"Leg stiffness and joint stiffness while running to and jumping over an obstacle"

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Abstract
During running, muscles of the lower limb act like a linear spring bouncing on the ground. When approaching an obstacle, the overall stiffness of this leg-spring system (kleg) is modified during the two steps preceding the jump to enhance the movement of the center of mass of the body while leaping the obstacle. The aim of the present study is to understand how kleg is modified during the running steps preceding the jump. Since kleg depends on the joint torsional stiffness and on the leg geometry, we analyzed the changes in these two parameters in eight subjects approaching and leaping a 0.65m-high barrier at 15kmh(-1). Ground reaction force (F) was measured during 5-6 steps preceding the obstacle using force platform and the lower limb movements were recorded by camera. From these data, the net muscular moment (Mj), the angular displacement (θj) and the lever arm of F were evaluated at the hip, knee and ankle. At the level of the hip, the Mj-θj relation shows that muscles are not ...
Leg stiffness and joint stiffness while running to and jumping over an obstacle

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ABSTRACT

During running, muscles of the lower limb act like a linear spring bouncing on the ground. When approaching an obstacle, the overall stiffness of this leg-spring system (k_leg) is modified during the two steps preceding the jump to enhance the movement of the center of mass of the body while leaping the obstacle. The aim of the present study is to understand how k_leg is modified during the running steps preceding the jump. Since k_leg depends on the joint torsional stiffness and on the leg geometry, we analyzed the changes in these two parameters in eight subjects approaching and leaping a 0.65 m-high barrier at 15 km h⁻¹. Ground reaction force (F) was measured during 5–6 steps preceding the obstacle using force platform and the lower limb movements were recorded by camera. From these data, the net muscular moment (M_j), the angular displacement (θ_j) and the lever arm of F were evaluated at the hip, knee and ankle. At the level of the hip, the M_j–θ_j relation shows that muscles are not acting like torsional springs. At the level of the knee and ankle, the M_j–θ_j relation shows that muscles are acting like torsional springs: as compared to steady-state running, the torsional stiffness k_j decreases from 1/3 to 1/3 during the last contact, and increases from 2/3 to 3/3 during the last contact. These modifications in k_j reflect in changes in the magnitude of F but also to changes in the leg geometry, i.e. in the lever arms of F.

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1. Introduction

During running, the muscles–tendons units of the lower limb act like a linear spring storing and releasing elastic energy during contact (Alexander, 1992; Blickhan, 1989; Cavagna et al., 1988; McMahon and Cheng, 1990). When the running conditions are changing, the bouncing mechanism is adapted by adjusting the stiffness of the leg-spring system (k_leg) and the angle swept during contact. When the speed of progression increases, k_leg does not change but the angle swept increases (Farley et al., 1993; He et al., 1991; Morin et al., 2005). If at a given speed the step frequency is increased, k_leg increases and the angle swept decreases (Farley and Gonzalez, 1996); k_leg is also adapted when subjects are running on an uneven ground (Seyfarth et al., 2002; Grimmer et al., 2008) or when the softness of the surface is modified (Ferris et al., 1999, 1998).

Mauroy et al. (2012) have shown that when approaching an obstacle, k_leg and the angle swept are adjusted during the last two contacts before the jump. Two contacts before the obstacle, k_leg decreases whereas the angle swept increases slightly, and the COM is lowered and accelerated forwards. Then, during the last contact before the obstacle, k_leg increases whereas the angle swept decreases, and the COM is raised and accelerated upwards, while its forward velocity decreases.

During running and hopping on place, the lower limb can be assimilated to a multi-jointed system composed of 4 segments – foot, shank, thigh, head-arms-trunk – and 3 torsional springs – ankle, knee, hip (Fig. 1). The overall leg-spring stiffness, k_leg, depends (1) on the torsional stiffness, k_j, of the joints and (2) on the geometry of the leg at touchdown (Farley et al., 1998; Farley and Morgenroth, 1999). Torsional stiffness of a joint is defined as the slope of the relation between the net muscular moment and the angular displacement at that joint (Stefanyshyn and Nigg, 1998); k_j determines how much the joint angle changes in response to a given external moment. It depends on muscle activation, reflexes and joint angle (Agarwal and Gottlieb, 1977; Gottlieb and Agarwal, 1978; Hunter and Kearney, 1982; Nielsen et al., 1994; Sinkjaer et al., 1988; Weiss et al., 1988; Weiss et al., 1986a,b). If the lower limb joints are stiffer, they undergo smaller angular displacements during contact, resulting in less leg compression and higher leg-stiffness.

