



Biomechanical behavior of the lower limbs and of the joints when landing from different heights

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ABSTRACT

Landing from a jump is a challenging task as the energy accumulated during the aerial phase of the jump must be fully dissipated by the lower limbs during landing; the higher the jump height, the greater the amount of energy to be dissipated. In the present study, we aim to understand (1) how the biomechanical behavior is tuned as a function of the mechanical demand, and (2) the relationship between the self-selected landing strategy and the behavior of the joints. Fourteen subjects were asked to drop off a box of 10 to 60 cm height and land on the ground. The ground reaction forces and the kinematics were recorded using force plates and a motion capture system. A model was used to estimate the properties, i.e. stiffness and damping, of the lower limbs and of the joints. Our results show that, whatever the amount of energy to be dissipated (i.e. height of the jump), the lower limbs and the ankle and knee joints behave first as a spring, then as a spring-damper system. However each joint plays a specific role: during the spring phase, the behaviour of the lower limb is associated with the stiffness of the ankle and with the landing constraints (i.e. force peak and loading rate), while during the spring-damper phase, it is associated with the stiffness of the knee and with the amount of energy to be dissipated. Our findings suggest that constraints and performance result from a distinct control of biomechanical parameters at the joints.

1. Introduction

Landing from a jump is a challenging task as the downward movement of the center of mass of the body (CoM) of the participant must be decelerated quickly to allow the subject to return to a standing still position. The energy accumulated during the aerial phase of the jump must indeed be fully dissipated by the lower limbs during landing; the higher the drop jump height, the greater the amount of energy to be dissipated. Depending on the participant and the circumstances, the landing strategy, i.e. the way to dissipate the energy, can be more or less stiff. Generally, a stiff strategy is associated with a higher risk of injury such as an ACL injury (Almonroeder et al., 2020; Laughlin et al., 2011; Southard et al., 2012). To prevent such injuries, basic verbal instructions targeting the knee joint, such as “focus on bending your knees when you land”, are often used in injury prevention programs to soften the landing and reduce constraints, e.g. the peak ground reaction force (Almonroeder et al., 2020). According to others, the role of the ankle should also be considered in prevention programs (Lee et al., 2018; Tait et al., 2022). Therefore, gaining insight into the role of lower limb joints in

adjusting the landing strategy can be helpful in reducing constraints and so the risk of injury.

One way to study the landing strategy is to measure the mechanical work done on the CoM to dissipate the energy accumulated during the aerial phase. Although the net mechanical work performed on the CoM is a function of the energy to be dissipated, one can do more or less negative and positive work. According to Zelik & Kuo (2012), the amount of negative and positive work done on the CoM reflects a subjective trade-off between economy of movement and other costs, such as the risk of injury. When landing in a stiff manner, a small amount of negative and positive work is done on the CoM at the expense of the risk of injury. The opposite is true when landing softly: additional negative and positive work is performed on the CoM, decreasing the risk of injury.

Another way is to investigate the mechanical work done at each joint using an inverse dynamics approach (Elftman, 1939; Mauroy et al., 2014). When the amount of energy to be dissipated increases due to an increased jump height, the proximal joint contribution to negative work increases (McNitt-Gray, 1993; S. Zhang et al., 2008; S.-N. Zhang et al., 2000). In contrast, the amount of negative work performed increases at

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the ankle when landing with instructions to adopt a stiff strategy (Devita & Skelly, 1992; S.-N. Zhang et al., 2000). However, as a part of energy absorbed during negative work is stored in elastic structures and then released, and as energy can also be transferred between the joints by two-joint muscles, determining the energy dissipated by each joint (i.e., net work) and thus the adjustments related to the mechanical demand and to the strategy become challenging (Prilutsky & Zatsiorsky, 1994).

A third way to study the landing strategy is to measure the biomechanical properties using a model. In running and hopping, the stiffness can be estimated by means of a simple spring-mass model with a constant stiffness explaining the behavior of the CoM (Blickhan, 1989; Cavagna et al., 1988; Farley et al., 1991). However, this model is not appropriate when landing because in this case energy has to be dissipated, and a spring does not take into account energy dissipation. Dyhre-Poulsen et al. (1991) suggested that the behavior of the muscles should be modified throughout the task, changing from a spring to a damping-unit. Following this suggestion, a model that first includes a spring to allow energy storage and then another spring associated with a compliant damper to allow energy dissipation was proposed and tested more recently (Gambelli et al., 2015). Using this model, it has been shown that the system's characteristics were adjusted depending on the circumstances. For example, Schepens et al. (2020) reported that the stiffness during the first part of the landing increased under height-induced threat, leading to an increase in the loading rate, while the characteristics during the second part of landing were not modified. In other circumstances, such as microgravity conditions, Gambelli et al. (2016) reported that the stiffness decreased during both parts of landing together with the decrease of the gravity. These authors also showed in parallel that an overly stiff behavior during the second part of landing resulted in a rebound (Gambelli et al., 2016).

