1$  and  $\sin \phi \approx \phi$  (2005). Therefore, these last authors assume a conservation of linear momentum in the direction orthogonal to the leg and energy changes are accounted for by changes in the component of velocity along the axis of the leg between the beginning and the end of the stance (i.e. from the collisional impulse).

The contact period can be divided into two parts: the first part of the stance defined as the *absorbing* part, during which the angle between  $\mathbf{F}$  and  $\mathbf{V}$  is  $< 90^\circ$  and  $\phi$  is negative and the second part of the stance, called the *generating* part, during which the angle

between  $\mathbf{F}$  and  $\mathbf{V}$  is  $> 90^\circ$  and  $\phi$  is positive. In the first phase, energy is absorbed ( $E_a$ ) by extending muscles and tendons as well as by deformation of other tissues and the ground. According to (2005),  $E_a$  can be computed as:

$$E_a = \frac{m(\phi^- v)^2}{2}, \quad (1)$$

where  $\phi^-$  is the collision angle at the initial instant of the *absorbing* phase,  $m$  is the mass of the subject and  $v$  is the average forward velocity of the runner. Indeed, due to the conservation of linear momentum in the direction orthogonal to the leg, (2005) consider that the velocity during the absorbing phase ( $v^-$ ) equals the velocity during the generating phase  $v^+$  which are both equal to  $v$  (i.e.  $v^- \approx v^+ \approx v$ ).

During the second part of stance, energy is generated ( $E_g$ ) by muscles, tendon recoil and can be defined as:

$$E_g = \frac{m(\phi^+ v)^2}{2}, \quad (2)$$

where  $\phi^+$  is the collision angle at the final instant of the *generating* phase.

(2005) characterizes the collision by the coefficient of generation  $e_g$ :

$$e_g = \frac{\phi^+ - |\phi^-|}{\phi^+ + |\phi^-|}, \quad (3)$$

where  $\phi^+ + |\phi^-|$  is the total deflection angle of the collision. When  $e_g = 0$ , the collision is equivalent to a 'pseudo elastic' collision, i.e.  $\phi^+ = \phi^-$ . If  $e_g = 1$ , the collision is exclusively generating, i.e.  $\phi^- = 0$  and if  $e_g = -1$ , the collision is a plastic collision exclusively absorbing, i.e.  $\phi^+ = 0$ .

The energy change after a collision with the ground is thus equal to  $\Delta E = E_g - E_a$ . From Eqs. (1), (2) and (3),  $\Delta E$  can be expressed as:

$$\Delta E = m v^2 (\phi^+ + |\phi^-|)^2 e_g / 2. \quad (4)$$

This energy change during stance can be negative, zero or positive. By estimating the cost of running with only one collision with a given total deflection angle, Ruina et al. (2005) showed that over all choices, energy balance  $E_g = E_a$  (i.e.  $e_g = 0$ ), minimizes the metabolic cost of running. If  $E_g > E_a$  (i.e.  $e_g > 0$ ) then at least some positive work need be done in the gait cycle and if  $E_g < E_a$  (i.e. if  $e_g < 0$ ), then at least some negative work or other dissipation occurs during the gait cycle.

## 2.2. Subject and experimental procedure

Data were previously collected by Dewolf et al. (2016) on 10 healthy recreational runners (3 ♀ and 7 ♂, age:  $31.8 \pm 8.3$  years, mass:  $68.8 \pm 10.2$  kg, height:  $1.78 \pm 0.07$  m, mean  $\pm$  SD). Subjects provided written informed consent. 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 9 different speeds (2.22, 2.78, 3.06, 3.33, 3.61, 3.89, 4.17, 4.44 and  $5.00 \text{ m s}^{-1}$ , corresponding to 8, 10, 11, 12, 13, 14, 15, 16 &  $18 \text{ km h}^{-1}$ , respectively) at each of the following inclinations:  $0^\circ$ ,  $\pm 3^\circ$ ,  $\pm 6^\circ$  and  $\pm 9^\circ$  (corresponding to 0%,  $\pm 5.2\%$ ,  $\pm 10.5\%$ ,  $\pm 15.8\%$ , respectively). The average speed of the belt over a stride ( $\bar{V}_{\text{belt}}$ ) differed by  $2.8 \pm 1.4\%$  (mean  $\pm$  SD) from the chosen speed and the instantaneous did not change by more than 5% of  $\bar{V}_{\text{belt}}$ . Note that on a  $+9^\circ$  slope, one subject was not able to run at  $5 \text{ m s}^{-1}$ .

