Changes in spring-mass behavior and muscle activity during an exhaustive run at $\dot{V}O_{2max}$

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ABSTRACT

Purpose: The aim of this study was to evaluate concomitantly the changes in leg-spring behavior and the associated modifications in the lower limb muscular activity during a constant pace run to exhaustion at severe intensity.

Methods: Twelve trained runners performed a running test at the velocity associated with $\dot{V}O_{2max}$ (5.1 ± 0.3 m s^{-1}; mean time to exhaustion: 353 ± 69 s). Running step spatiotemporal parameters and spring-mass stiffness were calculated from vertical and horizontal components of ground reaction force measured by a 6.60 m long force platform system. The myoelectrical activity was measured by wireless surface electrodes on eight lower limb muscles.

Results: The leg stiffness decreased significantly (-8.9%; $P < 0.05$) while the vertical stiffness did not change along the exhaustive exercise. Peak vertical force (-3.5%; $P < 0.001$) and aerial time (-9.7%; $P < 0.001$) decreased and contact time significantly increased ($+4.6\%$; $P < 0.05$). The myoelectrical activity decreased significantly for triceps surae but neither vastus medialis nor vastus lateralis presented significant change. Both rectus and biceps femoris increased in the early phase of swing ($+14.7\%$; $P < 0.05$) and during the pre-activation phase ($+16.2\%$; $P < 0.05$).

Conclusion: The decrease in leg spring-stiffness associated with the decrease in peak vertical ground reaction force was consistent with the decline in plantarflexor activity. The biarticular rectus femoris and biceps femoris seem to play a major role in the mechanical and spatiotemporal adjustments of stride pattern with the occurrence of fatigue during such exhaustive run.

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1. Introduction

The spring-mass model has been used to describe the effects of fatigue on the mechanics of running (Hunter and Smith, 2007; Morin et al., 2011a; Le Meur et al., in press). This model consists of a point mass bouncing on a linear spring (Blickhan, 1989; McMahon and Cheng, 1990). In running, two kinds of stiffness are usually characterized: (i) the leg stiffness (k_{leg}), maximal force to maximal leg compression ratio during the stance phase; and, (ii) the vertical stiffness (k_{vert}), maximal force to maximal vertical displacement of the center of mass ratio. As these parameters are the result of the integration by the central nervous system of all of the elements of the musculoskeletal system, this model is frequently used to describe the effects of fatigue as a result of exhaustive runs (Hobara et al., 2010; Morin et al., 2006).

Recent investigations dealing with the effect of fatigue on leg-spring behavior analyzed a large range of running intensities. For very low intensity/long duration runs, like a 24-h treadmill run (Morin et al., 2011a) or a 166 km mountain ultra-marathon run (Morin et al., 2011b), investigations reported an increase in both leg and vertical stiffness associated with an increased stride frequency. At intermediate intensity (~80% of the velocity associated with the maximal oxygen uptake, $v\dot{V}O_{2max}$), a decrease in k_{leg} and k_{vert} was observed between the beginning and the end of the exhaustive run (Dutto and Smith, 2002). These authors have shown that modifications in spring-mass behavior were primarily related to the leg compression increase without significant changes in peak vertical ground reaction force (F_{zmax}). For higher running velocity, Rabita et al. (2011), by imposing a run at 95% of $v\dot{V}O_{2max}$ until exhaustion, reported that (i) k_{leg} decreased while k_{vert} was unchanged throughout the run; and, (ii) the contribution of the changes in leg-spring properties were mainly and homogeneously related to F_{zmax}. To date, little is known in terms of modification in spring-mass behavior at higher running intensity. If one only focuses on studies where fatigue effects were evaluated

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during the course of the fatiguing run rather than in pre-post protocol, only self-selected pacing strategies were designed (Girard et al., 2010; Hobara et al., 2010). However, given the co-variance of changes in running speed and spring-mass parameters with fatigue, the relative contribution of these factors on the observed modifications cannot be precisely assessed. To date, no investigation has attempted to evaluate the leg spring stiffness during a single run imposed at a constant velocity higher than 95% of v$\dot{V}O_{2max}$.