A second factor influencing k_leg is the touchdown leg geometry (Farley et al., 1998; Farley and Morgenroth, 1999), i.e. the position of the joints relative to the ground force vector when landing. For a given ground reaction force and a given k_j, if the joints are more flexed during contact, the lever arms and thus the net external
2. Methods

In this section, the methods and experimental procedure are only explained shortly. A detailed description of the experimental setup and procedure and of the data analysis is proposed as Supplementary material online.

2.1. Subjects and experimental set-up and procedure

Experiments were realized on eighty young male recreational runners. Written informed consent was obtained. Experiments were performed according to the Declaration of Helsinki and approved by the local ethics committee.

Subjects ran at 15 km h⁻¹, jumped over a 0.65 m-high barrier and continued to move at the same pace. Ground reaction forces were recorded using a 13 m-long force platform (Genin et al., 2010). A barrier was mounted 3 m before the end of the platform.

Two pairs of photocells placed at each end of the plates on the level of the neck measured the average running velocity. Traces were analyzed if the average velocity of the first step(s) before the barrier ranged between 14.5 and 15.5 km h⁻¹. Steps were numbered as follows: step 0 corresponded to the last contact before the obstacle and the following arial phase over the obstacle, step 1 was the step before step 0, etc. Control steps, i.e. runs without any obstacle, were also recorded.

Reflective markers were glued on the skin at the level of the lower limb joints. Their position in the sagittal plane was measured each 5 ms by a high-speed video camera (BASLER A501k). Movements of the supporting leg were recorded during contact (three trials on step-1, three on step 0, six on control steps). Camera and force-plates were triggered by the photocells. Coordinates of the reflectors were measured using a semi-automatic tracking software (Lynxzone, Arsalis).

2.2. Data analysis

Data processing was performed using custom software (LABVIEW 10.0, National Instruments). The leg was assimilated to a simple linear spring with the COM located at its upper end. This leg-spring system swept on an arc during the contact and the overall stiffness (kleg) generated by the lower limb muscles was estimated by computer simulation (Mauroy et al., 2012). The kinetic, potential and total energy of the COM was computed using the method of Cavagna (1975).

The net muscular moment (Mj), power (Pj) and work (Wj) at the ankle, knee and hip were evaluated in the sagittal plane by an inverse dynamic method (Elliott, 1959). The Mj, Pj, and Wj at each joint were computed on the limb in contact when F was greater than 10% of body weight. The net work (Wnet) is the difference between the positive and negative work done during the contact at each joint. Throughout the text, the subscript j refers to any lower limb joint, the subscript a refers specifically to the ankle, k to the knee and h to the hip.

The torsional stiffness of each joint (kj) was determined from the ratio of the change in net muscle moment to joint angular displacement in the sagittal plane (∆Mj/∆θj) between the beginning of the ground contact phase and the instant when the joints were maximally flexed (Farley and Morgenroth, 1995; Kuitten et al., 2002; Stefanyshyn and Nigg, 1998).

Results were grouped in classes according to the step number (control step, step-1 and step 0). A one-way repeated measures ANOVA (Bonferroni post-hoc) was performed to evaluate the effect of the step number on the variables studied.

3. Results

3.1. Leg-stiffness and joint stiffness during steady-state running

During steady-state running, the leg-spring is bouncing and sweeping forward in a symmetric way. The magnitude of angle between the leg and vertical (θk) at touchdown and at takeoff are about equal, the distance between the hip and the fifth metatarsal moments are greater. In turn, the angular displacement of the joint and thus the compression of the overall leg-spring are increased. In such a situation, kleg is reduced. This statement is confirmed by the results of Greene and McMahon (1979): bouncing on a compliant board with greater knee flexion leads to lower the leg stiffness. Similarly, when humans run with exaggerated knee flexion, kleg is lower than during normal running (McMahon et al., 1987); and when humans land from a jump, kleg during landing decreases as the knee flexion at touchdown increases (Devita and Skelly, 1992).