## 2.3. Data processing

Force transducers measured the components of  $\mathbf{F}$  normal (n) and parallel (p) to the tread-surface. The force signals were digitized by a 16-bit analog-to-digital converter at 1000 Hz. The horizontal (y) and the vertical (z) components of  $\mathbf{F}$  and  $\mathbf{V}$  were then computed using the methods described in details in Dewolf et al. (2016). The stance phase was defined as the period during which  $F_z$  was greater than 10 N.

At each instant, the following parameters were calculated: the angle  $\theta$  between  $\mathbf{F}$  and the vertical, the angle  $\lambda$  between  $\mathbf{V}$  and the horizontal and the collision angle  $\phi$  the deviation from an orthogonal relationship of  $\mathbf{F}$  and  $\mathbf{V}$  (Fig. 1A). These parameters were computed as in Lee et al. (2013):

$$\theta = \sin^{-1}(\mathbf{F} \cdot \hat{\mathbf{y}} / F) \quad (5)$$

$$\lambda = \sin^{-1}(\mathbf{V} \cdot \hat{\mathbf{z}} / V) \quad (6)$$

$$\phi = \sin^{-1}(\mathbf{F} \cdot \mathbf{V} / FV) \quad (7)$$

where  $\hat{\mathbf{y}}$  is a unit vector pointing horizontally forward and  $\hat{\mathbf{z}}$  is a unit vector pointing vertically upward.

Gutmann et al. (2013), Lee et al. (2013) computed the average of these angles throughout the stance phase, meaning that they did not consider the difference between landing and takeoff. Here, the stance phase was divided in two parts: the absorptive part during which  $\phi$  was negative and the generative part during which  $\phi$  was positive. In their simplified theoretical model, Ruina et al. (2005) compare  $\phi$  at the initial and final instant of stance. At these

moments, the horizontal and vertical GRF are rather small and the angle  $\theta$  is highly variable. Instead in this study, the absolute value of the angles  $\theta$ ,  $\lambda$  and  $\phi$  were averaged over the absorptive part (respectively  $\Theta^-$ ,  $\Lambda^-$ ,  $\Phi^-$ ) and over the generative part of the ground contact (respectively  $\Theta^+$ ,  $\Lambda^+$ ,  $\Phi^+$ ). The coefficient of generation  $e_g$  was then evaluated from  $\Phi^+$  and  $\Phi^-$  as:

$$e_g = \frac{\Phi^+ - \Phi^-}{\Phi^+ + \Phi^-}. \quad (8)$$

Here, the collision is equivalent to a 'pseudo elastic' collision when  $e_g = 0$ , i.e.  $\Phi^+ = \Phi^-$  (Fig. 1B). If  $e_g = 1$ , the collision is exclusively generating, i.e.  $\Phi^- = 0$  and if  $e_g = -1$ , the collision is a plastic collision exclusively absorbing, i.e.  $\Phi^+ = 0$ .

When running on a slope, the difference between the velocity in the direction orthogonal to the leg during the absorbing and generating phase was  $\sim 4.5 \pm 2.3\%$  (mean  $\pm$  SD) of the average running speed. Because this result was similar to the difference obtained on the level ( $p = 0.236$ ), we also assumed -as (2005)- that the energy change is completely accounted for by changes in the component of the velocity normal to the leg and we applied this point-mass collision model to our experimental data.

## 2.4. Statistics

A two-way ANOVA with Bonferoni post-hoc (PASW Statistics 19, SPSS inc®, IBM company, USA) was performed in order to assess the effect of speed and slope and of the interaction 'speed  $\times$  slope' on the calculated variables ( $p$ -values were set at 0.05).