The effect of running fatigue on the neuromuscular system has been widely described using different techniques of surface EMG. Numerous studies have focused on the effect of long distance runs (i.e. 10 km or higher) (Hausswirth et al., 2000; Millet et al., 2002; Ross et al., 2010). For example, in experienced runners, Ross et al. (2010) observed a reduction in knee extensor MVC and associated EMG of the vastus medialis during the final 5 km of a 20 km treadmill run. Their results have shown that voluntary activation and neural drive rather than contractile processes are responsible for this decreased strength. In contrast, Girard et al. (2012) have shown that the muscle strength loss in plantarflexors as a result of a more intensive/shorter duration run (5 km) was mainly induced by peripheral fatigue, and in a lower extend by central mechanisms. These studies are useful to describe the neuromuscular effects of maximal running exercise, but they do not allow for explanation of the modification in myoelectrical activity specifically during the course of the fatiguing run given that, for technical reasons, the methods implied that the participants have to stop the run during the data collection. To our knowledge, only a few investigations (Avogadro et al., 2003; Paavolainen et al., 1999) have analyzed the fatigue effects on the activity of lower limb muscles during a single run at constant pace. For example, Paavolainen et al., 1999 showed that a 10 km running exercise led to a significant decline in the participant's neuromuscular characteristics tested during maximal 20 m sprints immediately after the fatiguing run. However, no significant fatigue-induced changes took place during the course of the 10 km run supporting the fact that fatigue does not necessarily result in marked changes in kinematics during the submaximal running.

Finally, relationships between EMG activity and spring-mass behavior have been explored in jumping (Horita et al., 2002; Kuitunen et al., 2007; Padua et al., 2006) and running (Müller et al., 2010, 2012; Le Meur et al., 2012; Avogadro et al., 2003). However, to our best knowledge, only Le Meur et al. (2012) and Avogadro et al. (2003) analyzed how the fatigue-induced changes in lower limb muscular activity is related to leg-spring stiffness modifications. The participants of these two studies were tested during treadmill runs until exhaustion at (i) lactate threshold (~85% of v$\dot{V}O_{2max}$) and, (ii) 90% of v$\dot{V}O_{2max}$, respectively. The experimentation carried out by Le Meur et al. (2012) do not allow to determine the specific effects of the run as the exercise was performed in a very particular context, a cycle-run test. Regarding the Avogadro et al. (2003) study, no significant change was reported in leg stiffness or in EMG parameters in treadmill tests. However, considering that kinematics and muscle activity have been shown to differ between treadmill and overground running (Baur et al., 2007; Wank et al., 1998), further studies carried out on a track are required.

Therefore, the aim of this study was to evaluate the changes in leg-spring behavior and the concomitant EMG modifications in lower limbs during a run to exhaustion at v$\dot{V}O_{2max}$. By investigating these parameters during a constant velocity run, we aimed (i) to supplement the aforementioned studies, which, taken together, specify how the run velocity/duration influences the fatigue-induced modifications in spring-mass behavior, and (ii) to highlight the implied neuromuscular mechanisms. On the basis on our previous results (Rabita et al., 2011), we hypothesized that the

leg stiffness would decrease with the onset of fatigue, while the vertical stiffness would remain unchanged. Regarding the above-mentioned current literature, we hypothesized that these changes would be accompanied by a decrease in knee extensors and ankle plantarflexors activity during pre-contact and contact phases.

2. Methods

2.1. Participants

The 12 male runners [29.3 (SD 6.7) years; 180 (SD 5) cm; 72.5 (SD 7.5) kg] who participated in the study gave their informed consent before the commencement of the experiments conducted according to the Declaration of Helsinki and approved by the local ethics committee.

2.2. Experimental protocol

Each participant performed two runs on an indoor 340 m track. Throughout the tests, participants adopted the required velocity with an audio rhythm providing the time allotted to cover 20 m intervals set. The graded exercise test (first test) was carried out to determine maximal oxygen uptake ($\dot{V}O_{2max}$) and its associated velocity (v$\dot{V}O_{2max}$). All the variables presented in the present study were measured during the second test, performed 2 days later. This last exercise consisted in a constant velocity run performed until exhaustion at v$\dot{V}O_{2max}$.

2.3. Data collection and analysis

2.3.1. Ground reaction force

During the constant run, the vertical and horizontal components of the ground reaction forces were measured by a 6.60 m long force platform system (KI 9067; Kistler, Switzerland; natural frequency ≥500 Hz) that consisted of 6 platforms (1.20 m × 0.60 m) connected in series and covered with a tartan mat. It allowed recording ground reaction forces of 3–4 steps per lap. Vertical (F_z) and horizontal (antero-posterior, F_y) force components were digitized at a 500 Hz sampling rate.