The goal of this study is to understand the mechanism by which kleg is regulated when approaching and crossing an obstacle. Is kleg modified during step-1 and step 0 because of a change in the joint torsional stiffness at the ankle, the knee and/or at the hip? What is the role of each of the joints in the modulation of kleg when approaching an obstacle and which joint is developing the additional power necessary to cross the obstacle? Furthermore, at the approach of the obstacle, the general orientation of the leg-spring system (i.e. the angle between a line joining the foot and the hip and the vertical) is modified: at takeoff of step-1 and at touchdown of step 0, the leg-spring is more horizontal than during steady state running, and at takeoff of step 0, the leg-spring is more vertical (Mauroy et al., 2012). Is this change in orientation accompanied by a change in the leg geometry at the joints, and how does this change in orientation (if any) modify kleg? To answer these questions, we examined the changes in the touchdown leg geometry, in the net muscular moment and power (by the inverse dynamic method) and in the joint torsional stiffness at the level of the hip, knee and ankle during the steps preceding the jump over an obstacle.

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The net muscular moment (contact phase and a plantar-exhibiting) is negative and consistent with the one of McMahon and Cheng (1990) and of Mauroy et al. (2012). The knee presents a dorsi- flexion during the second half (Fig. 5). The net muscular moment (Mk) is in plantar-flexion during the greatest part of the contact phase; Mk increases during dorsi-flexion (Fig. 3) and decreases during plantar-flexion. The Mn–θh relation is quasi-linear suggesting that the ankle muscles act like a torsional spring of stiffness kθ (Table 1). The knee flexes during the first ~40% of contact and extends during the last ~60% (Fig. 6). During most of contact, extensor muscles of the knee are contracting first eccentrically then concentrically. Knee muscles perform thus slightly more negative work than positive work (Figs. 4 and 6) and W_net,k is negative (Table 1). The Mn–θh relation is quasi-linear (Fig. 3), suggesting that knee muscles act like a torsional spring of stiffness kθ (Table 1).

At the level of the hip, Mk is a extension moment and presents a peak ~10% after touchdown (Fig. 7). During the first 20–30% of contact, hip movements are small and Ph is close to zero. Then the hip extends during the rest of the contact phase, however Mk and Ph are small. Hip muscles perform slightly more negative work than positive work (Figs. 4 and 7) and W_net,h is negative (Table 1). The Mn–θh curve does not present the classical “storage-release” relation of a torsional spring (Fig. 3).

3.2. Leg-stiffness and joint stiffness during step-1

During contact of step-1, the maximal F is smaller than during steady-state running (Fig. 2). Furthermore, the orientation of F (θh) becomes more vertical than the orientation of the lower-limb (θl) at the end of contact. The F–L relation is quasi-linear (Fig. 3); however, k_leg is reduced as compared to control steps (Table 1). Consequently, at takeoff, the leg is more horizontal than during control steps (Fig. 2). Due to the change in orientation (Mauroy et al., 2012), the COM is lowered and accelerated forward (Fig. 4). During this phase, due to the lowering of the COM, E_k (Fig. 4) is reduced by 0.71 ± 0.13 J kg⁻¹ (mean ± SD) whereas E_fl increases.

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from 0.69 ± 0.61 J kg⁻¹; as a consequence, W_net is close to zero (Table 1).

At the ankle, M_a is a plantar-flexion moment during the greatest part of contact (Fig. 5), however the maximal M_a and P_a are smaller than during control steps. The shape of the M_a-θ_a curve is similar to control steps (Fig. 3), although k_a is smaller (Table 1). As compared to steady-state running, θ_a at takeoff is smaller (Fig. 5).

At the knee, the shape of the M_k-θ_k curve is similar to control steps (Fig. 3) although M_k and also P_k are smaller (Fig. 6). As compared to control steps, k_k is reduced (Table 1) whereas W_net,k is not different (Table 1). During the second part of contact, the knee stays in flexion (Fig. 6).

At the hip, the shape of the M_h-θ_h curve is similar to control steps (Fig. 3), except at the end of contact where M_h is a flexion moment and where the negative P_h is greater (Fig. 7). Consequently the balance between negative and positive work done increases (Table 1).

### 3.3 Leg-stiffness and joint stiffness during step 0

During step 0, the maximal F (Figs. 2 and 3) and k_leg (Table 1) are greater than during control steps. Furthermore, θ_h becomes more horizontal than θ_h at the end of contact. During this step, the COM is lifted and accelerated upwards while its forward velocity decreases (Fig. 4). The energy gained by enhancing the vertical movement of the COM is greater than the kinetic energy lost by decreasing the velocity of progression and W_net is greater than during control steps (Table 1). The energy saving mechanism during step 0 is similar to the one observed in pole vaulting (Mauroy et al., 2012).