Interestingly the model could be applied to the joints and the relationship between the CoM and joint behavior could then be explored. When hopping, the behavior of the ankle and knee can be characterized by a torsional spring as energy must be stored and released successively (Farley & Morgenroth, 1999; Hobara et al., 2011). During this task, the lower limb stiffness is associated with the stiffness of the ankle and of the knee. When landing from a jump, the relationship between the biomechanical behavior observed at the CoM and that at the lower limb joints remains unknown. Therefore, we used the model of Gambelli et al. (2015) to investigate the landing strategy at the level of the joints, and to identify the role of each joint in conjunction with the behavior at the CoM.

The present study is intended to describe the biomechanics when performing double-leg landings from different heights, i.e., different amounts of energy to be dissipated. Our first aim is to test a biomechanical model to characterize the biomechanical behavior as a function of the mechanical demand. Our second aim is to analyse the relationship between the self-selected landing strategy and the behavior of the joints.

2. Materials and methods

a) Subjects and experimental procedures

Fourteen healthy male recreational athletes (i.e., non-professional athletes) were enrolled in the present study (Table 1). Experiments were performed according to the principles of the Declaration of Helsinki and were approved by the local ethics committee (Comité d'Éthique Hospitalo-Facultaire Saint-Luc-ULouvain, 2021-12FEV-064). Participants were asked to perform five jumps from 6 boxes of different heights (10, 20, 30, 40, 50 and 60 cm) in an ascending order. They were instructed to stay still ~ 3 s prior jumping, to hop off of the box at the operator's signal, land barefoot on the ground on both feet using a self-selected strategy, and then return to a standing still position for ~ 3 s. No further instruction were provided about the manner, speed or arm movements. A period of ~ 30 s rest was provided between trials and ~ 1–2 min between landing heights to control potential fatigue (Nordin & Dufek, 2017). Prior marker placement, participants were asked to performed 3 trials from the 10 cm box in order to check that instructions have been correctly understood. A total of 406 trials was analyzed (Table 1).

b) Experimental Setup

The vertical (F_v) and fore-aft ($F_{\text{fore-aft}}$) components of the ground reaction force (GRF) were measured at a sample rate of 1000 Hz using 4 force plates (1x1m); two force plates were placed beneath the box to record the GRF before the takeoff, and two in the landing area to record the GRF after touchdown. The movements of the right side of the participant were measured in the sagittal plan at a sample rate of 250 Hz using a motion capture system of 12 cameras (Oqus 600+, Qualisys). Reflective markers were glued on anatomical landmarks: chin-neck intercept (CN), greater trochanter (GT), lateral epicondyle of the femur (FC), lateral malleolus (LM) and 5th metatarsal head (5 M).

c) Acquisition and signal processing

The GRF and the kinematic data were synchronized by means of a trigger signal. The GRF were filtered with a second-order bi-pass Butterworth digital low-pass filter (50 Hz) and normalized by the body weight (BW). The kinematic data were resampled at 1000 Hz.

Computation of the vertical acceleration, velocity and position of the CoM.

The CoM is the average position of all the mass of the body and its linear acceleration is determined by the external force acting on the body (Cavagna, 1975; Gambelli et al., 2015; Tesio & Rota, 2019).

First the vertical acceleration of the CoM (a_v) was computed at each instant as:

$$a_v = \frac{F_v - (m g)}{m}$$

Table 1
Population characteristics and number of trials per energy class (E_{TD}) for each participant.

	Participant													
	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12	#13	#14
Age (y.o)	22	22	26	24	24	25	22	23	30	31	28	23	22	22
Height (m)	1.85	1.80	1.74	1.89	1.84	1.88	1.74	1.86	1.72	1.71	1.73	1.81	1.89	1.69
Weight (kg)	75.1	70.8	87.5	73.7	72.9	82.3	70.3	62.3	71.3	71.4	71.3	76.5	78.4	59.4
E_{TD} class	Number of trials analyzed													
[1]	3	–	4	5	4	5	2	5	5	6	1	–	2	4
[2]	5	6	5	5	6	5	8	6	5	5	9	8	6	3
[3]	6	6	5	5	5	7	5	7	5	3	5	6	5	6
[4]	5	8	5	4	6	7	6	8	6	8	4	6	8	5
[5]	4	7	6	5	4	4	5	4	6	6	5	6	5	4
[6]	2	2	4	5	5	2	4	–	3	–	4	4	4	6

where F_v is the vertical component of the ground reaction force recorded using force plates, m is the body mass and g is the gravitational acceleration (i.e. 9.81 m.s⁻²). When the vertical force exerted on the ground is equal to the bodyweight of the participant, the vertical acceleration of the CoM is zero, and when the vertical force exerted is equal to zero (during the aerial phase), the vertical acceleration of the CoM is equal to g .

Second, the vertical velocity of the CoM (V_v) was computed at each instant as:

$$V_v = V_{v0} + \int a_v dt$$

where V_{v0} is the initial velocity of the CoM. V_v was computed as the time-integration of a_v starting when the participant was static on the box before the hop-off (defined as the first point of the 300 ms window with the lowest standard deviation of F_v) to the touchdown + 2 s. V_{v0} was assumed to be zero at the beginning of the calculation of V_v .