The following parameters were calculated: contact (t_c, in s) and aerial (t_a, in s) times, peak vertical force (F_{zmax} in N), peak braking (F_{ymin}, in N) and push-off (F_{ymax} in N) forces, step frequency [$f = (t_a + t_c)^{-1}$ in Hz], step length (SL = $V_{forward} f^{-1}$, in m), braking (B_{imp}, in N s) and push-off (P_{imp}, in N s) impulses defined as the product of the effective negative (braking) and positive (push-off) horizontal forces (in N) and their respective duration (in s).

Force data were then used for calculating leg-spring behavior parameters using a classical method (Farley and González, 1996; McMahon and Cheng, 1990). Leg stiffness (k_{leg}, kN m^{-1}) was defined as

$$k_{leg} = F_{zmax}/\Delta L \tag{1}$$

where F_{zmax} is the maximal vertical ground reaction force and ΔL the leg compression, measured between the landing time and the time corresponding to F_{zmax} ($t_{F_{zmax}}$). In order to ensure that $t_{F_{zmax}}$ occurred when the leg compression is maximal (i.e. at $t_{\Delta L_{max}}$), the differences between these occurrences were calculated. The mean time differences ($t_{F_{zmax}} - t_{\Delta L_{max}}$) were of 0.2 ($\pm 4.2$) ms at the beginning and 0.4 (± 3.7) ms at the end of the run, confirming that (i) F_{zmax} and ΔL_{max} occurred almost synchronously and, (ii) the fatigue had a negligible influence on these temporal characteristics.

ΔL was calculated from: Δy, maximal vertical displacement of the center of mass (COM) calculated by integrating the vertical acceleration twice (Cavagna, 1975); L_0, initial length of the leg spring (vertical distance from the ground to the great trochanter during standing), and θ, angle swept by the leg spring between t_0 (ground contact) and $t_{F_{zmax}}$

$$\Delta L = \Delta y + L_0(1 - \cos\theta) \tag{2}$$

θ was calculated from the contact time, t_c, the forward speed, u, and L_0:

$$\theta = \sin^{-1}(ut_c/2L_0) \tag{3}$$

where ut_c represented the horizontal distance traveled by the COM (in m) during the contact phase.

The vertical stiffness (k_{vert}, kN m^{-1}) was defined by the following equation:

$$k_{vert} = F_{zmax}/\Delta y \tag{4}$$

Each mechanical parameter was computed over the steps recorded during the first and last laps, which corresponded to 5.7 (± 1.2) and 97.5 (± 3.0) % of the run to exhaustion, respectively. The obtained values were then averaged for the beginning (BEG) and the end (END) of the run.

2.3.2. Electromyography

The electromyography was recorded in eight muscles of the right lower limb [soleus (SOL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), tibialis anterior (TA), vastus medialis (VM), vastus lateralis (VL), rectus femoris (RF) and biceps femoris (BF)] using a wireless device (Zerowire, Aurion, Italy). The skin was prepared by surface abrasion and cleaned with 1/3 ether, 1/3 acetone and 1/3 alcohol. The bipolar surface electrodes (Blue Sensor Q-OO-S, Medicotest, France) were located according to the SENIAM recommendations. EMG signals were preamplified (×1000; 2 kHz), bandpass filtered (20–1000 Hz) and off-line synchronized with the kinetic data (OriginPro 8.1, OriginLab, USA).

The root mean square (RMS) envelope was calculated from raw EMG data over a 40 ms moving window. The data from 6 consecutive strides were averaged and smoothed (low pass FFT filter; cut-off frequency 40 Hz) to obtain a mean RMS profile for each muscle. EMGs were then normalized by their respective peak RMS value. The overall activity was characterized by the magnitude of 4 specific phases of RMS profiles: pre-activation (100 ms before ground contact), braking and push-off phases, and swing phase (excluding pre-activation phase).