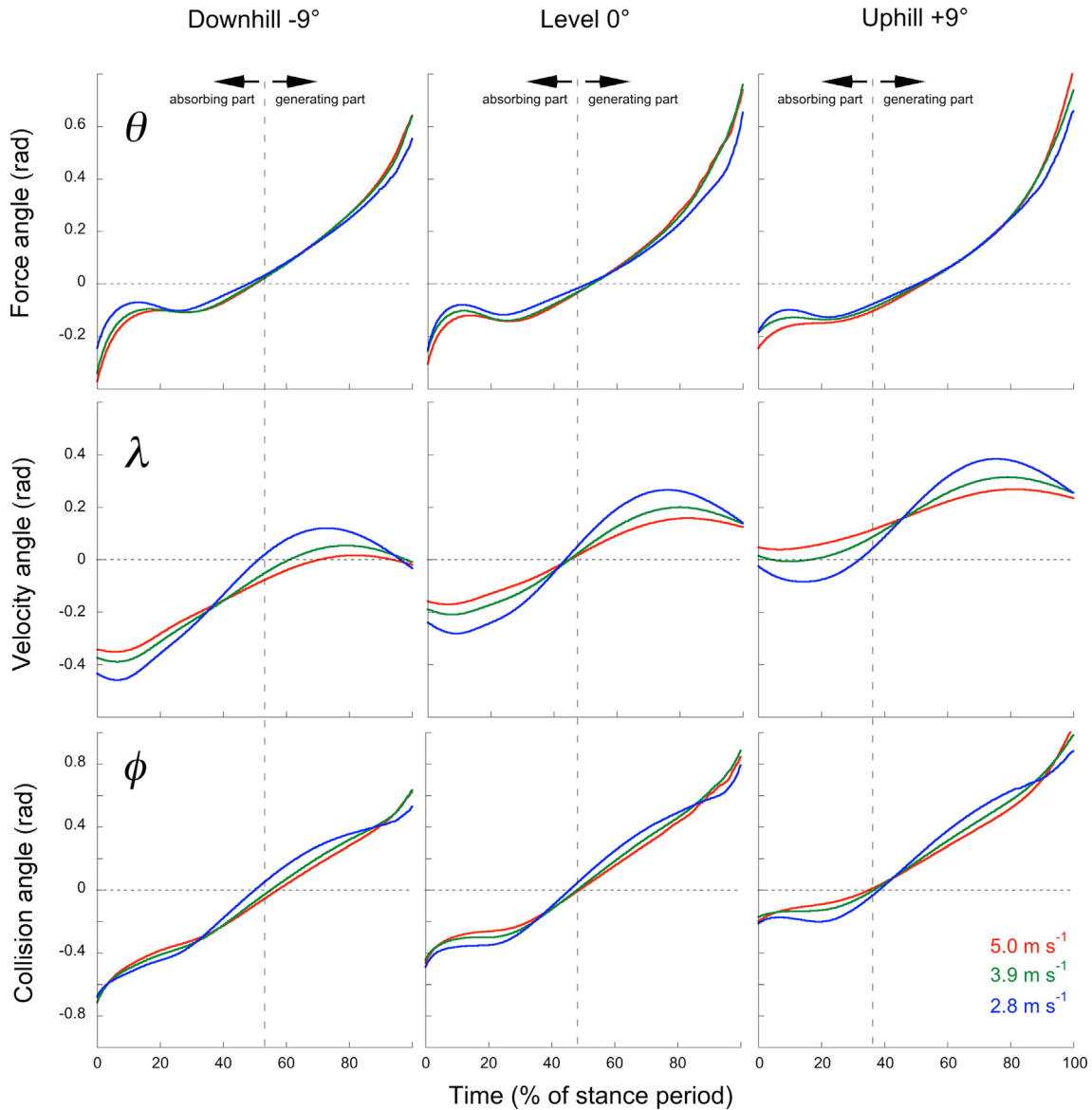
## 3. Results

The relative duration of the absorbing and the generating part change little with the speed of progression (Fig. 2). On the level, the absorbing part of the stance is somewhat shorter than the generating part, as described by Cavagna (2010). On a negative slope, the absorbing part becomes slightly longer whereas on a positive slope it is drastically reduced. During the absorptive part,  $\Theta^-$  and  $\Theta^+$  are hardly influenced by slope and speed.