Finally, the vertical position of the CoM (S_v) was computed at each instant as:

$$S_v = S_{v0} + \int V_v dt$$

where S_{v0} , the initial position of the CoM, is defined as the box height; S_v is therefore relative to the position of the CoM when the participant is on the box.

From V_v and S_v , the total energy of the CoM (E) was computed at each instant as the sum of the mass-specific vertical kinetic energy and the mass-specific gravitational potential energy.

$$E = \frac{1}{2} V_v^2 + g S_v$$

The amount of energy to be dissipated (E_{TD}) was defined as E at touchdown.

Computation of the angular position and velocity of the joints.

Rigid segments were defined from the markers: trunk from CN to GT, thigh from GT to FC, shank from FC to LM and foot from LM to 5 M. The angular position (θ_j) was calculated in the sagittal plane at each instant as the angle between segments (ankle between foot and shank, knee between shank and thigh, hip between thigh and trunk) and the angular velocity (ω_j) was computed as the time derivative of θ_j .

General characteristics of the task.

The touchdown (TD) was defined as the last point where $F_v < 0.01BW$ (Gambelli et al., 2015). After TD, the CoM goes down until reaching its lowest vertical position (S_{v-min}). The maximal value of F_v (F_{v-peak}) and the loading rate (LR, defined as the slope of the linear regression of the F_v -Time from TD to F_{v-peak}) were calculated. After the downward phase, the CoM goes up until returning to a standing still position (SP, defined as the first period of 500 ms where $0.9 < F_v/BW < 1.1$; Fransz et al., 2015). The time spent to reach SP relative to TD was named t_{SP} .

Biomechanical behavior.

The biomechanical behavior of the lower limbs was modeled by a spring from TD to F_{v-peak} and by a spring associated with a compliant damper from F_{v-peak} to SP (Fig. 1, see Gambelli et al. (2015) for more details). During the first phase, the mass-specific stiffness of the lower limbs (k_1) was calculated as the slope of the a_v - S_v curve, computed by a linear regression. During the second phase, the mass-specific stiffness (k_2) and damping coefficient (c_2) were calculated from the equation of a damped harmonic oscillator using a regression model:

$$a_v = k_2 S_v + c_2 V_v + \text{intercept}$$

To characterize the biomechanical behavior of the joints, the net muscular moment developed at each joint (M_j) was estimated by an

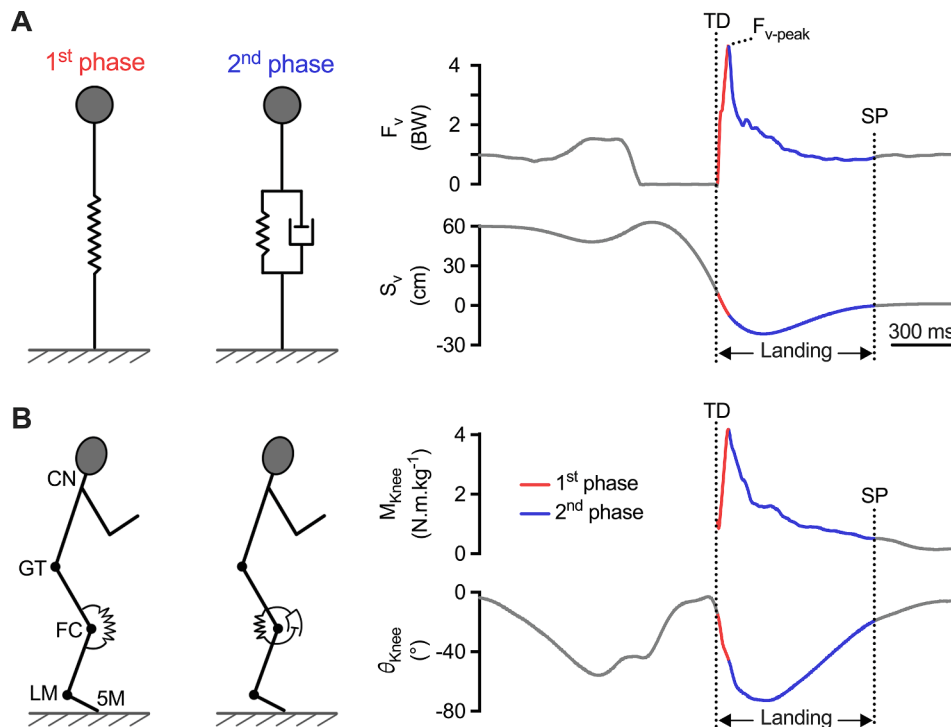


Fig. 1. Model to assess the biomechanical properties of the CoM (A) and of the joints (B) when landing from a jump. **A.** CoM: The 1st phase is modeled by a spring (red) and the 2nd phase by a spring associated with a damper (blue). The vertical component of the ground reaction force (F_v) normalized in BW and the vertical position of the CoM (S_v) are illustrated as function of time when hopping off a box of 60 cm. The first vertical dotted line indicates the instant of touchdown (TD) and the second vertical dotted line indicates the instant when the subject is returned to a standing still position (SP). **B.** Joints: The 1st phase is modeled by a torsional spring (red) and the 2nd phase by a torsional spring-damper (blue). The net muscular moment developed at the knee (M_{knee}) and the angular knee position (θ_{knee}) are illustrated as function of time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