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Fig. 3. Ground reaction force (F) vs. leg length (L) (three upper panels) and net muscular moment (M_j) as a function of the joint angle (θ_j) at the lower limb joints (nine lower panels) during the contact of steps preceding the jump over a 0.65 m-high barrier while approaching at ~ 15 km h⁻¹. Three upper panels The magnitude of F is normalized by body weight; the interrupted line corresponds to body weight. The distance between the great trochanter and the head of the fifth metatarsus L is normalized by the length measured while standing. Nine lower panels M_h, M_k and M_a are the net muscular moments at the hip, the knee and the ankle, respectively. The moments are normalized by body mass; the horizontal interrupted lines correspond to M_j = 0. The angles θ_h, θ_k and θ_a are the joint angles at the hip, knee and ankle, respectively. The vertical interrupted lines correspond approximately to the joint angle while the subject is standing. In the six lower panels, the slope of the lines corresponds to the torsional stiffness at the knee (k_k) and at the ankle (k_a). Note that the stiffness is calculated during the first part of contact when M_j increases (see Methods). Each of the 12 curves is the average of curves obtained on all trials across subjects. The interrupted curves in the middle and left panels are replications of the average curves obtained on control steps. The filled and open circles correspond to touchdown and takeoff, respectively. The arrows indicate how the curves change with time during contact.

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Table 1
Upper part: overall leg-spring stiffness ($k_{leg}$) and torsional joint stiffness at the knee ($k_k$) and at the ankle ($k_a$) during running in steady state (control step), two contact periods before the jump over the obstacle (step-1) and during the contact period preceding the jump over the obstacle (step 0). Lower part: net external work (i.e. positive external work minus negative external work) done during contact ($W_{net}$) to move the COM relative to the surroundings and net muscular work (i.e. positive minus negative work) done during contact at the level of the hip ($W_{net,h}$), the knee ($W_{net,k}$) and the ankle ($W_{net,a}$) of control steps, step-1 and step 0. Numbers are the mean ± SD of all the traces ($n=48$ for control steps, $n=24$ for step-1, $n=24$ for step 0).

<table>
<thead>
<tr>
<th>Control step</th>
<th>Step-1</th>
<th>Step 0</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Leg and joint stiffness</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$k_{leg}$ (N m$^{-1}$ kg$^{-1}$)</td>
<td>0.18 ± 0.02</td>
<td>0.13 ± 0.01*</td>
</tr>
<tr>
<td>$k_k$ (N m rad$^{-1}$ kg$^{-1}$)</td>
<td>8.46 ± 1.52</td>
<td>6.06 ± 1.15*</td>
</tr>
<tr>
<td>$k_a$ (N m rad$^{-1}$ kg$^{-1}$)</td>
<td>11.54 ± 2.02</td>
<td>7.03 ± 1.63*</td>
</tr>
<tr>
<td><strong>Mass-specific net work during contact</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$W_{net}$ (J kg$^{-1}$)</td>
<td>−0.01 ± 0.06</td>
<td>−0.02 ± 0.56</td>
</tr>
<tr>
<td>$W_{net,h}$ (J kg$^{-1}$)</td>
<td>−0.27 ± 0.24</td>
<td>−0.54 ± 0.34*</td>
</tr>
<tr>
<td>$W_{net,k}$ (J kg$^{-1}$)</td>
<td>−0.27 ± 0.11</td>
<td>−0.31 ± 0.21</td>
</tr>
<tr>
<td>$W_{net,a}$ (J kg$^{-1}$)</td>
<td>0.78 ± 0.16</td>
<td>0.40 ± 0.20*</td>
</tr>
</tbody>
</table>

* indicates that a significant difference was found between control steps and steps-1 or between control steps and step 0.

As in control steps and step-1, $M_a$ is generated by the plantar-flexor muscles during the greatest part of contact (Fig. 5), however the maximal $M_a$ and $P_a$ are greater. The $\theta_a$-time curve is shifted towards a greater plantar flexion. The slope of the $M_a$-$\theta_a$ curve (Fig. 3) is steeper showing that the stiffness $k_a$ is greater than during steady-state running (Table 1). During the first part of contact, the muscular moment in plantar flexion increases while the joint is performing a dorsiflexion, muscles are thus realising an eccentric contraction. During the second part of contact, the muscular moment in plantar flexion decreases while the joint is performing a plantar flexion; muscles are thus realising a concentric contraction. The surface under the $M_a$-$\theta_a$ curve represents the work done by the muscles; this surface is smaller during the eccentric phase than during the concentric phase. Consequently, $W_{net,a}$ is positive but not greater than during control steps (Table 1).