The angle  $\lambda$  is influenced by speed and slope (Fig. 2,  $p < 0.001$ ). During the absorptive part of stance,  $\Lambda^-$  decreases on positive slopes while it increases on negative slopes. At the opposite, during the absorptive part of stance,  $\Lambda^+$  decreases on negative slopes while it increases on positive slopes. Both  $\Lambda^-$  and  $\Lambda^+$  decrease as the speed of progression increases. At high speeds on a  $+9^\circ$  slope, the angle  $\lambda$  is positive during the whole stance period whereas on a  $-9^\circ$  slope, it is negative during the most part of the stance.

The collision angle  $\phi$  (Fig. 2),  $\Phi^-$  and  $\Phi^+$  (Fig. 3) are also influenced by slope ( $p < 0.001$ ): when the slope increases from  $-9^\circ$  to  $+9^\circ$ ,  $\Phi^+$  increases while  $\Phi^-$  decreases. The speed affects  $\Phi^-$ , which slightly but significantly decreases with increasing speed ( $p < 0.001$ ). On the contrary,  $\Phi^+$  does not change significantly with speed.

From  $-9^\circ$  to  $+9^\circ$ , the coefficient of generation  $e_g$  increases when the slope of the terrain increases (Fig. 4,  $p < 0.001$ ). On the steepest negative slopes,  $e_g < 0$  whereas on positive slopes,  $e_g > 0$ . Furthermore,  $e_g$  increases slightly but significantly with the speed of progression ( $p < 0.001$ ). At each speed, the slope at which  $e_g$  is nil is estimated from the coefficients of a linear regression (Table 1 and inset in Fig. 4):  $e_g$  is nil at a slope of between  $-3.5^\circ$  ( $2.2 \text{ m s}^{-1}$ ) and  $-7.5^\circ$  ( $4.2 \text{ m s}^{-1}$ ). The average  $e_g$  at each slope is also measured, neglecting the small variations of  $e_g$  due to speed (Fig. 4). Here also  $e_g$  is equal to zero around  $-6.2^\circ$ .



**Fig. 2.** Instantaneous force, velocity and collision angle during running on a slope. Time-evolution of the force angle  $\theta$  (top line), the velocity angle  $\lambda$  (middle line) and the collision angle  $\phi$  (bottom line) during the contact period while running downhill (left column), on the level (middle column) and uphill (right column), at different speeds:  $2.8 \text{ m s}^{-1}$  (blue),  $3.9 \text{ m s}^{-1}$  (green) and  $5 \text{ m s}^{-1}$  (red). The generative phase (when  $\phi < 0$ ) and the absorptive phase (when  $\phi > 0$ ) are defined by the vertical interrupted lines. The horizontal dotted lines correspond to an angle of zero. At  $\theta = 0$ , the force vector  $\mathbf{F}$  is vertical; at  $\lambda = 0$ , the velocity vector  $\mathbf{V}$  is horizontal and at  $\phi = 0$ ,  $\mathbf{F}$  is perpendicular to  $\mathbf{V}$ . For each subject, the curves obtained in a slope-speed class are averaged. Then, the curve of all subjects are averaged (grand-mean) and are presented here.