inverse dynamic method using F_v and $F_{\text{fore-aft}}$ and the kinematic (Elftman, 1939; Maury et al., 2014). A torsional spring was used to model the behavior from TD to the peak of M_j and the torsional stiffness (k_1) was calculated as the slope of the M_j - θ_j curve (see Fig. 1). A torsional spring-damper was used from the peak of M_j to SP, and the torsional stiffness (k_2) and the damping coefficient (c_2) were calculated from the equation:

$$M_j = k_2\theta_j + c_2\omega_j + \text{intercept}$$

Regardless the amount of energy to be dissipated, the model showed good correlations with the experimental data for the CoM, ankle and knee ($r^2 > 0.8$ for 96.6 %, 90.3 % and 98.4 % of cases, respectively), whereas it showed poorer correlations for the hip ($r^2 > 0.8$ for 43.8 % of cases, see r^2 in Supplementary Fig. S1). As the r^2 was below 0.8 for a substantial number of cases, the biomechanical properties at the hip will not be considered here.

d) Data analysis and Statistics

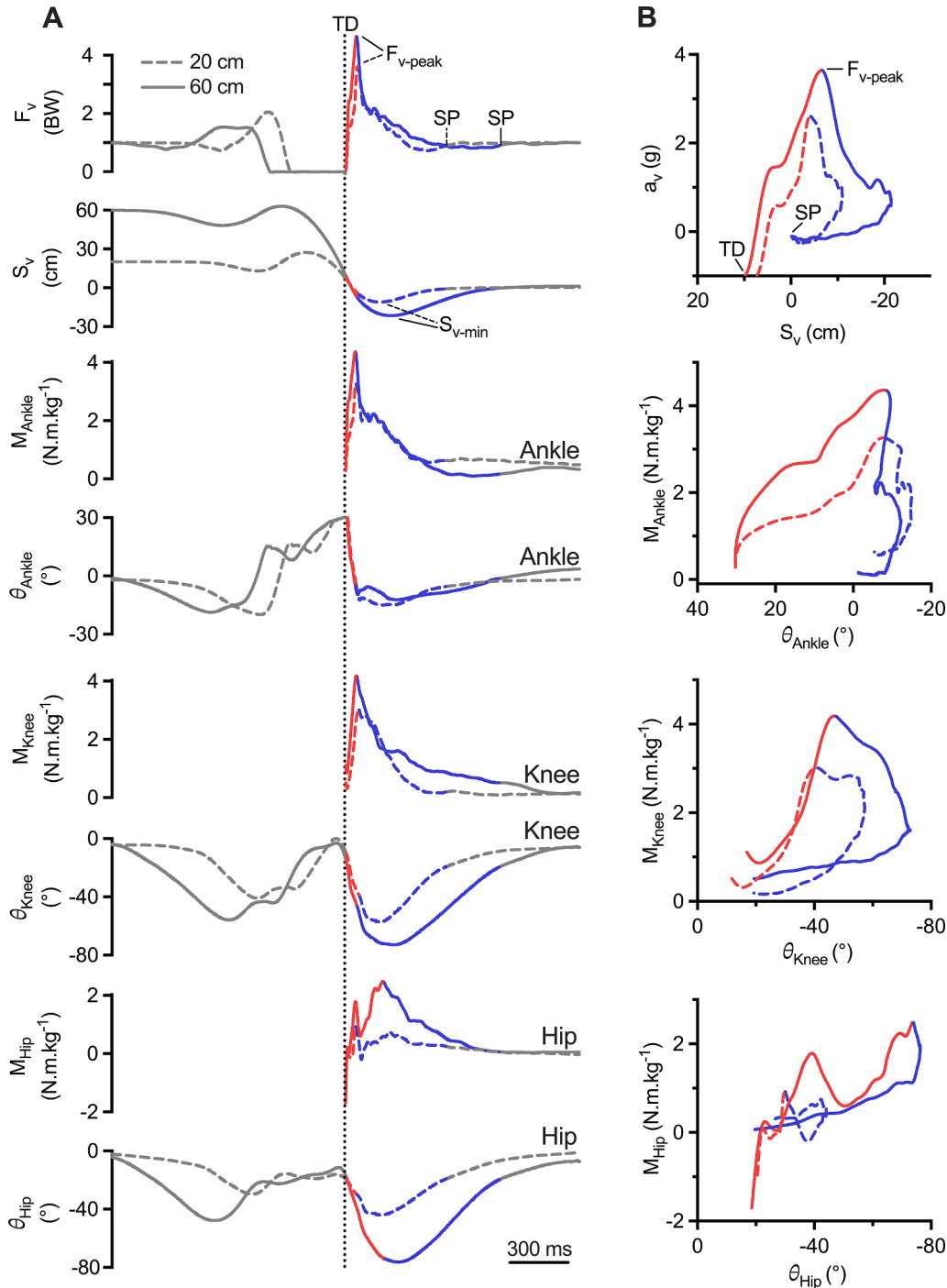


Fig. 2. Typical traces of landing when hopping off a box of 20 cm (dotted lines) and of 60 cm (solid lines). **A** Kinetics and kinematics are presented as a function of time. From top to bottom: vertical component of the ground reaction force normalized by BW (F_v), vertical position of the CoM (S_v), net muscular moment developed at the ankle (M_{Ankle}), angular position of the ankle (θ_{Ankle}), net muscular moment developed at the knee (M_{Knee}), angular position of the knee (θ_{Knee}), net muscular moment developed at the hip (M_{Hip}), angular position of the hip (θ_{Hip}). **B** From top to bottom: vertical acceleration of the CoM (a_v) as a function of S_v , net muscular moment developed at each joint (Ankle, Knee, Hip) as a function of its angular position (see Materials and Methods for more details).

Note that when performing the task, the way to hop off the box and therefore the energy to be dissipated during landing differ between trials of the same height (see [Supplementary Fig. S2](#)), so our results will be investigated according to the amount of energy to be dissipated (E_{TD}).

A linear mixed model was used to investigate the effect of E_{TD} (fixed effect, E_{TD} as a continuous variable) while taking into account the variability between participants (random effect). The normality of the residuals was checked with QQ-plots and was assumed for all variables. The significance level was fixed at $p < 0.05$.

A principal component analysis (PCA) with Varimax rotation was performed on the dataset to explore the relationship between the landing strategy and the joint behavior. The number of extracted components was determined using the Cattell's criteria. The correlation between the variables and the components, i.e. component loadings, were calculated and a threshold of 0.7 was used to identify the variables being associated with the extracted components ([Rojas-Valverde et al., 2020](#)).

In Tables and Figures, the grand mean and the standard deviation are reported in 6 classes of E_{TD} : [1] = [1;1.935 J.kg⁻¹]; [2] = [1.935;2.870 J.kg⁻¹]; [3] = [2.870;3.805 J.kg⁻¹]; [4] = [3.805;4.740 J.kg⁻¹]; [5] = [4.740;5.675 J.kg⁻¹]; [6] = [5.675;6.610 J.kg⁻¹] ([Fig. S2](#)).