2.3.3. Maximal oxygen uptake

Values of oxygen uptake were determined breath-by-breath during the incremental test (Cosmed K4b^2; Italy). The gas analyzer was calibrated prior to each test using ambient air (O_2: 20.93% and CO_2: 0.03%) and a gas mixture of known composition (O_2: 16.00% and CO_2: 5.00%). An O_2 analyzer with a polarographic electrode and a CO_2 analyzer with an infrared electrode sampled orally expired gases. The facemask, presenting a low dead space (70 mL), was equipped with a low-resistance turbine (28 mm diameter) calibrated before each test. The criteria used for the determination of $v\dot{V}O_{2max}$ were: a $\dot{V}O_2$ plateau, a HR over 90% of the predicted maximal HR and a respiratory exchange ratio (RER) greater than 1.15.

2.4. Statistical analysis

Descriptive statistics are presented as mean values (± SD). Normal distribution of the mechanical and EMG data was checked by the Shapiro-Wilk normality test. As the sample data did not always support the assumptions of normality, non-parametric statistical analyses were performed. A Wilcoxon test was used to analyze the effects of the exhaustive run by comparing mechanical and EMG values between BEG and END. All statistical analyses were conducted at $P < 0.05$.

3. Results

Mean values of $\dot{V}O_{2max}$ and $v\dot{V}O_{2max}$ were respectively of 60 (± 6.4) ml kg^{-1} min^{-1}, and 5.1 (± 0.3) m s^{-1}. The time to exhaustion was of 353 (± 69) s which corresponds to a mean distance of 1780 (317) m.

Fig. 1A,B presents the relative BEG–END changes in mechanical and temporal parameters. Raw values are reported in Table 1. The leg stiffness, k_{leg}, decreased (−8.9%; $P < 0.05$) while k_{vert} did not change significantly (+0.26%; $P > 0.05$). These results are explained by the fact that the significant decrease in F_{zmax} (−3.4%; $P < 0.001$) was associated with an increase trend (+7.4%; $P > 0.05$) in leg compression and a decrease trend (−2.8%; $P > 0.05$) in vertical displacement of the center of mass. Considering the anteroposterior force component, only F_{ymax} decreased significantly (−5.1%; $P < 0.05$). This maximal push-off force decrease was not associated with a similar decrease of the push-off impulse: the contact time increased significantly (+4.63%; $P < 0.05$), mainly because of the propulsion time increase (+7.9%; $P < 0.01$; Fig. 1B). Neither F_{ymin} nor B_{imp} changed significantly during the braking phase. Finally, we observed a 9.7% BEG-END decrease ($P < 0.05$) in aerial time, partially compensated by the increase in contact time such that the step frequency was unchanged (+0.84%; $P > 0.05$) Fig. 2.

Mean RMS in GM (−10.5%; $P < 0.05$) and GL (−8.7%; $P < 0.05$) presented a decrease during the pre-activation and the braking phases (−13.1% and −8.2%, respectively) while SOL activity decreased only during the braking phase (−6,2%; $P < 0.05$). TA decreased its activity at the end of the push-off phase (−4.7%; $P < 0.05$). A significant decrease value was observed for this muscle during the latter part of swing phase (−13.5%; $P < 0.05$).

Neither VM nor VL presented significant BEG–END changes.

RF increased its activity during the latest phase of the push-off (+5.4%; $P < 0.05$) and in the early phase of the swing phase
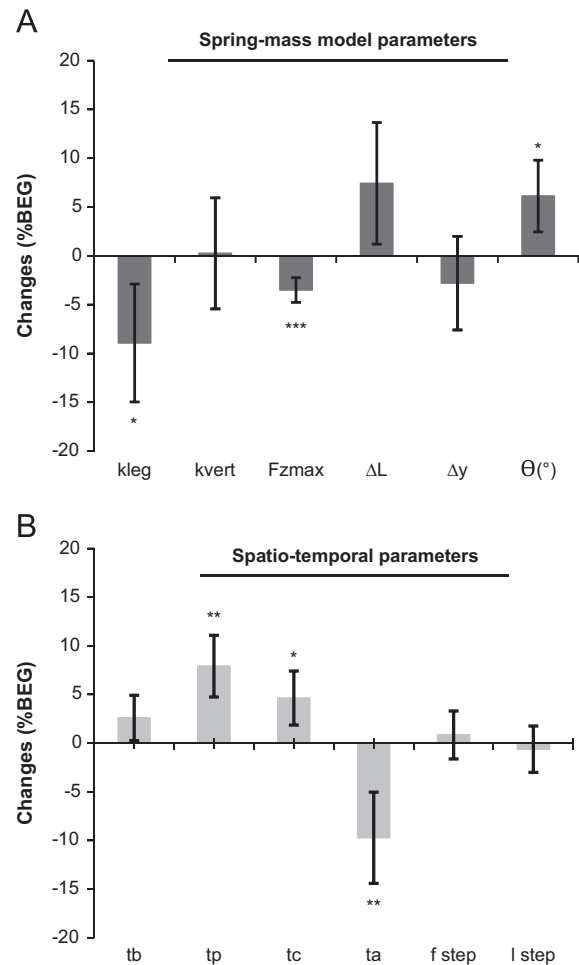