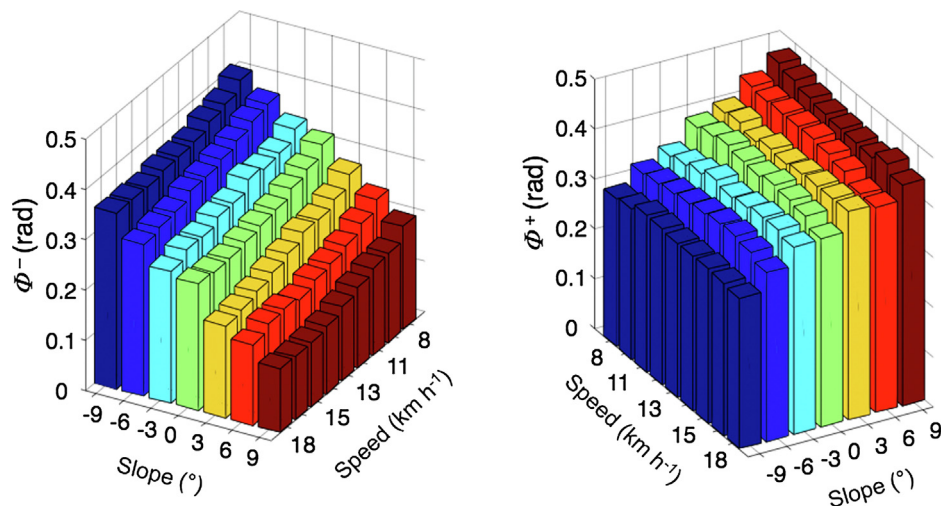
#### 4. Discussion

The studies of Margaria (1968) and Minetti et al. (1994) both show that when running on a slope, the minimum of oxygen consumption occurs on a negative slope around  $-6^\circ$ . In 1994, (Minetti et al., 1994) developed a model to predict the metabolic cost of running on a slope, assuming that the cost can be predicted only from the mechanical work after subtracting the “free” elastic energy. Notwithstanding the fact that the value of elastic energy recovery used in the model is in agreement with the literature, these authors assume that this value is not changing with slope and speed. However, running on different slopes at different speeds involves specific adaptations, among others changes in the foot strike pattern and in the ground reaction forces (Vernillo et al., 2017), which in turn affect the elastic energy storage and release in the muscle-tendon unit (Snyder et al., 2012). To our knowledge, no other study has suggested factors explaining the

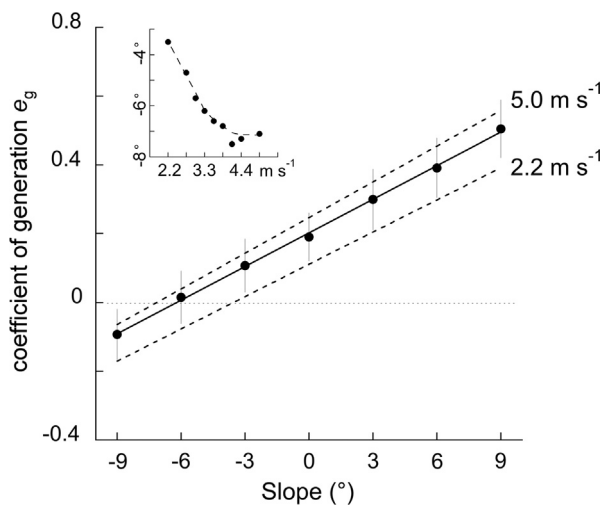
optimal slope at which the energy expenditure is minimal. The present study analyzes for the first time collision parameters to relate optimal coordination strategies (i.e. the pseudo-elastic collision) to the most economical slope.

In 2013, Lee et al. have developed a collision-based analysis of human gait [previously applied for quadrupedal locomotion (Lee et al., 2011)]: the authors have computed the average collision angle over the stance period and assert that it closely approximates the mechanical cost of transport. During running at  $1.9 \text{ m s}^{-1}$ , Lee et al. (2013) found an average collision angle of  $\sim 0.3$  rad. When their methods are applied at the closest running speed recorded here (i.e.  $2.2 \text{ m s}^{-1}$ ), our results are in agreement with their previous published values with an average collision angle of  $0.27 \pm 0.032$  rad. However, averaging the collision parameters across stance phase as in Lee et al. (2013) or Gutmann et al. (2013) does not take into account asymmetry that could occur between the absorbing and generating phases. Since running on





**Fig. 3.** Collision angle as a function of slope and running speed. Average collision angle during the absorptive phase,  $\Phi^-$  (left) and during the generative phase,  $\Phi^+$  (right) as a function of slope (one color per slope) and speed of progression. For each subject, the angles  $\Phi^-$  and  $\Phi^+$  obtained in a slope-speed class are averaged. The value obtained for each subject are then averaged (grand-mean) and are presented here.