3. Results

Whatever the amount of energy to be dissipated (E_{TD}), the landing is performed in a two phases-pattern ([Fig. 2](#)). During the 1st phase, S_v decreases while a_v increases (red in [Fig. 2B](#)); during the 2nd phase, S_v continues to decrease and then increases while a_v decreases (blue in [Fig. 2](#)). A similar pattern is observed at the level of the ankle and knee joints considering M_j and θ_j . As a result, the landing behavior can be modeled first by a spring, then by a spring associated with a compliant damper at the level of the CoM, ankle and knee (see Materials and methods).

When E_{TD} increases, F_{v-peak} , LR, S_{v-min} and t_{sp} increase: the estimated fixed effects indicate a change of, respectively, 0.3 BW, 8 BW.s⁻¹, 3 cm and 67 ms per 1 J.kg⁻¹ ([Table 2](#)). During the 1st phase, k_{1-knee} increases with E_{TD} , while k_{1-CoM} and $k_{1-Ankle}$ are not modified ([Fig. 3](#), [Table 2](#)). During the 2nd phase, $c_{2-Ankle}$ increases and k_{2-CoM} , k_{2-Knee} c_{2-CoM} decrease, while $k_{2-Ankle}$, c_{2-Knee} are not modified ([Fig. 3](#), [Table 2](#)).

The PCA highlights that two components could be extracted,

explaining 58.3 % of the total variance of the 13 variables data set. On the one hand, S_{v-min} , t_{sp} , k_{2-CoM} , c_{2-CoM} and k_{2-Knee} form a subset of variables associated with the 1st component (X-axis on [Fig. 4](#), [Table 3](#)); k_{2-CoM} , c_{2-CoM} and k_{2-Knee} are positively correlated with the component, while S_{v-min} and t_{sp} are negatively correlated. On the other hand, F_{v-peak} , LR, k_{1-CoM} and $k_{1-Ankle}$ form another subset of variables associated with the 2nd component (Y-axis on [Fig. 4](#), [Table 3](#)); all variables are positively correlated with the component. These two components are respectively named "2nd phase" and "1st phase", as they are associated with biomechanical variables (i.e., stiffness and damping) of the 2nd and 1st phase, respectively.

4. Discussion

When landing from a jump, a damper has to be implemented to explain the energy dissipation ([Dyhre-Poulsen et al., 1991](#)). Our results show that, regardless of the amount of energy to be dissipated, the behavior of the CoM can be modeled by a spring, which changes to a spring associated with a damper throughout the task. We also show that a similar model can be used to describe the behavior of the ankle and knee; both joints acting first as a torsional spring to absorb the impact with the ground, then as a torsional spring-damper to dissipate the energy. This two-phases pattern is consistent with the behavior of the musculo-tendinous units crossing the joints. During energy dissipation tasks, the mechanical energy is first stored in elastic elements, i.e. tendinous or connective tissue, and then released to be dissipated by fascicles lengthening ([Hollville et al., 2019, 2020](#); [Konow & Roberts, 2015](#); [Roberts & Azizi, 2011](#); [Roberts & Konow, 2013](#); [Werkhausen et al., 2017](#)). This two-phases pattern can help to prevent injury as the storage of energy in elastic elements delays and slows the dissipation of energy ([Reeves & Narici, 2003](#); [Roberts & Konow, 2013](#)).