At the knee, $M_k$ is a flexion moment at the beginning and at the end of contact of step 0 (Fig. 6). During the rest of the contact, $M_k$ is an extension moment. The maximum of $M_k$ and the maximal positive $P_k$ are not statistically different than during control steps (see numbers in Fig. 6). Knee extensor muscles perform more
negative than positive work (Figs. 3 and 4) and $W_{\text{net,k}}$ is negative (Table 1). The shape of $M_{\text{k}}$–$\theta_{\text{k}}$ curve is similar than in control steps although $k_{\text{k}}$ is greater (Table 1).

At the level of the hip, $M_{\text{h}}$ is an extension moment during most of contact (Fig. 7). As compared to control steps, $M_{\text{h}}$ is greater, however $P_{\text{h}}$ remains small. $W_{\text{net,h}}$ is positive (Table 1), showing
that extensor muscles are doing positive work to increase hip extension and lift the COM at the end of contact.

4. Discussion

When a runner prepares to cross an obstacle, $k_{leg}$ is modified during the two steps preceding the jump: $k_{leg}$ is first decreased then increased to verticalize the direction and amplify the magnitude of the velocity vector at takeoff (Mauroy et al., 2012). This last observation confirms the hypothesis of Farley et al. (1998) that, when running in nature at given speed, the leg-spring stiffness is modified to change direction or to leap an obstacle.

To analyze the influence of the torsional stiffness and of the lower limb geometry on $k_{leg}$, we evaluated the net muscular moment and the angular displacement at the level of the hip, knee and ankle during the steps preceding a jump. The results obtained at the level of the ankle and the knee during steady-state running, are in good agreement with those found in the literature (Arampatzis et al., 1999; Gunther and Blickhan, 2002).

Note that in our model, we assume that movement and muscle actions occur in the sagittal plane. However, Glitsch and Baumann (1997) and McClay and Manal (1999) highlighted the potential importance of non-sagittal plane dynamics during running and thus the work done at each is joint as estimated in our study is most likely underestimated.

4.1. Torsional springs during steady-state running

At the level of the knee, the $M_j-\theta_j$ curve presents the classical shape of a torsional spring (Fig. 3). However, the resilience of the spring is less than 100%, since the negative work is smaller than the amount of positive work done during contact.

Ankle muscles also act like a torsional spring. However, contrary to the knee muscles, ankle muscles do more positive than negative work (Figs. 3 and 4). Supposing a resilience of 100%, the surface between the two lines on the $M_j-\theta_j$ curve represents the additional positive work done by ankle during contact (Table 1).

At the level of the hip, the $M_j-\theta_j$ curve does not behave like a torsional spring. During the first 30% of contact, extensor muscles perform an isometric contraction to stabilize the hip during loading. Indeed, the leg-spring is in front of the COM and the $F$ vector is oriented more vertically than the leg-spring (Fig. 2): $F$ generates a moment that tends to rotate the subject backwards. As a consequence, hip extensor muscles are developing an important moment to counterbalance the action of $F$ (Fig. 7). During the last 70% of contact, $F$ and the leg-spring are more or less oriented in the same direction. So the net muscular moment and power are small suggesting that hip extends rather passively, when the leg-spring is sweeping forwards.

4.2. Influence of the segment masses on the net muscular moment

The influence of the segment masses on the computation of $M_j$ increases from distal to proximal (Gunther and Blickhan, 2002). At the level of the ankle and the knee, the moment generated at the joints by the ground reaction force $F$ (dotted line in the left panel of Figs. 5, 6 and 7) is close to the net muscular moment $M_j$, showing that the inertial effect (both in translation and in rotation) of the limb segments can be neglected in the estimation of the net muscular moment. At the level of the hip, the inertial effect is not negligible, although the dynamic deviations are small.