**Fig. 4.** Coefficient of generation  $e_g$  as a function of slope. The continuous line corresponds to the evolution of the coefficient of generation  $e_g$  neglecting the small variations of  $e_g$  due to speed (linear regression obtained from Kaleidagraph 4.5). At each slope, the closed circles and bars represent the mean and the standard deviations of the ten subjects at all speeds. The interrupted lines correspond to the relation between  $e_g$  and slope at the slowest ( $2.2 \text{ m s}^{-1} = 8 \text{ km h}^{-1}$ ) and at the fastest ( $5 \text{ m s}^{-1} = 18 \text{ km h}^{-1}$ ) running speed. The inset corresponds to the slope (in degrees) at which  $e_g$  is nil, as a function of running speed (in  $\text{m s}^{-1}$ ). In this inset, the dotted line is drawn through the data (weighted mean, Kaleidagraph 4.5).

**Table 1**  
Regression coefficients and optimum gradient for each running speed.

Speed ( $\text{km h}^{-1}$ )	$r^2$	Optimum gradient ( $^\circ$ )
8	0.90	−3.5
10	0.90	−4.7
11	0.90	−5.7
12	0.91	−6.2
13	0.91	−6.6
14	0.90	−6.8
15	0.90	−7.5
16	0.88	−7.3
18	0.89	−7.1

a slope affects the ratio between positive and negative work (Dewolf et al., 2016; Minetti et al., 1994), this asymmetry will be

affected by slope and speed and must be considered in collision parameters.

Lately, we have analyzed the collision parameters during level running and have shown that the average angle of the force vector ( $\Theta$ ) relative to the vertical is greater during the push than during the brake (Dewolf and Willems, 2017). This change in  $\Theta$  affects the collision angle between landing and takeoff. Here, we observe that when running on the level at all speeds,  $\Phi^- < \Phi^+$  showing that the angle between  $\mathbf{V}$  and  $\mathbf{F}$  is closer to  $90^\circ$  at the beginning than at the end of the stance. As a result, the stance phase deviates from a pseudo-elastic collision and is generative (i.e.  $e_g > 0$ ). Dissimilarities during the absorptive and generative phases of the stance were already observed by Cavagna (2006) during level running: he observed that the time of the absorptive phase is shorter than the time of the generative phase. These differences have been explained by a different response of the muscle-tendon unit during stretching and shortening (Cavagna, 2010). In addition, Cavagna et al. (2011) showed that in backward running the asymmetry is reversed (i.e. longer absorptive than generative). This last result could be explained by an asymmetry in the leg function mainly due to an asymmetry in the lever arms of the lower-limb muscles (e.g. Braunstein et al., 2010; Carrier et al., 1994; Maykranz and Seyfarth, 2014).

An alternative explanation could be the energy losses by soft tissues occurring at foot contact (DeVita et al., 2008). In 2017, Dewolf and Willems suggest that the deviation from a pseudo-elastic collision could be due to a greater energy production by muscles during the generative phases than the energy dissipation during the absorptive phases. This last hypothesis endorses the result of DeVita et al. (2008) showing that during running at a constant average speed, despite the maintenance of a constant average level of total mechanical energy, positive muscle work is greater than negative muscle work. Furthermore, DeVita et al. (2007) also observed that, in both ramp and stair gait, muscle work was larger in ascent than in descent, despite equivalent changes in vertical position. This means that the muscle contribution is greater to lift of the COM than to lower it. This observation is corroborated by (Zelik and Kuo, 2012) who showed that muscles generate a net positive amount of work to overcome various energy losses by other tissues. A similar result was also observed through direct measurement techniques in muscles of wild turkeys (Gabaldón et al., 2004).

When running on a slope, the average vertical velocity of the COM is tuned to raise or lower the COM each step (Dewolf et al., 2016; Minetti et al., 1994; Snyder et al., 2012). As a result, the major adaptation in COM dynamics is the change in the velocity angle  $\lambda$  whereas the force angle  $\theta$  hardly changes with speed and slope (Fig. 2). These changes affect the down-to-up redirection of the COM: in uphill running,  $\Phi^+$  increases while  $\Phi^-$  decreases whereas in downhill running,  $\Phi^+$  decreases while  $\Phi^-$  increases. The greater  $\Phi^+$  on positive slopes and the greater  $\Phi^-$  on negative slopes allow the runner to enhance the efficiency of the average positive and negative external power, respectively (Mauroy et al., 2013). Indeed, since the direction of the force is closer to the direction of the movement of the COM, the average external power is enhanced. For example, (Mauroy et al., 2013) showed that during level running, for a given  $\mathbf{F}$  and  $\mathbf{V}$ , an increase of  $\sim 0.1$  rad of  $\Phi^+$  increases the power by  $\sim 15\%$ . It is peculiar to note that in downhill running,  $\Phi^+$  decreases at a slower rate than  $\Phi^-$  in uphill running. This could be due, at least in part, to the fact that in downhill running, muscles must perform positive work to propel the lower extremity upward and forward to initiate the swing phase.