Fig. 1. Mean relative changes (± SD) in (A) spring-mass model parameters (k_{leg}: leg stiffness; k_{vert}: vertical stiffness; F_{zmax}: maximal vertical ground reaction force; ΔL: leg compression; Δy: vertical displacement of the center of mass; θ: angle of the spring-leg at touch-down) and (B) temporal parameters (t_b: braking time; t_p: push-off time; t_c: contact time; t_a: aerial time; f_{step}: step frequency; l_{step}: step length) between the beginning (BEG) and the end of the run. *, ** and *** denotes significant difference at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

Table 1
Raw values of mechanical and temporal parameters.

	BEG	END	P
Spring-mass parameters			
k_{leg} (kN/m)	13.9 ± 3.3	12.6 ± 2.9*	$P=0.027$
k_{vert} (kN/m)	40.4 ± 5.4	40.3 ± 5.9	$P=0.93$
F_{zmax} (N)	2009 ± 227	1940 ± 242***	$P<0.001$
ΔL (m)	0.149 ± 0.022	0.159 ± 0.026	$P=0.063$
Δy (m)	0.051 ± 0.006	0.049 ± 0.005	$P=0.33$
θ (°)	26.1 ± 2.8	27.7 ± 3.1*	$P=0.015$
Antero-posterior parameters			
F_{ymin} (N)	−391.9 ± 81.6	−402.7 ± 105.8	$P=0.47$
F_{ymax} (N)	334.4 ± 39.9	316.3 ± 34.0*	$P=0.017$
B_{imp} (N s)	17.26 ± 2.66	17.28 ± 2.57	$P=0.81$
P_{imp} (N s)	18.61 ± 2.41	18.88 ± 2.37	$P=0.26$
Spatio-temporal parameters			
t_b (s)	0.090 ± 0.011	0.093 ± 0.011	$P=0.080$
t_p (s)	0.110 ± 0.009	0.117 ± 0.011**	$P=0.001$
t_c (s)	0.201 ± 0.019	0.210 ± 0.020*	$P=0.015$
t_a (s)	0.117 ± 0.022	0.107 ± 0.026**	$P=0.0043$
f step (Hz)	3.14 ± 0.16	3.17 ± 0.24	$P=0.57$
l step (m)	1.60 ± 0.10	1.60 ± 0.14	$P=0.65$