Furthermore, we show that the biomechanical properties at the CoM is associated with the ankle stiffness during the 1st phase, i.e. from the touchdown to the force peak, and with the knee stiffness during the 2nd phase, i.e. from the force peak to the standing still position (results of PCA). These results suggest that the lower limb stiffness is tuned at the ankle during the 1st phase of landing and tuned at the knee during the 2nd phase. During the 1st phase of landing, the energy would be mainly stored at the ankle, whereas the knee would be mainly involved in energy dissipation process during the 2nd phase. As highlighted

Table 2

Statistical analysis: kinetic and kinematic characteristics (grand mean $\pm$ SD) as function of the amount of energy to be dissipated (E_{TD} class). The fixed effects were estimated using linear mixed models (significant effect in **bold**, p value < 0.05).

	E_{TD} class						Fixed effect / p value
	[1]	[2]	[3]	[4]	[5]	[6]	
E_{TD} (J.kg ⁻¹)	1.70 $\pm$ 0.15	2.40 $\pm$ 0.12	3.39 $\pm$ 0.16	4.34 $\pm$ 0.12	5.19 $\pm$ 0.17	5.92 $\pm$ 0.18	–
F_{v-peak} (BW)	3.5 $\pm$ 0.7	3.6 $\pm$ 0.6	4.0 $\pm$ 0.8	4.3 $\pm$ 0.8	4.5 $\pm$ 1.1	4.8 $\pm$ 1.1	0.312 / <0.001
LR (BW.s ⁻¹)	41.7 $\pm$ 11.5	42.3 $\pm$ 10.4	50.8 $\pm$ 16.9	58.7 $\pm$ 19.2	67.0 $\pm$ 22.6	73.6 $\pm$ 23.8	8.0 / <0.001
S_{v-min} (cm)	6.1 $\pm$ 2.2	8.5 $\pm$ 2.8	11.0 $\pm$ 4.0	14.0 $\pm$ 4.9	17.1 $\pm$ 5.7	18.6 $\pm$ 4.7	3.0 / <0.001
t_{sp} (ms)	439 $\pm$ 58	508 $\pm$ 67	581 $\pm$ 116	622 $\pm$ 119	670 $\pm$ 134	759 $\pm$ 169	66.8 / <0.001
k_{1-CoM} (s ⁻²)	291 $\pm$ 68	247 $\pm$ 58	243 $\pm$ 74	241 $\pm$ 75	245 $\pm$ 79	249 $\pm$ 75	–5.9 / 0.206
$k_{1-ANKLE}$ (N.m.kg ⁻¹ .deg ⁻¹)	0.12 $\pm$ 0.04	0.11 $\pm$ 0.04	0.12 $\pm$ 0.04	0.13 $\pm$ 0.04	0.14 $\pm$ 0.05	0.15 $\pm$ 0.07	0.007 / 0.053
k_{1-KNEE} (N.m.kg ⁻¹ .deg ⁻¹)	0.11 $\pm$ 0.04	0.13 $\pm$ 0.03	0.13 $\pm$ 0.03	0.14 $\pm$ 0.03	0.14 $\pm$ 0.05	0.15 $\pm$ 0.05	0.008 / <0.001
k_{2-CoM} (s ⁻²)	248 $\pm$ 116	195 $\pm$ 107	161 $\pm$ 99	114 $\pm$ 72	89 $\pm$ 64	64 $\pm$ 32	–39.0 / <0.001
$k_{2-ANKLE}$ (N.m.kg ⁻¹ .deg ⁻¹)	0.11 $\pm$ 0.05	0.10 $\pm$ 0.04	0.10 $\pm$ 0.05	0.10 $\pm$ 0.05	0.10 $\pm$ 0.06	0.08 $\pm$ 0.04	–0.003 / 0.052
k_{2-KNEE} (N.m.kg ⁻¹ .deg ⁻¹)	0.07 $\pm$ 0.01	0.06 $\pm$ 0.01	0.06 $\pm$ 0.02	0.05 $\pm$ 0.02	0.04 $\pm$ 0.02	0.04 $\pm$ 0.02	–0.006 / <0.001
c_{2-CoM} (s ⁻¹)	13.6 $\pm$ 4.8	12.4 $\pm$ 4.4	11.4 $\pm$ 4.1	10.7 $\pm$ 3.6	10.0 $\pm$ 4.0	9.4 $\pm$ 3.0	–0.86 / 0.005
$c_{2-ANKLE}$ (N.m.kg ⁻¹ .deg ⁻¹ .s)	0.008 $\pm$ 0.002	0.008 $\pm$ 0.002	0.009 $\pm$ 0.002	0.010 $\pm$ 0.003	0.010 $\pm$ 0.003	0.013 $\pm$ 0.005	0.0009 / <0.001
c_{2-KNEE} (N.m.kg ⁻¹ .deg ⁻¹ .s)	0.007 $\pm$ 0.002	0.006 $\pm$ 0.001	0.006 $\pm$ 0.001	0.006 $\pm$ 0.001	0.006 $\pm$ 0.001	0.006 $\pm$ 0.001	–0.0002 / 0.127

The grand mean and the standard deviation are reported for each E_{TD} class. The fixed effects of E_{TD} were estimated using the amount of energy to be dissipated as a continuous variable (See Materials and Methods).