When running uphill, as the slope becomes steeper the coefficient of generation  $e_g$  tends to one because the energy generated by muscles exceeds the energy dissipated. When running downhill on a shallow slope, the difference between  $\Phi^+$  and  $\Phi^-$  observed on the level disappears progressively and  $e_g$  equals zero around  $-6.2^\circ$  (Fig. 4). According to Ruina's model (2005), it would indicate that at that slope, the rebound is equivalent to a *pseudo-elastic collision*. Between  $0^\circ$  and  $\sim -6^\circ$ , the dissimilarities between the duration of the absorptive and generative phase progressively fades away since the time of negative work production is extended (Dewolf et al., 2016). Furthermore, on the level, the COM is higher at the end than at the beginning of the stance due to an asymmetry in the lever system of the limb (Maykranz and Seyfarth, 2014). When the slope becomes negative, this difference in height most likely disappears. On steeper negative slopes, the collision becomes absorptive and  $e_g < 0$ , suggesting that the energy dissipated by muscles exceeds the energy generated.

At all slopes, the collision becomes more generative with increasing speed; the fact that  $e_g$  becomes greater with speed both on positive and on negative slopes can be explained by the greater ground collision occurring at faster speed (Keller et al., 1996). Indeed, the larger ground forces with increasing speed cause larger shocks in the body tissues which in turn generate a greater energy-dissipation (Zelik and Kuo, 2012). Consequently, a greater amount of net positive work must be performed each step.

The inset in Fig. 4 and Table 1 show that the slope at which  $e_g$  is nil varies from  $\sim -4^\circ$  at slow speeds to  $\sim -8^\circ$  at fast speeds. This observation contrasts with the results on oxygen consumption of Minetti et al. (1994), showing that the optimal slope does not change with speed. Note that our results are an adaptation of a theoretical model based on a simple relationship between muscular work and energy consumption: we do not establish a direct link between the pseudo-elastic collision estimate here and the minimum metabolic cost of incline running. Indeed, other factors affect the metabolic cost such as the cost of swinging the limbs (Doke et al., 2005; Minetti et al., 1994), the amount of elastic energy stored in the muscle-tendon units (Willems et al., 1995) or which part of the force-length and force-velocity curves muscles are on (Griffin et al. (2003)).

Furthermore, factors other than work (and energy expenditure) also clearly influence the preferred movement strategy. By analyzing jump-landing strategy, Zelik et al. (2012) showed that subjects may alter their neuromuscular control strategy to modulate the amount of negative work, and its distribution between active and passive tissues. The deviation from the theoretically optimal

pseudo-elastic collision may also indicate a trade-off between work and other less easily quantified factors, which may explain why some tasks are performed less economically, e.g. power output limitation, stability, shock absorption, risk of injuries, etc. For example, Hunter et al. (2010) showed that, in downhill walking, ensuring stability was done at the expense of walking economy. This suggests that stability also plays a central role in shaping the movement and must be considered to understand preferred gait strategy.

Regardless of these limitations, the coefficient of generation  $e_g$  is nil at a gentle negative slope, close to the one at which the energy expenditure is minimal (Margarita, 1968; Minetti et al., 1994). This similarity supports the hypothesis that the dynamic collision strategy that decreases the mechanical cost of running is most effective close to the most economical slope. Interestingly, the model of the passive walker and runner of McGeer (1990) suggests that one could walk or run on a gentle downhill slope without any energy input, simply by taking advantage of gravity. In that case, the energy changes on a gentle negative slope balances the energy dissipated by joint friction, aerodynamic drag, etc. However, further studies should be considered to identify the reasons of the equality between the absorptive and generative collision angles on a  $\sim -6^\circ$  slope.

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## Competing interests

The authors declare no competing or financial interests.

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