*, **, *** denote significant changes between BEG and END at $P < 0.05$, $P < 0.01$ and $P < 0.001$.
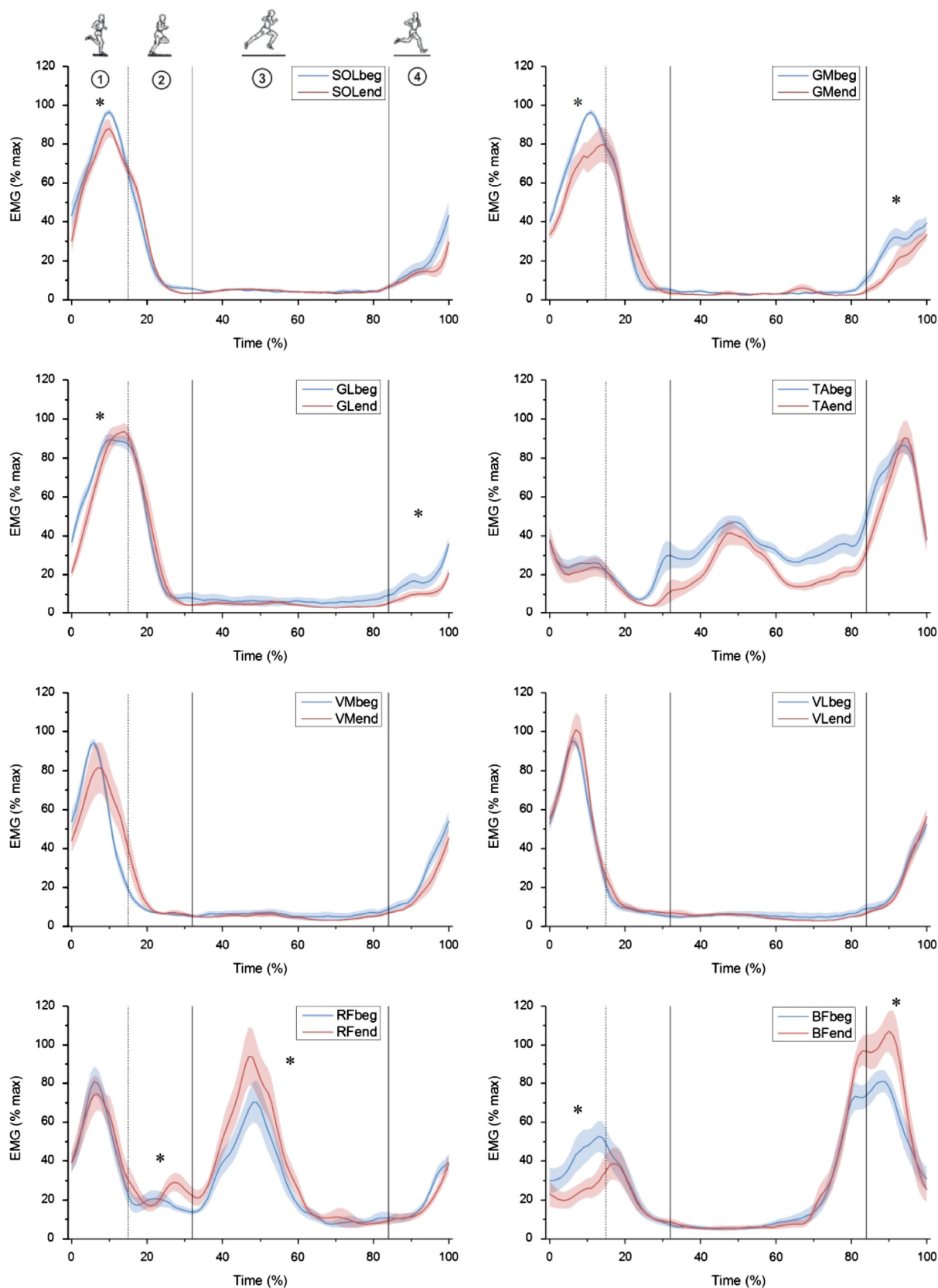
Fig. 2. Ensemble curves of EMG RMS linear envelope for 8 lower limb muscles obtained during the beginning (BEG) and the end (END) of run to exhaustion. Each profile represents the mean obtained from averaging individual data across 6 consecutive strides, normalized to the mean RMS calculated during the complete stride of BEG, and further averaging across the 12 runners. In abscissa, zero corresponds to the beginning of the contact phase. The different phases represent: ①: the braking phase; ②: the push-off phase; ③: the aerial phase (excluding the pre-contact phase) and ④ pre-contact phase (100 ms before ground contact). SOL, *soleus*; GL, *gastrocnemius lateralis*; GM, *gastrocnemius medialis*; TA, *tibialis anterior*; VM, *vastus medialis*; VL, *vastus lateralis*; RF, *rectus femoris*; BF, *biceps femoris*. * denotes significant difference between BEG and END at $P < 0.05$.

(+14.7%; $P < 0.05$). Finally, BF activity presented a significant increase during the pre-activation phase (+16.2%; $P < 0.05$) and a significant decrease during the braking phase (−15.8%; $P < 0.05$).

4. Discussion

The aim of this study was to evaluate the changes in leg-spring behavior and the associated modifications in the lower limb muscular activity during a run to exhaustion at severe intensity. The subjects modified their mechanical behavior toward lower leg stiffness while preserving a constant vertical stiffness. Analyses showed a decrease in plantarflexor activity during pre-activation and braking phases, while no change appeared in knee extensor activity. The increase in the biarticular RF and BF activation seems to greatly participate in the maintenance of the preset velocity when fatigue occurs.