Fig. 7. Joint angle ($\theta_j$), net muscular moment ($M_h$) and muscular power ($P_h$) at the hip during contact of steps preceding the jump over a 0.65 m-high barrier while approaching at $\sim 15$ km h$^{-1}$. In the angle-time graphs, the horizontal interrupted lines correspond approximately to the hip angle while the subject is standing. In the moment-time graphs, a positive moment corresponds to a moment developed by the extensor muscles of the hip; the dotted curve in the left panel represents the moment generated by the ground reaction force $F$ at the hip, i.e. the product $b_hF$ where $b_h$ is the effective lever arm of $F$ (see Figs. 1 and 8). In the power-time graphs, a positive power corresponds to a concentric contraction and a negative power to an eccentric contraction. Others indications are as in Fig. 2.
enough not to modify the conclusion of our observations: the moment generated at each joint depends essentially on the magnitude of the ground reaction force and on the geometry of the limb segments, i.e. of the position of each joint relative to the ground reaction force vector. In turn, the magnitude of the ground reaction force depends on the leg-spring stiffness, Devita and Skelly (1992) have shown that, when humans land from a jump, the magnitude of ground reaction force is greater the stiffer the joints during landing.

4.3. Work balance at the joint

During steady-state running and during step-1, the net external work done each step is nil (Fig. 4). However, it is peculiar to observe that $W_{\text{net}}$ done at each joint is not nil (Table 1). Muscles of the ankle are doing more positive than negative work, whereas at the level of the knee and the hip, muscles are doing more negative than positive work. During step 0, $W_{\text{net}}$ is positive. The work done at the level of the ankle and the knee are not modified, as compared to control steps. The additional work is provided by the hip extensor muscles (Figs. 4 and 7), which are doing positive work during contact (during control steps, these muscles are doing negative work).

However, the balance of the work presented in Table 1 does not take into account the work that can be transferred between joints through poly-articular muscles. Indeed, poly-articular muscles can do positive work at one joint and at the same time negative work at another joint. Furthermore the balance of work done on the COM and at each joint (Fig. 4) does not take into account the internal work done to move the limb segments relative to the COM.

Belli et al. (2002) showed that when running speed increases, peak joint power increases at all joints and that the highest changes were observed in the hip joint. Furthermore with increasing speed, no significant changes in the peak of the muscular moments were observed at the level of the ankle, but significant increases were observed at the level of the knee and the hip. Our results confirm these observations. When a runner jumps over a barrier, the biggest changes are observed at the level of the hip: the peak moment at the hip (Fig. 7) and $W_{\text{net,h}}$ (Table 1) are strongly increased. On the contrary at the level of the ankle, the peak moment, the peak power (Fig. 5) and $W_{\text{net,a}}$ (Table 1) hardly change. Belli et al. (2002) suggested that during running, the role of the ankle and knee extensors is to generate joint stiffness during contact, while hip extensors are the prime forward movers of the body. By contrast, when jumping over an obstacle, the power generated at the level of the hip seems too low to define the hip muscles as “prime movers”. Even if the muscular power generated at the hip is low, hip extensor muscles could contribute to the extension of the knee and plantar flexion of the ankle, through the action of bi-articular muscles. Indeed, Van Ingen Schenau et al. (1987) have demonstrated that in jumping, the gluteus maximus muscle could develop power that is used for knee extension and to plantar flexion work by the tendinous actions of both the rectus femoris and the gastrocnemius muscles. The same phenomenon could occur during step-1 to accelerate the COM forwards and during step 0 to lift and accelerate the COM upwards.

4.4. Changes in leg-stiffness, joint stiffness and lower limb orientation during step-1 and step 0

During step-1, the overall stiffness $k_{\text{leg}}$ is reduced (Table 1). As explained by Mauroy et al. (2012), this leads to a lowering and an acceleration of the COM. The lowering of the COM is due to the fact that during the second part of contact, the knee and the ankle are not extending as much as during steady-state running. The reasons for this preparatory step are discussed by Mauroy et al. (2012).

The lower $k_{\text{leg}}$ is due to a lower stiffness at the level of the knee and ankle (Table 1). In turn, the lower $k_a$ and $k_k$ are due to a smaller net muscular moment at these joints. At the level of the knee, the smaller $k_k$ is also due to change in the geometry of the leg-segments, especially at the end of contact (see average values in Fig. 8). This suggests that the lower $M_a$ is due to a lower

Fig. 8. Lever arm of the ground reaction force at the lower limb joints during contact of steps preceding the jump over a 0.65 m-high barrier while approaching at ~15 km h$^{-1}$. The lever arms $b_h$, $b_k$ and $b_a$ are the distance between the ground reaction force vector ($F$) and the center of rotation of the hip, knee and ankle, respectively. When $b_i$ is positive, the force $F$ generates a moment in (dorsi-)flexion, which generates a muscular moment in extension (or plantar flexion). When $b_i$ is negative, $F$ generates a moment in extension (or plantar flexion), which generates a muscular moment in (dorsi-)flexion. Others indications are as in Fig. 2.