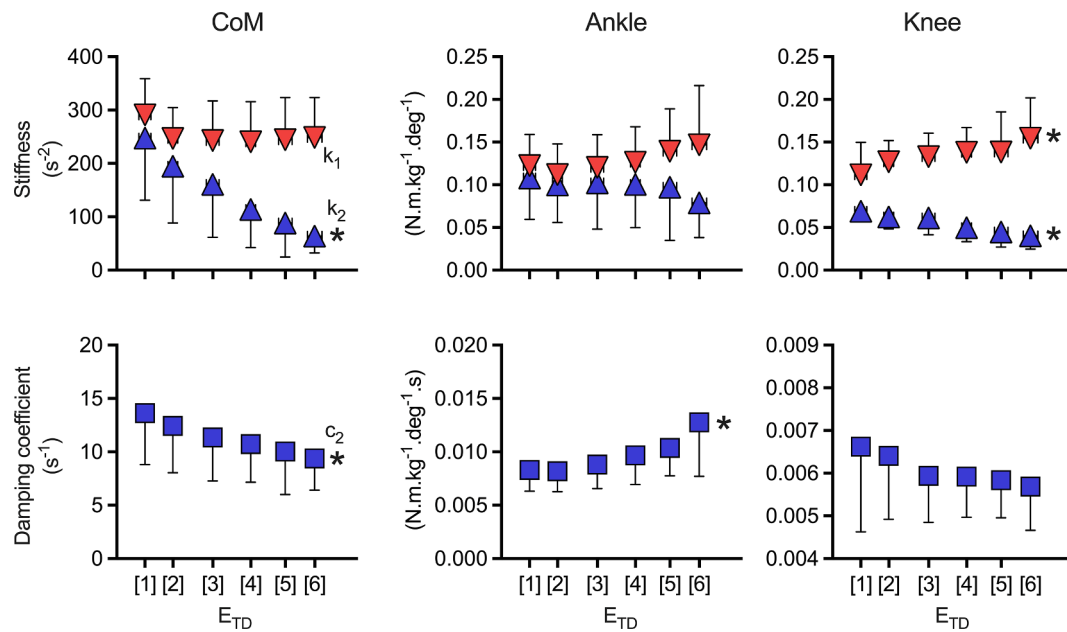


Fig. 3. Biomechanical properties computed from the CoM (left panel) and of the ankle (middle panel) and the knee (right panel) joints when landing. The stiffness during the 1st phase (k_1 , downward triangle, red) and the stiffness and the damping coefficient (respectively k_2 , upward triangle, and c_2 , square, blue) are illustrated as a function of 6 E_{TD} classes. Symbols represent the grand mean of all participants. Error bars error bars indicate one standard deviation and are drawn when they exceed the size of the symbol. * indicates a significant fixed effect estimated with E_{TD} as a continuous variable (p value < 0.05, see Table 2). See Fig. S2 in supplementary materials for information on energy classes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

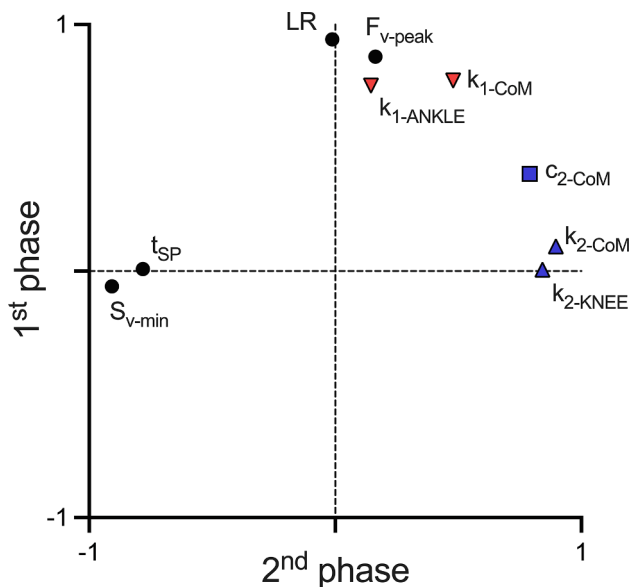


Fig. 4. Principal Component Analysis with Varimax rotation. The two first components are illustrated (explaining 58.3 % of the total variance) and the coordinates of each variable indicate the strength of the relationship between the variable and the two components. Only variables associated with the 1st and/or 2nd component are illustrated (component loading > |0.7|, see Material and Methods for more details). Downward triangle: k_1 ; upward triangle: k_2 ; square: c_2 ; circle: other variables (LR, F_{v-peak} , t_{SP} , S_{v-min}); red: first phase of landing; blue: second phase of landing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

previously, a part of the energy stored at the ankle is probably transferred from the ankle to the proximal joints by bi-articular muscles in order to be dissipated (Prilutsky & Zatsiorsky, 1994).