The present results complement well previous investigations (Dutto and Smith, 2002; Morin et al., 2011a) and confirm the BEG–END modifications observed in the only study that recorded these mechanical variables during an exhaustive run imposed at a constant velocity around $v\dot{V}O_{2max}$ in ecological conditions (Rabita et al., 2011). These include (i) the leg stiffness decreased together with a very significant and homogenous decrease in maximal vertical ground reaction force while the vertical stiffness was unchanged; (ii) neither leg compression nor maximal vertical displacement of the COM present significant changes with fatigue; and, (iii) regarding the spatiotemporal parameters, a decrease in the aerial time was observed while the contact time increased, leading to a stability of the step frequency. Thus, despite the differences in the exhaustive run duration, the fatigue-induced at a $v\dot{V}O_{2max}$ intensity (present study,~6 min) and 95% of $v\dot{V}O_{2max}$ (Rabita et al., 2011; ~11 min) lead to quite similar stride spatiotemporal and spring-mass behavior modifications.

In the present study, EMG was measured to enlighten the mechanical changes described above. Regarding plantarflexor muscles, the current results support our hypothesis: they decreased their activity during the pre-activation phase (GM and GL) and the beginning of the contact phase (SOL, GM and GL) as previously reported for well trained-runners (Le Meur et al., 2012; Nummela et al., 2006; Paavolainen et al., 1999). Without a concomitant reduction of antagonist activity (the TA activity did not change during these phases), this would imply a reduction in force and leg stiffness. The influence of the triceps surae pre-activation has been reported in running (Kuitunen et al., 2002). It participates to increase the stiffness of the muscle–tendon units to tolerate and absorb high impact loads at the beginning of the ground contact (Gollhofer et al., 1984). In contrast, as the fatigue occurs, a lower pre-activation leads to a reduced ability to sustain the impact loads and store elastic energy during stretch shortening cycles (Avela and Komi, 1998). Furthermore, the fact that leg stiffness is mainly determined by plantarflexor activity during running was recently strongly supported by Müller et al. (2010) who investigated the running kinematics and dynamics on uneven ground. They showed that (i) the ankle stiffness is adjusted to the vertical height of the obstacle in the same way that the global leg stiffness and (ii) the 100 ms GM pre-activation highly correlates with the activation at ground contact but also with kinematic and dynamic parameters (contact time, leg stiffness, ground reaction force, etc.). Finally, this decrease of the triceps surae activity is consistent with the neuromuscular mechanisms of fatigue induced by a middle distance running. Girard et al. (2012) showed that the decrease in plantarflexor maximal strength induced by a 5 km running trial reached 27% immediately after the race. This reduction was reported to be mainly caused by peripheral modifications, which are mainly attributable to a failure of the neuromuscular transmission and excitation–contraction coupling.

Regarding knee extensors, no change was observed in VM, VL and RF EMG during the pre-activation and braking phases. These results do not support our hypothesis of a BEG–END decrease in leg extensors activity notably based on the finding showing that the knee joint stiffness plays an important role in controlling the whole leg stiffness in running (Arampatzis et al., 1999; Kuitunen et al., 2002). Several assumptions could explain this result. In maximal middle distance running, the muscle fatigue in plantarflexors is around twice compared to that of knee extensors (MVC decrease between pre- and post-exercise of about –27% (Girard et al., 2012) vs –15% (Nummela et al., 2008), respectively). Moreover, previous findings have shown that different strategies can be selected to compensate for the fatigue in plantarflexors, one of them relying on the increased contribution of the quadriceps muscles (Bonnard et al., 1994; Kuitunen et al., 2007). The constancy (or even increase) in knee extensor activity after fatigue has often been called a quadriceps-dominant strategy (Kellis and Kouvelioti, 2009; Mizrahi et al., 2001; Padua et al., 2006) and has to be confirmed for middle distance running in future investigations.