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activation of the muscle, which, in turn, leads to a smaller $k_a$ and to a smaller amplitude of $F$. At the level of the knee, the lever arm is modified during the second part of contact: contrary to steady-state running, the knee extensor muscles are pushing at the end of contact to increase the forward velocity of the COM. At the level of the hip, the role of the increased eccentric contraction (Fig. 7) is to keep the COM in a low position while the ankle and knee muscles are pushing the COM forwards. In addition, during the last 20% of contact, the vector $F$ becomes more vertical than the leg-spring (Fig. 2). Consequently, $F$ generates a moment that tends to rotate the trunk downwards and helps to keep the COM in a low position. Van Caekenbergh et al. (2013) have also observed a change in the general direction of $F$ when the COM accelerates during running overground.

During step 0, the overall stiffness $k_{leg}$ is increased (Table 1), which induces an increase of the vertical velocity and a lift of the COM with a decrease of its forward velocity. The increase in $k_{leg}$ is due to both an increase in $k_a$ and $k_f$: this is most likely due to a greater muscular activation, which stiffens the ankle and the knee and generates a greater amplitude of $F$ (Devita and Skelly, 1992). In the knee, there are significant moments in flexion at the beginning and at the end of contact. As suggested by Gunther and Blickhan (2002), this initial flexor moment pre-determines the flexion of the shank since an extension of the knee at touchdown would be disastrous. During step 0, this flexor moment is increased because the leg is touching the ground more horizontally than in control steps. The role of the flexor moment at the end of contact is to brake the extension movement of the knee before takeoff. By contrast to step-1, the vector $F$ becomes more horizontal than the leg-spring during the last 20% of contact (Fig. 2). So, $F$ generates a moment that tends to rotate the trunk backwards and upwards, and participates to the lift of the COM.

When running speed increases, ankle joint stiffness ($k_a$) changes little and the knee joint stiffness ($k_f$) is the major modulator of $k_{leg}$ (Arampatzis et al., 1999; Brughelli and Cronin, 2008; Gunther and Blickhan, 2002). Several studies have also examined the relative influence of $k_a$ and $k_f$ on $k_{leg}$ during hopping, but results are, at best, ambiguous. According to Farley et al. (1998), humans adjust leg stiffness to accommodate for differences in surface stiffness primarily by modulating ankle stiffness and secondarily by modulating knee angle at touchdown. In their study, Hobara et al. (2009) evaluated leg and joint stiffness of the hip, knee and ankle: they found that knee stiffness was significantly higher than ankle and hip stiffness. Further, their regression model showed that only $k_a$ was significantly correlated with $k_{leg}$. The study of Kuitunen et al. (2011) suggests that when hopping with short contact period, $k_{leg}$ is modulated by $k_a$ and that $k_f$ is correlated with the jumping height. According to Butler et al. (2003), modulation of the joint stiffness may be related, at least in part, to the foot strike pattern: during hopping and running, if the forefoot strikes first the ground, the knee is stiffer than the ankle, conversely during rear foot landing, the ankle is stiffer than the knee. This hypothesis is corroborated by the observation of Laughton et al. (2003): as compared to rear foot runners, $k_a$ was greater and $k_f$ was lower in footre runners. These authors attributed the changes in joint stiffness to the decrease in knee excursion and increase in ankle excursion in the forefoot strike, as compared to the rear foot strike.

Vanrenterghem et al. (2004) have measured the net muscular moment at the level of the lower limb joints, during a vertical jump of different height (25%, 50%, 75% and 100% of the maximal height, $H$). These authors showed that the net muscular moment at the ankle does not increase anymore for jumps higher than 50% of $H$, while the muscular moment at the hip and the knee continues to increase with the height of the jump. In a following study, it should be interesting to vary the obstacle height and the approaching speed to understand how the net muscular moment and joint stiffness are modulated with these two factors.

Conflict of interest statement

There is no conflict of interest, i.e., there are no financial and personal relationships with other people or organization that could inappropriately influence this work.

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Appendix A. Supplementary material

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