Table 3

Component loadings of each variable as computed by the Principal Component Analysis.

Variable	Component	
	1	2
F_{v-peak}	0.16	0.87
LR	-0.01	0.94
S_{v-min}	-0.91	-0.06
t_{SP}	-0.78	0.01
k_1-CoM	0.48	0.77
$k_1-ANKLE$	0.15	0.75
k_1-KNEE	0.12	0.34
k_2-CoM	0.90	0.10
$k_2-ANKLE$	0.41	0.26
k_2-KNEE	0.84	0.01
c_2-CoM	0.79	0.40
$c_2-ANKLE$	-0.30	0.46
c_2-KNEE	0.21	-0.22

Bold indicates component loading > |0.7|.

During the 1st phase of landing, the biomechanical behavior of the lower limbs seems to be associated with the landing constraints: we show that the stiffness during this phase is associated with the force peak and the loading rate (PCA). Similar observations have been made in others environmental conditions such as when landing on an elevated surface inducing threat or in hyper-gravity conditions simulated in an aircraft (Schepens et al., 2020; Gambelli et al., 2015). As mentioned above, the ankle seems to play a key role in tuning the stiffness during the 1st phase; a stiff behavior at the ankle at touchdown being associated with a high force peak and loading rate. Several authors pointed out the ankle kinematics as a key feature (Choi et al., 2012; Jolingana-Seoka et al., 2023; Lee et al., 2018; Mizrahi & Susak, 1982; Shimokochi et al., 2013; Tait et al., 2022). When landing with a flat-foot, the peak of force and the loading rate increase and less energy is absorbed at the ankle joint, while when landing with plantar-flexed foot more energy is absorbed at the ankle. The higher amount of energy absorbed at the

ankle when landing with a plantar-flexed foot could result in slower energy transfer to proximal joints and lower constraints, whereas during a flat foot landing, the ankle does not store energy and the energy is instantaneously transferred to the knee leading to higher constraints. In agreement, Boden and Sheehan, 2022 described the behavior of the ankle as similar to that of an airbag in a car, which diminishes the impact forces before reaching either the knee or the passenger. So, as previously suggested by Lee et al. (2018), our results support that the role of the ankle joint should be considered when developing injury prevention programs.

During the 2nd phase of landing, the biomechanical behavior is adjusted in response to the mechanical demand; the stiffness decreasing with the amount of energy to be dissipated. The modulation of the stiffness has been shown to be crucial, in microgravity conditions it has been observed that an overly stiff behavior during the 2nd phase led to a rebound instead of a stable landing, probably due to a lack in energy dissipation (Gambelli et al., 2016). As mentioned above, the knee seems to play a key role in tuning the stiffness during the 2nd phase phase; in addition, the PCA analysis indicates that adopting a stiff strategy during the second phase is associated with a shorter time to return to the standing still position and a small displacement of the CoM, both key factors in terms of performance. Indeed, from a mechanical point of view, a small displacement of the CoM is economical because of the small amount of mechanical work performed. In agreement, several studies indicate that an increase in stiffness is associated with an increase in movement economy (Butler et al., 2003; Kerdok et al., 2002; Liu et al., 2022; McMahon & Cheng, 1990).

So, our results suggest that the constraints and the performance are independent variables: the constraints being associated with the stiffness during the 1st phase and controlled at the ankle, while the performance being rather associated with the stiffness during the 2nd phase and controlled at the knee. Note that the biomechanical behavior of the hip was not described in the present study as the data computed from the model did not fit with the experimental data; this does not imply that the hip is not involved in energy dissipation. For example, Yeow et al. (2011) observed that the hip's contribution to negative work is approximately 35 % when performing a double-leg landing from a height of 60 cm. In the present study, the discrepancy between the experimental data and the prediction of the model could be attributed either to the bottom-up inverse dynamics approach and its inherent limitation, i.e. errors are reported successively from the bottom to the top, resulting in large errors at the hip (Guelton et al., 2008; Riemer et al., 2008), or to a specific behavior at the hip not predicted by the model. We acknowledge that the characterisation of the hip behavior when landing remains a challenge and deserves further study.

5. Conclusion

The biomechanical behavior of the lower limbs and of the ankle and knee joints changes throughout landing from a spring to a spring associated with a damper to dissipate energy. Our results show that the ankle joint plays a key role during the 1st phase to reduce constraints by storing energy, while the knee joint plays a key role during the 2nd phase to dissipate energy. These results are encouraging for clinicians and sport instructors as they show that the constraints and the performance result from the control of different biomechanical parameters and suggest therefore that the risk of injury could be diminished while maintaining the performance.

CRedit authorship contribution statement

Thibaut D. Toussaint: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **B. Schepens:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration,

Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jbiomech.2024.112014>.

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