The biarticular hip-mobilizing muscles (RF and BF) have already been shown to be the lower limb muscles that present the earliest signs of change in their activity (Hanon et al., 2005). The increased RF activity at the beginning of the swing phase together with the increased BF activity during the pre-activation phase are consistent with (i) the greater distance traveled by the COM during contact (Rabita et al., 2011); and, (ii) the decreased aerial time. It is likely that the increase in BF and RF activity was primarily a consequence of the inability of the subjects to preserve constant the contact time. Without step length changes, the solution for the runners to maintain the preset velocity with fatigue was to keep a constant frequency, and thus, to balance the increased contact time by a decreased aerial time. These spatiotemporal modifications imply a reduced time for the hip flexors to induce maximal hip flexion around the middle of the swing phase. This can explain the greater activity in RF both at the end of the pushing phase, and at the beginning of the swing phase. A reduced time is also available for the hip extensors to efficiently anticipate the body propulsion before the contact phase by extending the hip joint. This change can explain the increase in BF activity just before the initial contact. This BEG–END increased activity of these two hip- and knee-mobilizing muscles could lead to a mechanical advantage. Indeed, biarticular muscles, particularly the RF and BF muscles have been shown to primarily participate to the transfer of energy between body segments in running (Novacheck, 1998). For instance, the hamstrings are activated at the end of the swing phase, when hip and knee are both extending. Then, an extensor moment is produced at the hip and a flexor moment at the knee. The moment produced at the knee being opposed to the knee motion, hamstrings absorb energy at the knee and generate energy at the hip. However, since the overall length change of the hamstrings is minimal, they can be considered to transfer energy from the tibia to the pelvis, and aid in hip extension. A similar type of analysis can be done for the rectus femoris during the first half of swing (Novacheck, 1998). This energy transfer principle was shown to contribute to energy efficiency (Jacobs et al., 1996). Then, it seems logical to assume that the increase in RF activity at the beginning of the swing phase and in BF activity at the end of the swing phase allows the neuromuscular system to compensate for the decrease in force production capacity in fatigued muscles, while preserving the preset velocity at the latter stage of the run.

4.1. Limitations

One of the main limitations of the present study is that we did not quantify the kinematic parameters on the basis of video analyses. This would have helped to explain some results induced

by eventual joint angle adjustments. Firstly, we assumed that the decrease in GM and GL activity without any change in TA activity may have implied a reduction in ankle stiffness. However, it was shown in other conditions [hopping in place (Farley and González, 1996) or running on uneven ground (Müller et al., 2010)] that the stiffness adjustment process primarily relies on rearrangement of the geometry of the three-segment leg rather than changes in muscle activation. For example, for a constant ankle angle, the length of the muscle–tendon unit of the biarticular GM and GL decreased with a more flexed knee, leading to a reduced gastrocnemii muscle force and ankle stiffness without any change in plantarflexors and dorsiflexors activity (Farley et al. 1998; Müller et al., 2010). Secondly, such eventual joint adjustment would also have influenced joint and leg stiffness via the different muscle fibers working range of the force–length relationship (Ishikawa et al., 2007; Müller et al. 2012). For instance, Ishikawa et al. (2007) have estimated that the working range of active GM fibers during running corresponds to the ascending limb of the force–length relationship (sarcomeres length shorter than for the plateau region). Consequently, a decreased activation of this muscle at an extended fibers length might have resulted in the same muscle force. Finally, a fatigue-induced change in foot strike would have contributed in the BEG–END modifications of the present study. It was shown that the types of running switched with fatigue from midfoot and forefoot landing styles to a rearfoot landing (Larson et al., 2011). As forefoot striking places a heavier eccentric load on the plantarflexors (Williams et al., 2000), fatigue in the triceps surae complex might have caused the runners to shift their gait during the run (Larson et al., 2011).

Thus, with regard to these abovementioned factors, kinematic data would have allowed to partly explain some of the dynamic or electromyographical results in case of fatigue induced changes in low limb joint angle. However, a significant rearrangement toward flexed posture at the end of the exhaustive run would have resulted in reduced vertical stiffness (McMahon et al., 1987).

5. Conclusion

The results have shown that the modifications in mechanical and spatiotemporal parameters are well explained by the changes in lower limb muscular activity between the beginning and the end of the exhaustive run. Plantarflexors were more affected by the run than knee extensors, which did not present changes in their activity. Biarticular rectus femoris and biceps femoris seem to play an important role in order to maintain the preset velocity at the latter stage of the run.

6. Conflict of interest

None of the authors have conflict of interest in connection with the submitted article to disclose.

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